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Air Quality Criteria for Ozone and Related Photochemical Oxidants

Review Draft (Do Not Cite or Quote)

Volume II of III

Notice

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PREFACE

In 1971, the U.S. Environmental Protection Agency (EPA) promulgated National Ambient Air Quality Standards (NAAQS) to protect the public health and welfare from adverse effects of photochemical oxidants. In 1979, the chemical designation of the standards was changed from photochemical oxidants to ozone (O_3). This document, therefore, focuses primarily on the scientific air quality criteria for O_3 and, to a lesser extent, for other photochemical oxidants like hydrogen peroxide and the peroxyacyl nitrates.

The EPA promulgates the NAAQS on the basis of scientific information contained in air quality criteria documents. The previous O_3 criteria document, *Air Quality Criteria for Ozone and Other Photochemical Oxidants*, was released in August 1986 and a supplement, *Summary of Selected New Information on Effects of Ozone on Health and Vegetation*, was released in January 1992. These documents were used as the basis for a March 1993 decision by EPA that revision of the existing 1-h NAAQS for O_3 was not appropriate at that time. That decision, however, did not take into account some of the newer scientific data that became available after completion of the 1986 criteria document. The purpose of this revised air quality criteria document for O_3 and related photochemical oxidants is to critically evaluate and assess the latest scientific data associated with exposure to the concentrations of these pollutants found in ambient air. Emphasis is placed on the presentation of health and environmental effects data; however, other scientific data are presented and evaluated in order to provide a better understanding of the nature, sources, distribution, measurement, and concentrations of O_3 and related photochemical oxidants and their precursors in the environment. Although the document is not intended to be an exhaustive literature review, it is intended to cover all pertinent literature available through the end of 1993.

This document was prepared and peer reviewed by experts from various state and Federal governmental offices, academia, and private industry for use by EPA to support decision making regarding potential risks to public health and welfare. The Environmental Criteria and Assessment Office of EPA's Office of Health and Environmental Assessment acknowledges with appreciation the contributions provided by these authors and reviewers as well as the diligence of its staff and contractors in the preparation of this document at the request of the Office of Air Quality Planning and Standards.

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AUTHORS, CONTRIBUTORS, AND REVIEWERS

CHAPTER 5. ENVIRONMENTAL EFFECTS OF OZONE AND RELATED PHOTOCHEMICAL OXIDANTS

Principal Authors

Dr. Richard M. Adams—Department of Agriculture and Resource Economics, Oregon State University, Corvallis, OR 97331

Dr. Christian Andersen—Environmental Research Laboratory, U.S. Environmental Protection Agency, 200 SW 35th Street, Corvallis, OR 97333

Dr. J.H.B. Garner—Environmental Criteria and Assessment Office (MD-52), U.S. Environmental Protection Agency, Research Triangle Park, NC 27711

Dr. Beverly A. Hale—Department of Horticultural Science, University of Guelph, Guelph, Ontario, N1G 2W1, Canada

Dr. William E. Hogsett—Environmental Research Laboratory, U.S. Environmental Protection Agency, 200 SW 35th Street, Corvallis, OR 97333

Dr. David F. Karnosky—School of Forestry and Wood Products, Michigan Technological University, Houghton, MI 49931

Dr. John Laurence—Boyce Thompson Institute for Plant Research at Cornell University, Tower Road, Ithaca, NY 14853

Dr. E. Henry Lee—ManTech Environmental Technology, Inc., 1600 W. Western Boulevard, Corvallis, OR 97333

Dr. Allen S. Lefohn—A.S.L. & Associates, 111 Last Chance Gulch, Suite 4A, Helena, MT 59601

Dr. Paul Miller—Pacific Southwest Forest and Range Experiment Station, USDA-Forest Service Fire Lab, 4955 Canyon Crest Dr., Riverside, CA 92507

Mr. Doug Murray—TRC Environmental Corporation, 5 Waterside Crossing, Windsor, CT 06095

Dr. Victor Runeckles—Department of Plant Science, University of British Columbia, Vancouver, British Columbia, V6T 1Z4, Canada

Dr. James A. Weber—Environmental Research Laboratory, U.S. Environmental Protection Agency, 200 SW 35th Street, Corvallis, OR 97333

Dr. Ruth D. Yanai—Boyce Thompson Institute for Plant Research at Cornell University, Tower Road, Ithaca, NY 14853

Reviewers

Ms. Vicki Atwell—U.S. Environmental Protection Agency, OAQPS MD-R, Research Triangle Park, NC 27711

Dr. Glen R. Cass—Environmental Engineering Science Department, Mail Code 138-78, California Institute of Technology, Pasadena, CA 91125

Dr. Arthur Chapelka—Auburn University School of Forestry, Auburn, AL 36849-4201

Dr. Robert Goldstein—Electric Power Research Institute, 3412 Hillview Ave., Palo Alto, CA 94303

Dr. Marcia Gumpertz—Department of Statistics, North Carolina State University, Raleigh, NC 27695

Dr. Allen Heagle—U.S. Department of Agriculture, ARS, 1505 Varsity Drive, Raleigh, NC 27606

Dr. Robert Heath—Dept. of Botany and Plant Science, University of California, Riverside, CA 92521

Dr. Thomas M. Hinckley—School of Forest Resources, University of Washington, Seattle, WA 98195

Dr. Robert Kohut—Boyce Thompson Institute, Cornell University, Tower Road, Ithaca, NY 14853-1801

Dr. Virginia Lesser—Department of Statistics, Oregon State University, Corvallia, OR 97333

Dr. Fred Lipfert—23 Carll Ct., Northport, NY 11768

Dr. Patrick McCool—SAPRC, University of California, Riverside, CA 92521

Dr. Delbert McCune—Boyce Thompson Institute, Cornell University, Tower Road, Ithaca, NY 14853-1801

Dr. Robert Musselman—U.S. Department of Agriculture, Forestry Service, Rocky Mountain Experiment Station, 240 West Prospect Road, Fort Collins, CO 80526

Dr. Eva Pell—Pennsylvania State University, Department of Plant Pathology, 321 Buckhout Laboratory, University Park, PA 16802

Dr. Phillip Rundel—Laboratory of Biomedical and Environmental Science, University of California, LA, 900 Veterans Ave., Los Angeles, CA 90024

Dr. Jayson Shogren—School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511

Dr. James Shortle—Department of Agricultural Economics, Pennsylvania State University, Armsby Building, 208C, University Park, PA 16802-5502

Dr. John Skelly—Pennsylvania State University, 108 Buckhout Laboratory, University Park, PA 16802

Dr. Boyd Strain—Department of Botany, 136 Biology Science Building, Duke University, Durham, NC 27708

Dr. George E. Taylor, Jr.—Biological Sciences Center, Desert Research Institute, 7010 Dandini Blvd., Reno, NV 89512

Dr. Patrick Temple—Statewide Air Pollution Research Center, University of California, Riverside, CA 92521-0312

Dr. David Tingey—U.S. Environmental Protection Agency, Environmental Research Laboratory, 200 SW 35th Street, Corvallis, OR 97333

Dr. Michael Unsworth—Department of Atmospheric Sciences, Oregon State University, Corvallis, OR 97333

Dr. David Weinstein—Boyce Thompson Institute, Cornell University, Tower Road, Ithaca, NY 14853-1801

Dr. John Yocom, 12 Fox Den Road, West Simsbury, CT 06092

U.S. ENVIRONMENTAL PROTECTION AGENCY
PROJECT TEAM FOR DEVELOPMENT OF AIR QUALITY CRITERIA
FOR OZONE AND RELATED PHOTOCHEMICAL OXIDANTS

Scientific Staff

Mr. James A. Raub—Health Scientist, Environmental Criteria and Assessment Office (MD-52), U.S. Environmental Protection Agency, Research Triangle Park, NC 27711

Dr. A. Paul Altshuller—Physical Scientist, Environmental Criteria and Assessment Office (MD-52), U.S. Environmental Protection Agency, Research Triangle Park, NC 27711

Mr. William G. Ewald—Health Scientist, Environmental Criteria and Assessment Office (MD-52), U.S. Environmental Protection Agency, Research Triangle Park, NC 27711

Dr. J.H.B. Garner—Ecologist, Environmental Criteria and Assessment Office (MD-52), U.S. Environmental Protection Agency, Research Triangle Park, NC 27711

Dr. Judith A. Graham—Associate Director, Environmental Criteria and Assessment Office (MD-52), U.S. Environmental Protection Agency, Research Triangle Park, NC 27711

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Mr. Richard N. Wilson—Clerk, Environmental Criteria and Assessment Office (MD-52), U.S. Environmental Protection Agency, Research Triangle Park, NC 27711

U.S. ENVIRONMENTAL PROTECTION AGENCY
PROJECT TEAM FOR DEVELOPMENT OF AIR QUALITY CRITERIA
FOR OZONE AND RELATED PHOTOCHEMICAL OXIDANTS
(cont'd)

Document Production Staff

Ms. Marianne Barrier—Graphic Artist, ManTech Environmental, P.O. Box 12313, Research Triangle Park, NC 27709

Mr. John R. Barton—Document Production Coordinator, ManTech Environmental Technology, Inc., P.O. Box 12313, Research Triangle Park, NC 27709

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5. ENVIRONMENTAL EFFECTS OF OZONE AND RELATED PHOTOCHEMICAL OXIDANTS

5.1 INTRODUCTION

Analyses of photochemical oxidants in the ambient air have revealed the presence of a number of phytotoxic compounds, including O_3, peroxyacyl nitrates, and NO_2. Ozone, the most prevalent photochemical oxidant, has been studied the most and its effects are better understood than those of other photochemically derived oxidants. Ozone affects vegetation throughout the United States, impairing crops, native vegetation, and ecosystems more than any other air pollutant (Heck et al., 1980). The phytotoxicity of nitrogen oxides has been assessed in Air Quality Criteria for Oxides of Nitrogen (U.S. Environmental Protection Agency, 1993) and will not be discussed here. On the basis of concentration, the peroxyacyl nitrates are more toxic than O_3, with PAN being about ten times more phytotoxic than O_3 (Darley et al., 1963; Taylor and MacLean, 1970; Pell, 1976). Although more phytotoxic than O_3, the peroxyacyl nitrates generally occur at significantly lower ambient concentrations, however, and phytotoxic concentrations are therefore less widely distributed than those of O_3. Ambient concentrations of O_3 and PAN, as well as their concentration ratios, are discussed in detail in Chapter 4.

The effects of photochemical oxidants were first observed as foliar injury on vegetation growing in localized areas in Los Angeles County, California (Middleton et al., 1950). In these early reports, foliar injury was described as glazing, silvering, and bronzing of the lower leaf surface of leafy vegetables and as transverse bands of injury on monocotyledonous species. Subsequent studies showed that these symptoms of photochemical oxidant injury were caused by peroxyacetyl nitrate (Taylor et al., 1960). The characteristic O_3 stipple on grape leaves reported in the late 1950s was the first observation of O_3 injury to vegetation in the field (Richards et al., 1958). Subsequent studies with tobacco and other crops confirmed that O_3 was injuring vegetation at sites near urban centers (Heggestad and Middleton, 1959; Daines et al., 1960). It is now recognized that vegetation at rural sites may be injured by O_3 transported long distances from urban centers (Edinger et al., 1972; Heck et al., 1969;

Heck and Heagle, 1970; Kelleher and Feder, 1978; Miller et al., 1972; Skelly et al., 1977; Skelly, 1980; Garner et al., 1989; see also Chapters 3 and 4).

Plant stress from O_3 exposures occur when the atmospheric concentrations exceed the limits of plant tolerance, not because the gas is unique. Not all plants are sensitive. The effects of O_3 on terrestrial vegetation begin with the responses of individual plants (see Figure 5-1). When there are many sensitive individuals within a population, populations are affected. Changes within sensitive populations, or stands, ultimately can affect community and ecosystem structure and function. The occurrence and magnitude of the effects depends on the pollutant concentration, duration of the exposure, length of time between exposures, genetic composition (i.e., sensitivity) of the plants, and various environmental and biological factors influencing plant response.

Foliar injury is usually the first visible sign of O_3 exposure and indicates impairment of physiological processes within the leaves. As illustrated in Figure 5-1, in order for O_3 to affect an individual plant, sufficient amounts of O_3 derived from atmospheric and various canopy processes must be able to reach the leaves of the plant. To cause injury, ozone must: (1) enter the plant through the leaf stomata; (2) dissolve in the aqueous layer lining the cell walls within the air spaces; and (3) O_3 or its decomposition products diffuse through the membrane into the cell, where it can react with cellular components and affect metabolic processes, unless the plant is able to detoxify or metabolize O_3 or its metabolites (Tingey and Taylor, 1982). Cellular injury has been shown to subsequently manifest itself in a number of ways. These include: (1) visible foliar injury; (2) premature needle senescence; (3) reduced photosynthesis; (4) reduced carbohydrate production and allocation; (5) reduced plant vigor; and (6) reduced growth or reproduction or both (McLaughlin et al., 1982; U.S. Environmental Protection Agency, 1986). The impact of pollutant exposure is determined by the developmental stage, the genetic composition, the complex interactions among natural and pollutant stresses, their temporal and spatial variation, and finally, the action these have on the biochemical and physiological processes within the plants. Most plants undergo some form of stress during the various stages of their life cycle; however, the multiple stresses they encounter during their lifetimes do not usually all occur at one time (Osmond et al., 1987).

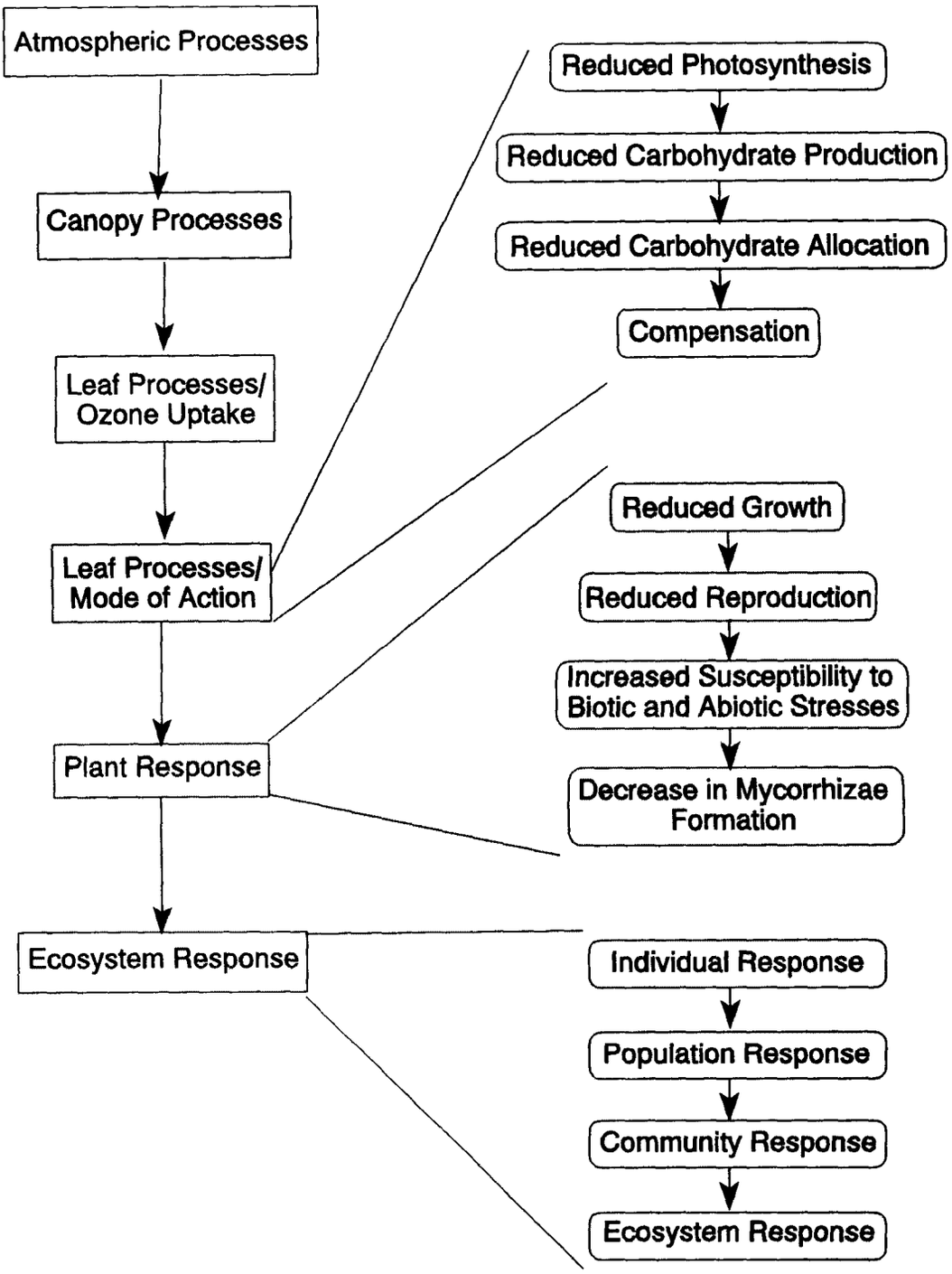

Figure 5-1. Leaf absorption and possible functional changes that may occur within the plant. Ecosystem response begins at the level of the individual and is propagated upward.

Ozone can affect all aspects of plant growth (Figure 5-1). Plants accumulate, store, and use carbon compounds to build their structure and maintain physiological processes (Waring and Schlesinger, 1985). Within the leaf, carbon dioxide absorbed from the atmosphere is converted to carbohydrates during the process of photosynthesis. The water and minerals necessary for growth are absorbed by plants from the soil. Growth and seed formation depend not only on the rate of photosynthesis and uptake of water and nutrients, but also on the subsequent metabolic processes and the allocation of the carbohydrates produced during photosynthesis. Most plants require a balance of resources (i.e, energy, water, and mineral nutrients) to maintain optimal growth, but these are seldom available in natural environments (Chapin et al., 1987). Plants compensate for injury and/or stresses by allocating their available resources to the point of injury or stress (McLaughlin et al., 1982; Miller et al., 1982; Tingey et al., 1976). Altering the allocation of carbohydrates has been shown to decrease plant vigor, increase susceptibility to insect pests and fungal pathogens, interfere with mycorrhizal formation and reduce plant growth and reproduction (McLaughlin et al., 1982; Miller et al., 1982; U.S.Environmental Protection Agency, 1986; Garner et al., 1989).

Most of our knowledge concerning the effects of O_3 on vegetation comes from studies of the responses of important agricultural crop plants and some selected forest tree species, mostly as seedlings or saplings. Crop plants, because of the importance of their yield to human food demand, usually have been selected for their productivity. In addition, crop plants usually are fertilized, weeded, frequently irrigated and grown in monocultures. In other words, competition for water, nutrients, space and light is greatly diminished when compared to plants growing in natural ecosystems.

The number of crop species and cultivars for which information regarding O_3 effects exists encompass a mere fraction of the total of those cultivated as crops or found growing in natural communities. It is not possible to predict the sensitivity of the species and cultivars that have not been investigated, except in very general terms, because of the wide range of sensitivities to O_3 known to exist among the species that have been studied and even among cultivars of individual crops. A number of attempts have been made to develop a general framework of response covering a range of species using the fragmented knowledge available. All of them have their shortcomings.

Ecosystem responses are hierarchical and range from those that are characteristic of individual organisms through populations to communities, and ultimately, to ecosystems (U.S. Environmental Protection Agency, 1978, 1986). Organisms, not ecosystems, respond to O_3 exposure (Sigal and Suter, 1987). The only well documented study of ecosystem change is that of the San Bernardino Forest ecosystem in southern California where the impact of O_3 on the keystone species, ponderosa and Jeffrey pine resulted in the degradation of the forest (Miller, 1982, 1984; U.S. Environmental Protection Agency, 1978, 1986). Studies within the forests of the eastern United States, until recently, have dealt with only a few plant species, chiefly eastern white pine, none of which have been critical in maintaining ecosystem structure and function (McLaughlin et al., 1982; Skelly, 1980; Skelly et al., 1984; U.S. Environmental Protection Agency, 1978, 1986). The absence of long term studies dealing with the impacts of O_3 on various ecosystem components and how these influence ecosystem structure and functions makes determination of the impact of O_3 on ecosystems in general difficult.

The sequential organization of this chapter closely follows the discussion dealing with the responses of plants to O_3 presented above. First, the methodologies (Section 5.2) that have been used to obtain the information on which the rest of the chapter is based are described. The next section (5.3) details the known biochemical and physiological responses occurring within leaf cells after O_3 entry into the leaves and how these responses affect plant vigor, growth, productivity and reproduction. Factors within and external to plants influence their response to O_3 and other stresses. How these factors, observed during experimentation or in the field, can modify functional and growth responses of plants exposed to O_3 is presented in the next section (Section 5.4).

A complicating factor in assessing plant response to O_3 exposure is determining the amount of O_3 entering the leaves. Entry of O_3 into plant leaves is not a simple uptake process, but involves gas exchange; the entry of O_3 through the stomata and carbon dioxide (CO_2) from the atmosphere at the same time oxygen and water vapor are exiting. For many years, attempts have been made to develop mathematical equations that quantify the relationship between pollutant exposure and agricultural crop yield. The problem is the need for combined incorporation of the age and the genetic composition of the plant, along with parameters for pollutant concentration, duration, frequency of exposure and the respite time

between exposures into an exposure statistic or index which may be used to predict crop yield loss. Section 5.5 discusses the strong points and shortcoming of the various indices that have been developed to aid in predicting the effects of O_3 on crops.

Some O_3 exposures (concentration and duration) result in foliar injury to the plant. Other exposures result in growth reduction and decrease in productivity. Section 5.6, exposure-response of plant species, presents the data from many different experiments and assesses the potential impact of different concentrations and exposure durations on growth of a variety of plants ranging from cultivated annual crops to woody perennials such as trees and shrubs. Of particular interest is the yield of crops. The majority of the data concerning the response of ecosystems deals with the response of individual organisms, populations or forest stands. Therefore, in section (5.7) the knowledge concerning ecosystem response to perturbations obtained from a variety of studies, and the California San Bernardino Forest study in particular, is used to present a view of what might be expected from continued O_3 exposure.

The costs to the nation of O_3 exposure of crops and ecosystems is discussed in Section 5.8. The scientific names of the plants cited in this chapter are presented in a table in Appendix A. Section 5.9 discusses the effects of O_3 on nonbiological materials, followed by an integrative summary and conclusions section (5.10) drawing together and interpreting key information from the earlier chapter sections concerning vegetation effects.

5.2 METHODOLOGIES USED IN VEGETATION RESEARCH

5.2.1 Fumigation Systems

The methodologies used in vegetation research have become more sophisticated over the years as new technology has developed. New exposure systems have been devised with pollutant dispensing systems that make it possible to more nearly duplicate the exposures plants receive in the field. These systems and their good points and short-comings are discussed below.

Air pollution exposure-response studies usually require exposure chambers or other apparatus for maintaining controlled pollutant exposures. Ozone exposure systems are designed to maintain a modified gaseous atmosphere around a plant for a period of exposure,

for the purpose of monitoring plant responses to that modified gaseous atmosphere. Whichever system is used, they all share some features in common, namely: general plant growth conditions (light, temperature, humidity, carbon dioxide, soil water) must be met, and differential concentrations of O_3 generated either artificially or naturally must be supplied to the fumigation system. Exposure systems have been established in controlled environments, greenhouses and the field, many of these were described in the earlier criteria document, Air Quality Criteria for Ozone and Other Photochemical Oxidants (U.S. Environmental Protection Agency, 1986). Exposure systems may range from cuvettes which enclose leaves or branches (Bingham and Coyne, 1977; Legge et al., 1979) to a series of tubes with calibrated orifices spatially distributed over a field to emit gaseous pollutants to a plant canopy (Lee et al., 1978). Each type of system was designed for specific objectives and operates most efficiently under the conditions for which it was intended. Each has advantages and limitations and must be evaluated in terms of the objectives it was designed to meet.

5.2.1.1 Methodologies Discussed in the Air Quality Criteria for Ozone and Other Photochemical Oxidants (1986)

Controlled Environment Exposure Systems

Controlled environment fumigation systems are those in which light sources, and control of temperature and relative humidity are artificial. Light quality and quantity are likely to be lower than in ambient environments, usually resulting in lower photosynthetically active radiation (PAR). Temperature and relative humidity will likely be more consistent in a controlled environment than in ambient air. Controlled environment exposure systems are typified by the widely-used continuous stirred tank reactor (CSTR), a system originally designed for mass balance studies of O_3 flux to vegetation. The main benefit of controlled environment chambers is that the environmental conditions during exposure can be very well characterized, controlled and replicated over time. They work very well for evaluating O_3 effects on physiological processes, which are themselves sensitive to changes in other environmental parameters. The major limitation of controlled environment exposure systems is the extrapolation of the data to field situations.

Greenhouse system designs are similar to those found in controlled environments, except that light, temperature and relative humidity conditions fluctuate with those occurring

in the greenhouse. Thus, they are more closely related to field studies than are controlled environments, but plant culture and environmental conditions are still quite different from those of field exposure chambers, making direct extrapolation difficult. These studies are, however, more applicable to phytotoxicity of O_3 to greenhouse grown ornamental and floriculture crops (U.S. Environmental Protection Agency, 1986). Some greenhouse exposure systems use activated charcoal filtration to remove pollutants from the incoming air prior to the addition of experimental O_3, and either vent directly to the outside, or use charcoal filtration of the outgoing air to prevent contamination of the greenhouse air supply. Other greenhouse exposure systems filter neither incoming nor outgoing air.

Field Exposure Systems

Fumigation of plants with O_3 in the field is most frequently carried out using open-top chambers. The most widely utilized design (U.S. Environmental Protection Agency, 1986) consists of a cylindrical aluminum frame, covered with transparent film. The bottom half of the transparent covering is doubled layered, the inside panel of which is perforated. Charcoal and particulate filtered air, non-filtered air or O_3 supplemented air is blown into the bottom layer, forced through the perforations into the plant canopy, and then escapes through the top of the chamber. The positive pressure maintained by the forced movement of air up through the chamber minimizes influx of ambient air into the chamber through the open-top. The open-top chamber exposure system was employed in the National Crop Loss Assessment Network (NCLAN) from 1980 to 1988 and a description and discussion of the chambers is provided in the 1986 criteria document Section 6.2.4 (U.S. Environmental Protection Agency, 1986). The design of these chambers has been modified with frusta to reduce such incursions by ambient air, making the chambers more viable under windy conditions. Canopies (moveable) have been added so that rain exclusion studies can be carried out. Finally, they have been modified in shape or increased in size so that species such as mature trees and grapevines can be enclosed. Crop loss studies conducted in open-top chambers more closely simulate field losses of crops due to O_3 than controlled environments or greenhouse fumigation chambers. However, there are some important differences in environmental conditions between open-top chambers and the field. Specifically, the frusta and walls of the chamber block some incoming light, as well as trap some long-wave

radiation within the chamber, so that PAR levels are lower and temperatures are higher in the chambers than in the field. The walls also cause a rain shadow necessitating irrigation. The rate at which air moves across the foliage contributes significantly to canopy resistance to O_3 uptake, and is similar between chambered and non-chambered plants. This suggests that O_3 uptake by the foliage is similar between open-top chambers and the field (U.S. Environmental Protection Agency, 1987). To promote normal dew formation, many studies turn off the blower fans during the night.

Limited use (for O_3 studies) has been made of chamberless field exposure systems, which rely on ambient wind conditions to move O_3 across an open field canopy. The O_3 is emitted from vertical pipes, which are spaced in a circle around the experimental plot of plants. The amount of O_3 emitted from each vertical pipe, as well as the number and compass direction of emitting pipes, depends on the wind direction and speed, this whole process usually being computer controlled.

5.2.1.2 Methodologies Referenced Since the Air Quality Criteria for Ozone and Other Photochemical Oxidants (1986)

Branch and Leaf Chambers

Most of the developments in exposure systems since 1986 have been modifications of existing systems. The tremendous interest in evaluation of mature tree response to O_3 has prompted the development of large branch chambers for estimating O_3 flux to trees. These branch chambers share many of the design characteristics of a CSTR. The chamber walls are transparent film spread over a supporting frame, there is a fan to reduce boundary layer resistance across the foliar surface, and an air inlet and outlet so that differential O_3, carbon dioxide (photosynthesis) and water vapor (leaf diffusive resistance) measurements can be taken (Ennis et al., 1990; Houpis et al., 1991; Teskey et al., 1991). The advantages of this system include the ease with which the Teflon bag can be replaced, uniform light transmission can be maintained, the branch chamber can be moved from plant-to-plant, can be used in situ, and can be modified for different sized branches. One of the disadvantages of the branch chamber, and indeed of any such cuvette which isolates one part of the plant under different environmental conditions than the rest of the plant, is whether the isolation leads to a response different from that which would have been observed if the branch was under the same environmental conditions as the rest of the plant. In addition, total tree

growth cannot be estimated using branch chambers, as only part of the plant is treated with O_3.

5.2.1.3 Flux Measurement

Estimation of O_3 flux to foliage can be made directly, by measuring the difference in O_3 concentration between air going into a leaf chamber and the same air stream exiting the chamber after passing over the leaf. It can also be inferred from measurements of leaf diffusive resistance during exposure of a leaf to O_3. The former method requires a chamber or cuvette fumigation system with uptake of O_3 which is quite small or extremely nonvariable relative to the amount being taken up by the leaf. Otherwise, it is difficult to detect O_3 flux to a leaf with good precision. Such cuvettes can be adapted from those commercially available for portable photosynthesis meters (Graham and Ormrod, 1989) or constructed from a novel design, such as that developed by Fuentes and Gillespie (1992) to estimate the effect of leaf surface wetness on O_3 uptake of maple leaves. The criteria for flux cuvette design include good light transmissibility, ease of leaf manipulation, minimal reaction of chamber wall surface with O_3 and good air mixing within the chamber. Good mixing of air is necessary to avoid a gradient in pollutant concentration, and to maintain a boundary layer resistance which is greater than stomatal resistance. Maintenance of leaf temperature close to that of the surrounding air, so that transpiration rates are not abnormally high, is another benefit of good air mixing. The physical design of the Fuentes and Gillespie chamber was simple, consisting of two glass hemispheres that were clamped together, separated by a Viton O-ring, over the petiole of the leaf under investigation. Inlet and outlet air attachments were on opposite sides of the cuvette. Other cuvette designs have been used to estimate leaf gas exchange responses to O_3; their principals of operation are similar, but there are differences in materials and design (Amiro et al., 1984; Freer-Smith and Dobson, 1989; Laisk et al., 1989; Moladau et al., 1991; Skarby et al., 1987).

Compared to the CSTR, which has been used for mass balance measurement of gas flux by whole plants during fumigation (LeSueur-Brymer and Ormrod, 1984), cuvette systems usually determine flux to one leaf at a time. This results in a more precise understanding of the interaction among leaf age, leaf diffusive resistance, leaf illumination and O_3 flux. However, these data are not particularly well adapted to estimating flux of O_3 to a large

vegetated surface. Finally, regardless of the methodology used to determine O_3 flux to foliage, there exist only very sketchy mechanistic-process models which would link O_3 fluxes to decreases in growth and productivity of plants. At this time, these data are mainly useful for developing a relationship between *internal* O_3 dose and plant response, and estimating the strength of vegetation as sinks for O_3 flux on a large scale.

Pollutant Dispensing Systems

Although exposure chambers have changed little in design in the last several years, the profile characteristics and method of dispensing pollutant profiles have. Whereas early studies utilized static or square-wave exposures, usually controlled by hand-set flowmeters, many more recent system expose plants with so-called dynamic exposures, during which the O_3 concentration gradually reaches a maximum, thus simulating diurnal variation in O_3 concentration (Hogsett et al., 1985a). These profiles may be achieved by mass flow controllers that are themselves computer controlled. Proportional add systems such as that used in NCLAN usually achieve ambient type profiles using rotameters instead of mass flow controllers. The O_3 concentration in each of the chambers is logged at pre-set intervals, so that the integrated exposure for the entire fumigation period can be calculated. Deviations from the planned O_3 episode can occur, due to failure in dispensing or monitoring equipment, as well as incursions of air through the tops of the chambers. The length of the interval between determinations of O_3 concentration in the chambers can be an important contribution to the control of O_3 profile. In general, longer intervals lead to less well-controlled and well-characterized O_3 exposure profiles (Lefohn et al., 1993). These deviations from the expected profiles can be mathematically quantified, and monitored among treatments and replications (Hale-Marie et al., 1991).

Open Air Field Fumigation Systems

Open air field fumigation systems have the potential to most closely estimate filed losses due to O_3, as the plants are grown and exposed under ambient field environmental conditions. However, of all the fumigation systems, this is the least controllable and repeatable. It has been used in the past to expose plants to "static" concentrations (desired concentration is the same throughout the exposure period) of such pollutants as sulphur

dioxide or hydrogen fluoride (Hogsett et al., 1987). The Zonal Air Pollution System (ZAPS) has been vastly modified and improved upon to enable fumigation of plants with the diurnally varying pattern of concentration typical of ambient O_3 fumigation (Runeckles et al., 1991). The system represents a significant advancement over earlier open-air field fumigation systems, in that 12 discrete seasonal treatments which simulate ambient patterns are achieved rather than the usual two or three. Ozone was supplied to plots, which were laid out in groups of four, through a manifold suspended over the plant canopy. The wind speed and direction determined the actual seasonal O_3 exposures, although the O_3 was released in concentrations proportional to that observed at the time in the ambient environment. While the twelve treatments are not repeatable over time, a regression relationship between pollutant exposure and plant response can be established for each growing season.

The Liphook study in England of long-term responses of *Picea sitchensis* (Bong.) Carr, *Picea abies* (L.) Karst., and *Pinus sylvestris* L. to sulphur dioxide and O_3 in combination consisted of seven growth plots, 50 m in diameter, five of which were surrounded by 64 vertical pipes from which pollutant gasses were emitted (McLeod et al., 1992). The 64 pipes were divided into four quadrants of 16 adjacent pipes, and each quadrant had diluted pollutant gases supplied to it from a computer controlled mass flow controller. The emitting quadrant(s) as well as the rate at which the gases were supplied to the quadrant depended on wind speed and direction. The gases were emitted from the vertical pipes into the plant canopy at two heights, 0.5 and 2.5 m above a reference height, which was approximately two-thirds of tree height. This pattern of gas dispersion resulted in a uniform horizontal distribution of hourly mean gas concentration across each central 25-m diameter experimental plot. Measured over a winter wheat canopy, SO_2 concentration differed by less than 1 $nl.l^{-1}$ over a 5-h period of measurement; measurement of consecutive 2-min mean values at five locations across the plots demonstrated high uniformity (McLeod et al., 1985). This exposure system, like all open-air exposure systems, clearly simulates field plant growth conditions far better than open- or closed-top chambers. The usefulness of the data is limited however, by the low number of treatments and lack of replication of those treatments. And, with five "enclosures", and two nonenclosed ambient plots, this is by far the largest of the very few of these systems which are in operation.

Field Chamber Exposure Systems

Open-top field chambers are used in most field studies of plant response to gaseous pollutants. They were first designed for studies on annual herbaceous crop plants (Mandl et al., 1973) but enlarged versions have been used successfully in tree seedling and sapling studies also (Adams et al., 1990; Chappelka et al., 1990; Qui et al., 1992; Kress et al., 1992; Hogsett et al., 1989; Andersen et al., 1990; Karnosky et al., 1993; Wang et al., 1991; Temple et al., 1991). Because the results from these studies using tree species are extrapolated to predict the effects of O_3 on forests, these studies require good exposure control in order to replicate ambient O_3 profiles characteristic of many low-elevation, rural areas of eastern North America. This condition could have been met using an open field exposure system. Open-top chambers which are large enough for mature trees to have been developed but are expensive (Grandl et al., 1989).

Microclimatic modification by open-top chambers as well as O_3 exposure schedules which are disconnected from typical O_3 episode meteorology have been addressed in a seasonal study of tree response to O_3 in the United Kingdom (Wiltshire et al., 1992). This study is using open top chambers with roll-up sides; except for fumigation days, the plants are maintained in ambient climatic conditions. The exposure episodes number between 27 and 30 throughout the growing season, and occur on days with ambient meteorology associated with naturally occurring O_3 episodes (i.e., high incident radiation and temperature with little air movement) (Wiltshire et al., 1992). The maintenance of near-ambient meteorological conditions during both growth and exposure periods ensures that this study will represent field grown plant responses to O_3 better than traditional open-top chamber studies.

Several designs of field fumigation chambers have been developed to overcome some of the disadvantages of the open-top chambers, namely small plot size and incursion of ambient air. Closed top chambers were first developed in the 1950's; generally, smaller in dimension to the open-top design, have been more recently constructed in California to assess crop loss to O_3. Closed top chambers were chosen because the authors wished to characterize the pollutant dose to the plants very precisely; pollutant gradients within the chamber were minimal (Musselman et al., 1986). The chambers were octagonal in shape and covered with Teflon® film; the soil was completely replaced with standard greenhouse mix. Temperatures

in the chamber were higher (2 to 4 °C at midday, 1 to 2 °C at night) than in the ambient air, and light levels were reduced by 11% (spectral quality of the light in the chambers was not reported). The authors concluded that, although the chambers were not suitable for studies requiring close approximation of field conditions, they were very useful when tight control over soil moisture and pollutant concentration were needed.

Closed-top chambers were constructed and installed in the United Kingdom to study responses of shrubs and large herbaceous species to long term, low (chronic) concentrations of sulphur dioxide, nitrogen dioxide and O_3 (Rafarel and Ashenden, 1991). They were a smaller version of an earlier design, as the larger chambers required pure gas sources of nitrogen dioxide and sulphur dioxide to be diluted into the ventilating air stream, which resulted in highly variable exposure concentrations. The flow rate of the smaller chambers meant that premixed gases were sufficient to maintain steady control of treatment concentrations. Because the gases were discharged from the source at constant concentrations, different treatments were achieved by placing one or more pollutant supply tubes in the fumigation chambers. Good air circulation (and moderate ambient temperatures) maintained the domes at near ambient conditions.

Ambient Gradients for Evaluation of Plant Response to Ozone

The exposure system which most simulates ambient conditions of O_3 exposure, temperature, humidity, soils, soil moisture, is the ambient gradient system. By this method, plants are grown along a transect of known differential pollutant concentrations, usually downwind of a major point source or urban area. The concentration of pollutant(s) is diluted as distance from the source increases. A study of four cultivars of red clover (*Trifolium repens* L) and spring barley (*Hordeum vulgare* L) was conducted along such a transect of gradient sulphur dioxide, nitrogen dioxide, and O_3 concentrations in the United Kingdom (Ashmore et al., 1988). Ozone concentration was inferred from injury to Bel W3 and Bel B cultivars of tobacco, but was found to have very little relationship to cultivar performance. The authors cautioned that these results must be interpreted with an understanding that differences among sites in other environmental parameters could contribute to the detection (or failure to detect) of O_3 effects on the crops. For ambient gradient studies to be interpretable, good characterization of site parameters (rainfall, temperature, radiation, soil

type) is needed. Additionally, the modeler needs to know how these factors should be used to adjust the apparent plant response. In order to know that, a good knowledge base of how all of these factors modify plant response to O_3 is needed.

At this time, although some information is available, the relationships are still incompletely understood. Many investigators consider that ambient gradients are impossible to find without major differences in environmental conditions which may affect plant response to O_3 and therefore confound interpretation of the results.

Comparison of Fumigation Systems

Each type of fumigation system is particularly well suited to certain types of studies of plant response to O_3. To gather data relevant to the mechanisms of plant response to O_3, chambers with a high degree of control over environmental conditions are needed. Many of the physiological bases of plant response to O_3 can be themselves highly influenced by small differences in light, humidity, and temperature. For example, measurements of O_3 effects on photosynthetic rates in chambers with illumination levels well below saturation for photosynthesis may be highly variable with very small changes in PAR, as the relationship between PAR and photosynthetic rates for many species is steeply linear at low light levels. Alternately, it is notoriously difficult to get reliable photosynthetic data from field chambers under ambient light, as cloud cover and diurnal changes in the solar angle cause change in instantaneous rates of photosynthesis. For high precision in estimating photosynthetic responses to O_3, controlled environment exposure chambers with saturating light sources are needed; such systems are not yet in wide-spread use.

A comparison of plant growth and plant response to O_3 fumigation in open-top chambers, closed-top chambers, and air exclusion systems has been carried out (Olszyk et al., 1986). The authors discovered that there was interaction between plant response to O_3 and type of exposure system for less than 10% of the growth parameters measured in California, suggesting that plant response to O_3 was the same regardless of fumigation system. Plants from exclusion systems were shorter than in open-top chambers, and generally weighed more. Of the three groups of plants, those in the control plots of the exclusion system (i.e., receiving ambient O_3 exposure) were most similar in size to plants grown in field plots. While this and another study (Olszyk et al., 1992) indicate that

environmental modification caused by chambers will affect plant growth, there is no evidence that there is a large effect of chambers on plant response to O_3. It is assumed that, because of the decreasing relative effects on plant environment caused by controlled environment, greenhouse, closed top field chambers, open-top field chambers, open air systems, and ambient gradients, the system effects on plant response to O_3 will decrease in the same order.

Considerable concern has been raised about plant response to trace pollutants in exposure chambers, specifically N_2O_5 and NO in chambers receiving O_3 generated from dry air, and NO_2 in chambers receiving ambient air. These trace pollutants may have a direct effect (positive or negative) on plant processes, or may change how plants respond to O_3, and without careful evaluation, these effects may go undistinguished from those of O_3. A comparison of alfalfa response to the same O_3 exposure, generated electrostatically from air or through nonfiltration of ambient air, indicated that the generated O_3 treatment was more phytotoxic than the ambient O_3 treatment, likely due to the co-generation of N_2O_5 and NO along with O_3 from dry air (Olszyk et al., 1990). The results of this study and the comparison among field exposure systems, suggest that estimates of plant response to O_3 from open field air exclusion systems will be most representative of true field response, as this system uses ambient O_3 and no chambers. Next in accuracy will be open-top chamber studies using filtered versus nonfiltered ambient O_3. The drawback of these two approaches is that plant responses to low ambient levels of O_3 as might occur in many years is quite subtle. To detect statistically significant differences between filtered and nonfiltered chamber grown plants requires a high number of replications (Rawlings et al., 1988). Since seasonal O_3 concentrations vary greatly with geographic location and year, the collection of data for yield loss estimates by either of these two methods will be much slower than if O_3-enriched chamber exposure systems are used.

5.2.2 Experimental Design and Data Analysis

The statistical design of an experiment is crucial in defining the types of analyses to which the data can be subjected, and consequently the kinds of information about plant response to O_3. For these reasons, the information goals of a study must be clearly defined in order to choose an appropriate experimental design. The various experimental designs and

approaches to data analysis have been well reviewed in the 1986 criteria document (U.S. Environmental Protection Agency, 1986) and will not be repeated here. In summary, it is clear that over the last 15 years, studies have more frequently used experimental designs which generate data suitable for determination of regression-type dose-response relationships. These exposure-response relationships generalize the mathematical relationship between the plant parameter of interest and O_3 exposure. Plant response to concentrations other than those used in the experiment can be interpolated from these relationships and thresholds of plant response can be determined (Ormrod et al., 1988). In the latter half of the NCLAN program, the Weibull model was chosen to characterize yield response to O_3 because of its flexibility to describe a wide range of data patterns (Rawlings and Cure, 1985) and, consequently to allow a common model to be fit when pooling data across years and sites (Lesser et al., 1990).

Experimental designs for exposure-response relationships can easily be expanded so that plant response to O_3 and another factor at multiple levels can be determined. Because of the need to contain each O_3 treatment by a chamber, incomplete factorial designs are a more efficient approach to multi-factor studies, leading to exposure-response surfaces (Allen et al., 1987). Choosing the appropriate incomplete factorial design for a response surface study requires forethought on whether all areas of the surface are of equal interest. For many O_3 plant response studies this is not so, as extremely high concentrations, although increasing the precision with which plant response to lower concentrations is estimated, are not as likely to occur in the ambient environment.

Because the U.S. Environmental Protection Agency (1986) decided to place greater emphasis on damage (i.e., effects that reduce the intended human use of the plant) than on injury, studies have more frequently used experimental designs which generate data suitable for regression and treatment mean separation analyses to model and test the impact of O_3 on plant response. While the impact at current O_3 levels is of primary interest and can be studied using two O_3 levels generated by charcoal-filtered (CF) and nonfiltered (NF) treatments, the development of exposure-response models necessitates the use of additional treatments at above ambient concentrations. The optimal number, range, and spacing of treatment levels depends upon the anticipated exposure-response model but, in the case of the Weibull and polynomial models, greater precision for estimation of relative yield loss at

ambient O_3 concentration is obtained when the lowest treatment level is near zero and the highest treatment level is well above ambient. For the Weibull model, the highest treatment should correspond to a concentration where yield loss is at least 63% of the yield at zero exposure (Dassel and Rawlings, 1988; Rawlings et al., 1988).

When studying the impact of mixtures of pollutants on plant processes in chambers, response surfaces can be generated from complete or incomplete factorial designs. These designs have been shown to increase the precision and efficiency of estimating relative yield loss at ambient concentrations (Allen et al., 1987). The optimal design cannot be specified *a priori* and necessitates the use of treatment levels from near zero to well above ambient for each pollutant. However, response surface designs have not been widely used in pollutant mixture studies to date. Nor have these designs been widely used to study the interaction between pollutant exposure and quantitative environmental parameters such as light, temperature or soil moisture. The interaction between O_3 and phytotoxic concentrations of other pollutants, in particular sulfur dioxide, has not been extensively studied because instances of co-occurrence of O_3 and other pollutants are not common in the United States. An analysis of pollution monitoring data showed fewer than 10 periods of co-occurrence between O_3 and phytotoxic concentrations of sulfur dioxide during the growing season at the sites where the two pollutants were monitored (Lefohn and Tingey, 1984; U.S. Environmental Protection Agency, 1986).

Design and analysis of pollutant effects studies have used various characterizations of exposure to determine optimum spacings of treatment levels and to relate exposure to response. Most notably, the daytime mean concentration index (i.e., either M7 or M12) has been adopted by the NCLAN program to determine the effects of O_3 on plant response. However, there has been considerable debate over the use of the mean index in exposure-response modelling; the variety of ways to compute the characterizations of plant exposure will be discussed elsewhere in this document (Section 5.5). When plant yield is considered, plant response is affected by the concentration of exposure as well as by other exposure-dynamic factors (e.g., duration, frequency, threshold, respite time) in combination with physiological, biochemical, and environmental factors which may mask treatment effects over the growing period. Research goals to understand the importance of exposure dynamic factors have utilized experimental designs that apply two or more different patterns of

exposure that are equal on some scaling (e.g., total exposure). Experiments designed specifically to address the importance of components of exposure may require the use of exposure regimes that are not typical of the ambient environment.

In experiments in which treatments are quantitative, the traditional approach is to use regression analysis which relates O_3 exposure to plant response (U.S. Environmental Protection Agency, 1986). The regression approach has been used to fit a common model to combined data from replicate studies of the same species when it is reasonable to assume that the primary cause of biological response is pollutant exposure and that differences in environmental, edaphic, and/or agronomic conditions among sites do not significantly change the shape of the regression relationships. When pooling data across sites and years, additional terms for site and year effects are often included in the model as either fixed or random components, depending upon the population of interest. Inferences over random environments implies that the environments sampled by the experiments are representative of the population of regions of interest under a variety of environmental conditions. In this case, site and year effects are incorporated as random components in the model when fitting a common model. The appropriate analysis is to use a mixed model analysis to fit an exposure response model with variance components. This analysis has been recently used to combine data from replicate studies of varying durations to test the importance of length of exposure in influencing plant response; this approach is described elsewhere in the document (Section 5.5).

5.2.3 Mechanistic Process Models

In addition to regression type models of plant response to O_3, which are empirical and statistical in nature, there are mechanistic-process models (Luxmoore, 1988; Kickert and Krupa, 1991; Weinstein et al., 1991). The key difference between these two types of models is how the changes in the dependent variable over time are handled. Empirical models treat a time period (e.g., a growing season) as a single point, and report the response of the dependent variable as a single point as well. Regression models may also over-simplify the characteristics of an O_3 exposure, in that the description of the O_3 exposure is compressed over time to a single number. The variety of ways to compute this single number will be discussed elsewhere in this document (Section 5.5).

Mechanistic-process models on the other hand describe the rate of change of a variable in response to the treatment (such as O_3) with change in time (dy/dt). The latter type of model has the potential to capture the interaction among plant age/stage of development, variability of ambient exposure concentrations and plant response to O_3. For this reason, mechanistic-process models have been rated much more highly than regression models for their realism, scientific value and applicability to other locations (Kickert and Krupa, 1991). However, compared to regression models, mechanistic-process models require more input data and the input data are less accessible. The mechanistic-process models are more complex than regression models, requiring more computer time and memory to develop. The precision of the output regression models is greater than mechanistic-process models (for interpolative examinations only), as is their ability to estimate response probabilities. The authors conclude that the popularity of single-equation time-lumped models is related to the fact that the studies of plant responses to O_3 are more oriented to air quality standard setting as an endpoint, rather than the physiological processes underlying plant responses. The problems with process-based models are the necessity for some large assumptions (in place of real data) and the lack of validation. Without that validation, using estimates from these models is questionable. If these estimations are used, the uncertainties associated with them must be identified and quantified.

5.3 SPECIES RESPONSE/MODE OF ACTION

5.3.1 Introduction

Plant adaptation to changing environmental factors or to stresses involves both short-term physiological responses and long-term physiological, structural, and morphological modifications. These changes help plants to minimize stress and maximize the use of internal and external resources. A great deal of information is available on the physiology of single leaves, however, relatively little is known about whole-plant systems and whether the physiological mechanisms involved are initiated wholly within the leaf or are the result of whole-plant interactions (Dickson and Isebrands, 1991).

The many regulatory systems contained in leaves change both as a function of leaf development and in response to different environmental stresses. Leaves function as the

major regulators of anatomical and morphological development of the shoot and control the allocation of carbohydrates to the whole plant (Dickson and Isebrands, 1991). This section discusses the movement of O_3 into plant leaves and what is known about their biochemical and physiological responses.

Movement of O_3 into plant leaves involves both a gas and a liquid phase. The phytotoxic effects of air pollution on plants appear only when sufficient concentrations of the gas diffuse into the leaf interior and pass into the liquid phase within the cells. Therefore, to modify or degrade cellular function O_3 must diffuse in the gas-phase from the atmosphere surrounding the leaves through the stomata into the air spaces and enter into the cells after becoming dissolved in the water coating the cell walls (U.S. Environmental Protection Agency, 1986). The exact site or sites of action are not known. Biochemical pathways are closely interrelated, and at the present time, we do not have sufficient knowledge of all the control and regulatory mechanisms (Heath 1987). The previous criteria document summarized quite well the overall processes controlling plant response to O_3:

> "The response of vascular plants to O_3 may be viewed as the culmination of a sequence of physical, biochemical, and physiological events. Ozone in the ambient air does not impair processes or performance, only the O_3 that diffuses into the plant. An effect will occur only if a sufficient amount of O_3 reaches the sensitive cellular sites within the leaf. The O_3 diffuses from the ambient air into the leaf through the stomata, which can exert some control on O_3 uptake to the active sites within the leaf. Ozone injury will not occur if (1) the rate of O_3 uptake is sufficiently small that the plant is able to detoxify or metabolize O_3 or its metabolites; or (2) the plant is able to repair or compensate for the O_3 impacts (Tingey and Taylor, 1982). The uptake and movement of O_3 to the sensitive cellular sites are subject to various physiological and biochemical controls" (U.S. Environmental Protection Agency, 1986).

Responses to O_3 exposure that have been measured include reduced net CO_2 exchange rate (photosynthesis minus respiration), increased leaf/needle senescence, increased production of ethylene, and changes in allocation patterns. Overall understanding of the response of plants to O_3 has been refined since the last criteria document (U.S. Environmental Protection Agency, 1986). Increased emphasis has been placed on the response of the process of photosynthesis to O_3, on identification of detoxification mechanisms, and on changes in biomass (sugar, carbohydrate) allocation.

As indicated above, entry of O_3 into leaves involves the gas-phase external to the plant and the liquid—phase within the leaf cells. A precondition for O_3 to affect plant function is that it be absorbed into the tissues. We will divide O_3 uptake into two components, adsorption to surfaces and absorption into tissues. Adsorption will affect surface materials (e.g., cuticles, and have little direct affect on physiological processes), whereas O_3 absorption can affect physiological function, if O_3 is not first detoxified. In the following section the processes that control movement of O_3 into the plant canopy and then into the leaf will be examined.

5.3.2 Ozone Uptake

Uptake of O_3 in a plant canopy is a complex process involving adsorption of O_3 to surfaces (stems, leaves, soil) and absorption into tissues, primarily leaves (Figure 5-2). Movement of O_3 from the atmosphere to the leaf involves micrometeoroloical processes (especially wind) and the architecture of the canopy (including the leaves). Within the canopy O_3 can be scavenged by chemicals in the atmosphere (Kotzias et al., 1990; Gäb et al., 1985; Becker et al., 1990; Yokouchi and Ambe, 1985; Bors et al., 1989; Hewitt et al., 1990) however the products of these reactions may themselves be phytotoxic (Kotzias et al., 1990; Gäb et al., 1985; Becker et al., 1990; Hewitt et al., 1990). The extent to which these scavenging processes affect O_3 absorption by leaves is not well known. Absorption of O_3 by leaves is controlled in large part by canopy and leaf conductances. The former is a shorthand for the complex of microclimate and canopy architecture that control movement of O_3 from the bulk air to the leaf. Leaf conductance is determined by leaf boundary layer conductance and stomatal conductance. In this section we will examine theoretical and empirical studies on O_3 uptake at the canopy and leaf levels.

5.3.2.1 Ozone Uptake by Plant Canopies

Integration of O_3 uptake at the stand level requires attention to several levels of organization (Enders et al., 1992; Hosker and Lindberg, 1982), because uptake at this level includes not only absorption by leaves, but adsorption by stems, the soil, and other structures with which O_3 can react. While the actual pathway, and therefore conductance, will vary within the canopy depending on position and wind profile, an integrated average conductance

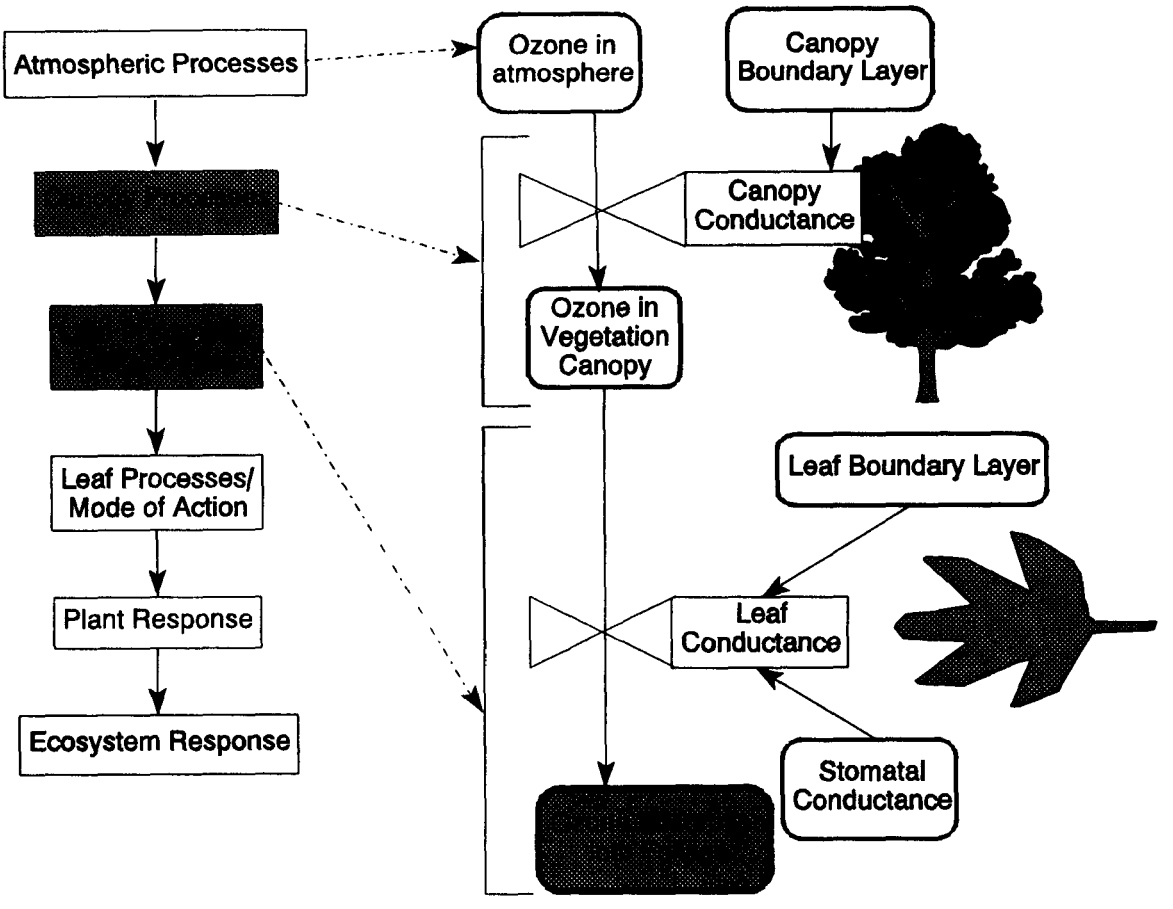

Figure 5-2. Uptake of O_3 from the atmosphere. Ozone is moved from the atmosphere above the canopy boundary layer into the canopy primarily by turbulent flow of air. Canopy conductance, controlled by the complexity of the canopy architecture and the wide distribution within the canopy, is a measure of the ease with which gases move into the canopy. Within the canopy, O_3 can be adsorbed by surfaces as well as being absorbed into the foliage. Foliage absorption is controlled by two conductances, leaf boundary layer and stomatal, which together determine leaf conductance. Solid black arrow denotes O_3 flow; gray stipled arrows connect factors and processes that affect O_3 flow; open arrows connect major processes. Shaded boxes at the left are those processes described in the figure. The shaded rounded box is end of pathway on this figure.

is frequently used to describe canopy conductance (Monteith and Unsworth, 1990). For most tree species canopy conductance tends toward high values while for crops it tends to be low.

Two general approaches have been used to estimate O_3 uptake by a plant stand: (1) measurement of gradients over the canopy using micrometeorological methods and

(2) simulation of canopy conductance. The results of the two methods are generally different because the micrometeorological techniques include O_3 uptake by all surfaces whereas simulation only accounts for O_3 absorbed by the surfaces simulated, primarily the foliage.

Two micrometeorological methods, Bowen ratio and eddy correlation, have been used to calculate canopy O_3 uptake. The Bowen ratio assumes a constant relationship (the Bowen ratio) between heat and water vapor fluxes (i.e., sensible and latent heat), then calculates O_3 uptake assuming a constant relation between water vapor and O_3 fluxes (Leuning et al., 1979a). The eddy correlation technique requires more elaborate instrumentation for measurement of variation in temperature, water vapor, and O_3 concentration over time and has stringent site requirements (Weseley et al., 1978).

Wesely et al. (1978), using eddy correlation, found a strong diurnal variation in the deposition velocity (the inverse of canopy conductance) and O_3 flux over a corn canopy. They also found evidence that 20 to 50% of the flux was to the soil and to the surface of the canopy. Ozone flux to a dead corn canopy also had a diurnal variation, but a lower magnitude, probably reflecting the absence of uptake through the response. Single time measures of deposition velocity, or canopy resistance, have been taken in a Gulf Coast pine forest (54 s m^{-1}; Lenschow et al., 1982) and in a New Jersey pine forest (120 and 300 s cm^{-1}; Greenhut, 1983. Ozone uptake in a maple forest varied diurnally in a pattern explainable by variation in leaf conductance and O_3 concentration (Fuentes et al., 1992). Ozone flux below the tree canopy at 10 m was about 10% of the flux above the canopy at 33 m. Measurements in specially constructed chambers showed that O_3 uptake, as well as photosynthesis, could occur when the foliage was wet (Fuentes and Gillespie, 1992). The fact that wet leaves could take up significant CO_2 is evidence that the response were not blocked by the water on the leaf surface. This result is counter to assumptions made in earlier work (Baldocchi et al., 1987) in which water on the surface of the leaf was presumed to interfere with O_3 uptake.

Simulation of canopy conductance requires scaling uptake from individual leaves to individual trees to that of a stand using a combination of canopy models (one for each species) and a stand model to handle interactions among individuals. Several assumptions are required for this approach: (1) the primary sink for O_3 is the foliage, (2) variation in stomatal conductance can be simulated through the canopy using either direct measurements

or models, and (3) canopy/plant models adequately simulate response when competition is occurring.

Leuning et al. (1979a,b) used a simple model to estimate canopy uptake in corn and tobacco. Comparison of the results of these simulations with estimates using the Bowen ratio technique indicated that about 50% of the O_3 absorbed by the stands entered the leaves. Baldocchi et al. (1987) presented a model for canopy uptake of O_3 that incorporated stomatal function, some aspects of canopy architecture, and soil uptake. The results of the simulation of O_3 uptake by a corn canopy correlated well with estimations using the Bowen ratio, but tended to overestimate the magnitude. These authors point out that results of model simulation are quite sensitive to the assumptions used. As part of a series of simulations, Reich et al. (1990) explored the effects of different O_3 exposures (daily average O_3 concentrations of 0.035, 0.05, 0.065, and 0.080 ppm) on canopy carbon gain in a mixed oak-maple forest. Depending on the response function and O_3 exposure used, reductions in carbon gain were between 5 and 60%. An important result of these simulations is that the effect of O_3 was strongest in the upper layer of the canopy, where most of the photosynthesis occurred. While all these simulations provide some interesting insights into how O_3 uptake (and response) varies with time and exposure, data for validating the models is still needed.

In summary, O_3 uptake (absorption to surfaces and absorption by tissues) by plant canopies has been measured only a few times. The results are consistent with the hypothesis that stomatal conductance plants a major role in the process. Modelling of O_3 absorption by leaves provides a means of assessing our understanding of the processes controlling O_3 absorption. Combining direct measurements over canopies with modelling will provide a means for assessing the dynamics of O_3 uptake in a canopy.

5.3.2.2 Ozone Absorption by Leaves

The importance of stomatal conductance for the regulation of O_3 uptake by a canopy has been hypothesized for some time (Heck et al., 1966; Rich et al., 1970). Absorption of O_3 by leaves is primarily controlled by stomatal conductance which varies as a function of stomatal aperture (Figure 5-3). Kerstiens and Lendzian (1989) found that the permeability to O_3 of cuticles from several species was about 0.00001 that of open response. Movement of guard cells, which control stomatal opening, are affected by a variety of environmental

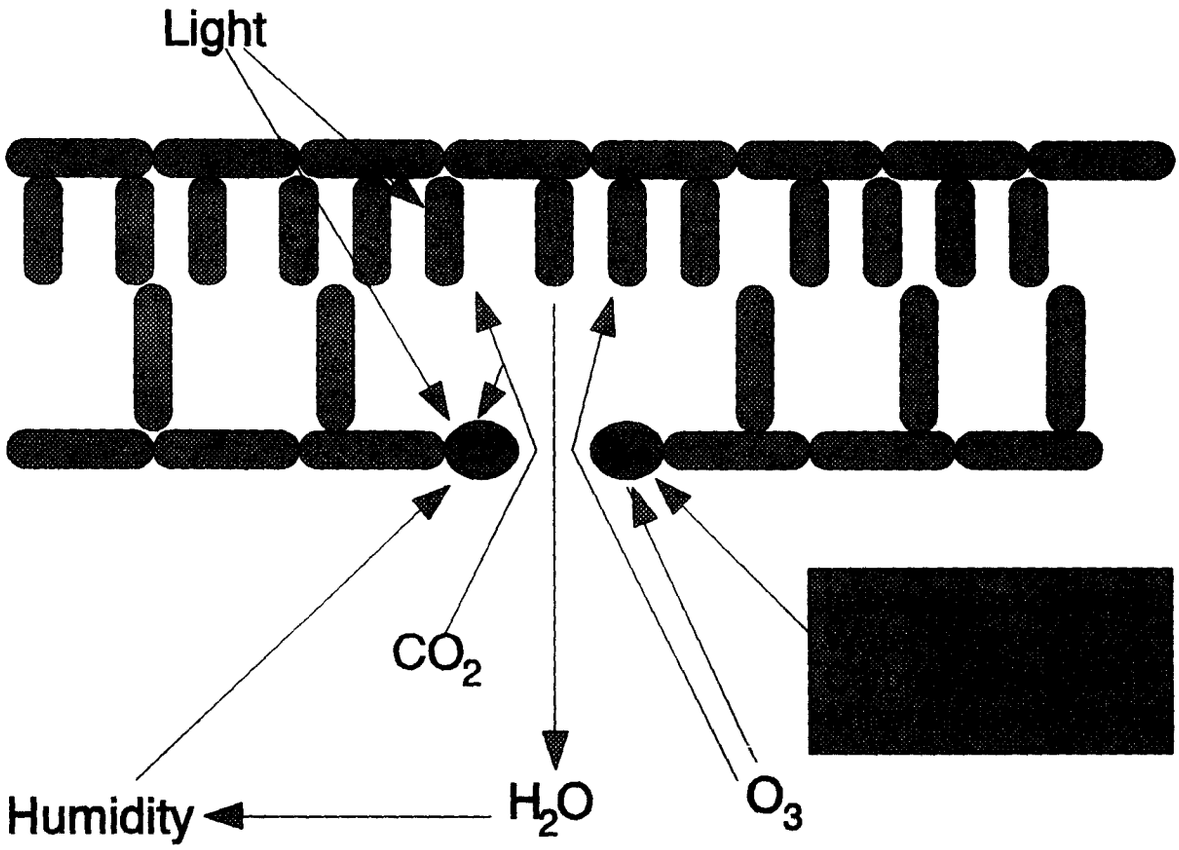

Figure 5-3. Movement of gases into and out of leaves is controlled primarily by the stomata—small openings in the leaf surface whose aperture is controlled by two guard cells. Guard cells respond to a number of external and internal factors, including light, humidity, CO_2, water stress. In general, the stomata open in response to light and increasing temperature and close in response to decreasing humidity, increased CO_2, and increasing water stress. They may also close in response to air pollutants, such as O_3.

and internal factors, including light, humidity, CO_2 concentration, and water status of the plant (Zeiger et al., 1987; Kearns and Assmann, 1993). Air pollutants, including O_3, may also affect stomatal function (U.S. Environmental Protection Agency, 1986).

For O_3 to be absorbed by a leaf, O_3 must be present in the atmosphere surrounding the leaf, and the stomata must be open. Any factor that affects stomatal opening affects O_3 absorption (Figure 5-3). Under drought conditions when stomatal conductance is reduced the relative effect of O_3 is less when compared with well-watered controls (Tingey and

Hogsett, 1985; Flagler et al., 1987; Temple et al., 1993, also see Section 5.4). Low humidity has been shown to modify plant response to O_3 (McLaughlin and Taylor, 1981), presumably due to reduced O_3 absorption (Wieser and Havranek, 1993).

To calculate O_3 absorption, some estimate of the internal O_3 concentration must be made. In earlier work, a finite O_3 concentration was assumed to exist in the intercellular air space of the leaf (Benett et al., 1973; Tingey and Taylor, 1982; Lange et al., 1989). Estimating this concentration is difficult because the rate of O_3 absorption into the leaf must be known. Recently Laisk et al. (1989) presented evidence that this concentration is near zero, a result that is consistent with the highly reactive nature of O_3. Further studies on other species must be made to test the hypothesis that internal O_3 concentration is negligible in leaves.

The other component of absorption, O_3 concentration outside the leaf, may vary greatly with time of day and season (Chapter 4). Data on the effect of variations in O_3 profile—from constant concentrations to equal daily peaks to variable (episodic) peaks—suggest that those profiles that have periodic high concentrations have a greater effect than those with low peaks even though the exposure is equivalent (Hogsett et al., 1985a; Musselman et al., 1986; see Section 5.6). Taylor and Hanson (1992) show how variations in conductance can affect O_3 absorption and conclude that conductances in and near the leaf surface have a major influence on absorption of O_3. Figure 5-4 shows a simulation of the effect of diurnal variation in stomatal conductance and O_3 concentration on the O_3 absorbed into the leaf. Amiro and Gillespie (1985) found that cumulative O_3 absorption correlated with visible injury in soybean. Weber et al. (1993) found that rate of uptake may play an important role in the response of ponderosa pine. The roles of cumulative uptake versus uptake rate have not been clarified and need further study.

Absorption of O_3 by leaves depends on variations in both stomatal conductance and O_3 concentration. The highly reactive nature of O_3 makes measuring its absorption difficult; therefore, models of stomatal conductance are used along with O_3 concentrations to estimate O_3 absorption. The relative importance of absorption rate versus cumulative absorption is not known at present.

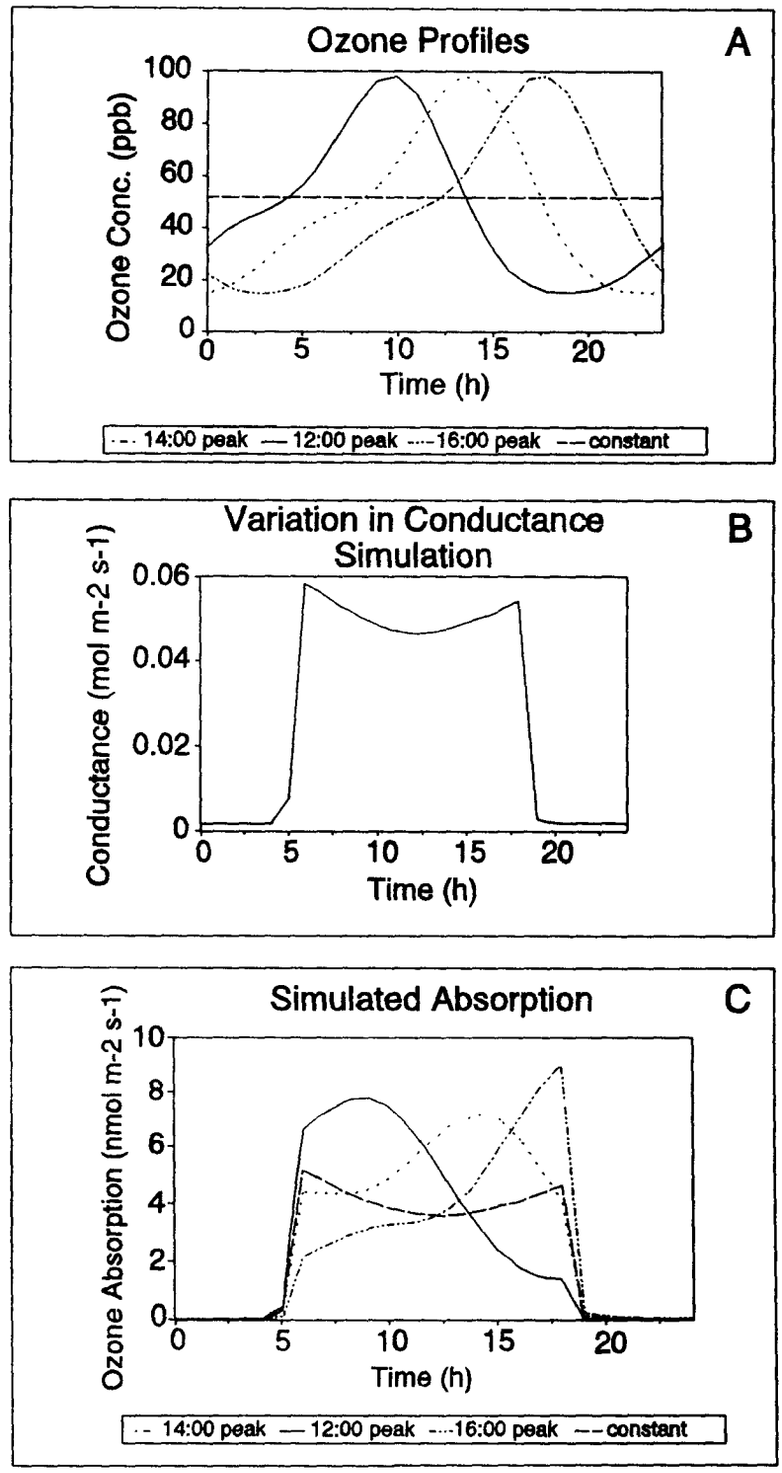

Figure 5-4. Simulation of the effects of diurnal variation in stomatal aperture and in O_3 concentration on O_3 uptake. A. Simulated conductance. B. Diurnal O_3 concentrations. C. O_3 Uptake.

5.3.3 Resistance Mechanisms

Resistance mechanisms can be divided into two types: (1) exclusion from sensitive tissue and (2) detoxification near or in sensitive tissue. For leaves the former involve response and cuticles, and the latter various potential chemical and biochemical reactions that chemically reduce O_3 in a controlled manner. While these systems potentially provide protection against O_3 damage to tissue physiology, they come at some cost, either in the reduction in photosynthesis in the case of stomatal closure or carbohydrate used to produce detoxification systems.

Injury to leaf/needle cuticles does not appear to have a major affect on leaf function; at least the data are not consistent. Barnes et al. (1988) found that O_3 exposure could damage leaf cuticles. However Lutz et al. (1990) found no consistent changes in Norway spruce.

5.3.3.1 Stomatal Limitation

As noted above, response can be affected by a wide variety of environmental factors. Some early research showed a decrease in leaf conductance (Figure 5-3) with O_3 exposure implying a direct effect of O_3 on stomatal conductance (U.S. Environmental Protection Agency, 1986). In studies at high O_3 concentrations (>300 ppb) stomatal response was rapid (Modlau et al., 1990). In other studies reduction in conductance in response to O_3 required hours to days of exposure (Dann and Pell, 1989; Weber et al., 1993). Several studies have shown that discrimination against 13C in C3 plants decreases with O_3 fumigation (Okano et al., 1985; Martin et al., 1988; Greitner and Winner 1988; Saurer et al., 1991; Matyssek et al., 1992). These data are consistent with an increased restriction to diffusion of CO_2 into the leaf (Farquhar et al., 1989). However, Matyssek et al. (1992) and Saurer et al. (1991) found that internal CO_2 increased with O_3 exposure and water use efficiency decreased, both the opposite of expectation, which indicates that photosynthesis decreased relatively more than conductance. While response limit O_3 uptake, whether this limitation results from direct effects of O_3 on guard cell function, indirectly through effects on internal CO_2 concentration, or a combination has not be clearly demonstrated.

5.3.3.2 Detoxification

When O_3 enters a cell, several highly reactive compounds can be produced (e.g., superoxide, free radicals, and peroxides) (Heath, 1987). The effects of these compounds depends on their reactivity, mobility, and half-life. For detoxification to occur oxidant and antioxidant must occur proximately. In addition, the rate of production of antioxidant must be a significant portion of the rate of oxidant entry into the system of effective detoxification to occur. Two general kinds of detoxification systems have been reported in plants: (1) those that utilize reductants (e.g., ascorbate) to reduce O_3, and (2) those that utilize enzymes (superoxide dismutase). In either case excess oxidizing power is dissipated in a controlled manner, effectively protecting the tissue from damage. These systems probably developed to protect cells from photooxidation which can occur, for example, at low temperatures (Powles, 1984).

Several antioxidants have been reported, the most studied being ascorbate and glutathione. Much of this work has occurred since the 1986 criteria document (U.S. Environmental Protection Agency, 1986). Alscher and Amthor (1988) reviewed the literature in this area. In the chloroplast, the process requires NADPH and may be a cause for the transient reduction in photosynthesis observed in some studies (Alscher and Amthor, 1988).

Evidence for the participation of antioxidants in protecting cells from O_3 injury is primarily indirect (i.e., changes in levels of antioxidants or of associated enzymes). In red spruce, glutathione levels increased in year-old needles in response to O_3, but not in current year needles (Hausladen et al., 1990; Madamanchi et al., 1991). Dohmen et al. (1990) found increased concentrations of reduced glutathione in Norway spruce in response to long-term O_3 fumigation. In a poplar hybrid, total glutathione increased with O_3 fumigation; however, the ratio of reduced to oxidized forms declined, indicating oxidation of glutathione was possibly stimulated by O_3 (Sen Gupta et al., 1991). Mehlhorn et al. (1986) found that both glutathione and ascorbic acid increased with O_3 fumigation in white fir (*Abies alba*) and Norway spruce. The potential for ascorbic acid to protect cells from O_3 damage was explored by Chameides (1989). He concluded that such protection was possible if ascorbic acid occurred in the apoplast at sufficient concentrations and sufficient production rates; however, experimental data are needed to test the hypothesis.

The response of enzymes involved in detoxification is not clear. Activities of enzymes involved in antioxidant production increased in response to O_3 in one study (Price et al., 1990); however, in several others no effect was found (Madamanchi et al., 1992; Pitcher et al., 1991; Anderson et al., 1992; Nast et al., 1993). Activity of superoxide dismutase, an enzyme that can reduce one of the products of O_3 interaction with the cytoplasm, can be increased by O_3 fumigation (Alscher and Amthor, 1988; Sen Gupta et al., 1991). There are both cytosolic and chloroplastic forms of this enzyme, but the role the different forms plant in detoxification of O_3 is not clear. Teppermann and Dunsmuir (1990) and Pitcher et al. (1991) found that increased production of SOD had no effect on resistance to O_3 in tobacco.

The extent to which these detoxification systems can protect tissue from O_3 damage is unknown. However, "If plants have detoxification mechanisms which are kinetically limited, the rate of O_3 uptake may be important, so that even an integrated absorbed dose may be insufficient to account for observed responses" (Cape and Unsworth, 1988). Potential rates of detoxification for given tissues are needed to estimate the importance of these systems to overall O_3 response. In addition, the sites in which the detoxification systems occur need to be identified.

5.3.4 Physiological Effects of Ozone

The initial reactions of O_3 with cellular constituents are not known. The high reactivity and non-specificity of O_3 reactions coupled with the absence of a useful isotopic tag for O_3 make studies of the initial reactions difficult at best. The data on changes in biochemical function resulting from O_3 exposure probably represent effects one or more steps beyond the initial reactions. Nonetheless, we do have data which indicate the wide range of cellular processes that can be affected by O_3.

Ozone that has not been neutralized by one of the detoxification systems (Figure 5-5) acts first at the biochemical level to impair the functioning of various cellular processes (Tingey and Taylor, 1982; U.S. Environmental Protection Agency, 1986). The result of these impairments are reflected in integrated changes in enzyme activities, membrane function, and energy utilization (Queiroz, 1988). Several related papers have shown that the activity of the primary carboxylating enzyme (RuBP-carboxylase) is reduced by O_3 exposures in the range of those measured at some sites (Dann and Pell, 1989; Enyedi et al., 1992; Pell

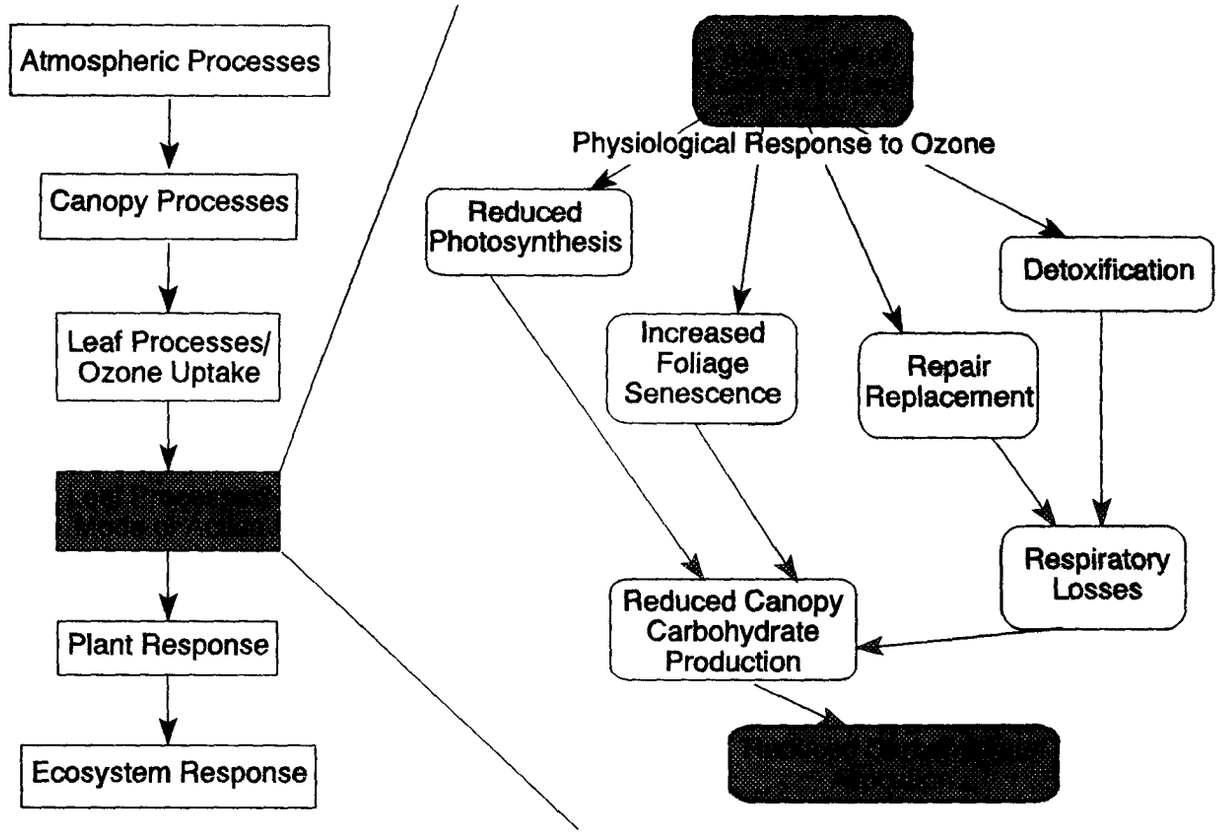

Figure 5-5. Effects of O_3 absorption into a leaf. Once inside the leaf O_3 can have a number of effects all of which affect carbohydrate production and utilization. Reduced photosynthesis, increased leaf senescence, production of detoxification systems, and increased respiration (both maintenance and growth) reduce the amount of carbohydrate available for allocation. Compensation through production of new leaves, for instance, can counter some or all of these effects depending on the O_3 exposure, physiological state of the plant, and the species. Integration of these processes leads to changes in the amount of carbohydrate available for allocation from the canopy. Solid black arrows denote O_3 flow; gray stipled arrows show the cascade of effects of O_3 absorption on leaf function.

et al., 1992; Landry and Pell, 1993). Membrane injury has been found in some experiments using acute levels of O_3 (Heath, 1987). Chronic exposure can lead to changes in lipid composition and changes in cold resistance (Brown et al., 1987; Davison et al., 1987; DeHayes et al., 1991; Lucas et al., 1988; Wolfenden and Wellburn, 1991). Recently, Floyd

et al. (1989) have been shown that O_3 can affect nuclear DNA through the formation of aducts.

Changes in the in vivo concentrations of various growth regulators in response to O_3 exposure could have important consequences for plant function. However, the effects of O_3 on levels and activities of growth regulators have not been studied extensively. Ozone has been shown to stimulate ethylene production and inhibitors of ethylene production have been found to reduce the effects of O_3 in short-term experiments (Pell and Puente, 1986; Rodecap and Tingey, 1986; Taylor et al., 1988; Mehlhorn et al., 1991; Telewski, 1992; Langebartels et al., 1991; Mehlhorn and Wellburn, 1987; Kargiolaki et al., 1991; Reddy et al., 1993). Ethylene is produced during ripening of fruit, during periods of stress, and during senescence (Abeles et al., 1992). Increased levels of ethylene in the leaves could play a role in the early senescence of foliage. In some cases there is a correlation between ethylene production and O_3 sensitivity; however, the relationship is complex and makes use of ethylene production as an index of sensitivity problematic (Pell, 1988).

Abscisic acid plays an important role in stomatal function (Davies et al., 1980). Atkinson et al. (1991) found that response from O_3 fumigated leaves were less sensitive to ABA than control leaves. These data could explain the observation that stomatal function is impaired by long-term O_3 exposure. Kobriger et al. (1984) found no effect of O_3 on whole-leaf content of abscisic acid, but changes in compartmentation could not be ruled out.

Physiological effects of O_3 uptake are manifest in two primary ways: (1) reduced net photosynthesis and (2) increased senescence (Figure 5-5). Both decreased photosynthesis and increased leaf senescence result in the loss of capacity for plants to form carbohydrates, thereby having a major impact on the growth of the plant (Figure 5-6).

Ozone-induced reduction in net photosynthesis has been known for some time (U.S. Environmental Protection Agency, 1986). Changes in stomatal conductance, in photosynthetic capacity, carbohydrate allocation and respiration have been documented. The relationship between O_3 exposure and photosynthesis is not well known. Photosynthesis provides plants with the energy and structural building blocks necessary for their existence. The photosynthetic capacity of a plant is an important aspect of plant response to stresses in natural environments and is strongly associated with leaf nitrogen content and with water

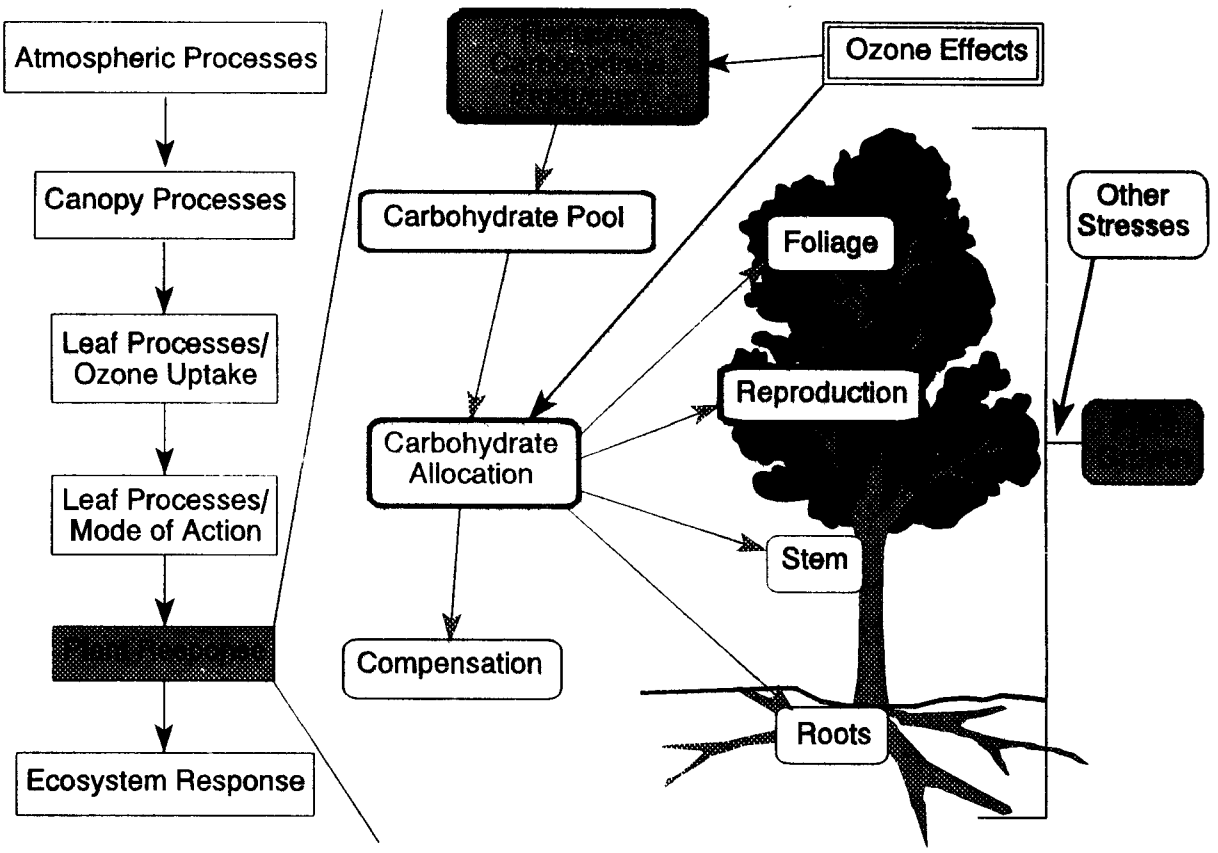

Figure 5-6. Effect of O_3 on plant function and growth. Reduction in carbohydrate allocation affects the pool of carbohydrates available for growth. Changes in relative growth rate of various organs as a function of O_3 exposure suggest that allocation patterns of carbohydrate is affected. Solid black arrows denote where O_3 absorption affects the allocation processes of the plant; gray stipled arrows show the cascade to plant growth.

movement. Both resources are essential if the process is to occur and involves the allocation of carbohydrates from the leaves to the roots for nitrogen acquisition and water uptake. Leaf photosynthetic capacity is also age dependent. As the plant grows, the canopy structure changes altering the amount and angle of light hitting a leaf. Allocation of carbohydrates and nutrients to new leaves is especially important in stimulating growth production (Pearcy et al., 1987). Reductions in photosynthesis are likely to be accompanied by as shift in growth pattern which favors shoots and by an increase or decrease in life span (Winner and Atkinson, 1986). Therefore, alteration of the processes of photosynthesis and carbohydrate

allocation affects plant response to stresses such as O_3. Reduction in photosynthesis, reduced carbohydrate formation and allocation to leaf repair or to new leaf formation decreases the availability of carbohydrates, alters the normal allocation pattern and, therefore, all aspects of plant growth and reproduction (Figure 5-6). The effects of a reduction in photosynthesis on growth and reproduction was discussed in the previous criteria document (U.S. Environmental Protection Agency, 1986).

Carbohydrate production by a single plant is controlled not only by photosynthetic capacity of the foliage but also by the amount and distribution of that foliage. Stow et al. (1992) and Kress et al. (1992) found that O_3 exposure affected needle retention in loblolly pine. Similar data have been reported for slash pine (Byres et al., 1992). Keller (1988) and Matyssek et al. (1993a,b) reported increased senescence with increased O_3 exposure in aspen, as did Wiltshire et al. (1993) in apple. Replacement of injured leaf tissue has been reported for some species when they are exposed to low O_3 concentrations (Held et al., 1992; Temple et al., 1993). Temple et al. (1993) also found increased photosynthetic capacity of new needles in O_3 treatments compared to controls.

Few direct effects of O_3 have been found outside leaves. Kargiolaki et al. (1991) found that intumescences appear on stems of poplar after 72 days of O_3 fumigation (70 to 80 ppb). Ozone probably enters the stem through the lenticles that occur on the surface of the stem and allow direct exchange of gases between the stem and the air. The consequence of this response to O_3 is not clear; however, it may be related to the reduction in phloem transport rate observed in loblolly pine (Spence et al., 1990).

5.3.4.1 Carbohydrate Production and Allocation

The importance of photosynthesis and carbohydrate allocation in plant growth and reproduction has been pointed out previously. The patterns of carbohydrate allocation directly affect growth rate. Plants require a balance of resources to maintain optimal growth, however, in natural environments optimal conditions seldom occur. Therefore, plants must compensate for differences in resource availability as well as for environmental stresses. They do this by changing the way they allocated carbohydrates (Chapin et al., 1987). Each response to stress affects the availability of carbohydrates for allocation from the leaves (Figure 5-5). The carbohydrate pool is affected both by a reduction in the carbohydrate

1 produced and by a shift of carbohydrate to repair and replacement processes. The effect is
2 particularly noticeable in the roots where O_3 exposure significantly reduces available
3 carbohydrate (Andersen et al., 1991; Andersen and Rygiewicz, 1991). Effects on leaf and
4 needle carbohydrate content have ranged from a reduction (Barnes et al., 1990; Miller et al.,
5 1989), to no effect (Alscher et al., 1989), to an increase (Luethy-Krause and Landolt, 1990).
6 Cooley and Manning (1987) reviewed the literature on carbohydrate partitioning and noted
7 that "storage organs...are most affected by O_3-induced partitioning changes when
8 O_3 concentrations are in the range commonly observed in polluted ambient air."
9 The above discussion supports the information in the previous criteria document (U.S.
10 Environmental Protection Agency, 1986), which pointed out that roots were usually more
11 affected by O_3 exposures than the shoots. Studies by Miller et al. (1969), Tingey et al.
12 (1976a), McLaughlin et al. (1982) and Price and Treshow, (1972) were cited in support of
13 the view. Miller et al., noted reduction in photosynthesis was accompanied by decreases in
14 sugar and polysaccharide fraction in injured needles of ponderosa pine seedlings and altered
15 allocation of carbohydrates. Exposure were for 30 days, 9 h/day to concentrations of 0.15,
16 0.30 or 0.40 ppm. These exposures reduced photosynthesis by 10, 70 and 85%,
17 respectively. The observations of Tingey et al. (1976) indicated that O_3 exposures
18 differentially affected metabolic pools in the roots and tops of ponderosa pine seedlings
19 grown in field. Further, this study indicated that the amounts of soluble sugars, starches,
20 and phenols tended to increase in the tops and decrease in plant roots of ponderosa pine
21 seedlings exposed to 0.10 ppm O_3 for 6 h/day for 20 weeks. The sugars and starched stored
22 in the tree roots were significantly less than those in the roots of controls. In another study
23 cited in the 1986 document, McLaughlin et al. (1982) also observed the reduced availability
24 of carbohydrate for allocation to the roots and stated that the result was reduced vigor and
25 enhanced susceptibility of trees to root diseases. Loss of vigor was due to a sequence of
26 events, including premature senescence and loss of older needles, lower gross photosynthetic
27 productivity, and reduced photosynthate (carbohydrates) available for growth and
28 maintenance, that were associated with exposure to O_3. Carbon-14 transport patterns also
29 indicated changes in carbon allocation. Older needles were found to be the source of
30 photosynthate for new needle growth in the spring and were storage sinks in the fall.

Retention of ^{14}C-photosynthate by foliage and branches of sensitive trees indicated that allocation to the trunks and roots was reduced.

Lost carbohydrate production has effects throughout the plant (Figure 5-6). The roots and associated mycorrhizal fungi are especially susceptible to reduced carbohydrate availability and quite frequently show the greatest decline in growth (Adams and O'Neill 1991; Edwards and Kelly, 1992; McQuattie and Schier, 1992; Meier et al., 1990; Taylor and Davies, 1990). However, in some cases, increased mycorrhizal formation has been reported (Goriseen et al., 1991; Reich et al., 1985). It might be expected that reduced allocation to roots would affect shoot growth through increased susceptibility to water stress, reduced nutrient availability (Flagler et al., 1987), and reduced production of growth factors (Davies and Zhang, 1991; Letham and Palni, 1983). Effects on production and retention of leaves and needles were described above. Effects on stem growth have been found in tree species (Hogsett et al., 1985b; Mudano et al., 1992; Pathak et al., 1986; Matyssek et al., 1992; Matyssek et al., 1993b). Changes in canopy density, root/shoot ratio, and stem growth will affect the functioning of the plant and may make plants more susceptible to environmental stresses, such as drought and nutrient limitation, that are characteristic of many ecosystems.

5.3.4.2 Compensation

Compensatory responses occur as plants attempt to minimize the effects of stress. Responses include adjustments to changes in physiological processes (e.g., photosynthetic capacity and foliage production) that tend to counteract the effects of O_3 absorption by the leaves. Pell et al. (in press) have reviewed the extensive literature produced in the ROPIS experiment. A wide range of compensatory responses have been identified, especially reallocation of resources leading to increased relative growth in the shoot compared to the root (see above). Compensation can take the form of production of new tissue (e.g., leaves) to replace injured tissue and/or biochemical shifts, including increased photosynthetic capacity in new foliage.

Changes in respiratory rate have been attributed to such repair processes (U.S. Environmental Protection Agency, 1986). Recent studies have found stimulation of dark respiration in Norway spruce (Barnes et al., 1990; Wallin et al., 1990) and bean (Amthor, 1988; Amthor and Cumming, 1988; Moldau et al., 1991). Repair of membranes (Sutton and

Ting, 1977; Chevrier et al., 1988, 1990) and of injured enzymes are two probable reasons for increased respiration. Ozone has been shown to increase the ATP/ADP ratio, which is consistent with increased respiratory activity (Weidmann et al., 1990; Hampp et al., 1990). As in the case of detoxification, the importance of repair processes in the overall carbohydrate budget of the plant and of their influence of apparent threshold is unknown.

Recovery of photosynthetic capacity after O_3 exposure has been noted in some studies. Early work indicated that recovery of photosynthetic capacity could occur after exposure of high concentrations (>0.25 ppm) of O_3 (e.g., Botkin, 1971, 1972). Dann and Pell (1989) found that photosynthetic rate, but not Rubisco activity, recovered within a few days in potato after exposure to 0.2 ppm O_3. In ponderosa pine, photosynthetic rates in O_3 treated needles recovered to that of controls within 40-50 days (Weber et al., 1993). To what extent this recovery can offset losses in carbohydrate gain is not known nor is the mechanism.

Replacement of injured foliage (see Section 5.3.4) is another method to counteract the effects of O_3 exposure. The extent to which increased leaf/needle production and increased photosynthetic capacity in the new foliage compensates for O_3 injury is not known.

The importance of various compensation mechanisms is not sufficiently well-known to allow an estimate of the degree to which they might mitigate the effect of O_3. The fact that increases in photosynthesis and in leaf production have been measured indicates that these processes, at least, may be important.

5.3.5 Role of Age and Size Influencing Response to Ozone

Plant age, physiological state of growth and the frequency to which plants are exposed play an important role in plant response to O_3. In annual species, effects of O_3 exposure can result in a reduction in the amount and size of seed production through changes in allocation that occur over the years. In perennial species, reduced growth occurs due to a reduction in the amount of carbohydrates available for storage. In both cases, carbohydrates will have been used to help the plants minimize the stress of O_3 exposure. It should also be noted that in absence of O_3 exposure, in hardwoods leaf photosynthetic capacity reaches an early peak and then gradually declines until senescence. Conifers, on the other hand retain leaves longer than one year (Pye, 1988).

Carry over effects of O_3 have been documented in growth of tree seedlings (Hogsett et al., 1989; Sasek et al., 1991; Temple et al., 1993) and in regrowth of roots (Andersen et al., 1991). Accumulation of these effects will affect survival and ability to reproduce. Data on cumulative effects of multiple years of O_3 exposure are extremely limited (Kress et al., 1992; Hogset et al., 1989). Controlled exposures have been for the most part 2 to 3 years.

A tacit assumption in much of the research on O_3 effects on trees is that seedling response to O_3 is a good predictor of large tree response. This assumption has been necessitated by the difficulty in exposing large trees for long times to O_3. Pye (1988) reviewed the problems of extrapolation from seedling/sapling experiments to large trees and noted several areas of difference between seedling/saplings and large trees. The problems include not only size but are those equivalent to a single tree growing in a field and a tree growing in a stand. There exists, between seedlings and large trees, a difference the ratio of photosynthetic to respiratory tissue; as a tree ages, the photosynthetically inactive tissue grows. Cambial tissues associated with stem, branch, and coarse roots also increase. Another difference is the existence of microclimatic and morphologic gradients across a canopy and altered water and nutrient regimes. Deep forest canopies generate a microclimatic gradient that is paralleled by a morphological gradient from sun leaves to shade leaves. Associated with this gradient is net radiation, which can vary by an order of magnitude within the canopy. Windspeed and air temperature decrease from above to below the crown, while air humidity and CO_2 increase. Ozone concentrations could also vary with forest crown depth, however, measurements have not been made. Cregg et al. (1989) also argue that these differences in scale can affect growth responses seen. Some studies have indicated that seedlings may be more sensitive (i.e., greater visible injury) than large trees (Kozlowski, Kramer, and Pallardy, 1992); however, Samuelson and Edwards (in press) have found that leaves on large red oak trees are more sensitive than those on seedlings. It is likely that a variety of factors determine sensitivity to O_3, including stomatal function and presence of detoxification systems, so that in some cases seedlings will be more sensitive and in others large trees will. While each of the four differences between small and large trees mentioned above can be supported on theoretical grounds, little direct information is available to evaluate the importance of these differences, especially with respect of O_3.

The microclimate of the canopy of mature trees is quite different from that of seedlings. Radiation intensity through the multilayer canopy can vary by an order of magnitude or more can be expected (Jones, 1992). In addition, gradients of other important microclimatic variables (temperature, humidity, wind speed) exist within the canopy. These will all affect stomatal conductance and some (e.g., wind speed), will affect canopy conductance.

The effect of size on transport processes and the subsequent response to O_3 is unknown. The simple fact of greater distance over which transport must occur will affect the timing of response of organs distant from the primary site of O_3 impact, the foliage. Studies using methods that integrate functions over the whole tree could provide useful information. For example, combinations of porometer measurements on foliage and whole plant water use measured (Schulze et al., 1985) on individuals of different sizes could provide very useful information on the coupling of leaf level processes to whole canopy and whole plant response. Greater evaporative demand in large than small trees as the result of greater leaf area and different microclimate could lead to transient water stress and stomatal closure, because of insufficient water transport capacity.

As a tree grows from a seedling to a large tree the ratio between photosynthesis and respiration declines as a greater portion of the plant tissue is non-photosynthetic. It is reasonable to assume that such a change could result in less resource being available for detoxification and repair as the plant grows. How this change affects the ability of a plant to survive O_3 (or any other stress) is not known. Recently, Samuelson and Edwards (in press) present data on northern red oak that show O_3 decreased photosynthetic capacity more on lower leaves within the canopy of large trees than on leaves near the top of the canopy—a result apparently counter to the model results of Reich et al. (1990). Seedling photosynthesis was not affected by the same O_3 exposure. A more interesting result of this work is the reduction in total canopy biomass found in large trees exposed to O_3. It is not possible to directly assess the relative importance of reduced photosynthesis versus loss of canopy from these data, but they do show that differences may exist between large trees and seedlings in their response to O_3. These differences may be due to changes in carbon budgets, stomatal characteristics, microclimate, and flushing patterns that develop as seedlings become trees. The ability of northern red oak seedlings to produce three flushes

and thus replace injured foliage may be an important defense mechanism in the seedling stage. The generality and physiological basis of these findings need further investigation.

In evergreen perennial plants, foliage must be maintained from one year to the next, frequently through periods unfavorable to growth. In evergreen species that retain a few to several years of leaves increased susceptibility to stress (e.g., frost) could further reduce potential canopy photosynthesis in subsequent years (Brown et al., 1987; Davison et al., 1987; DeHayes et al., 1991; Lucas et al., 1988). Fincher (1993) found that O_3 decreased frost tolerance in red spruce in both seedlings and trees. The consequences of this change to seedlings and large trees is in need of further work.

The effect of O_3 on storage of carbohydrates in large compared to small trees is not known. Changes in storage could affect the ability of the plant to withstand other stresses and/or to produce adequate growth during each growing season.

Dendrochronology (tree-ring analysis) provides the opportunity to do retrospective studies over the leaf of large trees. Reduction in annual radial growth has been found in the southern Sierra Nevada for Jeffrey pine but not for ponderosa pine (Peterson et al., 1987; 1989, 1991; Peterson and Arbaugh, 1988). One difficult with using tree-ring data to estimate O_3-related effects is that it is not always possible to separate reductions due to O_3 from other effects (e.g., drought).

Development of reliable methods for scaling from small to large trees are crucial to the prediction of the long-term effects of O_3 on forest function. Measurement of the response of different size trees to O_3 could provide useful data on the relative responses of small and large trees. However, problems exist in giving similar exposures to trees of widely different sizes. The most direct method is to fumigate trees over a significant portion of their life span. Time is the primary obstacle to these studies because they would require decades to complete. Whatever methods are used must be based on a good understanding of the physiological changes that occur as trees grow.

5.3.5.1 Summary

In the previous criteria document it was concluded that the "Critical effects, including reduction in photosynthesis and a shift in the assimilation of photosynthate, will lead to reduced biomass, growth, and yield" (U.S. Environmental Protection Agency, 1986).

In addition, changes in carbohydrate allocation patterns and affects on foliage were noted as important. Since that report additional information has been developed, especially on the effects of O_3 on photosynthetic capacity. However, at present there is still no clear understanding of the initial biochemical changes resulting within the leaf cells after the entry of O_3 and how these changes interact to produce the observed responses. Much of the earlier research used very high (0.25 ppm or greater) O_3 concentrations which produced what could be characterized as acute responses. More recent research has used lower concentrations, usually including near ambient O_3 level, so that the observed responses may be more relevant to field conditions. One characteristic of these more recent data is that a longer exposure (days to weeks instead of hours) is needed to show a response.

As a result of the research since the last criteria document, we have a better understanding of the reduction of photosynthesis as a result of O_3 exposure, especially its affects on the central carboxylating enzyme (ribulose-6-P-carboxylase/oxygenase). The rate of senescence of leaves has been shown to increase as a function of increasing O_3 exposure. At near-ambient exposures, leaf production has been shown to increase in some species, thereby off-setting the increased loss to due senescence. The mechanism of the increase in senescence is not known at the present time and deserves further study. Finally, the role that changes in allocation of resources plays in plant response to O_3 has gained greater prominence. Most studies have shown that allocation of photosynthate to roots is decreased by O_3. In some cases, allocation to leaf production has increased. Whether these changes are driven entirely by changes in carbohydrate availability or are controlled by other factors (e.g., hormones) is not known at present.

Some potentially significant processes have been investigated since the last Criteria Document, especially detoxification and compensatory processes. The role(s) of detoxification in providing a level of resistance to O_3 has been investigated; however, it is still not clear to what degree these processes can provide protection against O_3 damage. Data are especially needed on the potential rates of antioxidant production and on the subcellular localization of the antioxidants. Potential rates of antioxidant production are needed to assess whether they are sufficient to detoxify the O_3 as it enters the cell. The localization is needed to assess whether the antioxidants are in a location (cell wall or plasmalemma) which permits contact with the O_3 before it has a chance to damage

subcellular systems. Ozone exposure has been shown to decrease cold tolerance of foliage in some species. This response could have a major impact on long-lived evergreen species that retain leaves for several years. Various forms of compensation, especially stimulation of production of new leaves and higher photosynthetic capacity of new leaves, have been reported. While these processes divert resources away from other sinks, compensation may counteract the reduction in canopy carbon fixation produced by O_3. The quantitative importance of these processes is still in need of investigation. At the canopy level some additional evidence that diurnal stomatal variation is important in O_3 uptake. These data will provide important checks on the modelling of stand response to O_3.

Questions still remaining to be addressed include: How does the plant accumulate the effects of O_3 absorption? How important are cumulative O_3 absorption and O_3 absorption rate? How does the plant integrate injury due to O_3 absorption, detoxification, compensation, and other processes into a whole-plant response? What are the roles of growth regulators, especially ethylene? Are they significant? The major problem facing researchers trying to predict long-term O_3 effects on plants is how the plant integrates all of the response to O_3 into the overall response to the environment, including naturally occurring stresses. Little is now known about how response to O_3 changes with increasing age and size. This information is crucial to predicting the long-term consequence of O_3 exposure in forested ecosystems.

5.4 FACTORS THAT MODIFY PLANT RESPONSE

5.4.1 Modification of Functional and Growth Responses

Plant response to oxidants may be modified by various biological, physical, and chemical factors. Biological factors that modify plant response include those within the plant as well as those external to the plant. The genetic make up as well as their development stage play critical roles in the way individual plants respond to O_3 and other external stresses. For example, different varieties or cultivars of a particular species are known to differ greatly in their response to a given exposure to O_3, while the magnitude of the response of a particular variety, in turn, depends upon environmental factors such as temperature and humidity, soil moisture and nutrition, the presence of pests or pathogens,

and exposure to other pollutants or agricultural spray chemicals. In other words, response will be dictated by the plant's present and past environmental milieu, which also includes the temporal pattern of exposure, and the plant's stage of development. The corollary is also true: exposure to oxidants can modify response to other environmental variables. For example, exposure to O_3 reduces the ability of trees to withstand winter injury caused by exposure to freezing temperatures (Davison et al., 1988), and influences the success of pest infestations (Hain, 1987; Lechowiez, 1987). Hence, both the impact of environmental factors on response to oxidants and the effects of oxidants on responses to environmental factors have to be considered in determining the impact of oxidants on vegetation in the field. These interactions are summarized as the involvement of "other stresses" in the scheme shown in Figure 5-6 (Section 5.3). In the following review, the environmental factors are grouped into three categories: biological (including genetic and developmental components), physical, and chemical.

Runeckles and Chevone (1992) have recently provided a general review of the interactive effects of environmental factors and O_3. The subject is also treated in a National Acid Precipitation Assessment Program report (Shriner et al., 1990).

5.4.2 Genetics

The response of an individual plant within a species and at a given age is affected both by its genetic makeup and the environment in which it grows. This section examines the role of genetics in plant response to O_3 and its implication for both managed and natural ecosystems. In addition, major knowledge gaps in the understanding of genetic aspects of O_3 responses are pointed out.

The responses of plants to O_3 are strongly influenced by genetics as was summarized in the air quality criteria document for O_3 (U.S. Environmental Protection Agency, 1986). Thus, the plants of a given population or family will not respond to O_3 in the same way, even if they are grown in a homogenous environment. This has been amply demonstrated through intraspecific comparisons of O_3 sensitivity as determined by foliar sensitivity of ornamental plants, the aesthetic value of which are decreased by visible foliary injury, and of woody plants that are important components of natural ecosystems (Table 5-1). Ornamental plants and plants growing in wilderness areas, for example, have an intrinsic worth, apart

TABLE 5-1. EXAMPLES OF INTRASPECIFIC VARIATION OF FOLIAR SYMPTOMS IN OZONE RESPONSE

Species	Genetic Unit[a]	Concentration	Duration	Range of Response[b]	Reference
Ornamental, Non-Woody Plants					
Petunia sp. (Pentunia)	Cultivars	400 ppb - 4 h/day	4 days	20 to 60%(3)	Elkiey and Ormrod (1979)
Poa pratensis L. (Kentucky bluegrass)	Cultivars	400 ppb 300 ppb	2 h 4 h	0 to 90%(3) 30 to 60%(3)	Murray et al. (1975); Wilton et al. (1972)
Trees					
Acer rubrum L. (Red maple)	Populations	750 ppb - 7 h/day	3 days	19 to 34%(2)	Townsend and Dochinger (1974)
Fraxinus americana L. (White ash)	Half-sib families	500 ppb 250 ppb	7.5 h 6 h	0 to 50%(3) 2 to 33%(2)	Karnosky and Steiner (1981); Steiner and Davis (1979)
Fraxinus pennsylvanica Marsh. (Green ash)	Half-sib families	500 ppb 250 ppb	7.5 h 6 h	0 to 40%(3) 2 to 39%(2)	Karnosky and Steiner (1981); Steiner and Davis (1979)
Gleditsia triacanthos L. (Honeylocust)	Cultivars	Ambient	1 growing season	0 to 34% (3)	Karnosky (1981a)
Pinus ponderosa Dougl. ex P. Laws and C. Laws (Ponderosa pine)	Half-sib families	1.5 x ambient	3 growing seasons	0 to 28% (2)	Temple et al. (1992);
Pinus strobus L. (Eastern white pine)	Clones	300 ppb	6 h	0 to 60% (3)	Houston (1974)
Pinus taeda L. (Loblolly pine)	Half-sib families	250 ppb ambient + 60 ppb	8 h 1 growing season	3 to 29% (2) 1 to 42% (1)	Kress et al. (1982a); Adams et al. (1988)
Populus tremuloides Michx. (Trembling aspen)	Clones	200 ppb 150 ppb	3 h 6 h	7 to 56% (1) 10 to 91% (1)	Karnosky (1977); Berrang et al. (1991)

[a]Cultivars = a variety of agricultural or horticultural crops produced by selective breeding or a vegetatively propagated tree selection; half-sib seedlings = seedlings with one parent in common; full-sib seedlings = seedlings in which both parents are in common; clones = vegetatively propagated individual genotypes; populations = seedlings derived from a common gene pool.

[b]Range of response is expressed as percentage of leaves showing visible symptoms (1); percentage of leaf area injured (2); or percentage from a leaf injury rating scheme (3).

from any economic value related to growth (Tingey et al., 1990). Considerable genetic variation in O_3 sensitivity has also been demonstrated for growth responses of crop plants (Table 5-2). The range of responses displayed for visible foliar injury and growth, biomass or yield vary from species to species and from study to study. However, it is not uncommon to have genotypes varying from no response to well over fifty percent leaf area injured or fifty percent growth or yield reductions in the same study. Additional examples of genetic variation in O_3 response are shown in Figure 5-7 for visible foliar injury and in Figure 5-8 for growth. From Figure 5-7, we can see that depending on what population has been examined, white ash (*Fraxinus americana* L.) and green ash (F. *pennsylvanica* Marsh.) could have been classified as either O_3 sensitive or O_3 tolerant. Also noticeable from this figure is the large amount of variation in O_3 tolerance of individual half-sib (one parent in common) families from a given population. From Figure 5-8, the heterogeneity within a given loblolly pine (*Pinus taeda* L.) half-sib family in terms of growth is displayed. This variability has some interesting implications. First, since plants of a given species vary widely in their response to O_3 exposure, response relationships generated for a single genotype or small group of genotypes may not adequately represent the responses of the species as a whole (Temple, 1990). Second, because of the genetic variability and differential fitness existing among different genotypes in a population of plants, O_3 imposes a selective force favoring tolerant genotypes over sensitive ones (Roose et al., 1982; Treshow, 1980). Each of these implications will be discussed in this section.

Mechanisms and Gene Numbers

Little is known about the genetic bases for O_3 resistance mechanisms or about the numbers of genes involved in these mechanisms (Pitelka, 1988). Most O_3 resistance mechanisms involve a physiological cost which will result in decreased growth and productivity of resistant plants grown under O_3 stress. Partial or complete stomatal closure in the presence of O_3 is an example of a mechanism of resistance that has been demonstrated for several plants (Engle and Gabelman, 1966; Thorne and Hanson, 1976; Reich, 1987; Sumizono and Inoue, 1986; Tingey and Taylor, 1982) and that involves a high physiological cost as plants that have reduced stomatal conductivity will also have reduced carbon assimilation for growth (Ehleringer, 1991). Tolerance of internal leaf tissues to O_3 may

TABLE 5-2. EXAMPLES OF INTRASPECIFIC VARIATION IN GROWTH RESPONSES FOLLOWING OZONE EXPOSURES

Species	Genetic Unit[a]	Concentration	Duration	Range of Response[b]	Reference
Crops and Non-Woody Plants					
Agrostis capillaris L. (Bentgrass)	Populations	60 ppb	4 weeks	-45 to +20%(2)	Dueck et al. (1987)
Begonia semperflorens Hort. (Bedding begonia)	Cultivars	500 ppb-4 h/day 250 ppb-4 h/day	2 days 4 days	-59 to 0%(2) -16 to +10%(2)	Reinert and Nelson (1979); Reinert and Nelson (1980)
Festuca arundinacea Schreb. (Fescue)	Cultivars	400 ppb-6 h/day	7 days	-53 to -35%(2)	Flagler and Younger (1982)
Lycopersicon esculentum L. (Tomato)	Cultivars	400 ppb 1.5 x ambient	2 h 1 growing season	-50 to -4%(2) -54 to -17%(3)	Reinert and Henderson (1980); Temple (1990)
Phaseolus vulgaris L. (Snapbean)	Cultivars	60 ppb-7 h 72 ppb-7 h 80 ppb-7 h/day	mean-44 days mean-54 days 42 days	-26 to -2%(3) -73 to -44%(3) -68 to -50%(3)	Heck et al. (1988); Temple (1991); Eason and Reinert (1991)
Plantago major L. (Common plantago)	Populations	70 nl/1-7 h/day	2 weeks	-24 to 0%(1)	Reiling and Davison (1992a)
Raphanns sativus L. (Radish)	Within Cultivar	.1 μl/1-4 h/day - 3 days/week	3 weeks	-40 to -5%(2)	Gillespie and Winner (1989)
Silene cucabalus (Bladder campion)	Populations	35 ppb-12 h/day	4 weeks	-75 to -48%(2)	Ernst et al. (1985)
Solanum tuberosum L. (Potato)	Cultivars	150 ppb-6 h/day	8 days	-10 to 0%(2) -40 to 0%(2)	Pell and Pearson (1984); Ormrod et al. (1971)
Spinacia oleracea L. (Spinach)	Cultivars	130 ppb - 7 h/day	38 days	-56 to -28%(2)	Heagle et al. (1979)
Trees and Other Woody Plants					
Acer rubrum L. (Red maple)	Populations	750 ppb - 7 h/day	3 days	-36 to -17%(1)	Townsend and Dochinger (1974)
Abies alba Mill. (Silver fir)	Populations	250 ppb - 7 h/day	10 days	-18 to +3%(1)	Larsen et al. (1990)
Pinus elliottii Engelm. (Slash pine)	Half-sib families	3 x ambient	3 growing seasons	-20 to 0%(1)	Dean and Johnson (1992)

TABLE 5-2 (cont'd). EXAMPLES OF INTRASPECIFIC VARIATION IN GROWTH RESPONSES FOLLOWING OZONE EXPOSURES

Species	Genetic Unit[a]	Concentration	Duration	Range of Response[b]	Reference
Pinus taeda L. (Loblolly pine)	Full-sib families	50 ppb-6 h/day 1.9 x ambient	28 days 2 growing seasons	-18 to 0%(1) -19 to 0%(2)	Kress et al. (1982b); Shafer and Heagle (1989)
Pinus taeda L. (Loblolly pine)	Half-sib families	Ambient + 60 ppb 2.5 x ambient 250 ppb	1 growing season 1 growing season 8 h	-27.5 to +3%(2) -19 to -2%(2) -22 to +30%(2)	Adams et al. (1988); Qui et al. (1992); Winner et al. (1987)
Populus tremuloides Michx. (Trembling aspen)	Clones Ambient	26.4 ppm-h 3 growing seasons	92 days -24 to -12%(2)	-74 to -5%(2)	Karnosky et al. (1992); Wang et al. (1986)
Rhododendron obtusum (Lindl) Planch. (Azalea)	Cultivars	250 ppb-3 h/day	6 days	-43% to 0(2)	Sanders and Reinert (1982)

[a]Cultivars = a variety of agricultural or horticultural crops produced by selective breeding or a vegetatively propagated tree selection; half-sib seedlings = seedlings with one parent in common; full-sib seedlings = seedlings in which both parents are in common; clones = vegetatively propagated individual genotypes; populations = seedlings derived from a common gene pool.
[b]Range of response is expressed as decrease compared to charcoal-filtered-air control plants in terms of growth (1), biomass (2) or yield (3).

involve the production of antioxidant defense compounds (Lee and Bennett, 1982; Gupta et al., 1991) or other types of biochemical defense systems. The extent to which these internal tolerance mechanisms have physiological costs associated with them is not yet understood, but it is likely that increased defense compound production, triggered by O_3, will impact the amount of carbon available for growth (Ehleringer, 1991). The genetic regulation of these or other O_3 resistance mechanisms has not yet been thoroughly characterized.

Whether or not O_3 resistance is due to single gene or multi-gene control will affect the rate and the extent of resistance development (Roose, 1991). Rapid stomatal closing in the presence of O_3 appears to be under the control of either a single gene or a few genes in onion (*Allium cepa* L.) (Engle and Gabelman, 1966), some bean (*Phaseolus vulgaris* L.) cultivars (cultivated varieties) (Knudson-Butler and Tibbitts, 1979), soybean (*Glycine max* L.) (Damicone and Manning, 1987) and petunia (*Petunia* spp.) (Elkiey and Ormrod, 1979).

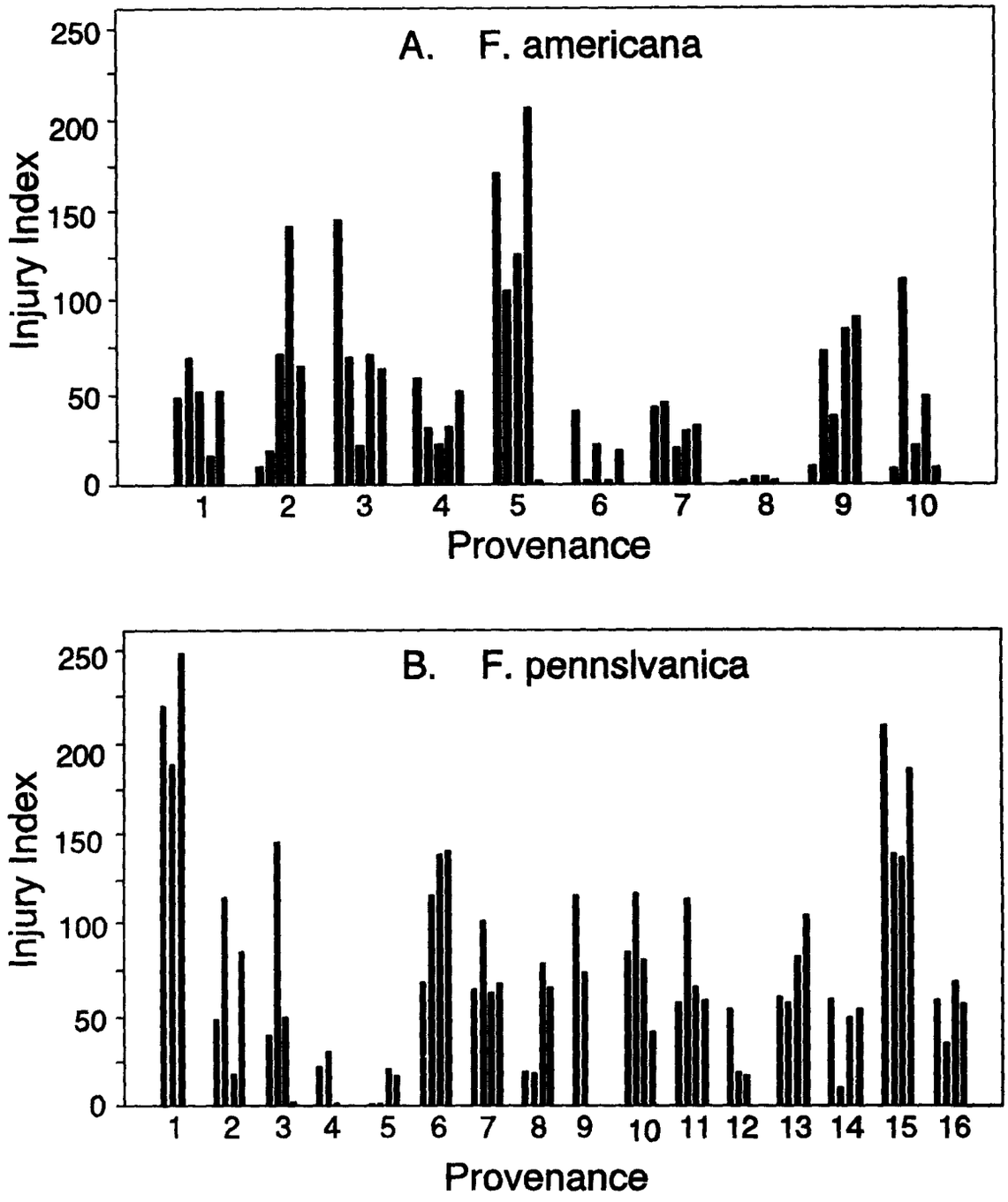

Figure 5-7. The average injury index for visible foliar injury after exposure of 1-year-old seedlings to 50 pphm O_3 for 7.5 h. Each mean shown represents the average of five trees per family. There were either four or five half-sib families for each white ash (*Fraxinus americana* L.) provenance (geographic location) and either three or four families for each green ash (*F. pennsylvanica* Marsh.) provenance. The specifics of the experimental design are reported in Karnosky and Steiner (1981).

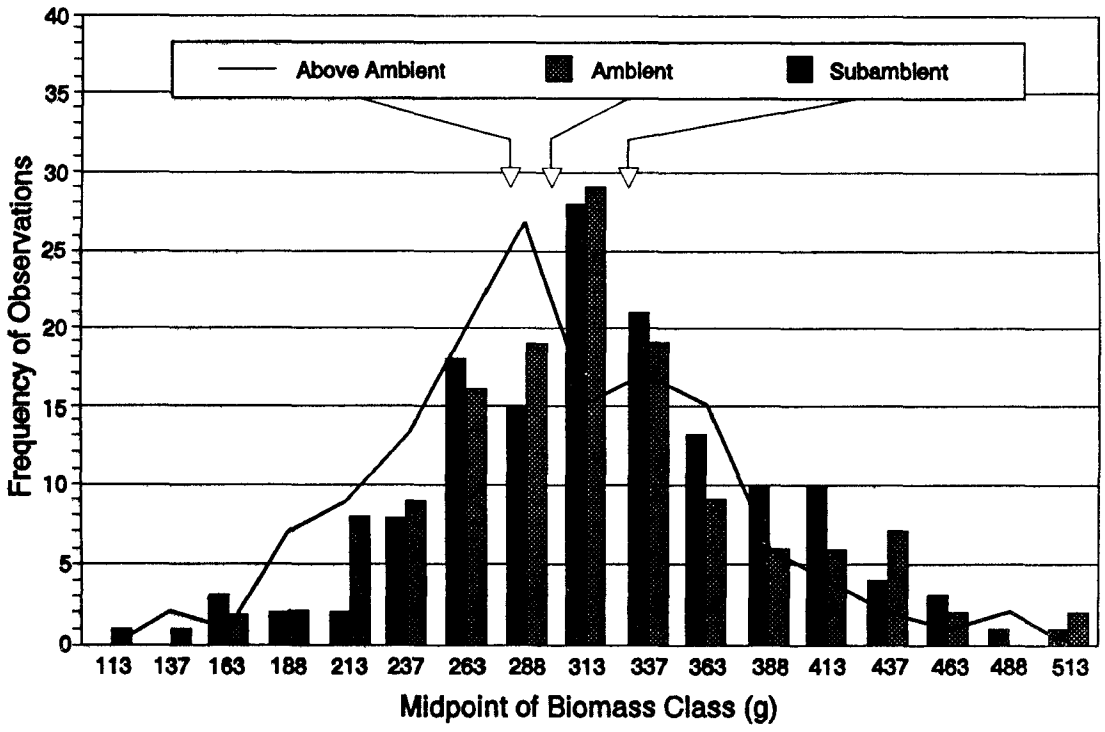

Figure 5-8. Frequency distribution showing the variability in O_3 response (midpoint of whole-plant biomass) within one half-sib family of loblolly pine (*P. taeda* L.) exposed to increasing levels of O_3 under chronic-level field conditions over several growing seasons (Adams et al., 1988). The arrows show the mean response for each of the three O_3 treatments (sub-ambient, ambient and above-ambient O_3). The specifics of the experimental design are reported by Adams et al. (1988). This figure was developed by Taylor (1993).

Generally, resistance mechanisms appear to be more complex (Karnosky, 1989a) and seem to involve multiple gene control as has been demonstrated in tobacco (*Nicotiana tabacum* L.) (Aycock, 1972; Huang et al., 1975, Povilaitis, 1967), some bean cultivars (Mebrahtu et al., 1990a,b,c), corn (*Zea maize* L.) (Cameron, 1975), tall fescue (*Festuca arundinacea* Schreb.) (Johnston et al., 1983), potato (*Solanum tuberosum* L.) (DeVos et al., 1982; Dragoescu et al., 1987) and loblolly pine (*Pinus taeda* L.) (Weir, 1977; Taylor, 1993).

Genetic Implications of Ozone Effects: Managed Ecosystems

Because of the high cost involved in conducting long-term growth studies to determine O_3 effects on plants, only a small proportion of the total number of commercial crop cultivars and of the important tree seed sources, families, clones and cultivars have been

adequately examined for O_3 sensitivity. Still, a tremendous amount of variation has been found, as was described previously in the first O_3 criteria document (U.S. Environmental Protection Agency, 1986) and in Tables 5-1 and 5-2 of this section.

Plant breeders and nurserymen working in locations with high O_3 concentrations have inadvertently developed selections more tolerant to O_3 than those developed in locations with low O_3 exposures (Reinert et al., 1982, Roose et al., 1982). "Team" alfalfa (*Medicago sativa*) and "Kennebec", "Pungo" and "Katahdin" potato were developed at the USDA Research Center at Beltsville, Maryland where 0.120 ppm O_3 is commonly exceeded (Lefohn and Pinkerton, 1988; Ludwig and Shelar, 1980). These cultivars have proven to be more O_3 tolerant than cultivars developed elsewhere (Reinert et al., 1982). Similarly, cotton (*Gossypium* spp.) and sugar beet (*Phaseolus* spp.) cultivars developed in southern California, where O_3 levels are among the highest in the county, are more O_3 tolerant than cultivars developed in low O_3 areas (Reinert et al., 1982).

Nurserymen, Christmas tree growers and seed orchard managers have all routinely discarded pollution-sensitive chlorotic dwarf and tipburned white pine trees because of their slow growth in areas with high O_3 exposures (Umbach and Davis, 1984). Thus, they have contributed to the selection of more O_3-tolerant commercial forests.

While these examples suggest that selection of O_3-tolerant genotypes is possible, this topic remains a highly debatable issue, and the general consensus of the scientific community is that top priority should be given to solving pollution problems at their source (Karnosky et al., 1989b) and not in selecting pollution-tolerant cultivars.

An interesting set of experiments by Barnes et al. (1990) and Velissariou et al. (1992) have described a concern about the modern crop varieties that have been developed in clean-air environments, but that are being routinely grown in areas with elevated O_3 exposures. These authors speculated that breeders of spring wheat (*Triticum aestivum* L.) grown in Greece had inadvertently selected varieties with increased O_3 sensitivity due to their higher rates of stomatal conductivity (Velissariou et al., 1992). Vellisariou et al. (1992) found a significant correlation between year of introduction and stomatal conductance with stomatal conductance increasing with the more modern introductions. The authors suggested that the selection for higher yields had resulted in a higher O_3 uptake for the modern spring wheat cultivars, contributing to their increased O_3 sensitivity. When they compared the relative

growth rates of spring wheat cultivars released over the period from 1932 to 1980, the modern cultivars had more foliar injury and more growth decrease when grown in the presence of O_3 (Barnes et al., 1990; Velissariou et al., 1992).

Genetic Implications of Ozone Effects: Natural Ecosystems and Biodiversity

Air pollutants can affect the genetics of plant populations in two ways: They may increase mutation rates or they may apply selection pressures which may eventually lead to adaptive responses (Cook and Wood, 1976). The issue of O_3-induced changes in mutation rate has not been adequately studied yet, but recent evidence by Floyd (1992) suggests that DNA may be affected by O_3 to induce mutation in plants. However, there is evidence that O_3 may be affecting plant populations via natural selection. According to Bradshaw and McNeilly (1991), there are three stages of selection-driven population change: Stage I. Elimination of the most sensitive genotypes; Stage II: Elimination of all genotypes except the most resistant; Stage III: Interbreeding of the survivors.

The first report of O_3 as a selective force in plant populations was that involving lupine (*Lupinus bicolor*) populations in the greater Los Angeles area (Dunn, 1959). Local Los Angeles area populations were more O_3 resistant than populations originating from cleaner-air areas. Berrang et al. (1986, 1989, 1991) have presented evidence for population change in trembling aspen (*Populus tremuloides* L.). Aspen clones from across the United States were sampled randomly from populations in polluted and non-polluted areas. Aspen from areas with high ambient O_3 concentrations were visibly injured to a lesser extent by experimental O_3 exposures than clones from areas with low O_3 concentrations (Berrang et al., 1986, 1991). Similar results were seen for field trials of O_3 injury (Berrang et al., 1989). More recently, growth rate and biomass differences have been reported for aspen clones differing in O_3 tolerance (Karnosky et al., 1992). Berrang et al. (1989) suggest that sensitive genotypes are not killed directly by O_3, but are eliminated through intraspecific competition for light, nutrients and water with their resistant neighbors. Spatial (population) variation in O_3 resistance that is related to background O_3 pollution has also been demonstrated in British populations of plantago (*Plantago major* L.) (Reiling and Davison, 1992a,b).

There have been three concerns raised regarding the spatial variation studies of O_3 resistance. First, since O_3 does not generally show steep concentration gradients, spatial studies must involve populations that are great distances from one another so that it is difficult to determine whether geographical differences in O_3 resistance are primarily related to local O_3 exposures or to other environmental factors (Reiling and Davison, 1992a). Second, spatial studies are limited by the general absence of historical records of ambient O_3 concentrations at the sites where the populations were sampled (Bell et al., 1991). Third, no O_3 study has collected plants from the same population over time to demonstrate O_3-induced population change over time (Bell et al., 1991) as has been demonstrated for other pollutants. However, Karnosky (1981b; 1989b) studied the O_3 symptom expression and survival of over 1,500 eastern white pine trees growing in southern Wisconsin and found that O_3-sensitive genotypes had a ten-times-higher rate of mortality than did the O_3-resistant genotypes over a 15-year study (Table 5-3). This is direct evidence of Stage I of natural selection occurring. Further evidence of this type was presented by Heagle et al. (1991) who found a population change in O_3 sensitivity over two years with white clover (*Trifolium repens* L.) exposed to O_3 in open-top chambers. A high O_3 dose at the end of the study caused significantly less foliar injury in plants which survived two seasons of exposure to high O_3 concentrations than on plants that had survived low O_3 concentrations.

TABLE 5-3. MORTALITY OF THREE OZONE SENSITIVITY CLASSES OF EASTERN WHITE PINE (*PINUS STROBUS* L.) TREES DURING THE PERIOD FROM 1971 TO 1986

Sensitivty Class[a]	Number Trees	Number Trees Dead	Percent Mortality
Resistant	1386	34	2.4%
Intermediate	98	3	3.1%
Sensitive	57	14	24.6%

[a]*Resistant* = Not showing visible foliar injury during the study; *Intermediate* = Showing visible injury, including foliar tipburn during one or two years; *Sensitive* = Showing visible injury, including foliar tipburn, short needles and poor needle retention for three or more years of the study.

Source: From Karnosky, (1989b).

The rate of evolution is dependent on: (1) the selection pressure; (2) the magnitude of the genetically controlled variability; and, (3) the number of genes involved (Roose, 1991). Long-lived species, such as trees, will evolve more slowly than annuals or biennials (Barrett and Bush, 1991). Gillespie and Winner (1989) found O_3 to be a strong and rapid selective force with radish. Ozone resistance was expressed within one generation following a series of artificial pollinations with various populations from the cultivar "Cherry Belle".

Whether or not the loss of some genotypes from plant populations is important is a debatable question. However, it is likely that sensitive genotypes are being lost from natural ecosystems with current O_3 exposures. Field studies documenting differential growth rates of O_3-sensitive and tolerant genotypes of eastern white pine in natural ecosystems influenced by O_3 were summarized in the original air quality criteria document for O_3 (U.S. Environmental Protection Agency, 1986). Similar findings have subsequently been reported for O_3-sensitive and tolerant Jeffry pine (*Pinus jeffrey*, Grev. and Balf.) trees in California (Peterson et al., 1987). It is likely that these growth rate differences affect the competitive ability of O_3-sensitive genotypes and increase their mortality rate (Karnosky, 1989b).

While some loss of rare alleles (one of a series of genes that are alternative in inheritance) and change in gene frequency is likely with loss of sensitive genotypes, the significance of these effects on biodiversity is unknown (Barrett and Bush, 1991). If the remaining population of O_3-resistant plants is less adaptable to subsequent change due to a reduced redundancy, as has been predicted by Gregorius (1989), or if O_3 sensitivity is linked to other traits such as rapid growth or high productivity, as has been suggested because of the inherently higher gas exchange rates of some O_3-sensitive genotypes (Barnes et al., 1990; Thorne and Hanson, 1976; Turner et al., 1972; Velissarious et al., 1992), then losing these sensitive genotypes is both biologically and economically important. This remains a point of scientific debate. While the evolution of resistance to air pollution is hypothesized to contribute to the loss of genetic variability (Scholz et al., 1989; Karnosky, 1991), other scientists suggest that there is little experimental evidence for concluding that genetic diversity is actually threatened by air pollution and that air pollution has less important implications for plant populations than do factors such as global climate change and habitat fragmentation (Parson and Pitelka, 1991; Taylor and Pitelka, 1991). Clearly, there is a need for additional research in this area of O_3 effects in plant biodiversity (Karnosky et al., 1989).

Reproductive Aspects and Related Genetic Implications

In the previous discussion in this section, only natural selection at the whole-plant level has been mentioned. This type of selection occurs as plants compete with their neighbors for survival and the ability to reproduce. Selection is thought to also occur during the reproductive process (Feder and Sullivan, 1969; Krause et al., 1975) and this is referred to as gametophytic selection (Mulcahey, 1979; Wolters and Martens, 1987) or fertility selection (Venne et al., 1989). The ability of gametophyte (haploid part of the plant-life cycle) selection to modify the sporophytic generation depends on two critical issues: pollen genes should be expressed after meiosis (cell divisions leading to production of gametes) and those same genes should also be expressed in the sporophytes (diploid part of the plant-life cycle) (Mulcahey and Mulcahey, 1983). This genetic overlap has been demonstrated in some species (Mulcahey, 1979; Searcy and Mulcahey, 1985; Walsh and Charlesworth, 1992). Indirect evidence for O_3-induced gametic selection was presented for Scot's pine (*Pinus sylvestris* L.) by Venne et al. (1989). Based on their studies of the effects of O_3 on the pollen germination and tube elongation of some thirty Scots pine clones, they found that O_3 could markedly change the relative male contribution to successful fertilization. However, this study did not actually examine offspring as would be needed to positively prove O_3-induced gametophytic selection.

Studies of O_3 effects on pollen germination and tube elongation have generally found a negative impact of O_3 on this critical element of reproduction (Table 5-4). Whether or not selection is occurring at the pollen level because of a selective disadvantage of the pollen from sensitive genotypes is a debatable issue. Feder (1986) and Krause et al. (1975) found that the pollen from O_3-sensitive genotypes of petunia and tomato (*Lycopersicon esculentum* L.) was more severely affected by O_3 than pollen from tolerant genotypes, suggesting that gametophytic selection could be occurring. Similar results were found for Scots pine clones by Venne et al. (1989). These authors found that the relative male contribution for charcoal-filtered air versus O_3-treated conditions was very different and could potentially lead to a strong gametophytic selection response caused by O_3. However, Hanson and Addis (1975) did not see any differences in the effect of O_3 on the pollen from sensitive and tolerant petunia genotypes, and Benoit et al. (1983) found no apparent differences in the susceptibility

TABLE 5-4. EXAMPLES OF OZONE EFFECTS ON POLLEN GERMINATION AND TUBE ELONGATION

Species	Pollen Germination	Pollen Tube Elongation	Reference
Nicotiana tobacum L. (Tobacco)	Decrease	Decrease	Feder, 1968; Feder and Shrier, 1990
Petunia hybrida (Petunia)	Not tested	Decrease	Feder and Shrier, 1990
Pinus strobus L. (Eastern white pine)	No effect	Decrease	Benoit et al. 1983
Zea mays L. (Corn)	Decrease	Not tested	Mumford et al. 1972

of eastern white pine pollen from O_3-sensitive or tolerant genotypes. Clearly, the question of whether O_3-induced gametophytic selection is occurring has not yet been resolved.

Reduced flowering as the result of prolonged fumigation with O_3 has been shown in Bladder campion (*Silene cucubalus*) (Ernst et al., 1985). Decreased floral initiation and decreased floral productivity under long-term O_3 exposures have also been reported in geranium (*Pelargonium* spp.) and carnation (*Dianthus caryophyllus*) (Feder, 1970). Ozone-induced impairment of flowering will reduce the fitness of the affected genotypes, populations or species and may result in the eventual loss of these genetic units from the O_3-stressed ecosystem. Reduced eastern white pine fecundity in air pollution-stressed ecosystems has been reported by Houston and Dochinger (1977).

Genetic Summary

Plant species, cultivars, populations and individuals within populations display variable responses to O_3. Variability in O_3 responses between and within species was described in the previous O_3 criteria document (U.S. Environmental Protection Agency, 1986). An important component of this variation is genetically controlled. The specific genes controlling O_3 response and involved in mechanisms of O_3 tolerance are as yet largely unknown. However, control of stomatal conductance and internal biochemical defense systems are among the most commonly described tolerance mechanisms. Ozone tolerance is generally thought to be controlled by multiple genes.

There are implications of genetic variation in O_3 response, both for managed and natural ecosystems. These are summarized below along with the relative degree of uncertainty attached to each.

It is known, with a great deal of certainty, that plants have a high degree of genetic variation in O_3 response. Thus, exposure-response equations and yield-loss equations developed for a single or small number of cultivars, genotypes, families or populations may not adequately represent the response of thespecies as a whole. As a corollary to this, sensitive responder genotypes will not be protected by air-quality standards based on mean responses.

The issue of O_3 effects on biodiversity via natural selection is a topic of debate within the scientific community. The potential for natural selection for O_3 tolerance and associated loss of sensitive genotypes is regional in nature, unlike well known, point-source pollution impacts which occur on local plant populations. However, the intensity of O_3 selection is generally thought to be quite low, 0.3 or less (Taylor and Pitelka, 1992), in the majority of the United States. The extent that germplasm has been or is continuing to be affected in terms of allele loss or gene frequency changes by O_3 and how this might be impacting the genetic adaptability of populations is an open and important research question.

While it is well known that individual plants within a species vary in their O_3 tolerance, the physiological costs to tolerant plants are not known in terms of carbon assimilation and allocation. Tolerance mechanisms based on reduced stomatal conductivity in the presence of O_3 would likely reduce growth of tolerant plants. Similarly, tolerance mechanisms based on the productivity of antioxidant compounds will likely shunt plant resources away from growth to the production of the defense compounds. The characterization of the extent and types of physiological costs involved in O_3 tolerance remains an important research question.

5.4.3 Environmental Biological Factors

The previous criteria document (U.S. Environmental Protection Agency, 1986) discussed pollutant-plant-pest and pollutant-plant-pathogen interactions together, and provided a tabular summary of pathogen effects. However, in light of the numerous studies of insect and pathogen interactions that have appeared in recent years, the topics are dealt with

separately below. Nevertheless, it is worth reiterating several points made in the previous criteria document:

- pests and diseases are natural components of managed and natural ecosystems;
- significant crop and timber losses result from pests and pathogens;
- the establishment of disease and pest infestations and their subsequent development involve complex interactions between host plant, the environment and the causal organism;
- the generalized disease (or pest infestation) cycle involves the arrival of the pathogen or pest on the host plant surface or its introduction into the host plant tissues through wounds or as a result of insect feeding activity;
- growth and development or propagation of the pathogen or pest only occurs if all environmental conditions are favorable;
- such development leads to various degrees of host tissue destruction or malfunction, and usually culminates in the causal organism entering a reproductive stage and producing propagules (e.g., spores or eggs) that facilitate its spread.

Ozone may modify any stage of the disease cycle directly, by affecting the causal organism itself, or indirectly by effects on the host plant (Lechowiez, 1987). Conversely, the plant-pest interaction may modify the sensitivity of the host plant to O_3.

The roots of many members of the pea family (including many important crops such as soybeans, beans and peas) are infected by symbiotic nitrogen-fixing bacteria (*Rhizobium spp.*) leading to the formation of bacteria-rich nodules that contribute to the nitrogen economy of the plant, through their ability to fix and convert atmospheric nitrogen, N_2, to biologically useful forms. Other nitrogen-fixing microorganisms are associated with the roots of several species, and in many cases roots are invaded by species of soil fungi to form mycorrhizal symbioses that assist in root functioning. These symbioses constitute micro-ecosystems and are discussed more fully in Section 5.7 as they relate to forest tree species.

Biological interactions also affect the growth of plants in populations (pure stands) and communities (mixtures of species) through the individual plants' competition for available resources (light, CO_2, water, nutrients). Such plant-plant interactions are features of all managed and natural ecosystems, but they operate at the indivdual plant level. Hence the

effects of oxidants on these interactions are discussed in both the present section and in Section 5.7 which deals will ecosystem responses.

5.4.3.1 Oxidant-Plant-Insect Interactions

The previous criteria document (U.S. Environmental Protection Agency, 1986), concluded that little was known at that time about O_3-insect interactions. Since then the topic has been covered in several reviews: Fluckiger et al. (1988), Hughes (1988), Manning and Keane (1988), and Hain (1987). Relevant studies of the effects of O_3 on the feeding preference of herbivorous insects, and on their growth, fecundity, and survival are presented in Table 5-5. As can be readily seen in this summary, the information is widely scattered among a wide range of host plants and pests. Nevertheless, there appears to be a general trend in the observations suggesting that O_3-induced changes in the host plants frequently result in increased feeding preference of a range of insect species, although this may or may not be reflected in effects on the growth of the insect.

However, in most studies, the effects have been far from clear-cut. For example, variable responses were observed with the aphid, *Aphis fabae*, on broad bean (Brown et al., 1992), with the aphids, *Acyrthosiphon pisum* and *Aphis rumicis*, on pea and dock, respectively, and the beetle, *Gastrophysa viridula* on dock (Whittaker et al., 1989), with the Mexican bean beetle, *Epilachna varivestis*, on Corsoy soybean (Endress and Post, 1984), and with the gypsy moth, *Lymantria dispar*, on white oak (Jeffords and Endress, 1984). Although statistically significant effects were frequently observed, they did not provide any consistent pattern of insect growth response to different levels or patterns of exposure.

Brown et al. (1992) observed that the response of *Aphis fabae* depended upon the dynamics of exposure: growth was stimulated in short-term (<24 h) continuous exposures or in episodic exposures over several days, whereas longer continuous exposures caused decreased growth. Chappelka et al. (1988c) found that O_3 consistently enhanced the feeding preference and larval growth of the Mexican bean beetle on soybean, leading to increased defoliation. Although the cultivar Forrest was significantly more sensitive to O_3 than Essex, this difference did not lead to any differences in insect behavior and development. Similarly, clear stimulatory responses were observed with pinworm, *Keiferia lycopersicella*, on tomato (Trumble et al., 1987), with an aphid, *Phyllaphis fagi*, and a weevil, *Rhynchaenus fagi*, on

TABLE 5-5. OZONE EFFECTS ON INSECT PESTS

Host Plant Insect	Exposure[a]	Experimental Conditions[b]	Effect of Ozone on Insect	Reference
CROP SPECIES				
Broad bean aphid	3 day, 0.085 ppm < 24 h, 0.1 ppm > 24 h, 0.1 ppm 8 h/day, episodic	chamber, whole plant chamber, whole plant chamber, whole plant chamber, whole plant	3-13% decreased growth rate 17% increased growth rate 12% decreased growth rate 15% increased growth rate	Dohmen (1988) Brown et al. (1992)
Pea/aphid	4-8 day, var.	chamber, whole plant	variable effects on growth	Whittaker et al. (1989)
Kidney bean/aphid	14 day, var.	OTC	15-50% reduction in growth of insect	Braun and Fluckiger (1989)
Soybean/beetle (cv Corsoy) (cvs Essex. Forrest)	16 day, var. 21 day, 7 h/day, var.	chamber OTC	variable feeding preference 0.11>0.0>0.05>0.03 ppm feeding preference increased and greater larval growth	Endress and Post (1985) Chappelka et al. (1988c)
Tomato/pinworm	2-4 day, 3 h/day, 0.28 ppm	chamber, detached leaf chamber, whole plant	80% in crease in larval development; no effect on fecundity	Trumble et al. (1987)
NATURAL VEGETATION				
Milkweed/monarch butterfly	17-19 day, 7 h/day 0.150-0.178 ppm	chamber, whole plant	no feeding preference but greater larval growth rate	Bolsinger et al. (1992)
Dock/aphid	15 day, var.	chamber, whole plant	10% increased growth rate	Whittaker et al. (1989)
Dock/beetle	15 day, var.	chamber, whole plant	10% larger egg batches; 4-fold greater larval survival	Whittaker et al. (1989)
TREES SPECIES				
European beech/aphid	2 mo., var.	OTC	75% increase in number	Braun and Fluckiger (1989)

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TABLE 5-5 (cont'd). OZONE EFFECTS ON INSECT PESTS

Host Plant/Insect	Exposure[a]	Experimental Conditions[b]	Effect of Ozone on Insect	Reference
TREE SPECIES (cont'd)				
European beech/weevil	72 h, var.	OTC	2-fold increase in feeding preference	Hiltbrunner and Fluckiger (1992)
Cottonwood/beetle	5 h, 0.2 ppm	OTC	22-60% greater consumption of foliage, but decreased fecundity	Jones and Coleman (1988) Coleman and Jones (1988)
Ponderosa pine/bark beetle	natural	none, field	increased infestation but in decreased survival	Hain (1987)
White oak/gypsy moth	11 day, 7 h/day. var.	chamber, leaf disks	variable feeding preference 0.15 > 0.03 > 0.09 ppm	Jeffords and Endress (1984)

[a]"var." indicates a range of exposures.
[b]"chamber" indicates closed chamber; OTC indicates open-top field chamber.

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European beech (Braun and Fluckiger, 1989; Hiltbrunner and Fluckiger, 1992), with the monarch butterfly, *Danaus plexippus*, on milkweed (Bolsinger et al., 1992), and with infestation by the willow leaf beetle, *Plagiodera versicolora*, on cottonwood (Coleman and Jones, 1988). However, there was less egg-laying by *Plagiodera* on O_3-treated foliage, and treatment had no effect on beetle growth rates and survival (Jones and Coleman, 1988).

In view of previous experiments in which it was clearly demonstrated that aphid growth was significantly stimulated by ambient pollutant mixtures containing O_3, SO_2, and NO_2, and in light of other reports of O_3-induced stimulations of insect growth, the inhibitory effects of O_3 on the growth of *Aphis fabae* on Broad Bean (dohmen, 1988), Or Kidney bean (Braun and Fluckiger, 1989), may be anomalous. The inhibitory effects on broad bean were only observed at low O_3 levels: exposure to higher concentrations resulted in a stimulation of aphid growth, which Dohmen (1988) attributed to the increased rate of leaf senescence of the host plant. The effects observed on kidney bean could not be accounted for by differences in the amino acid composition of the plant sap, although differences in other constituents or direct effects of O_3 on the pea aphid itself could not be ruled out (Braun and Fluckiger, 1988).

A well-established indirect stimulatory effect is the predisposition to bark beetle attack of ponderosa pine injured by exposure to O_3. However, the infested trees do not favor good brood production; O_3 injury results in a more susceptible but less suitable host (Hain, 1987).

In all of these studies, the focus was on direct or indirect effects of O_3 on the insect. With the exception of the work of Braun and Fluckiger (1988), any effects on the host plant that were reported were confined to observations on visible symptoms of foliar injury. The only report of an O_3-insect interaction affecting the response of the host plant appears to be that of Rosen and Runeckles (1976). This study showed that exposure to sub-acute levels of O_3 and infestation with the greenhouse whitefly, *Trialeurodes vaporariorum*, acted synergistically (i.e., more than additively) in causing leaf injury and accelerated senescence of kidney bean. However, the extent to which other insects with sucking mouthparts, such as aphids, might be involved in similar interactive responses is unknown, as is the nature of any interactions which involve pests that ultimately invade and develop within the host plant, such as those that cause the formation of galls.

The reports of O_3-insect-plant interactions are thus scattered among a wide range of host plant and insect species, and only represent a minute fraction of the plant-insect interactions that involve crop and native species. Although there appears to be a trend in the limited data available that suggests that exposures to moderate O_3 levels may increase the likelihood of insect attack and its consequences, there is insufficient information to decide whether extrapolation of this generalization is warranted or not. Even if the generalization is valid, it is not possible to generate any quantitative measure of response. Before such estimates will be possible on a broad scale, studies of a much wider range of plant insect-systems will be needed, together with systematic, in-depth studies of individual systems, aimed at determining the long-term effects on both the host plant and the insect. Such studies should include investigations of biological control systems employing beneficial insects which are increasing in use as alternatives to chemical insecticides and herbicides.

5.4.3.2 Oxidant-Plant-Pathogen Interactions

Plant disease is the result of infection by fungi, bacteria, mycoplasmas, viruses and nematodes. Recent reviews of pathogen-plant-O_3 interactions have been published by Dowding (1988) and Manning and Keane (1988), and extend the coverage of the previous criteria document (U.S. Environmental Protection Agency, 1986) in which the results of published studies of the effects of O_3 on disease development were summarized in tabular form. Interactions involving fungal pathogens occupied most of that review, and more recent studies have maintained this emphasis.

The previous criteria document concluded that it was "impossible to generalize and predict effects in particular situations." (U.S. Environmental Protection Agency, 1986;). However, Dowding (1988) has since concluded that pathogens which can benefit from injured host cells or from disordered transport mechanisms are enhanced by pollution insult to their hosts, whereas those that require a healthy mature host for successful invasion and development are depressed by pollutant stress to their host.

This conclusion is supported by evidence that the development of diseases caused by obligate parasites such as the rust fungi and bacterial pathogens is usually reduced by O_3. As shown by the observations summarized in Table 5-6, reductions in disease development were observed in five of the nine studies of obligate fungal parasites listed

TABLE 5-6. OZONE-PLANT-PATHOGEN INTERACTIONS

Host Plant	Pathogen	Effect of O_3 on Disease	Effect of Disease on O_3 Response	Reference
OBLIGATE FUNGI				
Kidney bean	*Uromyces phaseoli*	increased number of smaller pustules	reduced injury on severely diseased leaves	Resh and Runeckles (1973)
Barley	*Erysiphe graminis*	reduced infection but greater spore production	not reported	Heagle and Strickland (1972)
Cottonwood	*Melampsora medusae*	reduced infection and development	not reported	Coleman et al. (1987)
Lilac	*Microsphaera alni*	no effect	not reported	Hibben and Taylor (1975)
Oats	*Puccinia coronata*	reduced infection and development	no effect	Heagle (1970)
Wheat	*Erysiphe graminis*	increased infection and development	not reported	Tiedemann et al. (1991)
	Puccinia graminis	reduced infection and development	reduced leaf injury	Heagle and Key (1973a,b)
	Puccinia graminis	reduced development	not reported	Heagle (1975)
	Puccinia recondita	reduced infection and development	not reported	Dohmen (1987)
FACULTATIVE FUNGI				
Barley	*Drechslera teres*	increased infection	not reported	Tiedemann et al. (1990)
	Gerlachia nivalis	increased infection	not reported	Tiedemann et al. (1990)
	Helminthosporium sativum	no effect	not reported	Tiedemann et al. (1990)
Cabbage	*Fusarium oxysporum*	decreased development	not reported	Manning et al. (1971)

TABLE 5-6 (cont'd). OZONE-PLANT-PATHOGEN INTERACTIONS

Host Plant	Pathogen	Effect of O_3 on Disease	Effect of Disease on O_3 Response	Reference
FACULTATIVE FUNGI (cont'd)				
Corn	*Helminthosporium maydis*	increased development	not reported	Heagle (1977)
Cottonwood	*Marssonina brunnea*	increased infection	not reported	Coleman et al. (1988)
Geranium	*Botrytis cinerea*	decreased infection	not reported	Krause and Weidensaul (1978)
Onion	*Botrytis (3 spp.)*	increased infection and development	not reported	Wukasch and Hofstra (1977a,b)
Potato	*Botrytis cinerea*	increased infection and development	not reported	Manning et al. (1969)
	Alternaria solani	increased infection	not reported	Holley et al. (1985)
	Alternaria solani	increased infection	not reported	Bisessar (1982)
Soybean	*Fusarium oxysporum*	increased infection	increased leaf injury	Damicone et al. (1987)
Wheat	*Gerlachia nivalis*	increased infection	not reported	Tiedemann et al. (1990)
	Helminthosporium sativum	no effect	not reported	Tiedemann et al. (1990)
	Helminthosporium sativum	increased infection	not reported	Tiedemann et al. (1991)
	Septoria (2 spp.)	increased infection	not reported	Tiedemann et al. (1990)
	Septoria (2 spp.)	oncreased infection	not reported	Tiedemann et al. (1991)
Jeffrey pine	*Heterobasidium annosum*	increased development	not reported	James et al. (1980)

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TABLE 5-6 (cont'd). OZONE-PLANT-PATHOGEN INTERACTIONS

Host Plant	Pathogen	Effect of O_3 on Disease	Effect of Disease on O_3 Response	Reference
FACULTATIVE FUNGI (cont'd)				
Ponderosa pine	*Heterobasidium annosum*	increased development	not reported	James et al. (1980)
White pine	*Vertcicladiella procera*	slightly increased incidence	not reported	Costonis and Sinclair (1972)
	Lophodermium pinastre	slightly increased incidence	not reported	Costonis and Sinclair (1972)
BACTERIA				
Alfalfa	*Xanthomonas alfalfae*	reduced development	reduced leaf injury	Howell and Graham (1977)
Soybean	*Pseudomonas glycinea*	reduced incidence	no effect	Laurence and Wood (1978a)
	Pseudomonas sp.	reduced infection	reduced leaf injury	Pell et al. (1977)
White bean	*Xanthomonas phaseoli*	no effect	reduced leaf injury	Temple and Bisessar (1979)
Wild strawberry	*Xanthomonas fragariae*	reduced incidence	no effect	Lawrence and Wood (1978b)
NEMATODES				
Begonia	*Aphelenchoides fragariae*	reduced nematode reproduction	reduced leaf injury	Weber et al. (1979)
Soybean	*Belonolaimus longicaudatus*	stimulation or no effect	not reported	Weber et al. (1979)
	Heterodera glycines	reduced nematode reproduction	not reported	Weber et al. (1979)
	Paratrichodorus minor	reduced nematode reproduction	reduced leaf injury	Weber et al. (1979)
	Pratylenchus penetrans	no effect	not reported	Weber et al. (1979)
Tobacco	*Meloidogyne hapla*	possible stimulation[a]	increased leaf injury	Bisessar and Palmer (1984)

[a]Based on studies using the protectant EDU (see Section 5.3.2.4.1.3).

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whereas increases were observed in all but four of the studies of facultative fungal pathogens. Similarly, in four of the five bacterial systems, O_3 reduced infection or disease development. It should be noted that in three of the four studies of obligate fungi on which exposure to O_3 either had no effect or which resulted in stimulated fungal growth the pathogen was a powdery mildews (*Erysiphe*, *Microsphaera*). As discussed by Tiedemann et al. (1991), these species constitute a special case because they are ectoparasites whose hyphae merely penetrate the surface epidermal cells of the host plants leaves rather than the mesophyll tissues within the leaves. They noted that Heagle and Strickland (1972) observed greater pustule development of *Erysiphe* on exposed barley once infection was established, although the pathogen was sensitive during the early stages of infection. Tiedemann et al. (1991) suggest that the observed stimulations result from a differential weakening of the host's resistance response to the pathogen.

In a few of the studies summarized in Table 5-6, effects of disease development on the sensitivity of the host plant to O_3 were noted. Heagle and Key (1973b) and Resh and Runeckles (1973) confirmed the earlier observation of Yarwood and Middleton (1954) that infection with obligate rust fungi could reduce the severity of acute injury caused by exposure to O_3. However, with *Uromyces* on bean, the "protection" was only noted on severely infected leaves (Resh and Runeckles, 1973), and Heagle (1970) observed no such effect with crown rust, *Puccinia coronata*, on oats.

Infection with bacterial pathogens and nematodes also tends to reduce the impact of O_3, and almost all studies of the interactions of O_3 with virus infections appear to do so. The previous criteria document (U.S. Environmental Protection Agency, 1986) reviewed the supporting evidence from numerous studies with a range of host plants and viruses, and noted only two studies in which O_3 injury was apparently increased by virus infection (Ormrod and Kemp, 1979; Reinert and Gooding, 1978). However, with tomato infected by mosaic viruses, injury was reduced in the leaves of plants in which viral infection was well established (Ormrod and Kemp, 1979). Two more recent studies have indicated either no effect or variety-dependent increased sensitivity to relatively high O_3 levels. Heagle et al. (1991, 1992) found no effects of infection with several viruses on the response of two clonal strains of white clover. On the other hand, Reinert et al. (1988) reported that three cultivars of burley tobacco responded differently to O_3 when infected with either tobacco etch virus

(TEV) or tobacco vein mottling virus (TVMR). Although TEV-infection resulted in the protected all cultivars from O_3-induced growth suppression, TVMV infection enhanced the suppression of the growth of two cultivars, Burley 21 and Greenville 131, but had no effect on the third, Burley 49.

With the exception of one field study demonstrating the suppression of O_3 injury on tobacco infected with tobacco mosaic virus (Bisessar and Temple, 1977), the other investigations of virus interactions have all been conducted in laboratory or greenhouse chambers, which raises the question of their relevance to field conditions. As noted in the previous criteria document (U.S. Environmental Protection Agency, 1986), with few exceptions, the reports of viral protection are probably of little commercial significance, but may provide information at the mechanistic level of plant response. The same caveat is equally applicable to the significance of protective effects of other obligate pathogens.

No studies appear to have been conducted of interactions involving disease-causing mycoplasmas.

As in the case of plant-insect interactions, much more systematic study is needed before it will be possible to provide any quantitative estimates of the magnitude of the interactive effects. The patterns of pollutant modification of plant-pathogen relations suggested by Dowding (1988) are partly supported by the limited evidence available for O_3, but studies of a wider range of plant-pathogen systems will be needed before it will be possible to provide quantitative generalizations.

5.4.3.3 Oxidant-Plant-Symbiont Interactions

Exposure to O_3 can modify the symbiotic relationships between plants and microorganisms. In the case of *Rhizobium*, the important nitrogen-fixing symbiont of many leguminous species, the adverse effects of exposure of the host plant reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1986) were all observed at O_3 levels of 0.3 ppm or greater. However, Flagler et al. (1987) observed a consistent decline in total nitrogen-fixing activity of nodulated soybean roots with increasing O_3 concentrations up to 0.107 ppm (7-h/day seasonal average), with no effect on specific nodule activity. In a greenhouse study of soybean plants exposed at three different growth stages to a 12 h treatment in which the peak O_3 concentration (at 6 h) was 0.2 ppm, Smith

et al. (1990) observed a 40% decrease in specific nodule activity. Hence, there is limited evidence to indicate adverse effects on Rhizobial nitrogen-fixation at O_3 levels experienced in polluted air.

The effects of O_3 on mycorrhizal fungal symbioses have been reviewed by Manning and Keane (1988) and McCool (1988). Seasonal exposures averaging 0.079 ppm O_3 resulted in a 40% reduction in the growth of the vesicular-arbuscular endomycorrhizal fungus, *Glomus fasciculatus*, on soybean roots. However, mycorrhizal infection lowered the O_3-induced reduction in pod yield from 48 to 25% (Brewer and Heagle, 1983). Once-weekly exposures of tomato plants to 0.3 ppm for 3 h retarded the early development of the same fungus on tomato seedling roots, leading to reduced seedling growth (McCool et al., 1982). Greitner and Winner (1989) reported that the increased availability of nitrogen to alder seedlings resulting from the presence of root nodules containing the nitrogen-fixing actinomycete, *Frankia*, enabled plants to recover their photosynthetic integrity rapidly after exposure to O_3 However, they did not investigate effects on symbiont.

In spite of the inconsistencies in the available evidence, it appears that rhizobial and mycorrhizal growth is likely to be impaired as a consequence of long-term exposure to oxidant stress, probably because of reduced allocation of photosynthate to the root system (Chapter 7, U.S. Environmental Protection Agency, 1986). However, the implications of such effects on mycorrhizae are particularly difficult to predict because of our inadequate understanding of the functioning of the tree root-mycorrhiza-soil system.

5.4.3.4 Oxidant-Plant-Plant Interactions—Competition

In the field, the growth of any plant is to some extent dependent upon its ability to compete for resources with its neighbors. Some are better competitors than others for light, water, nutrients, and space. Grime (1977) characterized as "competitors" those with a rapid growth rate associated with a capacity to adjust to rapidly changing conditions. Factors such as light or soil nutrients are not available *ad libitum*, because of the mutual shading of leaves within the canopy and root competition. Competition may be either intra- or inter-specific, (i.e., the interference may be caused by neighboring members of the same species or by neighboring individual of other species). The planting densities and row spacings adopted for agricultural crops represent compromises between maximizing the number of plants per

unit area and the adverse effects of intra-specific competition. The planting densities and row spacings adopted for agricultural crops represent compromises between maximizing the number of plants per unit area and the adverse effects of intra-specific competition. Weeds are typical interspecific competitors. Interspecific competition also occurs in mixed plantings such as grass-clover forage and pasture plantings, and is an important feature of natural ecosystems.

Although competition from weeds may contribute more to crop losses on a global scale than any other factor, no studies appear to have been conducted on the effects of oxidant pollution on such competition. On the other hand, a few crop mixtures have been studied. A consistent finding with grass-clover mixtures has been a significant shift in the mixture biomass in favor of the grass species (Runeckles and Bennett, 1977; Blum et al., 1983; Kohut et al., 1988; Rebbeck et al., 1988; Heagle et al., 1989).

As the number of competing species increases, the interactions are more appropriately dealt with at the ecological level, but, as demonstrated by the work of Evans and Ashmore (1992), it is important to recognize that, because of the differential stresses imposed by competition, the impact of O_3 on the components of a mixture may not be predictable on the basis of knowledge of the responses of the individual species grown in isolation. A similar caution must be stated about extrapolating to field conditions results obtained in laboratory studies in which competition may be minimal. However, the development and use of field exposure systems have permitted many recent studies of crop species to be conducted at normal planting densities and hence have incorporated interspecific competition as an environmental factor. On the other hand, most forest tree studies have tended to be "artificial" in their use of individual seedlings or saplings or spaced trees, even when exposed in open-air systems (McLeod et al., 1992).

The significance of the effects of competitive interactions on the O_3 response of the competing species is thus largely unknown except for a few cases involving grass-legume mixtures. However, these are far from typical because they only involve two species, one of which is a legume with unique nitrogen nutrition conferred by the nitrogen-fixing capabilities of Rhizobial symbionts. Hence, at the present time, our lack of knowledge of the effects of O_3 on competitive interactions leads to considerable uncertainty in attempting to assess the

impact of O_3 on both managed and natural ecosystems, by extrapolation from effects on individual species.

5.4.4 Physical Factors

The physical components of the plant's aerial environment are light, temperature, humidity and surface wetness, while the physical, edaphic components affecting the plant roots are temperature, soil moisture and soil salinity. The previous criteria document (U.S. Environmental Protection Agency, 1986) also included soil fertility under this heading; in the present review, this topic is dealt with separately in the section dealing with chemical factors (Section 5.4.5). The effects of the physical climatic factors (light, temperature, and the availability of water) on plant growth and survival are major determinants of the geographic distribution of the earth's natural vegetation and of the distribution of agricultural lands and the suitability of the crops grown on them. Because of the control that these factors exert over plant growth, their variation, especially in the short term, can be expected to influence the magnitude of plant responses to oxidants. As in the previous criteria document, the factors are discussed individually, although their actions on plant growth and sensitivity are closely inter-related. A brief integration of their effects is presented in Section 5.4.8, which discusses the effects of global climate change.

At the time of the previous criteria document, much of our knowledge of the effects of these factors came from laboratory and greenhouse experimentation which focused the foliar injury response to high exposures to O_3 that exceeded those likely to be encountered in ambient air. Since then, more information has become available on growth effects, especially with regard to the key area of the interactions involving drought stress.

5.4.4.1 Light

Light influences plant growth through its intensity, quality (i.e., the distribution of wavelengths), and duration (i.e., daylength or photoperiod). Much of the early work on light-oxidant interactions is largely of academic interest since light intensity and daylength are uncontrolled in natural field situations. However, reduced intensities are needed for the production of shade-grown cigar wrapper tobacco and in many commercial greenhouse floriculture operations, in which photoperiod may also be controlled in order to induce

flowering. The general conclusion reported previously (U.S. Environmental Protection Agency, 1986) is that susceptibility to foliar injury is increased by low intensities and short photoperiods, although unpredictable responses had been observed when plants were subjected to increased or decreased intensities during and after exposure to O_3. One aspect of increased susceptibility to low light intensities that needs to be emphasized concerns the fact that many studies of oxidant effects have been conducted in controlled-environment chambers in which the light intensities used have rarely approached those of natural sunlight, and hence may have magnified the observed responses. Significant differences in the amounts of foliar injury were observed on soybean plants grown in a growth chamber, a shaded greenhouse or in an open-top chamber in the field when subsequently treated with a standard O_3 exposure, although the growing conditions other than light intensity and quality were comparable (Lewis and Brennan, 1977). Factors other than light intensity must have contributed to the observed differences since the descending order of sensitivity was greenhouse-growth chamber-field chamber, although the average light intensities in the greenhouse and growth chamber were 81% and 18%, respectively, of those in the field chamber.

Reduced light intensities have been measured in open-top chambers in the field, resulting form the build-up of dust on the walls. However, Heagle and Letchworth (1982) could detect no significant effects on soybean growth and yield in a comparison of plants grown in unshaded open-top chambers and chambers to which shading cloth was applied.

At the mechanistic level, Darrall (1989) has reviewed the effects of light intensity and suggests that, at high intensities, the potential for endogenous oxyradical production is greatest and that this, combined with the production of oxyradicals from O_3, might exceed the leaf's detoxification ability. However, at lower intensities, decreased carbon assimilation would limit the availability of energy for use in cellular repair.

In most species, light indirectly plays a major role in the opening and closing of stomata. Since stomata therefore tend to close at night and open during the day, light duration to some extent dictates whether or not O_3 can be taken up by foliage from the ambient air.

5.4.4.2 Temperature

Temperature affects almost all physical processes and chemical reactions within the plant. Hence it is the temperature within the plant tissues that is important. Although air temperature dictates the overall heat balance in the surrounding air, the temperature of the leaf is also determined by the absorption of infra-red radiation during the photoperiod (which increases the leaf temperature), and the loss of water vapor through transpiration (which provides evaporative cooling). Hence the effects of air temperature per se must be viewed in the context of these other physical factors. It is therefore not surprising that the few early studies of the effects of air temperature alone, using controlled environment chambers, led to variable and conflicting results, as noted in the previous criteria document (U.S. Environmental Protection Agency, 1986). In most of these studies, the relative humidity (RH) and light intensity were held constant. In water-saturated air with a relative humidity of 100%, the absolute humidity (or water vapor pressure) increases with temperature. Such increases occur at all RHs. Therefore, at constant RH, the increase in absolute humidity (or vapor pressure) with temperature, in turn, increases the vapor pressure deficit (VPD) (i.e., the difference between the absolute humidity) (or vapor pressure) and that of completely saturated air at the same temperature. Since VPD controls the rate of evaporation of water, at constant RH the effects of temperature are unavoidably confounded with effects on VPD. In a recent study with tomato seedlings, in which differences in VPD at different temperatures were minimized, Todd et al. (1991) showed that, out of 11 growth variables measured, the only significant modifications of the effects of O_3 caused by temperature were on stem fresh weight and specific leaf area (leaf area/leaf dry weight). The authors suggest that VPD probably plays a more important role in determining sensitivity to O_3 than temperature.

Although transpiration rate is dependent on VPD, it is also regulated by the opening and closing of stomata on the leaf surface, and factors such as O_3 that cause stomatal closure will indirectly cause leaf temperature to rise. Such stomatal and temperature changes have been observed during exposure to O_3 (Matsushima et al., 1985; Temple and Benoit, 1988).

An important O_3-temperature interaction affecting trees and other woody perennials is winter hardiness. Several studies have shown that exposures to O_3 at realistic levels may reduce the cold- or frost-hardiness of plants, as reviewed by Davison et al. (1988). Using

the pea plant as a laboratory model, Barnes et al. (1988) showed that daily 7-h exposures to 0.075 or 0.09 ppm O_3 for seven days significantly reduced plant survival after exposure to night-time temperatures that fell from 2 °C to -4 °C over a 2-h period and were than held at -4 °C for a further 4 h.

Various responses of coniferous trees to the exposure to O_3 during the growing season and freezing temperatures during the following winter have been reported. With Norway spruce, Eamus and Murray (1991) found that the recovery of photosynthetic rates after freezing was slower in O_3-treated seedlings. Brown et al. (1987) and Barnes and Davison (1988) observed severe necrosis of the older needle classes of seedlings of some Norway spruce clonal saplings exposed to O_3 and then to freezing temperatures although other clones showed no effect. Increased winter injury on plants exposed to O_3 was also observed with Sitka spruce (Lucas et al., 1988) and red spruce (Fincher et al., 1989). With loblolly pine, Edwards et al. (1990) observed variable results, but Chappelka et al. (1990) reported that a late winter frost resulted in severe tip die-back of the youngest needles of seedling trees exposed to 1.7 (350 ppm·h) and 2.5 (433 ppm·h) times the ambient (272 ppm·h) O_3 concentration during the previous growing season, in contrast to the effects observed on Norway spruce. The response also varied with plant genotype. A reason for the difference may be that, in the study with Norway spruce, the freezing period occurred soon after exposure to elevated O_3 levels, while in the loblolly pine study the frost occurred in late winter. The diversity of results led Eamus and Murray (1991) to develop a conceptual framework which recognizes that even in severe winters there are brief periods of mild temperatures that induce partial dehardening. While O_3 decreases frost hardiness per se, it also increases the trees' predisposition to dehardening given favorable conditions during winter. Such dehardening puts O_3-exposed trees at greater risk from subsequent low temperatures.

In a greenhouse study with one-year old red spruce seedlings, Neighbor et al. (1990) reported briefly that decreasing the level of nitric oxide at the time of exposure to O_3 prevented the appearance of O_3-induced frost injury. They suggest that the effects attributed to O_3 are probably due to the combination of O_3 with traces of NO above a critical level. However, this effect has not apparently been investigated further.

In a study of the sub-tropical trees, citrus and avocado, in Florida, Eissenstat et al. (1991) found that, although O_3 could reduce frost hardiness, the effects were subtle, and the authors concluded that the likelihood that frost resistance is adversely affected by current O_3 levels is slight.

The general consequences of global warming on O_3 responses are discussed in Section 5.4.8.

5.4.4.3 Humidity and Surface Wetness

A review of early investigations led to the conclusion that, in general, high relative humidity (RH) tends to sensitize plants to O_3 (U.S. Environmental Protection Agency, 1986). Such a conclusion is supported on mechanistic grounds. McLaughlin and Taylor (1982) studies indicated that measured O_3 uptake by bush bean plants increased with RH, and there are several reports that, at high RH, the rapid decrease in stomatal conductance caused by O_3 at lower relative humidities is inhibited (Otto and Daines, 1969; Rich and Turner, 1972; Elkiey and Ormrod, 1979). However, stomatal responses to O_3 show considerable variability among species and even among cultivars of the same species (Elkiey and Ormrod, 1979), and hence it is to be expected that the patterns of the O_3-RH interaction may not always be as clear. Thus with yellow poplar, five consecutive daily exposures to 0.15 ppm for 7 h at either 40% or 80% RH revealed considerable variation in stomatal conductance (Jensen and Roberts, 1986). At 40% RH, there was a tendency for O_3 to cause a decrease in conductance during the later exposures. Nevertheless, at 80% RH the conductances were generally greater and tended to increase during the later exposures.

Surface wetness also influences the foliar uptake of O_3 although there appear to have been no studies undertaken to investigate the consequences of such uptake. Until recently, it has been suggested that O_3 uptake is reduced when foliage is wet because the stomata may be covered with water (Hicks et al., 1987). However, Fuentes and Gillespie (1992) reported that both wetness from dew or raindrops on the upper surface of maple leaves can significantly increase O_3 uptake. While this may partly be due to a stomatal response to resulting increases in RH, the fact that increased uptake occurred in darkness when the stomata were largely closed led them to suggest that direct uptake into the surface water is

the more important mechanism. However, no information is yet available as to the consequences of such deposition.

5.4.4.4 Drought and Salinity

Short- and long-term variations in the availability of soil water have a profound influence on plant growth. In some agricultural situations, the use of irrigation may eliminate drought stress. However, the growth of crops and natural vegetation in many areas will adversely affected by the varying degrees of water shortage that occur, both during a growing season and from year to year. The previous criteria document (U.S. Environmental Protection Agency, 1986) summarized earlier studies and concluded that drought stress reduced the magnitude of adverse effects of O_3 including injury and growth or yield reductions. The effect was attributed to an increased rate of stomatal closure in drought-stressed plants in response to O_3 that effectively reduced uptake of the pollutant. These conclusions were based almost exclusively on studies with crop species. Since then, a number of studies with tree seedlings and further studies with crops species have shown that the interaction between drought and O_3 is more complex and variable than originally thought.

Heagle et al. (1988a) summarized the results of investigations into the drought-O_3 interaction in six soybean and three cotton studies, and one study each of alfalfa and a clover-fescue mixture. These studies were undertaken as part of the National Crop Loss Assessment Program (NCLAN) (Heck et al., 1984). The results of these investigations are included in Table 5-7. Significant interactions between O_3 and drought stress (soil moisture deficit, SMD) were reported only in three soybean and two cotton studies and the alfalfa study. The interaction was usually revealed by the fact that the clear negative relationships between yield and O_3 exposure observed with watered plants was either much reduced or could not be demonstrated with drought-stressed plants, bearing in mind that in most of these situations the yields were already depressed by the SMD. As a result, the lack of any significant response to O_3 in some cases with such stressed plants reflects the decreased range of yield responses within which an O_3 effect could operate. However, as shown in Table 5-7, Heggestad et al. (1988) found with Forrest soybean that SMD significantly enhanced the effects of low O_3 exposures. Heagle et al. (1988a) therefore were forced to conclude that the suppression of the response to O_3 caused by drought appeared to be

TABLE 5-7. FIELD STUDIES OF OZONE-DROUGHT STRESS INTERACTIONS IN CROP SPECIES
Adapted in Part from Heagle et al. (1988a)

Crop/Cultivar	Year	Response	Significant Interaction	Estimated Yield Loss (%) per Seasonal Mean O_3 Concentration (ppm)[2] 0.04	0.05	0.06	0.07	0.08	Reference
Soybean									
Williams	1982	Yield	No	7	13	19	24	30	Heggestad et al. (1985) Heggestad and Lesser (1990)
Williams and Corsoy 79	1983	Yield	WW	7	13	18	24	30	
		Yield	DS	6	11	15	19	23	Heggestad and Lesser (1990)
Williams		Root length	WW		no significant O_3 effect				Heggestad et al. (1988)
		Root length	DS		[33	36	52][3]		
Forrest	1982	Yield	WW	3	9	21	39	60	Heggestad et al. (1985)
		Yield	DS	13	21	28	35	41	Heggestad and Lesser (1990)
Davis	1983	Yield	WW	4	7	12	16	21	Heagle et al. 1987)
		DS							
	Yield	DS			no significant O_3 effect				
Davis	1984	Yield	No	4	7	12	18	24	Heagle et al. (1987)
Corsoy 79	1986	Yield	WW	2	4	8	13	21	Irving et al. (1988)
		Yield	DS	0	0	0	0	1	
Young	1986	Yield	No	6	11	17	25	34	Miller et al. (1989)

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TABLE 5-7 (cont'd). FIELD STUDIES OF OZONE-DROUGHT STRESS INTERACTIONS IN CROP SPECIES
Adapted in Part from Heagle et al. (1988a)

Crop/Cultivar	Year	Response	Significant Interaction	Estimated Yield Loss (%) per Seasonal Mean O_3 Concentration (ppm)[2] 0.04	0.05	0.06	0.07	0.08	Reference
Cotton									
Acala SJ-2	1981	Yield	WW	3	7	13	21	30	Temple et al. (1985)
		Yield	DS	1	2	3	7	12	
Acala SJ-2	1982	Yield	No	6	15	26	40	55	Temple et al. (1985)
McNair 235	1985	Yield	No	7	13	21	30	40	Heagle et al. (1988b)
Acala SJ-2	1986	Shoot dry mass	WW[4]		[22	26	42][5]		Temple et al. (1988b)
		Shoot dry mass	DS[4]		[20	37	44][5]		
		Shoot dry mass	DS (severe)[4]		[+14	+22	27][5]		
Alfalfa									
WL-514	1984	Yield	No	6	9	13	17	20	Temple et al. (1988a)
WL-514	1985	Yield	No[6]	4	7	10	14	18	
Tall fescue-Ladino clover									
Kentucky 31	1984	Yield	No	5	8	12	17	22	Heagel et al. (1989)
and Regal	1984	Yield	No	6	11	17	24	32	

[1]Where a significant interaction was observed, separate responses are listed for well-watered (WW) and drought-stressed (DS) plants; otherwise the pooled response is listed.
[2]Based on Weibull model estimates (Heagle et al., 1988a)
[3]Data presented are % reductions in root length per soil core at seasonal mean O_3 exposures of 0.074, 0.107 and 0.132 ppm relative to 0.052 ppm. Increased root lengths in DS treatments ranged from 136% to 11% with increasing O_3 exposure.
[4]Interaction not significant by analysis of variance, but significant suppression of O_3 response in DS (severe).
[5]Weibull model data not available. Data presented are actual % yield losses at seasonal mean O_3 exposures of 0.074, 0.094 and 0.111 ppm relative to 0.015 ppm.
[6]Polynomial regression analysis showed slightly greater response in WW than DS plots.

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dependent on the severity of the SMD-induced stress. This conclusion was supported empirically by the fact that the interaction was observed in hot, dry summers, but not in cool, cloudy seasons. However, because different measures of SMD or SMD-induced stress were used in different studies, it is not possible to quantify the relationship between the suppression the O_3 response and the level of drought stress. Furthermore, soil conditions at different sites and the depth of the water table in the soil also appeared to influence the interaction through effects on the vertical distribution of root growth (Heggestad et al., 1988). Moser et al. (1988) showed that impact of O_3 on the growth and yield of bush bean plants was reduced more by a period of SMD early in the reproductive phase of growth than at a later stage.

A retrospective analysis of three years' data involving four soybean cultivars led Heggestad and Lesser (1990) to conclude that, regardless of whether or not drought stress reduced the impact of ozone, in the majority of cases the yield curves showed comparable slopes with increasing O_3 exposure. This led them to question the justification for the 20% reduction in sensitivity to O_3 used by King (1988) in modelling the drought-O_3 interaction.

Brennan et al. (1987) suggested that the normal experimental protocols used in most NCLAN studies, which called for the use of irrigation to avoid possible complications due to drought, might have biased the yield loss data for soybean because it increased plant sensitivity to O_3. However, Heggestad and Lesser (1990) found no evidence to support this suggestion in view of the comparable estimates of yield losses predicted by the O_3-response curves.

Bytnerowicz et al. (1988) found no interaction between SMD and O_3 in 18 desert annual species. However, moderate SMD rendered the tropical fibre plant, kenaf, less sensitive to O_3 although sensitivity was enhanced by sever water stress (Kasana, 1992). A field survey of milkweed plants in two areas in the mid-Ohio River Valley revealed much less foliar injury attributable to O_3 in 1988, a dry year in which the maximum concentration recorded nearby reached 0.2 ppm, than in 1989, a year with ample precipitation and a nearby maximum of only 0.12 ppm (Showman, 1991).

Although there have been several recent studies of the effects of O_3 exposure and drought stress on tree species, they have little in common with respect to the treatments

applied or the measurements made. However, clear demonstrations of significant interactions have been obtained with beech, poplar and loblolly pine seedlings. Davidson et al. (1992) found that although O_3 reduced root growth in well-watered plants, SMD reversed this inhibition and led to slight O_3-induced stimulations. Drought reduced foliar injury caused by O_3 to poplar (Harkov and Brennan, 1980), ponderosa pine (Temple, 1992) and loblolly pine (Meier et al., 1990). In poplar, the effect was attributed to the reduced stomatal conductance observed which reduced O_3 uptake. Similar effects on stomatal conductance were observed in Norway spruce and sitka spruce (Dobson et al., 1990). In ponderosa pine, SMD also countered the inhibitory effects of O_3 on needle growth and retention (Temple et al., 1993). Tseng et al. (1988), however, observed no effects of O_3 on Fraser fir grown under three levels of SMD. No consistent patterns were found with various physiological measurements made on red spruce seedlings subjected to both O_3 and drought (Roberts and Cannon, 1992). Lee et al. (1990) observed reduced root conductivity in the second drought cycle following exposure to O_3.

Thus there is some evidence from tree species to support the view that drought stress may reduce the impact of O_3. However, the work with trees provides no additional information to help in resolving the quantitative nature of the drought-O_3 interaction.

Although drought stress may be the result of insufficient rainfall, conditions of effective SMD may also be induced by excessive soil salinity. Laboratory studies showed that increased salinity could reduce the impact of O_3 on injury and yield on various crops, as reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1996). However, in a more recent field study with alfalfa, Olszyk et al. (1988) found no overall interaction between O_3 and salinity on growth or yield. Although salinity decreased the number of empty nodes caused by exposure to above ambient levels of O_3, the effect was only statistically significant for the second of four harvests. In general, salinity was found to be a more harmful to alfalfa growth than exposure to O_3, but, as pointed out by Olszyk et al. (1988), the amount of information available is insufficient to permit the development of models for estimating losses due to O_3-salinity combinations.

The bulk of the available evidence supports the view that drought stress may reduce the impact of O_3 on plants. However, it must be emphasized that, in terms of growth and

productivity, any "protective" benefit will be offset by the effects of SMD per se, as noted in the previous criteria document (U.S. Environmental Protection Agency, 1986).

The O_3-water interaction is not confined to the effects of SMD on direct plant response to O_3. Numerous studies have shown that O3 may affect various aspects of plant water status, including water use efficiency (WUE), the ratio of the rates of photosynthetic carbon gain and transpirational water loss. For example, Reich et al. (1985) observed that daily exposures to 0.13 ppm O_3 for 6.8 h resulted in a 25% reduction in WUE in well-watered Hodgson soybean, when compared to exposure to 0.01 ppm. Similar findings have been reported for alfalfa (Temple and Benoit, 1988) and radish (Barnes and Pfirrmann, 1992). However, WUE is a complex resultant of both stomatal conductance and the activity of the photosynthetic system, both of which may be independently affected by O_3. Genetic or environmentally induced difference in the relative sensitivities of the stomatal and photosynthetic components will dictate the nature and magnitude of any effect of O_3 on WUE. Thus, with radish and soybean, Greitner and Winner (1988) observed effects on stomatal conductance and photosynthetic CO_2 assimilation that translated into O_3-induced increases in WUE, they point out, that this advantageous increase far outweighed the adverse effects of O_3 on growth.

However, these reports concern herbaceous weedy species, and there appears to be only one report concerning tree species. Johnson and Taylor (1989) reported that exposure to higher than ambient levels of O_3 results in adaptation to a more efficient use of water by the foliage of loblolly pine seedlings. The corollary to this observation is the trees exposed continuously to low O_3 levels may be more sensitive to recurrent drought stress than those grown under higher exposure levels. The corollary to this observation is that trees exposed continuously to low O_3 levels may be more sensitive to recurrent drought stress than those grown under higher exposure levels. As with most studies of tree species, these observations were made on tree seedlings, and their relevance to mature trees has still to be established.

It is therefore clear that not only does drought have a pronounced effect on the response of most species to O_3, but that O_3 also may also modify plant water relations including conferring drought tolerance. However, more study will be needed before it will be possible to generalize about the implications of the latter effect, and its importance to forest ecosystems.

5.4.5 Nutritional Factors

All land plants require an adequate supply of essential mineral elements from the soil in order to avoid adverse effects on growth and survival resulting from mineral deficiencies. Two of the essential elements needed for growth are nitrogen and sulfur, and although these are normally obtained from the soil through the root system, the plant's needs can, at least in part, also be met by the uptake of pollutant gases such as NO_2 and SO_2. Other nutrients such as phosphorus, potassium, magnesium and calcium are generally only available from the soil.

A supply of elements such as nitrogen, potassium, phosphorus, sulfur, magnesium and calcium is essential for plant growth, but optimal growth requires that the supply be balanced; with insufficiency (or excess) of any of them, growth will be sub-optimal. Not surprisingly, therefore, nutrient imbalance has been shown to affect response to O_3, although the previous criteria document (U.S. Environmental Protection Agency, 1986) concluded that work to that date had not clarified the relationship between soil fertility and sensitivity to O_3, largely because of the differences in nutrients and species selected for study and the experimental conditions used. This conclusion is still valid, in spite of the results of a limited number of more recent studies, and is not surprising in view of the vast number of possible permutations and combinations of nutrient elements and their levels that may exert effects on O_3 response. A comprehensive summary of the relevant studies is presented in Table 5-8.

Most information concerns nitrogen. Inspection of Table 5-8 shows that in three of the 13 studies, increased N supply increased susceptibility to foliar injury or enhanced adverse effects of O_3 on growth; three of the studies showed the opposite effects; in three studies, injury was greatest at normal N levels and less at lower or higher levels; in one study, injury was least at normal N levels; and in three studies, no interactions were observed. Knowledge of the tissue N levels resulting from the fertilizer treatments, as recommended by Harkov and Brennan (1980), might resolve these contradictions, but these were not reported in most studies. The contradictory evidence for tobacco was attributed by Menser and Hodges (1967) do the different cultivars used.

TABLE 5-8. OZONE-SOIL NUTRIENT INTERACTIONS
Based in part on Cowling and Koziol (1992)

Species	Response to Increase in Nutrient Level	Reference
Nitrogen (N)		
Loblolly pine	Decreased reduction of growth due to O_3	Tjoelker and Luxmoore (1991)
Ponderosa pine	No injury or growth interactions	Bytnerowicz et al. (1990)
Poplar	Maximum injury in mid range but no growth interaction	Harkov and Brennan (1980)
Yellow poplar	No growth interaction	Tjoelker and Luxmoore (1991)
Ladino clover/tall fescue	No growth interaction	Montes et al. (1982)
Mangel	Increased injury	Brewer et al. (1961)
Radish	Increased reduction of growth due to O_3	Ormrod et al. (1973)
	Reversal of reduction of shoot growth due to O_3	Pell et al. (1990)
Spinach	Increased injury	Brewer et al. (1961)
Tobacco	Decreased injury	Menser and Street (1962)
	Minimum injury in mid range	Macdowall (1965)
	Maximum injury in mid range	Leone et al. (1966)
	Maximum injury in mid range	Menser and Hodges (1967)
Phosphorus (P)		
Radish	No growth interaction	Ormrod et al. (1973)
Tomato	Increased injury	Leone and Brennan (1970)
Potassium (K)		
Norway spruce	Decreased reduction of CO_2 assimilation due to O_3	Keller and Matyssek (1990)
Pinto bean	Decreased injury	Dunning et al. (1974)
Soybean	Decreased injury	Dunning et al. (1974)
Sulfur (S)		
Bush bean	Decreased injury	Adedipe et al. (1972)
Magnesium (Mg)		
Loblolly pine	No growth interaction	Edwards et al. (1992b)
General fertility (N-P-K)		
Bush bean	Decreased injury	Heck et al. (1965)
Soybean	Maximum injury and growth reduction in mid range	Heagle (1979)

The limited evidence for phosphorus, potassium and sulfur consistently indicated a decrease in sensitivity with increased nutrient level. With respect to general fertility, both studies listed in Table 5-8 revealed decreased sensitivity to O_3 at high levels of nutrient supply, although with soybean, nutrient-deficient plants also showed decreased sensitivity. Heagle (1979) found that although injury and growth reductions tended to be greatest at normal levels of fertility, the effects were dependent upon the rooting medium used; in media containing peat, the impact of O_3 on growth was least at the lowest fertility level.

Cowling and Koziol (1982) have suggested that, in spite of the apparent contradictory evidence regarding the effects of nutrition on O_3 response, there is evidence to support the hypothesis that differences in sensitivity are ultimately linked to changes in the status of soluble carbohydrates in the plant tissues (Dugger et al., 1962). However, this hypothesis has yet to be systematically tested.

Nutritional nitrogen and sulfur can also be supplied directly to foliage in the form of nitrogen and sulfur oxides. The interactions of these gaseous pollutants with O_3, dealt with in the next section, focus on toxic rather than nutritional effects. However, one example of a beneficial effect concerns nitrogen pentoxide, N_2O_5. Since N_2O_5 is produced in trace amounts by high voltage corona discharge O_3 generators, it may contaminate O_3 produced from air by such generators for use in studies of effects of O_3 on vegetation, unless the O_3 stream is first passed through a water scrubber. Brown and Roberts (1988) reported that deposition of the nitrate formed by hydration of trace amounts of N_2O_5 in unscrubbed O_3 significantly increased the nitrogen status of the exposed plants, which may have confounded the effects attributed to O_3.

5.4.6 Interactions with Other Pollutants

The concurrent or sequential exposure of vegetation to different gaseous air pollutants has been found to modify the magnitude and nature of the response to individual pollutants. Some of the early work on the effects of gaseous pollutant combinations, reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1986), is of academic interest with little relevance to the present review because of the levels of exposure and the exposure profiles used and the fact that the experimental regimes usually involved concurrent exposures to two or more pollutants repeated daily. Lefohn and Tingey (1984) and Lefohn

et al. (1987) reviewed the patterns of co-occurrence of O_3, SO_2, and NO_2 in urban, rural, and remote sites in the United States for the years 1978 to 1982 and found that co-occurrences were usually of short duration and occurred infrequently. They noted that the most frequent types of co-occurrence were either purely sequential or a combination of sequential and overlapping exposures of short duration. Accordingly, the present review will focus on the evidence from experiments which simulated these naturally occurring patterns of combined exposure or at least which used exposure levels in the ranges of those occurring in polluted air. An exception is the co-occurrence of O_3 and PAN, which are both components of photochemical oxidant.

Over the past decade, the effects of pollutant mixtures have been reviewed by Wolfenden et al. (1992), Shriner et al. (1990), Mansfield and McCune (1988), Torn et al. (1987), Lefohn and Ormrod (1984), Reinert (1984), and Runeckles (1984).

5.4.6.1 Oxidant Mixtures

Because of their photochemical origins, elevated levels of O_3 and PAN can occur simultaneously. There appear to have been no further investigations of the effects of simultaneous or sequential exposures since the limited number of studies reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1986). Hence, there is no reason to question the general conclusion, based on the work of Tonneijck (1984) and Nouchi et al. (1984), that the two gases tend to act antagonistically in both concurrent and sequential exposures. Hydrogen peroxide, H_2O_2, is also a component of photochemically polluted atmospheres. Although Ennis et al. (1990) reported reduced stomatal conductances in red spruce needles exposed to a mixture of O_3, SO_2 and H_2O_2, no studies have been made of O_3/H_2O_2 interactions.

5.4.6.2 Sulfur Dioxide

Since SO_2 originates from point sources of combustion, the occurrence of high ambient concentrations at a given location is usually episodic because of its dependence upon wind speed, wind direction, and distance from the source. However, aggregations of point sources can lead to more widespread but less marked increases in ambient SO_2 levels. Thus the potential exists for elevated O_3 exposures to be superimposed on patterns of SO_2 ranging

from severe fluctuations to almost steady low-level concentrations. Concern over the importance of O_3-SO_2 interactions dates from the observations of Menser and Heggestad (1966) that simultaneous exposures of tobacco to SO_2 and O_3 acted synergistically (i.e., the effects of the mixture were greater than the sum of the responses to either pollutant alone). Indeed, in the Menser and Heggestad study, foliar injury was found to result from exposure to mixtures although exposures to either gas alone at the same concentrations as in the mixtures did not result in injury.

Although much of the early work was concerned with foliar injury responses to simultaneous exposures to high levels of O_3 and SO_2, more recent studies have tended to focus on the consequences of repeated exposures to lower level mixtures or sequences on growth or yield. Several have been aimed at obtaining statistical evidence for the existence of interactions. For example, Ashmore and Onal (1984), studying six cultivars of barley, found that SO_2 at 0.065 ppm for 6 h, an exposure that induced no adverse effects, acted antagonistically to a 6-h exposure to 0.18 ppm O_3, causing significant decreases in foliar injury, ranging from 46% to as much as 95%. However, only one cultivar, Golden Promise, showed a significant interaction on yield, with SO_2 completely reversing the decrease caused by O_3 alone. The results could not be explained by effects on stomatal uptake since stomatal conductances were found to be highest in the mixture. In contrast, with pea, Olszyk and Tibbetts (1981) reported that O_3+SO_2 caused the same degree of stomatal closure as SO_2 alone. A similar antagonism to that observed on Golden Promise was also observed in a field study of "Arena" barley (Adaros et al., 1991a) and of spring rape (Adaros et al., 1991b). However, with "Tempo" spring wheat, a synergistic interaction was observed: the adverse effect of O_3 on yield (-26%) was increased to -38% by SO_2 which by itself only reduced yield by 7% (Adaros et al., 1991a). On the other hand, neither Amundson et al. (1987) nor Kohut et al. (1987) observed any interaction in a field study with "Vona" winter wheat. Irving et al. (1988) observed no interaction on field corn.

In a series of experiments in which exposure to O_3 or an O_3/SO_2 mixture was preceded by exposures to SO_2 alone, an antagonistic response was observed on foliar injury to white bean (Hofstra and Beckerson, 1981). In contrast, the responses of cucumber and radish were synergistic, while there was no interaction on soybean or tomato. However, when followed

by exposure to an O_3/SO_2 mixture, SO_2 pretreatment resulted in an increase in injury to white bean, decreases on cucumber and tomato, and no effect on soybean and radish.

Field studies with soybean using an air-exclusion system to provide a range of exposures to O_3 and SO_2 at ambient and sub-ambient levels revealed an antagonistic interaction on yield at low concentrations (Jones et al., 1988). However, Kress et al. (1986) found no interaction in a soybean field study using open-top chambers. No interactions were found with potato (Pell et al., 1988) or with a red clover-timothy forage mixture (Kohut et al., 1988).

From the foregoing, it is apparent that no clearer pattern of the interactive effects of O_3 and SO_2 on crops has emerged since the previous criteria document (U.S. Environmental Protection Agency, 1986). The same is true for the responses of tree species.

With tree seedlings, Chappelka et al. (1988a) observed no interaction on white ash. Although a synergistic interaction was found on root growth of yellow poplar (Chappelka et al., 1985), only additive interactions were found on the growth of other parts of the plant. In a unique study, Kargiolaki et al. (1991) noted that SO_2 reduced the accelerated leaf senescence caused by O_3 on two poplar clones, but had no effect on other clones. They also observed additive or less than additive interactions on the formation of intumescences, due to hypertrophy of the stems, and bark cracking. They attributed the differences in clonal response to differences in the levels of pollutant-induced ethylene evolution.

Sulfur dioxide reversed the inhibition of photosynthesis caused by exposure to O_3 in two lichen species, *Flavoparmelia caperata* and *Umbilicaria mammulata* (Eversman and Sigal, 1987).

Several studies have attempted to quantify the magnitudes of joint responses to O_3 and SO_2. The earliest (Macdowall and Cole, 1971) showed that the synergistic injury response of tobacco occurred at concentrations of SO_2 less than the threshold for SO_2 injury, but not less than the O_3 threshold. Oshima (1978), working with kidney bean, found that the synergistic reduction due to intermittent exposures to O_3 was linear through a range of O_3 concentrations achieved by varying degrees of filtration of ambient air (expressed as 10 to 90 ppm-h of concentrations greater than zero), although the threshold for an O_3 response was approximately 47 ppm-h.

A selection of statistical models of injury- or yield responses to O_3/SO_2 is listed in Table 5-9. It is immediately apparent that the models reveal no consistent patterns of response. In part, this is because they were developed on the basis of individual experiments conducted under different environmental conditions at different locations in different years. Although each model was statistically significant, it was based on a unique data set. One study with soybean indicated an antagonistic interaction (Heagle et al., 1983) but another indicated no interaction (Kress et al., 1986). Cucumber (Hofstra et al., 1985) and snap bean (Heggestad and Bennett, 1981) were reported to respond synergistically, while white bean responded antagonistically (Hofstra et al., 1985).

All that can be concluded from these studies is that the type of interaction, and whether or not one exists, is probably highly dependent upon species and cultivar, and possibly dependent upon other environmental variables. The available evidence is insufficient to be able to decide in which way, and to what extent, SO_2 exposure will influence the effects of O_3 on a particular species or cultivar at a particular location. The original observations of synergism (Menser and Heggestad, 1966) certainly is not a general response.

5.4.6.3 Nitrogen Dioxide

As with SO_2, most of the few studies of O_3/NO_2 interactions that have utilized realistic concentrations have involved mixtures of the pollutants. Adaros et al. (1991a) found in a 2-year study of two cultivars each of barley and spring wheat that significant interactions could only be detected on wheat yield in one growing season. With both cultivars the interaction was antagonistic. NO_2 also reduced the adverse effect of O_3 on the yield of spring rape (Adaros et al., 1991b). Foliar injury to sunflower caused by daily exposures to O_3 (0.1 ppm, 8 h) was increased by continuous exposure to 0.1 ppm NO_2 (Shimizu et al., 1984). Plant dry weight was decreased by O_3 + NO_2 relative to growth in O_3 alone, but since O_3 exposure resulted in a slight increase in dry weight relative to the controls, the growth in the mixture and in the controls did not differ significantly.

The results of a study of seven tree species exposed to 0.1 ppm O_3 and/or 0.1 ppm NO_2 for 6 h/day for 28 days (Kress and Skelly, 1982) were reported in detail in the previous criteria document (U.S. Environmental Protection Agency, 1986). However, although several growth interactions were noted in the review, the only statistically significant effect

TABLE 5-9. SOME STATISTICAL MODELS OF COMBINED OZONE AND SULFUR DIOXIDE RESPONSES

Species	Type of Interaction	Model	Reference
Corn			
Golden Jubilee	Synergistic	Injury=-11.39+5.471ln(IHT)-9.59[O_3]+ 11.81[SO_2]-86.63[SO_2]^2+428.95[O_3][SO_2] (IHT=initial plant height, used as a covariate; [O_3] and [SO_2]: ppm)	Deveau et al. (1987)[a]
Cucumber			
National Pickling	Synergistic	Injury=2.70+1.95 n; at[SO_2]=0.10 ppm Injury=2.40+0.21 n; at[SO_2]=0.05 ppm Injury=2.39+0.39 n; at [SO_2]=0.03 ppm Injury=1.86+0.166 n; at [SO_2]=0.02 ppm (n=number of daily 8-h SO_2 exposures; O_3 exposure: 0.15 ppm, 6 h)	Hofstra et al. (1985)
Snap bean			
Maple Arrow interaction	Additive; no	Injury=4.44+34.19[O_3]+19.98[SO_2]([O_3] and [SO_2]: ppm)	Deveau et al. (1987)[a]
White bean			
Seafarer	Antagonistic	Injury=6.31-0.90 n; at [SO_2]=0.10 ppm Injury=5.95-0.45 n; at [SO_2]=0.05 ppm (n=number of daily 8-h SO_2 exposures; O_3 exposure: 0.15 ppm, 6 h)	Hofstra et al. (1985)
Potato			
Norchip	Additive; no interaction	Yield=1.27-0.0037[O_3]+0.00092[SO_2] (Yield=number of Grade #1 tubers per plant; [O_3]: ppm, 10 h/day seasonal mean; [SO_2]: ppm, 3 h/day)	Pell et al. (1985)
Soybean			
Davis	Antagonistic	Polynomial model: Yield=534.5-3988.6[O_3]-479.7[SO_2]+ 2661.0[O_3][SO_2]+1,0960[O_3]^2 Weibull model: Yield=531 x exp[-([O_3]/0.133)] x exp[-([SO_2]/0.892)] (Yield=g/m of row; [O_3]: ppm, seasonal 7 h/day mean; [SO_2]: ppm, seasonal 4 h/day mean)	Heagle et al. (1983)

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TABLE 5-9 (cont'd). SOME STATISTICAL MODELS OF COMBINED OZONE AND SULFUR DIOXIDE RESPONSES

Species	Type of Interaction	Model	Reference
Amsoy-71 and Corsoy-79 (pooled)	No interaction	$Yield = 1934.4*\exp[-([O_3]/0.124)^{2.666}]*\exp[-([SO_2]/1.511)^{1.044}]$ (Yield = kg/ha; $[O_3]$: ppm, seasonal 7 h/day mean; $[SO_2]$: ppm, seasonal 4 h/day mean)	Kress et al. (1986)
Tomato			
New Yorker		$Injury = -75.78 + 20.48\ln[PI] - 29.16[O_3] + 1{,}016[O_3]^2 + 9.02[SO_2] - 17.29[SO_2]^2 + 258.76[O_3][SO_2]$ (PI = plastochron index, used as a covariate; $[O_3]$ and $[SO_2]$: ppm)	Deveau et al. (1987)[a]

[a]Report includes models for other growth variables.

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was on top growth of pitch pine, in which NO_2 reversed a growth stimulation caused by exposure to O_3. In contrast, although Yang et al. (1982) also observed an antagonistic interaction on the needle dry weights of two eastern white pine clones, in these cases NO_2 reversed the adverse effect of O_3.

There appear to have been only three studies using sequential exposures of O_3 and NO_2. Runeckles and Palmer (1987) exposed radish, wheat, bush bean and mint daily to 0.08 to 0.1 ppm NO_2 for 3 h (09:00 to 12:00) or to 0.08 to 0.1 ppm O_3 for 6 h (12:00 to 18:00), or to the two gases in sequence. With each species except mint, pretreatment with NO_2 significantly modified the growth responses to O_3. In radish and wheat, the two gases acted conjointly to reduce growth more than O_3 alone, while in bean NO_2 was antagonistic. In studies with tomato, Goodyear and Ormrod (1988) found that sequential exposure to 0.08 ppm O_3 for 1 h followed by 0.21 ppm NO_2 for 1 h significantly reduced growth. No significant effects were found when the sequence was reversed or the two gases were used as a mixture. However, since the study did not include a treatment with O_3 alone, no information was obtained as to how NO_2 may have influenced the response to O_3. Bender et al. (1991) exposed kidney beans in open-top chambers in the field to the sequence: O_3 (08:00 to 16:00, ambient+0.50 ppm) followed by NO_2 (16:00 to 08:00, ambient+0.3 ppm), during two growing seasons. No significant treatment effects on growth were observed in 1988, but in 1989 a significant interaction on total plant biomass was noted after 48 days; the overnight NO_2 exposures negated the inhibition caused by O_3 with a change from -32% to +14%, relative to the controls. This type of response is similar to that observed on bean by Runeckles and Palmer (1987).

With such limited information, it is not possible to generalize, particularly since antagonistic and additive responses have been reported even for individual species. However, since on a daily basis changes in NO_2 levels tend to lead to maxima at times when O_3 levels are lowest, the evidence is sufficiently compelling to indicate that modifications of the O_3 response as a result of increased NO_2 are highly probable.

5.4.6.4 Hydrogen Fluoride and Other Gaseous Pollutants

The adverse effects of hydrogen fluoride, HF, released from the aluminum smelting process and superphosphate fertilizer manufacture are well documented, but information

about possible HF/O_3 interactions are limited to a single study. MacLean (1990) reported that exposures of corn plants on alternate days to 4 h at $1\mu g/m^3$ fluorine as HF or 0.06 ppm O_3 showed reduced rates of senescence, compared with plants exposed only to O_3.

5.4.6.5 Acid Deposition

The effects of acidic deposition have been extensively reviewed by Shriner et al. (1990). Although concerns over the possible role of exposures to acid rain or acid fog and O_3 in the forest decline syndrome led to several studies with forest tree species, studies have also been conducted on crops. Of over 80 recent reports of studies on over 30 species, more than 75% of the reports indicated no significant interactions between O_3 and acidity of simulated acid rain (SAR) or acid fog. The reports are summarized in Table 5-10. In 63 studies, there was either no effect of one or other of the pollutants (usually acid rain) or the effects of both pollutant stresses were simply additive.

However, in other studies, statistically significant interactions have been reported for several species, as also shown in Table 5-10. For example, although a large number of studies of loblolly pine revealed no interaction, Qiu et al. (1992) reported significant interactions on foliar and stem biomass with seedling trees of an O_3-sensitive family. However, since the study failed to show a significant main effect of acidity of the SAR, the authors question whether the interaction is meaningful.

With Norway spruce, antagonistic interactions were noted on stomatal conductance (Barnes et al., 1990a) and dark respiration (Barnes et al., 1990b). In contrast, Eamus and Murray (1991) reported greater than additive effects of O_3 and acid mist on photosynthetic rates. However, no interactions were noted in nine other investigations (Table 5-10).

Kohut et al. (1990) observed significant interactions on needle and shoot growth of red spruce. In both cases the inhibition caused by O_3 and SAR at pH 5.1 was reversed by more acidic rain at pH 3.1. However, there were unexplained inconsistencies in the trends since the combination of intermediate O_3 levels and low pH resulted in the greatest reductions in dry matter. Percy et al. (1992), also working with red spruce, observed an unexplained statistically significant interaction on the thickness of the needle epidermal cell cuticular membrane: at intermediate O_3 exposures, increased acidity led to reduced membrane thickness while at lower or higher O_3 levels led to thicker membranes.

TABLE 5-10. REFERENCES TO REPORTS OF INTERACTION OR NO INTERACTION BETWEEN OZONE AND ACID RAIN OR ACID FOG

Species	No.	Interaction References	No.	No Interaction References
Tree species:				
CONIFERS:				
Jeffrey pine	0	—	1	62
Loblolly pine	1	41	13	1, 10, 16-21, 26, 32, 43, 47, 55
Ponderosa pine	0	—	2	65, 66
Shortleaf pine	1	52	1	8
Slash pine	2	9, 13	0	—
White pine	1	47	3	44, 46, 56
Douglas fir	0	—	1	25
Norway spruce	1	3, 4	9	2, 5-7, 15, 24, 30, 36, 50
Red spruce	2	31, 39	5	33, 34, 38, 40, 62
Sequoia	1	63	0	—
Totals	9		35	
HARDWOODS:				
Green ash	0	—	1	23
White ash	0	—	1	23
European beech	1	14	1	35
Paper birch	1	29	0	—
Sugar maple	0	—	2	44, 45
Red oak	0		2	44, 45
Yellow poplar	3	11, 12, 27	1	48
Totals	5		8	
Crop species:				
FORAGES AND FIELD CROPS:				
Alfalfa	1	59	4	42, 53, 59, 64
Sorghum	1	51	0	—
Soybean	1	67	4	28, 37, 53, 57
Wheat	0	—	1	53
Totals	2		5	
HORTICULTURAL CROPS:				
Snap bean	0	—	1	53
Celery	0	—	1	60
Corn	0	—	1	60
Pepper	0	—	2	58, 60

TABLE 5-10 (cont'd). REFERENCES TO REPORTS OF INTERACTION OR NO INTERACTION BETWEEN OZONE AND ACID RAIN OR ACID FOG

Species	No.	Interaction References	No.	No Interaction References
HORTICULTURAL CROPS (cont'd):				
Strawberry	0	—	2	60, 61
Tomato	0	—	2	53, 60
Avocado	1	22	0	—
Citrus	1	22	0	—
Totals	2		9	
Others:				
Ivy	0	—	1	30
Lichen (Lobaria)	0	—	1	54
Totals	0		2	
TOTALS:	19		63	

References:
1. Adams and O'Neill (1991). 2. Barnes and Brown (1990). 3. Barnes et al. (1990a). 4. Barnes et al. (1990b). 5. Blank et al. (1990a). 6. Blank et al. (1990b). 7. Blaschke and Weiss (1990). 8. Boutton and Flagler (1990). 9. Byres et al. (1992). 10. Carter et al. (1992). 11. Chappelka et al. (1985). 12. Chappelka et al. (1988). 13. Dean and Johnson (1992). 14. Eamus and Murray (1991). 15. Ebel et al. (1990). 16. Edwards and Kelly (1992). 17. Edwards et al. (1990). 18. Edwards et al. (1991). 19. Edwards et al. (1992). 20. Edwards et al. (1992). 21. Edwards et al. (1992). 22. Eissenstat et al. (1991). 23. Elliott et al. (1987). 24. Fuhrer et al. (1990). 25. Gorissen et al. (1991). 26. Hanson et al. (1988). 27. Jensen and Patton (1990). 28. Johnston and Shriner (1986). 29. Keane and Manning (1988). 30. Kerfourn and Garrec (1992). 31. Kohut et al. (1990). 32. Kress et al. (1988). 33. Laurence et al. (1989). 34. Lee et al. (1990). 35. Leonardi and Langebartels (1990). 36. Magel et al. (1990). 37. Norby et al. (1986). 38. Patton et al. (1991). 39. Percy et al. (1992). 40. Pier et al. (1992). 41. Qiu et al. (1992). 42. Rebbeck and Brennan (1984). 43. Reddy et al. (1991). 44. Reich and Amundson (1985). 45. Reich et al. (1986). 46. Reich et al. (1987). 47. Reich et al. (1988). 48. Roberts (1990). 49. Sasek et al. (1991). 50. Senser (1990). 51. Shafer (1988). 52. Shelburne et al. (1993). 53. Shriner and Johnson (1987). 54. Sigal and Johnston (1986). 55. Somerville et al. (1992). 56. Stroo et al. (1988). 57. Takemoto et al. (1987). 58. Takemoto et al. (1988a). 59. Takemoto et al. (1988b). 60. Takemoto et al. (1988c). 61. Takemoto et al. (1989). 62. Taylor et al. (1986). 63. Temple (1988). 64. Temple et al. (1987). 65. Temple et al. (1992). 66. Temple et al. (1993). 67. Troiano et al. (1983).

Shelburne et al. (1993) reported that, in two growing seasons, needle biomass of shortleaf pine was significantly reduced in tree seedlings receiving the highest O_3 exposures (2.5 × ambient) and SAR at pH 3.3. However, there were no effects at lower O_3 exposure levels or higher pHs.

A three-year study of slash pine revealed a significant interaction on stem volume increment in each year (Dean and Johnson, 1992). This was attributed to a high rate of

increase observed with increasing acidity in trees exposed to an intermediate O_3 level (2 × ambient). In contrast, at higher or lower O_3 exposures, acidity of the SAR applied had little effect. Although another study with slash pine indicated a significant interaction on photosynthetic rates, no information was provided about its nature (Byres et al., 1992).

The mineral status (K, Ca and manganese, Mn) of white pine showed antagonistic interactions between O_3 and SAR (Reich et al., 1988). Increased acidity nullified the increase in foliar K and the decreases in root CA caused by O_3, while increased O_3 nullified the increase in root Mn that resulted from increased acidity.

Temple (1988) reported a synergistic response of root growth of giant sequoia. Yellow poplar showed no interactions in one study (Table 5-10), but a greater than additive response of root growth was observed by Chappelka et al. (1985). Chappelka et al. (1988b) found that although neither O_3 nor the pH of SAR caused any significant main effects on growth, at intermediate O_3 levels increased acidity caused significant decreases in stem and leaf biomass. Jensen and Patton (1990), on the other hand, reported significant antagonistic interactions on yellow poplar leaf and shoot growth. Based on estimates from growth models derived from experimental data, increased acidity (pH 5.5 to pH 3.0) of SAR reduced the decreases caused by O_3 by almost 50%.

Adverse effects of O_3 on the leaf area and shoot, leaf, and root biomass of paper birch were reversed by increased acidity of SAR (Keane and Manning, 1988). Similarly, in both avocado and lemon trees, Eissentstat et al. (1991) found that increased acidity offset the negative effects of O_3 on leaf growth.

Although there are four reports of no interactions on alfalfa, Takemoto et al. (1988b) observed significant interactions on leaf drop. In charcoal-filtered air, leaf drop increased by a factor of six as the pH of the fog treatment changed from 7.24 to the extremely acid pH 1.68, the lowest level recorded in the field in southern California. In unfiltered air, in contrast, leaf drop only increased 20%.

Several studies with soybean revealed no significant interactions. However, Troiano et al. (1983) reported a 42% reduction in seed yield between charcoal-filtered and unfiltered air with SAR at pH 2.8, versus a 6% reduction at pH 4.0. Increased acidity thus multiplied the effect O_3, due largely to a stimulation of seed yield caused by increased acidity. Shafer (1988) observed a stimulation of shoot growth of sorghum at pH 2.5 of SAR over growth at

pH 5.5 as a result of which greater growth occurred at low O_3 exposure levels, although there was no effect of acidity at the highest O_3 level (0.3 ppm).

In summary, although the majority of studies have not demonstrated the existence of interactions between O_3 and SAR, where statistically significant interactions on growth or physiology have been reported, the interactions were mostly antagonistic. The only synergistic interactions reported are in two studies of yellow poplar and single studies of sequoia and shortleaf and slash pines. In most cases where significant interactions were noted, the authors have had difficulty in providing any mechanistic explanation. It appears that, although the effects may have passed normally accepted tests of statistical significance, they may nevertheless have been spurious findings. Overall, it appears that exposure to acidic precipitation is unlikely to result in significant enhancement of the adverse effects of O_3 in most species. In the few cases of antagonistic interactions, the suggestion was made that these may have reflected a beneficial fertilizer effect due to the nitrate and sulphate present in the SAR applied.

5.4.6.6 Heavy Metals

Interactions of O_3 with several heavy metal pollutants were reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1986). The limited data for pollutants such as cadmium (Cd), nickel (Ni), and zinc (Zn) almost invariably showed that they enhanced the adverse effects of O_3, usually additively, but occasionally more than additively. To the results with Cd, Ni, and Zn on garden cress, lettuce, pea, tomato, and aspen, reviewed at that time, should be added similar findings with Zn on Pinto bean (McIlveen et al., 1975), with increased Zn resulting in significantly increased foliar injury and decreased infection mycorrhizal establishment. However, in a study of the effects of O_3, Ni, and copper (Cu) on tomato, Prokipcak and Ormrod (1986) found that as the levels of both O_3 and Ni increased, the interaction changed from additive to less than additive. Complex interactions were observed when the treatments included both Ni and Cu.

No information appears to be available about possible interactions with lead. Although qualitatively heavy metals appear to increase plant sensitivity to O_3, the limited information available precludes defining any quantitative relationships.

5.4.6.7 Mixtures of Ozone with Two or More Pollutants

Pollutant-pollutant interactions are not limited to mixtures or sequences of two pollutants. Several studies have been made of interactions of O_3 with various combinations of SO_2, NO_2 and acid rain. However, in some of these investigations, no treatment with O_3 was included in the experimental design and therefore no information was obtained on effects on the response to O_3. Some studies using only repeated daily exposures to high levels (>0.3 ppm) of one or more pollutants are excluded from this review.

Adaros et al. (1991b), in a field study of spring rape using open-top chambers, found no significant interactions between O_3 and NO_2 (sequential exposures) and SO_2 (continuous exposures). In a two-year study on spring barley and spring wheat, some statistically significant interactions were noted but they were scattered through the different growth measurements, cultivars and years with no consistent pattern (Adaros et al., 1990a). Additive effects with no interactions were observed in studies of shore juniper (Fravel et al., 1984), radish (Reinert and Gray, 1981), and azalea (Sanders and Reinert, 1982). Yang et al. (1982) reported a less than additive interaction on injury to white pine.

No significant three-way interactions were found in studies of soybean (Norby et al., 1985), yellow poplar (Chappelka et al., 1985, 1988b), nor on other hardwood species (Davis and Skelly, 1992; Jensen and Dochinger, 1989; Reich et al., 1985) exposed to O_3, SO_2 and SAR.

No information was collected on interactions in the few published studies involving O_3, SO_2, NO_2 and SAR.

The limited data make it difficult to draw any firm conclusions, but in general, the consequences of such exposures appear to be largely dictated by the dominant individual two-way interaction.

5.4.7 Interactions with Agricultural Chemicals

Agricultural chemicals are used for the control of insect pests, diseases, and weeds, and for the control of growth in specialized situations such as the selective thinning of fruit on orchard trees. The potential for some agricultural chemicals to modify plant response to O_3, first noted with certain fungicides on Pinto beans (Kendrick, 1954), led to numerous field and laboratory studies. As noted in the previous criteria document (U.S. Environmental

Protection Agency, 1986), protection against O_3 injury was found to be conferred by applications of numerous commercial fungicides, herbicides and growth regulators.

The available information is derived from studies involving a number of different commercial chemicals and species. No comprehensive and systematic studies have been reported, but the weight of evidence indicates that certain fungicides are consistent in providing protection. In particular, there have numerous reports of protection conferred by applications of benomyl (benlate; methyl-1-[butylcarbamoyl]-2-benzimidazolecarbamate). In addition to the studies reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1986), benomyl protection of grape (Musselman and Taschenberg, 1986) and bean cultivars (Pell, 1976; Pellisier et al., 1972) has also been reported. It is of interest to note that although several nematocides were found to increase sensitivity of tobacco and Pinto bean to O_3, applications of benomyl overcame this response and conferred resistance (Miller et al., 1976). However, benomyl was found to increase the injury caused by PAN (Pell and Gardner, 1979). It should also be noted that many of the effective fungicides are carbamates and have been used as antioxidants in other applications such as rubber formulations.

The need to distinguish between protective action against O_3 injury and fungicidal activity per se is shown by a study of fentin hydroxide (Du-Ter; tetraphenyltin hydroxide) on potato (Holley et al., 1985). The fungicide reduced foliar injury in the field and also the colonization of injured leaf tissue by the early blight fungus, *Alternaria solani*. However, yield increases appeared to result from the reduction of disease rather than from diminished O_3 injury.

The triazoles are a family of compounds with both fungicidal and plant growth regulating properties. Fletcher and Hofstra (1985) reported on the protective action of triadimefon (1-[4-chlorophenoxy]-3,3-dimethyl-1-[1H--1,2,4-triazo-1-yl]-2-butanone), and Musselman and Taschenberg (1986) found that triadimefon and the triazole, etaconazole (1-[[2,4-dichlorophenyl]-4-ethyl-1,3-dioxolan-2-yl]methyl-1H-1,2,4-triazole), were as effective as benomyl in protecting grape from oxidant injury; cultivar differences were noted, with the fungicides being more effective on Concord than on Ives foliage. Seed treatment with triazole S-3307 ([E]-1-[4-chlorophenoxy]-3,3-dimethyl-2-[1,2,4-triazol-1-yl]-1-penten-3-ol) resulted in a 50% reduction in the size of wheat plants but provided complete

protection from an excessive exposure to 0.5 ppm O_3 for 6 h that resulted in severe necrosis on the leaves of untreated plants (Mackay et al., 1987).

A range of commercial plant growth regulating compounds was studied by Cathey and Heggestad (1972). The plant growth retardants, CBBP (Phosfon-D; 2,4-dichloro-benzyltributyl phosphonium chloride) and SADH (Alar; succinic acid 2,2-dimethyl-hydrazide) and several of its analogs, were found to be more effective than benomyl in reducing O_3 injury on petunia.

Conflicting reports of the effects of herbicide-O_3 interactions were reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1986). Recent studies of metolachlor (2-chloro-N-[2-ethyl-6-methlphenyl]-N-[2-methoxy-1-methylethyl] acetamide); Mersie et al., 1989) and atrazine (2-chloro-4-ethylamino-6-isopropylamino-*s*-triazine); Mersie et al., 1990) revealed species-dependent effects: metolachlor sensitized corn to O_3 but offered protection to bean and soybean. The effects of atrazine on corn were additive to those induced by exposure to 0.2 ppm O_3 for 6 h/day twice weekly for three weeks, but antagonistic to exposures to 0.3 ppm. Mersie et al. (1990) also observed a protective action of the commercial antioxidant, n-propyl gallate, on corn.

In spite of reports to the contrary (Teso et al., 1979), Rebbeck and Brennan (1984) found that the insecticide, diazinon (O,O-diethyl-O-[2-isopropyl-4-methyl-6-pyrimidinyl] phosphorothioate), did not protect alfalfa from O_3 injury in a greenhouse study.

Our knowledge of the interactions of these different types of agricultural chemical with O_3 is still too fragmentary to be able to draw any general conclusions other than to note the general efficacy of the carbamate fungicides. As noted in the previous criteria document (U.S. Environmental Protection Agency, 1986), it is premature to recommend their use specifically for protecting crops from the adverse effects of O_3, rather than for their primary purpose.

5.4.8 Factors Associated with Global Climate Change

This section focuses solely on the ways in which features of global climate change may be expected to affect the impact of oxidants on vegetation. It is not intended to provide a comprehensive review of the issues and components of climate change per se.

The magnitudes and causes of some of the changes in features of the global climate that have been observed or are predicted to occur are currently the subject of controversy. However, there is clear evidence of increases in mean CO_2 levels (Keeling et al., 1989) which together with other anthropogenic emissions of radiatively active gases may contribute to the upward trend in mean surface level temperatures observed over the past century (Jones, 1989) and changes precipitation patterns throughout the world (Diaz et al., 1989). In addition, depletion of the stratospheric O_3 layer in the polar regions, caused by halofluorocarbons, results in increased penetration of the atmosphere by solar ultraviolet-B (UV-B) radiation (280 to 320 nm wavelengths). However, the intensity of UV-B radiation reaching the earth's surface may be attenuated by O_3-pollution in the lower troposphere (Brühl and Crutzen, 1989). Differences in the degree of this attenuation probably contribute to the discrepancies between recently observed trends in surface-level UV-B intensities (Scotto et al., 1988; Blumenthaler and Ambach, 1990).

Independent of any effects of ambient temperature, CO_2 level affects plant water relations through effects on stomatal aperture and conductance, leading to effects on leaf and canopy temperature and the uptake of gaseous pollutants. The effects of UV-B on numerous growth processes have been reviewed by Tevini and Teramura (1989) and Runeckles and Krupa (1993). Individual interactive effects of O_3 and several of these features of global climate change have been reviewed in the previous sections. However, it is important to recognize that, because of the interactions among the different components of climate change themselves, a holistic approach is essential, which includes their potential for modifying plant response to oxidants. Overall reviews of the interactions involving the factors of climate change and O_3 have been presented by Krupa and Kickert (1989) and Ashmore and Bell (1991).

The effect of increased CO_2 in stimulating photosynthetic rates may also lead to increased leaf area, biomass and yield (Allen, 1990). Increased CO_2 also leads to stomatal closure. However, with regard to water use, the result of decreased stomatal conductance in reducing transpiration is partly offset by the increase in leaf and canopy temperature resulting from reduced evaporative cooling, and the increase in leaf area. The net result is that increased CO_2 may lead to only slight increases in water use efficiency that are attributable more to increased photosynthetic activity than to reduced transpiration (Allen, 1990). On the

other hand, since the primary route of entry into the leaf of a gaseous pollutant such as O_3 is through the stomata, increased CO_2 levels would be expected to decrease the impact of O_3 by reducing uptake as a consequence of reduced stomatal conductance.

Allen (1990) provides a simulation of the effect of doubling the average ambient CO_2 level from 340 to 680 ppm on soybean yield, based on the Weibull response model to O_3 and SO_2 of Heagle et al. (1983), and the model of stomatal conductance developed for soybean by Rogers et al. (1983):

$$g_s = 0.0485 - 7.00 \times 10^{-5}[CO_2] + 3.40 \times 10^{-8}[CO_2]^2,$$

where g_s is stomatal conductance (m/s), and $[CO_2]$ is CO_2 concentration (ppm). According to this model, a doubling of the CO_2 level would reduce g_s by a factor of 0.69, effectively reducing the O_3 and SO_2 concentrations to 0.038 and 0.018 ppm respectively. At the current 340 ppm CO_2 level, the Weibull model predicts a yield of 340.5 g/m of row. Reduced pollutant entry at 380 ppm CO_2 gives a predicted yield of 390.6 g/m of row, an increase of 14.7%. This is a conservative estimate since it ignores the direct effect of the increased CO_2 level on soybean growth.

Although the calculation makes numerous assumptions, it is qualitatively supported by evidence from the few studies published to date on CO_2/O_3 interactions. Barnes and Pfirrmann (1992) reported that an increased CO_2 level of 765 ppm countered the adverse effects of O_3 on photosynthesis, shoot growth rate, leaf area, and water use efficiency of radish. Protection against the adverse effects of O_3 on soybean by elevated CO_2 was also reported by Kramer et al. (1991). The yield loss due to O_3 at ambient CO_2 was 11.9%, whereas in the presence of ambient+150 ppm CO_2, the loss was only 6.7%.

Although these studies support the prediction of Allen (1990), they were conducted in growth chambers (Brown and Pfirrmann, 1991) or open-top field chambers (Kramer et al., 1991; Mulchi et al., 1992), as were the studies on which Allen's model was based. Hence the plants would not have been subjected to the environmental conditions typical of the open field, particularly with respect to wind speed and its effects on transpiration and temperature. Nevertheless they support the view that increased CO_2 levels will reduce adverse effects of O_3 on crops.

It is unclear as to whether such CO_2-induced reductions of the impact of O_3 also apply to the long term growth of trees, and it is equally unclear as to how increased CO_2 will affect the impact of O_3 on ecosystems. These uncertainties arise because of the numerous compensatory feedback mechanisms that play important roles in both long-term perennial growth and in the behavior of ecosystems. Such feedbacks include changing demands for nutrients, increased leaf area and potential water loss, and changes in litter quality and quantity. For example, in terms of the effects of increased CO_2 alone, long-term studies of several species suggest that although photosynthesis may be demonstrably stimulated, there may be little or no net response at the ecosystem level (Bazzaz, 1990).

The consequences of global warming as a feature of climate change are difficult to assess since, as discussed in Section 5.4.4, the information on the effects of temperature on O_3-response is conflicting. However, as Ashmore and Bell (1991) point out, concerns over the effects of O_3 on sensitivity to freezing temperatures will become increasing unimportant as warming occurs.

Various models of climate change scenarios have indicated that changed precipitation patterns will lead to increased drought in some mid-latitude regions of the world. The bulk of the evidence reviewed in Section 5.4.4 suggests that this would reduce the impact of O_3. However, because of the major direct impact of drought per se, such protection would be of little practical significance.

Greater certainty surrounds the likelihood that global warming will increase the incidence and severity of losses caused by pests and diseases. Concurrent increases may also favor the competitiveness of many weed species. At present, it is not possible to quantify such changes or to determine how they would influence the interactions discussed in Section 5.4.3.

With regard to possible interactions of O_3 and UV-B, Runeckles and Krupa (1993) point out that, because of the episodic nature of O_3 pollution, including its typical diurnal pattern, surface level exposures to UV-B will also be episodic. They have described various possible O_3/UV-B scenarios that need to be considered. With low surface O_3 levels and increased UV-B irradiation due to stratospheric O_3 depletion, effects of UV-B will predominate. On the other hand, elevated surface O_3 levels will cause increased attenuation of UV-B resulting in reduced surface intensities. With no stratospheric O_3 depletion, this

condition implies that surface effects of O_3 will predominate over the effects of the effects of UV-B; with stratospheric O_3 depletion, the resulting surface level irradiation will be dependent upon the concentration and thickness of the surface O_3 layer and both O_3 and UV-B effects may occur.

To date there have been no experiments conducted specifically to simulate these different scenarios. However, Booker et al. (1992) exposed soybean in field open-top chambers within which lamps were suspended to provide increased intensities of UV-B. The O_3 treatments were ambient and 1.5 $\times$ ambient. No significant O_3/UV-B interactions were noted; the effects on growth were solely attributable to the O_3 exposure. However, increased UV-B irradiation resulted in increases in the foliar content of UV-absorbing constituents. In contrast, Miller and Pursley (1990) reported that a preliminary experiment revealed a less than additive interaction of O_3 and UV-B on soybean growth.

It is clear overall that the effects of O_3 on vegetation will be modified to some degree by various components of the complex mix of factors that constitute climate change. Considerably more research will need to be undertaken before quantitative assessments of the magnitudes of the changes will be possible.

5.4.9 Summary

Since the previous criteria document (U.S. Environmental Protection Agency, 1986), additional studies have been published on a wide range of biological, physical, and chemical factors in the environment that interact with plant response to O_3.

Biological components of the environment of individual plants include pests, pathogens and plants of the same or other species in competition. With regard to insect pests, although only a very limited number of plant-insect systems has been studied, there is a general trend in the observations that suggests that some pests have a preference for and grow better when feeding on plants that have been impacted by O_3. Unfortunately, because we have no knowledge of how the vast majority plant-insect systems will be affected by O_3, it is not possible to offer any quantitative overall assessment of the consequences of such interactions on the growth of crops and natural vegetation. At best, we may conclude that there is a reasonable likelihood that some insect pest problems will increase as a result of increased ambient O_3 levels, but there is no evidence to suggest that O_3 may trigger pest outbreaks.

Plant-pathogen systems are also affected by O_3 but here too, the available evidence is far from representative of the wide spectrum of plant diseases. Nevertheless, the suggestion of Dowding (1988) that diseases caused by obligate pathogens tend to be diminished by O_3 while those caused by facultative pathogens tend to be favored, is generally supported by the limited evidence available. In terms of its broader implications, this suggests that continued exposure to O_3 may lead to a change in the overall pattern of the incidence and severity of specific plant diseases affecting crops and forest trees. However, it is not possible with the limited evidence currently available to predict whether the net consequences would be more harmful or less.

A major level of uncertainty concerns the effects of O_3 at the population and community levels within natural ecosystems. Very few studies have been conducted on multi-species systems, and Woodward (1992) has pointed out the hazards of attempting to extrapolate from responses of the individual plant to responses of a population of such plants. This is borne out by the observations of Evans and Ashmore (1992) who showed that the behavior to O_3-exposure of a species growing in mixture with other species is not predictable from its behavior when grown in isolation. This has serious implications with regard to complex natural ecosystems, and identifies a serious gap in our knowledge of the effects of O_3 that can only be filled by a substantial research effort.

With regard to the physical environment, the combination of light, temperature and water availability largely determines the success of plant growth because of the influence of these factors on the processes of photosynthesis, respiration and transpiration. For agricultural crops, perhaps the most important of these potential interactions with O_3 concerns water availability and use. There is consistent evidence that drought conditions tend to reduce the direct adverse effects of O_3 on growth and yield. Conversely, the ready availability of soil water tends to increase the susceptibility of plants to O_3 injury. However, a lack of water should not be viewed as a potentially protective condition, because of the adverse effects of drought per se. The combination of drought conditions and exposure to O_3 is likely to result in adverse effects on growth and yield that are largely the result of lack of water. However, with perennial trees, there is evidence that prolonged exposures to O_3 may lead to greater water use efficiency which would enable such trees to be better able to survive drought conditions.

In contrast with crop species, with tree species the relative roles of light, temperature and water are shifted somewhat because of the differences in plant form. In particular, the photosynthetic function of the leaves is carried out by a much smaller proportion of the plant's biomass. Conversely, a larger demand is placed on temperature-dependent respiratory processes to maintain and support the tissues of the stem and root systems. In addition, in temperate regions, the perennial habit brings with it the requirement for storage of carbohydrates and other reserves, in order to permit survival during the winter season and to facilitate renewed spring growth. Hence, with tree species it becomes important to distinguish between the immediate effects of exposure to O_3 and the longer-term consequences of these effects.

Of particular importance in northern latitudes and at higher elevations is the demonstrated role of O_3 in adversely affecting cold hardiness, by reducing carbohydrate storage. Independent of effects on winter hardiness, there is also evidence to indicate that adverse effects on storage may also be a component of changes in growth occurring in subsequent seasons (Hogsett et al., 1989; Anderson et al., 1991; Sasek et al., 1991). However, it is not yet possible to assemble these observations into a general quantitative model.

The plant's environment also contains numerous chemical components, ranging from soil nutrients and other air pollutants to agricultural chemicals used for pest, disease and weed control. With regards to plant nutrients and their influence on plant response to O_3, the available evidence is highly fragmentary and frequently contradictory, and hence does not permit the drawing of any general conclusions. A large number of studies have been conducted on the effects of O_3 in conjunction with other gaseous air pollutants such as SO_2 and NO_2, although the information obtained in several of the studies is of no more than academic interest because of the unrealistic exposure conditions used. Although there is clear evidence to show that O_3 and SO_2 may act synergistically in increasing foliar injury in some species, the available evidence indicates that this type of response is not universal. Several empirical models of the O_3-SO_2 interaction have been developed, but they have little in common and are highly specific to the crop and exposure conditions used. Furthermore, the frequently observed lack of interaction implies that in many cases the impact of O_3 is

probably best assessed on its own. The same is true of the situation with regard to combinations of O_3 and acid rain or acid fog, and O_3 and NO_2.

Numerous agricultural chemicals have been found to influence the responses of plants to O_3. In particular, several fungicides have been shown to confer protection against visible injury, although none has been adopted for commercial application for this purpose. On the other hand, the experimental chemical, ethylenediurea, has been found consistently to provide protection of a wide range of species, both in the laboratory and in the field.

Since increased tropospheric O_3 is a component of global climate change, results from studies on the interactions of O_3 with increased levels of CO_2 and UV-B radiation are beginning to appear. Initial work with CO_2 suggests that increased CO_2 levels may ameliorate the effects of O_3. However, it is too soon to be able to generalize on the outcome of this interaction. At the present time, no investigations of the compound interactions involving O_3, CO_2, UV-B, increased temperature and changed soil moisture status have been reported.

In conclusion, in spite of the amount of work carried out to date on the interactions of O_3 with environmental factors, we are left with a very fragmented understanding from which to draw conclusions. This is probably inevitable in view of the vast scope of the possible interactions between O_3 and all the other environmental variables. It is also a result of the fact that most of the published work consists of studies resulting from personal interests of the investigators, rather than from coordinated programs of research that focus on systematic investigations.

5.5 EFFECTS-BASED AIR QUALITY EXPOSURE INDICES

5.5.1 Introduction

5.5.1.1 Biological Support for Identifying Relevant Exposure Indices

The effects of O_3 on individual plants and factors that modify plant response to O_3 are complex and vary with species, environmental conditions, and soil and nutrient conditions. Because of the complex effect of O_3 and its interactions with physical and genetic factors that influence response, the development of exposure indices to characterize plant exposure and to quantify the relationship between O_3 exposure and ensuing plant response has been and

continues to be a major problem. At best, experimental evidence of O_3's effect on biomass production can refine our knowledge of those factors of O_3 exposure that affect our ability to predict plant response using exposure indices. The impacts of measured O_3 concentrations on plant response are discussed and evaluated to determine the key factors of exposure that account for the variations in plant response and, if possible, to develop measures of pollutant exposure which relate well with plant response.

Considerable evidence of the primary mode of action of O_3 on plants (e.g., injury to proteins and membranes, reduction in photosynthesis, changes in allocation of carbohydrate, and early senescence), which eventually impacts biomass production, identifies O_3 uptake as the correct characterization of plant exposure (Section 5.3). Ozone uptake is controlled by canopy conductance, stomatal conductance, and ambient O_3 outside the leaf (see Figure 5-3). Any factor that will affect stomatal conductance (e.g., light, temperature, humidity, soil and atmospheric chemistry and nutrients, time of day, phenology, and biological agents) will affect O_3 uptake and, consequently plant response (i.e., yield or biomass). Biochemical mechanisms describe the mode of action of O_3 on plants as the culmination of a series of physical, biochemical, and physiological events leading to alterations in plant metabolism. Ozone-induced injury is cumulative, resulting in net reductions in photosynthesis, changes in allocation of carbohydrate, and early senescence, which ultimately lead to reductions in biomass production. In most cases, increasing the duration of exposure increases the effect of O_3 on plant response. Peak concentrations occurring during daylight when stomatal conductance is high have more influence in determining the impact of O_3 on plant response than lower concentrations or night concentrations because of a greater likelihood of intracellular impairment.

From a toxicological perspective, duration and peak concentrations above some level have value in determining plant response but interact with other factors such as respite time, temporal variation, phenology, canopy structure, physiological processes, environmental conditions, and soil and nutrient conditions in different fashions, depending upon species. Effects occur on vegetation when the amount of pollutant absorbed exceeds the ability of the plant to detoxify O_3 or repair the initial impact (Tingey and Taylor, 1982).

Although O_3 uptake integrates the above factors with atmospheric conditions and relates well with plant response, it is difficult to measure. Several empirical models to predict

stomatal conductance have been developed for particular species (Lösch and Tenhunen, 1981) but have not been used to estimate O_3 uptake or to develop exposure indices.

5.5.1.2 Historical Perspective on Developing Exposure Indices

For almost seventy years, air pollution specialists have explored alternative mathematical approaches for summarizing ambient air quality information in biologically meaningful forms that can serve as surrogates for dose for vegetation effects purposes. Some of the indices introduced have attempted to incorporate some of the factors (directly or indirectly) described above. Recognizing the importance of duration and peak concentrations in conjunction with stomatal conductance, the optimum exposure index can be written as:

$$\text{Index} = \Sigma_{i=1}\text{na } w_i \text{ x } f(C_i) \qquad (5\text{-}1)$$

where C_i is the hourly mean concentration, $f(C_i)$ is some function of C_i, and w_i is some weighting scheme that relates ambient condition and internal O_3 flux. The optimal weights are difficult to develop because of the complex relationship among exposure, environmental condition, and species.

Equation (5-1) represents a taxonomy of exposure indices that have been proposed as surrogates of dose in the literature. The exposure indices differ in the ways in which the values are assigned to w_i. Based on the weighting function, the exposure indices can be arranged into the following categories (description from Lee et al., 1989):

- One Event: $w_i=0$ for all C_i except for the few concentrations where $w_i=1$. Examples of such indices are the second highest daily maximum 1-h concentration (2ndHDM), the maximum of 7-h (P7) and 1-h (P1) maximum daily averages, and the 90th or higher percentiles of hourly distribution;

- Mean: $w_i=0$ for all C_i outside the period of interest, P, and $w_i=v_i/\Sigma_{i=1}n_i$ v_i for all C_i inside the period P where v_i is a function of C_i or some environmental variable. Examples are the seasonal mean of 7-h daily means (M7) (Heagle et al., 1979); the effective mean, denoted m_e, where m_e^v is the index in Equation (5-1) with $f(C_i)= C_i^{-1/v}$ and $w_i=1$ for some parameter v (Larsen and Heck, 1984); the solar-weighted mean where v_i is the hourly solar radiation value (Rawlings et al., 1988);

- Cumulative: $w_i=1$ for all C_i. An example is the seasonal sum of hourly concentrations (i.e., total exposure, denoted as SUM00);

- Concentration Weighting: $w_i=g(C_i)$ where g() is a monotonically non-decreasing function. Examples are the seasonal sum of hourly concentrations at or above a threshold level such as 0.06 ppm (SUM06) or 0.08 ppm (SUM08); the seasonal sum of the difference between an hourly concentration above a threshold level less the threshold value, such as 0.08 ppm (AOT08); the total impact with $w_i=C_i^{(-1-1/v)}$ for some v (Larsen et al., 1983); the index with the allometric function, $g(C_i)=C_i^a$, $a>0$; the index with sigmoidal weighting function, $g(C_i)=1/[1+M \times \exp(-AxC_i)]$, where M=4,403 and A=126, denoted as W126 by Lefohn et al. (1988a), and M=500 and A=100, denoted SIGMOID by Lee et al. (1989); total hours with concentrations at or above a threshold level, such as 0.08 ppm (HRS08), $g(C_i)=0$ for $C_i<0.08$ ppm and $w_i=1/C_i$ for $C_i \geq 0.08$ ppm;

- Multicomponent: $w_i=g(C_i, i)$. Examples are indices that incorporate several characteristics of exposure and crop development stage, including the phenologically weighted cumulative impact indices (Lee et al., 1987).

Oshima (1975) and Oshima et al. (1976) proposed an exposure index, where the difference between the value above 0.10 ppm and 0.10 was summed. This is referred to as the AOT10 exposure index with $f(C_i)=C_i-0.10$ and $w_i=0$ for $C_i<0.10$ ppm and $w_i=1$ for $C_i \geq 0.10$ ppm in Equation (5-1). Alternatively, Lefohn and Benedict (1982) introduced an exposure index based on the hypothesis that if the higher O_3 concentrations had greater value in predicting adverse effects on agricultural crops than the lower values, then the higher hourly mean concentrations should be given more weight than the lower values. This index summed all hourly concentrations equal to and above a 0.10 ppm threshold level. This index is referred to as the SUM10 exposure index with $f(C_i)=C_i$ and $w_i=0$ for $C_i<0.10$ ppm and $w_i=1$ for $C_i \geq 0.10$ ppm.

A 6-h long-term seasonal mean O_3 exposure index was used by Heagle et al. (1974). Also, Heagle et al. (1979) reported the use of a 7-h experimental period mean. The 7-h (0900 to 1559 h) mean, calculated over an experimental period, was adopted as the statistic of choice by the U.S. EPA's NCLAN program (Heck et al., 1982). The 7-h daily daylight period was selected by NCLAN because the index was believed to correspond to the period of greatest plant susceptibility to O_3 pollution. In addition, the 7-h period of each day (0900 to 1559 h) was assumed to correspond to the time that the highest hourly

O_3 concentrations would occur. However, not all monitoring sites in the United States experience their highest O_3 exposures within the 0900 to 1559 h 7-h time period (Lefohn and Jones, 1986; Lefohn and Irving, 1988; Logan, 1989). Toward the end of the program, NCLAN redesigned its experimental protocol and applied proportional additions of O_3 to its crops for 12-h periods. The expanded 12-h window reflected NCLAN's desire to capture more of the daily O_3 exposure. In the published literature, the majority of NCLAN's experiments were summarized using the 7-h experimental-period average.

As additional evidence began to mount that higher concentrations of O_3 should be given more weight than lower concentrations (summarized in U.S. Environmental Protection Agency, 1986), concerns about the use of a long-term average to summarize exposures of O_3 began appearing in the literature (Lefohn and Benedict, 1982; Tingey, 1984; Lefohn, 1984; Lefohn and Tingey, 1985; Smith et al., 1987). Specific concerns were focused on the fact that the use of a long-term average failed to consider the impact of peak concentrations. The 7-h seasonal mean contained all hourly concentrations between 0900 to 1559 h; this long-term average treated all concentrations within the fixed window in a similar manner. A large number of hourly distributions within the 0900 to 1559 h window could be used to generate the same 7-h seasonal mean, ranging from those containing many peaks to those containing none. Larsen and Heck (1984) pointed out that it was possible for two air sampling sites with the same daytime arithmetic mean O_3 concentration to experience different estimated crop reductions.

In the late 1980s, the focus of attention turned from the use of long-term seasonal means to cumulative indices (i.e., exposure indices that sum the products of concentrations multiplied by time over an exposure period). As indicated previously, the cumulative index parameters proposed by Oshima (1975) and Lefohn and Benedict (1982) were similar. Both parameters gave equal weight to the higher hourly concentrations, but ignored the concentrations below a subjectively defined minimum threshold (e.g., 0.10 ppm). Besides the cumulative indices proposed by Oshima (1975), Oshima et al. (1976), and Lefohn and Benedict (1982), other cumulative indices were suggested, including (1) the number of occurrences of daily maximum hourly averaged concentrations greater than a threshold level (Ashmore, 1984) and (2) the use of exponential functions (Nouchi and Aoki, 1979; Larsen and Heck, 1984) to assign unequal weighting to O_3 concentrations.

A possible disadvantage of applying an integrated exposure index, as defined by Oshima (1975) or Lefohn and Benedict (1982), is that the use of an artificial threshold concentration as a cutoff point eliminates any possible contribution of the lower concentrations to vegetation effects. Although this disadvantage may not be important when considering O_3 exposures that occur in the California South Coast Air Basin, where repeated high concentrations are experienced from day-to-day and there are relatively short periods between episodes, it is important when assessing the typical exposures experienced in other parts of the United States.

Recognizing the disadvantage, Lefohn and Runeckles (1987) suggested a modification to the Lefohn and Benedict (1982) exposure index by weighting individual hourly mean concentrations of O_3 and summing over time. Lefohn and Runeckles (1987) proposed a sigmoidal weighting function that was used in developing a cumulative integrated exposure index. The index included the lower, less biologically effective concentrations in the integrated exposure summation.

None of the exposure indices mentioned above fully characterize the potential for plant uptake of O_3 because the indices, being measures of ambient condition, ignore the biological processes controlling the transfer of O_3 from the atmosphere through the leaf and into the leaf interior (U.S. Environmental Protection Agency, 1986, 1992). Early studies with beans and tobacco, reviewed in the previous criteria document (U.S. Environmental Protection Agency, 1986), showed that short-term higher-peak exposures induced more injury than longer-term lower-peak exposures of the same total exposure, indicating that concentration has more value than exposure duration in eliciting a response. Other studies with soybean, tobacco, and bean, conducted prior to 1983 and described in U.S. EPA (1986), showed that the foliar injury response to subsequent peak exposures varies with temporal pattern. Predisposition to low levels of O_3 for a few days increases plant sensitivity to subsequent peaks (Johnston and Heagle, 1982; Heagle and Heck, 1974; and Runeckles and Rosen, 1977). Tobacco plants exposed to two consecutive days of peak exposures showed greater injury on the first day (Mukammal, 1965). Plants exposed to a series of successive short exposures suffered more injury than did those plants that received a continuous uniform exposure, with all plants receiving equal total exposure (Stan and Schicker, 1982).

When yield or growth are considered, "not only are concentration and time important but the dynamics of the O_3 exposure are also important" (U.S. Environmental Protection Agency, 1986). Musselman et al. (1983) and Hogsett et al. (1985a) were among the first to demonstrate that plants exposed to variable concentrations showed greater effect on plant growth than those exposed to a fixed or daily peak concentration of equal total exposure but lower peak concentrations. Musselman et al. (1986), in a subsequent experiment, exposed kidney bean plants to either a simulated ambient or a uniform concentration that had equal total exposure and peak concentration (at two levels of 0.30 and 0.40 ppm) and found that the effects of the two distributions did not differ significantly. Consequently, when peak concentrations and total exposures are equal, the diurnal distribution of concentrations appears to be unimportant.

More recent studies with bean (Kohut et al., 1988), soybean (Heagle et al., 1986), and tobacco (Heagle et al., 1987) (reviewed in U.S. Environmental Protection Agency, 1992) showed conflicting evidence of no significant differences in response to different exposure patterns of equal total exposure but varying peak concentrations. The value of peak concentrations in influencing response is inconclusive in these studies because of low statistical power. For the study with beans, plants exposed to peak exposures showed significant impairment in the early harvests, but at the final harvest, O_3 effects on growth and yield were not statistically significant. For the NCLAN studies with soybean and tobacco, differences in yield between the constant and proportional 7-h O_3 addition exposures were not significant, even though the proportional-addition treatments had greater peak concentrations. In reanalysis of the soybean and tobacco studies, Rawlings et al. (1988) stated that the differences between the constant and proportional O_3 additions were relatively small, thus limiting the power of the comparison test. However, 12-h exposures caused greater effects than 7-h exposures but the decrease in yield loss was not directly proportional to the increased length of exposure (Rawlings et al., 1988).

Considerable research since the publication of the previous criteria document (U.S. Environmental Protection Agency, 1986) has been directed at developing measures of exposure that were consistent with then-current knowledge of the mode of action of O_3 on plants and on factors including concentration, duration, and temporal dynamics of exposure influencing response. A number of retrospective studies of existing data to evaluate and

compare exposure indices based on statistical fit have been summarized in the literature between 1986 and 1988 and reviewed by the U.S. EPA (1992) (Rawlings et al., 1988; Adomait et al., 1987; Cure et al., 1986; McCool et al., 1986, 1987; Smith et al., 1987; Lee et al., 1987, 1988; Lefohn et al., 1988a; Tingey et al., 1989; Musselman et al., 1988). These studies support the conclusion that: (1) O_3 effects are cumulative; (2) peak concentrations are more important than lower concentrations in eliciting a response; and (3) plant sensitivity to O_3 varies with time of day and crop development stage. Exposure indices that cumulate the exposure and preferentially weight the peaks yield better statistical fits to response than the mean and peak indices.

Because the mean exposure index treats all concentrations equally and does not specifically include an exposure duration component, the use of a mean exposure index for characterizing plant exposures appears to be inappropriate for relating exposure with vegetation effects (U.S. Environmental Protection Agency, 1992). In particular, the weighting of the hourly O_3 concentrations of the mean is inconsistent with the weighting function of plant exposure to O_3 in Equation (5-1), which attempts to relate O_3 flux with ambient condition. The total exposure index includes an exposure duration component but does not adequately relate pollutant exposure with plant response because the index weights all concentrations equally and focuses on the lower concentrations, whose impact on vegetation is minimal.

Evidence supporting the use of peak-weighted, cumulative indices in relating O_3 exposure and plant response is growing. However, it is unlikely that the empirical modeling of plant response will determine the optimal weighting function of hourly O_3 concentrations for use in characterizing plant exposure, which vary with environmental factors and species. The development and comparison of exposure indices based on statistical fits is difficult because only a limited number of experiments have been specifically designed to test and evaluate the various exposure indices.

While much research has been conducted on O_3 effects on crops and trees between 1988 and the current period, our overall understanding of the mode of action of O_3 on plants and factors that modify plant response remains unchanged since the previous criteria document (U.S. Environmental Protection Agency, 1986) and its supplement (U.S. Environmental Protection Agency, 1992). Additional studies further support the value of

concentration, duration, and temporal pattern of exposure in describing plant exposure and its relation to plant response. Studies that applied two or more different exposure patterns of equal exposure but possibly different peak concentrations are reviewed in Section 5.5.2.2 to substantiate the value of exposure structure in influencing the magnitude of plant response. Recent papers that report results from replicate studies over time and/or space are summarized in Section 5.5.2.3 to test the value of duration and its relation with plant response. In addition, a few recent studies that provide additional insight to those factors that modify plant response are reviewed in Section 5.5.2.4.

5.5.2 Developing Exposure Indices

5.5.2.1 Experimental Design and Statistical Analysis

Controlled and field exposure-response studies, where extraneous factors influencing response are controlled or monitored, allow one to study concentration, duration, respite time, temporal fluctuations at general and specific stages of crop development in influencing response. These studies provide insight on the efficacy of exposure indices in explaining variation of response. A small number of experiments have been designed specifically to study the components of exposure and have applied two or more different patterns of exposure which measure the same SUM00 values. These designs provide the best evidence to determine whether plants respond differentially to temporal variations in O_3 concentrations. However, they may have limited application in developing a statistical relationship between O_3 exposure and plant response. Other design considerations, including the number, kind, and levels of O_3 exposure, the patterns of randomization, the number of replicates used in the experiment, and experimental protocol, determine the (1) strength of the statistical analysis that is applied to the treatment mean comparison tests and (2) range of ambient and environmental conditions over which generalizations may be made. These designs have been successfully used to test the value of components of exposure, particularly concentration, in influencing response (Musselman et al., 1983, 1986; Hogsett et al., 1985a). Different approaches that include either a mean separation procedure and/or a regression procedure have been used to identify those important components of exposure that influence response.

To identify the importance of exposure in contributing to variation of plant response, the majority of pollutant effects studies use regression-based designs that apply a single pattern of exposure at varying concentration levels. However, using these designs, the application of the results is limited; the order of plant response (i.e., plant yield) with respect to exposure is unchanged with different measures of exposure. The relative position and spacing between exposure levels is a function of how the exposure index weights the hourly O_3 concentrations and governs the statistical fit to response. The regression approach has been used to compare and evaluate various exposure indices but the ability to discriminate among indices is low for these studies. By their nature, those studies that have used regression-based designs that utilize data from single patterns of exposure cannot distinguish between mean exposure indices and sums constructed from means (i.e., mean $\times$ duration) and, consequently cannot be used to test the value of duration in explaining the variation of response.

Evidence to substantiate the value of duration in explaining the experimental variation of plant response may be obtained when combining data from replicate studies of the same species and cultivar over time and/or space. Pooling of data from replicate studies of the same species to evaluate duration effects and/or to compare various exposure indices assumes that the primary cause of biological response is pollutant exposure. This assumption may or may not be valid, particularly when plants from replicate studies are grown under varying environmental, edaphic, and/or agronomic conditions that tend to mask the treatment effects during the growth of the plant (Section 5.3). Hence, it is more difficult to substantiate the importance of exposure-dynamic factors from retrospective analyses of combined data from replicate studies of the same species than from experiments designed specifically to address the components of exposure. The comparison of environmental conditions, as well as the yields of plants exposed to charcoal-filtered air over replicate studies, is a simple check of interaction but does not ensure that O_3 effects on response can be isolated. In addition, when the main effect of O_3 is insignificant, the data may be limited for determining the value of duration or other components of exposure in predicting response. Nonetheless, if an air pollutant is the primary source of variability in plant response, the relationship between exposure and response should be consistent when data sets for the same crop are combined over several years and/or locations.

Sets of replicate studies of equal and varying duration are readily available in the published literature but only a few reports have combined the data to specifically test the value of duration in explaining variation of plant response or to evaluate exposure indices based on statistical fit. Lefohn et al. (1988a) were the first to fit a common response model to combined data from two replicate studies of varying duration using various exposure indices. Greater yield losses occurred when plants were exposed for the longer duration, indicating that the duration component of exposure was important in influencing response and that a cumulative-type index was able to describe adequately the relationship between exposure and yield. More recent papers have reported results of the two years of replicate studies and a few papers have used the regression approach with and without variance components for sites and/or years to evaluate various exposure indices based on the adequacy of fit of a common response model.

A number of the papers relevant to the study of components of exposure influencing plant response report only the mean and total exposure (i.e., sum of all hourly average concentrations—SUM00) indices. Because exposure indices weight hourly O_3 concentrations differently, it is almost impossible to transform one index into another. One must return to the original data, which in many cases are not available, to generate alternative exposure indices. Therefore, unless adequate information is given to allow calculation of exposure indices, the analysis of reported results from individual and combined data to evaluate different exposure indices is not possible, although it may be possible to perform retrospective evaluation of the structure of exposure in altering plant response.

Another concern relates to the experimental design, particularly the number, kind, and levels of exposure used in the study. Generalization of experimental results is largely dependent on the degree to which atmospheric and biospheric conditions mimic those of the target population. However desirable the need to mimic the real world, understanding the relationship between exposure and the ensuing response (i.e., plant yield) and to identify those components of exposure in influencing response may require the use of exposure regimes with temporal pattern, concentration, and/or structure that are not observed in nature. Research goals are difficult to attain when the investigator requires exposure levels between charcoal-filtered and near-ambient conditions, but the mathematician who is

modeling the experiment requires higher than ambient levels of O_3 to better describe the nature of plant response to O_3.

For example, the O_3 exposures utilized by the NCLAN program have been described as producing artificial regimes that do not mimic actual conditions. Lefohn and Foley (1992) have compared the O_3 exposures for the charcoal-filtered (CF) treatments from 13 NCLAN data sets with clean monitoring sites in the United States. The authors concluded that the exposures in the CF treatments were lower than those experienced under ambient conditions at clean O_3 monitoring sites and that the CF treatments did not mimic those exposures that occurred under ambient conditions at the cleanest sites in the United States. Most of these clean monitoring sites, as described by Lefohn and Foley (1992), are not representative of the crop-growing regions of interest, yet, it is doubtful that the ambient conditions inside the CF chambers would be experienced at any sites in the United States. The application of treatment levels so low that they are almost never observed anywhere may result in statistically significant differences that occur when growth comparisons are made between plants grown in CF and nonfiltered (NF) treatments that are not relevant. Ideally, each exposure in the design should be representative of ambient conditions experienced in the geographic area of interest and the lowest treatment level (i.e., CF) should be set at the cleanest of these sites. Because treatment levels are derived from ambient conditions experienced at the research site, CF chambers may not be identical to ambient conditions at the cleanest site in the region of interest, but may represent ambient conditions observed somewhere in the world.

In addition to the CF concentration regimes, Lefohn et al. (1988a) have reported that the highest treatments have a tendency to display bimodal distributions that are unrealistic (Figure 5-9). At this time, there is no evidence to suggest whether or not these higher ambient exposures provide realistic information on the impact of O_3 on plant response.

Studies that utilize exposures with peak concentrations above 0.40 ppm may not provide realistic evidence of O_3 impact on plant response in the United States. These studies provide limited evidence for substantiating the value of peak concentrations in influencing response. Consequently, these studies are not included in this section.

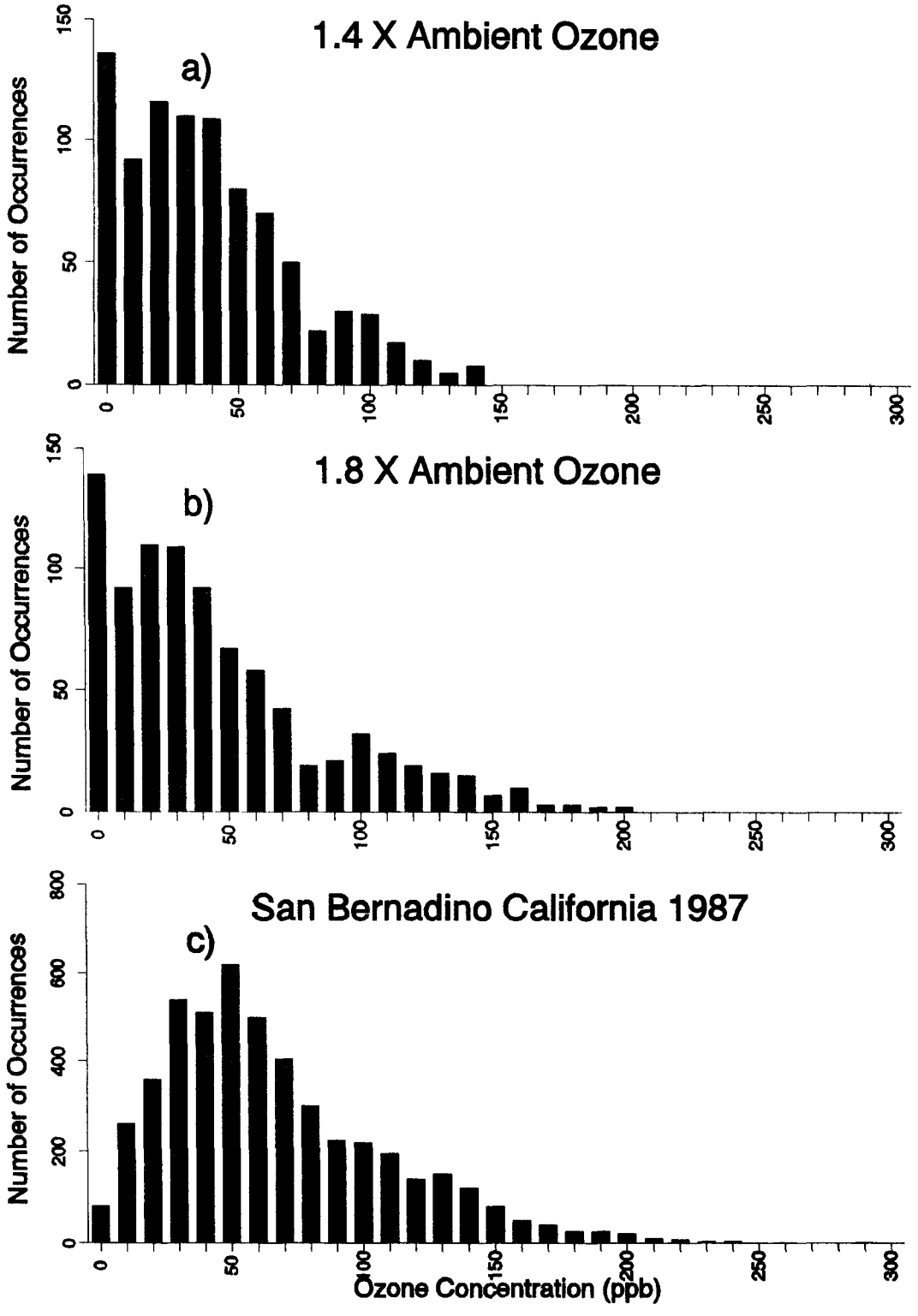

Figure 5-9. Distribution pattern showing the number of ozone concentrations within specified ranges for the 1983 winter wheat proportional addition experiment for the (a) 1.4 × ambient air; (b) 1.8 × ambient air treatments; and (c) for San Bernardino, California in 1987.

5.5.2.2 Studies with Two or More Different Patterns of Exposure

Experiments that focus on the structure of exposure have shown that plant response is differential to temporal patterns of O_3 exposure. For crop species, there is evidence to suggest that plant response is influenced more by higher concentrations than lower concentrations or exposure duration. Greater response to concentration occurred when plants were predisposed to low concentrations for a few days or when peaks occurred just prior to or at maximum leaf expansion (U.S. Environmental Protection Agency, 1978, 1986). Plants exposed to two (or more) different exposure patterns of equal exposure (i.e., same SUM00 value) showed greater foliar injury response to:

1. The short-term, high-concentration exposure than the longer-term exposure with lower peak concentrations (Heck et al., 1966; Heck and Tingey, 1971; Bennett, 1979; Nouchi and Aoki, 1979; Amiro et al., 1984; Ashmore, 1984; Tonneijck, 1984); and

2. The exposure that predisposes plants to low O_3 concentrations for a few days prior to a high O_3 concentration than exposures that have a set diurnal pattern of O_3 concentrations or less than two days of respite time between high concentrations (Heck and Dunning, 1967; Johnston and Heagle, 1982; Heagle and Heck, 1974; Runeckles and Rosen, 1977; Mukammal, 1965; Stan and Shicker, 1982).

The studies that applied the same exposure using different patterns of exposure have been reviewed in previous criteria documents (U.S. Environmental Protection Agency, 1978, 1986, 1992) and substantiate the role of concentration, temporal dynamics, respite time, and predisposition in influencing the magnitude of plant response to O_3.

Musselman et al. (1983) and Hogsett et al. (1985) were among the first to demonstrate that variable concentrations produced greater effect on plant growth than fixed or set diurnal patterns of exposure of equal total exposure with lower peak concentrations (Table 5-11). Musselman et al. (1986), in a subsequent experiment, exposed kidney bean plants to either a simulated ambient or a uniform concentration of equal total exposure and equal peaks (at two levels of 0.30 and 0.40 ppm) and found the effects of the two distributions were not significantly different (Table 5-11). Consequently, when peak concentrations and total exposures are equal, the diurnal distribution of concentrations appears not to be an important factor (U.S. Environmental Protection Agency, 1992).

TABLE 5-11. A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE FOR TWO OR MORE EXPOSURE PATTERNS ON THE GROWTH, PRODUCTIVITY, OR YIELD OF PLANTS

Species	Facility[a]	Total Number Chambers	Exposure Patterns[b]	Exposure Duration	Concentration (ppm)/Exposure (ppm-h)	Variable	Effect[c]	Reference
Glycine max L. Merrill cv. Davis, Forrest, Bragg, and Ransom	OTC in pots	24	16 combinations of CF or NF over 4 quarters (31-days/quarter)	124 days	M7 (ppm): CF range from .016 to .038 over the 4 quarters, NF range from 0.96 to 0.98 over the 4 quarters	Total seed weight	Forrest: greater effect in Q3 than in other quarters. Davis: no consistent effect Q1, significant but similar effects for Q2, Q3, and Q4. Ransom: no significant O_3 effects in Q1 or Q2, and equal responses in Q1, Q3, and Q4.	Heagle et al. (1991)
Medicago sativa L.	OTC in pots	8	Episodic (E), Daily Peak (DP)	133 days	Equal SUM07 (ppm-h): DPH=113, DPL=63, EH=117, EL=72 Equal SUM00 (ppm-h): DPH=183, DPL=140, EH=193, EL=145 M7 (ppm): DPH=.099, DPL=.074, EH=.084, EL=.064	shoot dry wt	91 and 67% reductions for EH and DPH (*). Significant difference between E and DP regimes. Treatment means are ordered CF<DPL<EL<DPH<EH.	Hogsett et al. (1985a)
Phaseolus vulgaris L. cv. Calif. Dark Red Kidney Bean	GC in pots	8	Uniform (U), Ambient (A)	3 weeks (1 day/week)	Equal SUM00 (ppm-h/day): UL=AL=0.69; UH=AH=0.92 Equal Max conc (ppm): UL=AL=0.30, UH=AH=0.40	pod and seed dry weights	6% less yield when exposed to Ambient (NS). Response to O_3 same in reproductive and vegetative growth stages.	Musselman et al. (1986)
Phaseolus vulgaris L. cv. Calif. Dark Red Kidney Bean	GC in pots	8	Uniform (U), Ambient (A)	3 weeks (1 day/week)	Equal SUM00 (ppm-h/day): UL=AL=1.20; UH=AH=1.68 Max conc. (ppm): UL=AL=0.30, UH=AH=0.40	pod and seed dry weights	38% less yield when exposed to Ambient (*). No significant difference between Low and High. Beans in reproductive growth stage when exposed.	Musselman et al. (1983)

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TABLE 5-11 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE FOR TWO OR MORE EXPOSURE PATTERNS ON THE GROWTH, PRODUCTIVITY, OR YIELD OF PLANTS

Species	Facility[a]	Total Number Chambers	Exposure Patterns[b]	Exposure Duration	Concentration (ppm)/Exposure (ppm-h)	Variable	Effect[c]	Reference
Phaseolus vulgaris L. cv. Calif. Dark Red Kidney Bean	GC in pots	10	Initial exposure of .3 ppm for 3-h and second exp of .3 ppm at 2-6 (or 1-5) days after initial exp.	2-6 days in 1984 and 1-5 days in 1985	Equal maximum concentration of 0.30 ppm.	total dry weight	Reductions due to the second exposure were significant when exposures were 3-6 days apart in 1984 and 5 days apart in 1985.	McCool et al. (1988)
Pinus ponderosa Laws, Populus tremuloides michx.	OTC in pots	15	Episodic (E), High Elev (HE), Daily Peak (DP)	111 days	Equal SUM00 (ppm-h): DPH=HEH=EH=170, HEL=EL=122.	leaf stem, stem, root, dry weight	At low level, 64 and 0% reductions for E and HE (*). At high level, 42%, 75%, and 7% reductions for E, HE, and DP(*). Treatment means are ordered E<HE<DP.	Hogsett and Tingey (1990)

[a]GC = controlled environmental growth chamber or CSTR, OTC = Open-top chamber.
[b]CA = Constant addition, PA = Proportional addition, CF = Charcoal-filtered, NF = Nonfiltered, E = Episodic, DP = Daily peak, U = Uniform, A = Ambient, HE = High elevation, H = High, L = low.
[c]Significant at the 0.05 level, NS = not significant.

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One recent study exposed bean plants to two consecutive exposures of 0.30 ppm for 3 h per day in the rapid vegetative growth stage and showed greater reductions in total dry weight when exposures were three to six days apart (McCool et al., 1988) (Table 5-11), consistent with earlier results on the role of predisposition in influencing response (e.g., Hogsett et al., 1988). Predisposition to a high concentration above the level that causes visible injury may increase plant sensitivity over time (Mukammal, 1965). As a result, the subsequent response to a high concentration following recovery may be greater than experienced in prior exposures. In future modeling efforts, this phenomenon may have to be taken into consideration by the weighting of hourly concentrations for properly characterizing plant exposure.

Sensitivity of plants to O_3 is a function of stomatal conductance and varies with phenology. To test the role of phenology, Heagle et al. (1991) applied 16 patterns of exposure in combinations of either charcoal-filtered (CF) or nonfiltered (NF) for each quarter of the experimental period (31 days/quarter) (Table 5-11). The authors concluded that plant response was differential to phenological stage of development and that exposures during mid- to late-growth stages caused a greater yield loss than early exposures. For crops, foliage appears to be most sensitive to O_3 just prior to or during maximum leaf expansion (U.S. Environmental Protection Agency, 1978). These results are consistent with earlier studies (Lee et al., 1987) that reported better statistical fits to response using exposure indices that preferentially weighted hourly O_3 concentrations during the period of anthesis to seed fill.

There is very limited information on the nature of seedling response to O_3 (see Section 5.3.7) and much less is known about the role of exposure-dynamic factors (e.g., concentration, duration, respite time, temporal variation) in influencing biomass response in long-lived species. In a study by Hogsett and Tingey (1990), ponderosa pine and aspen seedlings were exposed to three different exposure patterns of equal SUM00 over a 5-mo growing season (Table 5-11). One pattern simulated ambient conditions at high-elevation sites remote from urban influence. A second pattern (i.e., episodic) was representative of ambient conditions at low-elevation sites at rural or near-urban locations. A third pattern was artificial and had a diurnal pattern rising to a peak at 2 ppm, repeated daily for the length of the experimental period. Growth reductions in both ponderosa pine and aspen were

greatest in the episodic exposure pattern, which had the largest peak concentrations of the three patterns. The smallest growth reductions in both species were observed with the high-elevation pattern that had peak concentrations less than 0.10 ppm. The authors concluded that temporal pattern and concentration were important in influencing long-term growth response of tree seedlings, just as in crops, and, consequently, should be considered in measures of exposure.

When yield is considered, a number of exposure-dynamic factors, including concentration, temporal pattern, predisposition and respite times, as well as phenological stage of plant development, have been shown to influence the impact of O_3 on plant response. Evidence from studies of kidney bean (Musselman et al., 1983), alfalfa (Hogsett et al., 1985a), tobacco (Heagle et al., 1987), soybean (Heagle et al., 1986), ponderosa pine and aspen (Hogsett and Tingey, 1990) suggests that concentration and temporal variation of exposure are important factors in influencing biomass production and, consequently become considerations in measures of exposure. Because the SUM00 index weights all concentrations equally, the SUM00 is inadequate for characterizing plant exposure to O_3 (Lefohn et al., 1989). Other factors, including predisposition time (McCool et al., 1988) and crop development stage (Heagle et al., 1991), contribute to variations in biological response, which suggests the need for weighting O_3 concentrations to account for predisposition time and phenology. However, the roles of predisposition and phenology in influencing plant response vary with species and environmental conditions and are not understood well enough to allow specification of a weighting function for use in characterizing plant exposure.

5.5.2.3 Combinations of Years, Sites, or Species: Comparisons of Yield Losses with Different Exposure Durations

Duration has not been a focus in experimental designs of studies that applied two or more exposure regimes over the growing season. Several lines of evidence suggest that the ultimate yield depends upon the cumulative impact of repeated peak concentrations (U.S. Environmental Protection Agency, 1986, 1992) and that O_3-induced reductions in growth are linked to reduced photosynthesis, which is impaired by the cumulative O_3 exposure (Reich and Amundsen, 1985; Reich, 1987; Pye, 1988). In the Agency's reviews of the literature (U.S. Environmental Protection Agency, 1986, 1992), EPA concluded that, "When plant

yield is considered, the ultimate impact of an air pollutant on yield depends on the integrated impact of the pollutant exposures during the growth of the plant." As a measure of plant exposure, the appropriate index should differentiate between exposures of the same concentration but of different duration. For example, a mean index calculated over an unspecified time cannot accomplish this (Lefohn et al., 1988a; Hogsett et al., 1988; Tingey et al., 1989, 1991; U.S. Environmental Protection Agency, 1986, 1992).

The paper by Lefohn et al. (1988a), reviewed previously in U.S. EPA (1992) along with published criticisms and responses, was the first to fit a common response model to combined data from two replicate studies of unequal duration (71 and 36 days for the 1982 and 1983 wheat studies, respectively, conducted at Ithaca, NY) to specifically test the importance of duration in influencing plant response. Greater yield losses occurred in 1982 which can partially be attributed to the longer duration. Because the mean index ignores the length of the exposure period, the year-to-year variation in plant response was minimized by the use of several cumulative indices rather than the mean. Lefohn (1988) and Lefohn et al. (1988b) concluded that duration has value in explaining variation in plant response and that a cumulative-type index was preferred over a mean or peak index based on statistical fit.

When O_3 effects are the primary cause of variation in plant response, plants from replicate studies of varying duration showed greater reductions in yield or growth when exposed for the longer duration (Lee et al., 1991; Olszyk et al., 1993; Adaros et al., 1991a) (Table 5-12 Part A). Using NCLAN data for wheat, cotton, kidney bean, and potato (from Penn State) from replicate studies with markedly different exposure durations, Lee et al. (1991) showed that year-to-year variations in the magnitude of relative yield loss were minimized by the use of exposure indices that are cumulative and weight peak concentrations more than low concentrations, indicating that O_3 effects are cumulative (Figure 5-10). Olszyk et al. (1993), using the two NCLAN cotton studies summarized by Temple et al. (1985) and Lee et al. (1991), in addition to cotton studies replicated at four sites in California's San Joaquin Valley over two years, tested and compared various exposure indices (SIGMOID, SUM06, M7, and 2ndHDM) based on statistical fit of a common response model. A Weibull response model with variance components was fit to the combined data and used to test for a common response (Gumpertz and Rawlings, 1991, 1992; Gumpertz and Pantula, 1992). The likelihood ratio test of parallel exposure-response

TABLE 5-12. A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF PLANTS FOR TWO OR MORE REPLICATE STUDIES HAVING EQUAL TOTAL EXPOSURES AND EITHER VARYING DURATIONS (PART A) OR SIMILAR DURATIONS (PART B)

Part A Species	Facility[a]	Total No. of Plots	Duration	Concentration (ppm)/ Exposure (ppm-h)[b]	Variable	Effect[c]	Reference
Brassica napus L. var. napus cv. callypso	OTC in pots	'87: 18 '88: 24 '89: 16	'87: 05-13 to 08-10 (89) '88: 05-02 to 08-24 (113) '89: 05-08 to 08-01 (84)	'87: M24 (M8) in ppb range from 5 (9) to 16 (43). '88: M24 (M8) in ppb range from 3 (5) to 16 (48). '89: M24 (M8) in ppb range from 6 (5) to 22 (62).	seed dry weight	'87: 27% reduction at M8=43 ppb (***). '88: 18% reduction at M8=48 ppb (***). '89: 11% reduction at M8=62 ppb (***).	Adaros et al. (1991c)
Gossypium Hirsutum L. cv. Acala SJ2	OTC	'81: 12 '82: 12	'81: 07-06 to 09-15 (72) '82: 06-04 to 09-09 (98)	'81: M7 (SUM06) range from 18 ppb (0 ppm-h) to 138 (68). '82: M7 (SUM06) range from 12 ppb (0 ppm-h) to 111 (71).	lint dry wt	45% and 66% reductions at M7=111 ppb. 57% and 60% reductions at SUM06=68 ppm-h.	Lee et al. (1991), Olszyk et al. (1993)
Hordeum vulgare L. cf. Arena and Alexis	OTC in pots	'88: 24 '89: 16	'88: 04-29 to 08-15 (108) '89: 05-08 to 08-15 (99)	'88: M8 (max 8-h mean) in ppb range from 5 (15) to 48 (89). '89: M8 (max 8-h mean) in ppb range from 11 (27) to 62 (101).	seed dry wt	Arena: 14% (*) and 6% (NS) reductions at M8=48 ppb. Alexis: No reductions at M8=48 ppb (NS).	Adaros et al. (1991b)
Phaseoulus vulgaris L. cv. Calif Dark Red Kidney Bean	OTC	'80: 20 '82: 20	'80: 08-20 to 09-10 (22) '82: 08-11 to 10-06 (57)	'80: M7 (SUM06) range from 24 ppb (0 ppm-h) to 139 (19). '82: M7 (SUM06) range from 19 ppb (0 ppm-h) to 110 (40).	seed dry wt	13% and 59% reductions at M7=110 ppb. 28% and 8% reductions at SUM06=19 ppm-h.	Lee et al. (1991)
Phaseolus vulgaris L. cf. Rintintin	OTC in pots	'88 I: 4 '88 II: 6 '89 III: 8	'88 I: 06-15 to 08-04 (51) '88 II: 07-24 to 08-29 (37) '89 III: 06-04 to 07-25 (52)	I. M8 (Max) in ppb range from 3 (19) to 48 (70). II. M8 (Max) in ppb range from 2 (19) to 50 (105). III. M8 (Max) in ppb range from 6 (26) to 109 (159).	pod dry weight	I. 2% reduction at M8=48 ppb (NS). II. 0% reduction at M8=50 ppb (NS). III. 0% (NS) and 47% (*) reductions at M8=50 and 109 ppb.	Bender et al. (1990)
Solanum Tuberosum L. cv. Norchip	OTC	'85: 15 '86: 39	'85: 06-14 to 08-22 (70) '86: 06-20 to 08-20 (62)	'85: M7 (SUM06) range from 22 ppb (0 ppm-h) to 85 (47). '86: M7 (SUM06) range from 24 ppb (0 ppm-h) to 88 (38).	tuber weight	42% and 25% reductions at M7=85 ppb. 32% and 27% reductions at 12-H SUM06=38 ppm-h.	Lee et al. (1991)
Triticum aestivum L., cv. Vona	OTC	'82: 20 '83: 12	'82: 05-18 to 07-17 (61) '83: 06-12 to 07-17 (36)	'82: M7 (SUM08) range from 21 ppb (0 ppm-h) to 95 (40). '83: M7 (SUM08) range from 26 ppb (0 ppm-h) to 96 (21).	seed dry wt	74% and 49% reductions at M7=95 ppb. 49% and 62% reductions at SUM08=21 ppm-h. 55% and 60% reductions at 7-h SUM06=22 ppm-h.	Lefohn et al. (1988), Lee et al. (1991)

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TABLE 5-12 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF PLANTS FOR TWO OR MORE REPLICATE STUDIES HAVING EQUAL TOTAL EXPOSURES AND EITHER VARYING DURATIONS (PART A) OR SIMILAR DURATIONS (PART B)

Part A Species	Facility[a]	Total No. of Plots	Duration	Concentration (ppm)/ Exposure (ppm-h)[b]	Variable	Effect[c]	Reference
Triticum aestivum L., cv. Star and Turbo	OTC in pots	'88: 6 '89: 10	'88: 04-27 to 08-23 (118) '89: 05-09 to 08-15 (98)	'88: M8 (Max,SUM06) in ppb range from 4 (58,0) to 51 (106,8.2). '89: M8 (Max,SUM06) in ppb range from 10 (34,0) to 113 (162,87).	seed dry wt	Star: 20% (*) and 9% (NS) reductions at M8=51 ppb. Turbo: 25% (*) and 31% (*) reductions at M8=51 ppb.	Adaros et al. (1991a)
Triticum aestivum L., cv. Star and Turbo	OTC in pots	'88: 24 '89: 16	'88: 04-29 to 08-15 (108) '89: 05-08 to 08-15 (99)	'88: M8 (max 8-h mean) in ppb range from 5 (15) to 48 (89) '89: M8 (max 8-h mean) in ppb range from 11 (27) to 62 (101)	seed dry wt	Star: 26% (*) and 12% (*) reductions at M8=48 ppb. Turbo: 34% (*) and 17% (*) reductions at M8=48 ppb.	Adaros et al. (1991b)
Part B.							
Glycine max L. Merr. cv. Davis	OTC in pots	'77: 8 '78: 8	'77: 06-17 to 10-10 (116) '78: 06-28 to 10-21 (116)	'77: M7 (max) in ppb range from 27 (78) to 154 (277). '78: M7 (max) in ppb range from 28 (84) to 131 (241).	seed dry wt	47% and 37% reductions at M7=131 ppb.	Cure et al. (1986), Heagle et al. (1983)
Glycine max L. Merr. cv. Williams	OTC	'81: 31 '82: 31 '83: 31	'81: 07-20 to 09-22 (65) '82: 07-14 to 09-22 (71) '83: 07-23 to 09-23 (63)	'81: M7 in ppb range from 15 to 64. '82: M7 in ppb range from 17 to 99. '83: M7 in ppb range from 19 to 132.	bean dry weight	28%, 20%, and 32% reductions at M7=64 ppb. 43% and 41% reductions at M7=99 ppb in '82 and '83	Heggestad and Lesser (1990), Heggestad et al. (1988)
Medicago sativa L. cv. WL-514	OTC	'84: 30 '85: 30	'84: 03-16 to 10-10 (209) '85: 03-23 to 10-09 (201)	'84: M12 in ppb range from 16 to 109. '85: M12 in ppb range from 10 to 94.	top dry wt	29% (*) and 25% (*) reductions at M12=94 ppb.	Temple et al. (1988)
Pinus rigida Mill.	OTC in pots	Exp. 1: 4 Exp. 2: 4	Exp. 1: 13 weeks Exp. 2: 13 weeks	1: M8 in ppb range from 0 to 200 ppb (U). 2: M8 in ppb range from 0 to 200 ppb (U).	total dry wt	49% and 46% reductions at M8=200 ppb.	Schier et al. (1990)

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TABLE 5-12 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF PLANTS FOR TWO OR MORE REPLICATE STUDIES HAVING EQUAL TOTAL EXPOSURES AND EITHER VARYING DURATIONS (PART A) OR SIMILAR DURATIONS (PART B)

Part B Species	Facility[a]	Total No. of Plots	Duration	Concentration (ppm)/ Exposure (ppm-h)[b]	Variable	Effect[c]	Reference
Pinus taeda L.	GC in pots	'86: 15 '87: 15	'86: 09-15 to 12-04 (81) '87: 07-27 to 10-15 (81)	'86: SUM00 in ppm-h range from 0 to 99 (U). '87: SUM00 in ppm-h range from 0 to 99 (U).	total dry wt	43% and 28% reductions at SUM00=99 ppm-h averaged across all families. Individual families show similar reductions, e.g., 35% and 33% reductions at SUM00=99 ppm-h for family 5.56, 14% and 12% reductions at SUM00=99 ppm-h for family 1.68.	Shafer et al. (1993)
Picea rubens Sarg.	OTC in pots	'87: 12 '88: 12	'87: 05-30 to 12-15 (199) '88: 06-01 to 12-01 (184)	'87: SUM00 in ppm-h are 32, 61, 91 and 119. '87: SUM00 in ppm-h are 36, 70, 101 and 135.	total dry wt	0% (NS) reduction in biomass after 1st yr, 8% (*) reduction at SUM00=135 ppm-h after 2nd year of exposure	Alscher et al. (1989) Amundsen et al. (1991)
Pisum sativum L. cv. Puget	ZAPS	'86: 14 '87: 14	'86: last 58 days '86: last 52 days	M12 and D25 (# days with 1-h conc >25 ppb) used in simple linear regression	pea fresh wt	0% reductions at M12=100 ppb based on linear regression models	Runeckles et al. (1990)
Populus tremuloides Michx clones	OTC in pots	'88: 18 '89: 18	'88: 07-19 to 09-27 (71) '89: 07-20 to 09-20 (64)	'88: SUM00 in ppm-h are 5.0, 10.0, and 19.4 (U). '89: SUM00 in ppm-h are 7.7, 15.4, and 26.4 (U).	stem and leaf dry wts	36% (*) and 40% (*) reductions at SUM00=19.4 ppm-h.	Karnosky et al. (1992)
Triticum aestivum L., cv. Albis	OTC	'86: 12 '87: 16 '88: 16	'86: 05-06 to 07-31 (86) '87: 04-27 to 08-10 (92) '88: 05-04 to 08-01 (89)	'86: M24 (max) in ppb range from 12 (61) to 47 (181). '87: M24 (max) in ppb range from 12 (54) to 45 (175). '88: M24 (max) in ppb range from 17 (65) to 45 (148).	seed dry wt	'86: 61% reduction at M24=47 ppb. '87: 27% reduction at M24=45 ppb. '88: 65% reduction at M24=45 ppb.	Fuhrer et al. (1989)
Triticum aestivum L., cv. Albis	OTC	'89: 24 '90: 24	'89: 05-16 to 08-14 (91) '90: 05-14 to 08-09 (88)	'89: M7 (SUM06) range from 18 ppb (0 ppm-h) to 62 (3.8). '90: M7 (SUM06) range from 17 ppb (0 ppm-h) to 71 (5.6).	seed dry wt	29% and 22% reduction at M7=62 ppb. 29% and 17% reduction at SUM06=3.8 ppm-h.	Fuhrer et al. (1992)

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TABLE 5-12 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF PLANTS FOR TWO OR MORE REPLICATE STUDIES HAVING EQUAL TOTAL EXPOSURES AND EITHER VARYING DURATIONS (PART A) OR SIMILAR DURATIONS (PART B)

Part B Species	Facility[a]	Total No. of Plots	Duration	Concentration (ppm)/ Exposure (ppm-h)[b]	Variable	Effect[c]	Reference
Triticum aestivum L., cv. Severn, Potomac, Oasis, MD5518308	OTC	'84: 20 '85: 20	'84: 05-14 to 06-22 (40) '85: 05-06 to 06-15 (41)	'84: M4 (AOT03) in ppb (ppb-h) range from 32 (0) to 93 (10). '85: M4 (AOT03) in ppb (ppb-h) range from 30 (0) to 86 (9).	seed dry wt	31% (*) and 9% (NS) reductions at M4=86 ppb.	Slaughter et al. (1989)

[a]GC = controlled environmental growth chamber or CSTR, OTC= open-top chamber, ZAPS=zonal air pollution system.
[b]U = Uniform.
[c]* = significant at the 0.05 level, NS= not significant.

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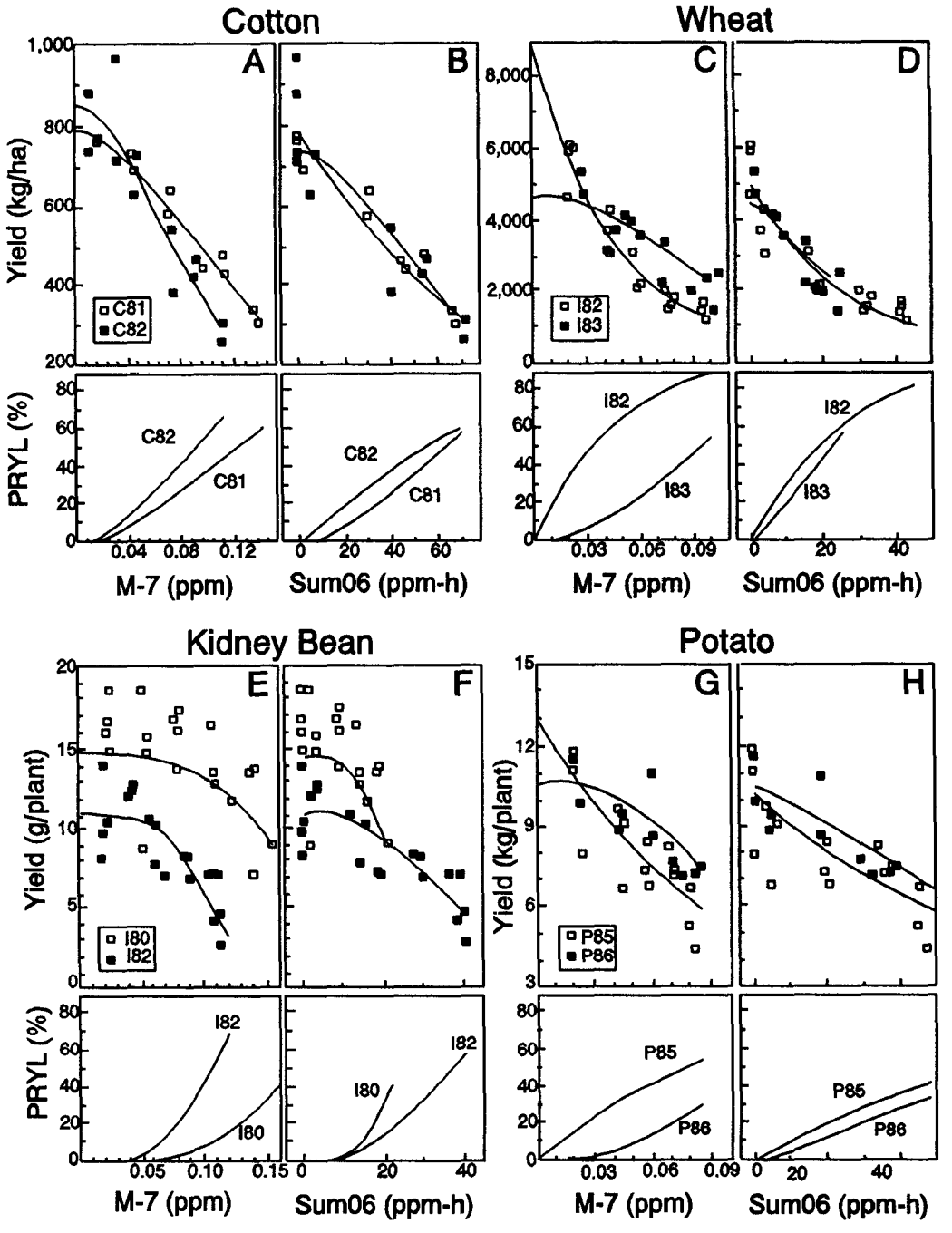

Figure 5-10. Comparison of the Weibull exposure-response functions and its predicted relative yield loss (PRYL) curves (relative to 0 ozone) using M-7 and daytime SUM06 for replicate years of National Crop Loss Assessment Network Program's data for (A) and (B) cotton (var. Acala SJ-2), (C) and (D) wheat (var. Vona), (E) and (F) kidney bean (var. California light red), and (G) and (H) potato (var. Norchip), respectively. Mean dry weights and the Weibull exposure-response functions for replicate studies are given in the top portion of the graphs (Lee et al., 1991).

curves was statistically significant for M7 and 2ndHDM for at least one set of cotton data, indicating significant differences in the magnitude of response across years and/or sites. On the other hand, the SIGMOID and SUM06 indices resulted in consistent patterns of response for both sets of cotton data, as well as between sets of cotton data (Figure 5-11). The authors concluded that the peak-weighted, cumulative indices minimized the temporal and spatial variations in crop yield and better predicted cotton yield responses than the M7 or 2ndHDM indices. The mean and peak indices did not differentiate between exposure seasons of differing duration and could not account for year-to-year differences in response.

The results of European studies with wheat (Adaros et al., 1991a,b), spring rape (Adaros et al., 1991c), barley (Adaros et al., 1991b) and kidney beans (Bender et al., 1990), using data from replicate studies with varying duration, are less conclusive as to the role of duration in determining plant response (Table 5-12 Part A). Exposures are reported using a mean index. Adaros et al. (1991a) showed a greater reduction in above ground dry weight when exposed for the longer duration for wheat cultivar, Star, but not for cultivar, Turbo (Figure 5-12). Adaros et al. (1991b), in another two-year study with barley (cv. Arena and Alexis) and wheat (cv. Star and Turbo) involving mixtures of O_3, SO_2, and NO_2, showed greater reductions in yield when exposed for the longer duration for all species and cultivars except barley cv. Alexis (Table 5-12 Part A). Ozone effects were insignificant in both years for barley cv. Alexis. The authors did not attribute the differential response in growth and yield to any single factor but the data suggested that O_3 effects are cumulative. When O_3 exposure is the primary source of response, the mean exposure index of unspecified duration could not account for the year-to-year variation in response.

The role of duration in influencing growth or yield is unclear for the other studies because of the following limitations in the data:

1. Treatment levels were below the levels to induce injury or damage to kidney bean plants in two of the three years. None of the years produced a significant O_3 effect at or below 70 ppb concentration (Bender et al., 1990). Similarly, the study with barley showed no significant O_3 effects.

2. Differences in growing conditions and varying kinds of interactions between O_3, SO_2, and NO_2 resulted in different sizes of control plants of spring rape over years and affected the magnitude of response to O_3.

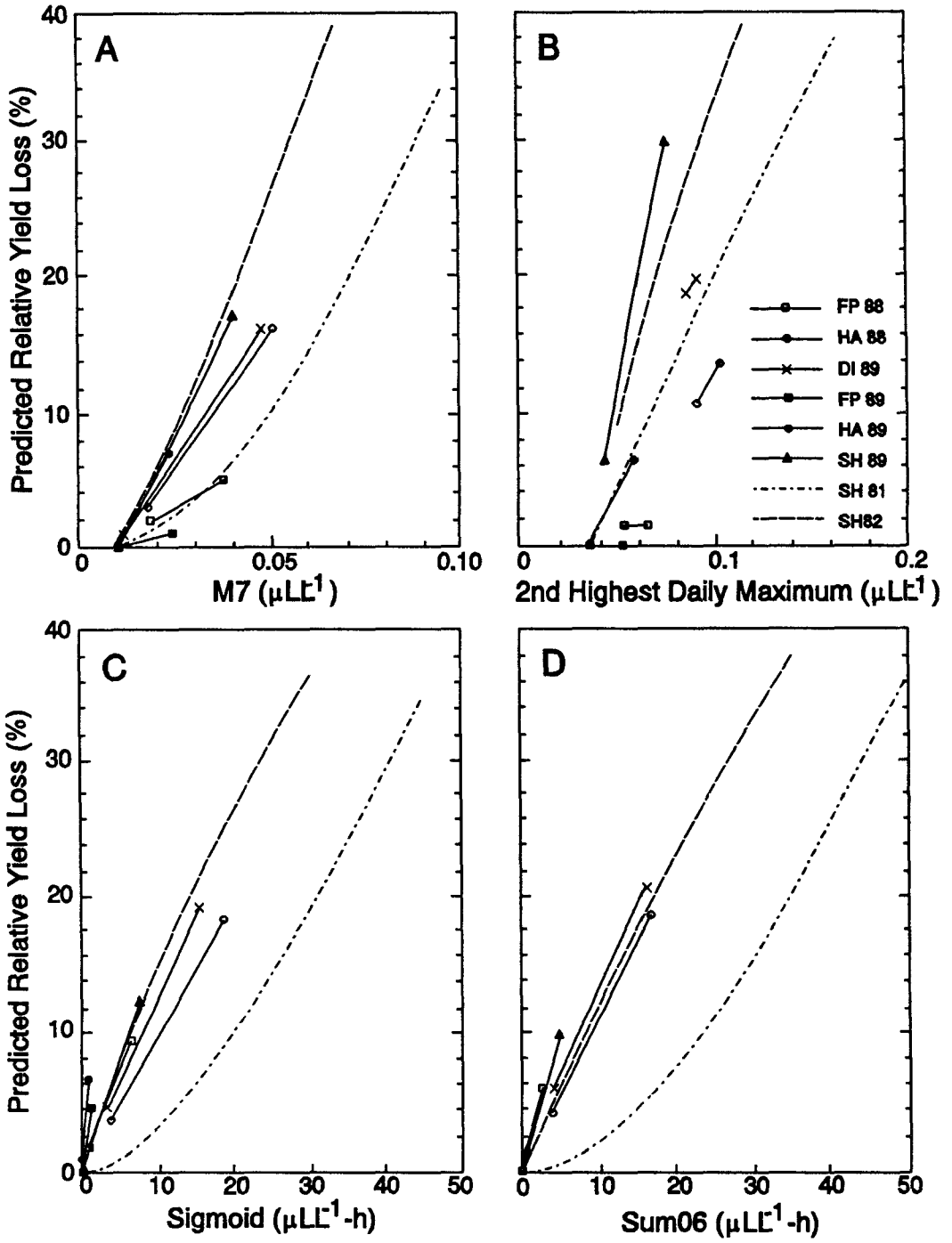

Figure 5-11. Predicted relative yield losses (lint weight) for Acala SJ-2 cotton for four sites and multiple years (1981, 1982, 1988, 1989) relative to 0.10 ppm for M7, 0.035 ppm for 2ndHDM, 0 ppm-h for SIGMOID, and 0 ppm-h for SUM06, which correspond to typical levels in the CF chambers. Predicted losses are based on M7 (A), 2ndHDM (B), SIGMOID (C), and SUM06 (D) exposure indices. Abbreviations: DI=Dinuba, FP=Five Point, HA=Hanford, SH=Shafter (Olszyk et al., 1993).

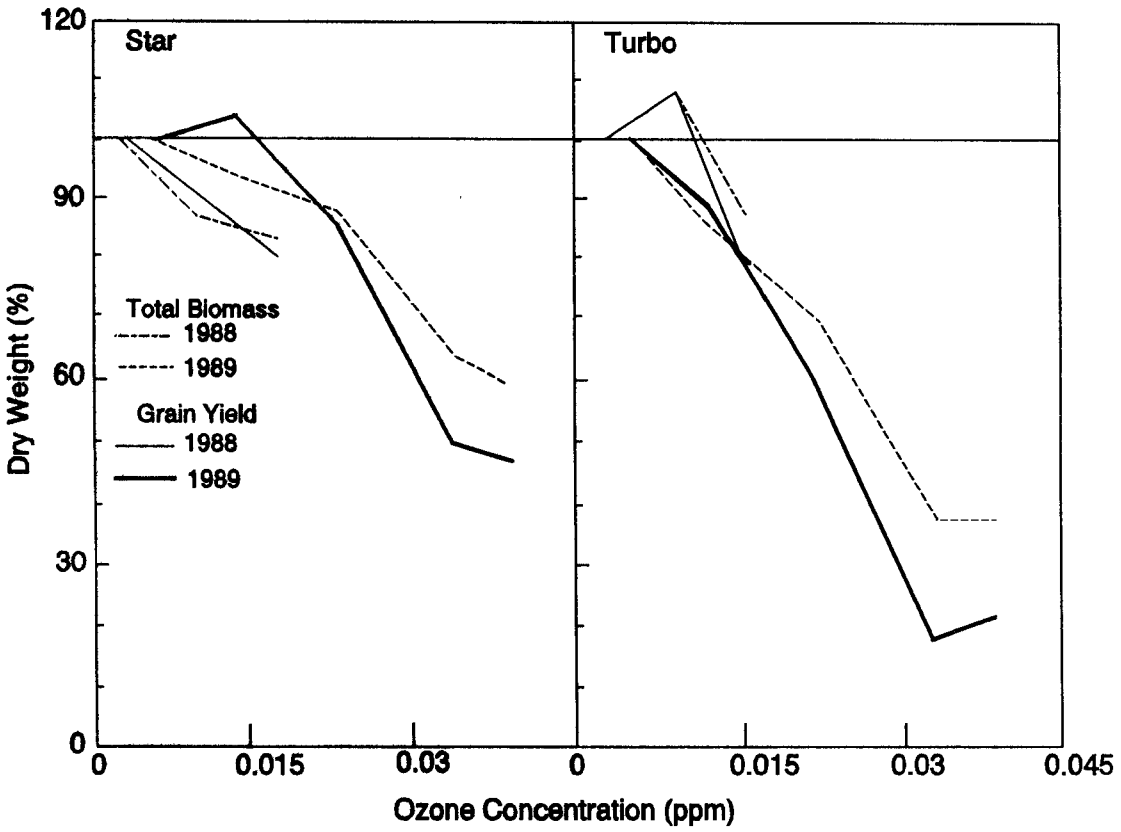

Figure 5-12. Relative effect of ozone on growth and yield of spring wheat cultivars (var. Star and Turbo) from two growing seasons (Adaros et al., 1991a).

Compared to 1987, yield of control plants increased by 32% in 1988 and by 94% in 1989 (Adaros et al., 1991c). Consequently, the evidence of duration as the primary cause of differences in response over years was difficult to substantiate.

When durations were nearly equal, plant response to O_3 were similar for 2- or 3-year studies with alfalfa (Temple et al., 1988), pea (Runeckles et al., 1990), soybean (Heagle et al., 1983; Heggestad and Lesser, 1990; Cure et al., 1986), wheat (Fuhrer et al., 1989, 1992), aspen clones (Karnosky et al., 1992), loblolly pine (Shafer et al., 1993), and pitch pine (Schier et al., 1990) (Table 5-12 Part B). For example, year-to-year variations in wheat yield response to O_3 were small for the three years having durations between 86 and 92 days to allow pooling of the data to fit a common Weibull model using Rawling's solar-radiation

weighted mean index (Fuhrer et al., 1989) (Figure 5-13). Different growing conditions were reported in a number of studies (Shafer et al., 1993; Fuhrer et al., 1989) but found no interaction between O_3 and climatic effects. On the other hand, Slaughter et al. (1989) reported reductions in wheat grain yield of 69% and 9% in a two-year study having equal durations, which the authors attribute to differences in rainfall and temperature. Environmental conditions in 1985 favored greater photosynthate partitioning for grain development rather than for vegetative growth, resulting in larger plants in 1985. Air pollution effects may not have been the primary source of variation in response and, consequently, the data are unable to substantiate the role of duration in influencing response.

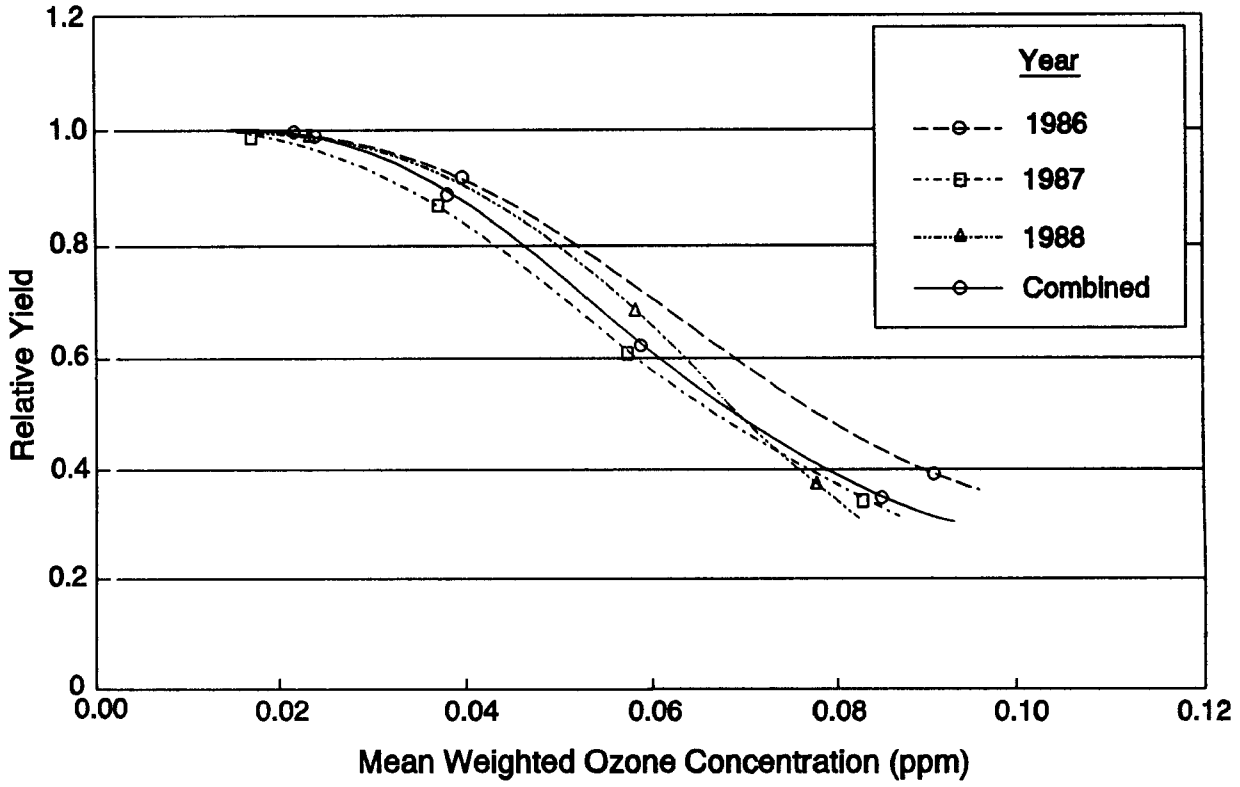

Figure 5-13. Weibull exposure-response curves for the relative effect of ozone on grain yield of spring wheat for three years, individually and combined (Fuhrer et al., 1989).

These studies report plant response as a function of a mean exposure index and do not evaluate or compare various exposure indices based on statistical fit. In a series of three papers that examined the response of spring wheat to O_3 at higher elevations, Grimm and Fuhrer (1992a,b) and Fuhrer et al. (1992) conducted a 2-year study in which the flux of O_3 was determined in open-top chambers. Plants were exposed to O_3 for periods lasting 44 and 50 days in 1989 and 1990, respectively and flux measurements were taken repeatedly over the experimental period. In addition to O_3 flux, exposures were characterized using M7, M24, SUM06, and the solar radiation-weighted mean index (Rawlings et al., 1988). The quadratic response curves relating the various indices with grain yield showed year-to-year variations were minimized using the mean O_3 flux index (Figure 5-14). The other three exposure indices showed slightly greater yield losses in 1989 than in 1990, in contrast with longer exposure in 1990 and drier conditions in 1989. The authors concluded that the O_3 flux related well with yield because the mean flux incorporated environmental factors, canopy structure, and physiological processes, which affected the uptake of O_3 from the air to the leaf interior. The measures of ambient condition ignored these factors and consequently, were unable to account for all of the year-to-year variability in wheat response. The authors suggested that O_3 flux was a surrogate of Fowler and Cape's (1982) "pollutant absorbed dose" and appeared to be the relevant measure for use in relating exposure and plant response.

Alscher et al. (1989) and Amundson et al. (1991) report on the impact of O_3 on growth, injury, and biomass response of 2-year-old red spruce seedlings after 1 and 2 years of exposure, respectively. Exposures were characterized using the M12 (or M7), M24, and SUM00 indices. No significant O_3 effects on biomass were detected in 1987 (Alscher et al., 1989) because stomatal conductances in red spruce are inherently low and, consequently, result in low rates of pollutant uptake (Seiler and Cazell, 1990). However, in the second year, O_3 reduced leaf and root starch, increased foliar antioxidant content, and reduced biomass of 1988 fixed-growth foliage. However, O_3 effects on biomass were slight in the second year. The authors concluded O_3 effects are cumulative because the onset of damage occurred in the second year rather than the first year of exposure.

When the concentrations are above the levels in which injury and damage occur, plant response is influenced by exposure duration. The results of these studies are in general

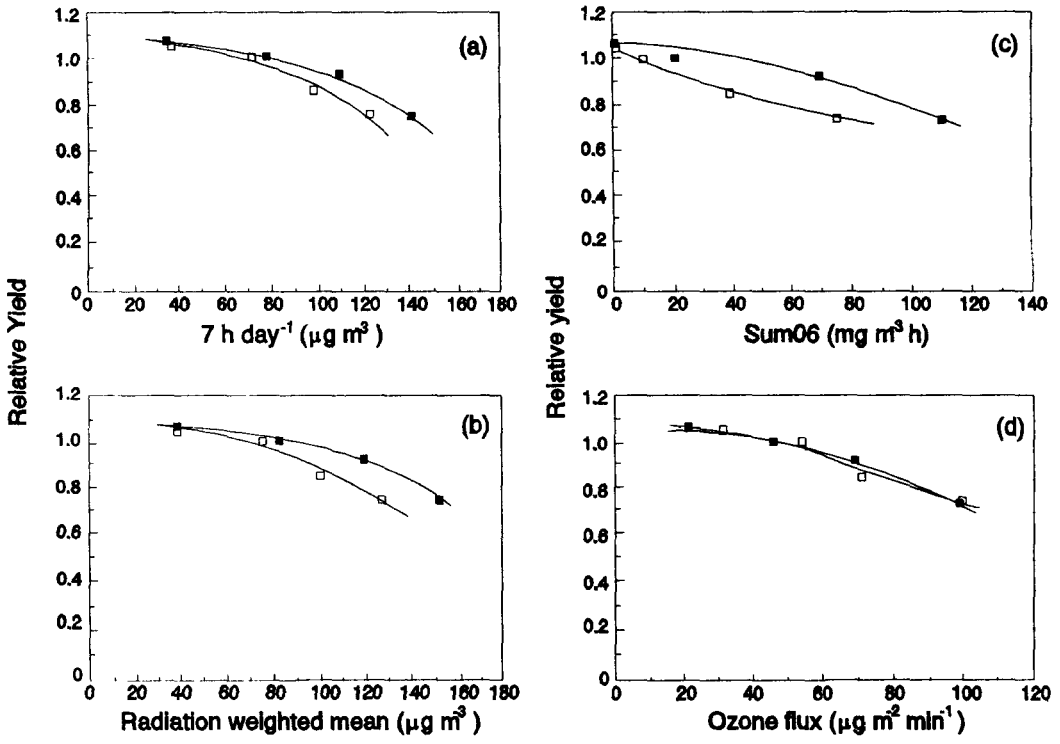

Figure 5-14. Quadratic exposure-response curves for the relative effect of ozone on grain yield of spring wheat in 1989 and 1990 using four different exposure indices (a-d) (Fuhrer et al., 1992).

agreement that O_3 effects are cumulative and the ultimate impact of long-term exposures to O_3 on crops and seedling biomass response depends on the integration of repeated peak concentrations during the growth of the plant. Consequently, the mean or peak indices are inappropriate since the length of exposure is unspecified and these indices cannot differentiate among exposures of the same concentration but varying in duration. These results support the conclusion that an appropriate O_3 index should cumulate hourly concentrations in some fashion to reflect the nature of O_3 on plant response. Fuhrer et al. (1992) suggested that the weighting function should reflect the relationship between ambient condition and internal O_3 flux, consistent with the mode of action of O_3 on plants and with earlier findings that peak-weighted, cumulative indices give better predictions of plant response than mean or peak indices.

5.5.2.4 Comparisons of Measures of Exposure Based on Reanalysis of Single-Year, Single-Species Studies

Studies cited in previous sections focused on the role of the structure of exposure in influencing plant response but do not specifically identify the weighting function for use in characterizing plant exposure to O_3. In addition to these types of studies, other studies have focused on comparison of measures of exposure based on reanalysis of single-year, single species studies. The variety of statistical approaches used to relate exposure and plant response range from informal description of the distributions of O_3 concentrations associated with response to more formal regression-based procedures.

The regression approach is designed to select those exposure indices that properly order and space the treatment means along the horizontal axis to optimize the fit of a linear or curvilinear model. However, because the experimental designs are not designed to evaluate various indices, the power of the regression approach to identify the important exposure-dynamic factors influencing plant response is less than desirable (Lefohn et al., 1992a). Consequently, these retrospective studies provide less substantiating evidence of the role of exposure-dynamic factors (e.g., concentration, duration, temporal pattern, and respite time) than those studies with experimental designs and analyses that focus on specific components of exposure.

Most of the early retrospective studies reporting regression results using data from the NCLAN program and/or from Corvallis, Oregon (Lee et al., 1987, 1988; Lefohn et al., 1988a: Tingey et al., 1989) or using data collected by Oshima (U.S. Environmental Protection Agency, 1986; Musselman et al., 1988) were in general agreement and consistently favored the use of cumulative peak-weighted exposure indices. These studies have been previously reviewed by the Agency (U.S. Environmental Protection Agency, 1992). Lee et al. (1987) suggested that exposure indices that included all the data (24 h) performed better than those that used only 7 h of data; this is consistent with the conclusions of Heagle et al. (1987) that found plants receiving exposures for an additional 5 h/day showed 10% greater yield loss than those exposed for 7-h/day. In a subsequent analysis using more of the NCLAN data, Lee et al. (1988) found the "best" exposure index was a general phenologically weighted, cumulative-impact index (GPWCI) with sigmoid weighting on concentration and a gamma weighting function as surrogate of time of increased plant sensitivity to O_3. For most cases, Lee et al. (1987) computed their exposure indices based

on the daylight exposure periods used by the NCLAN investigators. The exposure indices with minimum RSS were those indices that (1) cumulated hourly O_3 concentrations over the growth of the plant, (2) gave preferential weighting to peak concentrations, and (3) phenologically weighted the exposures to emphasize concentrations during the plant growth stage. The paper by Tingey et al. (1989) is a summarization of the results in Lee et al. (1988) and shows the limitations of the mean index.

Lefohn and Foley (1992) characterized the NCLAN exposures that had a SUM06 level closest to those that predicted a 20% yield loss, using the exposure-response equations as reported in Lee et al. (1991) and Tingey et al. (1991). Lefohn and Foley (1992) characterized the hourly average concentrations using percentiles, HRS06, HRS10, SUM06, and W126 for each of 22 NCLAN studies. The authors noted that the frequent occurrence in many cases of high hourly concentrations ($\geq$0.10 ppm) may have been partly responsible for the 20% yield loss. The number of hourly average concentrations ranged from 0 to 515 with only one of the 22 NCLAN experiments experiencing no hourly average concentrations $\geq$0.10 ppm, while the remaining experiments experienced multiple occurrences $\geq$0.10 ppm. The repeated occurrences of high hourly average concentrations were a result of the NCLAN protocol (Table 5-13). As a result of their analysis, Lefohn and Foley (1992) and Lefohn et al. (1992b) stressed that because the NCLAN experiments contained peak hourly average concentrations, it is important that any index selected to characterize those regimes responsible for growth reduction adequately capture the presence of these peak concentrations when attempting to predict biological responses using actual ambient air quality data.

For example, Tingey et al. (1991), using mostly NCLAN data, identified 24.4 ppm-h as the SUM06 value, calculated over a 3-mo period, that would protect 50% of the NCLAN crops analyzed at the 10% yield reduction level. There are monitoring sites in the United States that experience 3-mo cumulative SUM06 values greater than 24.4 ppm-h, but do not experience frequent occurrences of hourly average concentrations > 0.10 ppm. For example, 24% (1987), 10% (1988), 30% (1989), 25% (1990), and 31% (1991) of the rural agricultural sites listed in the U.S. EPA AIRS database experienced 3-mo cumulative SUM06 values greater than 24.4 ppm-h, but experienced fewer than 11 hourly average concentrations equal to or greater than 0.10 ppm. Lefohn and Foley (1992) noted that agricultural crops grown at a site experiencing a 3-mo cumulative SUM06 value greater than 24.4 ppm-h, but

TABLE 5-13. SUMMARY OF OZONE EXPOSURES THAT ARE CLOSEST TO THOSE PREDICTED FOR 20% YIELD REDUCTION PER SUM06 EXPOSURE RESPONSE MODELS USED BY LEE ET AL. (1991) IN SELECTED NCLAN EXPERIMENTS (ppm)

Experiment	Chamber	Min.	Percentiles 10	30	50	70	90	95	99	Max	Number of Obs.	Number of Occurrences ≥0.06	≥0.08	≥0.10	SUM 06 (ppm-h)	SUM 08 (ppm-h)	W126 (ppm-h)
A80S0 - Corsoy	NF+0.03-1	0.000	0.000	0.011	0.026	0.045	0.077	0.090	0.111	0.123	1,344	263	113	35	21.1	10.7	17.7
A83SO - Amsoy	NF+0.03-1	0.000	0.001	0.014	0.028	0.049	0.083	0.098	0.123	0.168	1,992	467	223	90	39.16	22.1	33.2
A83SO - Corsoy	NF+0.03-1	0.000	0.001	0.014	0.028	0.049	0.083	0.098	0.123	0.168	1,992	467	223	90	39.1	22.1	33.2
A85SO - Corsoy_79 D	NFx2.00-1D	0.000	0.000	0.008	0.023	0.051	0.110	0.129	0.160	0.194	2,352	657	495	319	67.5	56.2	63.0
A85SO - Corsoy_79 W	NFx2.00-1W	0.000	0.000	0.011	0.026	0.063	0.114	0.134	0.162	0.199	2,352	729	547	358	75.1	62.5	70.0
A86SO - Corsoy_79 D	NFx2.5-1D	0.000	0.002	0.016	0.035	0.085	0.137	0.161	0.207	0.279	2,040	784	654	515	92.1	83.2	88.6
A86SO - Corsoy_79 W	NFx2.0-1W	0.000	0.002	0.015	0.033	0.065	0.105	0.124	0.161	0.242	2,040	719	510	271	69.6	55.1	63.7
B83SO - Corsoy_79 D	NF-1D	0.000	0.002	0.006	0.018	0.037	0.063	0.074	0.087	0.111	1,512	184	51	5	13.5	4.4	10.6
B83SO - Corsoy_79 W	NF+0.03-1W	0.000	0.002	0.006	0.019	0.049	0.084	0.097	0.118	0.135	1,512	359	198	70	30.1	18.9	25.8
B83SO - Williams D	NF+0.03-1D	0.000	0.002	0.006	0.019	0.049	0.084	0.098	0.118	0.137	1,512	364	204	66	30.5	19.5	26.0
B83SO - Williams W	NF+0.03-1W	0.000	0.002	0.006	0.019	0.049	0.084	0.097	0.118	0.135	1,512	359	198	70	30.1	18.9	25.8
I81SO - Hodgson	NF+0.06-1	0.000	0.004	0.007	0.015	0.031	0.083	0.090	0.105	0.132	1,680	323	191	29	26.7	17.4	22.9
R81SO - Davis	NF-1	0.000	0.003	0.015	0.026	0.043	0.066	0.075	0.088	0.145	2,664	421	79	6	30.2	7.0	2.6
R82SO - Davis	NF+0.02-1	0.000	0.001	0.013	0.026	0.047	0.080	0.091	0.123	0.203	2,160	471	218	56	39.0	21.4	33.1
R83SO - Davis Dry	NF+0.02-1D	0.000	0.002	0.015	0.030	0.055	0.089	0.104	0.126	0.155	2,640	721	378	163	61.6	37.7	53.1
R83SO - Davis Wet	NF+0.02-1W	0.000	0.002	0.015	0.030	0.054	0.087	0.101	0.119	0.138	2,640	698	359	140	58.7	35.0	50.7
R84SO - Davis Dry	NF+0.015-1D	0.000	0.006	0.018	0.030	0.047	0.077	0.089	0.113	0.140	2,496	512	208	59	41.2	19.9	34.8
R84SO - Davis Wet	NF+0.015-1W	0.000	0.006	0.018	0.029	0.046	0.075	0.089	0.110	0.159	2,496	486	193	62	38.9	18.6	32.6
R86SO - Young Dry	NFx1.3-1D	0.000	0.003	0.013	0.024	0.047	0.089	0.107	0.137	0.206	2,568	597	345	175	53.7	36.2	47.7
R86SO - Young Wet	NFx1.3-1W	0.000	0.003	0.013	0.023	0.046	0.087	0.101	0.129	0.198	2,568	573	323	136	50.2	32.8	44.1
SORGHUM																	
A82SG - Dekalb	NF+0.10-1	0.000	0.001	0.010	0.023	0.055	0.145	0.160	0.185	0.223	2,040	599	557	516	79.1	76.3	78.2
WHEAT																	
A82WH - Abe	NF+0.03-1	0.000	0.002	0.015	0.027	0.047	0.079	0.094	0.113	0.149	1,344	300	130	43	24.1	12.5	19.8
A82WH - Arthur_71	NF+0.06-1	0.000	0.002	0.015	0.027	0.053	0.109	0.121	0.144	0.170	1,344	373	293	186	37.4	31.8	35.3

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TABLE 5-13 (cont'd). SUMMARY OF OZONE EXPOSURES THAT ARE CLOSEST TO THOSE PREDICTED FOR 20% YIELD REDUCTION PER SUM06 EXPOSURE RESPONSE MODELS USED BY LEE ET AL. (1991) IN SELECTED NCLAN EXPERIMENTS (ppm)

Experiment	Chamber	Min.	10	30	50	70	90	95	99	Max	Number of Obs.	Number of Occurrences ≥0.06	≥0.08	≥0.10	SUM 06 (ppm-h)	SUM 08 (ppm-h)	W126 (ppm-h)
						Percentiles											
A83WH - Arthur_71	NF+0.06-1	0.000	0.004	0.019	0.032	0.054	0.108	0.123	0.159	0.186	1,296	365	295	186	37.4	32.5	35.6
BTI82WH - VONA	NF-1	0.000	0.011	0.025	0.034	0.042	0.057	0.064	0.072	0.098	1,464	114	2	0	7.6	0.2	6.2
BTI83WH - VONA	NF-1	0.000	0.006	0.021	0.036	0.049	0.071	0.083	0.097	0.116	864	165	51	4	12.4	4.7	9.8
CORN																	
A81MA - PAG 397	NF+0.06-2	0.000	0.000	0.008	0.020	0.052	0.111	0.126	0.150	0.187	1,968	552	461	306	57.5	51.0	55.1
A81MA - Pioneer	NF+0.06-2	0.000	0.000	0.008	0.020	0.052	0.111	0.126	0.150	0.187	1,968	552	461	306	57.5	51.0	55.1
COTTON																	
R82CO - Stoneville	NF-1	0.000	0.003	0.018	0.029	0.044	0.065	0.074	0.087	0.152	2,856	390	64	7	28.2	5.8	22.7
R85CO (McNair) Dry	NFx1.99-1D	0.000	0.003	0.012	0.024	0.052	0.117	0.154	0.221	0.291	3,000	810	609	407	92.9	78.9	88.2
R85CO (McNair) Wet	NFx1.33-1W	0.000	0.003	0.012	0.024	0.041	0.073	0.091	0.129	0.166	3,000	487	226	118	41.4	23.5	35.9
PEANUT																	
R80PN - NC-6	NF+0.015-1	0.000	0.004	0.017	0.029	0.043	0.066	0.076	0.091	0.112	2,688	369	101	5	27.2	8.8	22.0
TOBACCO																	
R83TO - McNair 944	NF+0.020-1	0.000	0.003	0.018	0.037	0.061	0.089	0.104	0.121	0.155	1,968	611	288	117	50.7	28.4	42.6

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with infrequent high hourly average concentrations (e.g., ≥0.10 ppm), might experience less yield reduction than predicted using NCLAN experimental results. For rural forest sites, 21% (1987), 23% (1988), 54% (1989), 50% (1990), and 52% (1991) of the sites exhibited 3-mo cumulative SUM06 values greater than 24.4 ppm-h, but fewer than 11 hourly average concentrations equal to or greater than 0.10 ppm. Tables 5-14 and 5-15 illustrate that sites that experience 3-mo, SUM06 values ≥24.4 ppm do not necessarily have peaks, whereas sites that experience values <24.4 ppm-h do have peaks.

Krupa et al. (1993) tested the importance of ambient O_3 frequency distributions in eliciting a response based on comparisons of non-filtered (NF) and charcoal-filtered (CF) treatments using the NCLAN data. Eight cases where yields in NF were significantly lower than CF were matched with corresponding cases where the yields in CF and NF were not significantly different. The frequency distributions of NF treatments resulting in significant yield loss had a greater proportion of concentrations >50 ppb than those of NF treatments resulting in no significant yield loss, indicating that these intermediate concentrations may contribute to determining the magnitude of response. The authors conclude that concentrations between 50 and 87 ppb are more important than concentrations >100 ppb in eliciting plant response. These conclusions are difficult to substantiate with the selected data because: (1) the NF treatments had few occurrences of concentrations >100 ppb, and consequently, the relative importance of peak concentrations >100 ppb cannot be reliably tested with any degree of statistical power; and (2) the selected cases showing no significant yield loss for NF do not closely match the cases showing significant yield loss for NF in terms of environmental conditions, soil and nutrient condition, exposure periods and durations, sites, species and cultivars, and harvests (for clover studies). Because these factors interact with O_3 effects in determining plant response, differences in these factors confound the comparison of frequency distributions between cases having significant and non-significant yield losses for NF. Another concern is the inconsistency of harvests for the two clover studies conducted at Raleigh, NC, in 1984 and 1985, which have six and seven harvests, respectively (Heagle et al., 1989), not 12 as reported by Krupa et al. (1993).

Reich (1987) reviewed 44 studies on 45 species to study the effects of O_3 on net photosynthesis (Pn) and growth of crops and tree species. Plants responded differently to equivalent total exposures (i.e., SUM00) when peak concentrations differed widely, with

TABLE 5-14. SUMMARY OF PERCENTILES FOR OZONE MONITORING SITES IN 1989 (APRIL THROUGH OCTOBER) WITH A MAXIMUM THREE-MONTH SUM06 VALUE <24.4 ppm-h BUT WITH SECOND HOURLY MAXIMUM CONCENTRATION ≥0.125 ppm

AIRS Site	Name	Min.	10	30	50	70	90	95	99	Max.	Maximum Uncorrected SUM06 (ppm-h)	Number of Observ. Over 7-mo Period
						Percentiles						
060010003	LIVERMORE,CA	.000	.000	.010	.030	.040	.050	.060	.090	.140	17.0	5,067
060371301	LYNWOOD,CA	.000	.000	.010	.020	.030	.050	.070	.100	.140	18.1	4,793
060374002	LONG BEACH, CA	.000	.010	.020	.020	.030	.050	.060	.080	.160	13.6	4,876
060375001	HAWTHORNE, CA	.000	.000	.020	.030	.040	.060	.060	.080	.190	18.1	4,894
060830008	SANTA BARBARA, CA	.000	.010	.020	.030	.040	.050	.060	.080	.190	17.1	4,823
060830010	SANTA BARBARA, CA	.000	.010	.020	.030	.040	.050	.060	.080	.220	13.3	4,663
060833001	SANTA BARBARA CO, CA	.000	.010	.020	.030	.040	.050	.060	.080	.140	12.3	5,077
090010113	BRIDGEPORT, CT	.000	.002	.011	.022	.033	.048	.059	.091	.156	16.5	4,865
090091123	NEW HAVEN, CT	.000	.003	.010	.019	.029	.045	.056	.091	.156	12.9	4,502
220191003	WESTLAKE, LA	.000	.003	.013	.022	.033	.052	.061	.082	.137	12.2	4,811
220330003	BATON ROUGE, LA	.000	.001	.009	.021	.034	.059	.069	.094	.168	17.4	4,964
220330004	BATON ROUGE, LA	.000	.002	.008	.016	.028	.047	.057	.078	.138	8.4	4,791
220331001	E BATON ROUGE, LA	.000	.003	.012	.022	.034	.056	.066	.092	.171	14.4	4,890
220470002	IBERVILLE PAR, LA	.000	.005	.014	.023	.034	.057	.068	.093	.149	15.9	5,040
220770001	NEW ROADS, LA	.000	.001	.011	.021	.033	.052	.062	.083	.141	12.0	4,964
230052003	CAPE ELIZABETH, ME	.001	.017	.027	.034	.042	.055	.064	.093	.146	16.7	4,627
471630009	KINGSPORT, TN	.001	.001	.005	.017	.032	.054	.062	.078	.125	13.4	4,252
481410027	EL PASO, TX	.000	.010	.020	.030	.040	.050	.060	.080	.260	14.9	4,484
481990002	KOUNTZE, TX	.000	.000	.010	.020	.030	.050	.060	.080	.130	10.6	4,630
482010024	HARRIS CO, TX	.000	.000	.010	.020	.030	.060	.070	.110	.230	19.2	4,728
482010062	HOUSTON, TX	.000	.000	.010	.020	.030	.050	.070	.110	.170	16.8	4,600
482011034	HOUSTON, TX	.000	.000	.010	.010	.030	.050	.060	.100	.220	14.0	4,595
482011037	HOUSTON, TX	.000	.000	.010	.010	.030	.050	.060	.110	.250	16.3	4,729
490350003	SALT LAKE CO, UT	.000	.001	.008	.029	.042	.056	.062	.083	.125	17.4	4,585
490353001	SALT LAKE CITY, UT	.000	.002	.014	.029	.041	.053	.061	.079	.140	13.0	4,544

TABLE 5-15. SUMMARY OF PERCENTILES FOR OZONE MONITORING SITES IN 1989 (APRIL THROUGH OCTOBER) WITH A MAXIMUM THREE-MONTH SUM06 VALUE ≥ 24.4 ppm-h BUT WITH SECOND HOURLY MAXIMUM CONCENTRATION <0.125 ppm

AIRS Site	Name	Min.	10	30	50	70	90	95	99	Max.	Maximum Uncorrected SUM06 (ppm-h)	Number of Observ. Over 7-mo Period
						Percentiles						
040132004	SCOTTSDALE, AZ	.000	.006	.018	.031	.045	.062	.071	.084	.107	31.7	5,070
060070002	CHICO, CA	.000	.010	.020	.030	.040	.060	.070	.080	.100	33.5	4,690
060170009	SOUTH LAKE TAHOE, CA	.000	.020	.030	.040	.050	.060	.070	.080	.100	44.8	4,768
060430004	YOSEMITE NP, CA	.000	.008	.022	.035	.049	.065	.072	.083	.111	37.6	4,853
060710006	SAN BERNARDINO CO, CA	.000	.020	.040	.050	.060	.070	.080	.090	.100	70.5	4,856
061011002	YUBA CITY, CA	.000	.000	.020	.030	.040	.060	.070	.080	.100	29.0	4,623
120094001	COCOA BEACH, FL	.002	.017	.024	.032	.042	.059	.068	.077	.094	28.7	5,012
170190004	CHAMPAIGN, IL	.000	.008	.020	.029	.039	.065	.072	.078	.088	32.0	5,091
170491001	EFFINGHAM CO, IL	.000	.009	.023	.036	.046	.063	.070	.081	.104	25.3	4,600
180970042	INDIANAPOLIS, IN	.001	.006	.021	.034	.046	.063	.072	.085	.103	25.4	4,592
240030014	ANNE ARUNDEL, MD	.000	.006	.021	.032	.045	.064	.073	.090	.120	25.5	4,360
240053001	ESSEX, MD	.000	.002	.010	.024	.038	.059	.069	.089	.121	25.2	5,028
310550032	OMAHA, NE	.002	.021	.030	.037	.047	.062	.067	.075	.098	24.9	4,160
350431001	SANDOVAL CO, NM	.000	.010	.020	.030	.040	.060	.060	.070	.090	25.1	5,059
360310002	ESSEX CO, NY	.016	.033	.042	.050	.056	.067	.073	.086	.106	45.6	4,070
370270003	LENOIR, NC	.000	.007	.019	.032	.045	.062	.067	.078	.092	25.8	4,806
370810011	GUILFORD CO, NC	.004	.010	.023	.034	.046	.063	.070	.083	.113	27.7	4,853
371470099	FARMVILLE, NC	.000	.010	.023	.034	.044	.062	.070	.083	.100	26.4	4,833
390030002	ALLEN CO, OH	.000	.007	.022	.032	.043	.060	.068	.086	.107	24.5	4,854
391510016	CANTON, OH	.000	.008	.019	.030	.042	.060	.070	.088	.110	26.3	4,875
420070003	NEW BRIGHTON, PA	.000	.008	.021	.032	.043	.062	.070	.087	.102	29.4	5,055
420770004	ALLENTOWN, PA	.000	.003	.016	.028	.039	.060	.070	.087	.102	25.1	5,040
470090101	SMOKY MT NP, TN	.000	.025	.036	.044	.053	.065	.070	.081	.098	35.9	4,764
510130020	ARLINGTON CO, VA	.000	.001	.010	.023	.037	.059	.071	.088	.116	25.7	5,029
510610002	FAUQUIER CO, VA	.000	.009	.021	.033	.045	.061	.069	.084	.122	24.6	5,050
511870002	SHEN NP (DKY RDG), VA	.004	.027	.037	.045	.054	.065	.071	.082	.100	59.0	4,454
550270001	HORICON, WI	.002	.019	.029	.037	.047	.062	.070	.088	.111	24.6	4,142
551390007	OSHKOSH, WI	.002	.016	.028	.038	.048	.063	.070	.084	.121	27.9	4,206

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greater loss of net photosynthesis (Pn) for increasing concentrations (Figure 5-15). Short-term, high concentrations above 0.40 ppm (e.g., 0.50 ppm for 8 h) caused rapid and significant reduction in Pn. Longer-term exposures for weeks to lower concentrations had a significant effect on Pn; the observed reductions were less severe than at the higher concentrations. Based on short-term, high concentration studies, SUM00 alone was an inadequate descriptor of exposure for predicting response. However, for assessing the effects of long-term, low concentrations typical of ambient condition, SUM00 may be adequate, as the response of field-grown plants to SUM00 was roughly linear. SUM00 explained much, although not all, of the variation in net photosynthesis and growth of conifers, hardwood trees, and agricultural crops (Figures 5-16 through 5-18). Unexplained variation can be attributed to biological variation, inherent experimental error, experimental conditions, and differences in O_3 uptake. Imputed O_3 uptake calculated as the product of SUM00 and mean diffusive conductance (ks) for each species better correlated with Pn and growth than SUM00.

Kickert and Krupa (1991) criticized Reich's findings on the basis of insufficient reporting of statistical model parameters, possible non-normality of Pn and growth variables, exclusion of ks terms for imputing O_3 uptake for each species, and with no implication for any individual plant species. However, Reich's synthesis of Pn and growth, using the SUM00 index, would not necessarily be invalidated by non-normality of the variables and provides evidence on the importance of peak concentrations and duration in eliciting a response. Reich's use of a mean diffusive conductance to impute O_3 uptake is questionable as leaf diffusive conductance measurements vary with time of day, season, and environmental condition. Consequently, numerous measurements of conductance are required to weight hourly O_3 concentrations to calculate O_3 uptake over the growth of a plant.

Pye (1988) reviewed 15 studies on 26 seedling species and found reductions in biomass response increased with SUM00 (Figure 5-19). Seasonal sum of hourly concentrations values ranged from 4 to 297 ppm-h. However, there was substantial variation in response. Pines, poplars, sycamore, ash, and maple are relatively sensitive. Both concentration and duration are important factors governing impact on growth and photosynthesis, but they probably are not equally important. The biomass data suggest a nonlinear response to

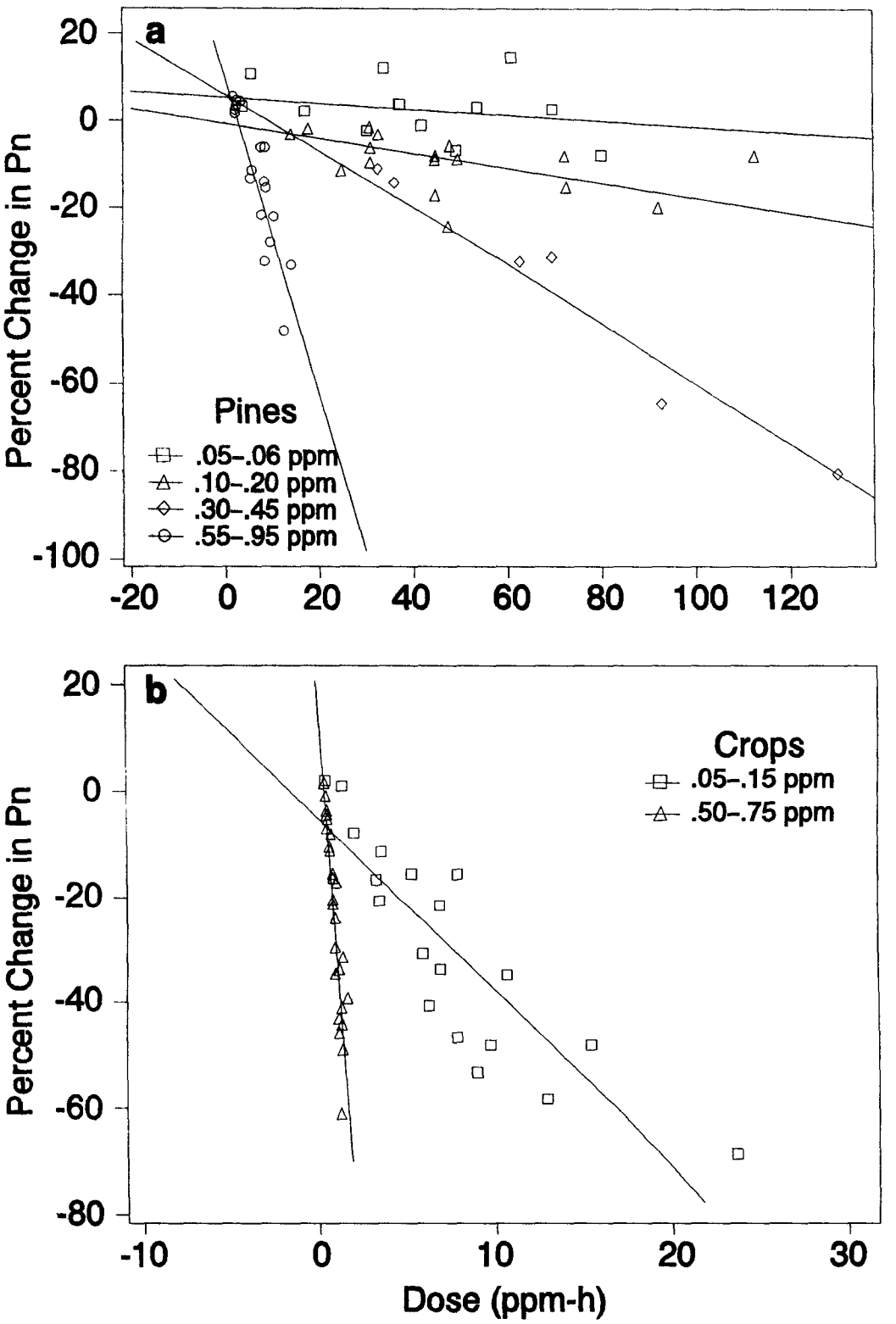

Figure 5-15. Percent reduction in net photosynthesis of (a) pines (including one point for red spruce) and (b) agricultural crops in relation to total ozone exposure (SUM00), for several ranges of peak concentrations (Reich, 1987).

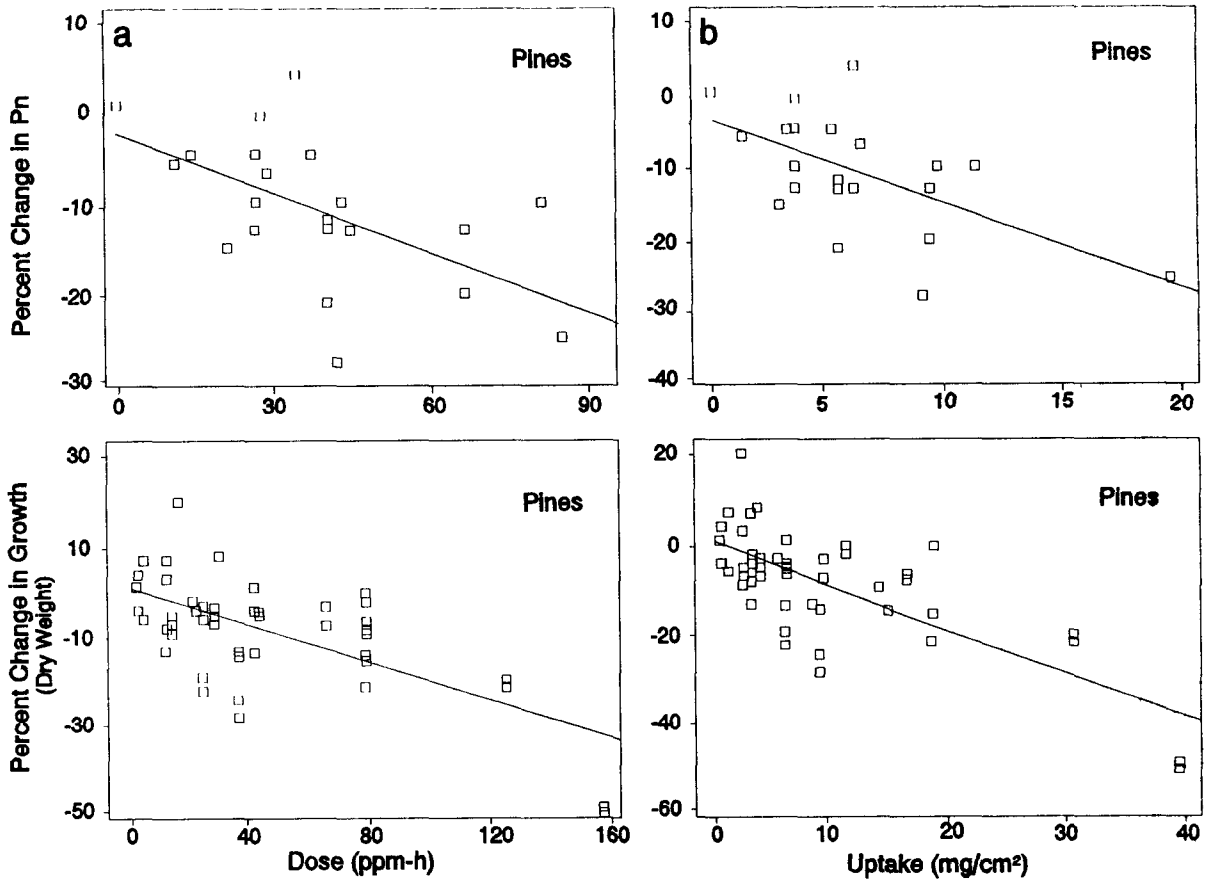

Figure 5-16. Percent reduction in net photosynthesis and biomass growth of coniferous species in relation to (a) total exposure (SUM00) and (b) estimated total ozone uptake (Reich, 1987).

fumigation and the presence of convexity of response implies that for similar mean O_3 exposures, damage will be greater when O_3 concentrations are more variable.

There is limited information for assessing the relative performance of exposure indices for relating to vegetation effects. Lefohn et al. (1992a) reported that it was not possible to differentiate among the SUM00, SUM06, W126, and SUM08 exposure indices because the indices were highly correlated with one another in the experiment (Figure 5-20). However, results based on biological experiments, reported by Musselman et al. (1983) and Hogsett et al. (1985a) have shown that different exposure regimes with similar SUM00 values resulted in those exposures experiencing capture peak concentrations exhibiting the greater effects. The authors demonstrated that plants exposed to variable concentrations showed

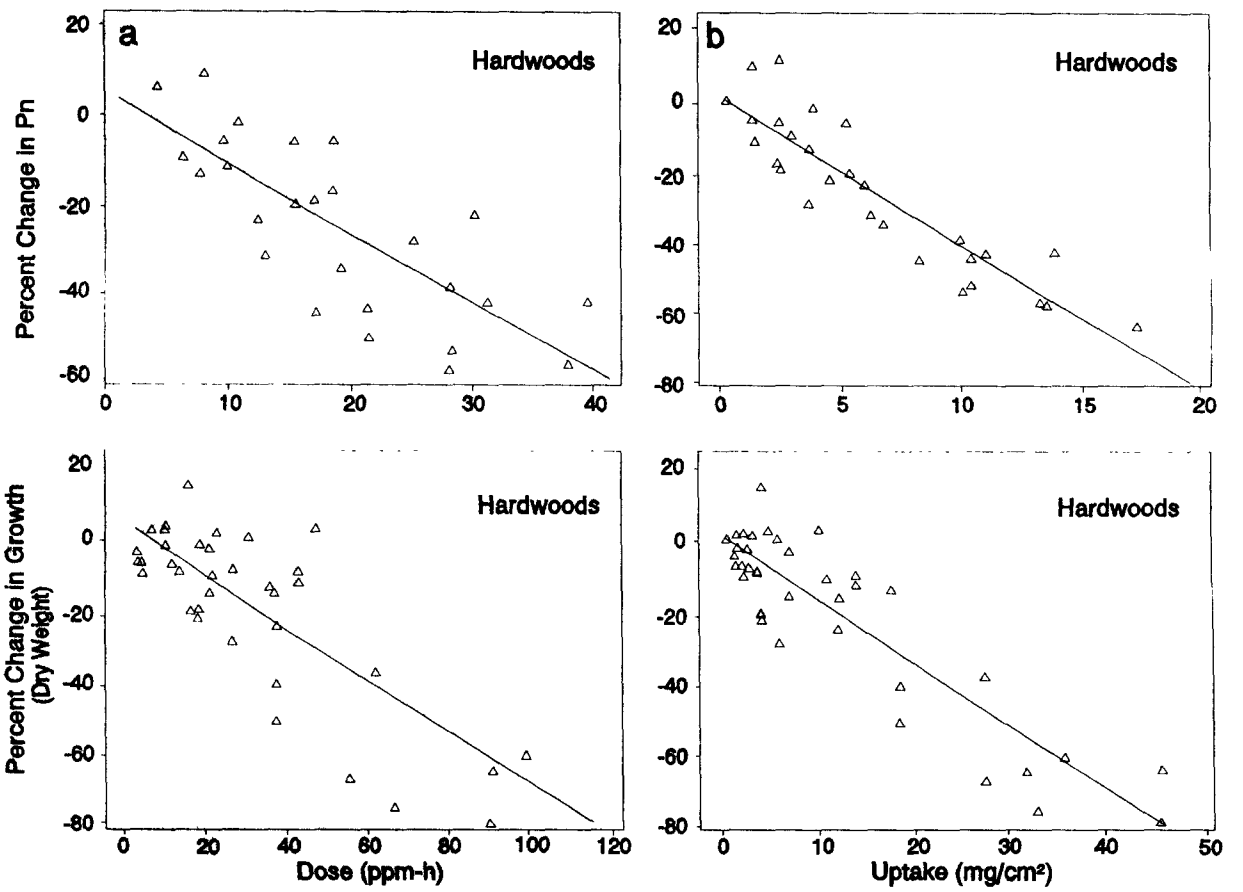

Figure 5-17. Percent reduction in net photosynthesis and biomass growth of hardwood species in relation to (a) total exposure (SUM00) and (b) estimated total ozone uptake (Reich, 1987).

greater effect on plant growth than those exposed to a fixed or daily peak concentration of equal SUM00 but lower peak concentrations.

Building upon the above cited results that biologically showed that the importance of the higher hourly average concentrations, Lefohn et al. (1989) concluded that the SUM00 index did not appear to perform adequately. Using air quality data, Lefohn et al. (1989) showed that the magnitude of the SUM00 exposure index was largely determined by the lower hourly average concentrations instead of the biologically relevant higher hourly average concentrations (Figure 5-21). Figure 5-21 illustrates that the slope of the curve that described the cumulative frequency for the SUM00 index (referred to as TOTDOSE) was greater than the slope of the curve for the W126 index until approximately 0.06 ppm.

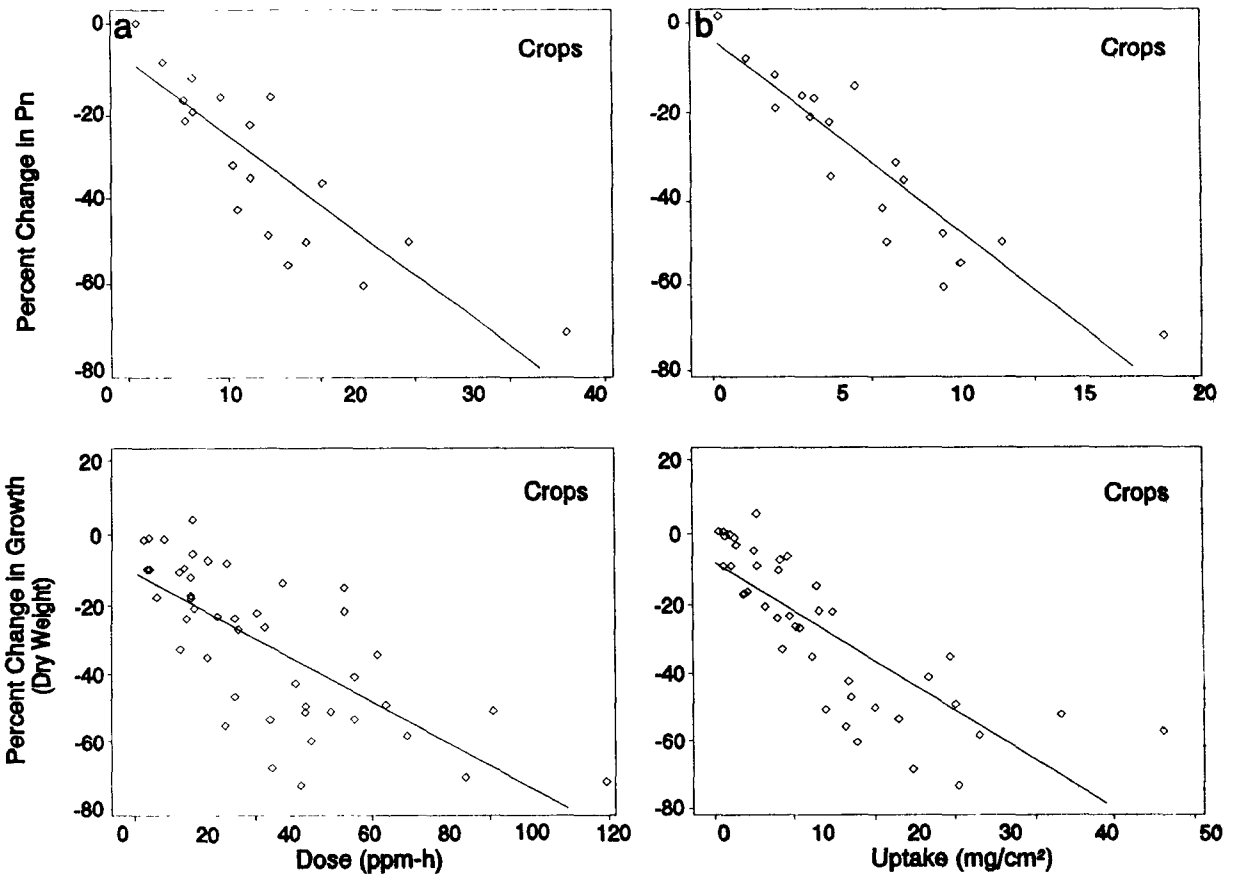

Figure 5-18. Percent reduction in net photosynthesis and biomass growth of agricultural crops in relation to (a) total exposure (SUM00) and (b) estimated total ozone uptake (Reich, 1987).

Thereafter, the reverse was true. This occurred because the W126 index weighted the higher concentrations more heavily than the lower ones, while the TOTDOSE index did not.

Supplementing the results in Lefohn et al. (1989), Lefohn et al. (1992a), using loblolly pine data exposed at Auburn, AL, to varying levels of O_3 over 555 days (Qiu et al., 1992) reported that the magnitude of the SUM00 values in the CF chamber, although experiencing hourly average values greater than those at the South Pole or Pt. Barrow, AK, was about 50% less than the SUM00 values experienced at the South Pole and Pt. Barrow, AK.

In a similar analysis using ambient data, Lefohn et al. (1992a) identified a separate set of ambient sites that experienced SUM00 values similar to those of the ambient treatments at

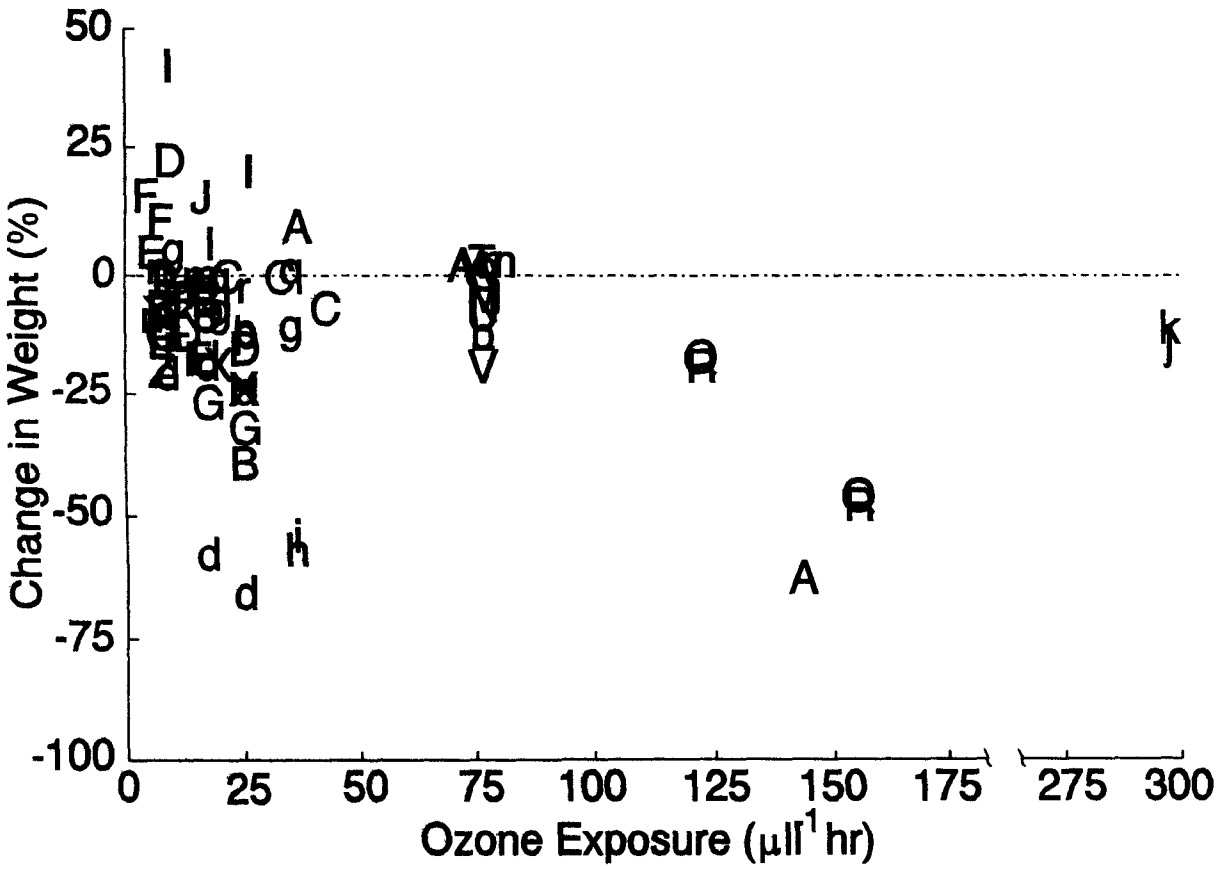

Figure 5-19. Percent reduction in biomass growth of tree seedlings in relation to total exposure (Pye, 1988).

Auburn; these ambient sites experienced fewer hourly concentrations above 0.07 ppm than did the ambient chambers. Similar to the results cited above, the authors noted that the magnitude of the SUM00 index was unable to capture the occurrence of the higher hourly average concentrations in the ambient treatments. The authors indicated that the SUM00 index was inadequate because of the observed inconsistences of the SUM00 value between chambers and selected monitoring sites.

When taken by themselves, the importance of these findings may be debatable because the clean sites are not representative of loblolly growing regions and there is no substantiating evidence of differing effects at these levels. However, the coupling of the air quality considerations, as described by Lefohn et al. (1989, 1992a), with the biological

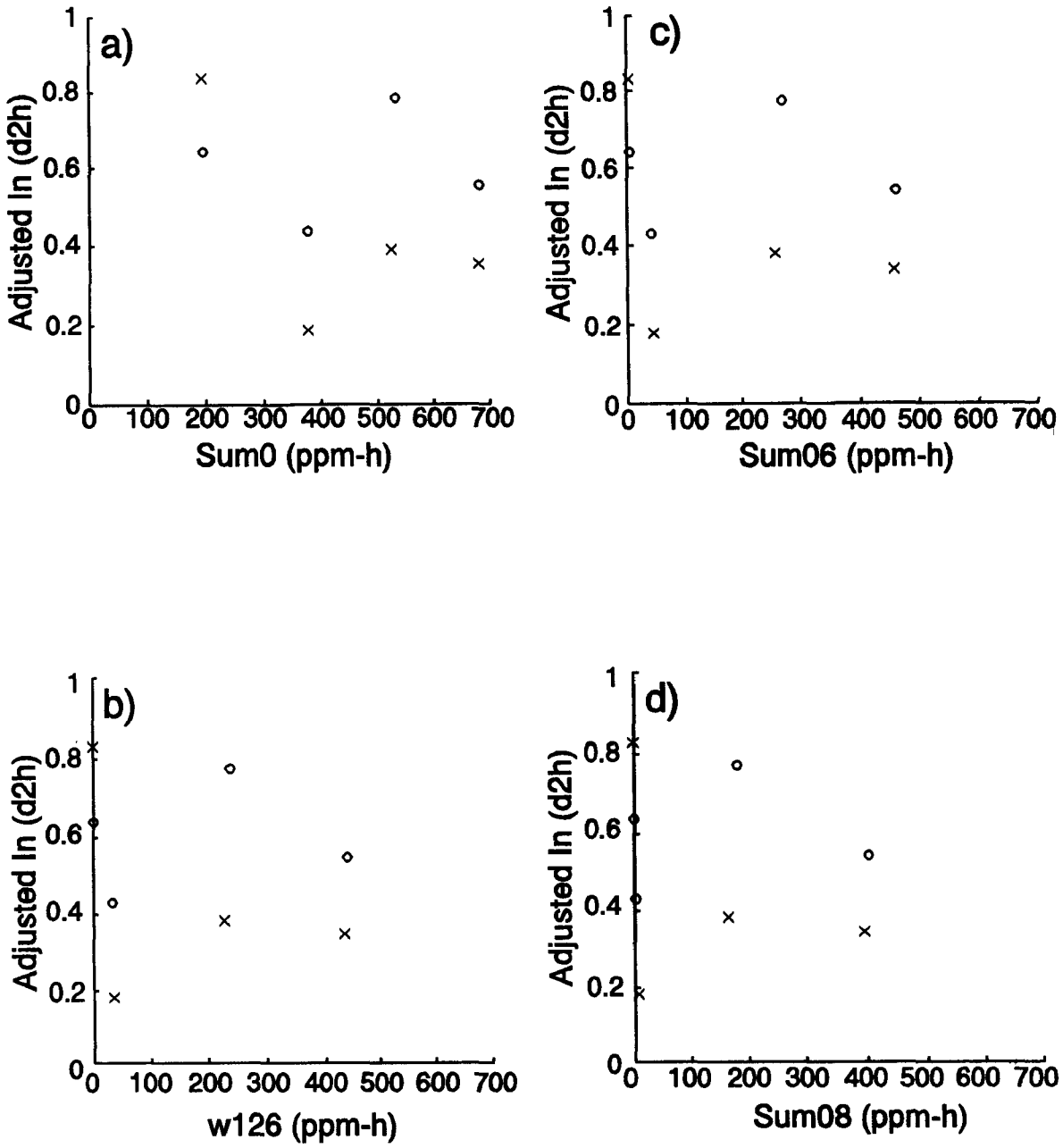

Figure 5-20. Reduction in volume production of loblolly pine seedlings (family 91) in relation to four exposure indices (a-d) (Lefohn et al., 1992a).

findings reported by Musselman et al. (1983) and Hogsett et al. (1985a), builds a consistent picture that the SUM00 index does not properly describe the occurrence of the higher hourly average concentrations.

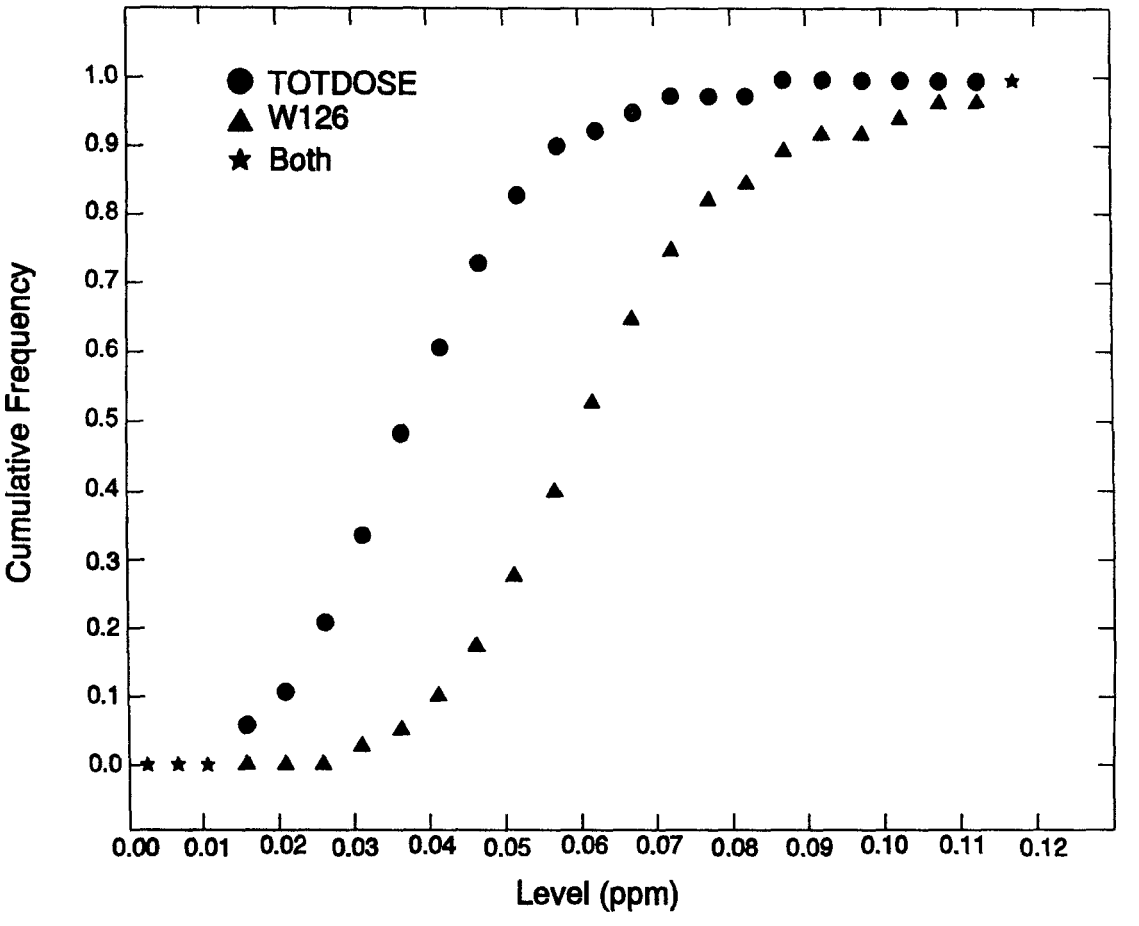

Figure 5-21. A comparison between the resulting cumulative frequencies for the exposure parameters (a) sum of all hourly average concentrations (SUM00) and (b) the sigmoidally weighted integrated exposure index, W126. The ozone data were collected in 1981 at a site located in the Mark Twain National Forest, Missouri. The U.S. EPA AIRS site number is 291230001 (Lefohn et al., 1989).

The selection of the weighting scheme of hourly O_3 concentrations for use in characterizing plant exposure and its relationship to plant response is difficult because of limitations in the data. The results of studies based on analysis of experimental and air quality data substantiate O_3 uptake as the determining factor of response. Stomata controls the rate of O_3 uptake. Stem et al. resistance is influenced by ambient conditions surrounding the plant, as well as other factors. Concentration has been identified as important in predicting response and concentrations as low as 50 ppb may contribute to response. Several lines of evidence suggest that the peak-weighted, cumulative indices yield better predictions

of yield loss than the mean and peak indices. The optimal weighting function to describe plant exposure has not been determined but should give greater weight to the peak concentrations. Because the NCLAN studies used ambient-added exposures that have considerably more concentrations above 0.10 ppm than ambient conditions in polluted monitoring sites, one must be careful in the selection of an exposure index based on statistical fit.

5.5.3 Summary

The effects of O_3 on individual plants and factors that modify plant response to O_3 are complex and vary with factors, such as species, environmental conditions, and soil and nutrient conditions. Because of the complex effect of O_3 and its interactions with physical and genetic factors that influence response, it is difficult to develop a measure of exposure that relates well with plant response based on experimental data. At best, experimental evidence of the impact of O_3 on biomass production can indicate important factors of O_3 exposure that modify plant response, which become considerations in developing an exposure index.

Considerable evidence of the primary mode of action of O_3 on plants (injury to proteins and membranes, reduction in photosynthesis, changes in allocation of carbohydrate, and early senescence), which ultimately lead to reductions in biomass production, identifies O_3 uptake as an important factor (see Section 5.2). Ozone uptake is controlled by canopy conductance, stomatal conductance, and O_3 concentration outside the leaf (see Figure 5-2). Any factor that will affect stomatal conductance (e.g., light, temperature, humidity, soil and atmospheric chemistry and nutrients, time of day, phenology, and biological agents) will affect O_3 uptake and, consequently plant response.

Evidence from studies that applied two or more different exposure regimes substantiate the importance of daytime peak concentrations, respite time, and phenology in eliciting a response. Ozone effects on plants exposed to two (or more) regimes having equal total exposure were greater for exposures experiencing the higher peak concentrations, respite time of 2 to 6 days, or peak concentrations during period of maximum leaf expansion. This conclusion is consistent with the mode of action of O_3 on plants and with the conclusions in the previous Environmental Protection Agency criteria document (U.S. Environmental

Protection Agency, 1986) and its Supplement (U.S. Environmental Protection Agency, 1992) and is equally true for seedlings based on a recent seedling study (Hogsett and Tingey, 1990).

Further, the biochemical mechanisms, discussed in Section 5.2, describe the mode of action of O_3 on plants as the culmination of a series of physical, biochemical, and physiological events leading to alterations in plant metabolism. Ozone-induced injury is cumulative, resulting in net reductions in photosynthesis, changes in allocation of carbohydrate, and early senescence, which lead to reductions in biomass production (Section 5.2). Increasing O_3 uptake will result in increasing reductions in biomass production. Retrospective analyses comparing replicate studies of equal and varying durations are in general agreement that the ultimate impact of O_3 on plant response depends upon the integration of repeated peak concentrations during the ecological period of growth.

The optimum exposure index that relates well with plant response should incorporate the factors (directly or indirectly) described above; unfortunately, such an index has not yet been identified. At this time, exposure indices that weight the hourly O_3 concentrations differentially appear to be the best candidates for relating exposure with predicted plant response. Peak concentrations in ambient air occur primarily during daylight thus, these indices, by providing preferential weight to the peak concentrations, give greater weight to the daylight concentrations rather than nighttime concentrations (when stomatal conductance is minimal).

Studies reported in the literature show that when O_3 is the primary source of variation in response, year-to-year variations in plant response are minimized by the peak-weighted, cumulative exposure indices. The data suggest that the exposure indices that cumulate hourly O_3 concentrations over the growing season and give preferential weight to the peak concentrations are biologically appropriate as characterizations and representations of plant exposure. Generally, the peak-weighted, cumulative indices relate well with plant response and order the treatment means in monotonically decreasing fashion with increasing exposure, based on studies that apply two or more types of exposure regimes and when combining data from replicate studies of the same species. No studies have been designed specifically to evaluate the adequacy of the peak-weighted, cumulative indices. Consequently, it is not possible to discriminate among the various peak-weighted, cumulative indices based on

experimental data. Functional weighting approaches including an allometric, sigmoid, or threshold weighting have been suggested and, in earlier retrospective studies compared, but there is no evidence to favor one approach over the other on the basis of statistical fits to the data.

The study of Fuhrer et al. (1992) illustrates some of the limitations in applying exposure indices. The study is significant for its use of the mean O_3 flux in minimizing the year-to-year variation in response when combining replicate studies, indicating the importance of environmental conditions in quantifying the relationship between O_3 exposure and plant response.

The factors such as respite time, temporal variation, phenology, canopy structure, physiological processes, environmental conditions, and soil and nutrient conditions, are important in determining the impact of O_3 on crops and trees but are not well understood and interact with concentration and duration in different fashions depending upon species. Ozone uptake integrates these factors with atmospheric conditions, relates well with plant response, but is difficult to measure. Empirical functions to predict stomatal conductance have been developed for particular species (e.g., Lösch and Tenhunen, 1981) but have not been used to estimate O_3 uptake or used in development of exposure indices.

The exposure-response studies in the published literature support the conclusion that O_3 effects are cumulative and peak concentrations are more important than lower concentrations in determining the magnitude of plant response. The peak-weighted, cumulative indices appear to have major advantages over the mean (e.g., 7-h seasonal mean), peak indices (e.g., 2ndHDM), and the index that cumulates all hourly average concentrations (i.e., SUM00). Crop yield loss and biomass reduction are better estimated using the peak-weighted, cumulative indices than the 2ndHDM index; when duration of exposure is taken into consideration, peak-weighted cumulative indices perform better than the seasonal mean indices. In addition, results have been published to indicate that the SUM00 index does not adequately relate exposure with biological effects because the index focuses on the lower hourly average concentrations.

For predicting the effects of O_3 on vegetation under ambient conditions using experimental exposure-response models, the types of exposure regimes used in the experiments should be taken into consideration. For example, NCLAN experiments

contained peak hourly average concentrations in their regimes. Any exposure index, based on the NCLAN experiments, should take into consideration the presence of these peak concentrations. By doing so, the situation may be avoided where two sites, which experience two distinct distributions of high hourly average concentrations, but have the same value of cumulation (e.g., same SUM06 or W126 value), exhibit differing biological effects.

Future research needs to focus on: (1) validation of the application of exposure-response relationships based on chambered studies to ambient conditions; (2) evaluation of peak-weighted, cumulative indices for quantifying the relationship of O_3 exposure to ensuing plant response; (3) a better understanding of the effects of O_3 and its interactions with environmental conditions, soil chemistry, and nutrient conditions; (4) development of mechanistic models of stomatal conductance for use in weighting O_3 concentrations in ambient air; and (5) more multi-year exposure studies on trees to predict the long-term effects on O_3 of biomass production.

5.6 EXPOSURE-RESPONSE OF PLANT SPECIES

5.6.1 Introduction

Determining the response of plants to O_3 exposures continues to be a major challenge. The effects of vegetational exposure are usually evaluated by exposing various plant species under controlled experimental conditions such as those discussed in Section 5.2. Plant responses are influenced not only by the biochemical and physiological changes that may occur within the plant after O_3 entry (Section 5.3, Mode of Action, see also Figure 5-5) but also by the many factors that modify plant response (Section 5.4). Of the factors discussed in Section 5.4, those that are most likely to apply under controlled experimental conditions are the genetic makeup and age of the plant. Compensatory responses (Section 5.3.4.2) will also influence plant response. This section will analyze, summarize, and evaluate what is known about the response of various plant species or cultivars, either as an individuals or in populations to O_3 exposure. Species as populations will only be considered in the case of pasture grasses, or forage mixes, which commonly occur as mixed stands. Emphasis will be placed on those studies conducted since the publication of the previous criteria document 1986 (U.S. Environmental Protection Agency, 1986). Much of the discussion of vegetational

response to O_3 exposure in the current document is based on the conclusions of both the 1978 and 1986 documents (U.S. Environmental Protection Agency, 1978, 1986). Therefore, to provide a basis for understanding the effects presented below, the conclusions of the two documents are summarized.

Finally, the results of O_3 exposure-response presented in this section must be related to one or more assessment endpoints. Historically, the dollar value of lost production was the endpoint of interest, however, other endpoints (e.g., biodiversity, habitat, aesthetics, recreation) must be considered now, particularly as the impacts of O_3 on long-lived species of ecological importance are evaluated (Tingey et al., 1990).

5.6.2 Summary of Conclusions from the Previous Criteria Documents

The experimental data presented in the 1978 and 1986 criteria documents dealt with the effects of O_3 primarily on agricultural crops species (U.S. Environmental Protection Agency, 1978, 1986). The chapter on vegetational effects in the 1978 criteria document (U.S. Environmental Protection Agency, 1978) emphasized visible injury and growth effects; however, the growth effects were not those that affected yield. This emphasis was dictated by the kind of data available at the time. The document also presented data dealing with the response of the San Bernardino ecosystem to O_3. This information was also discussed in the 1986 document (U.S. Environmental Protection Agency, 1986). It remains the best study of ecosystem responses to O_3 stresses (see Section 5.7).

The 1986 document emphasized the fact that though foliar injury on vegetation is one of the earliest and most obvious manifestations of O_3 exposure, the effects of exposure are not limited to visible injury. Plant foliage is only the primary site of plant response to O_3 exposures. Significant secondary effects, include reduced growth, both in foliage and roots. Impacts range from reduced plant growth and decreased yield to changes in crop quality and alterations in plant susceptibility to biotic and abiotic stresses. Also, the 1986 document noted that O_3 exerts a phytotoxic effect only if a sufficient amount reaches sensitive sites within the leaf (see Section 5.3). Ozone injury will not occur if (1) the rate of uptake is low enough that the plant can detoxify or metabolize O_3 or its metabolites; or (2) the plant is able to repair or compensate for the effects (Tingey and Taylor, 1992; U.S. Environmental Protection Agency, 1986). Cellular disturbances that are not repaired or

compensated are ultimately expressed as visible injury to the leaf or as secondary effects that can be expressed as reduced root growth, or reduced yield of fruits or seeds, or both. Ozone would be expected to reduce plant growth or yield if (1) it directly impacts the plant process e.g., photosynthesis that was limiting plant growth; or (2) it impacts another step sufficiently so that it becomes the step limiting plant growth (U.S. Environmental Protection Agency, 1986; Tingey, 1977). Conversely, if the process impacted is not or does not become rate-limiting, O_3 will not limit plant growth. These conditions also suggest that there are combinations of O_3 concentration and exposure duration that a plant can experience that will not result in visible injury or reduced plant growth and yield. Indeed, numerous studies have demonstrated this fact. This information is still pertinent today (Section 5.3)

Ozone can induce a diverse range of effects beginning with individual plants and then proceeding to plant populations and ultimately communities. The effects may be classified as either (1) injury or (2) damage. Injury encompasses all plant reactions such as reversible changes in plant metabolism (e.g., altered photosynthesis), leaf necrosis, altered plant quality, or reduced growth that does not impair yield or the intended use or value of the plant (Guderian, 1977). Thus, for example, visible foliar injury to ornamental plants, detrimental responses in native species, while reductions in fruit and grain production in cultivated plants are all considered damage or yield loss. Although foliar injury is not always classified as damage, its occurrence indicates that phytotoxic concentrations of O_3 are present and, therefore, studies should be conducted to assess the risk to vegetation.

The concept of limiting values used to summarize visible foliar injury in the 1978 document was also considered valid in the 1986 document (U.S. Environmental Protection Agency, 1978, 1986). Jacobson, (1977) developed limiting values by reviewing the scientific literature and identifying the lowest concentration and exposure duration reported to cause visible injury to a variety of plant species. Expressed in another way, limiting values were concentrations and durations of exposure below which visible injury did not occur. A graphical analysis presented in both of the previous documents indicated the limit for reduced plant performance was an exposure to 0.05 ppm for several hours per day for greater than 16 days. Decreasing the exposure period to 10 days increased the concentration required to cause injury to 0.1 ppm, and a short, 6 day exposure further increased the concentration to cause injury to 0.30 ppm.

By 1986, a great deal of new information concerning the effects of O_3 on the yield of crops plants had become available, both through the EPA National Crop Loss Assessment Network (NCLAN) and the results of research funded by other agencies. The NCLAN project was initiated by the Environmental Protection Agency in 1980 primarily to improve estimates of yield loss in the field and to estimate the magnitude of crop losses caused by O_3 (Heck et al., 1982). The primary objectives were:

1. To define the relationships between yields of major agricultural crops and O_3 exposure as required to provide data necessary for economic assessments and the development of National Ambient Air Quality Standards;

2. To assess the national economic consequences resulting from the exposure of major agricultural crops to O_3;

3. To advance understanding of the cause and effect relationships that determine crop responses to pullutant exposures.

The cultural conditions used in the NCLAN studies approximated typical agronomic practices. The methodology used in these studies is described in Section 5.2.

Yield loss in the 1986 document was defined as an impairment in the intended use of the plant. This concept included reductions in aesthetic values, the occurrence of foliar injury (changes in plant appearance), and losses in terms of weight, number, or size of the plant part that is harvested. Yield loss may also include changes in physical appearance, chemical composition, or the ability to withstand quality storage; which collectively are termed crop quality. Losses in aesthetic values are difficult to quantify. Foliar injury symptoms can substantially reduce the marketability of ornamental plants or crops in which the foliage is the plant part (e.g., spinach, lettuce, cabbage) and constitute yield loss with or without concomitant growth reductions. At that time (1986) most studies of the relationship between yield loss and O_3 concentration focused on yields as measured by weight of the marketable organ of the plant.

Open-top field chamber studies conducted to estimate the impact of O_3 on the yield of various crops species, e.g., the NCLAN program, were grouped into two types, depending on the experimental design and statistical methods used to a analyze the data: (1) studies that developed predictive equations relating O_3 exposure to plant response, and (2) studies that

compared discrete treatment level to a control. The advantage of the regression approach is that exposure-response models can be used to interpolate results between treatment levels (see Section 5.2.2).

Using NCLAN data as an example of plant response, the O_3 concentrations that could be predicted to cause 10 or 30% yield loss were estimated using the Weibull function (Table 5-16; Table 6-19, U.S. Environmental Protection Agency, 1986). The data in Table 5-16 are based on yield-response functions for 38 species or cultivars developed from studies using open-top chambers. Review of that data indicated that ten percent yield reductions could be predicted for 57% of the species or cultivars when 7-h seasonal mean concentrations were below 0.05 ppm, for 35% when seasonal mean concentrations were between 0.04 and 0.05 ppm, but only 19% required a 7-h seasonal mean concentrations in excess of 0.08 ppm to suffer a 10% loss in yield. Furthermore, approximately 11% of the 38 species or cultivars would be expected to have a yield reduction of 10% loss at 7-h seasonal mean concentrations below 0.05 ppm, suggesting that these plants are very sensitive to O_3.

Grain crops were apparently less sensitive than the other crops. The data also demonstrate that the sensitivity within species may be as great as difference between species. For example, at 0.04 ppm O_3, estimated yield losses ranged from 2 to 15% in soybean and from 0 to 28% in wheat. Year to year variations in plant response were also observed during the studies.

Discrete treatments were used to determine yield loss in some studies. These experiments were designed to test whether specific O_3 treatments were different from the control rather than to develop exposure-response equations and the data were analyzed using analyses of variance. When summarizing these studies using discrete treatment levels, as opposed to the variable concentrations used in NCLAN, the lowest O_3 concentration that significantly reduced yield was determined from analyses done by the authors. Frequently, the lowest concentration used in the study was the lowest concentration reported to reduce yield; hence it was not always possible to estimate a no-effect exposure concentration. In general, the data indicated that O_3 concentrations of 0.10 ppm (frequently the lowest concentration used in the studies) for a few hours per day for several days to several weeks

TABLE 5-16. ESTIMATES OF THE PARAMETERS FOR FITTING THE WEIBULL MODEL USING THE 7-HOUR SEASONAL MEAN OZONE CONCENTRATIONS[a,b]

Crop	Parameters for Weibull Model				Concentration for Predicted Yield Losses of:	
	$\hat{\alpha}$	$\hat{\sigma}$	$\hat{c}$	CF[c]	10%[d]	30%[d]
LEGUME CROPS						
Soybean, Corsoy	2785.00	0.133	1.952	0.022	0.048	0.082
Soybean, Davis (81)	5593.00	0.128	0.872	0.025	0.038	0.071
Soybean, Davis (CA-82)[e]	4931.00	0.12/	2.144	0.019	0.048	0.081
Soybean, Davis (PA-82)$_e$	4805.00	0.103	4.077	0.019	0.059	0.081
Soybean, Essex (81)	4562.00	0.187	1.543	0.014	0.048	0.099
Soybean, Forrest (82-I)	4333.00	0.171	2.752	0.017	0.076	0.118
Soybean, Williams (81)	4992.00	0.211	1.100	0.014	0.039	0.093
Soybean, Williams (82-I)	5884.00	0.162	1.577	0.017	0.045	0.088
Soybean, Hodgson	2590.00	0.138	1.000	0.017	0.032	0.066
Bean, Kidney (FP)[f]	2878.00	0.120	1.171	0.019	0.033	0.063
Peanut, NC-6	7485.00	0.111	2.249	0.025	0.046	0.073
GRAIN CROPS						
Wheat, Abe (82)	5363.00	0.143	2.423	0.023	0.059	0.095
Wheat, Arthur 71 (82)	4684.00	0.148	2.154	0.023	0.056	0.094
Wheat Roland	5479.00	0.113	1.633	0.023	0.039	0.067
Wheat, Vona	7857.00	0.053	1.000	0.022	0.028	0.041
Wheat, Blueboy II (T)	5.88	0.175	3.220	0.030	0.088	0.127
Wheat, Coker 47-27 (T)	5.19	0.171	2.060	0.030	0.064	0.107
Wheat, Holly (T)	4.95	0.156	4.950	0.030	0.099	0.127
Wheat, Oasis (T)	4.48	0.186	3.200	0.030	0.093	0.135
Corn, PAG 397	13968.00	0.160	4.280	0.015	0.095	0.126
Corn, Pioneer 3780	12533.00	0.155	3.091	0.015	0.075	0.111
Corn, Coker 16 (T)	240.00	0.221	4.460	0.020	0.133	0.175
Sorghum, DeKalb-28	8137.00	0.296	2.217	0.016	0.108	0.186
Barley, Poco	1.99	0.205	4.278	0.020	0.121	0.161
FIBER CROPS						
Cotton, Acala SJ-2 (81-I)	5546.00	0.199	1.228	0.018	0.044	0.096
Cotton, Acala SJ-2 (82-I)	5872.00	0.088	2.100	0.012	0.032	0.055
Cotton, Stoneville	3686.00	0.112	2.577	0.026	0.047	0.075
HORTICULTURAL CROPS						
Tomato, Murrieta (81)	32.90	0.142	3.807	0.012	0.079	0.108
Tomato, Murrieta (82)	32.30	0.082	3.050	0.012	0.040	0.059
Lettuce, Empire (T)	1245.00	0.098	1.220	0.043	0.053	0.075
Spinach, America (T)	21.20	0.142	1.650	0.024	0.046	0.082
Spinach, Hybrid (T)	36.60	0.139	2.680	0.024	0.043	0.082
Spinach, Viroflay (T)	41.10	0.129	1.990	0.024	0.048	0.080
Spinach, Winter Bloom (T)	20.80	0.127	2.070	0.024	0.049	0.080

TABLE 5-16 (cont'd). ESTIMATES OF THE PARAMETERS FOR FITTING THE WEIBULL MODEL USING THE 7-HOUR SEASONAL MEAN OZONE CONCENTRATIONS[a,b]

Crop	Parameters for Weibull Model				Concentration for Predicted Yield Losses of:	
	$\hat{\alpha}$	$\hat{\sigma}$	$\hat{c}$	CF[c]	10%[d]	30%[d]
Turnip, Just Right (T)	10.89	0.090	3.050	0.014	0.043	0.064
Turnip, Pur Top W.G. (T)	6.22	0.095	2.510	0.014	0.040	0.064
Turnip, Shogoin (T)	4.68	0.096	2.120	0.014	0.036	0.060
Turnip, Tokyo Cross (T)	15.25	0.094	3.940	0.014	0.053	0.072

[a]Data are from Heck et al. (1984b) and are based on individual plot means unless the crop name is followed by "(T)". The "T" indicates that the parameters were based on treatment means and the data are from Heck et al. (1983a). The parameters given in Heck et al. (1983a, 1984b) also contain the standard errors of the parameters.
[b]All estimates of $\hat{\sigma}$ are in ppm. The yield is expressed as kg/Ha for all crops except barley—see weight (g per head); tomato (both years)—fresh weight (kg per plot); cotton—lint + seed weight (kg/ha); peanut—pod weight (kg/Ha). In cases where the estimated $\hat{c}$ parameter is exactly 1.0, it has been bounded from below to obtain covergence in the nonlinear model fitting routine. Parameters were estimated from data not showing the expected Weibull form. Caution should be used in interpreting these Weibull models. Other models might better describe the behavior observed in these experiments. For those crops whose name is followed by "(T)" the yield is expressed as g/plant.
[c]The O_3 concentration in the charcoal filtered chambers expressed as a 7-h seasonal mean concentration.
[d]The 7-h seasonal mean O_3 concentration (ppm) that was predicted to cause a 10 or 30% yield loss (compared to charcoal-filtered air).
[e]CA and PA refer to constant and proportional O_3 addition.
[f]Only the bean data from the full plots are shown. The partial plot data are given Heck et al. (1984b).

Source: U.S. Environmental Protection Agency (1986).

generally caused significant yield reductions. The concentrations derived from the regressions studies were based on a 10% yield loss, while in the studies using the analysis of variance the 0.10 concentration frequently induced mean yield losses of 10 to 50%.

A chemical protectant, ethylene diurea (EDU) was used to provide estimates of yield loss. The impact of O_3 on yield was determined by comparing the yield data from plots treated with EDU with those that were not. Studies indicated that yields were reduced by 18 to 41% when ambient O_3 concentrations exceeded 0.08 ppm during the day for 5 to 18 days over the growing season.

In summary, the 1986 criteria document (U.S. Environmental Protection Agency, 1986) states that the following several general conclusions can be drawn from the various approaches used to estimate crop loss yield; (1) Based on the comparison of data obtained

from crop yield in charcoal-filtered and unfiltered (ambient) exposures clearly indicate that O_3 at ambient levels are sufficiently elevated in several parts of the country to impair the growth and yield of plants. This conclusion is supported by data from the chemical protectant studies and extends it to other plant species; (2) Both of the above mentioned approaches indicate that effects occur with only a few O_3 occurrences above 0.08 ppm; (3) The growth and yield data cited in the 1978 criteria document (U.S. Environmental Protection Agency, 1978) indicate that several plant species exhibited growth and yield effects when the mean O_3 concentration exceeded 0.05 ppm for 4 to 6 h/day for at least 2 weeks; and (4) The data obtained from regression studies conducted to develop exposure-response functions for estimating yield loss indicated that at least 50% of the species/cultivars tested were predicted to exhibit a 10% yield loss at 7-h season mean O_3 concentrations of 0.05 ppm or less. Though most of the data from the discrete treatment studies did not use concentrations low enough to support the values cited above, the magnitude of yield losses reported at 0.10 ppm under a variety of exposure regimes indicate that to prevent O_3 effects a substantially lower concentration is required.

The limiting values established in the 1978 were still deemed appropriate in the 1986 criteria document for ornamentals and certain vegetable crops where visible injury was still considered the response of interest because appearance is of importance (e.g., spinach, lettuce, cabbage) (U.S. Environmental Protection Agency, 1986). This remains the case today.

5.6.3 Information in the Published Literature Since 1986

The major question to be addressed in this section is whether the conclusions of the 1986 criteria document summarized in the previous section, remain valid given the results of research published since 1988. In particular, whether the response of plants to experimental treatments at or near concentrations of 0.05 ppm (7 h seasonal mean), characteristic of ambient concentrations in many areas, can be compared to a control, or reduced O_3 treatment to establish a potential adverse effect.

The 1986 (U.S. Environmental Protection Agency, 1986) made the following statement: "The characterization and representation of plant exposures to O_3 has been and continues to

be a major problem because research has not yet clearly identified which components of the pollutant exposure cause plant response". This is still true today (See Section 5.5).

The aim of most air pollution research experiments have been designed to quantify the relationship between pollutant exposure an agricultural crop yield. The problem is the incorporation of the concentration, duration, frequency, age, genetic composition and respite time into an exposure statistic or index which may be used to predict yield loss. The correct exposure representation is the amount of pollutant entering the plant, not the ambient concentration to which it is exposed (Taylor et al., 1982a; Tingey and Taylor, 1982). Most indices were not developed from a biological basis, nor were they developed using an experimental approach specifically designed to address all key factors (Lee et al., 1990). A number or exposure indices have been developed in an attempt for depicting plant response to O_3 exposure (See Section 5.5). Much of the data in this section is evaluated using these indices. For this reason several different exposure statistics are used to determine the effect of an exposure on plant response. It should be remembered that the SUM06, which is used more than any of the other indices, is the seasonal sum of hourly concentrations at or above 0.06 ppm (See Section 5.5).

Exposure indices calculated for each of 10 years (1982 to 1991) and two exposure periods, June through August (three month) and May through September (five month) are presented in Table 5-17 (modified from Tingey, et al., 1991). The monitoring data, collected at non-urban sites, show that ambient O_3 is frequently at, or near, the 7 h seasonal mean (M7) that would be expected to cause a yield loss in crops based on the conclusions of the 1986 criteria document. This table may be used for comparison of ambient-O_3 concentrations to those used in experiments. Thirty-five percent of the 38 species or cultivars under consideration would be predicted to have a 10% yield loss at a 7 h mean concentration of between 0.04 and 0.05 ppm, but only 19% required a 7 h mean concentration of greater than 0.08 ppm to suffer a predicted 10% loss in yield. Furthermore, 11% of the 38 species or cultivars would be expected to have a yield reduction of 10% at a 7 h mean or less than 0.028 to 0.035 ppm (Table 6-17, U.S. Environmental Protection Agency, 1986). It was also concluded that grain crops (with the exception of a few very sensitive cultivars) were generally less sensitive than others, but that within-species variability in sensitivity may be as great or greater than between species. These results are

TABLE 5-17. SUMMARY OF OZONE EXPOSURE INDICES CALCULATED FOR 3- OR 5-MONTH GROWING SEASONS FROM 1982 TO 1991

3 mo (June-August)

		HDM2 ppm		M7 ppm		SUM00 ppm·h		SUM06 ppm·h		SIGMOID ppm·h	
Year	No. Sites	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
1982	99	0.114	23.7%	0.052	18.7%	82.9	19.1%	26.8	68.8%	26.3	56.7%
1983	102	0.125	24.9%	0.056	21.9%	86.1	22.1%	34.5	58.1%	33.0	52.3%
1984	104	0.117	24.6%	0.052	18.2%	84.1	19.9%	27.7	58.4%	27.4	47.9%
1985	117	0.117	24.6%	0.052	17.1%	84.6	18.0%	27.4	59.6%	27.4	47.6%
1986	123	0.115	21.8%	0.052	19.1%	85.3	18.0%	27.7	65.0%	27.7	51.8%
1987	121	0.119	22.9%	0.055	17.6%	86.9	17.3%	31.2	56.4%	30.4	46.8%
1988	139	0.129	21.3%	0.060	17.8%	97.6	19.6%	45.2	46.8%	42.9	42.4%
1989	171	0.105	23.1%	0.051	17.5%	86.4	19.9%	24.8	78.7%	25.8	59.4%
1990	188	0.105	21.6%	0.053	18.3%	85.7	21.0%	25.8	76.2%	26.6	59.2%
1991	199	0.106	22.0%	0.054	18.4%	87.7	21.3%	28.3	74.2%	28.9	59.5%
Among Years		0.113	11.1%	0.054	10.0%	87.0	9.9%	29.5	42.1%	29.4	31.0%

5 mo (May-September)

		M7 ppm		SUM00 ppm·h		SUM06 ppm·h		SIGMOID ppm·h	
Year	No. Sites	Mean	CV	Mean	CV	Mean	CV	Mean	CV
1982	88	0.048	20.6%	122.9	22.3%	37.3	70.9%	37.1	57.8%
1983	87	0.051	22.1%	129.6	24.4%	44.4	61.9%	43.8	52.7%
1984	95	0.048	18.0%	126.2	19.1%	36.7	60.8%	37.6	46.9%
1985	114	0.048	18.4%	124.5	19.4%	36.2	63.8%	37.0	50.3%
1986	118	0.048	20.3%	123.3	21.4%	34.9	70.7%	35.6	55.7%
1987	116	0.050	20.3%	128.7	20.4%	42.2	62.0%	41.8	50.3%
1988	134	0.054	18.7%	141.7	22.0%	58.0	50.5%	55.6	45.0%
1989	158	0.047	18.6%	127.8	22.5%	32.7	87.8%	35.2	64.1%
1990	172	0.049	19.8%	129.4	22.7%	34.6	82.7%	37.0	62.1%
1991	190	0.050	19.8%	130.6	23.6%	36.8	80.7%	38.8	62.9%
Among Years		0.049	9.8%	129.0	9.9%	38.7	42.5%	39.6	29.8%

[a]Updated and additional years from data given in Table III of Tingey et al (1991) where the spatial and temporal variation in ambient O_3 exposures is expressed in terms of several exposure indices.
[b]No. sites indicates the number of separate monitoring sites included in the analysis. Fewer sites had 5 mo of available data than 3 mo of available data. The 2nd HDM index is calculated for sites with at least 3 mo of available data.
[c]SUM00, SUM06, M7, SIGMOID, and 2nd HDM are the cumulative sum above 0.0 ppm, the cumulative sum above 0.06 ppm, the 7 h seasonal mean, the sigmoid weighted summed concentration, and the second highest daily maximum 1 h concentration, respectively.
[d]CV = coefficient of variation.

Source: Tingey et al. (1991).

similar to those previously obtained from Table 6-19 in the 1986 document. Lee et al. (1993a) have revised Table 6-19 (see Table 5-16) in U.S. Environmental Protection Agency (1986) using re-calculated peak-weighted exposure indices (shown to be more appropriate than long-term means for relating effects to ambient concentrations) for the 54 studies (Tables 5-18 and 5-19).

In 1992, a Supplement to the Air Quality Criteria Document for Oxidants reviewed effects of oxidant exposure on vegetation. Considerable emphasis was placed on the appropriate exposure index for relating biological effects of O_3 on plants (U.S. Environmental Protection Agency, 1992). An analysis of the data at that time showed that a seasonal mean concentration (e.g., 7 or 24-h) might not be the best expression of the exposure since it did not weight high concentrations differently from low concentrations and it did not account for the variable length of growing seasons or exposure durations. Unfortunately, it is often impossible to calculate the different possible exposure indices (means, cumulative peak-or threshold-weighted, or continuously weighted [sigmoid] cumulative) from information given in published papers. Thus, difficulties remain in comparing exposure-response studies that utilize different exposure indices. However, reported responses and concentrations of O_3 can be compared to those that occur at ambient concentrations, and thence to other exposure indices (Table 5-17).

5.6.3.1 Effects of Ozone on Short-Lived (Less Than 1-Year) Species

Plant species can be characterized by their life-span, either short-lived annual species, or longer-lived perennials and trees. Physiological processes may be related to life-span (for instance, leaf gas exchange tends to be lower in longer-lived trees than in crop species) and so, the response to O_3 may be different (Reich, 1987). In addition, multiple year exposures and carry-over effects may be of importance in long-lived species, but of no concern in annuals. Accordingly, animals and perennials will be discussed separately. The response of plants to O_3 is also affected by interactions with other physical, chemical, and biological factors. Those interactions are discussed elsewhere in this document (Section 5.3). In most cases, the research analyzed here was conducted under near-optimal conditions of water and nutrient availability. While deviations from these conditions may affect the magnitude of

TABLE 5-18. COMPARISON OF EXPOSURE-RESPONSE CURVES CALCULATED USING THE 3-MONTH, 24-HOUR SUM06 VALUES FOR 54 NCLAN CASES

Species	Cultivar	Moisture[a]	Weibull/Linear Model Parameters[b] A	B	C	RMSE[c]	R^2[d]	3 mo 24-h SUM06[e] Values for Yield Losses of 10%	30%
Barley (Linear)	CM-72	DRY	7741.1	-4.412		1215	0.12	175.5	526.4
Barley (Linear)	CM-72	WET	8776.6	15.485		1175	NA	250.0	250.0
Corn (L)	PIO		9627.4	92.61	2.823	680	0.93	41.7	64.3
Corn (L)	PAG		10730.1	94.36	4.316	1248	0.80	56.0	74.3
Cotton (L)	ACALA	DRY	6465.0	92.59	2.361	1097	0.45	35.7	59.8
Cotton (L)	ACALA	WET	9808.0	71.17	1.997	521	0.96	23.1	42.5
Cotton (L)	ACALA	DRY	7009.8	83.78	1.849	949	0.80	24.8	48.0
Cotton (L)	ACALA	WET	7858.8	78.01	1.311	937	0.85	14.0	35.5
Cotton (L, Linear)	ACALA	DRY	5.693	-0.0011		104	0.06	94.9	321.3
Cotton (L, Linear)	ACALA	WET	5.883	-0.0017		90	0.20	60.3	204.0
Cotton	STONEVILLE		3576.1	94.6	2.012	226	0.91	30.9	56.7
Cotton	MCNAIR	DRY	3698.8	165.81	2.778	342	0.46	73.8	114.4
Cotton	MCNAIR	WET	4811.0	117.02	1.534	366	0.89	27.0	59.7
Kidney Bean	CAL LT RED		2488.2	27.41	3.885	333	0.72	15.4	21.0
Kidney Bean (L)	CAL LT RED		2484.3	44.24	2.691	397	0.71	19.2	30.2
Lettuce (T)	EMPIRE		7196.6	54.87	5.512	613	0.74	36.5	45.5
Peanut (L)	NC-6		6402.5	100.12	2.226	351	0.97	36.4	63.0
Potato	NORCHIP		5900.7	93.84	1.000	742	0.63	9.9	33.5
Potato	NORCHIP		5755.6	79.26	1.654	675	0.49	20.3	42.5
Sorghum	DEKALB		8046.2	178.05	2.338	441	0.48	68.0	114.6
Soybean	CORSOY		2652.6	57.1	1.726	166	0.91	15.5	31.4
Soybean	CORSOY		1891.7	65.21	5.160	282	0.63	42.2	53.4

TABLE 5-18 (cont'd). COMPARISON OF EXPOSURE-RESPONSE CURVES CALCULATED USING THE 3-MONTH, 24-HOUR SUM06 VALUES FOR 54 NCLAN CASES

Species	Cultivar	Moisture[a]	Weibull/Linear Model Parameters[b] A	B	C	RMSE[c]	R^2[d]	3 mo 24-h SUM06[e] Values for Yield Losses of 10%	30%
Soybean	AMSOY		1907.2	75.91	2.739	390	0.41	33.4	52.1
Soybean	PELLA		2619.9	174.13	1.000	311	0.51	18.3	62.1
Soybean	WILLIAMS		2368.4	146.37	1.000	527	0.27	15.4	52.2
Soybean	CORSOY	DRY	2229.8	92.0	9.593	193	0.16	72.8	82.6
Soybean	CORSOY	WET	2913.8	311.04	1.527	330	0.38	71.3	158.4
Soybean	CORSOY	DRY	3528.1	103.83	15.709	400	0.55	90.0	97.2
Soybean	CORSOY	WET	4905.0	117.98	3.590	401	0.80	63.0	88.5
Soybean	CORSOY	DRY	5676.1	97.46	1.000	508	0.81	10.3	34.8
Soybean	CORSOY	WET	5873.9	65.73	1.319	512	0.89	11.9	30.1
Soybean	WILLIAMS	DRY	6305.2	99.18	1.456	389	0.87	21.1	48.8
Soybean	WILLIAMS	WET	7338.4	78.71	1.344	377	0.94	14.8	36.5
Soybean	HODGSON		2052.4	79.97	1.000	361	0.78	8.4	28.5
Soybean	DAVIS		3929.7	131.57	1.000	524	0.64	13.9	46.9
Soybean	DAVIS		4815.5	85.71	1.734	346	0.87	23.4	47.3
Soybean	DAVIS	DRY	2007.1	542.36	1.000	556	0.04	57.1	193.4
Soybean	DAVIS	WET	4568.0	158.57	1.539	495	0.61	36.8	81.2
Soybean	DAVIS	DRY	5775.6	90.18	3.348	920	0.55	46.0	66.3
Soybean	DAVIS	WET	8082.7	113.89	1.442	927	0.71	23.9	55.7
Soybean	YOUNG	DRY	5978.8	183.63	1.448	244	0.93	38.8	90.1
Soybean	YOUNG	WET	7045.0	145.63	1.277	424	0.93	25.0	65.0
Tobacco (L)	MCNAIR		5177.4	172.55	1.186	306	0.81	25.9	72.3
Turnip (T)	JUST RIGHT		12.7	25.68	1.806	0.810	0.96	7.4	14.5
Turnip (T)	PURPLE TOP		5.7	29.26	1.437	0.590	0.92	6.1	14.3
Turnip (T)	SHOGOIN		4.4	29.18	1.548	0.660	0.81	6.8	15.0

TABLE 5-18 (cont'd). COMPARISON OF EXPOSURE-RESPONSE CURVES CALCULATED USING THE 3-MONTH, 24-HOUR SUM06 VALUES FOR 54 NCLAN CASES

Species	Cultivar	Moisture[a]	Weibull/Linear Model Parameters[b] A	B	C	RMSE[c]	R^2[d]	3 mo 24-h SUM06[e] Values for Yield Losses of 10%	30%
Turnip (T)	TOKYO CROSS		11.7	27.83	2.142	3.250	0.78	9.7	17.2
Wheat	ABE		5149.8	52.89	3.077	399	0.90	25.5	37.8
Wheat	ARTHUR		4455.8	60.87	2.176	264	0.92	21.6	37.9
Wheat	ROLAND		5028.9	52.32	1.173	405	0.91	7.7	21.7
Wheat	ABE		6043.1	47.39	7.711	226	0.74	35.4	41.5
Wheat	ARTHUR		5446.9	72.34	2.462	349	0.57	29.0	47.6
Wheat	VONA		5384.0	27.74	1.000	608	0.88	2.9	9.9
Wheat	VONA		4451.0	33.5	1.818	654	0.64	9.7	19.0

[a]Wet refers to experiments conducted under well-watered conditions while dry refers to experiment conducted under some controlled level of drought stress.
[b]For those studies whose species name is followed by "(Linear)" a linear model was fit. A Weibull model was fit to all other studies and estimates of B parameter are in ppm-h. The yield is expressed in kg/Ha for all crops except turnip (g/plant) and lettuce (g/m). In cases where the estimated C parameter is exactly 1.0, the shape parameter has been bounded from below to obtain convergence in the nonlinear model fitting routine. For those studies whose species name is followed by "(L)" a log transformation was used to stabilize the variance. For those crops whose name is followed by "(T)" the yield is expressed as either g/plant or g/m.
[c]The root mean square error based on individual plot means.
[d]R^2 or multiple correlation coefficient measures the proportion of total variation about the mean response explained by the regression on individual plot means..
[e]The 24-h SUM06 value (ppm-h) that was predicted to cause a 10 or 30% yield loss (compared to zero SUM06).

Source: Lee et al. (1993b).

response, it is important to understand the potential of O_3 exposure, and to understand the consequences.

Several papers (Lee et al., 1988, 1991, 1993a,b; Lefohn et al., 1988; Lesser et al., 1990; Tingey et al., 1991) present a re-analysis of NCLAN data and/or data from field

TABLE 5-19. COMPARISON OF EXPOSURE-RESPONSE CURVES CALCULATED USING THE 24-HOUR W126 VALUES FOR 54 NCLAN CASES

Species	Cultivar	Moisture[a]	Weibull[b] A	B	C	RMSE[c]	R^2[d]	24-h W126[e] Values for Yield Losses of 10%	30%
Barley	CM-72	DRY	8133.2	1109.6	1.000	1214	0.13	116.9	395.8
Barley	CM-72	WET	8927.2	57439.6	1.000	1175	NA	6051.9	20487.3
Corn (L)	PIO		9605.0	92.9	2.594	650	0.93	39.0	62.4
Corn (L)	PAG		10686.7	94.5	4.190	1253	0.80	55.2	73.9
Cotton (L)	ACALA	DRY	6482.8	89.9	1.949	1075	0.47	28.3	53.0
Cotton (L)	ACALA	WET	9817.3	66.6	1.603	514	0.96	16.4	35.0
Cotton (L)	ACALA	DRY	7022.7	81.3	1.540	948	0.80	18.8	41.6
Cotton (L)	ACALA	WET	7927.1	74.7	1.070	943	0.85	9.1	28.5
Cotton (L)	ACALA	DRY	310.1	174.1	2.189	104	0.06	62.3	108.7
Cotton (L)	ACALA	WET	393.2	582.6	1.000	90	0.20	61.4	207.8
Cotton	STONEVILLE		3592.1	94.1	1.582	223	0.91	22.7	49.1
Cotton	MCNAIR	DRY	3700.9	174.1	2.430	344	0.45	68.9	113.9
Cotton	MCNAIR	WET	4817.6	113.5	1.410	360	0.89	23.0	54.6
Kidney Bean	CAL LT RED		2484.7	28.0	3.706	332	0.72	15.3	21.2
Kidney Bean (L)	CAL LT RED		2475.2	44.2	2.353	401	0.70	17.0	28.5
Lettuce (T)	EMPIRE		7197.4	54.6	4.921	614	0.74	34.6	44.3
Peanut (L)	NC-6		6386.0	97.4	1.905	370	0.96	29.9	56.7
Potato	NORCHIP		5867.2	96.3	1.000	754	0.62	10.1	34.3
Potato	NORCHIP		5777.9	113.9	1.299	675	0.48	20.1	51.5
Sorghum	DEKALB		8049.7	205.9	1.963	439	0.48	65.4	121.8
Soybean	CORSOY		2660.3	58.8	1.455	169	0.91	12.5	28.9
Soybean	CORSOY		1895.6	63.3	4.032	280	0.63	36.2	49.0

TABLE 5-19 (cont'd). COMPARISON OF EXPOSURE-RESPONSE CURVES CALCULATED USING THE 24-HOUR W126 VALUES FOR 54 NCLAN CASES

Species	Cultivar	Moisture[a]	Weibull[b] A	B	C	RMSE[c]	R^2[d]	24-h W126[e] Values for Yield Losses of 10%	30%
Soybean	AMSOY		1926.1	79.0	1.977	390	0.41	25.3	46.9
Soybean	PELLA		2602.4	161.5	1.000	314	0.50	17.0	57.6
Soybean	WILLIAMS		2341.8	138.6	1.000	533	0.25	14.6	49.4
Soybean	CORSOY	DRY	2229.3	88.2	8.632	192	0.16	67.9	78.2
Soybean	CORSOY	WET	2929.7	470.2	1.128	329	0.39	64.0	188.6
Soybean	CORSOY	DRY	3533.5	113.2	11.095	403	0.54	92.4	103.1
Soybean	CORSOY	WET	4909.5	126.5	2.803	405	0.80	56.7	87.6
Soybean	CORSOY	DRY	5597.1	95.7	1.000	526	0.80	10.1	34.1
Soybean	CORSOY	WET	5884.8	65.6	1.139	515	0.88	9.1	26.6
Soybean	WILLIAMS	DRY	6314.1	106.3	1.243	391	0.87	17.4	46.4
Soybean	WILLIAMS	WET	7352.3	80.7	1.162	368	0.95	11.6	33.2
Soybean	HODGSON		2044.6	76.2	1.000	361	0.78	8.0	27.2
Soybean	DAVIS		3837.6	130.3	1.000	530	0.63	13.7	46.5
Soybean	DAVIS		4810.8	87.5	1.494	352	0.86	19.4	43.9
Soybean	DAVIS	DRY	1992.3	537.6	1.000	558	0.03	56.6	191.7
Soybean	DAVIS	WET	4595.4	170.9	1.253	496	0.61	28.4	75.1
Soybean	DAVIS	DRY	5770.1	90.6	2.796	928	0.54	40.5	62.7
Soybean	DAVIS	WET	8101.3	118.2	1.220	939	0.70	18.7	50.8
Soybean	YOUNG	DRY	5994.2	199.8	1.251	244	0.93	33.1	87.7
Soybean	YOUNG	WET	7075.0	149.7	1.133	418	0.93	20.5	60.2

TABLE 5-19 (cont'd). COMPARISON OF EXPOSURE-RESPONSE CURVES CALCULATED USING THE 24-HOUR W126 VALUES FOR 54 NCLAN CASES

Species	Cultivar	Moisture[a]	Weibull[b] A	B	C	RMSE[c]	R^2[d]	24-h W126[e] Values for Yield Losses of 10%	30%
Tobacco (L)	MCNAIR		5223.9	179.8	1.018	291	0.83	19.7	65.3
Turnip (T)	JUST RIGHT		12.7	24.1	1.473	0.96		5.21	2.0
Turnip (T)	PURPLE TOP		5.8	28.2	1.155	1	0.92	4.0	11.6
Turnip (T)	SHOGON		4.4	28.2	1.174	1	0.82	4.1	11.7
Turnip (T)	TOKYO CROSS		11.7	26.8	1.710	3	0.78	7.2	14.7
Wheat	ABE		5138.1	53.3	2.602	407	0.89	22.4	35.8
Wheat	ARTHUR		4467.4	63.8	1.747	264	0.92	17.6	35.4
Wheat	ROL		5074.4	51.2	1.000	397	0.91	5.4	18.3
Wheat	ABE		6042.8	48.5	5.843	225	0.75	33.0	40.6
Wheat	ARTHUR		5440.0	76.1	2.100	349	0.57	26.1	46.6
Wheat	VONA		5300.8	25.0	1.000	679	0.85	2.6	8.9
Wheat	VONA		4462.7	32.3	1.517	665	0.63	7.3	16.4

[a]Wet refers to experiments conducted under wll-watered conditions while dry refers to experiments conducted under some controlled level of drought.
[b]All estimates of B parameter are in ppm-h. The yield is expressed in kg/Ha for all crops except turnip (g/plant) and lettuce (g/m). In cases where the estimated C parameter is exactly 1.0, the shape parameter has been bounded from below to obtain convergence in the nonlinear model fitting routine. For those studies whose species name is followed by "(L)" a log transformation was used to stabilize the variance. For those crops whose name is followed by "(T)" the yield is expressed as either g/plant or g/m.
[c]The root mean square error based on individual plot means.
[d]R^2 or multiple correlation coefficient measures the proportion of total variation about the mean response explained by the regression on individual plot means.
[e]The 24-h W126 value (ppm-h) that was predicted to cause a 10 or 30% yield loss (compared to zero W126).

Source: Lee et al. (1993b).

studies conducted on potato that were not part of the NCLAN project. Lee et al. (1988, 1991) examined a number of measures of O_3 exposure in relation to response data collected in the experiments. They were particularly interested in examining the ability of a seasonal mean, a cumulative exposure index, and the second highest daily maximum concentration (2HDM) to predict the biological response of the plant. They found that no particular index of O_3 concentration dominated as best in all studies, but that cumulative indexes that weighted high concentrations at the "grain-filling" stage of the life cycle were better than a seasonal mean. Seasonal means did work well within a given experiment where treatments were highly correlated. The 2HDM was consistently a poor predictor of plant response.

In a re-analysis of NCLAN data, Lesser et al. (1990) presented composite exposure-response functions for a number of crop species, or groups of species. Predicted yield losses (compared to yield at an assumed background concentration of 0.025 ppm) of up to 20% occurred at a 12 h seasonal mean of 0.06 ppm, with a loss of 10% at a 12 h mean concentration of about 0.045 ppm.

Tingey et al. (1991) and Lee et al. (1993) went on to re-analyze the crop response data using three measures of exposure: (1) the SUM06 (the cumulative sum of all hourly O_3 concentrations greater than 0.06 ppm), (2) the 7 h seasonal mean, and (3) the 2HDM. Their analysis included crops that account for 70% of all crop land in the United States and 73% of the agricultural receipts. The analysis included 31 field experiments with 12 crop species, conducted in open-top chambers and resulted in composite exposure-response functions. The results of their studies and additional re-analyses done since then are summarized in Tables 5-20 and 5-21. They concluded that to limit yield loss to 10% or less in 50% of the cases (all experiments and crops), a SUM06 of 24.4 ppm·h (or 26.4 ppm·h based on 24 h), a 7 h seasonal mean of 0.049 ppm, or a 2HDM of 0.094 ppm would be required. A SUM06 of about 37 ppm·h should limit yield losses to 20% in 50% of the cases. If one standard error were added to or subtracted account for the variability, the metrics would be reduced to 21, 0.046, and 0.088 or increased to 27.8 ppm·h, 0.049 ppm and 0.10 ppm respectively. To limit the loss to 10% or less in 75% of the cases would require 14.2 ppm·h, 0.040 ppm and 0.051 ppm respectively (Table 5-20). These values are based on studies of both well-watered and drought stressed plants.

TABLE 5-20. THE EXPOSURE LEVELS (USING VARIOUS INDICES) ESTIMATED TO CAUSE AT LEAST 10% CROP LOSS IN 50 AND 75% OF EXPERIMENTAL CASES

50th Percentile No.	SUM06	SE*	SIGMOID	SE	M7	SE	2ndHDM	SE
NCLAN Data (N=49; Wet and Dry) (?)	24.4	3.4	21.5	2.0	0.049	0.003	0.094	0.006
NCLAN Data (N=39; Wet Only)	22.3	1.0	19.4	2.3	0.046	0.003	0.090	0.010
NCLAN Data (N=54; Wet and Dry) **	26.4	3.2	23.5	2.4	NA	NA	0.099	0.011
NCLAN Data (N=42; Wet Only) **	23.4	3.1	22.9	4.7	NA	NA	0.089	0.008
NCLAN Data (N=10; Wet)	25.9	4.5	23.4	3.2	0.041	0.001	0.110	0.042
NCLAN Data (N=10; Dry)	45.7	23.3	40.6	0.1	0.059	0.014	0.119	0.017
Cotton Data (N=5)	23.6	2.3	19.3	2.3	0.041	0.001	0.066	0.032
Soybean Data (N=13)	26.2	5.4	22.6	3.6	0.044	0.005	0.085	0.013
Wheat Data (N=6)	21.3	15.2	19.3	12.7	0.061	0.018	0.098	0.059
Cotton Data (N=5) **	30.0	12.7	27.2	12.8	NA	NA	0.075	0.012
Soybean Data (N=15) **	23.9	6.5	22.0	8.0	NA	NA	0.088	0.008
Wheat Data (N=7) **	25.9	10.5	21.4	9.4	NA	NA	0.097	0.028
75th PERCENTILE #								
NCLAN Data (N=49; Wet and Dry)	14.2	4.2	11.9	5.6	0.040	0.007	0.051	0.010
NCLAN Data (N=39; Wet Only)	14.3	2.7	12.6	2.3	0.039	0.005	0.056	0.006
NCLAN Data (N=54; Wet and Dry) **	16.5	4.3	14.5	3.2	NA	NA	0.073	0.006
NCLAN Data (N=42; Wet Only) **	17.2	3.0	14.7	2.4	NA	NA	0.070	0.006
NCLAN Data (N=10; Wet)	16.4	3.7	13.7	3.2	0.040	0.001	0.080	0.032
NCLAN Data (N=10; Dry)	24.0	0.8	22.3	0.1	0.053	0.022	0.093	0.003
Cotton Data (N=5)	21.8	5.0	17.5	2.8	0.041	0.001	0.065	0.014
Soybean Data (N=13)	14.2	0.1	12.4	0.1	0.041	0.006	0.069	0.004
Wheat Data (N=6)	11.7	2.5	10.9	2.4	0.054	0.032	0.062	0.035
Cotton Data (N=5) **	21.1	6.0	16.7	5.7	NA	NA	0.070	0.034
Soybean Data (N=15) **	15.3	4.1	13.4	4.1	NA	NA	0.078	0.007
Wheat Data (N=7) **	5.1	2.6	8.5	3.4	NA	NA	0.054	0.027

The numbers in parentheses are the number of cases used in deriving the various exposure levels.
* Standard error (SE).
? NCLAN data refers to studies conducted as part of the NCLAN project. Wet and dry refer to watery regimes used in the studies, wet being well-watered, and dry meaning some level of drought stress was imposed.
** 24-h exposure statistics reported in Lee et al. (1993). Relative yield loss for 2ndHDM is relative to yield at 0.04 ppm rather than 0.00 ppm as was used in Tingey et al. (1991).

Modified from: Tingey et al. (1991).

A further analysis by Lee et al. (1993b) provides composite exposure-response functions for all NCLAN studies, as well as for soybean and wheat experiments (Table 5-21). In the analysis, they calculated the SUM06 based on 24 h per day

TABLE 5-21. SUM06 LEVELS ASSOCIATED WITH 10 AND 20% YIELD LOSS FOR 50 AND 75% OF THE NCLAN CROP STUDIES

Weibull equations (all 54 NCLAN studies):

50th Percentile[a] PRYL = 1 - exp(-[SUM06/89.497]**1.84461)
75th Percentile PRYL = 1 - exp(-[SUM06/60.901]**1.72020)

Weibull equations (all 22 NCLAN soybean studies; 15 well-watered, 7 water-stress):

50th Percentile PRYL = 1 - exp(-[SUM06/117.68]**1.46509)
75th Percentile PRYL = 1 - exp(-[SUM06/88.99]**1.47115)

Weibull equations (15 NCLAN well-watered soybean studies):

50th Percentile PRYL = 1 - exp(-[SUM06/112.75]**1.46150)
75th Percentile PRYL = 1 - exp(-[SUM06/79.62]**1.36037)

Weibull equations (7 NCLAN wheat studies):

50th Percentile PRYL = 1 - exp(-[SUM06/49.02]**3.52788)
75th Percentile PRYL = 1 - exp(-[SUM06/29.56]**1.29923)

SUM06 levels associated with 10% and 20% yield loss for 50% and 75% of the crops.

All 54 NCLAN cases

		Percent of crops	
		50%	75%
Relative	10%	26.4	16.5
Yield Loss	20%	39.7	25.5

All 22 NCLAN soybean cases

		Percent of crops	
		50%	75%
Relative	10%	25.3	19.3
Yield Loss	20%	42.3	32.1

15 well-watered soybean cases

		Percent of crops	
		50%	75%
Relative	10%	24.2	15.2
Yield Loss	20%	40.4	26.4

All 7 NCLAN wheat cases

		Percent of crops	
		50%	75%
Relative	10%	25.9	5.2
Yield Loss	20%	32.0	9.3

[a]50th and 75th percentile refer to the percentage of studies analyzed in which loss of the stated magnitude would have been prevented.

Source: Lee et al. (1993a,b).

O_3 concentrations and the resulting exposure to prevent crops from yield loss is slightly higher than they previously calculated (26.4 ppm·h versus 24.4 ppm·h, Table 5-20). A composite exposure-response function based on uncited data using GIS, TRIGRO and ZELIG models is illustrated in Figure 5-22.

Research since 1986 has largely focused on understanding the response of trees and other perennials to O_3 (covered in the next section) and of five crop species: cotton, wheat, spring rape, *Phaseolus* bean, and soybean. A number of the studies were conducted as part of NCLAN, but many were also the result of research activity in Europe. Results of these studies, as well as those species studied less intensively, are summarized in Table 5-22.

Yield losses in cotton of 13 to 19% have been reported at 12 h mean concentrations of 0.050 or 0.044 ppm by Heagle et al. (1988), Miller et al. (1988), and Temple et al. (1988b) (Table 5-22). These are typical ambient concentrations as listed under M7 (Table 5-17). The same experiments showed that drought stress reduced the predicted yield loss due to O_3, but did not eliminate it.

Wheat yields have been reduced by 0 to 29%, depending on the cultivar and exposure conditions (Adaros et al., 1991a; Fuhrer et al., 1989; Grandjean and Fuhrer, 1989; Kohut et al., 1987; Pleijel et al., 1991) (Table 5-22). In no case was a 7 h average of greater than 0.062 ppm required to cause the reported loss, but Slaughter et al. (1989) suggest that hourly concentrations above 0.06 ppm during the period following anthesis may be particularly effective in reducing yield.

Studies with spring rape in Europe have documented yield losses of 9.5 to 26.9% at 8 h growing season average concentrations ranging from 0.03 to 0.06 ppm (Adaros et al., 1991b,c) (Table 5-22).

The yield of *Phaseolus* beans (fresh pods) was reduced by 17% at a 7 h average of 0.045 ppm (Schenone et al., 1992) or 20% at an 8 h growing season average of 0.080 ppm (Bender et al., 1990). In a similar study, Heck et al. (1988) the predicted yield of sensitive cultivars was reduced an average of 17.3% by exposure to a 7 h growing season mean of 0.05 ppm, but resistant cultivars suffered only a 1.6% loss. Temple (1991) reported reductions in dry bean yield of 44 to 73% in three cultivars grown in California and exposed to a 12 h seasonal mean of 0.072 ppm. One other cultivar increased in yield in non-filtered

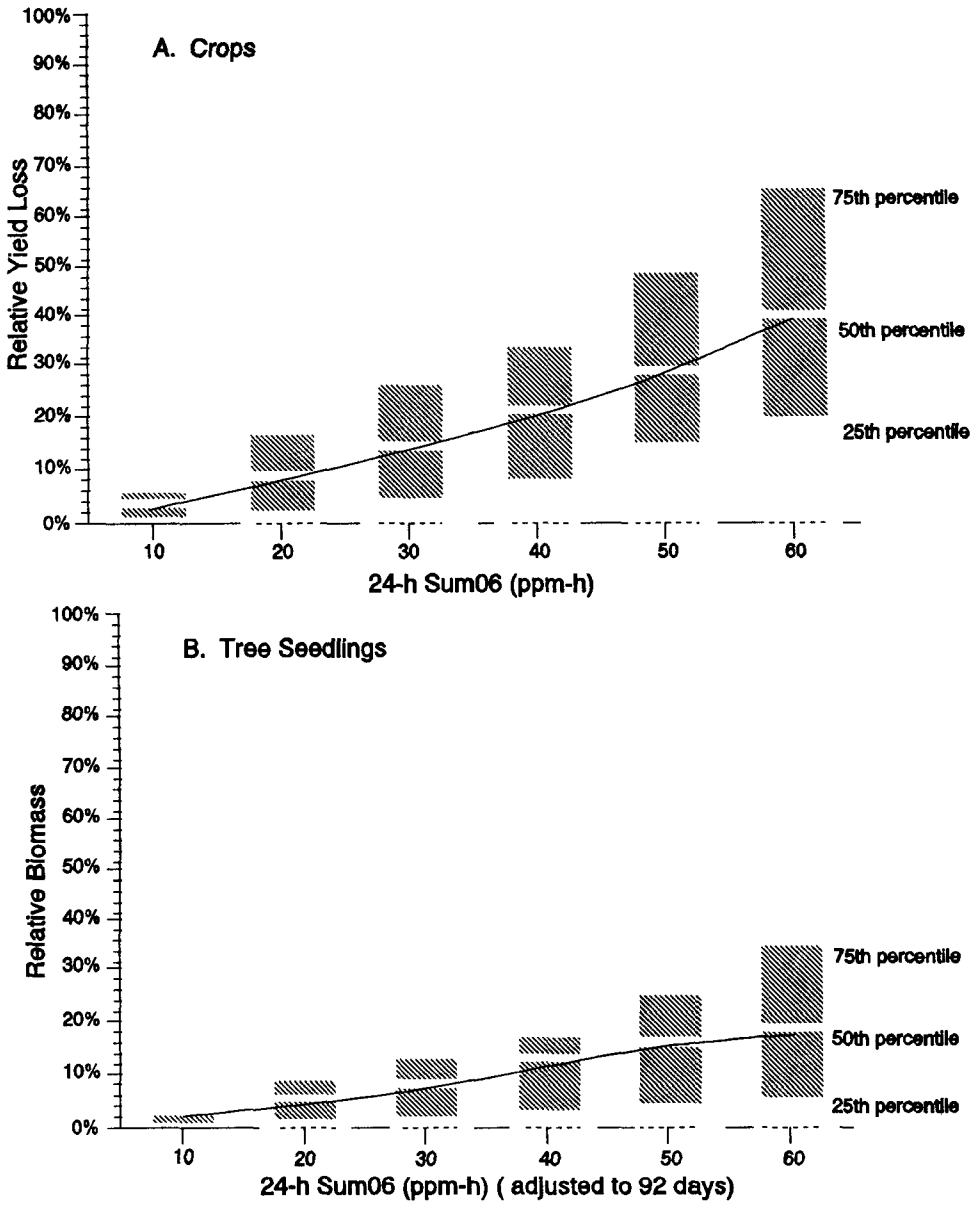

Figure 5-22. Box-plot distribution of biomass loss predictions from Weibull and linear exposure-response models that relate biomass and ozone exposure as characterized by the 24-h SUM06 statistic using data from (A) 31 crop studies from the National Crop Loss Assessment Network (NCLAN) program and (B) 26 tree seedling studies conducted at the Environmental Research Laboratory in Corvallis, Oregon; Smoky Mountain National Park, Tennessee; Michigan; Ohio; and Alabama. Separate regressions were calculated for studies with multiple harvests and/or cultivars resulting in a total of 54 individuals equations from the 31 NCLAN studies and 56 equations from the 26 seedling studies. Each equation was used to calculate the predicted relative yield or biomass loss at 10, 20, 30, 40, 50, and 60 ppm·h and the distributions of the resulting losses plotted. The solid line is the calculated Weibull fit at the 50th percentile. From Hogsett et al. (1993).

TABLE 5-22. A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Soybean	C	18 or 24 ppb vs. 59 or 72 ppb, 9 h mean	13 weeks, 2 growing seasons	OTC	seed yield	12.5% reduction over filtered air averaged over cultivars. Between cultivar differences as great as ozone effect.	Mulchi et al. (1988)
Soybean	C	23, 40, and 66 ppb 7 h mean	84 days	OTC	seed yield	15.8 and 29% reduction over 23 ppb.	Mulchi et al. (1992)
Soybean	C	97 ppb vs. 38, 23, 16, 23 ppb 7 h mean	4 31 day periods, 1 growing season	OTC in pots	seed yield	30 to 56% reduction over control, most loss in mid to late growth stage.	Heagle et al. (1991)
Soybean	C	17 to 122 ppb 7 h mean	69 days	OTC	seed yield	8% at 35 ppb to 41% at 122 ppb.	Kohut et al. (1986)
Soybean	C	25 and 50 ppb 7 h mean	about 90 days	OTC	seed yield	Predicted loss of 10%.	Heagle et al. (1986b)
Soybean	C	20 and 50 ppb 12 h mean	107 days	OTC	seed yield	Predicted loss of 13%.	Miller et al. (1989)
Soybean	C	25 and 55 ppb 7 h mean	64, 70, and 62 days, 3 growing seasons	OTC	seed yield	Predicted loss of 15%.	Heggestad and Lesser (1990)
Soybean	C	27 and 54 ppb 7 h means	about 109 and 103 days, 2 growing seasons	OTC	seed yield	Predicted loss of 12 and 14%.	Heagle et al. (1987)

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TABLE 5-22 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Soybean	C	filtered and non-filtered air-concentration not reported	about 125 days 2 growing seasons	OTC	seed yield	No difference.	Johnston and Shriner (1986)
Soybean	C	10 to 130 ppb	8 weeks, 6.8 h/day	GC	biomass	Predicted reduction of 16 or 33% at 60 and 100 ppb vs 25 ppb.	Amundson et al. (1986)
Soybean	C	200 ppb	12 h, up to 4 times	GC	shoot and root weight	No effect at maturity.	Smith et al. (1990)
Cotton	C	15 to 111 ppb 12 h mean	123 days	OTC	leaf, stem, and root weight	Up to 42% reduction in leaf and stem, and 61% reduction in root weights.	Temple et al. (1988c)
Cotton	C	10 to 90 ppb 12 h mean	102 days	OTC	lint weight	40 to 71% reduction at highest concentration determinant cultivars more susceptible.	Temple (1990b)
Cotton	C	25 to 74 ppb 12 h mean	123 days	OTC	lint weight	Predicted loss of 26.2% at 74 ppb.	Temple et al. (1988b)
Cotton	C	22 to 44 ppb 12 h mean	124 days	OTC	lint weight	Predicted loss of 19% at 44 ppb.	Heagle et al. (1988)
Cotton	C	26 to 104 ppb 7 h mean	119 days	OTC	lint weight	Predicted loss of 11% at 53 ppb.	Heagle et al. (1986a)

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TABLE 5-22 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Bean-Fresh	C	35 to 132 ppb 7 h mean	42 days	OTC in pots	green pod weight	Significant yield reductions of >10% in 8 lines at 63 ppb 7 h mean.	Eason and Reinert (1991)
Bean-Fresh	C	11 to 40 ppb 12 h mean, 7 to 42 ppm·h	69 days	OTC	pod weight	15.5% reduction at 45 ppb (39 ppm·h).	Schenone et al. (1992)
Bean-Fresh	C	26 to 126 ppb 7 h mean	26 days and 44 days, early and late in season	OTC in pots	pod weight	3.5 to 26% reduction in resistant and sensitive cultivars at 55-60 ppb.	Heck et al. (1988)
Bean-Fresh	C	24 to 109 ppb 8 h mean	43 days 34 days, 2 growing seasons	OTC	pod weight	20% reduction at 80 ppb.	Bender et al. (1990)
Bean-Dry	C	15 to 116 ppb 12 h mean, 339 ppb highest hour	54 days	OTC	seed yield	55 to 75% reduction at 72 ppb 12 h mean, 198 highest hour.	Temple (1991)
Bean-Dry	C	10 to 50 ppb, 7 h mean	86 days	OTC	seed weight	26-42% reduction at 38 to 50 ppb.	Sanders et al. (1992)
Bean-Dry	C	300 ppb	3 h- two exposures	GC	dry weight	growth response detected if exposure separated by 3 to 5 days.	McCool et al. (1988)
Wheat-Spring	C	14 to 46 ppb 24 h mean	79, 92 and 79 days in 3 growing seasons	OTC	seed weight	13% reduction at 40 ppb.	Fuhrer et al. (1989)

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TABLE 5-22 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[c]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Wheat-Spring	C	21.6 to 80 and 24.6 to 93.5 ppm·h	82 and 88 days in 2 growing seasons	OTC	seed weight	48 to 54% reduction at 80 and 93.5 ppm·h.	Grandjean and Fuhrer (1989)
Wheat-Spring	C	3 to 56 ppb 7 h mean	61 and 55 days in 2 growing seasons	OTC	seed weight	7% reduction at 15 and 22 ppb.	Pleijel et al. (1991)
Wheat-Spring	C	8 to 101 and 20-221 ppb 8 h mean	118 and 98 days in 2 growing seasons	OTC	seed weight	10% reduction at 17 to 23 ppb.	Adaros et al. (1991a)
Wheat-Spring	C	0 to 38 ppb 8 h mean	entire growing season	OTC	seed weight	5% reduction at 38 ppb.	DeTemmerman et al. (1992)
Wheat-Spring	C	17 to 77 ppb 7 h mean	90 and 87 days in 2 growing seasons	OTC	seed weight	9.5 to 11.6 reduction at 37 and 45 ppb.	Fuhrer et al. (1992)
Wheat-Spring	C	25 to 75 ppb 8 h mean	40 days	OTC	total weight	Reductions at 75 ppb.	Johnsen et al. (1992)
Wheat-Spring	C	6 to 10 ppb 6 h/day	21 days	GC	shoot dry weight	Decreased 35-60% at 101 ppb in low and high light.	Mortensen (1990b)
Wheat-Spring	C	10 to 125 ppb 6 h/day	21 days and 17 days	GC	top dry weight	Reduced by up to 35%.	Mortensen (1990c)

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TABLE 5-22 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Wheat-Winter	C	11 to 42 ppb 14 week mean	109 days	OTC	seed weight	No effect.	Olszyk et al. (1986)
Wheat-Winter	C	30 to 93 ppb 4 h mean	39 and 40 days in 2 growing seasons 5 day/week 4 h/day	OTC	seed weight	Exposures >60 ppb during anthesis reduce yield.	Slaughter et al. (1989)
Wheat-Winter	C	27 to 96 ppb 7 h mean	36 days	OTC	seed weight/ head	50% reduction at 96 ppb.	Amundson et al. (1987)
Wheat-Winter	C	22 to 96 ppb 7 h mean	65 days and 36 days in 2 growing seasons	OTC	seed weight	33% and 22% reduction at 42 and 54 ppb.	Kohut et al. (1987)
Wheat-Winter	C	23 to 123 ppb 4 h/day	5 days at anthesis	OTC	seed weight	Up to 28% reduction.	Mulchi et al. (1986)
Barley-Spring	C	6 to 45 ppb 7 h mean	96 days	OTC	seed weight	No effect.	Pleijel et al. (1992)
Barley-Spring	C	0.6-27 ppb monthly mean	growing season	OTC	seed weight	No effect.	Weigel et al. (1987)
Barley-Spring	C	0.8-83 ppb 8 h mean	97, 108 and 98 days in 3 growing seasons	OTC in pots	seed weight	0-13% reduction at highest.	Adaros et al. (1991b)

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TABLE 5-22 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Rape-Spring	C	25 to 75 ppb 8 h mean	31 days	OTC	premature senescence	Increased at 75 ppb.	Johnsen et al. (1992)
Rape-Spring	C	0.8-83 ppb 8 h mean	89, 113 and 84 days in 3 growing seasons	OTC in pots	seed weight	9.4-16% reduction at 30 or 51 ppb.	Adaros et al. (1991b)
Rape-Spring	C	43 to 60 ppb 8 h mean	89, 113 and 84 days in 3 growing seasons	OTC in pots	seed weight	12-27% reduction.	Adaros et al. (1991c)
Tomato	C	13 to 109 12 h mean 79.5 ppm h	75 days	OTC	fresh weight	17 to 54% reduction at 109, no reduction at ambient.	Temple (1990a)
Tomato	C	10 to 85 ppb 6 h/day	12-21 days	GC	shoot dry weight	35 to 62% reduction.	Mortensen (1992b)
Tomato	C	18 to 66 ppb 12 h mean	11 weeks	OTC	fresh fruit weight	No effect.	Takemoto et al. (1988c)
Silene acaulis		5 to 80 ppb 8 h/day	up to 90 days	GC	dry weight	25% reduction at 80 ppb.	Mortensen and Nilsen (1992)
Plantago lanceolata		5 to 80 ppb 8 h/day	up to 90 days	GC	dry weight	14% reduction at 50 ppb.	Mortensen and Nilsen (1992)
16 other species		5 to 80 ppb 8 h/day	up to 90 days	GC	dry weight	No effect.	Mortensen and Nilsen (1992)

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TABLE 5-22 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Radish	C	20 or 70 ppb 24 h mean	27 days	GC	shoot and root growth	36 and 45% reduction at 70 ppb.	Barnes and Pfirrman (1992)
Lettuce	C	21 - 128 ppb 7 h mean	52 days	OTC	head weight	Significant reduction at 83 ppb; 35% at 128 ppb.	Temple et al. (1986)
Lettuce	C	10 to 34 ppb 7 week mean	64 days	OTC	fresh weight	No effect.	Olszyk et al. (1986)
Faba bean	C	6 or 15 ppb 24 h mean	134 days	OTC	seed weight	No effect.	Sanders et al. (1990)
Fenugreek	C	120 ppb 7 h/day	4 weeks	CC	dry weight	No significant effect.	Kasana (1991)
Chickpea	C	120 ppb 7 h/day	4 weeks	CC	dry weight	No significant effect.	Kasana (1991)
Black-gram	C	120 ppb 7 h/day	4 weeks	CC	dry weight	No significant effect.	Kasana (1991)
Rice	C	0 to 200 ppb 5 h/day	5 days/week 15 weeks	OTC	seed weight	12 to 21% reduction at 200 ppb.	Kats et al. (1985)
Rice	C	50 ppb 24 h mean	8 weeks	GC	dry weight	No effect at 50 ppb.	Nouchi et al. (1991)
Watermelon	C	15 to 27 ppb 7 h mean	81 days	OTC	fresh weight and number (marketable)	20.8 and 21.5% reduction at 27 ppb.	Snyder et al. (1991)
Pea	C	10 to 35 ppb 12 h mean	58 and 52 days in 2 growing seasons	OF	fresh weight	linear decrease in yield with increasing O_3	Runeckles et al. (1990)

TABLE 5-22 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF ANNUAL PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Green pepper	C	19 to 66 ppb 12 h mean	77 days	OTC	fresh fruit weight	12% reduction at 66 ppb.	Takemoto et al. (1988c)
Green pepper	C	18 to 66 ppb 12 h mean	11 weeks	OTC	fresh fruit weight	13% reduction in fruit weight at 66 ppb.	Takemoto et al. (1988c)
Celery	C	18 to 66 ppb 12 h mean	11 weeks	OTC	shoot dy weight	12% reduction at 66 ppb.	Takemoto et al. (1988c)

[a]E = evergreen, D = deciduous, C = crop. PC = perennial crop.
[b]Means are seasonal means unless specified. Maximums are 1 h seasonal maxima unless otherwise specified. Cumulative exposures are SUM00 unless otherwise specified, accumulation based on 24 h/day unless otherwise noted.
[c]OTC = open-top chamber with plants in ground unless specified in pots; CC = closed chamber, outside; GC = controlled environment growth chamber or CSTR; GH = greenhouse; F = field; OF = open-field fumigation.
[d]The effect reported in the study that is a measure of growth, yield, or productivity.
[e]Effect measured at specified ozone concentration, over the range specified under concentration, or predicted (if specified) to occur based on relationships developed in the experiment.

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chambers, but was severely affected in higher concentration O_3 treatments. Sanders et al. (1992) also observed yield stimulation at an 7 h growing season mean of 25 ppb (often considered background in the U.S.), however, significant yield reductions were measured as O_3 concentrations increased to 50 ppb (7 h seasonal mean).

A number of studies have shown soybean yields to be reduced by 10 to 15% at 7 or 12 h seasonal mean concentrations of 0.05 to 0.055 (Heagle et al., 1986b, 1987; Heggestad and Lesser, 1990; Miller et al., 1989).

A number of the studies cited above, and some of those in Table 5-22, were conducted as part of NCLAN, are considered in the discussions of Tingey et al. (1991), Lee et al. (1993a,b), and Lesser et al. (1990), but many of the experiments (primarily those not part of NCLAN) were not included in their analyses. While the range of variability in species response to O_3 is apparent, these studies support, for the most part, the conclusions of U.S. Environmental Protection Agency (1986), Tingey et al. (1991), and Lesser et al. (1990). Table 5-22 summarizes the studies reporting the response of annual plants, particularly crops, as growth, dry weight, or yield to O_3 exposures (concentrations x time) under experimental conditions since the previous criteria document (U.S. Environmental Protection Agency, 1986). Based on the results of the studies reviewed in this section, including the reanalysis of NCLAN, exposures for a three month period to O_3 concentrations currently occurring in the ambient air (0.048 to 0.06 ppm, 7 h seasonal mean, See M7, Table 5-17) have been shown to cause losses of 10% or more in the yield of the majority of major crop plants grown in the country. A number of crop species are more sensitive, and greater losses could be expected (Tables 5-18 through 5-22). It should be noted that a variety of methodologies have been used to generate these data. Generally speaking, data obtained through growth chamber experiments, and experiments conducted using potted plants, may be less reliable when assessing the effects of O_3 than results from field growth plants.

5.6.4 Effects of Ozone on Long-Lived Plants

Quantifying exposure-response in the case of perennial plants (agricultural crops such as pastures, alfalfa and shrubs and trees) is complicated by they fact that they can receive multi-year exposures and because the results of exposures in a previous year, or over a number of years, may be cumulative. Reduction in growth and productivity, a result of altered carbon

(sugar) allocation, may appear only after a number of years or when carbohydrate reserves are depleted (U.S. Environmental Protection Agency, 1986; Lawrence et al., 1993b; Garner, 1991; Garner et al., 1989). A further complication is that in the case of evergreen plants, the life span of a leaf exceeds one year, and may be on the plant for several years. In such cases, loss of a leaf or a reduction in photosynthetic capacity may have a large effect on a plant's ability to survive and grow. Physiological differences among species (rates of gas exchange, for instance) may have a tendency to equalize exposure over a number of years, however, as shown in Reich's (1987) analysis of crops, hardwoods and conifers, and Pye's analysis of tree species (1988). Unfortunately, there is little experimental data regarding the effects of long-term O_3 exposure on perennial plants, as only a few experimental studies have extended exposures beyond a single growing season. Most of what is known regarding the effects of O_3 on mature trees is from field observations. Some studies that have extended observation of growth alterations into the season following exposures and thus observed "carry-over effects" in several species. Hogsett et al. (1989) reported altered bud elongation in ponderosa pine, lodgepole pine and western hemlock following a season of O_3. Altered root regrowth in ponderosa pine in the season following exposure that was correlated with root storage carbohydrate was observed by Andersen et al. (1991). Most studies have used seedlings due to the difficulty of exposing large trees. The extrapolation from seedlings to large trees and to forest stands is not straight-forward, and will, most likely, depend on the use of models (Hogsett et al., 1993; Laurence et al., 1993a,b; Taylor and Hanson, 1992). Correlative studies, such as those conducted in the San Bernadino mountains of California, indicate potentially large impacts on ecosystems (U.S. Environmental Protection Agency, 1986). This section will address three distinct types of long-lived plants: multiple-year agricultural crops, deciduous shrubs and trees, and evergreen coniferous trees.

5.6.4.1 Perennial Agricultural Crops

Cooley and Manning (1988) conducted a greenhouse study of the response of alfalfa to O_3 applied at 0.06 to 0.08 ppm for 6 h per day, 5 days a week for 8 weeks during two different years (to different plants). Ozone treatment reduced the growth and relative growth rate (by about 15 to 20% for tops and 20 to 40% for roots) of plants before cutting, when compared to a filtered-air control. The growth of roots was more affected than the growth of

tops, with a shift in the allocation pattern. In the second year of the study, O_3 exposure was continued after the plants were harvested and the impact of exposure on regrowth was determined. In this case, they found that the relative growth rate in O_3 exposed plants was higher, perhaps because of an increased demand for carbon by the root systems of the O_3-stressed plants. It is unclear whether these plants would sustain their increased growth, and in fact, the authors speculate that the increased growth, in lieu of partitioning carbon to other compounds, might alter the cold hardiness of the plants.

Ozone has been demonstrated to affect the growth of field grown alfalfa. Temple et al. (1988a) reported a two-year study of alfalfa in which O_3 at ambient concentrations (0.049 in 1984 and 0.042 ppm in 1985 for the seasonal 12-h means April to October) did not affect the growth and yield of the plants, but at 12 h seasonal means of 0.063 and 0.078 ppm, yield was reduced by about 15 and 19%. The exposure-response functions for the two years were homogeneous; there was no indication of cumulative effect of O_3 exposure, however, crown weight, an indicator of health and vigor, of exposed plants was significantly reduced.

In a different field experiment conducted to determine the interactive effects of O_3 and simulated acid fog on stomatal conductance, photosynthesis, foliar injury, and yield of an established stand of alfalfa, plants were exposed 12 h daily for 4 weeks (Temple et al., 1987). Ozone was added in proportion to its concentration in the ambient air. Ambient O_3 concentrations during the experiment were 0.043 ppm. Ozone injury symptoms appeared on the alfalfa exposed to 0.098 ppm (NF $\times$ 2.0), one week after the start of the regrowth period. When exposures were at 0.081 and 0.066 ppm (NF $\times$ 1.7 and NF $\times$ 1.3), more than a week was required for injury to appear. A one month exposure of the plants at the end of the growing season resulted in a reduction of about 2.5% in aboveground yield at a 12 h seasonal mean concentration of 0.04 ppm. At a concentration of 0.066 ppm, the exposure resulted in a reduction in yield of approximately 18%. It should be noted that the whole plant was exposed to ambient O_3 for the growing season, only new leaves that had developed after harvest received the one month exposure. Ozone exposures could shorten the productive life of alfalfa stands in addition to its effect on yield.

The sensitivity of alfalfa to O_3 had been demonstrated in an earlier study using filtered air in field chambers (Neely et al., 1977; U.S. Environmental Protection Agency, 1986). There was a 49% decrease in top dry weight when plants were exposed to 0.05 ppm,

7-h/day for 68 days. Increasing the concentration to 0.1 ppm produced a 51% loss in dry weight at harvest.

Kohut et al. (1988) and Heagle et al. (1989) experimented with forage mixtures characteristic of the northeast and southeast, respectively. In both cases, exposure to O_3 resulted in a reduction in total forage yield of about 10 to 20% at 12 h seasonal mean O_3 concentrations of 0.045 to 0.05 ppm. In both cases, the clover component of the mix was more sensitive than the grass, and was reduced in prevalence in the stand. The relevance of these studies to competition and species composition is discussed in the ecosystem response section (Section 5.7).

Results of studies or perennial plants conducted since 1986 are summarized in Table 5-23. As with single-season agricultural crops, yields of multiple-year forage crops are reduced at concentrations at, or near ambient (0.04 to 0.06 ppm) in many parts of the country (Table 5-17).

5.6.4.2 Effects of Ozone on Deciduous Shrubs and Trees

Most of the information concerning the response of deciduous shrubs and trees to episodes, season-long, or multiple-year exposures to O_3 is based on field observations. The longevity of perennial plants, and the size in the case of trees, makes experimental their study under experimental conditions difficult. For this reason, there is little experimental data concerning the response of deciduous shrubs and trees.

Most of the hardwood experiments included in Reich's analysis (1987), for example, were exposed under laboratory or greenhouse conditions to relatively high concentrations for short periods of time. Although exposures durations of weeks were conducted, square-wave exposure regimes that do not capture important characteristics of ambient exposure were used. In addition, in Pye (1988), the majority of the studies were conducted in laboratory or greenhouse. The results of a few open-top chamber studies are cited, however, the majority of these studies used O_3 concentrations 0.10 ppm or higher. While the studies reported in Table 6-23 of U.S. Environmental Protection Agency (1986) (see Table 5-16) document the sensitivity of the seedlings of some species grown in chambers, little information of value with regard to tree growth or biomass production in the long-term can be extrapolated from

TABLE 5-23. A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, PRODUCTIVITY, OR YIELD OF PERENNIAL CROP PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Strawberry	PC	18 to 66 ppb 12 h mean	11 weeks	OTC	fresh fruit weight	20% increase in fruit weight at 66 ppb.	Takemoto et al. (1988c)
Phleum pratense	PC	10 to 55 ppb 7 h mean	5 weeks	GC	shoot dry weight	45% reduction at 55 ppb.	Mortensen (1992a)
Dactylis glomerata	PC	10 to 55 ppb 7 h mean	5 weeks	GC	shoot dry weight	28% reduction at 55 ppb.	Mortensen (1992a)
Poa pratensis	PC	10 to 55 ppb 7 h mean	5 weeks	GC	shoot dry weight	28% reduction at 55 ppb.	Mortensen (1992a)
Festuca rubra	PC	10 to 55 ppb 7 h mean	5 weeks	GC	shoot dry weight	23% reduction at 55 ppb.	Mortensen (1992a)
Festuca pratensis	PC	10 to 55 ppb 7 h mean	5 weeks	GC	shoot dry weight	16% reduction at 55 ppb.	Mortensen (1992a)
Agrostis tenuis	PC	10 to 55 ppb 7 h mean	5 weeks	GC	shoot dry weight	No effect.	Mortensen (1992a)
Lolium perenne	PC	62 ppb 7 h mean	5 weeks	GC	shoot dry weight	No effect.	Mortensen (1992a)
Trifolium pratense	PC	6 to 59 ppb 7 h mean	5 weeks	GC	shoot dry weight	30% reduction at 59 ppb.	Mortensen (1992a)
Plantago major	PC	70 ppb 7 h mean	8 weeks	GC	total dry weight	Reduced up to 36% depending on growth stage.	Reiling and Davison (1992)
Red clover	PC	19 to 62 ppb 12 h mean	83 and 91 days in 2 growing seasons	OTC	dry weight	11% reduction at 62 ppb.	Kohut et al. (1988)

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TABLE 5-23 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, OR PRODUCTIVITY OF PERENNIAL CROP PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Timothy	PC	19 to 62 ppb 12 h mean	83 and 91 days in 2 growing seasons	OTC	dry weight	No effect.	Kohut et al. (1988)
Ladino clover tall fescue pasture	PC	22 to 114 ppb 12 h mean	5 3-4 week exposure periods. 6 3-4 week exposures in 2 years	OTC	shoot dry weight root dry weight	18 to 50% reduction SDW at 40 to 47 ppb clover 25% reduction RDW at 40 to 47 ppb. SDW increased by up to 50% in fescue.	Rebbeck et al. (1988)
Ladino clover	PC	28 to 46 ppb 12 h mean	180 and 191 days in 2 growing seasons	OTC	dry weight	Predicted yield of mix reduced 10% with 19% decrease in clover and 19% increase in fescue at 46 ppb.	Heagle et al. (1989)
Alfalfa	PC	14 to 98 ppb 12 h mean	32 days	OTC	dry weight	2.4% reduction at 40 ppb, 18.3% reduction at 66 ppb	Temple et al. (1987)
Alfalfa	PC	20 to 53 ppb 12 h mean	11 weeks	OTC	dry weight	22% reduction at 53 ppb.	Takemoto et al. (1988a)
Alfalfa	PC	18 to 66 ppb 12 h mean	11 weeks	OTC	shoot dry weight	22% reduction at 36 ppb.	Takemoto et al. (1988c)
Alfalfa	PC	10 to 109 ppb 12 h mean	208 and 200 days in 2 growing seasons	OTC	dry weight	0 to 25% reduction at levels of 38 ppb and above.	Temple et al. (1988a)
Alfalfa	PC	60 to 80 ppb 6 h day	5 days/week for 8 weeks	GH	relative growth rate	Reduced up to 40% in Saranac.	Cooley and Manning (1988)

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TABLE 5-23 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH, OR PRODUCTIVITY OF PERENNIAL CROP PLANTS PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Grape	PC	not reported	2 growing seasons	OTC	Yield	No effects of ambient air vs. filtration.	Musselman et al. (1985)

[a]E = evergreen. D = deciduous, C = crop, PC = perennial crop.
[b]Means are seasonal means unless specified. Maximums are 1 h seasonal maxima unless otherwise specified. Cumulative exposures are SUM00 unless otherwise specified, accumulation based on 24 h/day unless otherwise noted.
[c]OTC = open-top chamber with plants in ground unless specified in pots; CC = closed chamber, outside; GC = controlled environment growth chamber or CSTR; GH = greenhouse; F = field; OF = open-field fumigation.
[d]The effect reported in the study that is a measure of growth, yield, or productivity.
[e]Effect measured at specified ozone concentration, over the range specified under concentration, or predicted (if specified) to occur based on relationships developed in the experiment.

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the experiments. Trees, because of their size, are difficult to study under controlled conditions, therefore, most experiments have used seedlings in pots or in open top chambers. Since 1986, a number of studies have been conducted documenting the sensitivity of hardwoods to O_3 (Table 5-24). Some species, such as black cherry, are very sensitive (Davis and Skelly, 1992, 1992b; Simini et al., 1992), with SUM06 exposures as low as 12.9 ppm·h over 92 days (concentrations not given) predicted to cause a 10% yield loss (Hogsett et al., 1993; Table 5-25). Based on studies previously reviewed, the growth of some hardwood species, particularly those of the genus *Populus*, may be affected by ambient concentrations of O_3 (U.S. Environmental Protection Agency, 1978, 1986).

In a studies of the response of aspen clones to O_3 at two field sites in Michigan, Karnosky et al. (1992a,b) documented reductions in stem weight of up to 46% in sensitive aspen clones after 70 days of exposure in open-top chambers to 0.08 ppm for 6 h per day, 3 days per week.

Tjoelker and Luxmoore (1991) found leaf abscission on tulip poplar seedlings to be increased by exposure to a 7 h seasonal mean concentration of 0.108 ppm, resulting in a doubling of the leaf turnover rate, but this was not translated into an effect on growth, perhaps due to the indeterminate growth habit of the plant. In such plants, leaf production continues throughout the growing season, which may permit the tree to maintain an optimal leaf area. However, continued leaf growth could deplete carbon or nitrogen reserves.

Samuelson and Edwards (1993) found canopy weight of 30 year old northen red oak, exposed in large open-top chambers, to be reduced by 41% after exposure for 177 days at a 7-h seasonal mean of 0.069 ppm (87 ppm·h SUM00) compared to a sub-ambient treatment at a 7-h seasonal mean of 0.015 ppm (18 ppm·h SUM00) a concentration found nowhere in the world. Two-year old seedlings were not affected by similar exposures.

Hogsett et al. (1993) have developed exposure-response functions using uncited data for aspen, red alder, black cherry, red maple, and tulip poplar (Table 5-25), as well as composite functions for deciduous tree seedlings (Table 5-26). Their results show that, for 28 deciduous seedling cases, a SUM06 exposure of 31.5 ppm·h over 92 days a mean concentration of approximately 0.055 ppm) should result in less than a 10% yield (biomass) reduction in 50% of the cases. A 20% reduction in yield should result from a SUM06

TABLE 5-24. A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF DECIDUOUS SHRUBS AND TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Almond	D/PC	38 to 112 ppb 12 h mean	153 days	OTC	total dry weight	Linear reduction in 2 cultivars, no effect in three.	Retzlaff et al. (1992a)
Almond	D/PC	30 to 117 ppb 12 h mean	3.5 mo	OTC	cross sectional area	6% reduction at 51 ppb.	Retzlaff et al. (1991a)
Almond	D/PC	250 ppb 4 h/wk	16 weeks in each of 2 growing seasons	CC	net growth	28 and 36% reduction in year 1 and 2.	McCool and Musselman (1990)
Plum	D/PC	44 to 111 ppb 12 h mean	191 and 213 days	OTC	number of fruit per tree	29% fewer fruit at ambient and above.	Retzlaff et al. (1992b)
Plum	D/PC	30 to 117 ppb 12 h mean	3.5 mo	OTC	cross sectional area	19% reduction at 51 ppb.	Retzlaff et al. (1991b)
Pear	D/PC	30 to 117 ppb 12 h mean	3.5 mo	OTC	cross sectional area	8% reduction at 51 ppb.	Retzlaff et al. (1991b)
Apricot	D/PC	30 to 117 ppb 12 h mean	3.5 mo	OTC	cross sectional area	53% reduction at 117 ppb.	Retzlaff et al. (1991b)
Rhus trilobata	D	10 to 75 ppb 12 h mean	3 mo	OTC in pots	growth	Increase in leaf weight in ambient air. No other effect.	Temple (1989)

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TABLE 5-24 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF DECIDUOUS SHRUBS AND TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Black Cherry	D	16 to 67 ppb 12 h mean	3 growing seasons	OTC	growth and leaf dynamics	Leaf abscission increased with increasing ozone.	Simini et al. (1992)
Black Cherry	D	40 or 80 ppb 7 h/day 5 days/week	8 or 12 weeks	GC	growth	Reduced leaf, stem, and root dry weight, and height at 80 ppb.	Davis and Skelly (1992)
Red Oak	D	18 to 87 ppm·h 15 to 69 ppb 7-h mean	177 days	OTC	tree canopy	Reduced 41% at 82 ppm·h or 69 ppb 7-h mean.	Samuelson and Edwards (1993)
Red Oak	D	16 to 67 ppb 12 h mean	3 growing seasons	OTC	growth and leaf dynamics	No effect.	Simini et al. (1992)
Red Oak	D	40 or 80 ppb 7 h/day 5 days/week	8 or 12 weeks	GC	growth	Reduced root dry weight at 80 ppb.	Davis and Skelly (1992)
Red Maple	D	16 to 67 ppb 12 h mean	3 growing seasons	OTC	growth and leaf dynamics	No effect.	Simini et al. (1992)
Red Maple	D	40 or 80 ppb 7 h/day 5 days/week	8 or 12 weeks	GC	growth	Reduced stem diameter and dry weight at 80 ppb.	Davis and Skelly (1992)
Tulip Poplar	D	16 to 67 ppb 12 h mean	3 growing seasons	OTC	growth and leaf dynamics	Leaf abscission increased with increasing ozone.	Simini et al. (1992)

TABLE 5-24 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF DECIDUOUS SHRUBS AND TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Yellow Poplar	D	40 or 80 ppb 7 h/day 5 days/week	8 or 12 weeks	GC	growth	Reduced leaf dry weight and stem diameter at 80 ppb.	Davis and Skelly (1992)
European Beech	D	10 to 90 ppb weekly mean	5 years	OTC	growth	Reduced shoot growth and leaf area.	Billen et al. (1990)
Aspen	D	80 ppb 6 h/day 3 days/week	70 and 92 days in 2 growing seasons	OTC	stem weight	No effect on tolerant clones 46% reduction for sensitive clones in one year 5% (tolerant) and 74% (sensitive) reductions in the second year.	Karnosky et al. (1992b)
Aspen	D	filtered air or 80 ppb 6 h/day 3 days/week	93 days at 2 sites in Michigan	OTC	growth	18 to 26% reduction in diameter growth.	Karnosky et al. (1992a)
Aspen	D	ambient+ 27 51, or 102 ppb exposure period mean	105 days	CC	dry weight	40% reduction—44% reduction in early growth the following year.	Keller (1988)
Yellow Poplar	D	0 to 200 ppb 8 h/day 3 days/week	4.5 mo	GC	growth	Up to a 24% reduction at 200 ppb, but moderated by pH treatment.	Jensen and Patton (1990)
Paper Birch	D	60 to 80 ppb 7 h/day 5 days/week	12 weeks	GH	dry weight	Decreased shoot and root weight and leaf area.	Keane and Manning (1988)

TABLE 5-24 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF DECIDUOUS SHRUBS AND TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Betula pubescens	D	25 to 82 ppb 7 h/day	50 days	GC	dry weight	Shoot and root dry weight decreased linearly with ozone.	Mortensen and Skre (1990)
Betula pubescens	D	25 to 82 ppb 7 h/day	50 days	GC	dry weight	Shoot and root dry weight decreased linearly with ozone.	Mortensen and Skre (1990)
Alnus incana	D	25 to 82 ppb 7 h/day	50 days	GC	dry weight	Shoot and root dry weight decreased linearly with ozone.	Mortensen and Skre (1990)

[a]E = evergreen, D = deciduous, C = crop, PC = perennial crop.
[b]Means are seasonal means unless specified. Maximums are 1 h seasonal maxima unless otherwise specified. Cumulative exposures are SUM00 unless otherwise specified, accumulation based on 24 h/day unless otherwise noted.
[c]OTC = open-top chamber with plants in ground unless specified in pots; CC = closed chamber, outside; GC = controlled environment growth chamber or CSTR; GH = greenhouse; F = field; OF = open-field fumigation.
[d]The effect reported in the study that is a measure of growth, yield, or productivity.
[e]Effect measured at specified ozone concentration, over the range specified under concentration, or predicted (if specified) to occur based on relationships developed in the experiment.

TABLE 5-25. EXPOSURE-RESPONSE EQUATIONS THAT RELATE TOTAL BIOMASS (FOLIAGE, STEM, AND ROOT) TO 24-HOUR SUM06 EXPOSURES (C) ADJUSTED TO 92 DAYS (ppm-h/year)

Rate of Growth	Habit	Study	Species	Location (State)	Exposure[b] Days	Year	Harvests[a]	Weibull Parameters A	B	C	SUM06 for Loss of[c] 10%	30%
FAST	D	1	Aspen - wild	OR	84	1989	1	9.9	96.3	1.316	19.09	48.21
FAST	D	1	Aspen - wild	OR	84	1989	2	17.7	165.2	1.000	19.06	64.54
FAST	D	2	Aspen - wild	OR	118	1991	1	31.0	130.0	3.062	48.62	72.41
FAST	D	2	Aspen - wild	OR	118	1991	2	75.6	124.9	5.529	64.80	80.79
FAST	D	3	Aspen - wild	OR	112	1990	1	67.8	111.0	6.532	64.60	77.86
FAST	D	3	Aspen - wild	OR	112	1990	2	96.9	142.1	1.257	19.48	51.40
FAST	D	4	Aspen 216	MI	82	1990	1	54.5	121.1	1.609	33.56	71.60
FAST	D	4	Aspen 253	MI	82	1990	1	73.1	265.5	1.000	31.38	106.23
FAST	D	4	Aspen 259	MI	82	1990	1	79.1	92.7	1.000	10.96	37.10
FAST	D	4	Aspen 271	MI	82	1990	1	91.3	44.9	8.964	39.20	44.91
FAST	D	5	Aspen 216	MI	98	1991	1	37.4	128.6	1.000	12.72	43.06
FAST	D	5	Aspen 259	MI	98	1991	1	35.2	95.9	1.000	9.49	32.11
FAST	D	5	Aspen 271	MI	98	1991	1	35.7	73.1	4.012	39.16	53.07
FAST	D	6	Aspen - wild	MI	98	1991	1	19.0	263.1	1.000	26.02	88.08
SLOW	E	7	Douglas Fir	OR	113	1989-90	1	16.8	462.7	1.844	111.17	215.37
SLOW	E	7	Douglas Fir	OR	113	1989-90	2	27.9	3.8E+17	1.000	250.00	250.00
SLOW	E	7	Douglas Fir	OR	234	1989-90	3	33.3	438.9	5.383	113.61	142.49
SLOW	E	7	Douglas Fir	OR	234	1989-90	4	83.5	2887.0	1.000	119.61	404.91
SLOW	E	8	Douglas Fir	OR	118	1991-92	1	26.7	109.5	57.655	82.13	83.88
SLOW	E	8	Douglas Fir	OR	118	1991-92	2	85.9	-0.0058	(lin)	250.00	250.00
SLOW	E	8	Douglas Fir	OR	230	1991-92	3	119.1	218.7	12.254	72.80	80.42
SLOW	E	9	Ponderosa Pine	OR	111	1989	1	12.8	246.9	1.000	21.56	73.00
SLOW	E	9	Ponderosa Pine	OR	111	1989	2	25.8	365.2	1.000	31.89	107.95
SLOW	E	10	Ponderosa Pine	OR	113	1989-90	1	12.9	233.7	1.000	20.05	67.87
SLOW	E	10	Ponderosa Pine	OR	113	1989-90	2	25.7	358.8	1.000	30.77	104.18
SLOW	E	10	Ponderosa Pine	OR	234	1989-90	3	32.1	327.8	1.000	13.58	45.97
SLOW	E	10	Ponderosa Pine	OR	234	1989-90	4	90.1	634.3	1.000	26.27	88.94
SLOW	E	11	Ponderosa Pine	OR	118	1991-92	1	20.2	266.4	1.000	21.88	74.09
SLOW	E	11	Ponderosa Pine	OR	118	1991-92	2	47.1	206.5	1.000	16.96	57.42
SLOW	E	11	Ponderosa Pine	OR	230	1991-92	3	44.5	458.5	1.257	30.61	80.77
SLOW	E	12	Ponderosa Pine	OR	140	1992	1	134.6	235.8	2.570	64.56	103.76
SLOW	E	13	Ponderosa Pine	OR	84	1991	1	136.0	442.8	1.000	51.10	172.98
FAST	D	14	Red Alder	OR	121	1990	1	42.4	217.0	1.427	34.08	80.10
FAST	D	15	Red Alder	OR	113	1989	1	84.4	253.0	1.000	21.70	73.46
FAST	D	15	Red Alder	OR	113	1989	2	206.8	179.9	5.294	95.76	120.57
FAST	D	16	Red Alder	OR	118	1991	1	63.5	501.7	1.000	41.21	139.51
FAST	D	16	Red Alder	OR	118	1991	2	248.8	2.0E+13	1.000	250.00	250.00
FAST	D	17	Red Alder	OR	112	1992	1	54.1	274.4	1.107	29.50	88.79
FAST	D	18	Black Cherry	TN	76	1989	1	53.7	79.1	1.123	12.91	38.23
FAST	D	19	Black Cherry	TN	140	1992	1	37.1	176.6	1.168	16.90	48.00
SLOW	D	20	Red Maple	TN	55	1988	1	28.5	387.1	1.537	149.75	331.07
FAST	D	21	Tulip Poplar	TN	75	1990-91	1	45.8	46.4	4.518	34.56	45.27
FAST	D	21	Tulip Poplar	TN	184	1990-91	3	334.1	623.5	1.000	32.85	111.19
FAST	D	22	Tulip Poplar	TN	81	1992	1	150.1	50.8	1.852	17.12	33.07

TABLE 5-25 (cont'd). EXPOSURE-RESPONSE EQUATIONS THAT RELATE TOTAL BIOMASS (FOLIAGE, STEM, AND ROOT) TO 24-HOUR SUM06 EXPOSURES (C) ADJUSTED TO 92 DAYS (ppm-h/year)

Rate of Growth	Habit	Study	Species	Location (State)	Exposure[b] Days	Year	Harvests[a]	Weibull Parameters A	B	C	SUM06 for Loss of[c] 10%	30%
FAST	E	23	Loblolly GAKR 15-91	AL	555	1988-89	3	22.7	4,402.5	1.000	76.89	260.30
FAST	E	23	Loblolly GAKR 15-23	AL	555	1988-89	3	20.4	13,125.4	1.000	229.24	250.00
SLOW	D	24	Sugar Maple	MI	83	1990-91	1	4.12	100.0	40.069	104.79	108.03
SLOW	D	24	Sugar Maple	MI	180	1990-91	3	24.63	110.2	5.987	38.68	47.42
SLOW	E	25	E. White Pine	MI	83	1990-91	1	0.35	63.1	4.191	40.90	54.72
SLOW	E	25	E. White Pine	MI	180	1990-91	3	1.21	719.5	1.000	38.74	131.16
SLOW	E	26	Virginia Pine	MI	98	1992	1	78.3	3,045.1	1.000	250.00	250.00

[a]Harvest 1 occurs immediately following end of first year of exposure. Harvest 2 occurs in spring following first year of exposure. Harvest 3 occurs immediately following end of second year of exposure. Harvest 4 occurs in spring following second year of exposure.
[b]Duration corresponds to the length in days of the first year of exposure for Harvests 1 and 2 and to the total length of the first and second years of exposure for Harvests 3 and 4.
[c]"To compare the results from seedling studies of varying exposure duration," the SUM06 value is calculated for an exposure of fixed period of 92 days per year. "For example, Study 1 Harvest 1 has an exposure duration of 84 days and a" SUM06 value of 19.09 ppm-h over 92 days which corresponds to a SUM06 value "of 19.09*84/92 = 17.43 ppm-h over 84 days, at which biomass loss is 10%." The calculation assumes that exposures can be scaled up or down in uniform fashion.
[d]Based on GIS, TREGRO and ZELIG models projections. No data given in paper.

Source: Hogsett et al. (1993).

exposure of greater than 52.1 ppm·h. Comparison with Table 5-17 shows a SUM06 for 3 mo of 29.5 ppm·h at ambient concentrations, a value near that (33.3 ppm·h) expected to prevent a 10% yield reduction in 50% of the cases Table 5-24). An individual year, such as 1988, might be significantly above the no-injury exposure value (Table 5-17). By further grouping the seedlings by rate of growth (fast or slow), they were able to refine estimates of the SUM06 exposure that would protect seedlings based on growth strategy. Deciduous seedlings and/or fast growing species are more sensitive than evergreen and/or slow growing seedlings (Table 5-24).

The response of a number of fruit and nut trees to O_3 has been reported (McCool and Musselman, 1990; Retzlaff et al., 1991, 1992a,b). Almond has been identified as the most sensitive, but peach, apricot, pear, and plum have also been affected. Net growth of almond, as well as stem diameter of peach and the stem diameter and number of shoots produced on apricot were reduced by four months (the exposure duration specified by the authors) of once-weekly exposure to 0.25 ppm for 4 h, a relatively small exposure cumulatively (16 ppm h as a SUM00 or as a SUM 06) (McCool and Musselman, 1990) but

TABLE 5-26. SUM06 LEVELS ASSOCIATED WITH 10 AND 20% TOTAL BIOMASS LOSS FOR 50 AND 75% OF THE SEEDLING STUDIES (The SUM06 value is adjusted to an exposure length of 92 days per year)

Weibull Equations (all 51 seedling studies):
50th Percentile PRYL = 1 - exp(-[SUM06/176.342]**1.34962)
75th Percentile PRYL = 1 - exp(-[SUM06/104.281]**1.46719)

Weibull equations (27 fast-growing seedling studies):
50th Percentile PRYL = 1 - exp(-[SUM06/150.636]**1.43220)
75th Percentile PRYL = 1 - exp(-[SUM06/89.983]**1.49261)

Weibull equations (24 slow to moderate growing seedling studies):
50th Percentile PRYL = 1 - exp(-[SUM06/190.900]**1.49986)
75th Percentile PRYL = 1 - exp(-[SUM06/172.443]**1.14634)

Weibull equations (28 deciduous seedling studies):
50th Percentile PRYL = 1 - exp(-[SUM06/142.709]**1.48845)
75th Percentile PRYL = 1 - exp(-[SUM06/87.724]**1.53324)

Weibull equations (23 evergreen seedling studies):
50th Percentile PRYL = 1 - exp(-[SUM06/262.911]**1.23673)
75th Percentile PRYL = 1 - exp(-[SUM06/201.372]**1.01470)

Levels associated with prevention of a 10% and 20% total biomass loss for 50% and 75% of the seedlings.

All 51 seedling cases

		Percent of seedlings	
		50%	75%
Relative	10%	33.3	11.4
Biomass Loss	20%	58.0	23.8

27 fast-growing seedling cases

		Percent of seedlings	
		50%	75%
Relative	10%	31.3	19.4
Biomass Loss	20%	52.9	32.4

24 slow to moderate growth seedling cases

		Percent of seedlings	
		50%	75%
Relative	10%	42.6	24.2
Biomass Loss	20%	70.2	46.6

28 deciduous seedling cases

		Percent of seedlings	
		50%	75%
Relative	10%	31.5	20.2
Biomass Loss	20%	52.1	33.0

TABLE 5-26 (cont'd). SUM06 LEVELS ASSOCIATED WITH 10 AND 20% TOTAL BIOMASS LOSS FOR 50 AND 75% OF THE SEEDLING STUDIES (The SUM06 value is adjusted to an exposure length of 92 days per year)

23 Evergreen Seedling Cases		Percent of seedlings	
		50%	75%
Relative	10%	42.6	21.9
Biomass Loss	20%	78.2	45.9

[a]Based on GIS, TREGRO and ZELIG model projections. No data given in paper.

Hogsett et al. (1993).

one with a high peak value. Cross-sectional area of almond, plum, apricot, and pear stenis decreased linearly with increasing O_3, with a significant reduction at a 12 h seasonal mean of 0.051; dry weight of roots, trunk, and foliage was also reduced in one variety (Retzlaff et al., 1991, 1992a,b).

Finally, two studies report the response of citrus and avocado to O_3 (Eissenstat et al., 1991; Olszyk et al., 1990). These species retain their leaves for more than one year, but fit best in the deciduous category because, while evergreen, leaves are replaced more frequently than in most evergreen species. Valencia orange trees (during a production year) exposed to a seasonal 12 h mean of 0.04 or 0.075 ppm had 11 and 31% lower yields than trees grown in filtered air at 0.012 ppm and atypical concentration. During an off-production year, yield was not affected. Growth of Ruby Red grapefruit was not affected by concentrations of 3 times ambient (Eissenstat et al., 1991). Avocado growth was reduced by 20 or 61% by exposure during two growing seasons at 12 h seasonal mean concentrations of 0.068 and 0.096.

In summary, deciduous trees appear to be less sensitive to O_3 than most crop plants, but there are species that are as, or more sensitive due to their genetic composition, than crops (e.g., *Populus* species, and perhaps black cherry—see discussion in Section 5.4.2). Analysis of the crop data presented in Table 5-24 and discussed above suggests that a 7 h seasonal mean exposure of approximately 0.055 ppm over a three month period would prevent injury to tree seedlings. However, the absence of multiple-year studies, or studies

using older, more mature trees leaves unanswered the question of long-term and cumulative effects.

5.6.4.3 Effects of Ozone on Evergreen Trees

As with hardwoods, little long-term data from controlled studies was available at the time the literature was reviewed for U.S. Environmental Protection Agency (1986). The 1986 document did point out, however, that studies conducted on eastern white pine on the Cumberland Plateau in Tennessee indicated that ambient O_3 may have reduced the radial growth of sensitive individuals as much as 30 to 50% annually over a period of 15 to 20 years (Mann et al., 1980). Also, field studies in the San Bernardino National Forest indicated that over a period of 30 years O_3 may have reduced the growth in height of ponderosa pine by as much as 25%, radial growth by 37%, and total volume of wood produced by 84% (Miller et al., 1982). Calculations of biomass in these studies were based on apparent reductions in radial growth without standardization of the radial growth data with respect to tree age. Since 1986, studies on the effects of O_3 on evergreen trees have focused primarily on three species or groups: red spruce in the eastern United States, southern pines (loblolly and slash), and western conifers (primarily ponderosa pine). For the most part, the research has been conducted with tree seedlings or saplings, and has involved exposures lasting one to four growing seasons. In many cases, the research has concentrated on defining the mode of action of O_3 in conifers, and is discussed elsewhere in this document (Section 5.3). Results of studies with evergreen trees are summarized in Table 5-27.

Hogsett et al. (1993) summarized the results from uncited data and produced composite exposure-response functions for douglas-fir, ponderosa pine, eastern white pine, Virginia pine, and loblolly pine (Table 5-25). They predict that a 10% loss in 50% of the experimental cases could have been prevented by a SUM06 exposure of 42.6 ppm·h (O_3 concentrations and exposure times were not given).

Studies of the response of red spruce to O_3 exposures, regardless of whether they have been conducted in growth chambers (Lee et al., 1990a,b; Patton et al., 1991; Taylor et al., 1986), or in the field (Kohut et al., 1990; Laurence et al., 1993b; Thornton et al., 1992) have failed to detect effects on growth of seedlings or saplings, even after exposure to 12 h seasonal means of up to approximately 0.09 ppm each year for up to four years;

TABLE 5-27. A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF EVERGREEN TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Avocado	E/PC	10 to 108 ppb 12 h mean	4 and 8 mo in 2 growing seasons	OTC in pots	leaf mass	20 and 61% reduction in leaf mass at 86 and 108 ppb.	Eissenstat et al. (1991)
Orange	E/PC	10 to 108 ppb 12 h mean	4 and 8 mo in 2 growing seasons	OTC in pots	leaf mass	No effect.	Eissenstat et al. (1991)
Orange	E/PC	12 to 75 ppb 12 h mean	7 mo/season for 5 years	OTC	fruit weight	"On" production year - 11 and 31% reduction at 40 and 75 ppb "off" year - no effect.	Olszyk et al. (1990)
Ponderosa Pine	E	ambient	—	F	radial growth rate	No change in growth rate on symptomatic trees.	Peterson and Arbaugh (1988)
Ponderosa Pine	E	13 to 95 ppb 12 h mean 47 to 350 ppm·h over 3 years	3 growing seasons	OTC	growth	19.5% reduction at 95 ppb.	Beyers et al. (1992)
Ponderosa Pine	E	11 to 87 ppb 12 h mean	3 growing seasons	OTC	leaf weight	70 and 48% loss of 2 and 1 year old needles at 87 ppb.	Temple et al. (1993)
Ponderosa Pine	E	5, 122 or 169 ppm·h	112 days	OTC in pots	root growth	43% reduction in coarse and fine non-growing roots; 50, 65 and 62% reduction in coarse, fine and new growing roots.	Andersen et al. (1991)
Ponderosa Pine	E	67 to 71 ppb 7 h mean	134 days	OTC in pots	leaf, stem and root dry weight	20 to 33% reduction from filtered air at 67 ppb.	Hogsett et al. (1989)

TABLE 5-27 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF EVERGREEN TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Lodgepole Pine	E	67 to 71 ppb 7 h mean	134 days	OTC in pots	leaf, stem and rot dry weight	No effect.	Hogsett et al. (1989)
Jeffrey Pine	E	0-200 ppb 4 h/day 3 days/week	44 and 58 days in 2 growing seasons	GC	root, stem and needles dry weight	Reduced 10-20% ppb in one year.	Temple (1988)
Jeffrey Pine	E	ambient	—	F	radial growth	11% reduction in symptomatic trees.	Peterson et al. (1987)
Western Hemlock	E	67 to 71 ppb 7 h mean	134 days	OTC in pots	leaf, stem and root dry weight	11 to 305 reduction at 71 ppb.	Hogsett et al. (1989)
Western Red Cedar	E	67 to 71 ppb 7 h mean	134 days	OTC in pots	leaf, stem and root dry weight	No effect.	Hogsett et al. (1989)
Douglas Fir	E	67 to 71 ppb 7 h mean	134 days	OTC in pots	leaf, stem and root dry weight	No effect.	Hogsett et al. (1988)
Giant Sequoia	E	0-200 ppb 4 h/day 3 days/week	44 and 58 days in 2 growing seasons	GC	root, stem and needles dry weight	No effect.	Temple (1988)
Red Spruce	E	8 to 166 ppb 8 h mean 8 to 156 ppm·h	135 days	OTC	scion growth	No effect on juvenile or mature scion growth.	Rebbeck et al. (1992)
Red Spruce	E	23 to 87 ppb 12 h mean	2 growing seasons	OTC in pots	dry weight	No effect.	Kohut et al. (1990)

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TABLE 5-27 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF EVERGREEN TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Red Spruce	E	120 ppb 4 h/day twice/week	4 mo	GC	growth	No effect.	Taylor et al. (1986)
Red Spruce	E	0, 150 ppb 6 h/day or 150 ppb 6 h plus 70 ppb 18 h/day	195 days	GC	dry weight	No effect.	Patton et al. (1991)
Red Spruce	E	25 or 100 ppb 4 h/day 3 day/week	10 weeks	GC	growth	No effect.	Lee et al. (1990b)
Red Spruce	E	27 to 54 ppb 12 h mean	3 growing seasons	OTC in pots	dry weight, diameter, height	No effect.	Thornton et al. (1992)
Norway Spruce	E	80 to 100 ppb 7 to 8 h/day	100 days	GC	dry weight	0-14% reduction vs. filtered air - 5 provenances.	Mortensen (1990a)
Norway Spruce	E	14 to 70 ppb 8 h mean	5 to 6 mo in 2 growing seasons	OTC in pots	growth	No effect.	Nast et al. (1993)
Norway Spruce	E	10 to 90 ppb weekly mean	5 years	OTC	growth	Reduced lateral shoot growth in last year.	Billen et al. (1990)
Sitka Spruce	E	5 to 170 ppb 7 h/day 5 days/week	65 days	GH	growth and winter hardiness	No effect on growth, reduced winter hardiness.	Lucas et al. (1988)
Silver Fir	E	10 to 90 ppb weekly mean	5 years	OTC	growth	Increased dry matter production.	Billen et al. (1990)
Fraser Fir	E	20 to 100 ppb 4 h/day 3 times/week	10 weeks	GC	biomass	No effect.	Tseng et al. (1988)
White Pine	E	20 to 140 ppb 7 h/day 3 day/week	3.5 mo	GC	dry weight	No effect.	Reich et al. (1987)
Loblolly Pine	E	21 to 86 ppb 7 h mean	96 days	OTC in pots	dry weight	18% reduction at 86 ppb 20% reduction in foliage at 40 or 86 ppb.	Adams et al. (1988)

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TABLE 5-27 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OR EVERGREEN TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Loblolly Pine	E	21 to 117 ppb 7 h mean	3 growing seasons	OTC in pots	growth	No effect on 5 families.	Adams et al. (1990)
Loblolly Pine	E	22 to 94 ppb 7 h mean	3 growing seasons	OTC in pots	dry weight	4% reduction at 30 to 38 ppb, 8% reduction at 51 to 65 ppb.	Edwards et al. (1992)
Loblolly Pine	E	32 to 108 ppb 7 h mean	18 weeks	OTC in pots	dry weight	20% reduction in needles at 108 ppb.	Tjoelker and Luxmoore (1991)
Loblolly Pine	E	23 to 90 ppb 12 h mean 46 to 209 max 12 h	150 days	OTC in pots	growth	10% reduction at 46 ppb.	Shafer et al. (1987)
Loblolly Pine	E	22 to 92 ppb 12 h mean 37 to 143 ppb 1 h maximum	3 growing seasons	OTC in pots	dry weight	0 to 13% reduction after 3 years at about 45 to 50 ppb 12 h seasonal mean, depending on family.	Shafer et al. (1989)
Loblolly Pine	E	7 to 166 ppb 12 h mean 12 h maximum 248 ppb	245 days	OTC in pots	foliar weight	35% reduction at 166 ppb.	Qiu et al. (1992)
Loblolly Pine	E	7 to 132 ppb 12 h mean 17 to 382 ppm·h	3 growing seasons	OTC	foliage abscission	Initiated above 130 to 220 ppm·h in trees exposed to ambient or above.	Stow et al. (1992)
Loblolly Pine	E	21 to 137 ppb 12 h mean 60 to 397 ppm·h	241 days	OTC	shoot growth	Shoot length reduced 30% at 137 ppb.	Mudano et al. (1992)
Loblolly Pine	E	20 to 137 ppb 12 h mean 50 to 286 ppb maximum 12 h mean	2 growing seasons	OTC	needle retention, fascicle length	Needle retention decreased in elevated ozone—fascicle length reduced by ozone in early flushes, increased in later flushes.	Kress et al. (1992)

TABLE 5-27 (cont'd). A SUMMARY OF STUDIES REPORTING THE EFFECTS OF OZONE ON THE GROWTH OR PRODUCTIVITY OF EVERGREEN TREES PUBLISHED SINCE U.S. ENVIRONMENTAL PROTECTION AGENCY (1986)

Species	E/D/ PC/C[a]	Concentration[b]	Duration	Facility[c]	Variable[d]	Effect[e]	Reference
Loblolly Pine	E	0 to 150 ppb 5 h/day 5 days/week	6-12 weeks	GC	dry weight	8% reduction at 150 ppb.	Meier et al. (1990)
Loblolly Pine	E	0 to 320 ppb 6 h/day 4 days/week	8 weeks	GC	height and diameter growth	20 % reduction in height growth 36% reduction in diameter growth in three open-pollinated families.	Horton et al. (1990)
Loblolly Pine	E	0 to 120 ppb 7 h/day 5 days/week	12 weeks	GC	dry weight	Top dry weight increased up to 60% root dry weight reduced 6%.	Spence et al. (1990)
Loblolly Pine	E	0 to 320 ppb 8 h/day 4 days/week	9 weeks	GC	relative growth rate (RGR)	36% reduction in height RGR 10% reduction in diameter RGR.	Wiselogel et al. (1991)
Loblolly Pine	E	20 to 100 ppb 4 h/day 3 days/week	10 weeks	GC	dry weight	No effect.	Lee et al. (1990a)
Slash Pine	E	76 to 104 ppb 7 h mean 126 ppb 1 h maximum 122 and 155 ppm·h	112 days	GC	top and root dry weight	18% reduction in top dry weight and 39% reduction in root dry weight at 122 ppm·h.	Hogsett et al. (1985)
Slash Pine	E	200 to 1,000 ppm·h	28 mo	OTC	litterfall	Twice as much litterfall at ozone above 220 ppm·h.	Byres et al. (1992)
Slash Pine	E	179 to 443 ppm·h 24 h SUM00 multiples of ambient	28 months	OTC	leaf area	Reduced up to 33% by 443 ppm·h.	Dean and Johnson (1992)

[a]E = evergreen, D = deciduous, C = crop, PC = perennial crop.
[b]Means are seasonal means unless specified. Maximums are 1 h seasonal maxima unless otherwise specified. Cumulative exposures are SUM00 unless otherwise specified, accumulation based on 24 h/day unless otherwise noted.
[c]OTC = open-top chamber with plants in ground unless specified in pots; CC = closed chamber, outside; GC = controlled environment growth chamber or CSTR; GH = greenhouse; F = field; OF = open-field fumigation.
[d]The effect reported in the study that is a measure of growth, yield, or productivity.
[e]Effect measured at specified ozone concentration, over the range specified under concentration, or predicted (if specified) to occur based on relationships developed in the experiment.

concentrations that are considerably greater than those expected in ambient air. There was an indication that total non-structural carbohydrate content was reduced by O_3, which might be an indicator of cumulative stress (Woodbury et al., 1991). However, results of these studies indicate red spruce is tolerant of O_3, at least for exposures of a few years.

Growth of seedlings of loblolly pine (a much faster growing species than red spruce) has been reduced by O_3 under some conditions. In growth chamber experiments, height growth was reduced after exposure to 0.10 ppm for 4 h per day, three days per week for 10 weeks, but only in combination with a "control" rain treatment. The effect was not observed in trees that received significant inputs of potential nutrients in simulated rain. Conversely, Tjoelker and Luxmoore (1991) reported a significant reduction in the weight of current year needles following an open-top chamber exposure to O_3 at a 7 h seasonal mean of 0.056 or 0.108 ppm only in a high nitrogen treatment.

Multiple-year open-top chamber exposures of loblolly pine have resulted in decreased foliar weight, partly through accelerated abscission, and decreased root surface area in the first year following exposure to a 2.5 times ambient O_3 treatment (0.10 ppm 12 h seasonal average, 318 ppm·h) (Qiu et al., 1992). In a two year study, Kress et al. (1992) found that fascicle length and number of early season needle flushes decreased linearly with increasing O_3, but the reverse was true in flushes produced later in the season. This may only occur in seedlings that produce more than two leaf flushes per year. Foliage retention decreased with O_3, and fewer fascicles were retained on trees exposed to ambient concentrations of O_3 (12 h seasonal mean of 0.045 averaged over two years). Shafer and Heagle (1989) exposed seedlings of four families of loblolly pine to O_3 over three growing seasons and, based on their data, predicted growth suppressions of above ground plant parts at a 12 h seasonal mean of 0.05 ppm of 0 to 19% (depending on the sensitivity of the family) after two years, and of 13% in the most sensitive family after three years. Cumulative effects of multiple-year exposures were not apparent from the above study, but no measures of root growth, which has been reported to be affected in other species (Andersen et al., 1991; Edwards et al., 1992; Temple et al., 1993) were reported. Edwards et al. (1992) also conducted a three year exposure and found a 4% reduction in whole plant biomass after exposure to a 7 h seasonal concentration of about 0.050 ppm. An 8% reduction was

associated with a 7 h concentration of about 0.10 ppm. Growth reductions occurred in both above and below ground plant parts.

Many studies with loblolly pine have used multiple families with a range of reported tolerance to O_3 (Adams et al., 1988, 1990; Kress et al., 1992;, Qiu et al., 1992; Shafer and Heagle, 1989; Wiselogel et al., 1991). These studies have demonstrated the range of response, from tolerant to sensitive, in the species. Adams et al. (1990) suggest that resistance to natural stresses, such as drought, may be linked to tolerance to O_3, thereby affecting the response of the species to multiple stresses.

The response of slash pine to O_3 has also been characterized. Dean and Johnson (1992) found leaf area to be reduced by O_3 in all three growing seasons studied, with an intensification of the effect each year at an O_3 exposure of about 0.03 to 0.04 ppm (12 h seasonal means) or 77 to 216 ppm·h. Leaf litterfall was also increased by O_3 (Byres et al., 1992). Volume increment of the trees was affected, with an increased sensitivity to simulated acid rain in trees exposed to twice ambient. Hogsett et al. (1985) found reduced height (22%), diameter (25%), top (18%), and root growth (39%) in slash pine exposed to a 7 h seasonal mean of 0.076 ppm, with a maximum concentration of 0.094 ppm. From these studies, it is clear that slash pine is relatively sensitive to O_3 on an annual basis.

Hogsett et al. (1989) report the results of exposing 5 western conifers to O_3 at a seasonal 7 h mean concentration of 0.067 or 0.071 ppm (SUM07 for 134 day was 49.5 and 63 ppm·h; SUM00 was 140 and 153 ppm·h). Ponderosa pine and western hemlock had reduced needle, stem, and root dry weight after 134 days of exposure. Douglas-fir and western redcedar were not different from the charcoal-filtered air control, but douglas-fir showed consistent decreases in weight of plant components. Lodgepole pine was not affected by either O_3 treatment. Carry-over effects were observed in bud elongation the following spring in lodgepole pine, ponderosa pine and hemlock. Andersen et al. (1991) also observed reduced root dry weight in ponderosa pine after exposure to SUM00 of 122 or 169 ppm·h during a 120-day growing season. In addition, they observed a reduction in the weight of newly formed roots the following spring, possibly due to reduced levels of root starch.

In a three year field study, Temple et al. (1993) and Beyers et al. (1992) found that ponderosa pine trees exposed to a 24 h seasonal mean of 0.087 ppm had a 48 and 70% loss of 2 and 3 year old needles, respectively. Radial stem growth and coarse root growth were

also reduced, but not as severely as needle weight (due to abscission). After three seasons of exposure, current year needles in elevated O_3 treatments had a higher photosynthetic capacity than those in filtered air. The compensation was apparently due to higher foliar nitrogen in O_3-exposed needles, a product of redistribution of nitrogen before abscission of needles. Cumulative responses would suggest that eventually, reductions in growth of the trees would occur at lower concentrations of O_3.

A number of field studies have been conducted in North America in which an attempt was made to relate air quality to growth or injury of forest trees. Two field studies have correlated radial growth with visible injury in ponderosa and Jeffrey pine in California (Peterson and Arbaugh, 1988; Peterson et al., 1987). An 11% reduction in radial growth was measured in symptomatic Jeffrey pine compared to trees that did not show symptoms of O_3 injury, but no reduction could be demonstrated in ponderosa pine, however, the authors point out that the trees they measured were not under competitive stress, which might alter their response.

The response of evergreen trees varies widely, depending on species, and genotype within species. It is clear, however, that major forest species, such as ponderosa, loblolly, and slash pine are sensitive to O_3 at, or slightly above the concentrations of O_3 (0.04 to 0.05 ppm) that occur over wide areas of the United States. Furthermore, because of the long life span of these trees, including those that have not been reported sensitive to O_3, there is ample opportunity for a long-term, cumulative effect on growth of the trees. Most of the experiments are conducted over only 2% or less of the life expectancy of the tree; an equivalent exposure in field crop plants would be two to three days. Consideration must also be given to the fact that most of these trees grow as part of mixed forests, in competition with many other species. Small changes in growth might be translated into large changes in stand dynamics, with concomitant effects on the structure and function of the ecosystem.

5.6.5 Assessments Using Ethylene Diurea (EDU) as a Protectant

Vegetational response to air pollutants can be modified by agricultural chemicals commonly used by growers to control diseases, insects and other pests on crops (see Section 5.4.7; U.S. Environmental Protection Agency, 1986). A chemical protectant, ethylene diurea (EDU; N-[2-(2-oxo-1-imidagolidinyl)ethyl]-Ń-phenylurea), has been used to

study the response of plants to O_3 without attempting to control the concentration of the pollutant during the exposure (U.S. Environmental Protection Agency, 1986) Table 5-28.

Disadvantages of the use of open-top chambers for assessing the effects of O_3 on the growth of plants include relatively high cost, the need for electrical power, and potential effects of the chambers themselves on the growth of the plants. In many cases, no chamber effects can be detected, and since most studies compare against a control, chamber effects would have a minimal effect on interpretation of results. While the number of experiments conducted with open-top chambers has led to a firm understanding of plant response to a chamber environment, the possibility of interactions with treatment cannot be ruled out. The use of EDU is attractive due to low cost and ease of application, however, it is essential to establish the correct dosage for protection from O_3 without direct effects of EDU on the plant, and an estimate of the level of protection from O_3 achieved (Kostka-Rick and Manning, 1992a,b, 1993). EDU is known to be phytotoxic, so studies under controlled O_3 conditions to establish an effective level of protection without phytotoxicity are essential before it can be used as an assessment tool.

Previous studies with EDU led to the conclusion, as did experiments with open-top chambers, that ambient concentrations of O_3 were sufficient to reduce crop yields (U.S. Environmental Protection Agency, 1986). If hourly O_3 concentrations exceeded 0.08 ppm for 5 to 18 days during the growing season, yields of crops might be reduced 18 to 41% (U.S. Environmental Protection Agency, 1986).

Inspection of Table 5-28 shows that in many cases there were clear-cut reductions in O_3-induced injury, and increases in yield resulting from the application of EDU. However, the conflicting results for field-grown soybean indicated that, at the rate of EDU application used, no beneficial effects could be demonstrated. Similarly, experiments with corn and cotton suggest that any possible effects of O_3 may have been confounded by direct effects on growth of EDU itself.

A few studies using EDU have been conducted since 1986. Kostka-Rick and Manning (1992a,b, 1993) conducted studies to determine the direct effects of EDU on growth and to develop an understanding of dose-response to EDU itself. Their studies using EDU and radish in the presence or absence of a controlled O_3 fumigation in a greenhouse and found that the chemical did suppress O_3-induced reductions in below-ground plant organs. It also

TABLE 5-28. EFFECTS OF ETHYLENE DIUREA (EDU) ON OZONE RESPONSES

Crop/Species	EDU Application	O_3 Exposure	Effects of EDU	Reference
White bean	Spray to runoff, 2,000 ppm	Field; 34 h >0.08 ppm	Reduced O_3 injury, 38%; delayed defoliation; increased yield, 24%	Temple and Bisessar (1979)
	Spray to runoff, 2,000 ppm	Field; hours >0.08 ppm = 518 ppmh	Reduced O_3 injury, 20-80%; increased yield up to 35%	Toivonen et al. (1982)
	Soil drench, 500 ppm, 0.5l/pot	Greenhouse (charcoal-filtered)	No effect on growth	Brennan et al. (1990)
	Soil drench, 500 ppm, 4l/6m row	Field; 78 h >0.12 ppm (0.2 ppm max.)	Reduced O_3 injury up to 50%; retarded maturation	Brennan et al. (1990)
Corn	Spray to runoff, 500 ppm	field (no details)	19% yield reduction	Heggestad (1988)
Cotton	Spray to runoff, 500 ppm	Greenhouse (no details)	Increased yield in non-filtered air; reduced yield in filtered air	Heggestad (1988)
Potato	Spray to runoff, 1.1 kg/ha 5 applications	Field; >0.08 ppm on 18 days (0.138 ppm max.)	Reduced O_3 injury, 50%; increased tuber weight, 35%	Bisessar (1982)
	Soil drench, 6.7 kg/ha 4 applications	Field; 282 h >0.08 ppm	Reduced O_3 injury; increased tuber weight, 20-30%	Clarke et al. (1990)
Radish	Soil drench, 100 mg/l, 2l/m of row	Field; 0 h >0.1 ppm, hours >0.05 ppm = 0.76 ppmh	(No response to O_3) Reduced growth rates at low O_3 exposures	Kostka-Rick and Manning (1992a)
	Soil drench, up to 800 mg/l, 100 ml/pot	Greenhouse, <0.025 ppm	Increased shoot growth at <300 mg/l; reduced shoot growth at >300 mg/l Reduced hypocotyl growth at all EDU levels	Kostka-Rick and Manning (1993)
	Soil drench, up to 400 mg/l, 100 ml/pot	Greenhouse, 0.075 ppm/7 h, 6 day/week, with one weekly peak to 0.14 ppm	Complete protection against O_3 injury at 100 mg/l	Kostka-Rick & Manning (1993)

TABLE 5-28 (cont'd). EFFECTS OF ETHYLENE DIUREA (EDU) ON OZONE RESPONSES

Crop/Species	EDU Application	O_3 Exposure	Effects of EDU	Reference
Radish (cont'd)				
	Soil drench, 150 mg/l, 60 ml/pot	Greenhouse, 0.07 ppm/7 h, 5 day/week, with two weekly peaks to 0.12 ppm	Reduced O_3 injury, 90-100%; less reduction in hypocotyl weight	Kostka-Rick & Manning (1992b)
Soybean	Soil drench, 500 ppm, 0.5l/pot	Greenhouse; 0.2 ppm, 6 h/day, 2 days	Reduced O_3 injury, 80-90%	Brennan et al. (1987)
	Soil drench, 500 ppm, 4l/6m row	Field; 78 h >0.12 ppm (0.2 ppm max.)	No effect on loss of chlorophyll; no effect on seed weight Increased growth, 22%	Smith et al. (1987) and Brennan et al. (1990) Bisessar and Palmer (1984)
Tobacco	Spray to runoff, 1 kg/ha 7 applications	Field; >0.08 ppm on 2 days		
Beech	Stem injection 1 g/l; 0.25 ml	OTC; ambient and ambient +0.08 ppm, 8 h/day	No consistent effect	Ainsworth and Ashmore (1992)
Black cherry	Spray to runoff, 1,000 ppm 7 applications/year	Field; 75 h >0.08 ppm (over 4 years)	2-fold increase in growth	Long and Davis (1991)
Other woody species:				
Red maple	Spray to runoff, 500 ppm or soil drench, 500 or 2,000 ppm, 250 ml/pot	Up to 0.95 ppm, 3 h	Reduced O_3 injury	Cathey and Heggestad (1982)
Paper birch			Reduced O_3 injury	
White ash			Reduced O_3 injury	
Honey locust			Reduced O_3 injury	
Golden-rain			Reduced O_3 injury	
London plane			Reduced O_3 injury	
Lilac			Reduced O_3 injury	
Basswood			Reduced O_3 injury	

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protected the plants from foliar injury. The EDU itself did not cause effects on growth at a concentration of 150 mg l^{-1} applied as a 60 ml drench to each plant, a dosage much lower than has often been used (e.g., Long and Davis, 1991; Smith, et al., 1987 discussed below). Kosta-Rick and Manning emphasize that it is essential to establish the appropriate dose for the species under consideration. Armed with this background, they used EDU in a field study and found an O_3-induced decrease in the relative growth rates of sink organs of field-grown radish plants above a threshold level of about 0.052 to 0.058 ppm (7 h daily mean), an exposure that is near ambient O_3 concentrations.

EDU has also been used to estimate the effect of O_3 on field-grown soybean in New Jersey (Smith, et al., 1987; Brennan, et al., 1990). In this case, the researchers did not establish the appropriate dose level for O_3 protection as was done by Kostka-Rick and Manning. No differences in yield were found and the authors conclude that O_3 does not impact soybean yield of the tested cultivars in New Jersey. However, they did not demonstrate that EDU was an effective protectant at the concentrations used and on the cultivars grown.

In a similar study, potato yields were measured and related to foliar injury in EDU treated and non-treated plots over a four year period (Clarke, et al., 1990). The cumulative O_3 dose ranged from 45 to 110 ppm·h, depending on the year, producing a range of foliar injury from 1 to 75%. The authors found that significant differences in yield between EDU-treated and control plants occurred only when foliar injury on untreated plants was 75% of leaf area. No level of protection, other than from foliar injury, could be assessed.

In a three-year study of potted green ash, no significant effects on growth were measured using EDU (two years) or by comparison of filtered and non-filtered air in open-top chambers (one year) (Elliot, et al., 1987). Foliar injury was observed only late in the season of the first year in the non-filtered chambers.

An effort by Ensing, et al. (1986) to assess the impact of O_3 on yield of peanut in Ontario found that year-to-year variation was greater than that they could account for either by correlation of O_3 concentration with yield of test plots or by EDU treatment. They conclude that a correlative approach to assessing losses due to O_3 will not work.

Finally, a 4 year study of black cherry using EDU as a protectant was conducted by Long and Davis (1991). They found significant effects with a 47% reduction in above

ground biomass compared to EDU-treated trees. The authors do not believe the difference was due to a stimulation in growth due to nitrogen in the EDU, but did not conduct studies as recommended by Kostka-Rick and Manning to characterize the EDU system for black cherry.

The consistency of the results on field-grown white bean in southern Ontario led to the development of an economic loss model based on the improved yields obtained as a result of applications of EDU (Adomait et al., 1987).

In summary, the EDU method for assessing the impact of O_3 is promising, particularly for remote areas, or as a validation tool for existing crop-loss models. The system must be carefully characterized, however, as pointed out by many of its users.

It should be noted that, in spite of the promise shown by EDU as a field protectant over many years, it has not been developed commercially, and until recently was unavailable for further experimentation.

5.6.6 Summary

Several conclusions were drawn from the various approaches used to estimate cropyield loss. In 1986, U.S. Environmental Protection Agency (1986) established that 7 h/day growing season mean exposures to O_3 concentrations above 0.05 were likely to cause measurable yield loss in agricultural crops. At that time, few conclusions could be drawn about the response of deciduous or evergreen trees or shrubs because of the lack of information about the response of such plants to season-long exposures to O_3 concentrations of 0.04 to 0.06 ppm and above. However, the 1978 and 1986 criteria documents (U.S. Environmental Protection Agency, 1986) indicate that the limiting values for foliar injury to trees and shrubs was 0.06 to 0.10 ppm for 4 h. Since 1986, considerable research has been conducted and the sensitivity of many tree species has been established.

Based on research published since U.S. Environmental Protection Agency (1986), the following conclusions can be drawn:

1. An analysis of 10 years of monitoring data from more than 80 to almost 200 nonurban sites in the U.S. established ambient 7 h growing season average concentrations of O_3 for 3 or 5 mo of 0.051 to 0.060 and 0.047 to 0.054 ppm, respectively. SUM06 exposures ranges from 25.8 to 45.2 ppm·h for 3 mo, and 32.7 to 44.4 ppm·h for 5 mo (Tingey et al., 1991).

2. The results of open-top chamber studies that compare yields at ambient O_3 exposures with those in filtered-air, and retrospective analyses of crop data summarized in this section, establish that the current ambient concentrations of O_3 at some sites are sufficient to reduce the yield of major crops in the United States. The results of research since 1978 do not invalidate the conclusions of the U.S. Environmental Protection Agency (1976, 1986) that visible injury due to O_3 exposures reduces the market value of certain crops and ornamentals (spinach, petunia, geranium and poinsettia, for instance), and that such injury occurs at O_3 concentrations (0.04 to 0.10) that presently occur in the United States.

3. A growing season SUM06 exposure of 26.4 ppm·h, corresponding to a 7 h growing season mean of 0.049 ppm and a 2HDM of 0.094 ppm will prevent a 10% loss in 50% of the 54 experimental cases analyzed by Tingey, et al., (1991) and Lee, et al., (1993a,b). A 12 h growing season mean of 0.045 should restrict yield losses to 10% in major crop species (Lesser, et al., 1990).

4. Concentrations of O_3 and SUM06 exposures that occur at present in the U.S. are sufficient to affect the growth of a number of trees species. Given the fact that multiple year exposures may cause a cumulative effect of the growth of some trees (Simini, et al., 1992; Temple, et al., 1992), it is likely that a number of species are currently being impacted, even if threshold exposures are not being reached.

5. A study of 51 cases of seedling response to O_3 (Hogsett, et al., 1993), including 11 species representing deciduous and evergreen growth habits, concluded that a SUM06 exposure for 5 mo of 31.5 ppm·h would protect hardwoods from a 10% yield (growth) loss in 50% of the cases studied. A SUM06 exposure of 42.6 ppm·h would provide the same level of protection for evergreen seedlings. Research by others support these conclusions. It should be noted that these conclusions do not take into the account the possibility of effects on growth in subsequent years, an important consideration in the case of long-lived species.

6. Studies of the response of trees to O_3 have established that, in some cases (*Populous* and black cherry, for instance) trees are as sensitive to O_3 as annual plants, in spite of the fact that they are longer lived and have lower rates of gas exchange, and therefore a lower uptake of O_3.

7. The use of the chemical protectant, EDU is of value to establish O_3 related losses in crop yield and tree growth, providing care is exercised in establishing the appropriate dosage of the compound to protect the plants without affecting growth. EDU cannot be used to predict the response of plants at concentrations greater than those that exist in ambient air.

5.7 EFFECTS OF OZONE ON NATURAL ECOSYSTEMS

5.7.1 Introduction

The previous section presents the response of different species of crops and cultivated plants, as well as data from deciduous shrubs and trees (Table 5-25) and evergreen tree species (Table 5-26) to a variety of O_3 exposure times and concentrations. The exposure-response studies cited in the tables in the previous section, whether conducted in chambers, greenhouses, or open-tops suggest that all sensitive plants will respond to O_3 concentrations above 0.06 ppm within hours. In general, depending upon the length of exposure, the number and height of peaks, and the sensitivity of the vegetation, data from the field supports this contention.

The environment in both natural and agricultural ecosystems is seldom optimal for plant growth. In fact, most natural environments are suboptimal with respect to one or more environmental parameters. Plant attempting to maintain a balance of resources by integrate their responses (Chapin, 1991). Most plants undergo some form of stress during the various stages of their life cycle, however, the multiple stresses they encounter during their lifetimes do not usually all occur at once. In addition, the sensitivity to stress varies with the age of the plant (Osmond et al., 1987). Cultivated plants are fertilized and frequently watered so that they will have a balance of resources and produce better crops. Plants growing in their natural habitats must compensate not only for the lack of resources but also for the multiple stresses they usually encounter. How plants respond to O_3 exposures and may compensate for stresses is pointed out in the section on Mode of Action (5.3). The importance of genetic variability in plant response, plant competition, and also the multiple biological and physical factors that may modify plant response and, in some cases cause stress, are discussed in Factors That Modify Plant Response (5.4). The discussion regarding modifying factors is of particular importance in understanding ecosystem response to stresses because plants growing in their natural habitats are much more likely to encounter them.

In order to place the known plant responses to O_3 exposure in the ecosystem context, a brief presentation of ecosystems characteristics and their importance to human existence is given in the next section. The responses of forest ecosystems to pollutant exposure have received more study than unmanaged ecosystems of other biomes (grasslands, shrublands, or deserts). The following discussion relies mainly on forest ecosystems for its examples.

5.7.2 Ecosystem Characteristics

5.7.2.1 Expected Sequence of Events

Ecosystems are composed of populations of "self-supporting" and "self-maintaining" living plants, animals and microorganisms (producers, consumers, and decomposers) interacting with one another and with the nonliving chemical and physical environment within which they exist (Odum, 1989; U.S. Environmental Protection Agency, 1993). Mature ecosystems are seldom stable. They must continually respond and adapt to changing environments (Koslowski, 1985). Structurally complex communities, they are held in an oscillating steady state by the operation of a particular combination of biotic and abiotic factors. Ecosystems usually have definable limits, the boundaries of which, and the organisms that can live there, are determined by the environmental conditions of that particular area or region. They may be large or small (e.g., fallen logs, forests, grasslands, cultivated or uncultivated fields, ponds, lakes, rivers, estuaries, oceans, the earth) (Odum, 1971). Together, the environment, the organisms, and the physiological processes resulting from their interactions form the life-support systems that are essential for the existence of any species on earth, including man (Odum, 1993).

The importance of ecosystems to human existence is pointed out in the nitrogen oxides criteria document (U.S. Environmental Protection Agency, 1993).

Human welfare is dependent on ecological systems and processes. Natural ecosystems are traditionally spoken of in terms of their structure and functions. Ecosystem structure includes the species (richness and abundance) and their mass and arrangement in an ecosystem. This is termed an ecosystem's standing stock—nature's free "goods" (Westman, 1977; U.S. Environmental Protection Agency). Society reaps two kinds of benefits from the structural aspects of an ecosystem: (1) products with market value such as fish, minerals, forest products and pharmaceuticals, and genetic resources of valuable species (e.g., plants for crops and timber and animals for domestication); and (2) the use and appreciation of ecosystems for recreation, aesthetic enjoyment, and study (Westman, 1977; U.S. Environmental Protection Agency).

More difficult to comprehend, but no less vital, are the functional aspects of an ecosystem. They are the dynamics of ecosystems and impart to society a variety of benefits, nature's free "services". Ecosystem functions encompass the interactions of the ecosystem

components and their environment and maintain clean air, pure water, a green earth, and a balance of creatures; the functions that enable humans to obtain the food, fiber, energy, and other material needs for survival (Westman, 1977; U.S. Environmental Protection Agency).

Ecosystems have both structure and function. The several most visible levels of biological organization are (1) the individual and its environment; (2) the population and its environment; (3) the community and its environment; and (4) the ecosystem (Billings, 1978). These populations of plants, animals, and microorganisms (producers, consumers and decomposers) in an ecosystem, live together and interact as communities. Individual organisms within a population vary in their ability to withstand the stress of environmental changes. The range of variability within which they can exist and function, determines the ability of the population to survive. Communities, due to the interaction of their populations, respond to pollutant stresses differently from individuals (U.S. Environmental Protection Agency, 1993).

Intense competition among plants for light, water, nutrients, and space, along with recurrent natural climatic (temperature) and biological (herbivory, disease, pathogens) stresses, can alter the species composition of communities by eliminating those individuals sensitive to specific stresses, a common response in communities under stress (Woodell, 1970; Guderian, 1985). Those organisms able to cope with stresses survive and reproduce. Competition among different species results in succession (community change over time) and ultimately produces ecosystems composed of populations of plant species that have a capacity to tolerate the stresses (Kozlowski, 1980). Pollutant stresses, such as those caused by exposure to O_3, are superimposed upon the naturally occurring competitional stresses mentioned above (See also Section 5.4). Air pollutants are known to alter the diversity and structure of plant communities (Guderian et al., 1985). The extent of change that may occur in a community depends on the condition and type of community as well as the pollutant exposure.

In unpolluted atmospheres, the number of species in a community usually increases during succession. Productivity, biomass, community height, and structural complexity increase. Severe stresses, on the other hand, divert energy from growth and reproduction to maintenance and alter succession (Waring and Schlesinger, 1995). In addition, biomass accumulation and production decrease and structural complexity, biodiversity, environmental

modification, and nutrient control are reduced (Borman, 1985). When catastrophic disturbances or injury, whether from natural (e.g., fire, flood, or windstorm) or anthropogenic stresses (e.g., O_3), alter the species composition (biodiversity) of a forest enough to disrupt food chains and modify rates of energy flow and nutrient cycling, succession is returned to and earlier less complex stage. The effects of stresses upon ecosystems, unless they are catastrophic disturbances are frequently difficult to determine (Koslowski, 1985; Garner et al., 1989). In a mature forest, a mild disturbance becomes part of the oscillating steady state of the forest community or ecosystem. Responses to catastrophic disturbances, however, as a rule are readily observable and measurable (Garner, 1993).

The structural changes within ecosystems are the result of functional changes that occurred within the individuals, populations and community (e.g., altering of nutrient cycling Miller et al., 1982). Ecosystem functions include the processes and interactions among the various components and their environments that involve the movement of nutrients and energy through a community as organic matter. Vegetation, through the process of photosynthesis, plays and integral role in energy and nutrient transfer through ecosystems. During photosynthesis, plants utilize energy from sunlight to convert carbon dioxide (CO_2) from the atmosphere and water from the soil into carbohydrates (See Section 5.3). The energy accumulated and stored by vegetation as carbohydrates is also available to other organisms such as herbivores, carnivores, and decomposers. As energy and nutrients move from organism to organism in food chains or webs, they become more complex as ecosystem diversity increases (Odum, 1993). Energy flow through the food chains is unidirectional. At each step some is dissipated until ultimately, the amount left is dissipates into the atmosphere as heat and must be replaced. Nutrients and water can be recycled, fed back into the system, and used over and over again (Odum, 1993). The plant processes of photosynthesis, nutrient uptake, respiration, translocation, carbon allocation, and biosynthesis are directly related to the ecosystem function of energy flow and nutrient cycling. Reduction in structure and diversity in ecosystems shortens food chains, reduces the total nutrient inventory, and returns the ecosystems to a simpler successional stage (Woodwell, 1970). How changes in these processes influence an ecosystem is discussed in the following text.

5.7.3 Ecosystem Response to Stress

5.7.3.1 Forest Ecosystems

Ecosystem response to stress begins with individuals (Figure 5-23). Individuals, not ecosystems respond to O_3 exposure. Ecosystem responses are hierarchical ranging from those that are characteristic of individuals to those characteristic of the entire ecosystem (see Section 5.7.2). Table 5-29 lists the components that might be adversely affected by air pollutants in hierarchical level, the possible functional responses that might occur at each level of organization and the associated structural changes that might be expected (Sigal and Suter, 1987). Changes in ecosystems begin with the death of individual plants. Even though ecosystems integrate individual responses and propagate them through trophic and competitive relationships, there can be no ecosystem response without an individual having first responded. How the structural and functional components interact beginning with the death of sensitive individuals as observed in the San Bernardino Forest ecosystem are described below. Individuals sensitive to O_3 have been described from the forests of both coasts of the United States (U.S. Environmental Protection Agency, 1986). The impacts on the west coast, however, have been much more severe, possibly because the exposures have been chronic, continuing day and night at higher levels and the overall O_3 concentrations have been higher. In the Appalachian Mountains and the east in general O_3 exposures have been episodic varying in length from days to weeks (see U.S. Environmental Protection Agency, 1986). The varying responses of the two ecosystems to O_3 stress will be discussed in the text that follows.

The extent of injury an ecosystem will experience from O_3 exposure is determined by the responses of its individuals. Leaf injury, as has been stated previously, is usually the first visible indication of O_3 exposure. Structural effects develop when functional responses are severe enough (see Table 5-29). Stresses, whose primary effects occur at the molecular or cellular physiology level in the individual, must be propagated progressively up through more integrative levels of organ physiology (e.g., leaf, branch, root) to whole plant physiology, stand dynamics, and then to the landscape level to produce ecosystem effects (Figure 5-24; Table 5-29). Particularly, this is true if the stress is of low-level because only a small fraction of stresses at the molecular and cellular level become disturbances at the tree, stand, or landscape level. Insect defoliation, for example, may severely reduce the

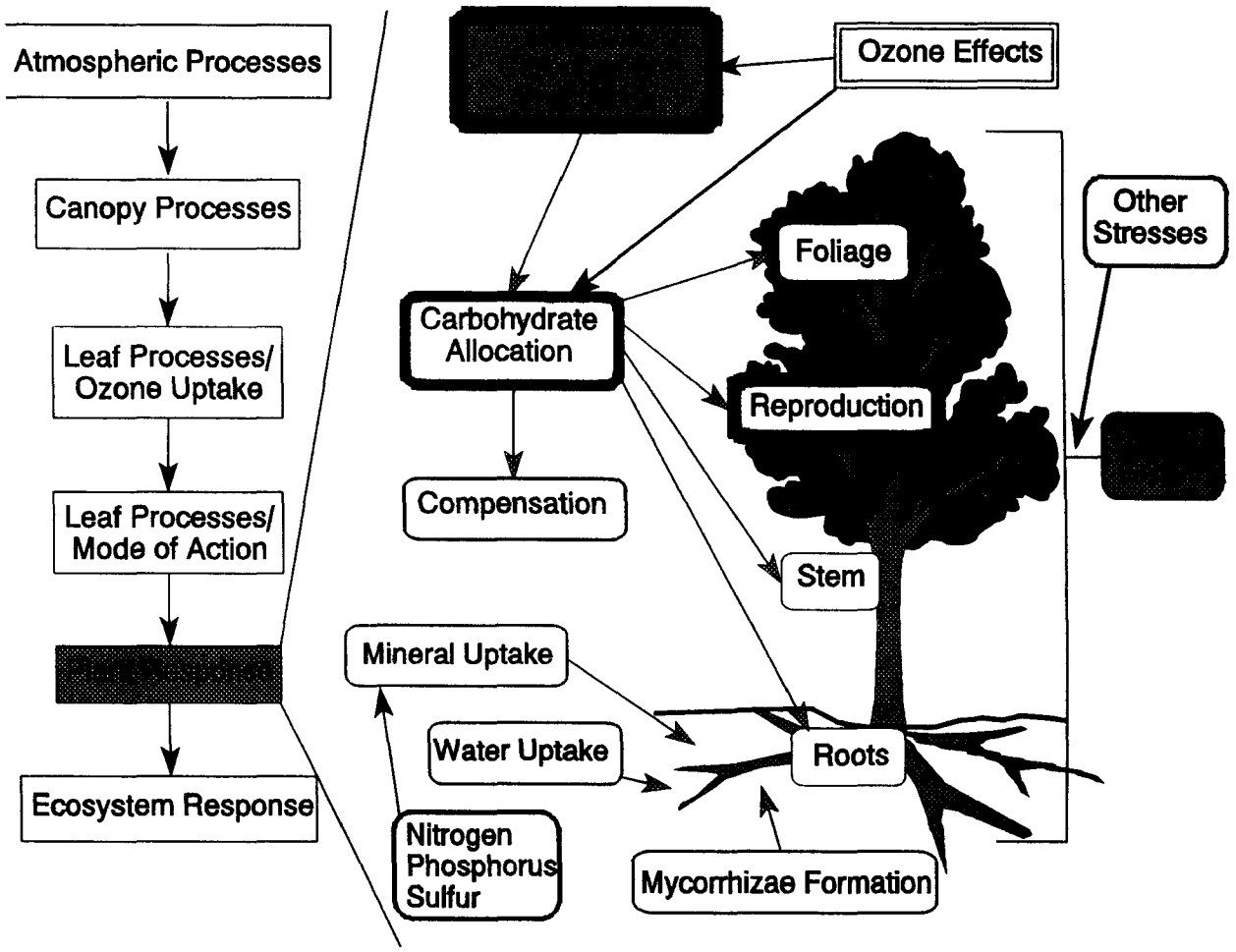


Figure 5-23. Effects of ozone on plant function and growth. Reduced carbohydrate production decreases allocation to for resources need for plant growth processes. Solid black arrows indicate affects of ozone absorption; gray stripped arrows indicate affects on plant growth.

growth of one or several branches while growth of the tree appears not to be affected (Hinckley et al., 1992).

Two properties that are important in determining the effect a stress at one hierarchial level of organization will have on a higher level are variability and compensation. Variability in response to stress may mean that, because of genetic variation, not all trees are equally susceptible. At the stand level, the slower growth of some trees may be compensated for by the relatively faster growth of others that are experiencing reduced competition so that the overall growth of the stand is not affected (Hinkley et al., 1992). These properties when taken together will determine the extent and rate at which stress at one hierarchical level will

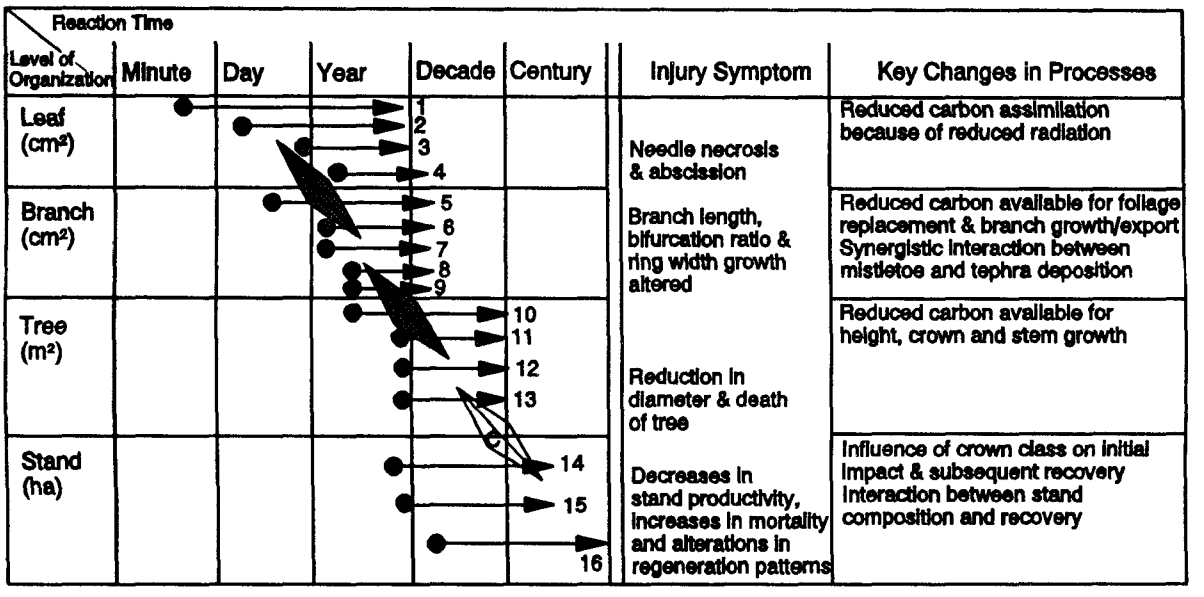
TABLE 5-29. PROPERTIES OF ECOLOGICAL SYSTEMS SUSCEPTIBLE TO OZONE AT FOUR LEVELS OF BIOLOGICAL ORGANIZATION

Level of Organization Properties	Structural	Functional Properties
Organism	Leaf area and distribution Biomass and allometry	Photosynthesis, respiration Nutrient uptake and release Carbon allocation
Population	Age and size structure Population density Genetic composition Spatial distribution Dispersion (spatial pattern)	Natality (reproduction, mortality) Competition Productivity
Community	Species composition (diversity) Trophic levels and food webs Physical structure (leaf area index)	Redundancy and resilience Succession (the integration of all species processes such as competition and predation)
Ecosystem	Biomass Element pools Soil properties	Ecosystem productivity Nutrient cycling Hydrologic cycling Energy flow

Source: Adapted from Sigal and Suter (1987).

impact the next highest level. To understand the effects of a stress, one must utilize the framework of hierarchical scales (Figure 5-24) developed by Hinckley et al. (1992) to provide a means by which the effects on forest trees of the eruption of St. Helens could be followed and understood. This figure is also applicable for use when considering O_3 effects and can be used to explain the difference between the response of the San Bernardino Forest ecosystem and the forests in the eastern United States. As pointed out above, variability and compensation determine the severity of the response of the individual.

Variability and compensation can also occur at the population level, all populations do not respond equally (Taylor and Pitelka, 1992). Plant populations can respond in four different ways: (1) no response, the individuals are resistant to the stress; (2) mortality of all individuals and local extinction of the extremely sensitive population—the most severe



Evaluating Impacts within a Level of Organization

Leaf Level	Carbon exchange 1 Carbon pools 2 Needle #/size 3 Needle retention/abscission 4	Tree Level	Hgt. & diameter growth 10 Crown shape & size 11 Tree vigor 12 Mortality 13
Branch Level	Carbon allocation 5 Branch growth 6 Branch morphology 7 Branch vigor 8 Branch retention 9	Stand Level	Productivity 14 Mortality 15 Species composition 16

Evaluating Interactions between Different Levels of Organization

The diagonal arrow indicates the interaction between any two levels of organization.
The types of interaction are due to the properties of variability, and compensation.

A - refers to the interaction between the leaf and branch levels where, for example, variability at the branch level determines leaf quantity and compensation at the leaf level in photosynthesis may compensate for the reduction in foliage amount.

B - refers to the interaction between the branch and the tree where variability in branches determines initial interception, branch vigor and branch location in the crown, and compensation may be related to increased radiation reaching lower branches.

C - refers to the interaction between the tree and the stand. Both genetic and environmental variability, inter- and intraspecific compensations and tree historical and competitive synergisms involved.

Figure 5-24. Effects of environmental stress on forest trees are presented on a hierarchial scale for the leaf, branch, tree, and strand levels of organization. The evaluation of impacts within a level of organization are indicated by horizontal arrows. The evaluation of interactions between different levels of organization are indicated by diagonal arrows.

Source: Hinckley et al. (1992).

response; (3) physiological accommodation, growth, and reproductive success of individuals are unaffected because the stress is accommodated physiologically; and (4) differential response, members of the population respond differentially with some individuals exhibiting better growth and reproductive success due to genetically determined traits (Taylor and Pitelka, 1992). Differential response results in the progressive elimination over several generations of the sensitive individuals and a shift in the genetic structure of the population toward greater resistance (microevolution). Physiological accommodation or microevolution, with only the latter affecting biodiversity, are the most likely responses for exposure to chronic stress (i.e., stresses that are of intermediate-to-low intensity and of prolonged duration). The primary effect of O_3 on the more susceptible members of the plant community is that the plants can no longer compete effectively for essential nutrients, water, light, and space and are eliminated. The extent of change that can occur in a community depends on the condition and type of community, as well as the exposure (Garner, 1993). Forest stands differ greatly in age, species composition, stability, and capacity to recover from disturbance. For this reason, data dealing with the responses of one forest type may not be applicable to another forest type (Kozlowski, 1980).

5.7.3.2 The San Bernardino Forest Ecosystem—Before 1986

The mixed conifer forest ecosystem in the San Bernardino Mountains of southern California is one of the most thoroughly studied ecosystems in the United States. The changes observed in the mixed conifer forest ecosystem exemplify the information presented in the foregoing discussion. Chronic O_3 exposures over a period of 50 or more years caused major changes in the San Bernardino National Forest ecosystem. The primary effect was on the more susceptible members of the forest community, individuals of ponderosa and Jeffrey pine, in that they were no longer able to compete effectively for essential nutrients, water, light and space. As a consequence of altered competitive conditions in the community, there was a decline in the sensitive species, permitting the enhanced growth of more tolerant species (Miller et al., 1982; U.S. Environmental Protection Agency, 1978, 1986). The results of the studies of the San Bernardino Forest ecosystem were reported in both the 1978 and 1986 criteria documents (U.S. Environmental Protection Agency, 1978, 1986). The information summarized below is from these two documents.

An inventory of the forest was begun in 1968 and conducted through 1972 to determine the results of more than 30 years of exposure to O_3. Based on that inventory and accompanying studies, the conclusions reached at that time are presented in Table 5-30. Data from the inventory indicated that for 5 mo per year from 1968 through 1972 trees were exposed to O_3 concentrations greater than 0.08 ppm for more than 1300 h with concentrations rarely decreasing below 0.05 ppm at night near the crest of the mountain slope, elevation approximately 5,500 ft (Miller, 1973). The importance of altitude in plant response was discussed in the 1986 criteria document (U.S. Environmental Protection Agency, 1986).

TABLE 5-30. SAN BERNARDINO FOREST—STATUS 1972

1. Ponderosa and Jeffrey pine were suffering the most injury. Mortality of one population of ponderosa pine (n = 160) was 8% Between 1969 and 1971 (p = 0.01); in a second population (n = 40), mortality was 10% between 1968 and 1972. White fir populations had suffered slight damage, with scattered individual trees showing severe symptoms. Sugar pine, incense cedar, and black oak exhibited only slight foliar injury from oxidant exposure.
2. A substantial shift occurred in ponderosa pines from the "slight injury" category in 1969 to the "moderate injury" category in 1971, indicating that there was continuing oxidant stress and that the selective death of ponderosa pines was occurring.
3. Suppression of photosynthesis in seedlings was observed (Miller et al., 1969). In ponderosa pine saplings, needles shortened by exposure to oxidants returned to normal length when the seedlings were moved to ozone-free air during 1968 to 1973 (Miller and Elderman, 1977).
4. Bark beetles were judged to be responsible for the death of weakened trees in the majority of cases. Elimination of ponderosa pine from the mixed-conifer forest was postulated to occur in the future if the rate of bark beetle attack were to continue unabated (Cobb and Stark, 1970).
5. Aerial portions of ozone-injured pine trees showed a decrease in vigor that was associated with deterioration of the feeder root system (Parameter et al., 1969).
6. Seed production was decreased in injured pines. Ordinarily, trees 25 to 50 inches dbh produce the most cones, but they were also the most sensitive to oxidants (Luck, 1980).
7. Understory plant species sensitive to oxidant pollution may already have been removed by air pollution stress at the time of these early studies (Miller and Elderman, 1977).

Source: U.S. Environmental Protection Agency (1986).

The survey cited above indicated the need for further information and resulted in the development of an interdisciplinary research team to more accurately determine the effects of the 30 years of exposure to O_3 of the San Bernardino Forest ecosystem. The study was designed to answer two questions: How do organisms and biological processes of the conifer forest response to different levels of chronic oxidant exposure? and (2) How can these responses be interpreted within and ecosystem context?

The research plan included study of the limited aspects of the following ecosystem processes: (1) carbon (energy) flow (the movement of carbon dioxide into the plants, its incorporation into carbohydrates; and then its partitioning among, consumers, decomposers, litter, and the soil; and finally its return to the atmosphere); (2) the movement of water in the soil-plant-atmosphere compartments; and (4) the shift in diversity patterns in time and space as represented by changes in structure, and density in the composition of tree species in communities.

The major abiotic components studied were water (precipitation), temperature, light, mineral nutrients (soil substrate, and oxidant pollution. The biotic components studied included producers (an assortment of tree species and lichens), consumers (wildlife, insects, disease organisms), and decomposers, (populations of saprophytic fungi responsible for the decay of leaf and woody litter (U.S. Environmental Protection Agency, 1978, 1986).

During the period of the study, 1973 to 1978, average 24 h O_3 concentrations ranged from a background of 0.03 to 0.04 ppm in the eastern part of the San Bernardino Mountains to a maximum of 0.10 to 0.12 ppm in the western part during May through September. In addition to total oxidant, PAN and NO_2 concentrations were measured. Peroxyacetyl nitrate injury symptoms could not distinguished from O_3 symptoms on herb-layer plant species, while NO_2 remained at non-toxic concentrations (Miller et al., 1982; U.S. Environmental Protection Agency, 1978, 1986).

The study indicated that the major changes in the ecosystem began with injury to ponderosa and Jeffrey pine.

Ponderosa pine was the most sensitive of the trees to O_3 with Jeffrey pine, white fir, black oak, incense cedar, and sugar pine following in decreasing order of sensitivity. Foliar injury on sensitive ponderosa and jeffrey pine was observed when the 24-h-average O_3 concentrations were 0.05 to 0.06 ppm (Miller et al., 1982). Foliar injury, premature

senescence, and needle fall decreased the photosynthetic capacity of stressed pines and reduced the production of carbohydrates needed for use in growth and reproduction by the trees. Nutrient availability to the trees was also reduced by their retention of smaller amounts of green foliage (Miller et al., 1982). Decreased carbohydrate resulted in a decrease in radial growth and in height of stressed trees (McBride et al., 1975; Miller and Elderman, 1977).

Tree reproduction also was influenced by a reduction in carbohydrate. Injured ponderosa and Jeffrey pines older than 130 years produced significantly fewer cones per tree than uninjured trees of the same age (Luck, 1980). Tree ring analysis indicated declines in ring width indices for many trees. Stand thinning however reversed the trend (Miller et al., 1982).

Summarized, the responses of individual conifers sensitive to O_3 include (1) visible foliar injury; (2) premature needle senescence; (3) reduced photosynthesis; (4) reduced carbohydrate production and allocation; (5) reduced plant vigor; and (6) reduced growth or reproduction or both (Miller et al., 1982). The majority of these same responses were observed on the eastern white pine growing in the Appalachian Mountains of the eastern United States (McLaughlin et al., 1982; Skelly et al., 1984; U.S. Environmental Protection Agency, 1986).

Injury to or changes in the functioning of other living ecosystem components affected, either directly or indirectly, the processes of carbon (energy) flow and mineral nutrient cycling, water movement and changed vegetational community patterns (Miller et al., 1982). Change in decomposition patterns, altered nutrient cycling. Early senescence and abscission caused an accumulation of pine needles into a thick layer under the stands of O_3 injured trees and changed the successional patterns of the fungal microflora as well. Altering the taxonomic diversity and population density of the microflora that normally develop on needles while they are on the tree, influenced its relationship with the decomposer community. Change in the type of fungi on needles weakened the decomposer community and the rate of decomposition (Bruhn, 1980). Carbon and mineral nutrients accumulated in the heavy litter and the thick needle layer under stands with the most severe needle injury and defoliation and influenced nutrient availability.

A comparison of lichen species found on conifers during the years 1976 to 1979 with collections from the early 1900's indicated 50% reduction in species in the more recent period. Marked morphological deterioration of the common species *Hypogymnia enteromorpha* was documented in areas of high oxidant concentrations (Sigal and Nash, 1983).

Biotic interactions associated with predators, pathogens, and symbionts were influenced by changes in the energy available to the trees. The decrease in vigor and lack of ability to recover from ozone injury associated with reduced carbohydrates made the ponderosa pines more susceptible to attack by predators and pathogens (Stark and Cobb, 1969). Dahlsten and Rowney (1980) have pointed out that oxidant-weakened pines can be killed by fewer western pine beetles than are required to kill healthier trees. In stands with a high proportion of O_3-injured trees, a given population of western pine beetles could therefore kill more trees. James et al. (1980a,b) observed that the root rot fungus, *Heterobasidium annosum*, increased more rapidly because freshly cut stumps and roots of weakened trees were more vulnerable to attack (U.S. Environmental Protection Agency, 1986).

From the presentation above, it can be seen that temporal dynamics at the level of the individual organisms can upset the equilibrium and be disorganizing in ecosystems that are dominated by nonmoble organisms (Shugart, 1987). In forests with large canopy trees, a canopy tree dominates the space where it is growing, reduces the amount of light reaching the forest floor and alters the microclimate, conditions that help to determine the plant species that can survive beneath the canopy. Death of a canopy tree increases the resources of light, nutrients, water, and energy available to other organisms. This change initiates a struggle for dominance among understory trees and seedlings. In time a new canopy becomes established (Shugart, 1987; Garner et al., 1989).

The mode of death of a tree is ecologically important as it determines the regeneration success of trees that form the next forest generation. Trees may dies catastrophically as when high winds or ice storms break off the crown or branches or when they are blown over, exposing roots; or they may dies slowly and tend to waste away as in the case of those injured by pathogens or insects (Shugart, 1987). Tree death, as influenced by O_3, is usually gradual rather than catastrophic unless the tree is extremely sensitive or the pollutant concentration is extremely high. Growth responses require time. Therefore, because growth

responses to cumulative stresses require time and trees are continually being subjected to many other stresses, the cause of death is frequently difficult to determine (Garner et al., 1989). The continuum of vegetation changes associated with increasing pollutant stress as seen in the San Bernardino mixed forest ecosystem is presented in Table 5-31 (Garner et al., 1989; U.S. Environmental Protection Agency, 1986).

TABLE 5-31. ECOSYSTEM RESPONSE TO POLLUTANT STRESS

Continuum	Stage of Response of Vegetation	Response of Ecosystem
0	Anthropogenic pollutants insignificant.	Unaffected; systems Pristine.
I	Pollutant concentrations low; no measurable physiological response.	Ecosystem functions unaffected; pollutants transferred from atmosphere to organic or available nutrient compartments.
II	Pollutant concentrations injurious to sensitive species; (1) Reduced photosynthesis, altered carbon allocation, reduced growth and vigor; (2) Reduced reproduction; (3) Predisposition to entomological or microbiological stress.	Altered species composition; populations of sensitive species decline; some individuals are lost. Their effectiveness as functional ecosystem members diminishes; they could be lost from the system. Ecosystem reverts to an earlier stage.
III	Severe pollution stress. Large plants of sensitive species die. Forest layers are peeled off; first trees, tall shrubs and, under most severe conditions, short shrubs and herbs.	(1) Simplification, basic ecosystem structure changes, becomes dominated by weedy species not previously present. (2) Reduced stability and productivity; loss of capability for repairing itself. Runoff increases, nutrient loss, and erosion accelerates; a barren zone results. Ecosystem collapses.

Source: Garner et al. (1989); adapted from Bormann (1985); Kozlowski (1985); Smith (1974).

5.7.3.3 The San Bernardino Forest Ecosystem—Since 1986

The source for pollutants transported to the mixed conifer forests of the San Bernardino Mountains is the South Coast Air Basin of southern California. Between 1976 and 1991 the weather adjusted O_3 data for the May through October "smog season" indicates that the number of Basin days exceeding 0.12 ppm, 1 h average have declined at an average annual rate of 2.27 days per year (Davidson, 1993). The number of days with episodes greater than 0.2 ppm, 1 h average have declined at an average annual rate of 4.70 days per year over the same time period. The total days per year with concentrations greater than 0.12 ppm was as high as 159 in 1978 with the lowest number being 105 days in 1990. The 1974 to 1988 trends of the May through October hourly average and the average of monthly maximum O_3 concentrations for Lake Gregory, a forested area in the western section of the San Bernardino Mountains, have also shown a decline (Miller et al., 1989). Similarly there has been an improvement shown in the injury index used to describe chronic injury to crowns of ponderosa and Jeffrey pines between 1974 and 1988 in 13 of 15 plots located on the gradient of decreasing O_3 exposure in the San Bernardino Mountains (Miller et al., 1989). The two exceptions were plots located at the highest exposure end of the gradient.

Miller et al. (1991) reported that for the 1974 to 1988 period the basal area increase of ponderosa pines was generally less than competing species at 12 of the 13 plots evaluated. The total basal area for each species as percent of the total basal area for all species (Figure 5-25) shows that ponderosa and Jeffrey pines lost basal area in relation to competing species that are more tolerant to O_3, namely, white fir, incense cedar, sugar pine and black oak at plots with slight to severe crown injury to ponderosa or Jeffrey pine. In effect stand development has been forced in reverse, that is, the development of the normal fire climax mixture dominated by fire tolerant ponderosa and Jeffrey pines is altered. The accumulation of more stems of O_3 tolerant species in the understory presents a fuel ladder situation that jeopardizes the remaining overstory trees in the event of a catastrophic fire. The O_3 tolerant species are inherently more susceptible to fire damage because of thinner bark and branches close to the ground. The important question for the future is whether the declining O_3 exposure will eventually allow ponderosa and Jeffrey pine to resume dominance in basal area.

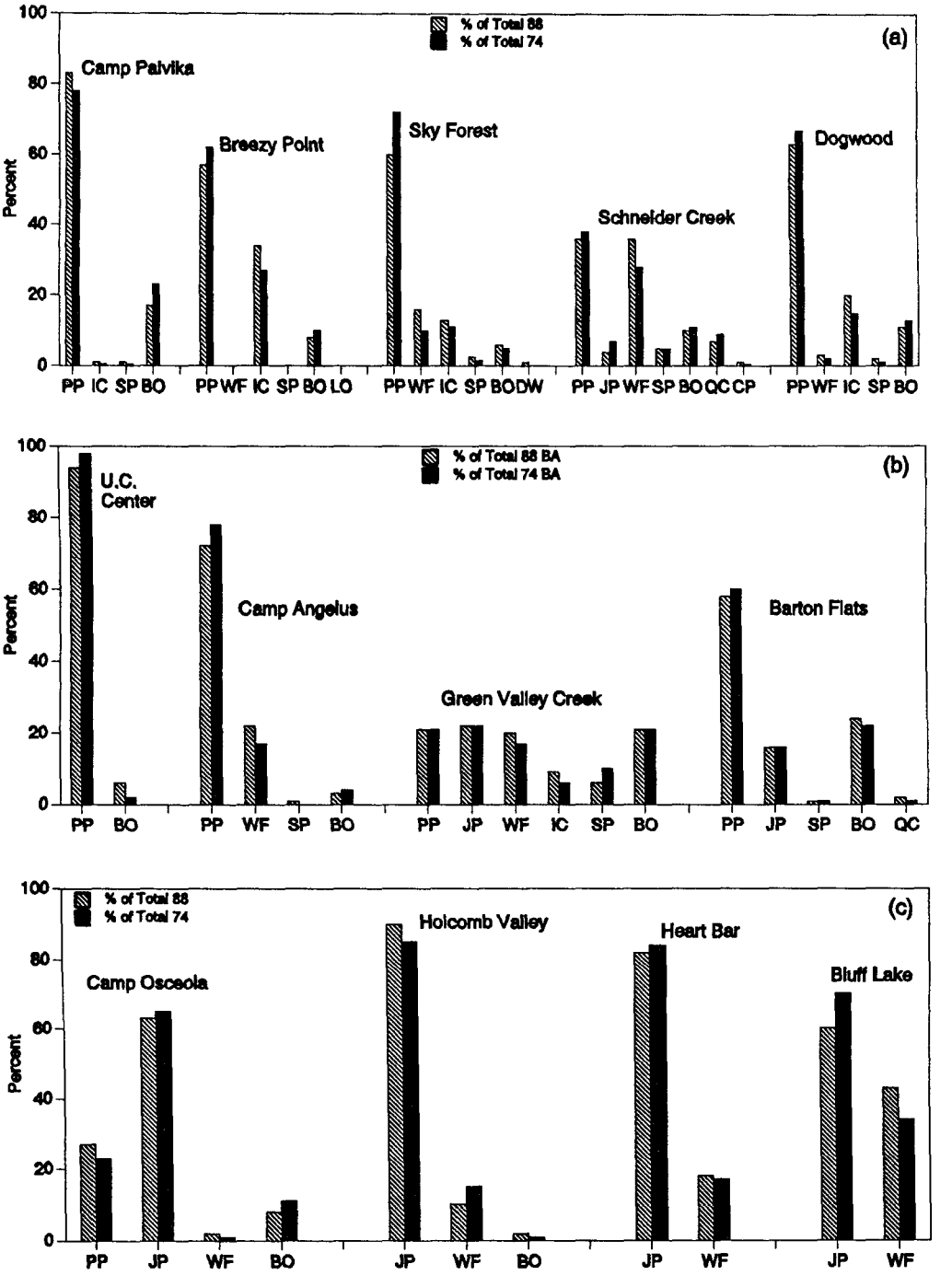


Figure 5-25. Total basal area for each species as percent of the total basal area for all species in 1974 and 1988 on (a) plots with severe to moderate damage, (b) plots with slight damage, and (c) plots with very slight damage or no visible symptoms.

Source: Miller, McBride, and Schilling (1991).

5.7.3.4 The Sierra Nevada Mountains

Since 1991 there has been an annual survey of the amount of crown injury by O_3 to the same trees in approximately 33 sample plots located in the Sierra Nevada including Tahoe National Forest, Eldorado National Forest, Stanislaus National Forest, Yosemite National Park, Sierra National Forest, Sequoi-Kings Canyon National Park, and Sequoia National Forest plus the San Bernardino National Forest. In general, the results of this study document the regional nature of the O_3 pollution problem originating primarily from the San Jaoquin Valley Air Basin (as well as the San Francisco Bay Air Basin further to the west). Oxidant air pollution is transported southward in the San Jaoquin Valley Air Basin until it reaches the southern boundary of the air basin—the Tehachipi Mountains. Because of this barrier polluted air masses circulate back northward. This circulation cell causes higher O_3 levels to be adverted to the southernmost administrative units, namely the Sequoia National Forest and the Sequoia-Kings Canyon National Park. The early tree injury results (unpublished) corroborate the north to south increase of chronic O_3 symptoms described by Peterson et al. (1991). The most important long-range object of the study is to provide a data base that will allow hypothesis testing regarding exposure response of ponderosa and Jeffrey pines as a function of O_3 concentration statistics, summer meteorology, and stomatal conductance measurements.

The region-wide survey (Peterson et al., 1991) of ponderosa pine provides a useful backdrop for reporting a number of other studies or surveys in the Sierra Nevada that were more narrowly focused. Another tree ring analysis and crown injury study concentrated on Jeffrey pines in Sequoia-Kings Canyon National Park (Peterson et al., 1989). This study suggested that decreases of radial growth of large, dominant Jeffrey pines growing on thin soils with low moisture holding capacity and direct exposure to upslope transport of O_3 amounted to as much as 11% less in recent years when compared with similar trees without symptoms.

Both permanent plots and cruise surveys have been employed in Sequoia, Kings Canyon and Yosemite National Parks to determine the spatial distribution and temporal changes of injury to ponderosa and Jeffrey pine within the Parks (Duriscoe and Stolte, 1989). In Sequoia—Kings Canyon, O_3 injury to individual trees and the number of trees injured in each plot increased between 1980 to 1982 and 1984 to 1985 evaluations was the most

common response among the 28 plots studied. Ozone injury tends to decrease with increasing elevation of plots. The O_3 concentrations associated with the highest levels of tree injury in the Marble Fork drainage of the Kaweah River at approximately 1,800 m elevation are hourly averages frequently peaking at 80 to 100 ppb but seldom exceeding 120 ppb.

During a cruise survey in 1986 (Duriscoe and Stolte, 1989) to identifiy the partial distribution of injury, there were 3,120 ponderosa or Jeffrey pines evaluated for O_3 injury in Sequoia, Kings Canyon and Yosemite National Parks. Approximately one third of this number were found to have some level of chlorotic mottle. At Sequoia, Kings Canyon symptomatic trees comprised 39% of the sample (574 out of 1,470) and at Yosemite they comprised 29% (479 out of 1,650). Ponderosa pines were generally more severely injured than Jeffrey pines.

In Sequoia, Kings Canyon observations at field plots showed that giant sequoia seedlings developed O_3 injury symptoms at both ambient O_3 concentrations and 1.5 $\times$ ambient O_3 (0.08 to 0.1 ppm hourly peaks) (in open top chambers) during the 8 to 10 weeks following germination (Miller and Grulke, submitted). Field plot observations of seedling health and mortality in natural giant sequoia groves over a 4 year period showed that seedling numbers were reduced drastically from drought and other abiotic factors. Any variable such as O_3 that could stress seedlings sufficiently to reduce root growth immediately after germination could increase vulnerability to late summer drought. Significant differences in light compensation point, net assimilation at light saturation, and dark respiration were found between seedlings in charcoal filtered air treatments and 1.5 $\times$ ambient O_3 treatments (0.08 to 0.1 ppm hourly peaks) (Grulke et al., 1989). One interpretation of these results is that O_3 could be a new selection pressure during the regeneration phase of giant sequoia, possibly reducing genetic diversity.

The Lake Tahoe Basin is located at the northern end of the Sierra Nevada sampling transect (near the Eldorado National Forest) (Peterson et al., 1991). Because it is an air basin unto itself the air quality situation is distinct from other Sierra Nevada sites. In 1987, a survey of 24 randomly selected plots in the basin included a total of 360 trees of which 105 (29.2%) had some level of foliar injury (Pedersen, 1989). Seventeen of these plots had FPM injury scores (Pronos et al., 1978) that fell in the slight injury category. Of 190 trees

in 16 cruise plots that extended observations to the east outside the basin 21.6% had injury—less than in the basin.

Site Variables Affecting Ozone Response in the California Ecosystems

Structural changes in forest stands are highly related to their position on the landscape, sometimes referred to as site. Site variables can be defined at regional and local levels. For example, the regional level is defined in California by the location of forested mountain slopes and summits in relation to polluted urban air basins. In both the Sierra Nevada mountains and the San Bernardino mountains in California the worst tree injury is found on ridges that overlook the polluted air basins. The polluted air masses are transported up-slope or up-canyon in terrain that is usually sunlit in the afternoon and early evening, thus the thermal convection on warm slopes is a major means by which O_3 and associated pollutants are delivered to the first forested ridges. Both vertical mixing and horizontal diffusion into cleaner air results in a distinct gradient of decreasing O_3 concentration in more distant forest stands. Two such gradients have been described in the San Bernardino mountains (Miller et al., 1986). Across the longer axis of the west to east orientation of the mountain range O_3 concentrations range from the highest summer months 24 h averages of 90 to 140 ppb nearest the polluted South Coast Air Basin to 40 to 50 ppb at a downwind distance of 35 to 40 km. In the more narrow south to north direction the same concentration gradient is seen over a much shorter distance of 5 to 8 km because of a more rapid transition to the warm desert influence which causes mixing and dilution (Miller et al., 1972). Accordingly, O_3 injury to sensitive vegetation ranges from severe to none over these distances.

In the Sierra Nevada mountains a gradient of decreasing injury is observed from west to east and south to north (Peterson and Arbaugh, 1992). But the worst level of chronic injury is generally much less than observed in the San Bernardino mountains.

With respect to localized site variables there is evidence from repeated surveys in Sequoia and Kings Canyon National Parks that percent of trees injured and the severity of foliar injury both increased with decreasing elevation in the 1,500 to 2,500 m zone on generally west facing slopes adjacent to the polluted San Joaquin Valley Air Basin (Stolte et al., 1992). In Sequoia-Kings Canyon National Parks radial growth reductions in Jeffrey pine with foliar injury by O_3 was documented only for large, dominant trees growing on

shallow soils (Peterson et al., 1987). Soil moisture availability is generally lower on such sites. One hypothesis for explaining radial growth decline on these sites and not more favorable sites with greater moisture holding capacity is that O_3 defoliation in favorable moisture years and water stress in dry years integrate sequentially to suppress growth.

In the San Bernardino mountains, radial growth of ponderosa and Jeffrey pines in plots along the decreasing O_3 gradient was not well correlated with level of chronic injury but was better correlated with soil moisture holding capacity. Within a single plot with relatively uniform moisture availability there was a good correlation between increased radial growth and a decreasing level of chronic O_3 visible injury to crowns. Chappelka et al. (1992) have suggested that some of the variability in foliar injury response of hardwood species to O_3 in Shenandoah National Park and the Great Smoky Mountains National Park is due to elevation and microsite conditions, including the proximity to streams.

5.7.3.5 The Appalachian Mountains—Before 1986

Oxidant induced injury on vegetation in the Applachian Mountains has been observed for many years but has not produced the same ecosystem responses. Results of studies in the eastern United States was reported in the 1986 criteria document and is summarized in the following passages (U.S. Environmental Protection Agency, 1986). Needle blight of eastern white pine was first reported in the early 1900s but it was not known until 1963 that it was the result of acute and chronic O_3 exposure (Berry and Ripperton, 1963). The U.S. Forest Service in the 1950s studied the decline of eastern white pine in an area covering several hundred square miles on the Cumberland Plateau in Tennessee and concluded that atmospheric constituents were the cause (Berry and Hepting, 1964). Despite this and other early reports of field observations by Berry (1962, 1964), no concerted effort was made to determine the effects of O_3 on the vegetation of the Appalachian Mountains until the 1970s when Skelly and his coworkers began monitoring total oxidants and recorded associated injury to eastern white pine in three rural Virginia sites between April 1975 and March 1976 (Hayes and Skelly, 1977). Reductions in overall growth of eastern white pine was reported by Benoit (1982). The mean ages of trees in the study plots classified as O_3-tolerant, intermediate and O_3-sensitive were 53, 52 and 56 years, respectively. A comparison of growth from 1974 to 1978 with that from 1955 to 1959 based on tree rings showed decreases

of 26, 37, and 51% for tolerant, intermediate and sensitive trees, respectively (Benoit, 1982). The authors assumed the reduction in radial growth had occurred because there had been no significant changes in seasonal precipitation between the 1955 to 1959 and the 1963 to 1978 periods. Ozone concentrations for 1 h at the study cites for 1979 to 1982 ranged from a low of 0.063 ppm to a high of 0.129 ppm (U.S Environmental Protection Agency, 1986).

Growth reductions in trees growing on the were studied by Mann et al. (1980) and McLaughlin et al. (1982). A steady growth decline in annual ring increment was observed during the years 1962 through 1979. Reductions in average annual growth and 90% of bole growth of 70% in sensitive trees when compared to the growth of tolerant and in intermediate trees were observed. Tolerant trees consistently showed a higher growth rate of from 5 to 15% than intermediate trees for the 1960 to 1968 interval, similar growth from 1969 through 1975, and a reduction in growth of 5 to 15% for the period 1976 through 1979 when compared to trees intermediate in sensitivity. The decline was attributed to chronic O_3 which frequently exceeded 1-h average concentrations greater than 0.08 ppm. Maximum 1-h concentrations ranged from 0.12 to 0.20 ppm (U.S Environmental Protection Agency, 1986).

McLaughlin et al. (1982) observed that the decline in vigor and reduction in growth in trees and the production of carbohydrates (carbon flow) were associated with the following sequence of events and conditions: (1) premature senescence of mature needles at the end of the growing season; (2) reduced carbohydrate storage capacity in the fall and reduced resupply capacity in the spring to support new needle growth; (3) increased reliance of new needles of self-support during growth; (4) shorter new needles, resulting in lower gross photosynthetic productivity; and (5) higher retention of current photosynthate (carbohydrate) by foliage, resulting in reduced availability for transport to for external use including repair of chronically stressed tissues of older needles (U.S. Environmental Protection Agency, 1986).

5.7.3.6 The Appalachian Mountains—Since 1986

In a survey of eastern white pine stands in the southern Appalachians fifty white pines were examined for foliar symptoms (chlorotic mottle) believed to be O_3-caused at 201 sites distributed on a 24 × 24 km grid across the natural range of the species in South Carolina,

Tennessee, Virginia, North Carolina, Kentucky and Georgia (Anderson et al., 1988). The survey was conducted from September through November 1985. The percentage of stands with at least one symptomatic tree was highest in Kentucky (77%), followed by Tennessee (31%), and the lowest in Georgia (10%). The mean percentage of symptomatic trees per plot for all six states was 27%. The mean volume difference of 48 pairs of symptomatic and non-symptomatic trees was 49% less for symptomatic trees. Elevation and percent slope were not correlated with occurrence of symptomatic trees but most symptomatic trees were found on southwest-facing slopes. Plantations had a higher percentage of symptomatic trees than did natural stands. Ozone exposure concentrations were not reported but it may be possible to make estimates of exposure at the nearest O_3 monitoring sites.

Shenandoah National Park and Great Smoky Mountains National Park are contained within the survey area investigated by Anderson et al. (1988). These parks have been the subject of several surveys for O_3 injury to native vegetation. For example, Winner et al. (1989) surveyed 7 to 10 individuals of 5 native species at 24 sites in Shenandoah National Park. These species included tulip poplar (*Liriodendron tulipifera*, wild grape (*Vitis sp.*), black locust (*Robinia pseudoacacia*, virgin's bower (*Clematis virginiana*), and milkweed (*Asclepias sp.*). Visible foliar injury due to O_3 was most prevalent on milkweed species (up to 70%) while the remaining species had injury approaching 20%. In each case the level of foliar injury increased with elevation of the sites. The summer monthly 24-h mean O_3 concentrations at Blacksburg, Rocky Knob, Salt Pond and Big Meadows did not exceed 0.06 ppm and still foliar injury was observed.

Another recent survey in the Shenandoah National Park included black cherry, yellow poplar, and white ash; and, in the Great Smoky Mountains National Park black cherry, sassafras and yellow poplar (Chappelka et al., 1992). Black cherry exhibited symptoms in both parks. In former the percentage of leaves injured ranged from 18 to 40 while in the latter the range was 8 to 29% in 1991. Black cherry at Cove Mountain in the latter exhibited the highest percentage of symptomatic trees (97%). This site also had the highest number of hours exceeding 0.08 ppm. The majority of occurrences of concentrations exceeding 0.08 ppm occurred during evening hours.

In the previous O_3 document (U.S. Environmental Protection Agency, 1986f), Duchelle et al. (1982, 1983) reported that exposing native tree seedlings and herbaceous vegetation in

the Big Meadows area of the Shenandoah National Park in the Blue Ridge Mountains of Virginia to ambient O_3 reduced both the growth of the native trees other than eastern white pine and the productivity of the native herbaceous vegetation found growing in forested areas. Comparison of growth of seedlings in open plots or open-top chambers with charcoal-filtered air suppressed the growth of wild-type seedlings of tulip poplar, green ash, sweet gum, black locust (*Robinia pseudoacacia* L.), Eastern hemlock [(*tsugs canadensis* (L.) Carr.), Table Mountain (*Pinus pungens* Lamb.), Virginia (*P. virginiana* Mill,) and pitch (*P. rigida* Mill.) pines, usually without visible foliar injury symptoms. Open-top chambers were operated continuously from May 9 until October 9 during the 1979 and from April 24 until September 15 in 1980 (U.S. Environmental Protection Agency, 1986). Common milkweed (*Asclepias syriaca* L.) and common blackberry (*Rubus allegheniensis* Porter) were two species of native vegetation to exhibit visible injury symptoms (Duchelle and Skelly, 1981).

It was mentioned previously that though there has been evidence of widespread injury to native tree and other vegetation from exposure to O_3 the amount of injury has not been great enough for it to be transferred from the tree level to the stand level (Figure 5-23). Undoubtably, there has been selection for and removal of the most sensitive tree species of eastern white pine, for example. However, the numbers of sensitive individuals in a stand have not been great enough to make a visible impact on the forest. Simulations suggest that in forests with mixed species of uneven-aged stands suggest that long-term responses are likely to be shifts in species composition rather than widespread degradation (Taylor and Norby, 1985; U.S. Environmental Protection Agency, 1986).

5.7.3.7 Foliage and Soil-Mediated Effects—Combined Stress

Previously, it has been mentioned that the environment is seldom optimal in either natural or agricultural ecosystems. It is not unusual, therefore, for plants growing in natural habitats to encounter multiple stresses. Plant response to multiple stresses depend on resource, particularly, carbohydrate and nitrogen, interactions at levels ranging from the cell to the ecosystem (Chapin et al., 1987). Plant responses are either foliage-mediated, soil-mediated or both. The discussions in the previous section has focused on the foliaged-mediated response of plant species in an ecosystem to O_3. This section discusses the possible

interactive effects of soil-mediated responses. It has usually been thought that nitrogen input to natural ecosystem alleviated deficiencies in the soil and increased plant growth (U.S. Environmental Protection Agency, 1993). Increased nitrogen additions can lead to nutrient deficiencies of other elements (e.g., calcium and magnesium). Aber et al., (1989) state that when nitrogen becomes readily available, other resources (e.g., phosphorus for plants and carbon for microorganisms) become limiting. Changes in nitrogen supply can have an impact on an ecosystem's nutrient balance and alter many plant and soil processes (U.S. Environmental Protection Agency, 1993).

The possible interactive effects of nitrogen on the forests of the San Bernardino Mountains has come under consideration more recently. For some time there has been a concern that O_3 is not the only pollutant in the photochemical mixture that may be causing lasting changes in the mixed conifer forest ecosystem. A multidisciplinary study to investigate the possibility of the combined impacts on ecosystem processes from chronic O_3 injury and both wet and dry deposition of acidic nitrogen compounds has been under way since 1991 at Barton Flats in the San Bernardino Mountains. The data base includes frequent measurements of stomatal conductance in relation to weather and O_3 exposure.

The nitrogen oxides criteria document (U.S. Environmental Protection Agency, 1993) explored the possible effects of increased nitrogen on litter content and decomposition. That discussion is presented here.

An increase in the nitrogen litter content and in litter decomposition rates and an alteration in nitrogen cycling have been observed in the more highly polluted areas when compared with moderate- and low-polluted areas of the San Bernardino Mountains of Southern California (Fenn and Dunn, 1989). A pollutant concentration gradient exists with 24-h O_3 concentrations at the high sites in the west averaging 0.1 ppm or higher, moderate sites ranging from 0.06 to 0.08 ppm, and low sites in the east averaging 0.05 ppm or less (Fenn, 1991). Nitrogen and sulfur compounds also occur in the pollutant mixture to which the mountains downwind of the Los Angeles Basin are exposed (Bytnerowicz et al., 1987a,b; Solomon et al., 1992). A nitrogen deposition gradient from west to east parallels the decreasing O_3 gradient. Deposition of nitrogen exceeds that of sulfur (Fenn and Bytnerowicz, 1992). Annual average HNO_3 concentrations in 1986 ranged from 1.2 ppb

near the Southern California coast to 2.7 ppb in the San Gabriel Mountains (Solomon et al., 1992).

The effects of O_3 exposure and injury to ponderosa (*Pinus ponderosa* Laws.) and Jeffrey pine (*P. jeffreyi* Grev. & Balf.) on a mixed conifer forest in the San Bernardino Mountains, east of Los Angeles, have been studied for many years (Miller, 1973; Miller, 1984; U.S. Environmental Protection Agency, 1986). The litter layers under trees severely injured by O_3 is deeper than that under trees less severely injured (Fenn and Dunn, 1989). A comparison study of litter decomposition rates of L-layer litter indicates that litter from the more polluted areas in the west decomposed at a significantly ($p = 0.01$) faster rate than litter from moderate to low pollution levels (Fenn and Dunn, 1989; Fenn, 1991). Nitrogen content of litter was greatest at the high pollution sites and was positively correlated with the litter decomposition rate. The higher nitrogen and lower Ca content of the litter suggests that litter in the western plots originated from younger needles than at the less polluted sites, possibly due to O_3-induced needle abscission. Fungal diversity was also greater in the litter from the western San Bernardino Mountains (Fenn and Dunn, 1989).

When the factors associated with enhanced litter decomposition were investigated, it was found that nitrogen concentrations of soil, foliage, and litter of ponderosa and Jeffrey pine were greater in the plots where pollution concentrations were high than in moderate- or low-pollution sites. This was also true for sugar pine (*Pinus lambertiana* Dougl.) and for incense cedar (*Calocedrus decurrens* [Torr.] Florin.), two O_3-tolerant species. The rate of litter decomposition for all three pine species was greater at the high-pollution sites. Therefore, the increased rate of litter decomposition in the high-pollution plots does not appear to be related to O_3 sensitivity or premature needle abscission, but rather due to higher levels of nitrogen in the soils (Fenn, 1991).

Nitrogen is the mineral nutrient that most frequently limits growth in both agricultural and natural systems (Chapin et al., 1987). The uptake of nitrogen and its allocation is of overriding importance in plant metabolism and governs, to a large extent, the utilization of phosphorus, potassium, and other nutrients, and plant growth. Plants usually obtain nitrogen by absorbing ammonium (or ammonia) or nitrate (or nitrite) through their roots or through fixation by symbiotic organisms. Nitrogen availability via the nitrogen cycle typically controls net primary productivity. Normally, the acquisition of nitrogen is a major carbon

expense for plants. Plants expend a predominant fraction of the total energy available to them in the form of carbohydrates in the acquisition of nitrogen through the processes of (1) absorption, bringing nitrogen into the plant from the environment; (2) translocation, moving inorganic nitrogen within the plant; and (3) assimilation, conversion of inorganic to organic nitrogen (Chapin et al., 1987). Absorption of nitrogen from the soil requires constant and extensive root growth to meet the needs of a rapidly growing plant because the soil pools of mineral nitrogen, ammonium, or nitrate in the immediate vicinity of the roots are usually so small that they are quickly depleted. A crude estimate suggests that the fraction of carbon budget spent on absorption, translocation, and assimilation ranges from 25 to 45% for ammonium, 20 to 50% for nitrate, 40 to 45% nitrogen fixation, and 25 to 50% for formation of mycorrhizae (Chapin et al., 1987).

Nitrogen is the mineral that most frequently limits growth in both natural and agricultural ecosystems (Chapin et al., 1987). The uptake of nitrogen and its allocation is of overriding importance in plant metabolism and governs, to a large extent, the utilization of phosphorus, potassium, and other nutrients, and plant growth. Nitrogen availability via the nitrogen cycle typically controls net primary productivity. Normally, the aquisition of nitrogen is a major carbohydrate expense for plants.

Nitrogen uptake influences photosynthesis because in the leaves of plants with C_3 photosynthesis (the pathway used by most of the world's plants), approximately 75% of the total nitrogen is contained in the choloroplasts and is used during photosynthesis. The nitrogen-photosynthesis relationship is, therefore, critical to the growth of trees (Chapin et al., 1987). As a rule, plants allocate resources most efficiently when growth is equally limited by all resources. When a specific resource such as nitrogen limits growth, plants adjust by allocating carbohydrates to the organs that acquire the most strongly limiting resources (Figure 5-26).

Among boreal and subalpine conifers, nitrogen added to the soil may not increase growth. Depending on the plant species, nitrogen use efficiency above a critical level decreases. All plants do not necessarily benefit from the added nitrogen in the leaves. More nitrogen in the soil is not mirrored directly by increased nitrogen uptake except at low levels. This is particularly true of conifers that are adapted to low-resource environments and tend to have low potential growth rates. The photosynthetic capacity of conifer foliage is low and

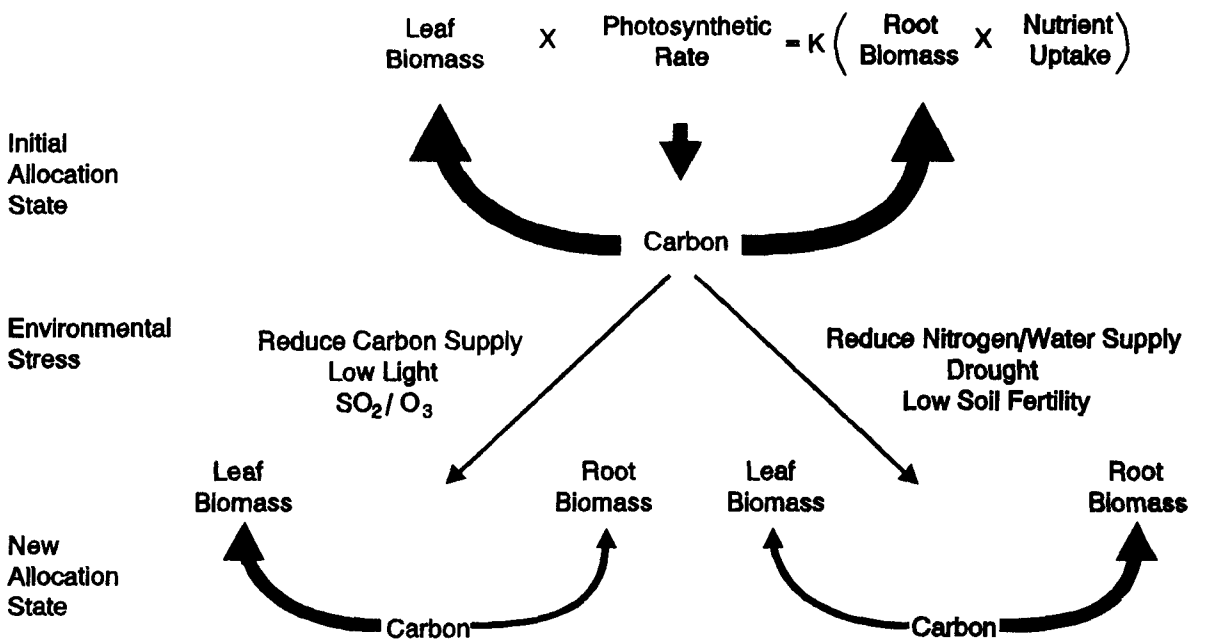


Figure 5-26. Impact of a reduced supply of carbon to the shoot, or water and nitrogen to the roots, on subsequent allocation of carbon.

Source: Winner and Atkinson (1986).

not greatly enhanced by increased nitrogen content (Waring, 1985; Chapin, 1991). High leaf nitrogen content is not always an advantage when other resources, among which are light and water, are limited. At the present time, data dealing with the response of trees or other vegetation to the combined stresses of O_3 exposure above ground and nitrate deposition through the soil are sparse. Tjoelker and Luxmoore (1991), however, have assessed the effects of soil nitrogen availability and chronic O_3 stress on carbon and nutrient economy in 1-year-old seedlings of loblolly pine (*Pinus taeda* L.) and yellow poplar (*Liriodendron tulipifera* L). Elevated O_3 concentrations altered biomass partitioning to needles of the current year. Ozone concentrations of 0.108 ppm reduced the biomass of current-year needles in loblolly pine seedlings grown at the highest (172 μg/g) nitrogen supply by 20%, but not those grown with a low (59 μg/g) supply of nitrogen. The interaction between O_3 and nitrogen suggests that plants grown with a high nitrogen supply are more sensitive to chronic O_3 stress in terms of biomass reduction (Tjoelker and Luxmoore, 1991). Similar results in the growth of domestic radish (*Raphanus sativa* L., cv. Cherry Bell) were obtained by Pell et al. (1990). Brewer et al. (1961) and Harkov and Brennan (1980) observed

increased foliar injury when plants were grown with an adequate nitrogen supply (U.S. Environmental Protection Agency).

5.7.3.8 Mycorrhizae-Plant Interactions

Mycorrhizae are quite literally, "fungus-roots", an association between plant roots and fungi that is beneficial to both. The majority of plants develop this relationship and could not reach optimum growth without it. Mycorrhizal fungi increase the uptake of mineral nutrients for the host plants, protect roots against pathogens, produce plant growth hormones, and move carbohydrates from one plant to another (Hacskaylo, 1972). The fungi in return receive food in the form of simple sugars from the plant roots. Ozone has the capability of disrupting the association between the mycorrhizal fungi and host plants by inhibiting photosynthesis and reducing the amount of sugars available for transfer from the shoots to the roots (see Figure 5-25). The benefits of this relationship was discussed in the previous criteria document (U.S. Environmental Protection Agency, 1986).

Mycorrhizal fungi are an integral part of the below-ground ecosystem of terrestrial communities. Some plants appear to be obligately mycorrhizal, while others are facultative or non-mycorrhizal; however, mycorrhizae form on the vast majority of terrestrial plants and contribute substantially to ecosystem function (Allen, 1991; Harley and Smith, 1983). The symbiotic association is mutually beneficial and is characterized by a flow of nutrients from fungus to host and flow of carbohydrates from host to fungus. Since oxidants have been shown to alter photosynthesis and carbohydrate allocation within the plant, often decreasing allocation to roots, they can disrupt the association by reducing carbohydrate availability to the fungus. Any change in the vigor of the association will influence the nutrient harvesting capability of the mycorrhizal hyphae, the physiology of the host plant, and subsequently ecosystem function.

Several studies of the effects of O_3 on tree species have included investigations of the effects on ectomycorrhizal associations. The topic has been discussed in a series of articles in a special issue of the journal Environmental Pollution (Vol. 73, No. 2), and selected studies are summarized in Table 5-32. The understanding of oxidant effects on root symbioses has not changed substantially since 1986 (U.S. Environmental Protection Agency, 1986), however, understanding of the importance of symbiotic organisms in ecosystem

TABLE 5-32. INTERACTIONS OF OZONE AND FOREST TREE ECTOMYCORRHIZAE INTERACTIONS

Host Plant	Mycorrhizae	Exposure Condtions[1]	Effect of O_3 on Mycorrhiza	Reference
Loblolly pine	*Pisolithus tinctorius*	OTC, field	reduced root infection	Adams and O'Neill (1991)
	not stated	OTC, field, 3 years	reduced root infection	Edwards and Kelly (1992)
	not stated	CEC	no effect	Mahoney et al. (1985)
	not stated	CSTR	reduced root infection	Meier et al. (1990)
Scots pine	10 spp.	open air, field, 3 years	no significant effects	Shaw et al. (1992)
White pine	*Pisolithus tinctorius*	CEC	reduced root infection	Stroo et al. (1992)
Norway Spruce	6 spp.	open air, field, 3 years	no significant effects	Shaw et al. (1992)
	4 spp.	CEC	no consistent effects	Blaschke and Weiss (1990)
Paper Birch	*Pisolithus tinctorius*	CEC	no effects	Keane and Manning (1988)
Red Oak	not stated	CEC and OTC	significant increase	Reich et al. (1985)

[1]CEC: controlled environment chamber; CSTR: continuous stirred tank reactor; OTC: open-top filed chamber.

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function has improved. The basic hypothesis on mechanisms remains the same (i.e., effects are mediated through host carbohydrate metabolism) since oxidants do not penetrate the soil more than a few centimeters. Most of the research has been conducted on individual plant species in controlled environments, and while the role of mycorrhizae in community structure has been recognized, it has not specifically been addressed experimentally. Below is a review of recent studies addressing oxidants effects on mycorrhizae.

Several studies have refined our understanding of oxidant stress effects on roots. In *Pseudotsuga menziesii* [Mirb.] Franco root/soil respiration was significantly reduced during the first 1 to 2 weeks after exposure to O_3 or SO_2, followed by a recovery period which resulted in similar total respiratory release between treatments and controls (Gorissen and Van Veen, 1988; Gorissen et al., 1991). Total allocation to roots did not appear to be reduced, but O_3 apparently reduced translocation to roots in that respiration of ^{14}C was suppressed. Edwards (1991) found that root and soil respiration were reduced in *Pinus taeda* L. seedlings exposed to O_3 levels ranging from 0.07 to 0.11 ppm (7 h mean) compared to seedlings exposed to levels below ambient (0.02 to 0.04 ppm). Nouchi et al. (1991) found that O_3 at 0.1 ppm reduced root respiration by 16% in *Oryza. sativa* L. after one week of exposure. However, exposure to 3 to 7 weeks of 0.1 ppm O_3 resulted in elevated levels of root respiration.

Several studies have examined the effects of O_3 on carbohydrate allocation to roots and subsequent shifts in biomass allocation (Cooley and Manning, 1987; Kostka-Rick and W.J. Manning, 1992; Karnosky et al., 1992; Temmerman, Vandermeiren and Guns, 1992; Qui et al., 1992; Sharpe et al., 1989; Gorissen and Van Veen, 1988; Gorissen et al., 1991; Spence et al., 1990). Gorissen et al. (1991) examined the combined effects of O_3 and ammonium sulfate application to *Psuedotsuga menziesii* [Mirb.] Franco in association with *Rhizopogon vinicolor* A.H. Smith and *Lactarius rufus* (Scop.:Fr.)Fr. They found greater needle retention of 14C labelled compounds in the new needles of O_3 treated plants, and a trend towards less 14C labelled substrates recovered in roots and root/soil fractions. Short-term transport of ^{11}C labelled substrates were followed throughout *P. taeda* (Spence et al., 1990). A 45% reduction in transport of photosynthates to roots occurred in O_3 treated plants compared to controls. Collectively, the studies have shown a general trend of diversion of carbohydrate resources from roots and retention in the photosynthetically active

portions of plants. A reduction in allocation to roots may be associated with a change in the availability of carbohydrate for maintenance of root symbioses.

The effects of O_3 on mycorrhizal colonization have varied depending on the experimental conditions and the species used. Stroo et al. (1988) studied the effects of O_3 on mycorrhizal infection in *Pinus strobus* seedlings grown for 4 mo in several soils. Results varied by soil type and nitrogen availability; however, in several soils the number of mycorrhizal short roots increased slightly at low O_3 levels and decreased significantly at higher O_3 concentrations. Reich et al. (1986) found similar results in *P. strobus* L. and *Quercus rubra* L., and concluded that O_3 may stimulate mycorrhizal infection at low O_3 concentrations. Simmons and Kelly (1989) observed a trend of greater mycorrhizal short roots in *Pinus taeda* seedlings exposed to subambient O_3 treatment than those exposed to ambient or twice ambient O_3 levels; results were not statistically significant. In another study with two families of *P. taeda*, Adams and O'Neill (1991) found that mycorrhizal colonization tended to increase with O_3 during the first 6 weeks of exposure, and decrease with O_3 after 12 weeks of exposure. Meier et al. (1990) found a decrease in ectomycorrhizal root tips and percentage of feeder roots in *P. taeda* L. seedlings. Keane and Manning (1988) found significant interactions among O_3, soil type and pH, however the direct effects of O_3 were difficult to elucidate. Collectively, these results suggest that O_3 does impact colonization of roots by mycorrhizal fungi; however the results illustrate the variability in response due to such factors as soil condition, duration of experiment, and timing of measurements.

Altered root carbohydrate allocation resulting from O_3 exposure may affect host-fungus compatibility (Edwards and Kelly, 1992; Simmons and Kelly, 1989). Combined effects of O_3, rainfall acidity and soil Mg status on growth and ectomycorrhizal colonization of *Pinus taeda* L has been studied (Simmons and Kelly, 1989). Although variation was high, there was a trend towards altered species composition and reduced mycorrhizal infection in O_3 treated seedlings. Edwards and Kelly (1992) found high variability in morphotype (morphologically different) frequency in response to O_3 treatments in *P. taeda* L., and noted changes in morphotype frequency over the 3 year study that suggested fungal succession had occurred. Fungal succession and the effects of oxidant stress on normal successional patterns

are poorly understood. Shaw et al. (1992), using an open field exposure system, found no differences in morphotype frequency or fruit-body succession in response to O_3 treatments.

In summary, there is evidence that O_3 affects mycorrhizal symbioses in a number of plant species. The mechanism appears to be through altered carbohydrate allocation and availability in the root. Efforts are currently underway to address successional patterns of mycorrrhizal fungi under oxidant stress and should provide a more integrative understanding of the effects at the ecosystem level.

5.7.3.9 Rhizosphere and Soil Processes

The importance of the below-ground ecosystem has largely been overlooked when evaluating ecological responses to oxidant exposure. Although the soil system is part of the larger terrestrial ecosystem, it is a system that operates independently and therefore is itself an ecosystem (Richards, 1987). While above-ground components of the terrestrial ecosystem are dominated by producers, the below-ground system is composed primarily of consumers. Thus, the below-ground system is dependant on the above-ground system for inputs of energy-containing substrates. Bacteria, fungi, protozoa, nematodes, microarthropods, earthworms and enchytraeids all serve various functions in maintaining biological, physical and chemical characteristics of soil, and all are dependent on plant residues for their maintenance. While the uniqueness of the below-ground ecosystem needs to be recognized, the interdependence between the above- and below-ground systems cannot be over emphasized.

Even though the effects of O_3 on rhizosphere and soil processes have not been studied, potential impacts can be hypothesized based on known plant responses to O_3. As noted above, O_3 stress reduces photosynthesis and growth, and roots often are more affected than shoots (Winner et al., 1991; McCool and Menge, 1984; Blum and Tingey, 1977; Manning et al., 1971; Tingey and Blum, 1973; Hogsett, 1985; Tingey et al., 1976; Spence et al., 1990; McLaughlin et al., 1982). Oxidant stress has been shown to affect both leaf senescence and root production in plants, thereby disrupting carbon availability for maintenance of the below-ground system (Gorissen et al., 1991; Andersen and Rygiewicz, 1991).

The availability of current photosynthate for root growth appears to be reduced under O_3 stress, and maintenance of below-ground processes dependent on roots for their carbon substrates may be affected. As noted in the previous section, a 45% reduction in transport of photosynthates to roots occurred in O_3 treated *P. taeda* (Spence et al., 1990). Ozone reduces concentrations of root carbohydrates (Jensen, 1981; Tingey et al., 1976; Meier et al., 1990, Andersen et al., 1991). Starch in roots was significantly reduced in *P. ponderosa* by the end of one growing season of O_3 exposure (Tingey et al., 1976). Reductions in coarse and fine root starch concentrations persisted over the winter in O_3-treated *P. ponderosa* and were lower during the subsequent years shoot flush (Andersen et al., 1991). In this study, lower starch concentrations in O_3-treated seedlings were associated with suppressed growth of new roots. The consequences of a reduction in carbon allocation below-ground includes reduced substrate availability for soil flora and fauna, altered soil physical characteristics such as total organic matter and aggregation, and altered soil chemical characteristics including cation exchange capacity.

Premature leaf senescence has been observed in plants exposed to O_3 stress (U.S. Environmental Protection Agency, 1986). Premature senescence affects the below-ground ecosystem by reducing canopy photosynthesis and carbon availability for transport to the below-ground system, and by increasing leaf litter inputs to the forest floor (Miller, 1982; Fenn and Dunn, 1989). The result is increased flux of nutrients, especially N, below-ground due to oxidant exposure.

The increased flux of nitrogen due to premature needle senescence in oxidant exposed plants may act to disrupt nutrient flow of the ecosystem. Allocation of carbon resources throughout a plant is based on a priority scheme that is driven by carbon and nutrient availability (Waring and Schlesinger, 1985). When soil nutrient levels are high, allocation to the shoot is favored over the roots. By shifting carbon allocation to organs in this fashion, plants can adjust to shifts in resource availability in their environment. Oxidant stress alters typical allocation schemes and in the process may impair the plant's ability to cope with drought or other stresses. In addition, reductions in allocation to roots can alter root system size, architecture and spatial arrangement, which in turn can influence populations of soil organisms.

Bacteria and fungi are particularly important in nutrient cycles and act to immobilize N, C, P, and other nutrients in their biomass. The turnover of these nutrient pools are relatively short as bacterial and fungal preditors act to release these nutrients. The majority of plant available N during the growing season comes from these predatory interactions in the soil (Kuikman et al., 1991; Ingham et al., 1985), emphasizing their importance in the maintenance of terrestrial ecosystems. Currently there are no data available on the effect of O_3 on soil fauna.

5.7.4 Summary

Ecosystems are composed of populations of "self-supporting" and "self-maintaining" living plants, animals and microorganisms (producers, consumers, and decomposers) interacting with one another and with the nonliving chemical and physical environment within which they exist (Odum, 1989; U.S. Environmental Protection Agency, 1993). Mature ecosystems are seldom stable. They must continually respond and adapt to changing environments (Koslowski, 1985). Structurally complex communities, they are held in an oscillating steady state by the operation of a particular combination of biotic and abiotic factors.

Ecosystem response to stress begins with individuals. Intense competition among plants for light, water, nutrients, and space, along with recurrent natural climatic (temperature) and biological (herbivory, disease, pathogens) stresses, can alter the species composition of communities by eliminating those individuals sensitive to specific stresses, a common response in communities under stress (Woodell, 1970; Guderian, 1985). Those organisms able to cope with stresses survive and reproduce. The effects of stresses upon ecosystems, unless they are catastrophic disturbances are frequently difficult to determine (Koslowski, 1985; Garner et al., 1989) In a mature forest, a mild disturbance becomes part of the oscillating steady state of the forest community or ecosystem. Responses to catastrophic disturbances, however, as a rule are readily observable and measurable (Garner, 1993).

Ecosystem responses are hierarchical ranging from those that are characteristic of individuals to those characteristic of the entire ecosystem. Ecosystems integrate individual responses and propagate them through trophic and competitive relationships. Two properties that are important in determining the effect a stress at one hierarchial level of organization

will have on a higher level are variability and compensation. Variability in response to stress may mean that, because of genetic variation, not all trees are equally susceptible. At the stand level, the slower growth of some trees may be compensated for by the relatively faster growth of others that are experiencing reduced competition so that the overall growth of the stand is not affected (Hinkley et al., 1992). These properties when taken together will determine the extent and rate at which stress at one hierarchical level will impact the next highest level.

The mixed conifer forest ecosystem in the San Bernardino Mountains of southern California is one of the most thoroughly studied ecosystems in the United States. The changes observed in the mixed conifer forest ecosystem exemplify those expected in a severly disturbed ecosystem. Chronic O_3 exposures over a period of 50 or more years caused major changes in the San Bernardino National Forest ecosystem. The primary effect was on the more susceptible members of the forest community, individuals of ponderosa and Jeffrey pine, in that they were no longer able to compete effectively for essential nutrients, water, light and space. As a consequence of altered competitive conditions in the community, there was a decline in the sensitive species, permitting the enhanced growth of more tolerant species (Miller et al., 1982; U.S. Environmental Protection Agency, 1978, 1986). The results of the studies of the San Bernardino Forest ecosystem were reported in both the 1978 and 1986 criteria documents (U.S Environmental Protection Agency, 1978, 1986). The more recent data from the San Bernardino Forest and from other ecosystems in California indicate that there continue to be O_3 concentrations injurious to forest vegetation. The concentrations and durations, however, are not as high nor for as long periods as in former times. For this reason, the vegetational injury has not been as great.

There is some indication from new data that O_3 may not have been the only stress encountered by the San Bernardino Forest ecosystem. Nitrate deposition gradients similar to those measured for O_3 suggests the possible soil-mediated exposures to nitrate could have been anc continue to be combined with the foliage-mediated O_3 exposures. Research in this area is continuing.

Studies of O_3 induced vegetational injury in the Appalachian Mountains and the southeastern United States is ongoing. Preliminary results indicate that injury to sensitive vegetation continues to occur.

Inhibition of photosynthesis by O_3 exposure alters carbohydrate allocation from the shoot to the roots. Reduced carbohydrate allocation to the roots has been shown to affect mycorrhizae formation. Mycorrhizae are extremely important for mineral nutrient uptake by trees and other vegetation reduction in their formation has been shown to have an detrimental impact on plant growth.

5.8 EFFECTS OF OZONE ON AGRICULTURE, FORESTRY, AND ECOSYSTEMS: ECONOMICS

5.8.1 Introduction

Evidence from the plant science literature cited in the 1986 O_3 Criteria Document (U.S. Environmental Protection Agency, 1986) and in the present document is unambiguous with respect to the adverse effects of tropospheric O_3 on some types of vegetation. For example, findings from U.S. EPA's multiyear NCLAN program provides rigorous corroboration of at least a decade of previous research which showed that O_3 at ambient levels caused physical damage to important species. Specifically, NCLAN established that ambient O_3 levels resulted in statistically significant reductions in yields for these crops. Literature reviewed in Section 5.6 of this document assesses the state of natural science findings regarding O_3 effects on crops, forests and other types of vegetation in more detail.

Information on the benefits and costs of alternative policy options or states of the world (such as changes in air pollution) is of use to decision makers in a variety of settings. For example, economic information provides one means by which to choose from alternative policies or public investments. The role of cost-benefit analysis in federal rule making or standard setting was enhanced in 1981 by President Reagan's Executive Order 12291 (February 19, 1981) which required that such calculations be performed on any rule or regulation promulgated by the federal government. That executive order provided the stimulus for a large increase in the use of economic analysis in evaluating federal actions, including environmental policies. While the Clean Air Act and its amendments do not allow the use of cost-benefit analysis in the standard setting process for primary (human health) effects, economic information has been introduced into the discussion of secondary or

welfare effects. A number of economic studies addressing vegetation and other welfare effects have been performed in the last decade.

Assessments of the economic consequences of O_3 on vegetation reflect the state of natural science information on each vegetation category. The natural science evidence concerning effects of O_3 on individual tree species or plant communities is less secure than for agricultural crops (see Section 5.6). As a result, most economic assessments focus on agricultural crops. The economics literature on effects of O_3 and other air pollutants on forest productivity is very sparse; the few assessments are confined to evaluations of assumed or hypothetical changes in output (e.g., board feet of lumber). The economic effects of O_3 on plant communities or ecosystems have not been measured in any systematic fashion.

This section reviews economic assessments across these vegetation categories. The discussion of economic valuation of ecosystem effects is limited to conceptual and methodological issues in performing such assessments, given the absence of empirical analyses in this category.

5.8.2 Agriculture

In view of the importance of U.S. agriculture to both domestic and world consumption of food and fiber, reductions in crop yields could adversely affect human welfare. The plausibility of this premise resulted in numerous attempts to assess, in monetary terms, the losses from ambient O_3 or the benefits of O_3 control, to agriculture. Fourteen assessments of the economic effects of O_3 on agriculture were reviewed in the 1986 document (U.S. Environmental Protection Agency, 1986). Since the preparation of the 1986 document, there have been at least nine other studies published in the peer review literature which provide estimates of the economic consequences of O_3 on agriculture.

The 1986 document highlighted key issues in judging the validity of economic assessments which are applicable to post-1986 studies (i.e., how well the biological, aerometric, and economic inputs used in the assessment conform to specific criteria). First, the evidence on crop response to O_3 should reflect how crop yields will respond under actual field conditions. Second, the air quality data used to frame current or hypothetical effects of O_3 on crops should represent actual exposures sustained by crops at individual sites or production areas. Finally, the assessment methodology into which such data are entered

should (1) capture the economic behavior of producers and consumers as they adjust to changes in crop yields and prices that may accompany changes in O_3 air quality; (2) should accurately reflect institutional considerations, such as regulatory programs and income support policies (e.g., provisions of federal "Farm Bill" legislation), that may result in market distortions; and (3) use measures of well-being that are consistent with principles of welfare economics.

5.8.2.1 Review of Key Studies from the 1986 Document

Assessments of O_3 damages to agricultural crops reported in the 1986 document displayed a range of procedures for calculating economic losses, from simple monetary calculation procedures to more complex assessment methodologies which conform to some or all of the economic criteria above. As noted in the 1986 document, the simple procedures calculate monetary effects by multiplying predicted changes in yield or production resulting from exposure to O_3 by an assumed constant crop price. By failing to recognize possible crop price changes arising from yield changes and not accounting for potential producer responses, such assessments are flawed, except for highly restricted situations such as localized pollutant events. Conversely, some assessments provide estimates of the economic consequences of O_3 and other air pollutants that reflect producer-consumer decision-making processes, associated market adjustments, and some measure of distributional consequences between affected parties. The distinctions between studies based on naive or simple models and those based on correct procedures is important at the regional or national level, since the simple procedures may be biased, leading to potentially incorrect policy decisions.

Most of the economic assessments reviewed in the 1986 document (nine of the fourteen) focused on O_3 effects in specific regions, primarily California and the Corn Belt (Illinois, Indiana, Iowa, Ohio, and Missouri). There have been a number of additional regional assessments since the 1986 document; most are non-peer reviewed reports arising from consulting or contract research. This regional emphasis in the earlier literature may be attributed to the relative abundance of data on crop response and air quality for selected regions, as well as the importance of some agricultural regions, such as California, in the national agricultural economy. Most of the recent state or regional assessments are commissioned by state public utility commissioners or similar regulatory agencies and use

variants of the simple "price times yield" approach, where yields are calculated from response functions arising from the NCLAN data. While perhaps of use to Public Utility Commissioners concerned with effects from single power plants or other localized sources, these studies generally contribute little to the assessment of pollution effects at the national level. (Most local or regional studies abstract from physical and economic interdependencies between regions, which limits their utility in evaluating secondary national ambient air quality standards or NAAQS.)

National-level studies which account for economic linkages between groups and regions can overcome some limitations of regional analyses. A proper accounting of these linkages, however, requires additional data and more complex models, and frequently poses more difficult analytical problems. Thus, detailed national assessments tend to be more costly to perform. As a result, there are fewer assessments of pollution effects at the national level than at the regional level.

Two national studies reported in the 1986 document were judged to be "adequate" in terms of the three critical areas of data inputs. Together, they provided a reasonably comprehensive estimate of the economic consequences of changes in ambient air O_3 levels on agriculture. Because of their central role in the 1986 document, these two studies are reported in Table 5-33 and are reviewed briefly below.

In the first of these studies, Kopp et al. (cited as 1984 in the earlier document but subsequently published as a journal article in 1985) measured the national economic effects of changes in ambient O_3 levels on the production of corn, soybeans, cotton, wheat, and peanuts. In addition to accounting for price effects on producers and consumers, the assessment methodology used is notable in that it placed emphasis on developing producer-level responses to O_3-induced yield changes (from NCLAN data available at the time) in 200 production regions. The results of the Kopp et al. study indicated that a reduction in O_3 from 1978 regional ambient levels to a seasonal 7-h average of approximately 0.04 ppm would result in a $1.2 billion net benefit in 1978 dollars. Conversely, an increase in O_3 to an assumed ambient concentration of 0.08 ppm (seasonal 7-h average) across all regions produced a net loss of approximately $3.0 billion.

The second study, by Adams et al. (originally cited as 1984b, but subsequently published as a journal article in 1986a), was a component of the NCLAN program. The

TABLE 5-33. RECENT STUDIES OF THE ECONOMIC EFFECTS OF OZONE AND OTHER POLLUTANTS ON AGRICULTURE[a]

Region	Pollutant and Concentration	Model Features: Price Changes	Output Substitutions	Input Substitutions	Quality Changes	Crops	Results (Annual 1980 U.S. Dollars): Consumer Benefits	Producer Benefits	Total Benefits (Costs)	Study
Illinois	Ozone, 10% increase from 46.5 ppb[b]	No	Yes	Yes	No	Corn, soybeans	None	$226 × 10^6	$226 × 10^6	Garcia et al. (1986)
U.S.	Ozone, 25% reduction from 1980 level for each state[a]	Yes	Yes	Yes	No	Corn, soybeans, cotton, wheat, sorghum, barley	$1.160 × 10^6	$550 × 10^6	$1,700 × 10^6	Adams et al. (1986)[d]
U.S.	Ozone, universal reduction from 53 ppb to 40 ppb[b]	Yes	Yes	Yes	No	Corn, soybean, wheat, cotton, peanuts	Not reported	Not reported	$1,300 × 10^6	Kopp et al. (1985)[d]
U.S.	Ozone, universal reduction from 53 ppb to 49 ppb[a]	Yes	No	No	Yes	Soybeans	$880 × 10^6	$-90 × 10^6	$790 × 10^6	Shortle et al. (1986)
U S	Acid deposition, 50% reduction in wet acidic deposition	Yes	Yes	Yes	No	Soybeans	$172 × 10^6	$-30 × 10^6	$142 × 10^6	Adams et al. (1986)
U.S	Ozone, 10% reduction from annual levels (1986-1990) for rural areas. Includes adjustments for 1985 Farm Bill.	Yes	Yes	Yes	No	Corn, cotton, soybeans, wheat	NA	NA	$2,500 × 10^6 (sum of discounted values at 5%, 1986-1990)	Kopp and Krupnick (1987)
U.S.	Ozone, seasonal standard of 50 ppb with 95% compliance[c]; includes adjustments for 1985 Farm Bill.	Yes	Yes	Yes	No	Corn, soybeans, cotton, wheat, sorghum, rice, hay, barley	$905 × 10^6	$769 × 10^6	$1,674 × 10^6	Adams et al. (1989)
U.S.	Increased UV-B radiation and associated increase of tropospheric O_3 (of 16%)	Yes	Yes	Yes	No	Soybeans (for UV-B) and all crops in Adams et al. (1989) for tropospheric O_3	NA	NA	-830 × 10^6 (for the increase in tropospheric O_3 only)	Adams and Rowe (1990)

[a]All studies except Garcia et al. use NCLAN data to generate yield changes due to ozone.
[b]Seven-hour growing season geometric mean. Given a log-normal distribution of air pollution events, a 7-h seasonal ozone level of 40 ppb is approximately equal to an hourly standard of 80 ppb, not to be exceeded more than once a year Heck et al. (1982).
[c]Seven and 12-h growing season geometric mean. Analysis includes both fixed roll-backs (e.g., 25%) and seasonal standards (with variable compliance rates).
[d]Reported in 1986 Criteria Document.

results were derived from an economic model of the U.S. agricultural sector that includes individual farm models for 63 production regions integrated with national supply and demand relationships for a range of crop and livestock activities. Using NCLAN data, the analysis examined yield changes for six major crops (corn, soybeans, wheat, cotton, grain, sorghum, and barley) that together account for over 75% of U.S. crop acreage. The estimated annual benefits (in 1980 dollars) from O_3 adjustments are substantial, but make up a relatively small percentage of total agricultural output (about 4%). Specifically, in this analysis, a 25% reduction in O_3 from 1980 ambient levels resulted in benefits of $1.7 billion. A 25% increase in O_3 resulted in an annual loss (negative benefit) of $2.4 billion. When adjusted for differences in years and crop coverages, these estimates are close to the Kopp et al. (1986a) benefit estimates.

The Kopp et al. (1985) and Adams et al. (1986a) studies indicated that ambient levels of O_3 were imposing substantial economic costs on agriculture. However, both Kopp et al. (1985) and Adams et al. (1986a) were judged to suffer from several sources of uncertainty. These include the issue of exposure dynamics (7-h per day exposures from the NCLAN experiments versus longer exposure periods, such as 12-h exposures), and the lack of environmental interactions, particularly O_3-moisture stress interactions, in many of the response experiments. Also, the O_3 data in both studies are based on a limited set of the monitoring sites in the AIRS system, mainly sites in urban and suburban areas. While the spatial interpolation process used for obtaining O_3 concentration data (Kriging) resulted in a fairly close correspondence between predicted and actual O_3 levels at selected validation points, validation for rural sites was limited (Lefohn et al., 1987). The economic models, with their large number of variables, and parameters, and the underlying data used to derive these values, were also noted as potential sources of uncertainty, including the effects on economic estimates of market-distorting factors such as the federal farm programs. Concern over farm programs stems from the evidence that reductions in O_3 will increase yields and hence total production of some crops. If the crop is covered (eligible for deficiency payments) under the provisions of the farm program, then the total costs to the government (of the farm program) may *increase* as a result of reduced O_3 (McGartland, 1987). Thus, the benefits of the O_3 reduction may not be as great as estimated.

The 1986 criteria document concluded that these possible improvements in future assessments were not likely to alter greatly the range of agricultural benefit estimates for several reasons. First, the studies covered about 75 to 80% of U.S. agricultural crops (by value). For inclusion of the other 20% to change the estimates significantly would require that their sensitivities to O_3 be much greater than for the crops included to date. Second, model sensitivity analyses reported in past studies indicate that changes in plant exposure response relationships must be substantial to translate into major changes in economic estimates. For example, it was believed unlikely that use of different exposure measures or inclusion of interaction effects would greatly alter the magnitude of the economic estimates. Third, it was believed that there were likely to be countervailing effects that would mitigate against large swings in the estimates (e.g., longer exposure periods may predict greater yield losses), but O_3-water stress tends to dampen or reduce the yield estimates. Finally, the document noted that potential improvements in economic estimates are policy-relevant only to the extent that they alter the relationship between total benefits and total costs of that policy. The possible exception to this generally optimistic assessment of the robustness of the estimates was inclusion of market-distorting factors (i.e., farm programs), an issue which is addressed in some of the post-1986 assessments reviewed below.

5.8.2.2 A Review of Post-1986 Assessments

The 1986 document concluded that the O_3 assessments by Kopp et al. (1985) and Adams et al. (1986a) provided the most defensible evidence in the literature at that time of the general magnitude of such effects. These two studies, in combination with the underlying NCLAN data on yield effects, were judged to be the most comprehensive information available on which to evaluate the economic impact of ambient air quality (O_3) on crops.

Seven national-level assessments performed since the last criteria document are reported in Table 5-33. Of these, all use defensible economic approaches to quantify dollar effects, where "defensible" is measured in terms of conforming to the criteria cited earlier. An evaluation of these studies in terms of the adequacy of critical plant science, aerometric, and economic data is presented in the table, along with estimates of benefits or damages associated with changes in O_3.

The concluding statements in the 1986 document are a benchwork against which to judge these seven national level studies published since the last document. Most of the contemporary studies build on either Kopp et al. (1985) or Adams et al. (1986a); indeed, the motivation of some of the more recent studies is to test whether the problems noted above (such as exclusion of farm programs) are sufficient to alter the original estimates in a meaningful manner. A relevant question is whether these new studies provided any "surprises" in terms of magnitude of economic effects. These studies are summarized in Table 5-33.

In discussing these latest evaluations, there are several points which relate to their comparability with Kopp et al. (1985) and Adams et al. (1986a). First, all studies use NCLAN response data to generate yield effects (for inclusion in the respective economic models). In most cases, data used in the post-1986 assessments reflect improvements of earlier NCLAN data. Second, these studies may be characterized as second generation assessments. They build on the first generation of studies reported in the 1986 document by refining selected aspects of those earlier studies, including (1) interactions with other stresses; (2) use of aerometric data and assumptions which, in some cases, more closely follow the seasonal and regional characteristics of O_3 exposure (Adams et al., 1989); and (3) effects of O_3 on quality of commodities (Shortle et al., 1986). Several of the studies use updated versions of the economic models in Adams et al. (1986a) and Kopp et al. (1985). In addition, some of the studies model the effects of government programs to judge the potential consequences of such distortions on economic estimates (Kopp and Krupnik, 1987; Adams et al., 1989). Third, there are differences in underlying aerometric assumptions; some studies include both O_3 and other environmental stresses (e.g., acid deposition, UV-B radiation); others reflect O_3 data for more recent time periods. Since ambient O_3 levels vary across years, the choice of year will influence the yield estimates and ultimately the economic estimates.

Common themes or findings from these (and earlier) O_3 and other air pollution studies have been summarized in two recent synthesis papers (Adams and Crocker, 1989; Segerson, 1991). The results of the post-1986 assessments in Table 5-33 and the recent synthesis papers corroborate the general findings of the 1986 document. Specifically, the agricultural effects of tropospheric O_3 at ambient levels impose economic costs to society (or conversely,

that reductions in ambient O_3 result in societal benefits). The magnitude of the economic costs reported in the more recent studies is similar to the estimates in Kopp et al. (1985) and Adams et al. (1986a). Such a similarity is not surprising, given the points noted above concerning use of similar data and economic models.

One important recent finding pertains to farm program. In each case, the inclusion of farm programs in the economic models resulted in modest changes (reductions) in the economic benefits of O_3 control (due to increased farm program costs). As Segerson notes, however, it is not clear that these increased costs should be charged against the potential benefits of an O_3 regulatory standard but rather as an additional cost associated with the inefficiencies of the federal farm program. Even with the inclusion of farm programs and other elements the general magnitude of further effects reported in the 1986 document are only reduced by approximately 20%.

In addition to including farm programs, there are a couple of other notable additions to the assessment literature. One study (Adams et al., 1989) attempts to analyze economic benefits under a regulatory alternative involving a seasonal (crop growing season) O_3 exposure index measured as a 12 h mean, instead of hourly levels or percent changes from ambient reported in earlier studies. Specifically, a seasonal average of 50 ppb O_3 (measured as a 12-h seasonal average) with a 95% compliance level, is reported in Adams et al. (1989). The result (of a $1.7 billion benefit) is similar to the assumed 25% reduction across all regions reported by Adams et al. in 1986a. At least one study has also combined environmental stresses (e.g., O_3, UV-B, radiation) in preforming economic assessments. Adams and Rowe (1990), using the same model as Adams et al. (1986a, 1989), report that a 15% depletion of stratospheric O_3 (which results in a 13% increase in tropospheric O_3) caused an economic loss of approximately $0.8 billion attributed to the tropospheric O_3 increase.

5.8.2.3 Limitations and Future Research Issues

The recent literature (post-1986) on economic effects of O_3 on agriculture supports the general conclusions drawn in the 1986 document. That is, ambient levels of O_3 are imposing economic costs on producers and consumers. However, there are at least three issues which are not addressed in the extant literature on the topic. First, the existing assessments do not

consider the external costs of changes in agricultural production arising from changes in O_3 exposures (Sergerson, 1990). These costs are important if changes in O_3 result in changes in crop mixes or production practices, which in turn result in changes in soil erosion, fertilizer and pesticide runoff or other agricultural externalities. For example, if reductions in O_3 increase the relative profitability of a crop which uses higher levels of chemical inputs, then some increase in chemical effluent may result. Given that some assessments suggest that such changes in crop mixes and production practices are likely to accompany O_3 changes, these costs/benefits need to be addressed.

A second issue not directly assessed in the current literature is the relationship between climate change and tropospheric O_3 effects. This relationship is important if global warming is expected to increase tropospheric O_3 levels. In addition, research indicates that global climate change will lead to a relocation of crops (Adams et al., 1990). This relocation may change the vulnerability of crop species to O_3, given the spatial distribution of O_3 across the U.S. (i.e., increased crop production in areas of relatively low ambient O_3, such as the Pacific Northwest, implies lower O_3 damage).

A third issue involves the institutional setting in which agricultural production occurs. Several recent studies have assessed O_3 effects in the presence of federal farm programs. However, the U.S. and most industrialized economies are moving away from price supports, production quotas and import restrictions, the traditional form of government intervention in agriculture. At the same time that these market distortions are being removed, there is increasing government regulation of agricultural production practices to reduce agricultural externalities. Future assessments of O_3 effects may need to pay less attention to farm program effects and instead include other institutional features of U.S. Agriculture.

5.8.3 Forests (Tree Species)

The plant science literature on O_3 and other air pollutant effects on tree species is evolving rapidly as a result of recent research initiatives by EPA and other agencies. The long-term nature of air pollution effects of perennial species creates challenges to plant scientists in sorting out the specific effects of individual stresses from among the many potential explanatory factors, such as O_3 (Skelly, 1989). It also creates problems in terms of

measuring impacts of direct economic value, such as reductions in board-feet of lumber produced per unit of time.

To date, most natural science literature on forest species reports O_3 effects in terms of foliar injury or similar measures (Taylor and Hanson, 1992; Davis and Skelly, 1992; Simini et al., 1992; Freer-Smith and Taylor, 1992). This emphasis on foliar effects (rather than marketable yield) is similar to the state of science for agricultural crops prior to 1975. Such visible foliar effects information is of limited use in economic assessments . The exception is in measuring the economic value of aesthetic changes in a forest stock (see Crocker, 1985a).

The lack of usable data concerning changes in marketed output, such as board-feet of lumber (or even changes in growth rates), has limited the number of economic assessment of O_3 effects on forests. The few studies which attempt to measure economic losses arising from O_3 or other pollutants circumvent the lack of plant science data by assuming (arbitrary) reductions in forest species growth or harvest rates (Callaway et al., 1985; Haynes and Adams, 1992 ; Adams, 1986; Crocker and Forster, 1985).

These studies are summarized in Table 5-34. While the economic estimates reported in Table 5-34 are comparable to these reported for agricultural crops (e.g., $1.5 billion for eastern Canada, $1.7 billion for eastern U.S. forests), the lack of defensible natural science data makes these studies suggestive at best, of possible economic consequences of forest (tree species effects) of O_3 or other environmental stresses. In addition, the economic methodology used in the assessments varies, from simple price times quantity calculations (e.g., Crocker, 1985b) to the use of large, econometric-based representations of the U.S. timber market (Haynes and Adams, 1992). With appropriate data, the TAMM methodology laid out by Haynes and Adams holds promise for assessing the economic consequences of O_3 when requisite natural science data become available.

In summary, the plant science literature shows that O_3 adversely influences the physiological performance of tree species; the limited economic literature also demonstrates that changes in growth have economic consequences. However, the natural science and economic literature on the topic is not yet mature enough to conclude unambiguously that ambient O_3 is imposing economic costs. The output from on-going natural science research

TABLE 5-34. STUDIES OF THE ECONOMIC EFFECTS OF OZONE AND OTHER POLLUTANTS ON FORESTS

Pollutant/Coverage	Response and Air Quality Data	Economic Model	Annual Damages or Benefits of Control ($ billion)	Study
All pollutants. Forest products (hardwood and softwood) in the eastern U.S.	Assumes three arbitrary growth reductions (10%, 15% and 20%) for hardwood and softwood tree species.	Spatial equilibrium models of softwood and hardwood stumpage and forest products industries in the U.S.	-270×10^6 to 563×10^6 damage in 1984 dollars for assumed reductions in growth levels	Callaway et al. (1985)
Acid deposition. Forest products and forest ecosystem service flows for eastern U.S.	Assumes a 5% reduction in products due to acid deposition: assumes a pristine background pH of approximately 5.2	Naive; assumed changes in output multiplied by average value of those goods or services.	$-1,750 \times 10^6$ damage in 1978 dollars from current levels of acid deposition	Crocker (1985b)
Acid deposition. Forest products and forest ecosystem services for eastern Canada.	Assumes 5% reduction in forest productivity for all eastern Canadian forests receiving ≥ 10 kg/ha/year sulphate deposition.	Naive; assumed changes in output multiplied by average value of goods or services.	$-1,500 \times 10^6$ damage in 1981 Canadian dollars from current levels of acid deposition	Crocker and Forster (1985)
Air pollutants, including acid precipitation. Losses estimated for eastern U.S softwoods.	None; paper demonstrates a methodology for assessing economic effects of yield (growth and inventory) reductions due to any course. Assumes losses from 6 to 21% for softwoods.	Econometric model of U.S. timber sector (TAMM).	$-1,500 \times 10^6$ to $-7,200 \times 10^6$ in 1986 dollars	Haynes and Adams (1992)

on this topic will be important to our understanding of this potentially important class of effects.

5.8.4 Valuing Ecosystem Service Flows

5.8.4.1 Background

Over the last thirty years economists have developed a variety of techniques for assessing the value of nonmarket goods and services [recently surveyed by Braden and Kolstad (1991) and Smith (1993)]. "Nonmarket" refers to those goods and services not priced and traded in markets. While most applications are to natural resources and environmental assets, the concepts extend to a range of goods not usually traded in markets. Early applications focused primarily on commodities used directly by the consumer, such as outdoor recreation. Within the last decade, attention has shifted to estimating nonuse (or passive) values, such as what individuals are willing to pay to insure the existence of species or unique natural settings. The values elicited with these techniques are being used in an increasing array of settings; however, their use is not without controversy.

Valuing complex ecological functions and the associated range of ecosystem service flows is relatively uncharted territory and raises a number of conceptual and practical issues. Some difficulties in valuing ecosystem services lie in the inability of ecologists to unambiguously define and measure ecosystem performance and endpoints (see Section 5.7 of this chapter). Other problems arise from the inability of economic science to measure adequately the consequences of long-term and complex phenomenon. A related problem is the difference in disciplinary perspectives between ecologists and economists. As a result, the current state-of-the-art for valuing ecosystem service flows is inadequate for benefit-cost assessments used in environmental regulatory processes. As Costanza et al. (1991) state:

> Because of inherent difficulties and uncertainties in determining values, ecological economics acknowledges several different independent approaches. There is no consensus on which approach is right or wrong — they all tell us something — but there is agreement that better valuation of ecosystem services is an important goal for ecological economics. [Bold emphasis added]

Improvement in valuation of ecosystem service flows will require increased interdisciplinary cooperation and research between ecologists and economists, including the development of a shared language. The objectives of this section are to provide a brief background on

nonmarket valuation techniques, outline some of the conceptual issues which require resolution, and to offer an agenda for future research.

5.8.4.2 The Economic Perspective

Economic analysis is one input to the full social accounting of environmental planning and management. For example, Tingey et al. (1990) discuss a variety of viewpoints for defining "adverse effects" from ambient air quality, with economics being just one perspective. More specifically, economic values are only one type of assigned values (Brown, 1984). They reflect human preferences for a good or service, and are not inherent in the good or service itself. Further, economic values are exchange values; they reflect the terms of trade—dollars for services. Decision criteria which are based on economic values, such as efficiency and benefit-cost analysis (BCA), reflect a particular utilitarian philosophical perspective. Such a perspective is typically based on the notions of "welfarism" (only individual assessments of value count), and "consequentialism" (assessment of value is based on identified outcomes or consequences) (Sen, 1987). While economists do not deny the existence or validity of alternative perspectives of value, they do assert the importance of economic values in making some types of private and social choices.

For example, terms such as "ecosystem management" are likely to reflect a broad spectrum of choices for policy makers. Each choice may imply an alternative path for attaining a given "state" of biological diversity or ecological health. Each state will, in turn, imply a different mix of endpoints (or outputs). Ecosystem management will alter the mix of goods and services provided by a natural system, requiring tradeoffs between these endpoints. Accurate assessment of these tradeoffs in selecting the optimal path and subsequent endpoints poses numerous challenges. Economists believe that economic values can aid in making such difficult social choices.

A critical first step in applying economy reasoning is the distinction between different economic value components. The most familiar component involves market values. Market values (prices) convey incentive information that guides the numerous independent decisions that directly affect ecosystems (Perrings et al., 1992). However, market values typically will not reflect the full social welfare change that results from a change in ecosystem service

flows. The distinction between market values and total social valuation requires the introduction of nonmarket values and the notion of total economic value.

One taxonomy of economic values can be given as follows:

(1) Direct use values (DUV): determined by the contribution of an environmental asset to current production or consumption (e.g., timber harvest, recreation).

(2) Indirect use values (IUV): determined by the functional service flows from the environment which support current and future production and consumption (e.g., watershed protection, natural filtration of polluted water, ecological functions).

(3) Option value (OV): refers to the value individuals place on the potential future use of a resource (willingness to pay today for option to exercise future use of an environmental asset).

(4) Bequest value (BV): refers to the present generation's preference for bequest to future generations.

(5) Existence value (EV): contemplative values for the existence of a resource arising independent of any current or future in situ use of the resource).

A number of similar value taxonomies exist (e.g., Munasinghe, 1992; Pearce, 1993). The critical distinction for decision-making is between goods and services whose economic values are or are not fully captured in market prices. For example, timber products may have a direct use value which is accurately reflected by market prices. Recreation may also have a direct use value, but minimal or nonexistent fees do not accurately reflect this value. Nonuse values, by definition, have no discernible link to market behavior. Specialized techniques must be used to assess these values in a manner commensurate with more conventional commodities (e.g., timber production sold in a market). Of the class of nonmarket goods and services, the critical distinction is between use values and nonuse values.

The measurement of total economic value (TEV) refers to systematic attempts to assess the combined economic values of an environmental asset or resource system (Pearce, 1993; Peterson and Sorg, 1987; Randall, 1991b). In the same way that physical resource functions are interconnected, economic values for the various goods and services produced are

interconnected. A valid TEV measurement must account for this interconnectedness (e.g., substitution and complementarity issues, and non-additivity of component parts). While the concept of TEV is generally accepted by economists, systematic attempts to measure TEV in a regional policy or planning context are rare.

5.8.4.3 Nonmarket Valuation: Implications for Ecosystem Service Flows

Nonmarket valuation techniques consist of two basic types. Indirect approaches rely on observed behavior to infer values. Direct approaches use a variety of survey-based techniques to directly elicit preferences for nonmarket goods and services. Both sets of techniques share a common foundation in welfare economics, where measures of willingness-to-pay (WTP) and willingness-to-accept (WTA) compensation are taken as the basic data for individual benefits and costs.

Indirect Approaches

Indirect approaches, sometimes referred to as revealed preference approaches, rely on observed behavior to infer values. Examples include the travel cost method (TCM) where the relationship between visits and travel expenditures is used to infer the value of a recreational site, and hedonic pricing method (HPM) which attempt to decompose the value of market goods, say recreational real estate adjacent to a national forest, to extract the embedded values for environmental assets. Travel cost methods encompasses a variety of models ranging from the simple single site travel cost model, to regional and generalized models which incorporate quality indices and account for substitution across sites. Hedonic pricing method encompasses both land price and wage models which account for variations due to environmental attributes (e.g., air and water quality, noise, aesthetics, environmental hazards). The indirect approaches can only measure use values. This limitation is brought out in one fairly strong assumption (weak complimentarity) which requires that associated with consumption of an environmental good or service is the purchase of some market good, and when consumption of the market good is zero then demand for the environmental good or service is almost zero (Adamowicz, 1991). Recent summaries of the indirect approaches can be found in Braden and Kolstad (1991), Mendelsohn and Markstrom (1988), Peterson et al. (1992) and Smith (1989, 1993).

A brief hypothetical example illustrates the use of an indirect approach to measuring nonmarket value. The HPM can be applied to housing prices to estimate the value of environmental attributes, such as "clean air" or proximity to wetlands, which vary across a region. It is assumed that variations in housing prices can be linked to real or perceived variations in these environmental attributes, (controlling for a variety of other statistical determinants). In practice, the approach involves collection of cross sectional data on house sales (or possibly assessed values) and information on a menu of potential determinants of value (lot size, number of bedrooms, etc.). These factors would include one or more indices of environmental attributes or services. Through multivariate statistical techniques, the marginal value of either positive or negative environmental externalities can be inferred. For example, it might be found that the average homeowner in a particular county would pay $X to be Y meters closer to an open-water wetland, and would require a reduction in price of $Z to be Y meters closer to a smoke-producing factory.

Applications of HPM are limited to use values and work best where there is some identifiable spatial distribution of value. Continued improvements in available natural science information (e.g., geographic information systems—GIS) will improve the efficacy and precision of future HPM applications to environmental services. While direct use of GIS-based information is rare in HPM models (Doss and Taff, 1993), this is a likely area of future research expansion.

Direct Approaches

Direct approaches to nonmarket valuation are survey-based techniques to directly elicit preferences. The hypothetical nature of these experiments requires that markets (private goods or political) be "constructed" to convey a set of changes to be valued. While there are a number of variants on these constructed markets, the most common is the contingent valuation method (CVM).

Contingent valuation method can be viewed as a highly structured conversation (Smith, 1993) which provides respondents with background information concerning the available choices and specific increments or decrements in one or more environmental goods. Values are elicited directly in the form of statements of maximum WTP or minimum WTA compensation for the hypothetical changes in environmental goods. For example,

recreational anglers may be asked about their WTP for specific increments in run size for a fishery (Johnson and Adams, 1989). Typically, multivariate statistical techniques are used to model a WTP function. Such models allow the analyst to control for variation in the personal characteristics of the respondents, check for consistency of results with economic theory, and possibly estimate an entire WTP response surface across varying levels of environmental goods.

The contingent valuation method can be applied to both use and nonuse values. The flexibility of constructing hypothetical markets accounts for much of the popularity of the technique. There are numerous methodological issues associated with application of CVM including how the hypothetical environmental change is to be specified, the elicitation format for asking valuation questions, the appropriate welfare measure to be elicited (i.e., WTP or WTA), and various types of response biases. Randall (1991a) argues that because of the importance of nonuse values, CVM is likely to be the primary tool for measuring the environmental benefits of biodiversity. Recent summaries of CVM can be found in Mitchell and Carson (1989) and Carson (1991).

Nonuse Values

From a measurement perspective, "passive" or nonuse values (i.e., option, existence and bequest) are the most problematic component of TEV. The contingent valuation method is the only technique available for assessing these values. The topic of existence values for environmental assets is one of the most controversial in environmental economics (Bishop and Welsh, 1992; Edwards, 1992; Kopp, 1992; Rosenthal and Nelson, 1992). Evidence shows that individuals will contribute to environmental organizations, and express positive WTP to preserve environmental assets on CVM surveys, with no expectation of current period or future use of the resource. However, evidence that existence values "exist" is something less than arguing that they can be measured on a sufficiently comprehensive and reliable basis for use in formal decision rules (Castle and Berrens, 1993; Rosenthal and Nelson, 1992).

An example of some of the ambiguities in existence value estimation can be seem in a CVM study by Stevens et al. (1991a) on bald eagles, wild turkeys, and Atlantic Salmon in New England. While Stevens et al. (1991a) found substantial economic benefit from

protection and restoration programs, their results also indicate that in a setting of potential irreversibility, existence values were difficult to quantify and sensitive to how the species were aggregated. Further, a majority of respondents viewed species protection as important, but were unwilling to pay anything. Follow-up questions indicated that many respondents were uncertain of their values or protested the WTP question for ethical reasons.

Much of the controversy over nonuse values has been stimulated by debates surrounding natural resource damage assessment and liability cases (e.g., the Exxon Valdez oil spill in Alaska). This controversy among economists is highlighted by the recent blue-ribbon panel, containing several Nobel Laureate economists, convened by the U.S. Department of Commerce's National Oceanic and Atmospheric Administration (NOAA) in 1992. The panel was convened to provide guidance concerning the potential use of CVM in measuring lost passive or nonuse values in promulgating regulations, pursuant to the Oil Pollution Control Act of 1990. The potential for assessing nonuse values through application of CVM was essentially reaffirmed by the NOAA panel, provided rigorous guidelines are followed (Arrow et al., 1993).

There are a variety of recent examples of the application of CVM to measure existence values, including Columbia River salmon (Olsen et al., 1991), and forest protection (Hagen et al., 1992; Loomis et al., 1993; Rubin et al., 1991). Some economists remain skeptical that existence values can be reliably measured for endangered species and irreversibility problems (Castle and Berrens, 1993; Stevens et al., 1991b), and turn from the traditional benefit-cost framework towards more ecologically conservative decision criteria such as the safe minimum standard (SMS) of conservation (Ciriacy-Wantrup, 1952).

Use Values

Empirical estimates of nonmarket use values are less controversial, and are important inputs to some types of research planning processes. The extant literature contains hundreds of site-specific studies valuing recreational services and environmental quality. Recent examples involving natural resources include Donnelly et al. (1990), Duffield et al. (1992), Johnson and Adams (1989), Morey et al. (1991). Viewed in the aggregate, the numerous valuation studies document the considerable economic worth of nonmarket goods and services.

An emerging issue in the valuation literature is the need to develop acceptable procedures for transferring values (Brookshire and Neil, 1992; Walsh et al., 1992). Benefit transfer refers to the transfer of some existing valuation estimate (or function) from the study site to a policy site. For example, incorporation of "typical" nonmarket values for recreation, fish and wildlife occurs in the U.S. Forest Service planning process under the Resource Planning Act (RPA) of 1974, as amended (Duffield, 1989). It should be noted, however, that these "RPA values" differ greatly from state-of-the-art primary data studies (Olsen, 1989), perhaps because the RPA values do not incorporate nonuse values (Duffield, 1989).

5.8.4.4 Challenges in Linking Valuation Techniques to Ecosystem Service Flows

The need for and interest in values of nonmarket goods and services has arisen independently of concerns regarding ecosystem management and sustainability. As environmental planning and management change to accommodate new issues, the need for de novo valuation studies may increase (e.g., standard RPA values may be poor indicators of the economic benefits and costs produced by forest quality changes under, say, alternative air pollution regimes). The process of developing a tractable framework for ecosystem management may require that valuation studies also co-evolve to aid critical management decisions. For example, explicitly linking valuation techniques to physical resource functions through bioeconomic models, remains an important research area (Adams et al., 1990a). Linking valuation measures, from both market and nonmarket studies, to indices of biological diversity is a fundamental challenge (e.g., Niese and Strong, 1992).

Ecologists have a traditional skepticism of attempts to assign monetary values to ecosystem functioning, due both to inherent limitations in BCA and the inadequacy of quantitative information about ecological and social factors (Westman, 1977; Higgs, 1987). Attempts to monetize environmental benefits are also seen as having an inherent "quantitative bias"; poorly understood ecological functions are neglected, while traditional commodities (outdoor recreation) are paid full attention (Foy, 1990).

A further question is whether TEV really captures total value. Economists make no claim that all values are being considered, only total economic value. But do traditional measurement approaches really capture all economic value? As Pearce (1993) states:

> There is in some sense a "glue" that holds everything together and that glue has economic value. If this is true, and it is difficult to pinpoint what is at issue here, then there is a total value to an ecosystem or ecological process which exceeds the sum of the values of the individual functions. Total economic value may not, after all, be total.

Can complex ecological functions be accurately expressed in monetary terms? It is tempting to think that because of its inherent flexibility CVM may be up to the task (Russell 1993). The contingent valuation method has been applied to an impressive array of nonmarket goods. While the traditional focus has been on outdoor recreation, applications include endangered species and unique natural landscapes. However, precise valuation of ecosystem services with CVM will require a precisely defined commodity. As researchers move from valuing single environmental endpoints or services to addressing more complex "bundles" of endpoints and services, it will become more difficult to define the commodity in a CVM survey. This may prevent unambiguous estimation of such values.

Indirect Use Values

The common use/nonuse dichotomy may miss the fundamental interconnectedness and transparency of complex ecological functions. The full range of ecosystem services is comprised of multiple endpoints. This vector of endpoints is supported by complex interactions. Uniqueness of the system lies in its functional structure, rather than discrete environmental commodities—often the visual or spectacular—which satisfy human preferences. Within the TEV taxonomy, indirect use values comes the closest to capturing the system characteristics of complex ecological functions (Pearce, 1993).

Potential Misuse/Abuse of Economic Values

If understanding of functional structure of ecosystems is inadequate, then can any attempt to express the valuation of ecosystem service flows be satisfactory? While services may indeed be important, grossly imperfect attempts at monetary valuation may do more harm than good (Norton, 1987; Rolston, 1988; Sagoff, 1988).

The first possibility is that precise quantification may introduce a degree of rigidity or inflexibility that reduces the efficacy of future planning and management. There may be an inherent need to seize onto any monetary value, no matter how poorly measured. Once

seized, the value can then take on a life of its own. A second possibility is that focusing on satisfaction of preferences of the current generation and distributional status quo ignores other collective social priorities. Examples include intergenerational equity and the notion of preserving critical natural capital (biogeochemical cycles, genetic information, etc.) embodied in the vast literature on sustainable development (Pezzey, 1992; Pearce, 1993).

If attempts at assigning monetary values are found to be unsatisfactory for the full complex of ecosystem service flows, then alternative decision rules must be given closer scrutiny. One such decision rule is the often-discussed safe minimum standard.

Safe Minimum Standard

The safe minimum standard (SMS) of conservation for ecosystem or other resources which give rise to a steady stream of benefits or servcies ("flow resources") was originally introduced by Ciriacy-Wantrup (1952). The SMS is a decision rule to protect critical flow resources unless the costs of doing so are intolerably large (Randall, 1989, 1991). The SMS rule is designed to provide flexibility and protect future options in the presence of true uncertainty (where probability assessments cannot be meaningfully made), and the possibility of irreversible ecological changes exist (Westman, 1977). Determination of "intolerable" is a social choice which can be informed by both economists (by identifying the costs associated with alternative degrees of protection or preservation), and ecologists (by identifying ecological indicators and threshold effects which can be tied to preservation costs). The SMS concept has received increasing attention (e.g., Bishop and Woodward, 1993; Randall, 1991) and is closely linked to the notion of "critical natural capital" that occurs in some formulations of sustainable development in agriculture and forestry.

Recent discussions of the SMS to threatened and endangered species applications include Hyde (1989), Castle and Berrens (1993), and Stevens et al. (1991).

5.8.4.5 The Research Agenda

The previous sections highlight some deficiencies in the natural science and economics literature which prevent valuation of ecosystem services. This section offers a set of opportunities for future research efforts to addresses these deficiencies. No priority is assigned and some opportunities are obviously overlapping.

(1985) suggests that the value of additional natural science information (in terms of reducing confidence materials around economic estimates) declines rapidly. Thus, not all sources of uncertainty need be removed before economic analyses can proceed.

Explore Relationship of Ecosystem Functions and Service Flows to Economic Values

An important research question is whether measures based on subjective preferences (e.g., stated WTP from a CVM study, or observed WTP from an HPM study) have any relationship to indices of ecosystem functions and service flows (Costanza et al., 1991). For example, Hanley and Ruffell (1993) find that "forest characteristics are in general poor predictors" of recreational value in a CVM study. However, they also conclude that the chief problem lies in quantifying changes in natural science information. Utilization of GIS-based tools offer new opportunities for connecting natural science information with a variety of economic models.

A critical building block in identifying such connections is the development of a shared language. For example, the connections between the concept of "endpoints" for ecological risk assessment and economic valuation are unclear. The EPA (1992) framework for risk assessment defines an assessment endpoint as: "an explicit expression of the environmental value that is to be protected." However, as Suter (1990) makes clear, assessment endpoint, "must be valued by society, but they are not ultimate values." An important, but not the sole, measure for expressing social value are economic values.

Future valuation studies may demonstrate that complex, and often transparent, ecological functions do not map into individual preferences. This would appear to be useful information worthy of documentation. It would also not be a reason to discard experimental techniques such as CVM.

Identify Limits to Application of Valuation Techniques

The measurement of nonuse values using the contingent valuation method remains controversial. Given ethical limitations to markets in various social spheres (Anderson, 1990), there is a limit to the things to which we can meaningfully assign values. As one example, the assignment of monetary values as expressions of the worth of certain personal or social relations may change the nature of the relationship. As a second example,

following Bishop and Woodward (1993), and Howarth and Norgaard (1992), we cannot expect nonmarket values to resolve large-scale sustainability and intergenerational equity issues. Economic efficiency criteria provide no guarantee of the protection of any particular environmental assets (Foy, 1990) or ecological sustainability (Common and Perrings, 1992).

Identify the Degree of Substitutability Between Natural and Man-Made Capital

Neoclassical economics has no traditional notion of sustainability other than intertemporal efficiency. A critical issue in the sustainability literature is the degree of substitutability between man-made and natural capital. Substitutability can occur on several levels. The first question is whether man-made capital is an adequate substitute for the full range of complex ecological functions. The corollary question is the degree of substitutability within the structure of human preferences. Valuation methods based on willingness to pay and willingness to accept compensation assume an underlying substitutability. Economic values are exchange values based on the notion of indifference—they express the terms of trade (money for environmental services) and money is the good which accesses other exchange commodities. In short, assigning an economic value to critical natural capital assumes an inherent substitutability for that asset in individual preference functions.

5.8.4.6 Valuing Ecosystem Service Flows: Summary

Economists have a variety of valuation techniques to help guide policy choices concerning the effects of air pollution or other environmental change on environmental assets. Applying these techniques to ecosystem management issues and valuing the full range of ecosystem service flows is a new, and as yet, unresolved challenge. Current state-of-the-art assessment methods are judged inadequate for environmental regulations. Many scholars, in both ecology and economics, are inherently skeptical of any economic valuation of the full complex of ecosystem services, and turn towards other value indicators. Costanza (1991) argues for methodological pluralism, where the imperfect information gained from multiple approaches is combined in an integrated informational structure. The identified research agenda for valuing ecosystem service flows crosses traditional disciplinary boundaries (Russell, 1993). Interdisciplinary dialogue, cooperation, and development of

shared language are necessary for successfully designing future valuation experiments concerning ecosystem service flows, and determining the proper role for such valuation.

5.8.5 Summary

The 1986 Criteria Document contained a review of assessments of the economic consequences of O_3 on U.S. agriculture. This section has evaluated selected post-1986 literature on the same topic. In addition, the review has been expanded to include potential economic effects on forests and ecosystems.

Based on economic assessments and scientific data available at the time, the previous criteria document (U.S. Environmental Protection Agency, 1986) concluded that O_3 at ambient levels was imposing economic costs on society. The review of more recent (post-1986) literature on agriculture corroborates that earlier conclusion. Specifically, the recent literature, using the full set of NCLAN data and addressing some deficiencies in the pre-1986 assessments, confirms the finding of economic losses from ambient O_3 concentrations.

The exact level of these economic effects is a function of cropping patterns, O_3 concentrations (both ambient and episodic), and the spatial and temporal characteristics of projected or observed O_3 levels. The current economic assessments represent improvements in the scientific understanding of O_3 effects on agriculture. However, the assessments of economic effects initially incident on the agricultural sector remains incomplete.

Only a few assessments consider the economic effects of O_3 on forest trees as well as urban trees, shrubs, and ornamentals. These studies assess the economic effects of hypothetical changes resulting from O_3 or other stressors on forest productivity and aesthetics and are best viewed as measures of the potential effect of O_3 on these receptors. Improvements linking O_3 effects data to productivity and aesthetic effects will improve the utility of such economic analyses.

The effects of O_3 on ecosystems have not been addressed in the published literature. There is, however, an emerging interest in applying economic concepts and methods to the management of ecosystems. Ecological research is also addressing the challenging conceptual and practical issues in understanding and managing ecosystem functions. Economic research continues to develop, refine, and apply techniques for valuing market and nonmarket products and services that will be of help in estimating the economic effects of O_3

on ecosystems. Increased dialogue between the disciplines is needed before empirical analyses of the economic consequences of ecosystem management are feasible.

In summary, the state of science concerning O_3 economic effects on agricultural crops is sufficient to conclude that O_3 imposes costs on society. Conclusions regarding effects on forests and ecosystems must await the acquisition of additional data and possible refinements in ecological and economic methods.

5.9 INTEGRATIVE SUMMARY AND CONCLUSIONS FOR VEGETATION AND ECOSYSTEM EFFECTS

5.9.1 Introduction

Review of the post-1986 literature has not altered the conclusions of the earlier Criteria Document (U.S. Environmental Protection Agency, 1986) or Supplement (U.S. Environmental Protection Agency, 1992). In the 1986 criteria document, several general conclusions were drawn from various experimental approaches: (1) current ambient ozone concentrations in many areas of the country were sufficient to impair growth and yield of plants; (2) effects occur with only a few hourly occurrences above 0.08 ppm; (3) growth and yield data cited in the 1978 criteria document (U.S. Environmental Protection Agency, 1978) indicate several species exhibited growth and yield effects when the mean ozone concentration exceeded 0.05 ppm for 4 to 6 h/day for at least 2 weeks; and (4) regression analyses of NCLAN data developing exposure-response functions for yield reductions indicated that at least 50% of the crops were estimated to exhibit a 10% yield reduction at 7 h seasonal mean ozone concentrations of 0.05 ppm or less. These conclusions remain valid today. The 1992 Supplement reviewed the literature concerning the appropriate exposure index for expressing O_3 effects on vegetation, including evaluation of the (1) role of exposure duration, (2) the role of peak concentrations, (3) the 7- and 12 h mean concentrations, and (4) comparison of many possible exposure indices to summarize seasonal exposures and relate to yield loss. It was concluded that the 7- and 12 h seasonal mean was not appropriate because of its treatment of all concentrations equally, and the lack of consideration of exposure duration. Experimental studies had indicated the influential role of episodic, peak concentrations and the length of the exposure. A comparison of possible

exposure indices concluded that the preferred indices cumulated all hourly concentrations during the growing season and preferentially weighted the higher concentrations. These conclusions remain valid today.

The review of the post-1986 literature has revealed additional analyses of the NCLAN database as well as several European crop yield loss studies, substantiating the effects observed in this country. There has been only limited publication of experimental studies directly addressing the role of each of the exposure components to further our understanding of what should be appropriate exposure indices relating ambient O_3 concentration to effects. There have been, however, several retrospective analyses of NCLAN data that increase confidence in the use of the peak-weighted, cumulative indices. Studies of forest tree seedlings have substantiated pre-1986 studies indicating the sensitivity of a number of species, at least as seedlings. Data concerning the response of large mature trees as individuals or in stands are limited. Seedling growth response of some species is altered at O_3 concentrations observed in many areas of the United States. Studies of the role various biotic and abiotic environmental factors play in the response of plants to O_3 indicate the complexity of determining the response of plants in natural ecosystems wherein the interaction of species, genotypes, and the multitude of environmental influences dictate the eventual response of the species or community in question.

5.9.2 Species Response and Ecosystem Response

Ozone injury was first observed on crop plants. Therefore crop plants have been studied more intensively than those plant species growing in natural habitats. As a result, most of the information concerning species response, to O_3 comes from the studies of crop plants. The number of crop species/cultivars for which response data is available, however, is a mere fraction of the total plants grown as crops. This is especially true for native herbaceous plants and trees where the studies are far fewer in number. Because of the known wide range of sensitivities to O_3 among the species that have been studied and even among cultivars of individual crops (see Section 5.4.2), it is not possible to estimate the sensitivity of any given species and/or cultivar that has not been investigated directly except in very general terms.

One attempt at using our fragmented knowledge to develop a general framework of response covering a range of species has been presented by Reich (1987). He described a conceptual model for conifers, hardwoods and agricultural crops, based on considerations of the carbon balance and growth of individual plants in relation to O_3 exposure or uptake (estimated from O_3 concentration and stomatal conductance). For equivalent exposures to O_3 during a single growing season, he ranked these groups in order of decreasing sensitivity as: crops, deciduous hardwoods, evergreen conifers. A similar ranking results when the published response data are reviewed. The concentration of ozone causing yield losses in crop species is slightly less than that observed to cause biomass reduction in deciduous species. A slightly greater concentration of ozone causes reductions in total biomass in some coniferous species. However it is important to note that the variation of this biomass response within these large groupings by growth strategy is as great or greater than the variation in response between the groups. Caution is also needed with such generalizations because these groupings compare annual versus perennial growth of long-lived species, as well as the influence on growth response of a vast array of environmental factors at play on these species in natural ecosystems.

The focus of research for developing quantitative relationships between O_3 exposure and biological effects has been on the response of individual species for three reasons: (1) Single species studies are achievable experimentally, including ease of developing adequate experimental design and exposure technology. (2) In many instances the plants are grown in monoculture (e.g., most crop plants, ornamentals, fruit and nut species, plantation forests), and the inter-specific competition and diversity, which typifies natural communities is not an issue. The predicted response may also include the environmental influences of its growing environment (e.g., drought) that modify the exposure-response relationship. (3) In systems that are comprised of a multitude of species (e.g., mixed forest stands, pastures or grasslands) it is important to understand the response of the individual components so that behavior of the system might be analyzed in a systematic fashion. The underlying assumption is that understanding how a forest stand responds to O_3 requires knowledge of the response of each species within that stand as a starting point. The interactions that typify the community are subject to O_3 effects as well and may manifest themselves as a measurable effect some time later as a result of these interactions. Up to this

time, aside from the study of the San Bernardino forests, the holistic approach to understanding O_3 effects has not been pursued. Exposing large woody and herbaceous species growing in natural species assemblages and subjected to a large array of climatic and biotic environmental factors over decades has not been possible.

It is important to note that there may be a limited potential for using individual plant (species) responses to an environmental stress (such as O_3 exposure) to predict population and community response (Woodward, 1992). As one progresses from knowledge of a tissue or organ's stress-response to the whole plant, population, community and ecosystem levels, various feedback mechanisms may modify the propagation of the effect. Important components of such feedback are the mechanisms of homeostasis which involve injury repair (at the metabolic level) or various types of compensation (Tingey and Taylor, 1982). Compensation, which may occur at all levels of organization, from the subcellular to the ecosystem,invokes processes that counteract the detrimental effects of the stress. At the ecosystem level, an effect on the growth rate of a particular species may not be translated into a comparable effect on the growth rate of a population of the species, because of changes in the intensity of competition (Woodward, 1992).

At the present time, most of our knowledge of O_3 exposure concerns the effects on individual plants or their parts. Although we have some information about effects at the population level with some agricultural crops and some forest tree populations, the information regarding the propagation of effects upward through the different hierarchical levels within natural and forest ecosystems is limited.

5.9.3 How Does Ozone Affect Plants?

Plant growth and yield are the product of a series of biochemical and physiological processes related to uptake, assimilation and translocation of ozone in the individual plant. Ozone exerts a phytotoxic effect only if a sufficient amount reaches the sensitive cellular sites within the leaf. To do this, it must diffuse from the ambient air into the leaf through the stomata, which exert control on O_3 uptake. Ozone effects will not occur if (1) the rate of ozone uptake is low enough that the plant can detoxify or metabolize O_3 or its metabolites; or (2) the plant is able to repair or compensate for the effects. Cellular disturbances that are not repaired or compensated are ultimately expressed as visible injury to the leaf and/or

effects on growth, yield, or both (Tingey and Taylor, 1982; U.S. Environmental Protection Agency, 1986). Ozone effect is cumulative, resulting in net reductions in photosynthesis, changes in allocation of carbohydrate, and early senescence, which leads to reductions in biomass and productivity, and alterations in susceptibility to abiotic and biotic stresses and/or decreased reproduction.

Ozone is expected to reduce growth or yield only if (1) it directly impacts the plant process that is limiting to plant growth (e.g. carbon fixed); or (2) it impacts another step sufficiently so that it becomes the step limiting plant growth (e.g., allocation of carbohydrates to roots and nutrient uptake becomes limiting to plant growth) (Tingey, 1977). Conversely, O_3 will not limit plant growth if the process impacted by O_3 is not growth-limiting. This implies that not all effects of O_3 on plants are reflected in growth or yield reductions. These conditions also suggest that there are combinations of O_3 concentration and exposure duration that the plant can experience that may not result in visible injury or reduced plant growth and yield (U.S. Environmental Protection Agency, 1986). However, subtle physiological effects which may not result in immediate growth reductions may result in increased plant susceptibility to other environmental factors and competition.

The mode of action of O_3 on plant species described in the 1986 criteria document (U.S. Environmental Protection Agency, 1986) still holds true. The plant leaf is the site O_3 action and the critical effect is on the plant's carbon budget (the amount of carbohydrate produced). Inhibition of photosynthesis limits carbohydrate production and allocation resulting in reduced biomass, growth and yield. Studies since 1986 corroborate this understanding, adding information on the effect of O_3 on photosynthetic capacity, respiration, leaf dynamics, and on the detoxification and compensatory processes. In particular, exposure to O_3 concentrations at or near current ambient levels (see Table 5-17 Section 5.6) has an effect on photosynthesis, but a longer exposure duration is necessary to produce a growth response, taking days to weeks rather than hours as in earlier studies with higher concentrations (0.25 ppm or greater). The loss of leaves prematurely as a result of O_3 exposure has been observed in several species and is particularly important in coniferous tree species. This O_3-induced loss in leaf area can be a significant factor in the reducing the amount of carbohydrate produced by the plant. Both a reduced photosynthetic capacity and a reduced leaf area contribute to the reduction in carbohydrate production by plants. However,

the mechanism of premature senescence is not understood. In addition to leaf loss, reports of stimulation of production of new leaves and higher photosynthetic capacity of new leaves represent compensation processes that operate in some species of trees. These mechanisms may counteract the reduction in canopy carbohydrate production resulting from O_3. Some quantitative understanding of these processes is needed to be able to predict long-term effects of O_3 on tree species. More information is needed as well in understanding O_3 uptake at the canopy level and how the plant integrates the effects of O_3 to enable prediction of long-term effects of O_3 exposure in ecosystems, i.e., species response as a function of interactions with other species, abiotic and biotic environmental factors. Unfortunately, there is little experimental evidence to date regarding effects of long-term O_3 exposure on perennial plants. Few experimental studies have extended exposures beyond one season and only in a limited number of studies have observations of growth been extended into the following year, thus observing "carry-over" effects in several tree species. These carry-over effects are significant to long-lived species such as trees since they affect the elongation of new spring shoots or root growth in the year following exposure to O_3. In at least one instance this has been correlated with reduced storage carbohydrate in roots. The implication of these effects on long-lived species is significant. Reduction in growth and productivity, a result of altered carbohydrate produced and allocated, may appear only after a number of years or when carbohydrate reserves in the tree are depleted below some threshold concentration.

5.9.4 Factors That Modify Plant Response to Ozone

Plant response to O_3 exposure is modified by factors within and external to the plant species; cultivars and individuals within populations display variable response to O_3. The plant's response and the variation of that response is dictated by genetics and the plant's present and past environmental milieu. The environment includes biotic and abiotic factors of the species' growing environment, the temporal pattern of exposure concentrations, and the plant's phenotypic stage during exposure.

5.9.4.1 Genetics

An important component of this variation is genetically controlled. The specific genes controlling O_3 response and involved in mechanisms of O_3 tolerance are as yet largely

unknown. However, control of stomatal conductance and internal biochemical defense systems are among the most commonly described tolerance mechanisms. Ozone tolerance is generally thought to be controlled by multiple genes. The implications of genetic variation for managed and natural ecosystems are several-fold: (1) The potential for natural selection for O_3 tolerance and associated loss of sensitive genotypes is regional in nature, unlike well known point-source pollution impacts which occur on local plant populations. However, the intensity of O_3 selection is generally thought to be quite low, 0.3 or less (Taylor and Pitelka, 1992) across most U.S. areas. (2) While it is known that individual plants within a species vary in their O_3 tolerance, the physiological costs to tolerant plants are not known in terms of carbohydrate assimilation (energy production) and allocation. Tolerance mechanisms based on reduced stomatal conductivity in the presence of O_3 would likely reduce the growth of tolerant plants. Similarly, tolerance mechanisms based on the productivity of antioxidant compounds will likely shunt plant resources away from growth to the production of the defense compounds. (3) Exposure-response equations and yield-loss equations developed for a single or small number of cultivars, genotypes, families or populations may not adequately represent the response of the species as a whole. As a corollary to this, the sensitivity of responder genotypes can not be determined by measuring effects just in relation to mean O_3 concentrations.

5.9.4.2 Environmental Factors

Since the previous criteria document (U.S. Environmental Protection Agency, 1986), additional studies have been published on a wide range of biological, physical, and chemical factors in the environment that interact with plant response to O_3. While understanding the plant's response to O_3 requires an understanding of the role of environmental factors that modify that response (primarily to reduce uncertainty in the estimation of species' exposure-response), the corollary is also important to understand, and in fact has not received as much attention, i.e., the exposure to O_3 can modify the plant's ability to integrate its environment. For example, exposure to O_3 reduces the tree's ability to withstand winter injury caused by exposure to freezing temperatures and influences the success of pest infestations.

Biological components of the environment of individual plants include pests, pathogens and plants of the same or other species in competition. With regard to insect pests, although

only a very limited number of plant-insect systems have been studied, there is a general trend in the observations which suggests that some pests have a preference for and grow better when feeding on plants that have been impacted by O_3, but there is no evidence to suggest that O_3 may trigger pest outbreaks. Unfortunately, because we have no knowledge of how the vast majority of plant-insect systems will be affected by O_3, it is not possible to offer any quantitative overall assessment of the consequences of such interactions on the growth of crops and natural vegetation. At best, we may conclude that there is a reasonable likelihood that some insect pest problems will increase as a result of increased ambient O_3 levels. Indeed, this was seen in the San Bernardino Mountains where ponderosa pine experienced bark beetle infestations with higher O_3 exposures (U.S. Environmental Protection Agency, 1986).

Plant-pathogen interactions also appear to be affected by O_3. The suggestion that diseases caused by obligate pathogens tend to be diminished by O_3 while those caused by facultative pathogens tend to be favored (Dowding, 1988), is generally supported by the limited evidence available. In terms of its broader implications, this suggests that continued exposure to O_3 may lead to a change in the overall pattern of the incidence and severity of specific plant diseases affecting crops and forest trees.

With regard to the physical environment, the combination of light, temperature and water availability largely determines the success of plant growth because of the influence of these factors on the processes of photosynthesis, respiration and transpiration. For agricultural crops, perhaps the most important of these potential interactions with O_3 concerns water availability and use. There is consistent evidence that severe drought conditions tend to reduce the direct adverse effects of O_3 on growth and yield. Conversely, the ready availability of soil water tends to increase the susceptibility of plants to O_3 injury. However, a lack of water should not be viewed as a potentially protective condition, because of the adverse effects of drought *per se*. With perennial trees, there is some evidence that prolonged exposures to O_3 may lead to greater water use efficiency which may enable such trees to be better able to survive drought conditions.

The plant's environment also contains numerous chemical components, ranging from soil nutrients and other air pollutants to agricultural chemicals used for pest, disease and weed control.

A large number of studies have been conducted on the effects of O_3 in conjunction with other gaseous air pollutants such as SO_2 and NO_2, although the information obtained in several of the studies is of no more than academic interest because of the unrealistic exposure conditions used. Preliminary evidence suggests that nitrate deposition in the soil could influence plant response to O_3.

Since increased tropospheric O_3 is a component of global climate change, results from studies on the interactions of O_3 with increased levels of CO_2 and UV-B radiation are beginning to appear. Initial work with CO_2 suggests that increased CO_2 levels may ameliorate the effects of O_3. However, it is too soon to be able to generalize on the outcome of this interaction. At the present time, no investigations of the compound interactions involving O_3, CO_2, UV-B, increased temperature and changed soil moisture status have been reported.

In conclusion, in spite of the amount of work carried out to date on the interactions of O_3 with environmental factors, there is not a strong quantitative database to generalize and extend the effects of O_3 on species across environments. Uncertainty about the extent of modification of the exposure-response relationship as a result of different growing environments remains, as well as the uncertainty associated with understanding O_3's role in altering a species' ability to integrate its environment.

5.9.5 Exposure Dynamics

The effects of O_3 on individual plants is not only a function of inter- and intra-specific differences in tolerance (genetics), and growing environment affecting the uptake of O_3 (e.g., soil water, nutrient), but also the characteristics of the exposure itself which affect the uptake of O_3 from ambient air, and thus the ultimate growth response. From the studies prior to 1986 and after 1986, evidence indicates that the components of exposure, i.e. peak concentration, frequency of occurrence and duration, play various roles in the plant response. The temporal pattern of hourly concentrations in the exposure influence the response. There is a reported greater influence on growth in annual and perennial crop species (bush beans and alfalfa), and in tree seedlings (ponderosa pine and aspen) of episodic peak exposures compared to either daily peak occurrences in the case of crops or non-diurnal, continuously elevated exposures typical of remote regions in the case of tree seedlings. The results

suggest a variation in the growth response of species as a function of the dynamics of the exposure. In addition to the temporal distribution of concentration during a day and during a season, there is also the distribution of the exposure during the growing season and the phenology of the plant. Some phenotypic stages of growth are more sensitive to O_3 than others. In most instances of crop exposure studies, in particular the NCLAN database, the exposure treatments used in developing response functions have used ambient concentrations as a base. Thus, the variation in the response as the result of a variation in regime type is not known. The same reservation is applicable to the growth response reported for tree seedlings. It is not possible at this time to quantify the alterations in the growth or yield response as a result of different exposure patterns. However, it is possible to suggest which components of an exposure play a relatively greater influence in growth alterations than do other components of the exposure. For example, peak concentrations are more effective than lower concentrations in altering growth; and the episodic occurrence of peak events seems to be more damaging than the daily occurrence of the same peak value or a continually elevated concentration over a growing season. The variation in species' response as a function of exposure concentration and duration suggests the importance of a measure of the ambient air exposure to relate to the biological effects.

5.9.6 What Measure of Exposure Characterizes Species Effects?

A measure is needed to relate ambient exposure to the observed biological effect(s). The amount of O_3 taken up from the atmosphere by the plant (either rate of uptake or cumulative seasonal uptake) is the ultimate measurement of O_3 exposure, but this is not a practical measure to make directly. The uptake rate and total cumulative uptake can be calculated from ambient concentrations and species' gas exchange characteristics. A measure of uptake integrates all those environmental influences on stomatal conductance controlling the effect, e.g., temperature, humidity, soil water status, etc., but it is not practical for most experimental approaches used in determining what ambient concentrations of O_3 can be tolerated by vegetation. Thus an index of ambient exposure is required as a surrogate of uptake. Any index that relates well to plant response should incorporate these environmental and exposure dynamic factors, directly or indirectly, in weighting the hourly O_3 concentrations differentially.

Given the evidence suggesting a relatively greater contribution to effects of higher concentrations, episodic occurrence of peak concentrations, and the duration of the exposure, an index that cumulates hourly concentrations during the season and gives greater weight to the higher concentrations appears to be an appropriate index for relating ambient exposure to growth or yield effects. A number of different forms of a peak-weighted, cumulative index have been examined, e.g., SUM06, SIGMOID, W126, for their ability to properly order yield response in the large number of crop yield studies of NCLAN. All perform equally well and it is not possible to distinguish between them on the basis of statistical fits of the data. In retrospective analyses when O_3 is the primary source of variation in response, year to year variations in plant response are minimized by the peak-weighted, cumulative exposure indices. No experimental studies, however, have been designed specifically to evaluate the adequacy of the various peak-weighted indices.

This document's conclusions are no different than those of the 1986 criteria document or the 1992 Supplement (U.S. Environmental Protection Agency, 1986, 1992): (1) mean indices are not among the best exposure indices; and (2) the preferred indices are those cumulating hourly values over the growing season and preferentially weighting the peak or higher concentrations.

The 7- and 12-h seasonal means were earlier indices used to describe plant response. The mean indices have been shown to be inadequate in ordering growth response in experimental studies as well as retrospective analysis of NCLAN data (U.S. Environmental Protection Agency, 1986). This is not surprising since a mean index implies that all concentrations are equal in their effect on plants, and does not consider duration of exposure. Exposure duration is influential in the response, as well as the timing of exposure during a growing season coinciding with sensitive plant growth stages. Phenology is one factor, other than peak events and duration, that is influential in response. Others such as respite time, canopy structure, environmental conditions, e.g., soil and nutrient conditions, are considered important but not well understood. All these factors interact with concentration and duration in different fashions depending on species. The peak-weighted cumulative indices do a better job of considering at least a part of this information on environment, phenology, etc., than the mean or single-event peak indices, because of their inclusion of concentration weighting and duration. Recently, the mean O_3 flux was used as an index and it minimized the year to

year variation in response when combining replicate studies, indicating the importance of environmental conditions in quantifying the relationship between O_3 exposure and plant response.

5.9.7 What Is the Estimated Crop Yield or Biomass Change with Ozone Exposure?

In the 1986 criteria document (U.S. Environmental Protection Agency, 1986) and its supplement (1992) a distinction was made between foliar injury and damage. Yield loss was defined as an impairment in the intended use of the plant. This concept included reductions in aesthetic values, foliar injury (changes in plant appearance), and losses in terms of weight, number, or size of the harvested plant part. Yield loss may also include crop quality. Losses in aesthetic values are difficult to quantify. Foliar injury symptoms can substantially reduce the marketability of ornamental plants or crops where foliage is the plant part (e.g., spinach, lettuce, cabbage), and they constitute yield loss with or without concomitant growth reductions. It should also be recognized that foliar injury to vegetation in national parks constitutes reduction in aesthetic value. At that time (1986), most studies of the relationship between yield loss and O_3 concentration focused on yields as measured by weight of the marketable organ of the plant. From this perspective, damage can be segregated into several categories: (1) economic; (2) ecological value of structure and function; (3) genetic resources; and (4) cultural values (Tingey et al., 1990). In the instance of crop species, the effect of interest was yield, at least in the NCLAN research program. In the instance of tree species, much of the research has sought to measure changes in biomass or productivity, which could relate to all four of the above effect categories.

Diverse experimental procedures, ranging from field exposures without chambers to open-top chambers and to exposures conducted in chambers under highly controlled climates, have been used to study effects on crops and tree seedlings. In general, the more controlled conditions are most appropriate for investigating specific responses and for providing the scientific basis for interpreting and extrapolating results. These systems are powerful tools for adding to an understanding of the biological effect of air pollutants. However, to assess the economic impact of O_3 on crop yield or biomass partitioning in tree species, exposures should have minimum deviations from the typical field environment in which the plant is grown. Much of the data reviewed in this document and in the 1986 ozone criteria document

(U.S. Environmental Protection Agency, 1986) utilized the open-top chamber methodology. This approach has been the primary methodology for developing the empirical database of O_3 effects on crop yield during the last 15 years. These are used because of the control they offer over exposures and still offer some semblance of relevance to field condition, and the ability to replicate studies from year to year. The NCLAN studies used sufficient treatments to allow development of exposure-response functions and became the largest database available for establishing a quantitative relationship between exposure and biological effect in crop and tree species (as seedlings). The response functions allow estimations and generalizations of biological response to O_3 unlike information from multiple comparisons.

Two different approaches to re-analysis of NCLAN data have occurred. The National Crop Loss Assessment Network studied the major agronomic crop species,including corn, soybean, wheat, cotton, bean, and alfalfa, as well as several other regionally important species accounting for 70% of all crop land in the United States and 73% of the agricultural receipts. One approach estimated yield reduction of up to 20% at 12 h seasonal mean of 0.06 ppm and a 10% reduction at 0.045 ppm. In another approach, they compared estimated yield reduction in 54 studies and 12 crop species with 3 measures of exposure. The average duration of the studies was 74 days. It was concluded that 50% of the crops would experience 10% yield reduction at a 3 mo Sum06 concentration of 26.4 ppm-h, 7 h seasonal mean of 0.049 ppm, or a 2HDM of 0.094 ppm. These are averaged yield losses for all species; more sensitive species would experience greater yield losses at these concentrations. The SUM06 has been examined in many papers; therefore, it has been used as an example in the discussions of O_3 effects that follow.

Similar results have been reported from European crop studies. Wheat yields were reduced up to 29% depending on the exposure and cultivars, but in no instance were O_3 concentrations greater than a 0.062 ppm 7 h seasonal mean. Spring rape yields were reduced 9 to 26% at 8 h seasonal means of 0.03 to 0.06 ppm. Seasonal 7 h means of 0.045 ppm reduced bean yields 17%.

5.9.8 Ozone Concentration Across the United States

The O_3 concentrations causing 10% or greater yield reductions in crop species are concentrations that are not atypical of O_3 air quality during the past 10 years across the U.S.

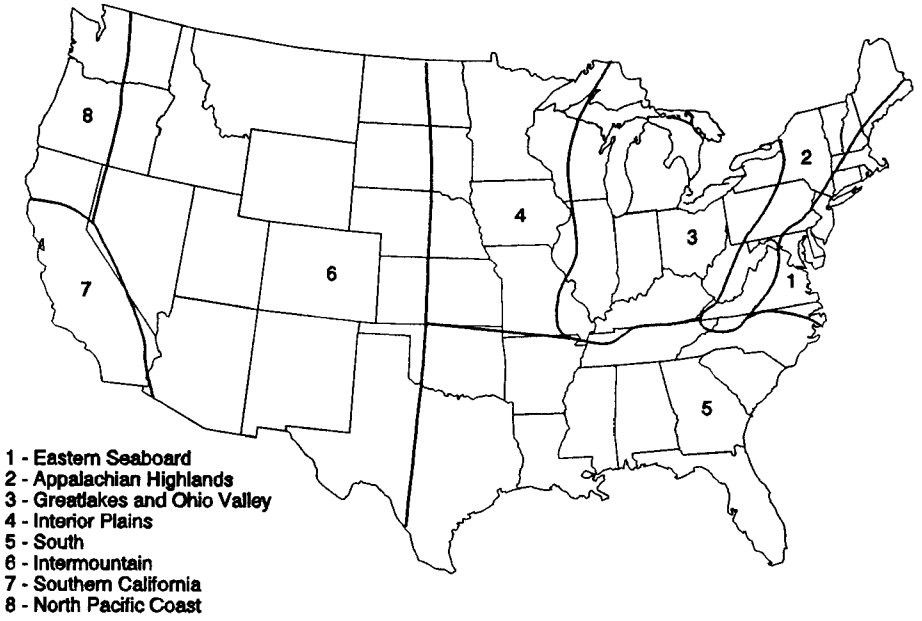


Figure 5-27. Regions of the United States for analysis of trends of ozone concentration.

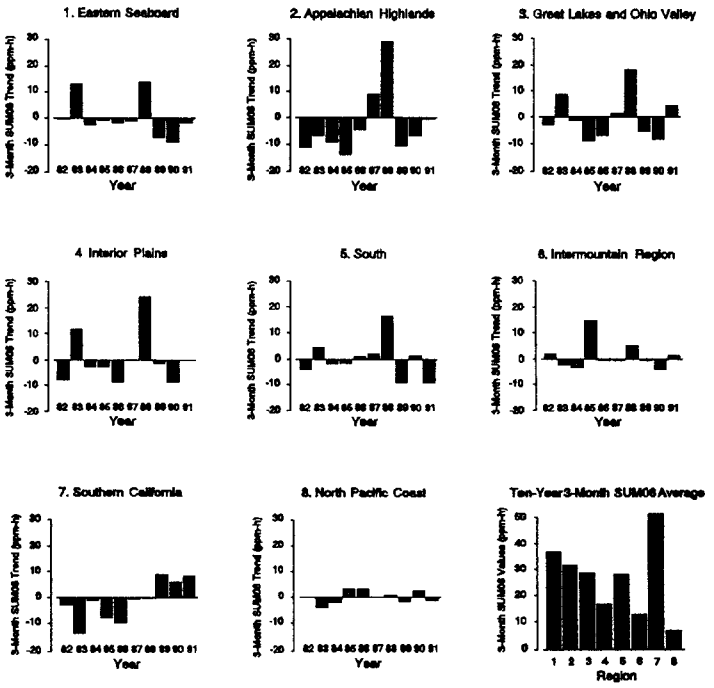


Figure 5-28. Ten-year trends in 3-mo SUM06 values by region at rural monitoring sites.

Table 5-17 (Section 5.6) summarizes the average of air quality by year (1982 to 1991) across the U.S. at rural or remote monitoring designations. Trend data for each of the 10 years from 8 different regions of the U.S. (Figure 5-27) are shown in Figures 5-28 to 5-30. The

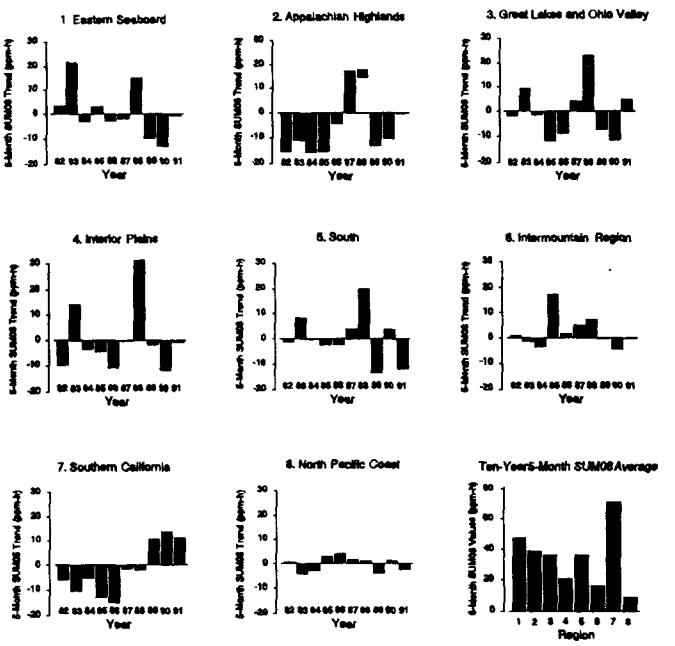


Figure 5-29. Ten-year trends in 5-mo 24-h SUM06 values by region at rural monitoring sites.

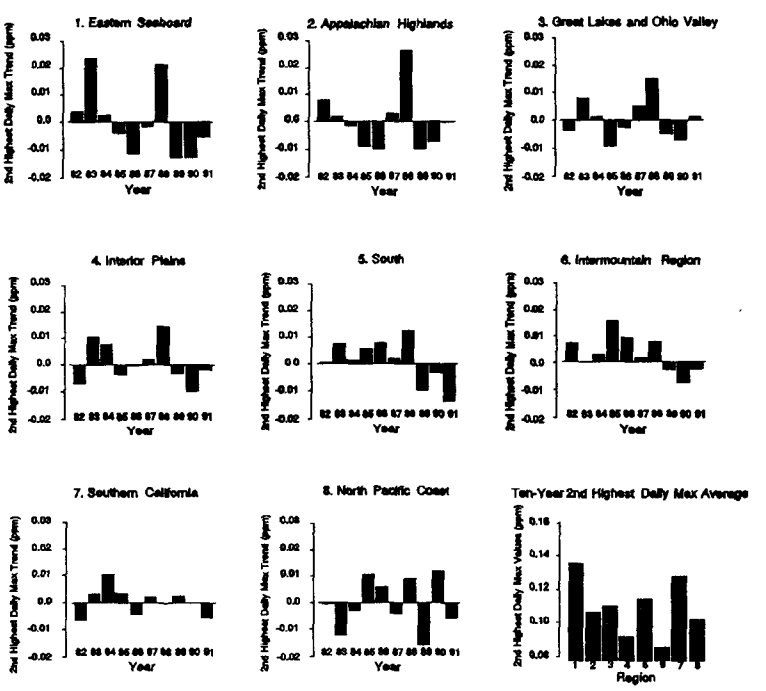


Figure 5-30. Ten-year trends in second highest daily maximum values by region at rural monitoring sites.

values estimated to cause 10% or greater yield losses in at least 50% of the crops are exceeded in every year regardless of exposure index. The average among years for the 3 mo

using SUM06 is 29.5 ppm-h, 0.054 ppm 7 h seasonal mean, and 0.113 2HDM (Table 5-17; Section 5.6). Both the seasonal mean and peak index (2HDM) were shown to be inadequate indices of exposure to relate to biological effects, but the values are given here for comparison since these are frequently used to express air quality or relate plant exposure effects.

Trends and year-to-year variation in regional exposures are expressed as peak-weighted, cumulative indices (SUM06) for 3 or 5 mo (Figure 5-28 and Figure 5-29) and the event-based second highest daily maximum (Figure 5-30). The O_3 concentration is variable from year to year during the 10 year period; and depending on the region of the country, each year exhibits variation to a more or less greater extent from the 10 year average. In the Eastern Seaboard (Region 1) 1983 was well above the 10 year average. Several regions show 1988 as the highest O_3 year. In the west, variation between years, and deviation from the 10 year average is not as great as in the east and the south. The 10 year averages for only rural sites are generally higher that those using all O_3 monitoring sites (includes urban, as well as near-urban designations). All but 3 regions, the Interior Plains, Intermountain, and Pacific Northwest, have average exposures greater than estimated to cause crop yield losses greater than 10% for 50% of the crop species, i.e., > 29 ppm h 3-mo SUM06 (Figure 5-28). There does not appear an obvious trend in direction of O_3 concentration by either of the exposure indices, but the year-to-year variation is great in several of the regions and for most regions of the country 1983 and 1988 were noteworthy 'high O_3' years. This variation in exposure would effect plant growth and is "coupled" to climatic conditions of that year, all of which are important growth factors in plants.

5.9.9 What Are the Exposure Effects on Other Species—Trees and Ornamentals?

Quantifying exposure-response in perennial plants (e.g., pasture grasses, shrubs, trees) is complicated by the fact that they can receive multi-year exposures and because the results of exposures in a previous year or over a number of years may be cumulative. Yield of multiple year forage crops (e.g., alfalfa and forage mixtures), as with single season crops, are reduced at concentration at or near ambient (0.04 to 0.06 ppm 12-h mean) in many parts of the growing areas for these crops. The question of cumulative effects from year to year

has been addressed in only one instance (a two year alfalfa study in southern California) and there was no indication of such carryover effects (Temple et al., 1988a).

As in the case of perennial crops, there is very little experimental evidence of the long-term effects of O_3 on trees and shrubs. There are studies reported in the earlier criteria document (U.S. Environmental Protection Agency, 1986) documenting sensitivity of seedlings in chambered exposure studies, but little information can be garnered from these studies regarding biomass or productivity. Recent exposure studies of black cherry and aspen suggest these are sensitive species and may have annual biomass changes with current ambient concentrations of O_3 in the regions where they are indigenous. In an interesting observation, 30-year-old red oak was reported to have 41% reductions in canopy weight after 177 days exposure to a 7 h mean of 0.069 ppm, but seedlings were not affected by this exposure (Samuelson and Edwards, 1993). A number of species, as seedlings, may be experiencing biomass loss as indicated by a compilation of results of a number of deciduous seedling studies (Figure 5-21; Section 5.5 and Table 5-26; Section 5.6) that indicate 10% biomass loss in 50% of the seedling studies at concentrations of 31.5 ppm h (SUM06 in 92 days) or 0.055 ppm (7 h mean).

Exposure-response functions for 11 species of trees as seedlings indicate total biomass losses in some species at concentrations of O_3 currently experienced in many regions of the United States. At concentrations of 33.3 ppm h for 92 days total biomass losses of 10% would be predicted to occur for 50% of these seedlings. When considered by growth strategies, deciduous species appear to be more sensitive that evergreen species and less sensitive than most crops species on the basis of estimated annual biomass or yield loss. A 10% annual biomass loss in deciduous species is estimated for 7 h mean of 0.055 or a SUM06 of 31.5 ppm h compared to 0.049 7 h mean and 26.4 ppm h causing 10% reduction in yield of 50% of the crops.

Changes in biomass of evergreen forest species, such as ponderosa pine, loblolly and slash pine are evident from the limited exposure studies of O_3 at or near concentrations typical of ambient (Table 5-17; Section 5.6) during a growing season (0.04 to 0.05 ppm 7 h seasonal means and 20 to 30 ppm h SUM06 for 92 days). Estimated biomass loss of 10% in 50% of the conifer seedlings examined occurs at a SUM06 92 day exposure of 42.6 ppm h.

The effects of O_3 exposure on fruit and nut tree species have received limited study. There are reported growth reductions in almond, pear, plum and apricot at 12 h means of 0.051 ppm.

Like crop species, tree species exhibit a wide range of response, depending on species, and genotypes within species. Alterations in gas exchange, needle retention, carbohydrate reserves, root growth and total biomass and productivity are reported. Like other perennial species, the alteration by O_3 of processes that alter total carbohydrate produced by the the canopy (i.e., photosynthetic capacity, needle retention), results in shifts in carbon allocation priorities and changes in growth. In particular, root growth is often observed to be reduced while shoot growth is maintained. This reduction in root growth can result in reduced water and nutrient uptake by seedlings thus reducing seedling establishment. Overall changes in carbon budgets as a result of O_3 exposures can hypothetically result in long-term changes in growth. However, most of the experiments are conducted on seedlings and during 1 to 3 seasons, only 2% or less of the life span of the tree. Whether or not these exposure-response functions for seedlings are representative of the larger, mature tree is unknown at present. Thus, the long-term effects are unknown and will undoubtedly require model simulations.

Furthermore, because of the long life span of trees, there is ample opportunity for a long-term cumulative effects on growth. Small changes (even less than 1 to 2% biomass loss per year) which may not be detectable statistically, might be translated into large changes during the life span of the tree, and may result in changes in stand dynamics, with concomitant effects on the structure and function of the ecosystem. The implication of these effects on long-lived species is significant. Reduction in growth and productivity, a result of altered carbon fixed and carbon allocated, may appear only after a number of years or when carbohydrate reserves are depleted. Consideration must also be given to the fact that most of these trees grow as part of mixed forests, in competition with many other species.

5.9.10 Spatial Characterization of Ozone Effects

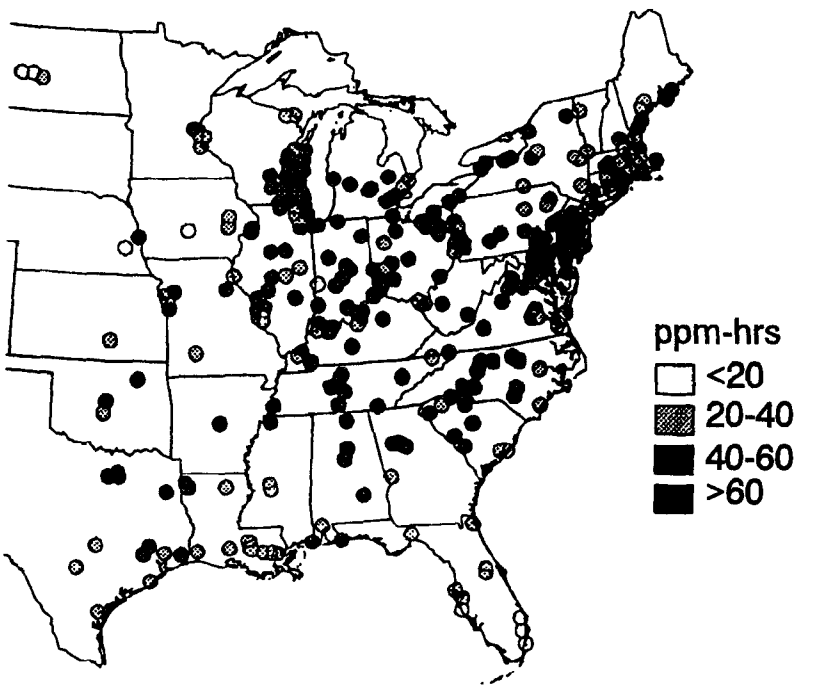
As reported for reductions in crop yield, tree species biomass reductions, based on seedling growth response, have also been reported at concentrations of O_3 currently occurring in regions of the United States. The decade average 3 mo SUM06 is 29.5

(Table 5-17; Section 5.6), only slightly below the 31.5 ppm h value estimated as capable of causing a 10% annual biomass loss in 50% of the deciduous species examined in seedling studies. Individual species, such as black cherry or aspen, would be estimated to experience 10% biomass loss at much lower concentrations, 16 to 20 ppm-h 3 mo SUM06 (Table 5-25; Section 5.6). These concentrations are exceeded in those regions of the U.S. where these species occur (Figure 5-28). Although the 10% annual biomass loss in conifers was estimated to occur at a 3 mo SUM06 of 42.6 pm h, this O_3 exposure is higher than the decade average O_3 in the U.S., but this concentration has been experienced in at least one region of the U.S. and in certain years, e.g., 1988, in several regions (Figure 5-28).

The spatial variation of ambient O_3 exposure across the U.S. and the distribution of crop or tree species can be depicted visually in maps using the Geographical Information System (GIS), and the effects of O_3 characterized in a geographical context by providing some estimate of the spatial extent of current ambient O_3 exposures to vegetation (and the variation about that estimate). Such approaches have been used for the crop species studied in NCLAN (Tingey et al., 1991, 1993) and a number of forest tree species as seedlings (Hogsett et al., 1993). These spatial characterizations have combined estimates of O_3 exposure from the AIRS monitoring network, geographical distributions of individual crop and tree species' growing regions, and the exposure-response functions developed for each species. The crop maps of Tingey et al. (1993) were revised using estimates of O_3 exposure developed by Herstrom et al. (1993) which estimate O_3 concentration across non-monitored areas. To illustrate year-to-year variation in exposure, 1988 and 1989 monitored O_3 concentrations reported as maximum 3 mo SUM06 are shown in Figure 5-31. The maps of the estimated O_3 exposure from these two years is shown in Figure 5-32. The peak index, 2HDM, is illustrated for the years 1988 and 1989 in Figure 5-33.

Exposure-response functions combined with the O_3 exposure result in a spatially-distributed yield loss. The year-to year variation in the estimated yield reduction for all crops is shown in Figure 5-34. Individual crop species soybean and wheat estimate with yield losses from 1988 are shown in Figure 5-35. Tree species distribution and variation in estimated total biomass reduction due to spatial variation in O_3 exposure are mapped in Figures 5-36 to 5-38. As with crop species, these maps show possible exposures for each species based on its distribution. An example of year-to-year variation in exposure-response

A. Monitored 3 Month SUM06 Exposures (1988)



B. Monitored 3 Month SUM06 Exposures (1989)

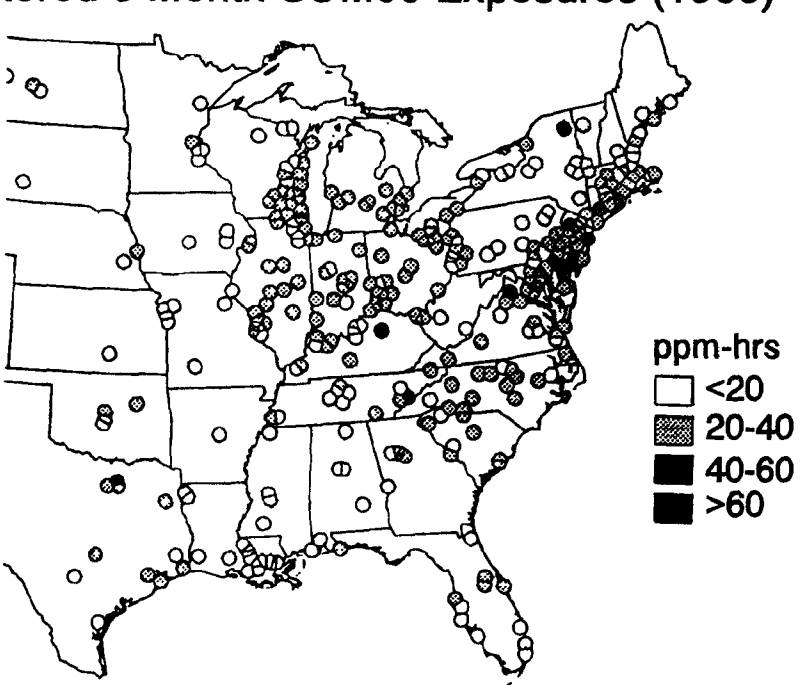


Figure 5-31. A) 1988 ozone monitoring site locations and calculated 3-mo SUM06 at each site. B) 1989 ozone monitoring site locations and 3 mo SUM06 at each site. All sites regardless of landscape designation included.

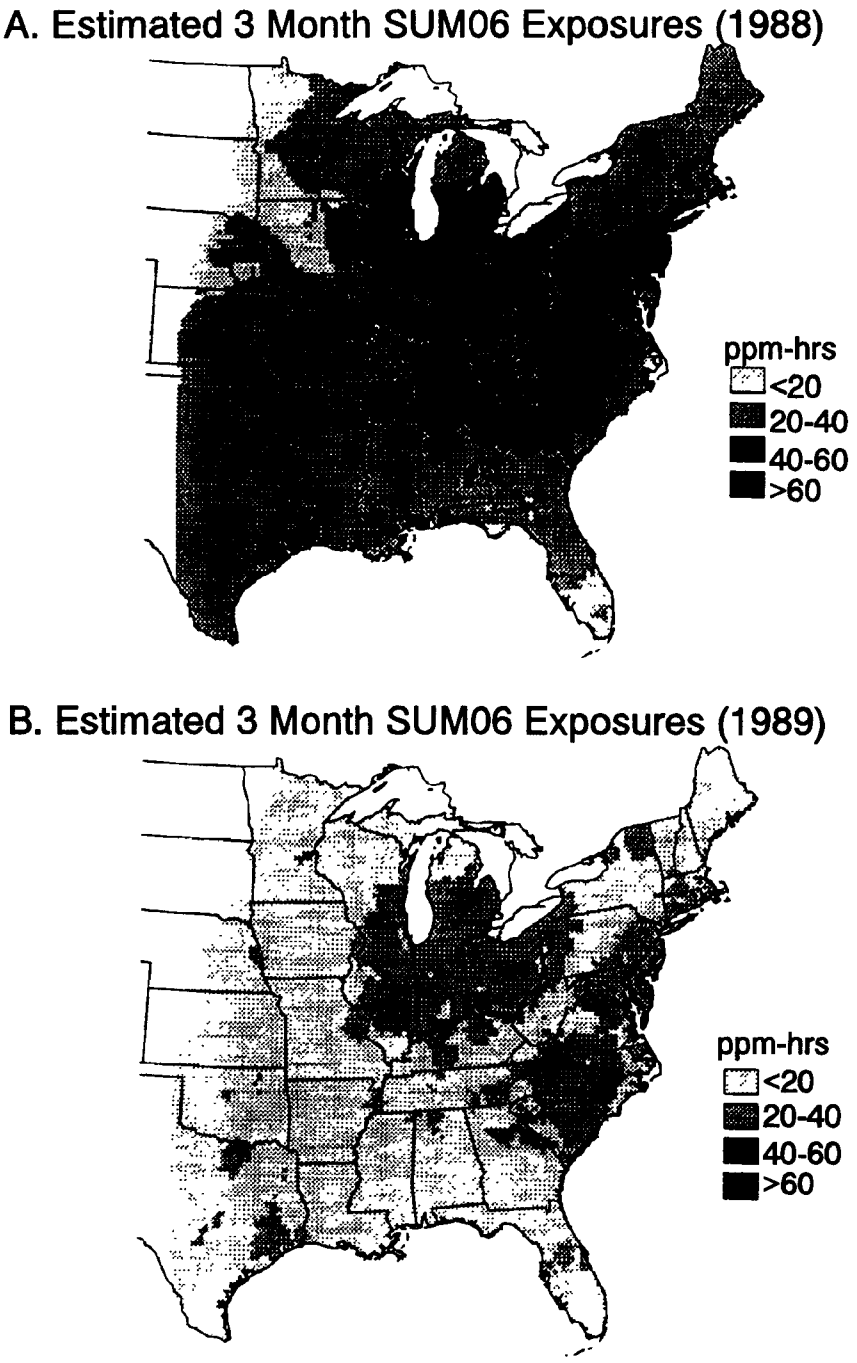


Figure 5-32. Estimated ozone exposure across the eastern half of the United States for 1988 (A) and 1989 (B). SUM06 exposure values based on actual monitoring regions based on the regression relationship with the exposure potential surface.

Source: Herstrom et al. (1993).

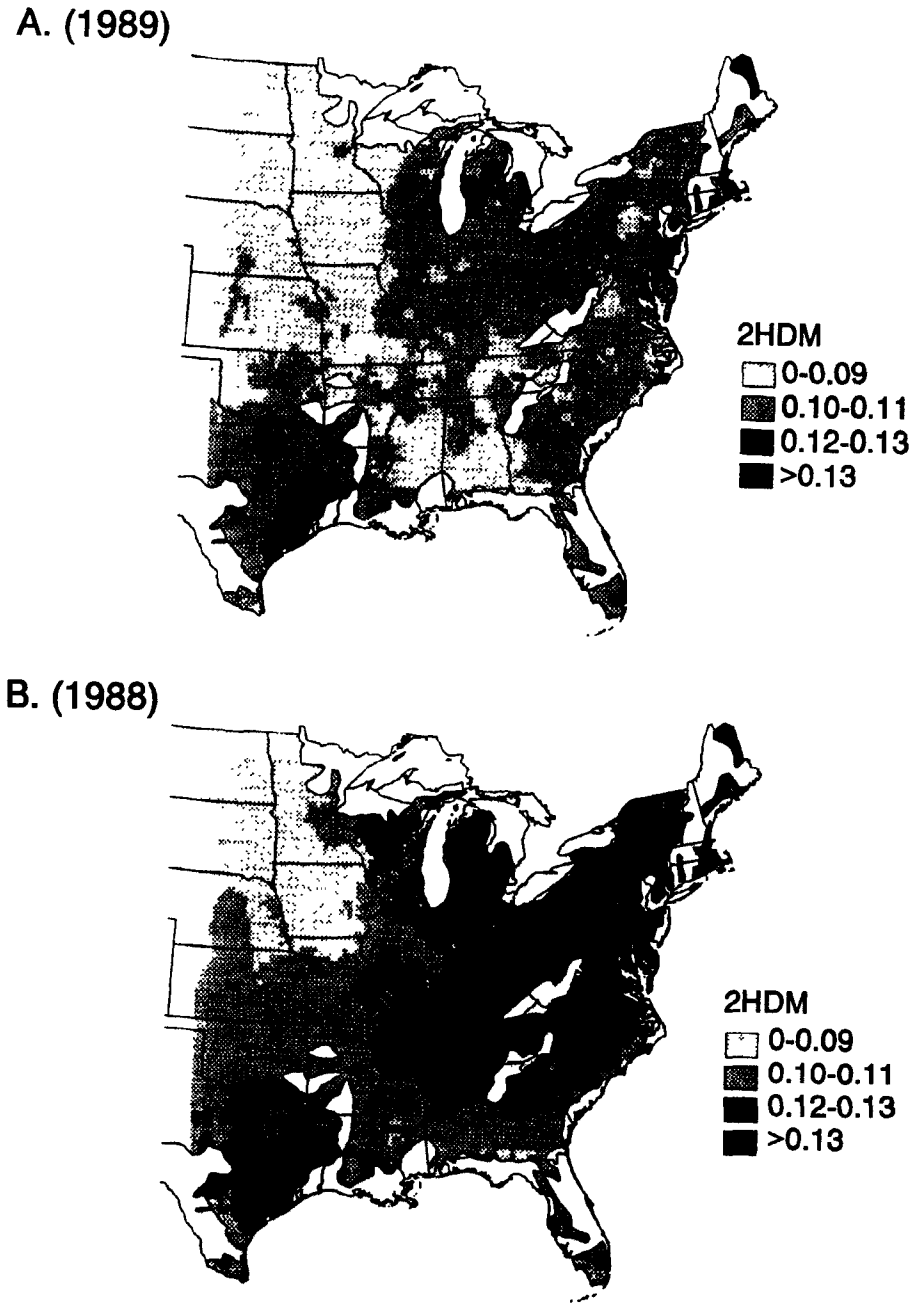


Figure 5-33. Second highest daily maximum (2HDM) for 1989 (A) and 1988 (B) estimated across crop growing regions in the eastern half of the country. 2HDM interpolated across non-monitored regions based on the regression relationship with an exposure potential surface and monitored sties for those years.

Source: Herstrom et al. (1993).

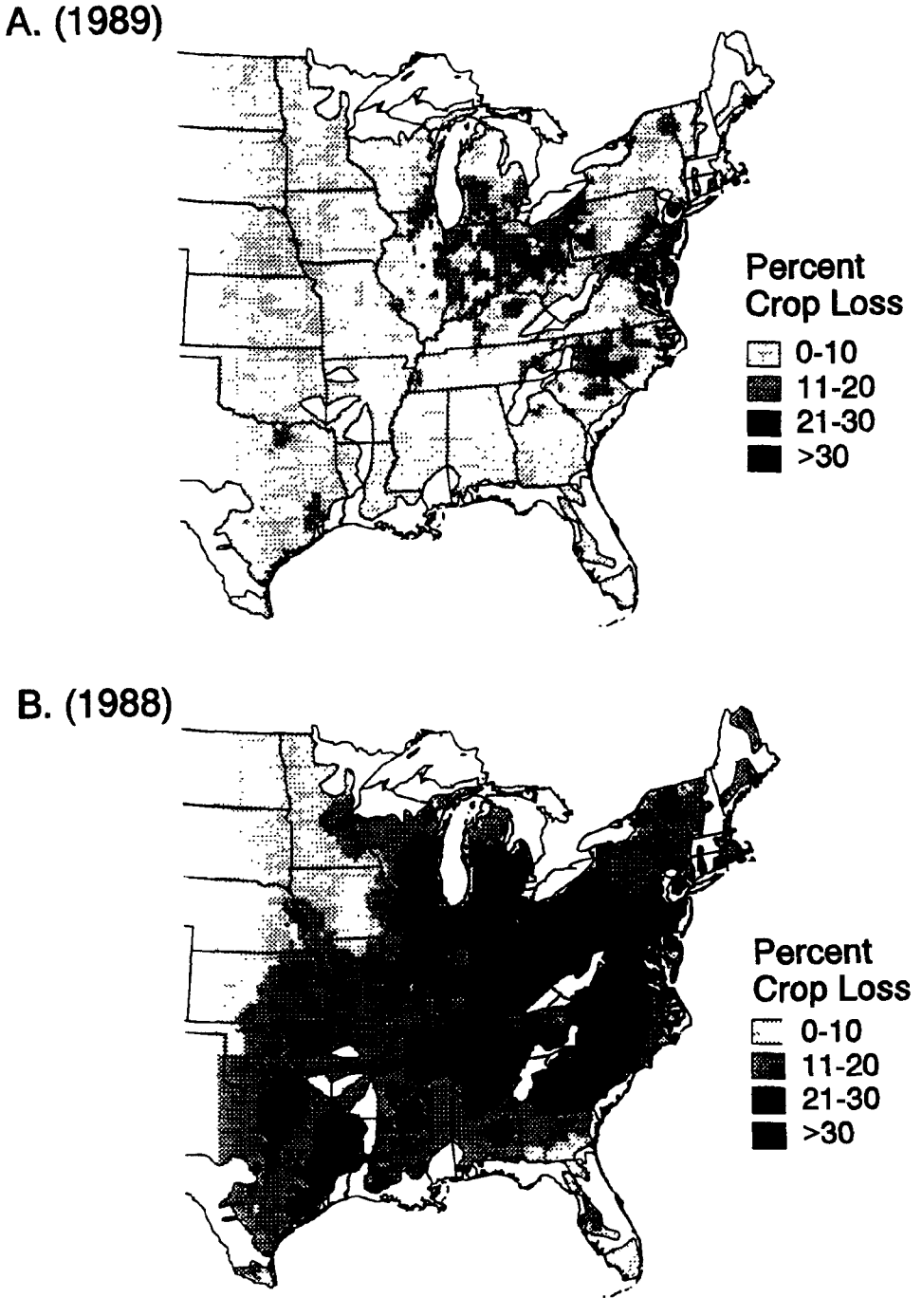


Figure 5-34. Estimated relative yield loss (ERYL) for all crops from NCLAN database across crop growing regions of the eastern half of the United States in 1989 (A) and 1988 (B). Estimated relative yeild loss calculated for each 20 km cell based on estimated ozone exposure value (3-mo SUM06) and Weibull parameters for all species' response function.

Source: Tingey et al. (1991).

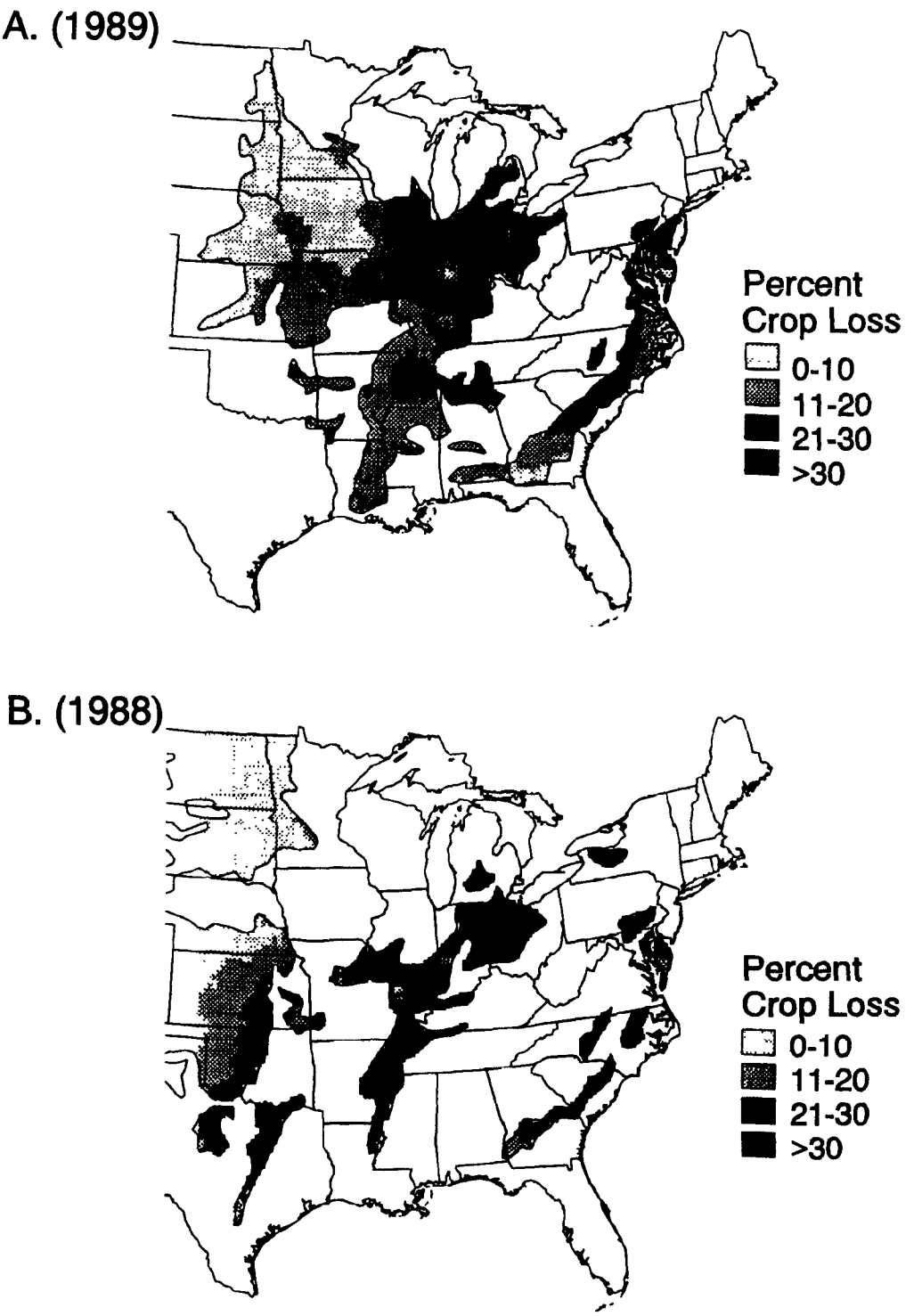


Figure 5-35. Estimated relative yield loss (ERYL) in 1988 for soybean (A) and wheat from NCLAN database across crop growing regions of the eastern half of the United States in 1989 (A) and 1988 (B). Estimated relative yield loss calculated for each 20 km cell based on estimated ozone exposure value (3-mo SUM06) and Weibull parameters for all species response function.

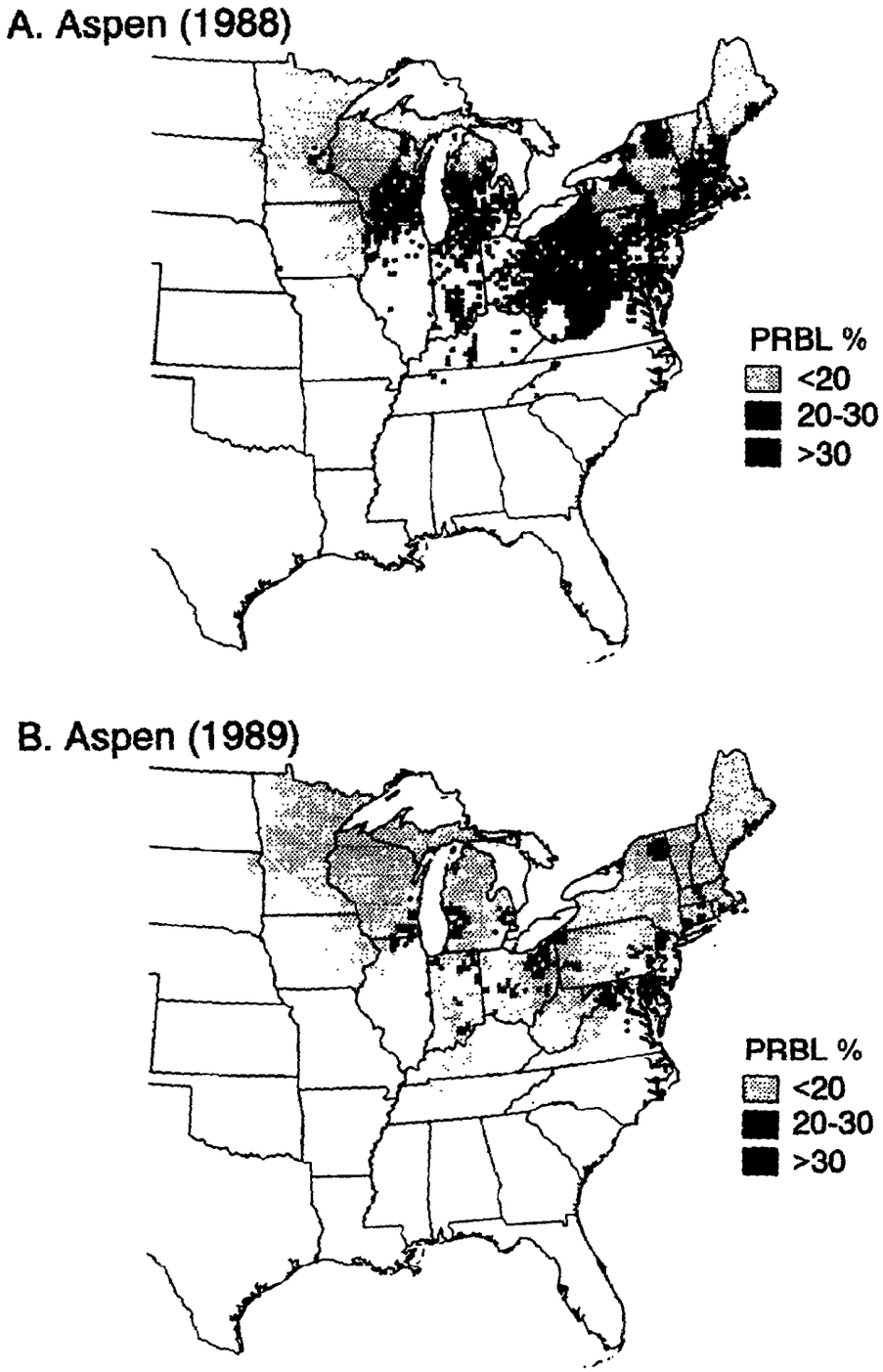


Figure 5-36. Variation in biomass reduction with year-to-year exposure variation. Aspen biomass reduction in 1988 (A) and 1989 (B) estimated exposures. Probable reduction in biomass caluculated for each 20 km cell based on estimated ozone exposure value (3-mo SUM06) and Weibull parameters for each species response function.

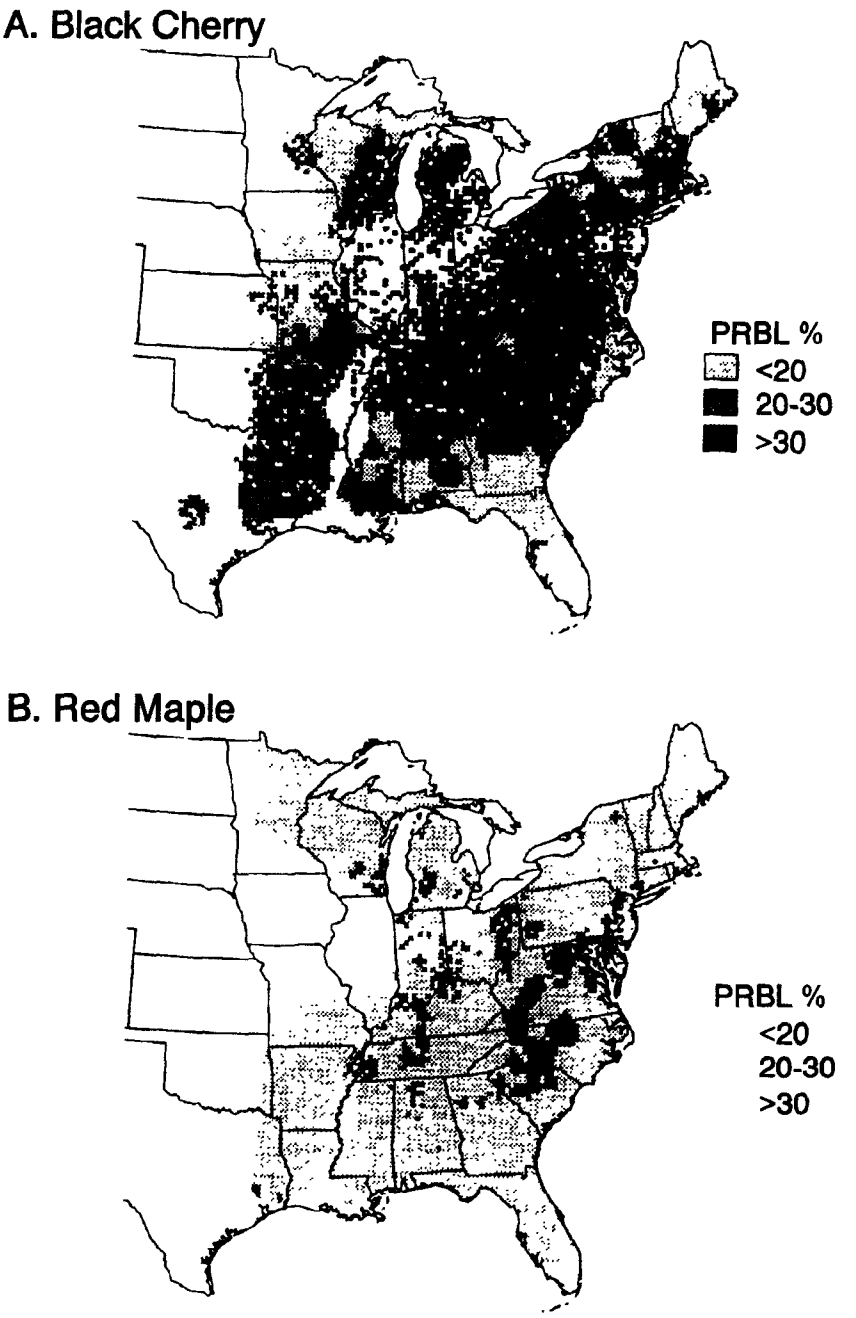


Figure 5-37. Estimated biomass reduction (EBR) for black cherry (A) and red maple (B) with 1988 ozone exposure. Estimated biomass reduction calculated for each 20 km cell based on estimated ozone exposure value (3-mo SUM06) and Weibull parameters for each species response function. Note the different scales for the two species. The EBR ranges from <20 to >30% in black cherry, but red in maple, EBR is <2 to >4% over its entire range.

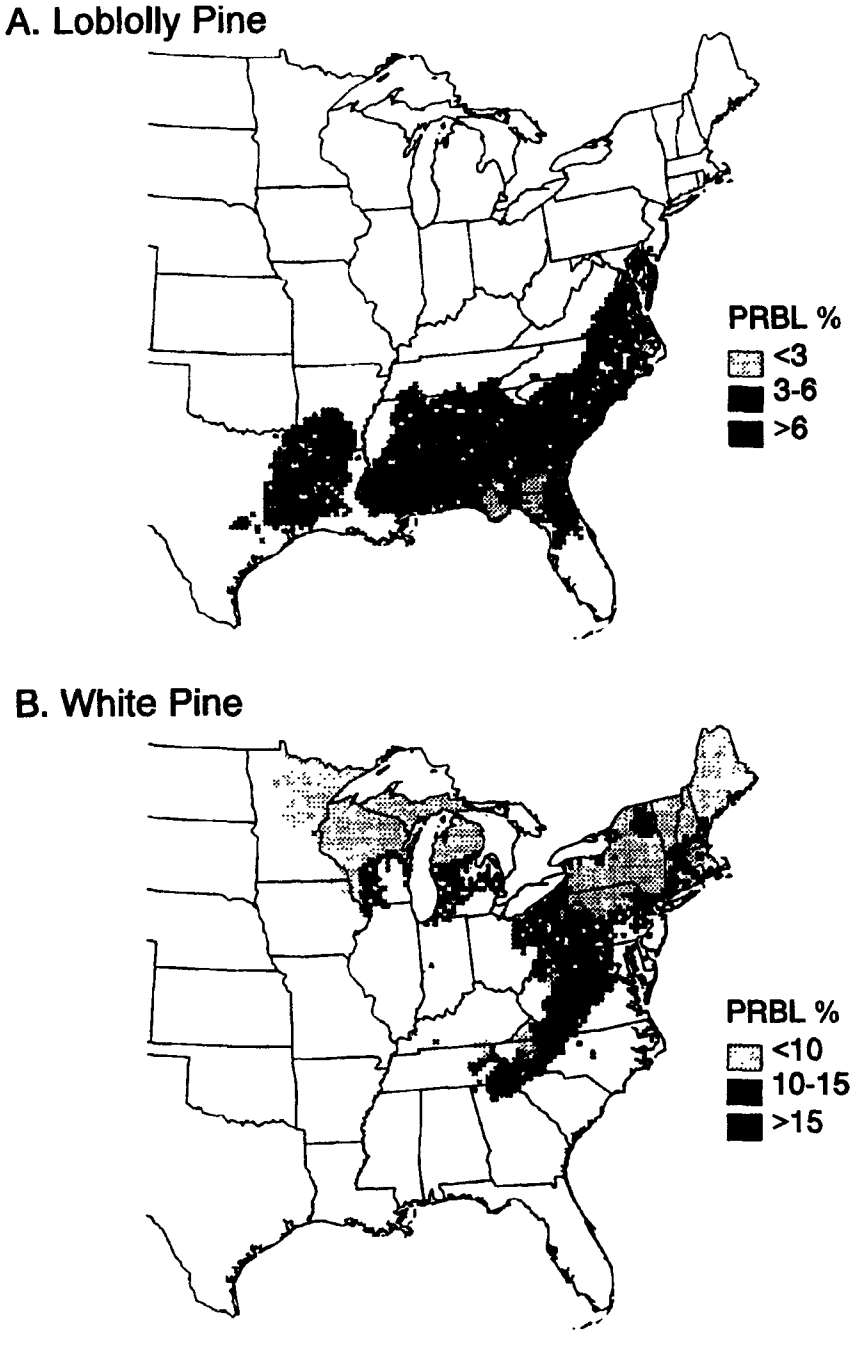


Figure 5-38. Estimated relative biomass reduction (ERBR) for loblolly pine (A) and eastern white pine (B) with 1988 ozone exposure. Estimated relative biomass reduction calculated for each 20 km cell based on estimated ozone exposure value (3-mo SUM06) and Weibull parameters for each species response function. Note the scale difference for the two species. Loblolly pine ranges from <3 to >6% ERBR, and eastern white pine range from <10 to >15%.

of a species is shown in Figure 5-36, using wild populations of trembling aspen seedling estimated total biomass reduction. Species-dependent variation in response to O_3 is illustrated in Figure 5-37. A vast difference in exposure-response is observed between two species that occupy the same area geographically, black cherry and red maple. Red maple, even in the high O_3 year of 1988, is relatively insensitive compared to black cherry. Red maple shows less than 2% reduction in growth across its range, whereas black cherry shows a large portion of its range experiencing greater than 30% annual biomass reduction. Pine species of the eastern U.S. also exhibit a difference in response to O_3. Loblolly pine and eastern white pine are shown in Figure 5-38 for 1988. Only a small portion of the range of loblolly pine is estimated to have greater than 2% reduction in total biomass, and eastern white pine is estimated to have total biomass reduction greater than 10% over more than half of its range.

The range of estimated yield reduction for each of the crop species (Figure 5-39) and the estimated annual total biomass reduction for each of the tree seedling species (Figure 5-40) across all the area (10th to 90th percentile) is variable depending on the species and year. Corn is the least, ranging from 1 to 20%, and wheat has the widest range from 2 to 80% yield reduction. The median (50% of the range) estimated yield reduction across all crop growing areas is 18.9% in 1988 and only 3.1 % in 1989 illustrating the year-to-year variation in response. The median for the four species indicates corn to be less sensitive and wheat to be the most sensitive, based on area-weighted estimated yield reduction across the area where the species are grown.

Tree species show a similar range of responses across their ranges. A relatively small range in response is estimated across all the area of loblolly pine (4 to 7%) compared to sugar maple (0 to 50%) (Figure 5-40). The median (50% of the range) annual biomass reduction across all species range from 0% in Virginia pine and red maple to 33% in the sensitive aspen clone. Based on the median value for each species, the relative sensitivity of seedlings based on area-weighted annual biomass reduction in relation to estimated 1988 exposures are: (1) Sensitive: Aspen and black cherry with annual growth reductions of 14 to 33%; (2) Moderately Sensitive: tulip poplar, loblolly pine, eastern white pine, and sugar maple having reductions of 5 to 13%; and (3) Insensitive: Virginia pine and red maple

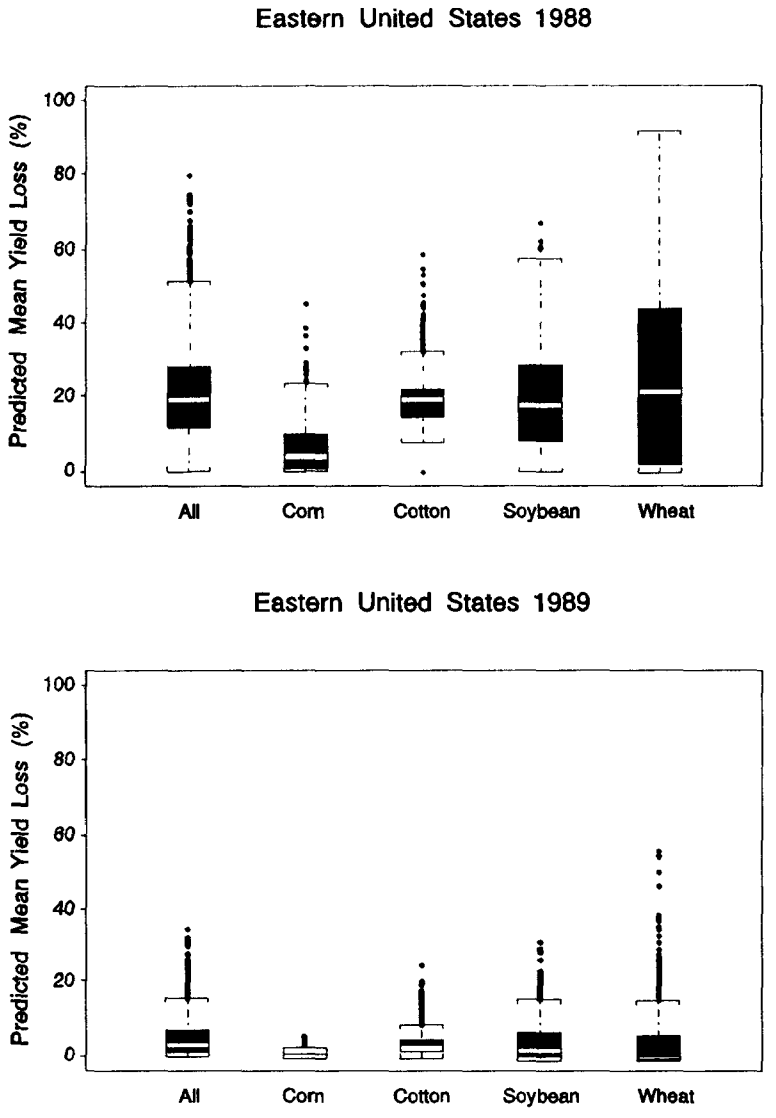


Figure 5-39. Box-plots of annual area-weighted yield reduction for the four major agronomic crop species and all crops from NCLAN with estimated 1988 (A) and 1989 (B) ozone exposure. The estimated yield reduction is taken from each 20 km cell in the species' distribution, weighted for area and the distribution plotted showing 10th (bracket), 25th (lower shaded box), 50th (clear bar in shaded box), 75th (upper shaded box), and 90th (bracket) percentile. The single values outside these percentiles are also plotted (closed circles). The percentiles represent the area of the species exhibiting that level or less of yield reduction.

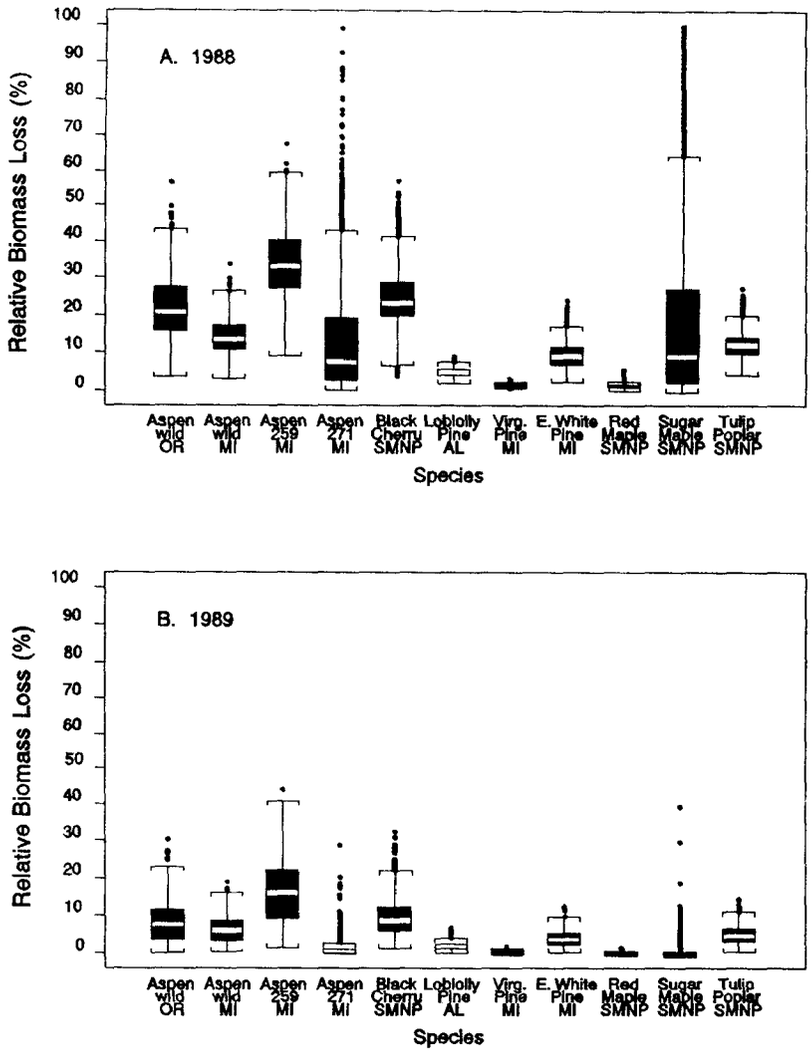


Figure 5-40. Box-plots of annual area-weighted biomass reduction for the eight tree species with estimated 1988 (A) and 1989 (B) ozone exposure. The estimated biomass reduction is taken from each 20 km cell in the species' distribution, weighted for area and the distribution plotted showing 10th (bracket), 25th (lower shaded box), 50th (clear bar in shaded box), 75th (upper shaded box), and 90th (bracket) percentile. The single values outside these percentiles are also plotted (closed circles). The percentiles represent the area of the species exhibiting that level or less of biomass reduction. OR = Oregon site, MI = Michigan site, SMNP = Smoky Mountain National Park, AL = Alabama.

having losses of 0 to 1% per year. The biomass losses for 1989 are significantly less (Hogsett et al., 1994).

There are uncertainties attached to these estimates, including: (1) the estimations of O_3 exposure in non-monitored areas; (2) the exposure-response functions for each species; (3) the climate and meteorological data; and (4) the accuracy of species distribution and the lack of any species density data. This listing is a rough order of significance, although it would be difficult to distinguish between the first two. In addition to the variation about the exposure-response function itself, there is the critical issue of the response function being developed from seedlings and under optimal growing conditions. As such they probably do not reflect mature tree response, and certainly do not reflect the response of species within an ecosystem context. But the estimated biomass loss is a potential risk that species may experience at least for seedling establishment, reforestation or natural regeneration. Again, the interactions that define a community response or an ecosystem response are not included in these spatial estimates.

5.9.11 What Is the Effect of Ozone on Ecosystems?

Most of the information dealing with the responses of ecosystems to O_3 stress is based on the study of the San Bernardino Forest ecosystem.

The mixed conifer forest ecosystem in the San Bernardino Mountains of southern California is one of the most thoroughly studied ecosystems in the United States. Chronic O_3 exposures over a period of 50 or more years produced major changes in the San Bernardino National Forest ecosystem. The primary effect was on the more susceptible members of the forest community, individuals of ponderosa and Jeffrey pine, in that they were no longer able to compete effectively for essential nutrients, water, light and space. As a consequence of altered competitive conditions in the community, there was a decline in the sensitive species, permitting the enhanced growth of more tolerant species (Miller et al., 1982; U.S. Environmental Protection Agency, 1978, 1986). The results of the studies of the San Bernardino Forest ecosystem were reported in both the 1978 and 1986 criteria documents (U.S Environmental Protection Agency, 1978, 1986).

Ecosystem responses to stress are hierarchical. They begin with the response of the most sensitive individuals of a population. Therefore, the response of an ecosystem to O_3 is

determined by how the responses of its most sensitive individuals affect the population. Foliar injury is usually the first visible indication of O_3 exposure. Stresses, the primary effects of which occur at the molecular level of the individual, must be propagated progressively up through more integrated levels of organ physiology (e.g., leaf, branch, root) to whole plant physiology, to stand dynamics, and then to the landscape level to produce ecosystem effects (Hinckley et al., 1992). This is particularly true if the stress is of low-level because only a small fraction of stresses at the molecular level become disturbances at tree, stand, or landscape level. Insect defoliation, for example, may severely reduce the growth of one or several branches while growth of the tree appears not to be affected (Hinckley et al., 1993). The time required for a stress to be propagated from one level to the next determines how soon the effects of the stress can be observed or measured. Therefore, to understand the effects of a stress, one must utilize a framework of hierarchical scales (Figure 5-24; Section 5.7) such as that developed to provide a means for following and understanding the effects of the eruption of St. Helens on forest trees (Hinckley et al., 1992).

The effect a stress at one hierarchial level will have on a higher level are determined by variability and compensation. Variability in response to stress may mean that, because of genetic variation, not all trees are equally susceptible as was observed not only in the case of the sensitive ponderosa and Jeffrey pine in the San Bernardino Forest but also was true of the eastern white pine in the Appalachian Mountains. In both instances, trees were designated sensitive, intermediate and tolerant. At the stand level, the slower growth of some trees may be compensated for by the relatively faster growth of others that are experiencing reduced competition so that the overall growth of the stand is not affected (Hinkley et al., 1992). These properties, when taken together, will determine the extent and rate at which stress at one hierarchical level will impact the next highest level. The stand level was affected in the San Bernardino Forest but was not apparent in the Appalachian Mountains. Figure 5-24 (Section 5.7), therefore, is also applicable for considering the effects of O_3 on forest stands and can be used to help explain the difference between the response of the San Bernardino Forest ecosystem and the forest ecosystems in the eastern United States. As pointed out above, variability and compensation determine the severity of the response of the individual and the length of time required for it to be expressed structurally and functionally.

Variability and compensation can also occur at the population level, all populations do not respond equally but are influenced by the number of sensitive individuals (Taylor and Pitelka, 1992). Plant populations can respond in four different ways: (1) no response, the individuals are resistant to the stress; (2) mortality of all individuals and local extinction of the extremely sensitive population—the most severe response; (3) physiological accommodation, growth, and reproductive success of unaffected individuals because the stress is accommodated physiologically; and (4) differential response, members of the population respond differentially with some individuals exhibiting better growth and reproductive success due to genetically determined traits (Taylor and Pitelka, 1992). Differential response results in the progressive elimination over several generations of the sensitive individuals and a shift in the genetic structure of the population toward greater resistance (microevolution). Physiological accommodation or microevolution, with only the latter affecting biodiversity, are the most likely responses for exposure to chronic stress (i.e., stresses that are of intermediate-to-low intensity and of prolonged duration). The primary effect of O_3 on the more susceptible members of the plant community is that the plants can no longer compete effectively for essential nutrients, water, light, and space and are eliminated. The extent of change that can occur in a community depends on the condition and type of community, as well as the exposure (Garner, 1993). Forest stands differ greatly in age, species composition, stability, and capacity to recover from disturbance. For this reason, data dealing with the responses of one forest type may not be applicable to another forest type (Kozlowski, 1980).

The factors explaining ecosystem responses at both the individual species and population level discussed above can be used to explain why the San Bernardino Forest ecosystem has suffered more severe injury than ecosystems such as those in the Appalachian Mountains and in other parts of the United States. Changes in ecosystems begin with the death of individual plants. Major changes in the San Bernardino ecosystem began with injury to ponderosa and Jeffrey pine. Ecosystem responses, therefore, began with the biochemical changes in the leaves of sensitive individuals and were transferred ultimately to the whole ecosystem. Individuals of ponderosa pine were most sensitive to O_3 exposure, with Jeffrey pine, white fir, black oak, incense cedar, and sugar pine following in decreasing order. Foliar injury on sensitive ponderosa and Jeffrey pine was observed when

24-h-average O_3 concentrations were 0.05 to 0.06 ppm (Miller et al., 1982). Structural changes within ecosystems are the result of functional changes that began within the individuals and were propagated to populations and to the community and then to the ecosystem (e.g., altering of nutrient cycling Miller et al., 1982). Biochemical changes within the trees resulting from O_3 exposure that were not repaired or compensated for were expressed as: (1) visible foliar injury; (2) premature needle senescence; (3) reduced photosynthesis; (4) reduced carbohydrate production and allocation; (5) reduced plant vigor; and (6) reduced growth or reproduction or both (Miller et al., 1982). These changes at the individual plant level lead to reduced root growth, and reduced yields of fruits and seeds or both, and change in competitive ability or reduced plant vigor. Subsequently, they were manifested as changes in plant populations and communities and ultimately ecosystems.

In addition, the functional changes lead not only to injury to or changes in the functioning of other living ecosystem components, either directly or indirectly, by altering the processes of carbon (energy) flow and mineral nutrient cycling, water movement and changed vegetational community patterns (Miller et al., 1982). Change in decomposition patterns, the result of early leaf senescence and changed successional patterns of leaf microflora, altered nutrient cycling. Carbon and mineral nutrients accumulated in the heavy and thick needle layers. Biotic interactions associated with predators (insect pests), pathogens (fungi), and symbionts (mycorrhizae) were altered by loss of tree vigor. In stands with a high proportion of O_3-injured trees, a given population of western pine beetles could, therefore, kill more trees. The root rot fungus (*Heterobasidium annosum*) increased more rapidly because freshly cut stumps of weakened trees were more vulnerable to attack (U.S. Environmental Protection Agency, 1976, 1986). The continuum of changes (Table 5-31; Section 5.7) beginning with injury to the individual trees resulted finally in ecosystem breakdown. A shift in dominance from ponderosa and Jeffrey pine to O_3-tolerant shrub and oak species was observed.

In the San Bernardino Mountains of California, O_3 concentrations greater than 0.08 ppm for 1300 h, with concentrations rarely decreasing below 0.05 ppm at night near the crest of the mountain slopes, have been observed over a period of 10 to 20 years.

Injury to sensitive vegetation in California continues to occur. To date, such injury has not resulted in as extensive ecosystem change.

Ozone-induced injury to vegetation has also been observed on the Cumberland Plateau in the eastern United States. In a study of 25-year old white pine, a reduction of 70% was observed over a 17-year period, when annual growth in diameter of sensitive trees was compared with that of intermediate and tolerant trees (McLauglin, 1982). Maximum 1-h O_3 concentrations ranged from 0.12 to 0.3 ppm for the years 1975 through 1979. Decline in vigor and reduced growth was associated with premature senescence, a loss of older needles and a reduction in photosynthesis.

In the Appalachian Mountains, monthly 8-h average O_3 concentrations ranging from 0.35 to 0.65 ppm with peak hourly concentrations from 0.08 to 0.13 ppm caused foliar injury, growth reductions and death of sensitive eastern white pine and growth reductions of other indigenous forest tree species.

Despite the injury to the sensitive eastern white pine which resulted in a decline in vigor and growth, the injury was apparently not severe enough to be propagated to the stand or ecosystem levels, except for possibly on Mt. Mitchell, NC. On Mt. Mitchell the death of Fraser fir and red spruce have also been attributed to the balsam wooly adelgid. Therefore, the extensive injury observed in the San Bernardino Mountains has not been observed in the Appalachian Mountains.

Preliminary studies suggest that a nitrogen deposition gradient coincident with the O_3 gradient in the San Bernardino Mountains may play an important interactive role in forest tree response.

The fact that changes in carbohydrate allocation from the leaves to the roots in the ponderosa, Jeffrey and eastern white pine can alter the process wherein fungi and plant roots form an important symbiotic relationship (mycorrhizae) has been mentioned. These relationships between plant roots and fungi are critical for both. Fungi take up minerals (e.g., nitrogen) and make it available to plants for their use. Plants, on the other hand, through their roots supply the fungi with energy (sugars) for their growth. Without the nutrients, particularly nitrogen which is critical in the process of photosynthesis, trees are more vulnerable to abiotic stresses such as resulting from O_3 exposure and to insect pests and pathogens.

5.9.12 Economic Assessments

Based on economic assessments and scientific data available at the time, the previous criteria document (U.S. Environmental Protection Agency, 1986) concluded that O_3 at ambient levels was imposing economic costs on society. The review of more recent (post-1986) literature on agriculture corroborates that earlier conclusion. Specifically, the recent literature, using the full set of NCLAN data and addressing some deficiencies in the pre-1986 assessments, confirms the finding of economic losses from ambient O_3 concentrations.

The exact level of these economic effects is a function of cropping patterns, O_3 concentrations (both ambient and episodic), and the spatial and temporal characteristics of projected or observed O_3 levels. The current economic assessments represent improvements in the scientific understanding of O_3 effects on agriculture. However, the assessments of economic effects initially incident on the agricultural sector remains incomplete.

Only a few assessments consider the economic effects of O_3 on forest trees as well as urban trees, shrubs, and ornamentals. These studies assess the economic effects of hypothetical changes resulting from O_3 or other stressors on forest productivity and aesthetics and are best viewed as measures of the potential effect of O_3 on these receptors. Improvements linking O_3 effects data to productivity and aesthetic effects will improve the utility of such economic analyses.

The effects of O_3 on ecosystems have not been addressed in the published literature. There is, however, an emerging interest in applying economic concepts and methods to the management of ecosystems. Ecological research is also addressing the challenging conceptual and practical issues in understanding and managing ecosystem functions. Economic research continues to develop, refine, and apply techniques for valuing market and nonmarket products and services that will be of help in estimating the economic effects of O_3 on ecosystems. Increased dialogue between the disciplines is needed before empirical analyses of the economic consequences of ecosystem management are feasible.

In summary, the state of science concerning O_3 economic effects on agricultural crops is sufficient to conclude that O_3 imposes costs on society.

5.10 EFFECTS OF OZONE ON MATERIALS

5.10.1 Introduction

Photochemical oxidants are capable of reacting with a number of man-made and natural materials. Nearly all materials damage research on photochemical oxidants has focused on economically important or abundant materials that are susceptible to oxidant damage. These include elastomers (natural rubber and certain synthetic polymers), textile fibers and dyes, and, to a lesser extent, paints. Recent research has been conducted on culturally important materials, such as artists' paints and pigments. It has been shown that oxidants harden and embrittle elastomers, causing cracking and a loss in physical integrity. Oxidant exposure weakens certain textile fibers (i.e., reduces the breaking strength and increases the rate of wear) and changes the color of some dyes. The effects of oxidants on paints are not defined well, but they may be similar to some of the effects on elastomers; damage from other gaseous pollutants, such as sulfur dioxide and from natural damaging agents such as sunlight, moisture, oxygen, and temperature fluctuations tend to overshadow the role of ambient O_3 in causing paint damage.

The literature selected for review in this section includes research previously reported in the 1978 and 1986 criteria documents (U.S. Environmental Protection Agency, 1978, 1986) and a limited number of other references published before and after 1986. Because little recent work has been reported on the effects on materials, reference to older studies is necessary for unity and coherence. This assessment of the effects on materials includes a review of the mechanisms of damage and protection; it also presents dose-response information from laboratory and field studies and evaluates previously reported economic assessments.

5.10.2 Mechanisms of Ozone Attack and Antiozonant Protection

5.10.2.1 Elastomers

Most elastomeric materials found in the marketplace are composed of unsaturated, long-chain organic molecules. That is, the molecules contain carbon-carbon double bonds. Natural rubber and synthetic polymers/copolymers of butadiene, isoprene, and styrene account for the bulk of elastomer production for products such as automobile tires (Mueller and Stickney, 1970). These types of compounds are particularly susceptible to O_3 attack.

In contrast, synthetic elastomers with saturated chemical structures, such as butyl rubber, polymers of silicones, ethylene, propylene, hypalon, and polyurethanes, have an inherent resistance to O_3 damage, but higher cost and limiting physical and chemical properties have constrained their use in outdoor environments.

Ozone is thought to attack elastomers by adding a chain of three oxygen atoms directly across the double bond, forming a five-membered ring structure (Mueller and Stickney, 1970). This structure quickly rearranges (via Criegee ozonolysis) to form a zwitterion and an aldehyde (see Figure 5-41). The aldehyde/zwitterion pair can be formed on either side of the point of chain scission. Subsequent reactions of the zwitterion lead to a permanently oxidized elastomer. Ozone damage in the form of cracking is a surface phenomenon. It is greatly accelerated by mechanical stress, which produces fresh surface area at crack boundaries. At very high concentrations and high mechanical stress, O_3 damage can result in a large number of surface microcracks that produce a frosted appearance and mechanical weakening (Crabtree and Malm, 1956). At pollutant concentrations normally encountered outdoors (and in many indoor environments), the elastomer hardens or becomes brittle and cracked, which results in a loss of physical integrity.

According to Fisher (1957), work at the Rock Island Arsenal by R. F. Shaw, Z. T. Ossefa and W. J. Tonkey in 1954 led to the development of effective antioxidant additives to protect elastomers from O_3 degradation. Subsequently, antiozonants were generally incorporated into elastomeric formulations during mixing, and their protection was effective even when elastomers were stretched or flexed (Fisher, 1957; Mueller and Stickney, 1970).

Several theories (Andries and Diem, 1974) have been advanced to explain the mechanism of antiozonant protection. The two best supported theories are the scavenger theory and the protective film theory. The scavenger theory suggests that the antiozonant diffuses to the surface, where it reacts with the O_3 at a faster rate than with the carbon-carbon double bonds of the rubber, thereby protecting the rubber sacrificially. The protective film theory also includes diffusion to the surface, but assumes that the resulting layer is less reactive with O_3 than is the rubber and thus constitutes a protective layer.

The work of Razumovskii and Batashova (1970) on the mechanism of protective action by the antiozonant N-phenyl-N'-isopropyl-*p*-phenylenediamine (PIPP) is most consistent with

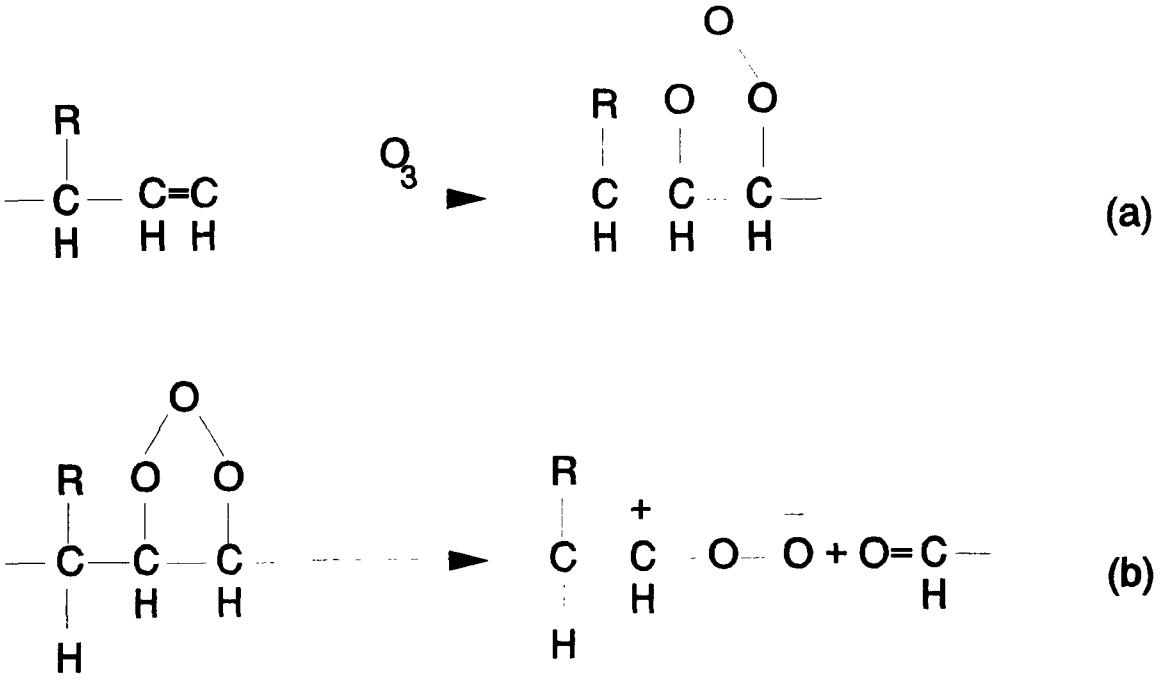


Figure 5-41. Postulated mechanism for damage to elastomers by ozone.

Source: Mueller and Stickney (1970).

the scavenger mechanism. These investigators showed that O_3 reacts preferentially with PIPP at a ratio of three O_3 molecules per one PIPP molecule.

Andries et al. (1979), using carbon-black-loaded natural rubber (NR) compounds with and without antiozonants, attempted to distinguish among possible mechanisms with attenuated total reflectance spectroscopy and scanning electron microscopy. Their experiments indicated that a combination of the scavenger and protective film mechanisms best explains antiozonant protection. Examination of the surface of the rubber samples with antiozonant showed that only ozonized antioxidant and not ozonized rubber was present. This layer of ozonized antioxidant functioned as a relatively nonreactive film over the surface, preventing the O_3 from reaching and reacting with the rubber below.

Lattimer et al. (1984) conducted a series of experiments on cross-linked rubber (*cis*-polyisoprene and *cis*-polybutadiene) containing N,N'-di-(1-methylheptyl)-*p*-phenylenediamine antiozonant. They concluded that while a number of O_3-rubber reactions and mechanisms are possible, these reactions do not become significant until the antiozonant

is nearly completely consumed (i.e., the antiozonant preferentially reacts with the O_3). They concluded that the "scavenger-protective film mechanism" is primarily responsible for antiozonant protection.

In addition to reactive antiozonants, paraffinic and microcrystalline waxes are used to protect the elastomers in rubber products such as tires. The wax migrates to the surface of the rubber and forms a barrier against O_3 attack. Dimauro et al. (1979) studied the ability of 18 waxes to protect rubber against degradation from O_3. Dimauro found that no wax by itself provided an optimal level of protection; blending with a reactive antiozonant was required. The paraffinic waxes protected best at lower exposure temperatures, and the microcrystalline waxes were more effective at higher temperatures. Wax blends, which combine the best effects of each type of wax, offered the best protection over a wide range of temperature (Lake and Mente, 1992). It was found, however, that wax alone can be detrimental to dynamic O_3 resistance. Wax can induce localized stresses in the rubber that can lead to premature rubber failure under dynamic testing conditions.

5.10.2.2 Textile Fibers and Dyes

Cellulose-based fibers, acrylic fibers, and nylon fibers are affected by O_3 (Zeronian et al., 1971); however, it is difficult to distinguish O_3-induced damage from oxidation by molecular oxygen. Reduction in breaking strength and an increased rate of wear are the types of damage most commonly observed. As stated by Bogaty et al. (1952), however, for most uses of textile fibers the action of O_3 is less important in affecting product lifetime than physical abrasion, biological degradation, soiling, fashion, and other factors. Furthermore, most textiles are used and spend most of their life indoors where O_3 concentrations are usually less than outdoor O_3 concentration (Yocom et al., 1986). Accordingly, the economic significance of O_3 damage to textile fibers is relatively low, and the differences in the mechanisms of attack are not important.

Many textile dyes react with O_3. Figure 5-42 illustrates the reaction of Disperse Blue #3 with O_3 and with nitrogen oxides (Haylock and Rush, 1976). Ozone attacked the quinoid portion of the molecule, completely rupturing the ring system chromophore and oxidizing the dye to phthalic acid, which is colorless. Matsui et al. (1988) investigated the reactions of O_3 with aromatic azo compounds. Ozone was found to attack both the aromatic

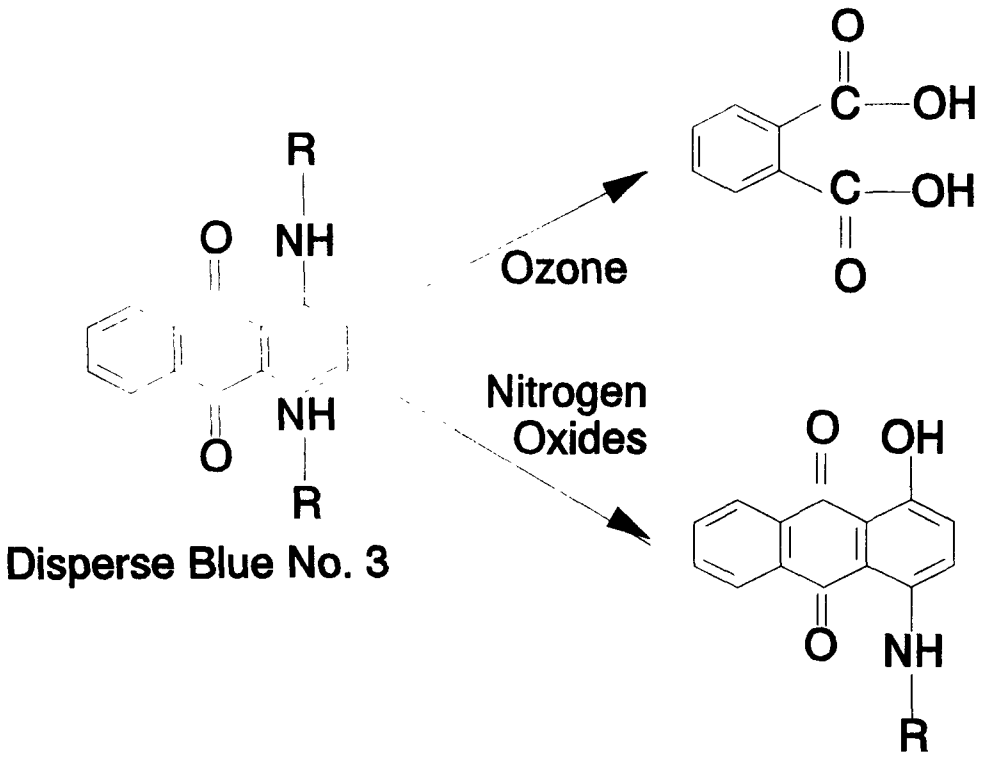


Figure 5-42. Reaction of anthraquinone dyes with ozone and with nitrogen oxides.

Source: Haylock and Rush (1976).

rings and the more electron-rich nitrogen atoms. Both the direct attack on the azo dye structure and the production of daughter products alter the original dye color.

The reactions between various dyestuffs and O_3 are influenced by the chemical nature of the fiber to which the dye is applied and the manner in which the dye is applied. Additional factors include the presence of protective agents; effects of temperature, air moisture, and other pollutants; and even the degree of strain of the base fiber caused by folding or creasing. In a study of O_3 fading of anthraquinone dyes on nylon, Haylock and Rush (1976, 1978) found that fiber properties such as cross-section shape, draw ratio, and the degree of steam heat setting had significant effects on the rate and severity of O_3 damage, even for chemically identical systems. Moore et al. (1984) found that the rate of O_3 fading of acid and disperse dyes on polyamide fibers appeared to be a function of rate of dye migration to the surface of the fibers. Thus using dyes that diffuse slowly (high molecular weight dyes) improved resistance to O_3 fading. Given this complexity and sensitivity for

both dye and fiber type, it is not possible to relate a specific mechanism of damage to a broad class of damage situations.

5.10.2.3 Paint

The mechanisms of architectural paint and coil coating damage caused by O_3 have not been well defined. Damage is probably related to oxidation of the organic binders that hold the pigment and form the protective seal over the surface. Damage is likely to be similar to that of elastomers; that is, embrittlement and cracking as the result of chain scission and cross-linking. The data available on O_3 damage to architectural paints, however, come primarily from studies of surface erosion caused by gaseous pollutants, and the suspected O_3 damage patterns (embrittlement and cracking) are not quantified. Because the polymeric structure of dried paint film is significantly different from that of an elastomer under elongation stress, direct comparisons should be made with great caution.

In a series of experiments (Shaver et al., 1983; Grosjean et al., 1987; Grosjean et al., 1988a,b; Grosjean et al., 1989) the direct attack of O_3 on artists' pigments and paints was investigated. Ozone was found to react with alizarin pigments, indigoes, curcumin and triphenylmethane colorants. The exact mechanism and site of the attack (e.g., carbon-carbon unsaturated bonds, aromatic rings, or carbon-nitrogen bonds) and subsequent reactions with the daughter products depended on the initial structure of the pigment. Often the products of these reactions were colorless or of a noticeably different color than the original pigments, resulting in fading or color changes.

5.10.3 Exposure-Response Data

Laboratory exposure-response studies are criticized for their reliance on artificial environments that do not contain all the critical variables encountered under ambient conditions. Scientists realize the limitations of laboratory tests; no model could simulate conditions identical to an ambient environment. Nevertheless, many laboratory tests have represented the outdoor environment to some extent, and the findings from these tests have been used in conjunction with field tests to estimate the nature and amount of damage to materials. Controlled field tests have the advantage of being carried out under real exposure

conditions, but, because of the highly variable nature of real exposure conditions, data interpretation is difficult.

5.10.3.1 Elastomer Cracking

Table 5-35 presents an overview of the available laboratory and field studies of the effects of O_3 on elastomers. Hofmann and Miller (1969) demonstrated correlations between laboratory tests and the actual service use of passenger vehicle tires in the Los Angeles area. Basically, three laboratory test methods were used: indoor and outdoor belt flex, indoor and outdoor wheel, and stress relaxation. They found that the behavior of rubber exposed to O_3 under laboratory conditions correlated well with the service behavior of tires in localities where atmospheric O_3 concentrations were high.

Bradley and Haagen-Smit (1951) evaluated a natural rubber (NR) formulation for susceptibility to O_3 cracking. Strips were strained approximately 100% by bending and then exposed in a small chamber to 20,000 ppm of O_3; these specimens cracked almost instantaneously and broke completely within 1 s. When these NR formulations were exposed to lower concentrations of O_3 (approximately 0.02 to 0.46 ppm) time periods of about 5 min to over an hour were required for cracks to develop.

Meyer and Sommer (1957) exposed thin polybutadiene specimens to constant load, ambient room air, and O_3. Specimens exposed in the summer to average O_3 concentrations of about 0.048 ppm broke after 150 to 250 h. In the fall, at average O_3 concentrations of 0.042 ppm, specimens failed after exposures of 400 to 500 h. In the winter, at average O_3 concentrations of 0.024 ppm, failures occurred between 500 and 700 h. These data show the strong dependence of breakage on O_3 dose over the average time of exposure at which failure occurred (average concentrations $\times$ time).

Edwards and Storey (1959) presented data demonstrating the O_3 resistance of two styrene-butadiene rubber (SBR) compounds (Polysar S and Polysar Krylene). Both compounds were exposed without and with different levels of antiozonant protection to 0.25 ± 0.05 ppm of O_3 at 120 °F (49 °C) under 100% strain (twice the original sample length). Without antiozonants, a linear relationship was found between O_3 dose (ppm·h) and cracking depth. Increasing the amount of antiozonants significantly reduced the rate of cracking for both rubber compounds in a dose-related manner.

TABLE 5-35. LABORATORY AND FIELD STUDIES ON EFFECTS OF OZONE ON ELASTOMERS

Conditions	Material/ Product	Pollutant	Concentration, ppm	Exposure	Environmental Variables	Dose, ppm-h	Effects	Comment	Reference
Laboratory/ field	Automotive tires	Ozone	0.25 to 0.5	NA	Tires under stress	—	Cracking of white side wall.	Purpose was to correlate lab and field tests. Exposure time, detailed pollutant measurements, and statistical analyses were not reported.	Hoffman and Miller (1969)
		Ambient air	0.04 (annual average)	>1 year	Los Angeles environment; actual service use	>350	Positive correlation between laboratory and ambient air tests.		
Laboratory	Vulcanized rubber strips	Ozone	0.02 to 0.46. 20,000	3 to 65 min	Physical stress	~0.02 to 0.03	Surface cracking.	Test was designed to establish dose/response curves on O_3-sensitive rubber for use an analytical method.	Bradley and Haagen-Smit (1951)
Field	Rubber tires and various polymers	Ambient air	0.023 to 0.048	150 to 700 h	Physical stress and ambient environment	9 to 20	Time of cracking	Cracking occurred over a broad range of values and was related to stress.	Meyer and Sommer (1957)
Laboratory	SBR: Plysar S Plysar Krylene with and without antiozonants	Ozone	0.25	19 to 51 h	120 °F, 100% strain	4.75 to 12 75	Percent antiozonant was related to cracking depth rate.	Demonstrated dose/response linear relationship for O_3 on unprotected rubber.	Edwards and Storey (1959)
Laboratory	White sidewall tire specimens	Ozone	0.05 to 0.5	250 to 1,000 h	10 and 20% strain	20 to 500	Mean cracking rates were determined for different stress and O_3 levels.	Detailed data not available to verify author's statement that 2 to .5 years of ambient conditions were required for O_3 cracks to penetrate cord depth.	Haynie et al. (1976)
Laboratory	Polyisoprene	Ozone	0 to 1.8	2 h	22 °C	Up to 3.6	Cracking, stress relaxation	Rate of attack rapid and proportional to O_3 concentration	Razumovskii et al. (1988)

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TABLE 5-35 (cont'd). LABORATORY AND FIELD STUDIES ON EFFECTS OF OZONE ON ELASTOMERS

Conditions	Material/ Product	Pollutant	Concentration, ppm	Exposure	Environmental Variables	Dose, ppm-h	Effects	Comment	Reference
Laboratory	Ten different NR, SBR, CR formulations with and without protection	Ozone	0.5	Up to 300 h	30 °C	Up to 50	Time to 10 to 20% relaxation	Both formulation and protection affected relaxation.	Ganslandt and Svensson (1980)
Laboratory	Natural rubber, epoxidised rubber, copolymers	Ozone	0.05 to 1,000	to 16 h	−20 to 70 °C, 10 to 100% strain	0 to 240	Time to first cracking	Temperature dependence of antiozonant protection.	Lake and Mente (1992)
Laboratory	Several NR/SBR blends with and without protection	Ozone	0.05 to 0 15	~3 to 16 h	Sunlight, humidity	~0.15 to 2.4	Interply adhesion affected at 0.05 ppm and above.	Both waxes and antiozonants needed for protection against sunlight plus O_3.	Davies (1979)
Laboratory	Tire cords (66 nylon; Dacron polyester; Kevlar aramid)	Ozone	0 to 1 5	0 to 48 h	UV light; heat (100 °C); RH (20 to 90%); NO_2	Up to 72	RFL adhesion loss occurred primarily during 6 h exposure to high RH and 0.2 ppm O_3.	Synergism between O_3 and RH; RFL deterioration occurred at surface.	Wenghoefer (1974)

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Haynie et al. (1976) conducted a chamber study to evaluate the effects of various pollutants, including O_3, on several materials. In one part of the study, white sidewall specimens from a top-quality, steel-belted radial tire were exposed (strained at 10 and 20%) for 250, 500, and 1,000 h to O_3 concentrations of 0.082 ppm (160 $\mu g/m^3$) and 0.5 ppm (1,000 $\mu g/m^3$). The O_3 level was found to be statistically significant in the rate of cracking of this rubber. However, cracking rates were not directly proportional to O_3 concentrations for these two levels. Using the mean cracking rate calculated after long-term (1,000 h) exposure to conditions representative of the primary air quality standard for O_3 and the annual average standard for nitrogen dioxide (NO_2), Haynie et al. (1976) concluded that it would take a minimum of 2.5 years for a crack to penetrate to the cord depth. For this particular premium tire, therefore, sidewall failure from O_3 damage does not appear to be the cause of reduced tire life. Tread wear, rather than sidewall failure, probably determines the life of a typical rubber tire.

Razumovskii et al. (1988) studied the decrease in stress (stress relaxation) of polyisoprene vulcanizates in an exposure chamber at 22 °C at five O_3 concentrations ranging from O_3 free to 3,450 $\mu g/m^3$ (1.76 ppm). Stress relaxation resulting from the growth of surface cracks caused irreversible changes in the dimension of the elastomer and decreased tensile strength. Figure 5-43 presents the rate of change of stress as a function of time for various O_3 concentrations. The rate of stress reduction was proportional to O_3 concentration, with virtually no change for the O_3-free samples and progressively more rapid relaxation as O_3 levels increased. Razumovskii et al. (1988) concluded that O_3 absorption, attack of the C=C bonds, cracking and resulting stress relaxation were fast processes for unprotected elastomers.

Ganslandt and Svensson (1980) tested 10 different mixtures of three rubber compounds, NR, SBR, and CR (a compound not defined by the authors), with the isoelastic force method. The O_3 protection afforded each rubber formulation is summarized in Table 5-36. The samples at 50% elongation were exposed to O_3 concentrations of 0.5 ppm at 30 °C. The time to 10 and 20% relaxation of the isoelastic force in the rubber test samples was used to gauge the O_3 resistance of the formulation. Compounds GL 2073 B, SS 202, and SS 200 C showed greatest resistance to the effects of O_3, and those formulations that were unprotected (GL 2073 D, SS 200 B, SS 202 A, SS 202) and the formulations protected only

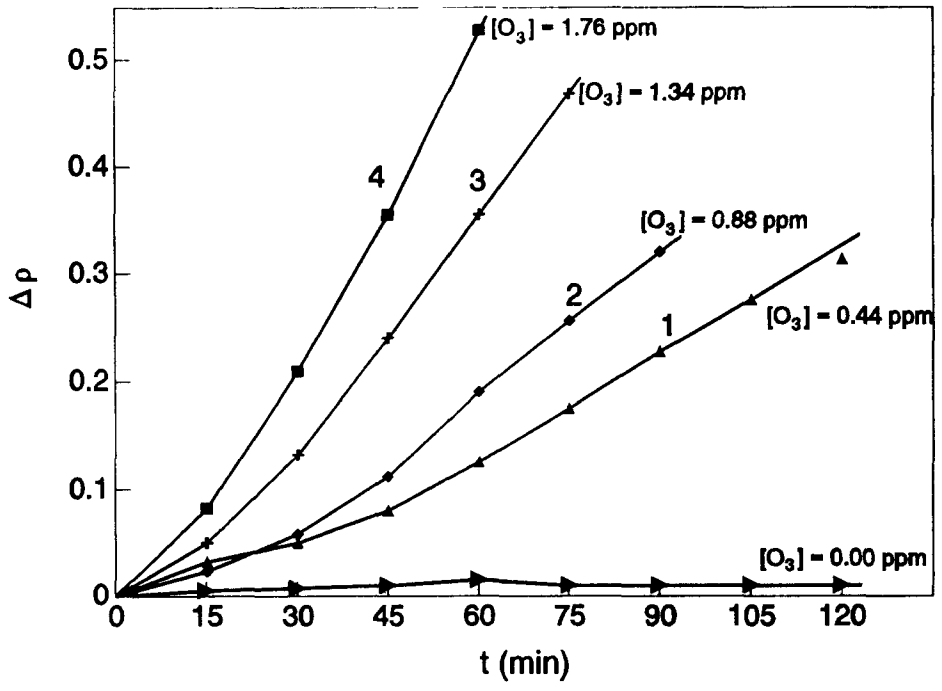


Figure 5-43. Relative decrease in stress with time as a function of ozone concentration for polyisoprene vulcanizate.

Source: Razumovskii et al. (1988).

TABLE 5-36. PROTECTION OF TESTED RUBBER MATERIALS

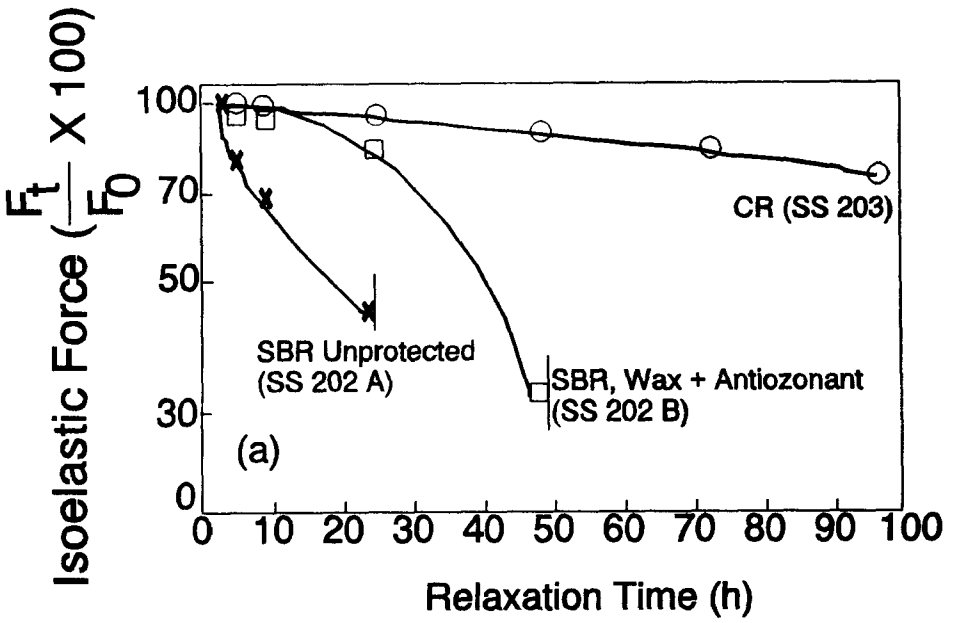
			Protected	
Rubber Formulation		Unprotected	Wax	Antiozonant
GL 2073	B, C		X	X
	G		X	
	D	X		
SS 200	A, C		X	X
	B	X		
SS 202	A	X		
	B		X	X
SS 203		X		

Source: Ganslandt and Svensson (1980).

by paraffin wax (GL 2073 G) demonstrated the least resistance to O_3 attack. The testing showed great variety in the kinds of visible cracking effects as a result of the exposure. The compounds with no protection often showed a large number of small cracks over the entire surface of the material, but those compounds protected by a combination of wax and antiozonant or by wax alone sometimes showed only a single crack, which grew rapidly. These effects are demonstrated in Figure 5-44. Compounds SS 202 B (Figure 5-44a) and SS 200 C (Figure 5-44b), both protected with wax and antiozonant, showed fairly good resistance when gauged by the 10 and 20% stress relaxation tests but failed after approximately 50 h and 58 h of exposure, respectively. On the other hand, compounds SS 203 and SS 200 B, both unprotected, exhibited small surface cracking and outlasted some of the protected compounds. Moreover, protection with wax and antiozonant may afford long-term protection, but when one crack appears, it can grow rapidly and cut off the test piece, as shown in Figure 5-44b.

Lake and Mente (1992) exposed natural rubber, epoxidised rubber and two acrylonitrile-butadiene copolymers with chemical antioxidants, waxes or a combination of antioxidants and waxes to a variety of O_3 concentrations and temperatures in environmental testing enclosures. Ozone concentrations ranged from 0.05 ppm to 1,000 ppm with temperatures from −20 to 70 °C. Samples were kept under constant strain between 10% and 100%. Antiozonant chemicals in the concentration range from 2 to 20 p.h.r. (parts per hundred of rubber by weight) were tested and wax/antiozonant combinations at 6 p.h.r. wax and 3 p.h.r. antiozonant were also tested. Lake and Mente found that O_3 protection was most effective at higher temperatures, when diffusion of the antiozonant and wax to the surface of the elastomers was most rapid. This relationship is fortunate as ambient O_3 concentrations correlate well with higher temperatures. Antiozonants became generally less effective as temperatures dropped; however, dialkyl paraphenylenediamine provided reasonable protection for natural rubber to −17 °C.

Davies (1979) reported on the effects of O_3 and other environmental factors on interply adhesion of natural and synthetic rubber compounds. Excellent adhesion of plies is essential to the proper manufacturing of tires. The rubber strips must make interlocking contact at the joint boundary or the strength of the tire will be inadequate. Ozone attack on synthetic poly isoprene and polybutadiene produces a surface layer of ozonides. With NR, the film consists



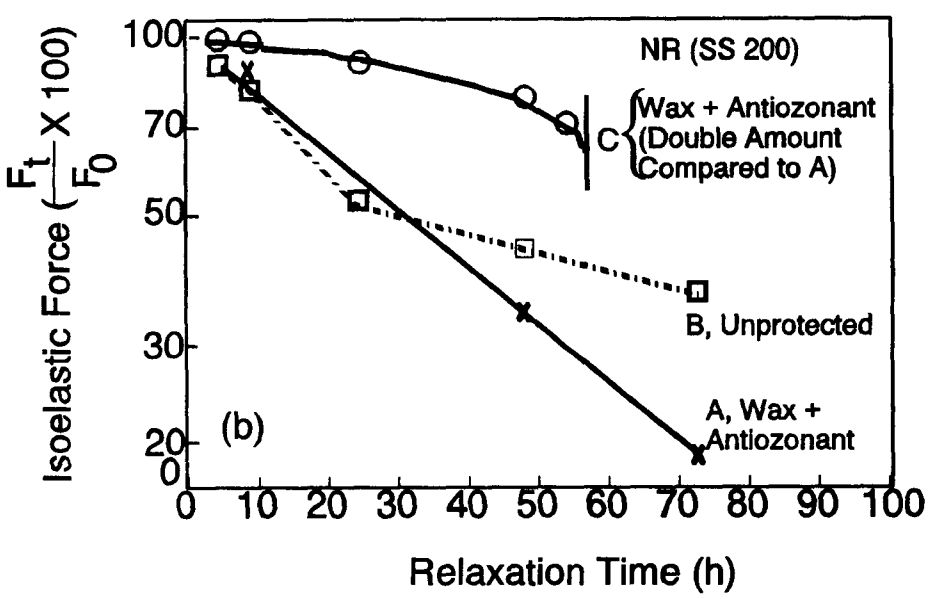


Figure 5-44. Relaxation of rubber compounds in ozone is affected by the combination of rubber formulation and type of ozone protection. Compounds were tested at ozone concentration, 0.5 ppm; temperature, 30 °C; elongation, 50%. Vertical line at the end of a curve means total failure, and vertical axis represents relaxation where F_0 is the initial force and F_t is the force after time t.

Source: Ganslandt and Svensson (1980).

of ozonides and carbonyl groups (Andries and Diem, 1974; Andries et al., 1979). The results of the Davies (1979) tests indicated that before curing, the adhesion of SBR compounds is unaffected by exposure to O_3 concentrations of 0.15 ppm, but the adhesion of the NR/SBR blend decreases by approximately 30%. Large reductions (on the order of 70%) in adhesion between plies were noted with the NR compounds; even exposure for a few hours at 0.05 ppm reduced adhesion considerably. The adhesion tests on cured NR, SBR, and isoprene rubber (IR) compounds after exposure to various levels of O_3 and humidity are summarized in Table 5-37. The adhesion of the SBR compound is superior to that of the other two compounds, which were greatly affected by increased RH.

TABLE 5-37. EFFECT OF OZONE AND HUMIDITY ON INTERPLY ADHESION[a]

		Final Adhesion[b]		
Compound	Initial Adhesion	0.15 ppm O_3 (294 $\mu g/m^3$), 30% RH	0.25 ppm O_3 (490 $\mu g/m^3$), 30% RH	0.15 ppm O_3 (294 $\mu g/m^3$), 60% RH
NR	5	2 to 3	1	1
IR	5	4 to 5	2 to 1	1
SBR	5	4 to 5	3 to 4	3 to 4

[a]Adhesion is rated from 1 (bad) to 5 (excellent), based on visual scale standardized by the authors.
[b]All exposures were 16 h in duration.

Source: Adapted from Davies (1979).

Wenghoefer (1974) studied the effects of O_3 on adhesion of tire cords dipped in resorcinal-formaldehyde latex (RFL). Many fibers and dip formulations were studied to determine their sensitivity to O_3, humidity, nitrogen dioxide (NO_2), UV light, and heat. Wenghoefer exposed these materials at a constant temperature of 100 °F (37.8 °C) to O_3 levels that varied between 0 and 1.5 ppm (0 and 2,940 $\mu g/m^3$) and to relative humidity (RH) levels ranging from 20 to 90%. Adhesion deteriorated from changes in surface properties of the RFL-dipped cords as a result of exposure to O_3, humidity, UV light, and heat. The adhesion losses from O_3 and the combined effects of O_3 and humidity were most

notable in the first 6 h of exposure. The detrimental effects of heat, NO_2, and the synergistic interaction of NO_2 and humidity were much less pronounced.

5.10.3.2 Dye Fading

Color fading of certain textile dyes has been attributed to the effects of ambient O_3. Although NO_2 was originally identified as the pollutant most important to color fading, the effects of O_3 were noted by Salvin and Walker (1955). The primary products affected were permanent press garments (polyester and cotton) and nylon carpeting. Table 5-38 summarizes studies on the effects of ozone on dyes. By using a combination of laboratory chamber studies and outdoor exposures, Salvin and Walker (1955) demonstrated that O_3 was responsible for dye fading observed on drapery fabrics. Blue anthraquinone dyes and certain red anthraquinone dyes were markedly bleached after exposure to just 0.1 ppm of O_3. Azo red and yellow dyestuffs and diphenylamine yellow dyes were shown to be resistant to fading at these concentrations, also confirming the results of the field study. The use of known antiozonants, such as diphenyl-ethylenediamine and diallyl phthalate, in combination with disperse blue dyes was effective against O_3 fading, thus providing additional evidence of the effects of O_3 on dyed fabrics.

Ajax et al. (1967) summarized the results of a study of 69 dye-fabric combinations that were exposed outdoors in light-free cabinets at 11 sites. These sites were Sarasota, Florida; Phoenix, Arizona; Cincinnati, Ohio; and four urban-rural combinations: Chicago and Argonne, Illinois; Washington, D.C., and Poolesville, Maryland; Los Angeles and Santa Paula, California; and Tacoma and Purdy, Washington. Among those fabrics exhibiting a high degree of fading at both urban and rural sites in the first 6 mo, fading was much greater at the urban sites than at the rural sites. The samples exposed in Phoenix, Sarasota, and Purdy showed the lowest amount of fading, which indicated that humidity and temperature are not, by themselves, the primary factors in fading. The highest fading rate occurred in samples exposed in Los Angeles, Chicago, and Washington, D.C. In addition, there was a marked seasonal variation in the test results, with greater fading during the spring and summer seasons. Generally, the results correspond with seasonal peaks in O_3 concentrations.

Ajax et al. (1967) also exposed the fabrics to irradiated and nonirradiated auto exhaust with and without sulfur dioxide (SO_2) for 9 h/day for six consecutive days. From the results

TABLE 5-38. LABORATORY AND FIELD STUDIES OF THE EFFECTS OF OZONE ON DYE FADING

Dye	Fabric	Concentration (ppm)	Exposure	Environmental Variables	Effects	Comments	Reference
Blue and red	Drapery	0.1	—	—	Both dyes were markedly bleached. No fading occurred when antioxidants were added.	Insufficient data for dose-response determinations. This study followed a field study showing that oxidants other than NO_x caused fading.	Salvin and Walker (1955)
Disperse Direct, fiber reactive vat, sulfur, azo Disperse Disperse, basic Disperse, acid Direct Premetolized, acid	Cellulose Acetate Cotton Polyester Orlon Nylon taffeta Viscose Wool	Laboratory 0.02 to 0.55 Field exposure concentrations not reported	54 h 3 mo	Light-proof cabinets, 11 rural and urban sites	Photochemical agents caused more fading than nonradiated samples. Urban locations produced more fading and temperature/humidity are not the primary causes of fading	Both laboratory and field measurements. Reported laboratory O_3 concentrations questionable. SO_2 was also present in laboratory exposures.	Ajax et al., (1967)
Direct red 1 Reactive red 2 Sulfur green 2 Azoic[a] red Direct red 1 Acid red 151 Acid yellow 65 Acid violet 1 Basic red 14 Basic yellow 11 Acid orange 45 Disperse blue 3 Disperse blue 3 Disperse blue 3 Disperse blue 27 Disperse blue 27 AATCC O_3 ribbon	Cotton Cotton Cotton Cotton Rayon Wool Wool Wool Acrylic Acrylic Nylon Nylon Cellulose Acetate Acetate Polyester Acetate	0.05 0.5	12 wk	Temperature = 130 °C 32 °C RH = 50%, 90%	Induced fading at both levels but at a nonlinear rate. Both temperature and humidity increased fading rate, and RH was more important Eight of the tested fabric-dye combinations faded measurably in response to O_3. Only trace amounts of fading occurred in the remaining fabrics.	Insufficient data to show detailed dose-response relationships. Although samples were measured throughout the exposure, only the 12-week data were presented.	Beloin (1973)

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TABLE 5-38 (cont'd). LABORATORY AND FIELD STUDIES OF THE EFFECTS OF OZONE ON DYE FADING

Dye	Fabric	Concentration (ppm)	Exposure	Environmental Variables	Effects	Comments	Reference
Olive I and II Disperse blue 3 and 7	Nylon fibers Nylon fibers	0.2 0.9	1 to >6 h	RH = 70 to 90% Temperature = 40 °C	Visible fading in Olive I after 16 h at 70% RH; same effect after 4 h at 90% RH. Linear increase in fading at 0.9 ppm O_3.	Both RH and O_3 concentration affected fading and in a nearly linear fashion. Sleeve form was more susceptible than skein form. Haylock and Rush (1976) found that: (1) increased fiber draw ratio reduced fading; (2) increased heat-setting temperature increased fading; (3) increased fiber surface area increased fading.	Haylock and Rush (1976)
Disperse blue dye in an avocado green mixture	Nylon 6 yarn	0.5	—	RH = 85% Temperature = 40 °C	Fading was closely correlated with fiber surface area (diameter).	Insufficient data for dose-response relationship determinations.	Huevel et al. (1978)
2 Disperse dyes and 2 acid dyes	Nylon 6 and Nylon 66 Carpet		3 mo to 3 years	28 homes in different parts of the country	Geographic and seasonal variation in fading.	Field study.	Nipe (1981)
Disperse blue 3	Nylon 6 yarn	0.2	2 to 120 h	RH = 65%, 85%, 90% Temperature = 40 °C	Nearly linear increase in fading with time. RH had a major influence on fading rate.	This study focused more on mechanisms of O_3 fading rather than dose-response relationships.	Kamath et al. (1983)

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TABLE 5-38 (cont'd). LABORATORY AND FIELD STUDIES OF THE EFFECTS OF OZONE ON DYE FADING

Dye	Fabric	Concentration (ppm)	Exposure	Environmental Variables	Effects	Comments	Reference
Disperse, basic Disperse Direct vat, sulfur, fiber reactive Disperse Disperse, acid Direct Acid, mordant	Acrylic Cellulose acetate Cotton Polyester Nylon Viscose rayon Wool		2 years in 3-mo blocks	Light-proof cabinets, 8 rural and urban sites	Two-thirds of samples exhibited substantial fading, O_3 was significant for 8 fabric/dye combination.	Field study.	Beloin (1972)
Disperse blue 3 Acid blue 25 Acid blue 40 Acid blue 45 Acid blue 80 Acid blue 127	Nylon 6 yarn Nylon 66 yarn	0.2	0 to 96 h	RH = 85% Temperature = 40 °C	Fading proceeded consistent with diffusion of dye to fiber surface	Study of mechanisms of O_3 fading, follow-on the Kamath et al. (1983).	Moore et al. (1984)
Royal blue Red Plum	Drapery fabric Rayon acetate Rayon acetate Cotton duck	0.5 and 1.0	250 - 1,000 h	50 and 90% RH, NO_2 and SO_2.	O_3 was not statistically significant cause of fading.	Laboratory study.	Haynie et al. (1976)

[a]Coupling component 2, azoic diazo component 32.

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of this chamber study, they noted that "photochemically produced byproducts of automobile exhaust are a prime cause of fading compared to fading caused by nonirradiated auto exhaust or by clean air with sulfur dioxide added." In the presence of SO_2, however, a more than additive effect was seen in the dye fading tests for both chamber and field studies. Although their conclusions concerning O_3 itself are easily substantiated in the research literature, the O_3 levels measured in their chamber are questionable. The daily 9-h average O_3 concentrations (measured by neutral KI, Mast instrument) were identical for irradiated (UV) and nonirradiated exhaust (0.02 ppm); irradiated exhaust plus SO_2 produced 0.55 ppm of O_3.

Beloin (1972, 1973) investigated the effects of air pollution on various dyed textiles by conducting field and controlled-environment laboratory studies. For the field study, a wide range of dyed fabric was exposed in light-tight cabinets at the same four urban and four rural sites used in the Ajax studies. The study was carried out over a 2-year period, in eight consecutive 3-mo seasonal exposure periods. Color change data and air pollution and weather measurements were analyzed to identify the factors that caused fading. About two-thirds of the fabrics studied showed appreciable fading. Most of these fabrics faded significantly more at urban sites than at rural sites. The small amount of fading evidenced by the samples exposed at extreme temperatures and/or humidity indicated that these factors by themselves have no effect on fading. The samples also showed some seasonal variations in fading. In areas of high oxidant concentration, maximum fading occurred primarily in summer and fall. Fabrics exposed in Chicago, where SO_2 concentrations are higher in the winter, showed greater fading during this season.

The results of the outdoor fading study were used in a multiple regression analysis. The analysis focused on 25 fabric dye samples, 23 of which showed SO_2 to be a significant variable. Ozone was also a significant contributor to fading of eight dyed fabrics and NO_2 to fading of seven dyed fabrics. The dominance of SO_2 as a factor in fading may have been complicated by soiling.

Beloin's laboratory study was designed to assess the effects of air pollutants, temperature, and RH on the colorfastness of 30 samples selected from those exposed during the field study. Fabric samples were exposed to two concentrations of O_3: 0.05 ppm and 0.50 ppm. The laboratory studies demonstrated that high O_3 levels produced more

significant fading in more fabric samples than did low levels. Visible fading did occur in about one-third of the sensitive fabrics (cellulose acetate, viscose, and cotton muslin with red and blue dyes) exposed to O_3 concentrations of 0.05 ppm. These levels are similar to those frequently found in metropolitan areas. The laboratory study also demonstrated that high RH (90%) is a significant factor in promoting and accelerating O_3-induced fading.

Haynie et al. (1976) and Upham et al. (1976) reported on the degree of fading of three different drapery fabrics exposed in a laboratory chamber to combinations of high and low O_3 concentration (0.5 and 0.1 ppm, respectively), high and low RH (90 and 50%, respectively), and high and low concentrations of NO_2 and SO_2. The three commercially obtained fabrics selected for this study were a royal blue rayon-acetate, a red rayon-acetate, and a plum cotton duck. The samples were exposed in the chamber for periods of 250, 500, and 1,000 h; the degree of fading was measured with a color difference meter. The fading of the plum-colored material was statistically related to RH and the NO_2 concentration. For the red and blue fabrics, only RH appeared to be a significant factor. The effects of concentrations of O_3 on the amount of fading of these dyes were not statistically significant, even after exposure for 1,000 h to 0.5 ppm, levels much higher than typical ambient exposures.

Haylock and Rush (1976, 1978) studied the fading of anthraquinone dyes on nylon fibers. In the first test, nylon carpet yarn dyed with Olive I (0.081% Celliton Pink RF, 0.465% Celliton Yellow GR, 0.069% Celliton Blue FFRN) and Olive II (0.082% Latyl Cerise Y, 0.444% Celliton Yellow GA, 0.143% Cellanthrene Blue CR) was exposed to varying levels of temperature, RH, and O_3. Material dyed with Olive I and exposed at 70% RH, 40 °C (104 °F), and 0.2 ppm of O_3 showed visible fading after 16 h of exposure. At 90% RH, similar fading occurred in less than 4 h. Under the same RH and temperature conditions, increasing the O_3 concentration from 0.2 to 0.9 ppm resulted in a parallel increase in fading. Samples in knitted sleeve form demonstrated much greater susceptibility to O_3 attack than samples in skein form.

Using Disperse Blue 3 and Disperse Blue 7 dyes exposed to constant conditions of 40 °C (104 °F), 90% RH, and 0.2 ppm of O_3, Haylock and Rush (1976) investigated the effect on fading of changing the fiber cross section, the fiber draw ratio, and the method of setting the nylon fibers with steam heat. They found that increasing the surface area of the

fibers resulted in an increased fading rate. Increasing the fiber draw ratio reduced dye fading, and increasing the heat-setting temperature decreased resistance to fading in disperse dyes.

The effect of high temperature and high humidity for induction of O_3 fading in nylon was further confirmed by the additional work of Haylock and Rush (1978). Their studies showed a good correlation between accelerated O_3 fading in the laboratory and in outdoor, in-service exposure, during which temperature and humidity extremes were common. Control samples exposed indoors, however, where temperatures and humidities were lower, did not exhibit nearly the same magnitude of fading as the laboratory samples.

Huevel et al. (1978) investigated the importance of the physical nature of Nylon 6 yarns on the O_3 fading behavior of a disperse blue dye. Samples of Nylon 6 yarns dyed avocado green with a dye mixture including Disperse Blue 3 were exposed in a laboratory cabinet to 0.5 ppm of O_3 at 40 °C and an RH of 85%. Huevel et al. found that the microfibril diameter and specific surface area of the fiber were the fiber characteristics most closely related to O_3 fading, thus confirming suspicions expressed earlier by Salvin (1969).

Nipe (1981) summarized the results of a 3-year study to establish the relationship between in-service fading of carpets in a home versus O_3 fading as determined by the American Association of Textile Chemists and Colorists (AATCC) Standard Test Method 129, Colorfastness to Ozone in the Atmosphere Under High Humidities. (Measurements were also taken to compare the fading caused by oxides of nitrogen.) The test carpets were made of Nylon 6 and 66 dyed with two disperse and two acid dye formulas. Test samples from the homes of 28 participants were returned every 3 mo for the 3-year period. The exposure sites selected for this long-term study represented variations in home heating and cooling, utilities, climate, and geographical locations. The carpet samples were placed in areas as close as possible to the kitchen but away from exposure to sunlight or any traffic. No measurements of O_3 concentrations were collected; however, an ozone sensitive sample strip was included with each carpet sample. Analysis of the sample strip enabled the researchers to determine the relative ozone exposure of each carpet sample.

Geographical location appeared to have a significant effect on fading. Test samples from sites in the southeast and northeast showed far more O_3 fading than those in the west and far west. Test samples in homes with air conditioning exhibited less fading during the

summer than those without air conditioning. In all samples, much greater fading was caused by O_3 during July, August, and September than in January, February, and March. Typically, O_3 levels indoors are higher during the summer, when doors and windows are more likely to be open, thus allowing a greater exchange between inside and outside air. The results of the study of in-service interior carpet exposures were compared with the results of AATCC Test 129. In a sample that performs satisfactorily through 1.08 cycles of O_3 exposure in AATCC Test 129, there is a 98% probability against in-service fading over a 1-year period. A sample that performs satisfactorily through only 0.6 cycles of O_3 testing has only a 90% probability of satisfactory performance after 1 year of in-service exposure.

Kamath et al. (1983) studied the effect of atmospheric O_3 dye fading on nylon fibers. Prior studies had postulated that O_3 does not penetrate into the fiber to destroy the dye, but instead attacks the dye at the surface of the fiber. Dye then diffuses outward from the fiber interior because of the concentration gradient set up as the surface dye is destroyed. Using microspectrophotometry to test this postulated mechanism, Kamath et al. studied the diffusion and destruction of C.I. Disperse Blue Dye 3 on Nylon 6 continuous filament yarn measuring about 45 μm in diameter. With this method, they were able to generate a dye distribution profile across the cross section of the fiber and to determine the diffusion coefficient of a dye in the fiber. The fibers were exposed in a controlled environment to O_3 concentrations of 0.2 ppm for 2 to 120 h at a temperature of 40 °C and RH levels of 90%, 85%, and 65%. The results of these laboratory studies indicated that RH has a significant positive effect on fading, that destruction of the dye begins near the surface of the fiber in the early stages of exposure, and that O_3 penetration into the fiber may be an important mechanism in O_3 fading. The dependence of fading rates on humidity was substantial. Even slight rises in humidity from 85 to 90% caused a significant increase in the extent of fading. At 65% RH, the fading rate drops dramatically. This effect was attributed to the breakage of hydrogen bonds in the presence of water, which leads to a more open structure with high segmented mobility; this condition is more favorable to diffusion of O_3 and disperse dyes.

A follow-on study by Moore et al. (1984) used the Kamath et al. (1983) approach with a variety of dyes, yarns and treatments. Moore and coworkers used untreated, phenol treated and steam treated Nylon 6 and Nylon 66 continuous filament yarns, with six disperse blue and acid blue dyes. Molecular weights of the dyes ranged from MW = 296 (Disperse Blue

No. 3) to MW = 872 (Acid Blue No. 127). Dyed filaments were exposed to 0.2 ppm O_3 at 40 °C and 90% relative humidity for various periods up to 96 h. For Nylon 6, steam treated fibers faded more quickly than untreated fibers, while phenol treated fibers faded less quickly. In Nylon 66, both treatments increased the rate of dye loss. The authors attributed this effect, at least in part, to the change in morphology of the treated fibers. Faster fading was attributed to higher diffusion rates of the dye in the fiber. They also observed that low molecular weight dyes faded faster than high molecular weight dyes, again suggesting the dye mobility within the fiber (rate of diffusion of the dye molecules to the surface of fiber) played a significant role in the fading process. Cross-sectional analysis of the exposed fibers showed that most of the dye loss appeared to occur due to reactions at the fiber surface and that penetration of O_3 into the fiber did not seem to be significant.

Salvin (1969) reported that O_3 and (to a lesser extent) NO_2 caused dye fading of cotton polyester/permanent press fabrics. As summarized by Dorset (1972), O_3 was found to be the major fading agent, with nitrogen oxides also capable of causing fading, though to a lesser extent. Remedial measures to avoid this problem include selecting dyes more resistant to reaction with O_3 and NO_2, avoiding the use of magnesium chloride catalyst in the permanent press process, and using different surfactants and softeners. The use of magnesium chloride as a catalyst makes O_3-sensitive dyes more sensitive to O_3 (Dorset, 1972). When the catalyst is zinc nitrate, dyes are more washfast and resistant to O_3 fading. The present use of a zinc nitrate catalyst appears to have generally eliminated the problem of the prefading of dyes in permanent press fabrics from O_3 exposure.

Much of the research reported on dye fading is qualitative in nature. Earlier studies relied on comparisons among various geographical locations and seasonal variations with little attention given to actual concentration and exposure characterizations. For several of the initial field investigations reported here, neither O_3 nor oxidant concentrations were given; rather, notations such as high versus low or urban versus rural were the only description of oxidant levels. The few laboratory studies employed only two concentrations of O_3 at most, making it nearly impossible to derive meaningful exposure-response relationships. Comparisons among studies are difficult owing to the various dye and fabric combinations tested. Also, the importance of relative humidity on O_3 fading rate confounds comparisons among many of the studies that did not use the same RH percentages. Despite

these shortcomings, the existing body of research clearly demonstrates a strong relationship between dye fading and O_3 exposure. A definitive study to develop exposure-response functions that covers a broad spectrum of fabric/dye combinations, O_3 exposures, humidities and temperatures has not been undertaken, although the available literature establishes the likely significant variables for such a study.

5.10.3.3 Fiber Damage

Sunlight, heat, alternate wetting and drying, and microorganisms are causative factors in the weathering and deterioration of fabrics exposed outdoors. The influence of O_3 at normal ambient levels is generally small by comparison. Table 5-39 summarizes the experiments of the effects of ozone on textile fibers.

Bogaty et al. (1952), as part of a program aimed at segregating some of the elements that cause weathering, carried out experiments to study the possible role of O_3 in the deterioration of cotton textiles. These investigators exposed samples of duck and print cloth to air containing 0.02 and 0.06 ppm of O_3. Samples were exposed both dry and wet and tested for 50 days. The wet samples were water-saturated once per week, and moisture was added regularly so that the moisture content of the cloth was never less than 50%. Similar fabric samples were exposed to similar O_3 concentrations with no moisture added, and another control group was similarly wetted but exposed to clean (O_3-free) air. After exposure to O_3, the wetted samples showed a loss in breaking strength of approximately 20%. The wet print control cloth showed a loss in breaking strength of only half this amount. The study showed that low levels of O_3 degrade cotton fabrics if they are sufficiently moist. Bogaty et al. surmised that an estimated 500 to 600 days of natural exposure might be required to reach a stage of degradation similar to that caused by a 50-day exposure to O_3 alone. Because unprotected fabrics typically reach a much more advanced state of decay after such long exposures to weathering, Bogaty et al. concluded that the effect of O_3 is slighter than that of other agents. Although not noted by Bogaty et al., the O_3 and increased moisture may have caused the formation of hydrogen peroxide (H_2O_2), which could account for the loss in breaking strength.

Morris (1966) also studied the effects of O_3 on cotton. Samples were exposed in the absence of light to 0.5 ppm of O_3 (more than four times the National Ambient Air Quality

TABLE 5-39. LABORATORY AND FIELD STUDIES OF THE EFFECTS OF OZONE ON FIBERS

Fiber	Concentration (ppm)	Exposure	Environmental Variables	Effects	References
Cotton	0.02 and 0.06	50 days	Cloth, both wet and dry	O_3 exposed wetted samples had 20% loss of breaking strength.	Bogaty et al. (1952)
Cotton	0.5	50 days	21 °C, 72% RH	No loss of breaking strength.	Morris (1966)
Cotton	1.0	60 days	25 °C, periodic washing or wetting	Washed O_3 exposed fabrics had 18% loss of breaking strength.	Kerr et al. (1969)
Modacrylic, Acrylic, Nylon 66, Polyester	0.2	7 days	48 °C, 39% RH Artificial sunlight, wetting	No effect on modacrylic and polyester. Slightly reduced breaking strength in acrylic and nylon.	Zeronian et al. (1971)
Nylon	0.03	Up to 445 days	Exposed in industrial warehouse	Loss of dyeability	Makansi (1986)

Standard [NAAQS] of 0.12 ppm) for 50 days in a chamber maintained at 70 °F (21 °C) and 72% RH. No appreciable effect on breaking strength was found. Apparently, the moisture content of the cotton was not high enough to produce the degradation that Bogaty et al. (1952) measured in wet cotton samples, even though the concentration of O_3 was considerably higher.

The laboratory study of Kerr et al. (1969) examined the effects of the periodic washing of dyed cotton fabrics exposed to O_3 and the amount of fading and degradation of moist, dyed fabrics exposed to O_3. They exposed samples of print cloth, dyed with CI Vat Blue 29, in a chamber to a continuous supply of purified air containing O_3 concentration levels of 1 ± 0.1 ppm. The samples were exposed at room temperature (25 °C) in the absence of light, and a shallow container of water was kept on the chamber floor to increase the humidity. Samples were withdrawn from the chamber after 12, 24, 36, 48, and 60 days. After an exposure period of 60 days, which included either 20 washing or 20 soaking treatments, the change in strength of control fabrics was not significant. By comparison, the fabrics exposed to O_3 changed significantly; the loss in strength of the washed fabrics was 18%, and that of the soaked fabrics, 9%. Fading was also evident in the fabrics exposed to O_3, but not in the control samples. Differences in the amount of fading between the washed and soaked samples were evident, but the reason for the differences was not. Kerr et al. concluded that washing in hot, soapy water may have affected the properties of the dye.

In laboratory studies, Zeronian et al. (1971) simultaneously exposed modacrylic (dynel), acrylic (orlon), Nylon 66, and polyester (dacron) fabrics to artificial sunlight (xenon arc) and charcoal-filtered air contaminated with 0.2 ppm of O_3 at 48 °C (118 °F) and 39% RH. During exposure, the fabric samples were sprayed with water for 18 min every 2 h. Ozone damage was measured by comparing these samples with fabrics exposed to the same environmental conditions without O_3. After exposure for 7 days, Zeronian et al. found that O_3 did not affect the modacrylic and polyester fibers. The exposure did seem to affect the acrylic and nylon fibers slightly by reducing breaking strength. The degree of difference, however, in the change of fabric properties between those exposed to light and air and those exposed to light and air containing 0.2 ppm of O_3 was not significant.

Ageing of nylon yarns causes a reduction in the dyeability of the yarn. Ageing is caused by the reaction of amine end groups in the filament skin with O_3 as well as other

pollutants (NO_x, SO_2, etc.). This phenomenon is well known within the textile trade and procedures such as minimizing time from yarn production to yarn dyeing are in place to reduce problems of ageing. Makansi (1986) investigated the relationship between yarn ageing as defined by reduction in dyeability and pollutant levels in yarn storage warehouses. Makansi assessed the yarn dyeability with Acid Blue 45 and Acid Blue 122 dyes of exposed test fiber versus unexposed control samples. Gaseous pollutant concentrations in the warehouse were either estimated using nearby air quality station data or measured twice weekly during the tests using commercial sampling tubes (Draeger™ Tubes). Yarn samples were exposed for up to one-year of ageing. Makansi found that dyeability decreased proportionally with the O_3 exposure during storage. Dyeability as weight of dye absorbed for Acid Blue 45 decreased over 75% for Nylon 66 stored in the warehouse at an average concentration of .03 ppm O_3. It was not possible to statistically isolate the effects of O_3 exposure from other pollutant exposures for the samples for these tests; thus other factors besides O_3 may have contributed to the loss in dyeability. Makansi suggested that yarns should be dyed as quickly as possible after manufacture or should be stored in airtight wrappings to prevent ageing.

In general, the contribution of O_3 to degradation of fabrics has not been quantified well. Bogaty et al. (1952) concluded that the effects of other factors (sunlight, heat, wetting and drying, and microorganisms) far outweighed the effects of O_3 on cotton duck and print cloth. The work by Morris (1966) and Kerr et al. (1969) does point to the synergistic effect of moisture and O_3 as an important ingredient in material degradation, possibly caused by the formation of a more potent oxidizing agent. Finally, the work of Zeronian et al. (1971) also indicates little if any effect of O_3 on synthetic fibers. Thus, it appears that O_3 has little if any effect on textiles, fibers, and synthetic cloth exposed outdoors. Because most fabrics are used primarily indoors where they are partially shielded from O_3 exposure, O_3 damage to textile fibers is considered an insignificant problem. This was a finding of Murray et al. (1985) in a study of material damage and costs in the Los Angeles area, an area with relatively high ambient ozone concentrations.

5.10.3.4 Paint Damage

A paint surface may suffer several types of damage that affect its usefulness, including cracking, peeling, erosion, and discoloration. Of these, erosion (i.e., wearing away of the paint surface) is the type of damage most often studied with respect to the impact of gaseous pollutants on architectural and coil coating finishes. (Coil coatings are industrial, continuous-dip process finishes typically applied to sheet metal). Studies of paint cracking and peeling have focused on the effects of moisture and have not dealt with the possible influence of ambient pollutants on these types of finishes.

Several damage functions for O_3-induced erosion of paint have been reported in the literature. Such reports are based on either accelerated chamber studies or long-term outdoor exposure studies. Unfortunately, all studies to date have shortcomings that render their results questionable in regards to actual exposures. Damage to a paint surface is the cumulative effect of the conditions to which the surface is exposed, including various combinations of temperature, moisture, sunlight, and pollution level. No exposure study to date has been able to match all factors exactly to separate the impact of O_3 from the other factors. Table 5-40 summarizes the studies of the effect of O_3 on architectural and industrial paint and coating systems.

In a laboratory chamber exposure study, Haynie et al. (1976) exposed oil-based house paint, latex house paint, vinyl coil coating, and acrylic coil coating to 0.5 and 0.05 ppm concentrations of SO_2, NO_2, and O_3 in various combinations. Statistically significant effects of O_3-caused damage were observed on the vinyl coil coating and the acrylic coil coating. There was a positive interaction between O_3 and RH on the vinyl coil coating and a positive direct O_3 effect on the erosion rate of the acrylic coil coating. The rate of erosion was low, however, and both vinyl and acrylic coil coatings were shown to be very durable. A linear regression for the acrylic coil coating data gives:

$$\text{Erosion rate} = 0.159 + 0.000714\ O_3 \qquad (5\text{-}1)$$

where erosion rate is in μm/year and O_3 is $\mu g/m^3$.

Although the O_3 effect on this coating was found to be statistically significant, it has no practical significance because the erosion rate is so slow; at 0.12 ppm of O_3, the erosion rate

TABLE 5-40. LABORATORY AND FIELD STUDIES OF THE EFFECTS OF OZONE ON ARCHITECTURAL/INDUSTRIAL PAINTS AND COATINGS

Paint/Coating Type	Substrate	Concentration (ppm)	Exposure	Environmental Variables	Effects	Comments	Reference
Latex house paint Oil house paint Vinyl coil coating Acrylic coil coating	Aluminum panels	0.05 and 0.5	to 1,000 h	Chamber exposures with SO_2, NO_2, O_3, 50 and 90% RH 13 and 35 °C, artificial dew and sunlight cycles.	Very slow erosion of coil coatings		Haynie et al. (1976)
Automotive refinish Latex Coil coating Industrial maintenance coating Oil house paint	Stainless steel panels	0.1 and 1.0	to 1,000 h	Chamber study with SO_2, 70 to 100% RH, 50 to 65 °C, artificial dew and sunlight cycles.	Although 1 ppm O_3 produced significant changes in finishes, 0 1 ppm O_3 did not produce statistically increased erosion		Cambell et al. (1974)
		4 sites, rural to industrial	to 24 mo	Field study.	Erosion greater in urban areas.	No environmental measurements conducted.	
Latex house paint Oil house paint	Stainless steel	0.006 to 0.055	3 to 30 mo	Field study.	Effects of O_3 not independently statistically significant.	Nine sites around St. Louis	Mansfeld (1980)

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is 0.33 μm/year. At an average annual O_3 level of 0.05 ppm, this regression predicts that a 20-μm-thick coating would last over 80 years.

In a comprehensive study by Campbell et al. (1974), panels painted with different exterior paints (automotive refinish, latex coating, coil coating, industrial maintenance coating, and oil-based house paint) were exposed to air pollutants in an environmental chamber under accelerated weathering conditions. The panels were exposed to low (0.1 ppm) and high (1.0 ppm) concentrations of O_3 and SO_2. After exposure, the panels were examined by measuring erosion, gloss, surface roughness, tensile strength, attenuated total reflectance (ATR), and the surface effects revealed by scanning electron microscopy and infrared examination. The panels were examined after 0, 400, 700, and 1,000 h of chamber exposure (considered as equivalent to 0, 200, 350, and 500 days, respectively, of exposure).

In general, exposures to 1 ppm of O_3 produced greater increases in erosion rates than did clean air. Concentrations of this magnitude, however, do not represent typical ambient exposure levels of O_3. At the more representative level of 0.1 ppm, O_3 did not produce statistically significant increases in erosion rates. The various finishes produced a variety of changes for the other measures. Some finishes lost gloss or showed changes in ATR, but O_3 exposure did not produce consistent changes over the suite of finishes examined.

In conjunction with Campbell's chamber studies, field measurements were made of the erosion of paint from test panels exposed to outdoor environments consisting of a clean, rural atmosphere (Leeds, North Dakota); a moderately polluted atmosphere (Valparaiso, Indiana); a heavily polluted (SO_2) atmosphere (Chicago, Illinois); and a high-oxidant, moderately polluted atmosphere (Los Angeles, California). The results of this study showed that paint erosion was much greater in the polluted areas than in relatively clean, rural areas. The highest erosion rates were observed for the coil coating and oil-based house paints at the Chicago and Los Angeles exposure sites. Since meteorology and air quality were not measured at the exposure sites, correlation of film damage with the environmental parameters was not possible. The study does suggest that SO_2 exerts an adverse effect on exterior paints with calcium carbonate as an extender pigment. The coil coating and oil house paints were formulated with calcium carbonate. Oxidants were probably reacting with the organic binder of the coil coating and oil house paints, although no mechanism for this reaction was developed from this exposure study.

In an outdoor exposure test of the effects of air pollutants on materials, Mansfeld (1980) exposed latex and oil-based house paints as well as galvanized steel, weathering steel, stressed aluminum, silver, marble, and nylon at nine test sites in St. Louis, Missouri. In conjunction with the material exposures, measurements of meteorological parameters, O_3, oxides of nitrogen, total hydrocarbons, total sulfur, SO_2, and hydrogen sulfide were made.

Haynie and Spence (1984) analyzed Mansfeld's (1980) St. Louis data accounting for covariances among the pollutant and meteorological variables. They analyzed the paint damage data and found significant correlations of O_3 flux with time, temperature, and NO_2 flux for the experimental period. While Haynie and Spence expected O_3 to attack the binder in latex paint, multiple regression analysis showed little dependence of paint erosion on O_3 flux. They speculate that the effects of O_3 are masked by the covariance of O_3 with temperature and oxides of nitrogen.

5.10.3.5 Cultural Properties Damage

Ozone-induced degradation of cultural properties (e.g., fine arts paintings) contributes to the deterioration and ultimately the loss of these unique objects. Many cultural properties are expected to last indefinitely, and irreversible damage, even at a slow rate, is considered unacceptable by curators and the art community.

A significant series of tests of the effects of O_3 on a variety of artist's pigments and dyes was reported by Shaver et al. (1983); Grosjean et al. (1987); Whitmore et al. (1987); Grosjean et al. (1988a,b); Whitmore and Cass (1988); Grosjean et al. (1989); Cass et al. (1991) and Grosjean et al. (1993). The experiments are summarized in Table 5-41. The doses of O_3 applied during these tests were the equivalent of less than 10 years exposure in a typical air conditioned indoor environment. Many pigments, and notably traditional organic pigments such as indigo, were found to be very sensitive to O_3 exposure. Many of the affected pigments underwent significant color changes upon exposure to O_3, and some were virtually completely consumed producing colorless reaction products. Cass et al. (1991) noted that O_3 damage to artwork is proportional to the O_3 exposure (concentration $\times$ time). Because artworks are intended to have long service lives and their appearance is important, fading is generally considered to be unacceptable, and even low concentrations for long

TABLE 5-41. LABORATORY STUDIES OF THE EFFECTS OF OZONE ON ARTISTS' PIGMENTS AND DYES

Pigment Types	Substrate	Concentration	Exposure	Environmental Variables	Effects	Comments	Reference
Seventeen Artists' watercolor pigments	Paper	0.4 ppm	95 days	23 °C 47% RH	Alizarin-based watercolors were very sensitive; other pigments showed lesser degrees of fading.	Also investigated fading on Japanese wood-block print.	Shaver et al. (1983)
Alizarin, Alizarin crimson, anthraquinone	Silica Gel Cellulose — Teflon	0.4 ppm 0.4 ppm — 10 ppm	95 days 95 days — 18-80 h	22 °C 50% RH — 24 °C ≤40% RH	Each pigment tested faded on all substrates.	Presented possible reaction mechanisms and products.	Grosjean et al. (1987)
Sixteen traditional organic colorants	Paper	0.4 ppm	12 weeks	23 °C 50% RH	Eleven colorants were reactive with O_3, three were possibly reactive.		Whitmore et al. (1987)
Indigo, dibromoindigo, thioindigo, tetrachlorothioindigo	Teflon	10 ppm	4 days	24 °C 5% RH	All indigo, dibromoindigo consumed. Thioindigo and tetrachlorothioindigo were much less reactive and still retained much color.	Presented possible reaction mechanisms.	Grosjean et al. (1988a)
Curcumin	Cellulose, Watercolor Paper, Silica Gel — Teflon	0.4 ppm 0.4 ppm — 10 ppm	95 days 95 days — 4 days	25 °C 50% RH — 24 °C ≤20% RH	Faded rapidly on all substrates producing colorless products.	Somewhat slower fading on watercolor paper.	Grosjean et al. (1988b)

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TABLE 5-41 (cont'd). LABORATORY STUDIES OF THE EFFECTS OF OZONE ON ARTISTS' PIGMENTS AND DYES

Pigment Types	Substrate	Concentration	Exposure	Environmental Variables	Effects	Comments	Reference
Traditional Japanese colorants and dyes	Paper, Silk Cloth	0.4 ppm	12 weeks	22 °C 50% RH	Several organic and one inorganic pigment faded significantly.	Also investigated fading on c. 1810 Japanese woodblock print.	Whitmore and Cass (1988)
Triphenylmethane colorants	Teflon	10 ppm	4 days	24 °C ≤20% RH	Found that while some are not affected, those colorants with unsaturated C-C bonds may fade.	Presented possible reaction mechanisms.	Grosjean et al. (1989)
Alizarin Crimson	Watercolor Paper	0.4 ppm	7 days	22 °C 50% RH	Severe fading.	Framed sample behind glass exhibited virtually no fading.	Cass et al. (1991)
Various artists' colorants	Watercolor Paper Cellulose	Mixture 0.2 ppm O_3 0.01 ppm PAN 0.08 ppm NO_2	12 weeks	16 to 26 °C 46 to 83% RH	11 colorants-negligible changes 12 colorants-small changes 3 colorants-modest changes 9 colorants-substantial changes.		Grosjean et al. (1993)

periods of time can lead to noticeable fading. Grosjean et al. (1987) suggest that formulations of substitute pigments be developed with O_3 sensitivity in mind.

Druzik et al. (1990) investigated the indoor/outdoor O_3 concentration ratios at 11 museums, art galleries, and historical houses in the Los Angeles, CA, area. They found that the indoor/outdoor ratio of 8-h average O_3 concentrations ranged from 0.10 to 0.87. The ratio was strongly dependent on the type of building ventilation. Buildings with high air exchange rates (ca. 2 to 3 air changes per hour) air ventilation had the highest indoor/outdoor ratios. Low exchange rate buildings (ca. less than one air change per hour) and buildings with air conditioning systems had significantly lower indoor/outdoor O_3 concentration ratios.

De Santis et al. (1992) investigated concentrations of SO_2, HNO_3, HONO, and O_3 as well as particulate sulfate, nitrate and ammonium in the Galleria degli Uffizi in Florence for a five day period. Although the museum was equipped with an air conditioning system, O_3 concentrations in the galleries correlated strongly with outdoor O_3 concentrations. Indoor hourly average O_3 concentrations ranged from 0.019 to 0.030 ppm. To reduce concentrations in the galleries, they suggested that the Uffizi's air handling system be upgraded to include filtration and modified to include less make-up air. Cass et al. (1991) and Grosjean et al. (1993) suggest that museums design and maintain air conditioning and air filtration systems to control the concentrations of oxidants in order to protect their collections. Cass et al. (1991) note that framing behind glass is an effective means of protecting oxidant sensitive pigments. Grosjean and Parmar (1991) found that activated carbon and Purafil (4% potassium permanganate on neutral activated alumina) could be used to reduce ozone and oxidant concentrations in museum display cases.

5.10.4 Economics

5.10.4.1 Introduction

Damage to materials from O_3 is usually expressed in terms of one or both of the following two general classes of costs to producers and consumers: (1) O_3-accelerated replacement and repair costs, as when the service life and/or aesthetics of a material are impaired, and (2) increased avoidance costs, as when certain industries (e.g., tires, plastics, paints, dyes, and fabrics) are obligated to incur expenditures for antiozonant research and

development, substitute processes and materials, additives and formulations, product packaging, advertising, etc., in order to offset sales losses that would otherwise occur.

In theory, the approach selected should depend on the observed behavior of the producers and consumers of the materials in question, and the type of damage to which they are reacting. In practice, the existing empirical estimates of O_3 damage to materials are far from reliable.

5.10.4.2 Methods of Cost Classification and Estimation

Computation of accelerated replacement is probably the most widely applied method of estimating the costs of materials damage to air pollutants. In this approach a materials damage function is developed to show the increase in physical damage for an increase in the dose of the pollutant. Then a cost schedule is constructed to show how maintenance or replacement schedules are influenced by the pollutant level. Hershaft et al. (1978) note, however, that this method usually assumes existing inventories, and does not take into account substitutions of materials with more (or less) resistance to pollution. As a result, this method tends to overestimate the cost of damage from pollutant increases and to underestimate the net savings realized from pollutant reductions.

A second approach considers avoidance costs. This refers to practices such as adopting alternative production processes and materials. Some industries add antiozonants to their products, or change the chemical formulation of their output. All of these measures mitigate the impact of O_3 on the service life or aesthetics of the products in question. Moreover, these measures also require research, development, and implementation expenditures. As such, estimation of these costs is conceptually and empirically difficult, since the opportunity to use different materials changes in response to the level of O_3 concentration.

A number of factors complicate the use of both the replacement and the avoidance methodologies. Data on key variables are generally missing or merely assumed. Lessening the reliability of the final cost estimates are deficiencies in knowledge of (1) the physical damage functions; (2) the quantities and types of materials exposed to O_3 indoors, outdoors, and in respective regions of the country; (3) the actual expenditures incurred for increased replacement, maintenance, and avoidance that can be directly attributed to O_3; (4) the threshold O_3 damage levels that prompt mitigating action; and (5) the range of substitution

strategies that can be used to ameliorate degradation. On this latter point, few attempts have been made to identify current technology practices and possibilities. The variety of rubber compounds, paint mixtures, and fabric dyes reflects the number of proprietary formulations, and each formulation presumably has a different response to O_3 exposure.

An additional complication is that repair, replacement, and substitution are frequently dominated by factors unrelated to O_3 concentrations. This can lead to spurious correlations if studies are accepted uncritically. For example, tire replacement may be high in a given region of the country because of high O_3 levels associated with automotive exhaust. Alternatively, it may be high simply because the total miles of automotive use per year are higher in that region than in the nation as a whole.

5.10.4.3 Aggregate Cost Estimates

The important caveats identified in the preceding discussion qualify the empirical data presented in this and following sections. Table 5-42 summarizes reports of highly aggregated estimates of oxidant damage to all materials. Unfortunately, there are no known recognized studies that are more recent than those reported in the table. For purposes of gross comparison only, the figures are expressed in 1984 currency equivalents alongside 1970 currency equivalents, the base data for the reference studies. They do *not*, however, represent 1984 supply-demand relationships, production technologies, or O_3 concentrations. It must be emphasized that the costs cited in 1984 currency equivalents therefore cannot be considered true 1984 costs. Although the data in Table 5-42 is reported to four significant figures, the real accuracy of this information is much less.

Salmon (1970) was among the first to attempt to estimate the annual cost of air pollution damage to materials. His computation included the dollar value of annual materials production, a weighted average economic life of each material included in his study, a weighted average factor for the percentage of the material exposed to air pollution, and a factor for increased labor to treat damaged materials. Cost was defined as the value of the material multiplied by the difference between the rate of material deterioration in a polluted urban versus an unpolluted rural environment. All data, except for annual production levels of materials, were assumed.

TABLE 5-42. SUMMARY OF DAMAGE COSTS TO MATERIALS BY OXIDANTS (in Millions of 1970 and 1984 Dollars)

	Materials Costs		
Study	Elastomers/Plastics	Fabric/Dye	All
Barrett and Waddell (1973)	ND[a]	(260)	(3,878)
Mueller and Stickney (1970)	500.0 (1,500)[b]	ND	ND
Salmon (1970)	295.2 (915)	358.4 (1,111)	653.6 (2,026)
Salvin (1970)	ND	83.5 (259)	ND
Waddell (1974)	ND	ND	900.0 (2,790)
Yocom and Grappone (1976)	ND	ND	572.0 (1,773)
Freeman (1979)	ND	ND	505.0 (1,566)

[a]ND = No data. Investigator(s) did not develop estimates in this category.
[b]1984 dollars are listed parenthetically below 1970 dollars and reflect inflation (consumer price index) rather than real increases in costs.

If it is assumed that O_3 affected all of the fibers, plastics, and rubber in the study by Salmon, then annual damage costs attributed to O_3 would have been $2,026 million (1984$). Salmon did not consider O_3-related damage to paint, since the dominant paint-damaging mechanisms are soiling and gaseous sulfur dioxide. His costs refer to maintenance and replacement only, and do not allow for materials protection, substitution, etc.

In discussing other limitations of his study, Salmon cautioned that his estimates were of potential loss, not of actual observed loss. Despite this and other qualifications that lessen the usefulness of the figures derived, the Salmon study has been cited extensively and used quantitatively in a number of the subsequent studies cited here.

For example, the materials estimate by Barrett and Waddell (1973) is based primarily on the work of Salmon (1970). Barrett and Waddell supplemented this by drawing on

Mueller and Stickney (1970) for damage costs on elastomers, and on Salvin (1970) for damage costs related to dye fading. Combining some of these numbers, Barrett and Waddell stated that materials damage costs attributable to oxidants alone were $3,878 million (1984$).

Freeman (1979) reviewed earlier studies that categorized the cost of damage to materials. Using the work of Waddell (1974) and Salvin (1970), Freeman calculated that the materials damage costs attributable to oxidants and oxides of nitrogen were $2,031 million (1984$). Of this total, roughly 46% was damage to textiles and dyes (from Salvin 1970), while the remaining 54% was damage to elastomers (from Mueller and Stickney, 1970). Freeman then assumed a 20% reduction in oxidant levels since 1970, and went on to conclude that the monetary benefits of controlling oxidants, oxidant precursors, and oxides of nitrogen were between $170 and $510 million (1984$). Freeman computed the savings attributable to oxidant controls alone as $128 to $383 million (1984$).

Waddell (1974) likewise depended primarily on existing studies to calculate the national cost of air pollution in 1970. Waddell used Salmon (1970), Salvin (1970), Mueller and Stickney (1970), and Spence and Haynie (1972) to derive an estimate of $6,820 million (1984$) as the total gross annual damage for materials losses in 1970 resulting from air pollution. The component attributable to O_3 and oxidants alone was $2,790 million (1984$), within a wide range of $1,550 to $4,030 million (1984$).

Yocom and Grappone (1976), in work for the Electric Power Research Institute, estimated that the cost of air pollution damage to materials was about $6,820 million (1984$) in 1970. Of this total, O_3 was estimated to be responsible for $1,773 million (1984$), or some 26% of the total.

Because of the reliance of the later studies on the questionable data and unverified assumptions contained in the earlier ones, the results compared here are of extremely limited usefulness for cost-benefit purposes. Updated research, using current economic evaluation approaches, should be undertaken to determine the costs of O_3-induced damage.

5.10.5 Summary and Conclusions

Over four decades of research show that O_3 damages certain materials. The materials most studied in O_3 research are elastomers and textile fibers and dyes. The amount of

damage to actual in-use materials and the economic consequences of that damage are poorly characterized.

Natural rubber and synthetic polymers of butadiene, isoprene, and styrene, used in products like automobile tires and protective outdoor electrical coverings, account for most of the elastomer production in the United States. The action of O_3 on these compounds is well known, and dose-response relationships have been established and corroborated by several studies. These relationships, however, must be correlated with adequate exposure information based on product use. For these and other economically important materials, protective measures have been formulated to reduce the rate of oxidative damage. When antioxidants and other protective measures are incorporated in elastomer production, the dose-cracking rate is reduced considerably, although the extent of reduction differs widely according to the material and the type and amount of protective measures used.

The effects of O_3 on dyes have been known for nearly four decades. In 1955, Salvin and Walker exposed certain red and blue anthraquinone dyes to a 0.1 ppm concentration of O_3 and noted fading, which until that time was thought to be caused by NO_2. Subsequent work confirmed the fading action of O_3 and the importance of relative humidity in the absorption and reaction of O_3 in vulnerable dyes. Both the type of dye and the material in which it is incorporated are important factors in a fabric's resistance to O_3. Researchers found no effects from O_3 on royal blue rayon-acetate, red rayon-acetate, or plum cotton. On the other hand, anthraquinone dyes on nylon fibers were sensitive to fading from O_3. Field studies and laboratory work showed a positive association between O_3 levels and dye fading of nylon materials. At present, the available research is insufficient to quantify the amount of damaged material attributable to O_3 alone.

The degradation of fibers from exposure to O_3 is poorly characterized. In general, most synthetic fibers like modacrylic and polyester are relatively resistant, whereas cotton, nylon, and acrylic fibers have greater but varying sensitivities to the gas. Ozone reduces the breaking strength of these fibers, and the degree of reduction depends on the amount of moisture present. The limited research in this area indicates that O_3 in ambient air may have a minimal effect on textile fibers, but additional research is needed to verify this conclusion.

The effects of O_3 on paint are small in comparison with those of other factors. Past studies have shown that, of various architectural and commercial paints, only vinyl and

acrylic coil coatings are affected, and that this impact has a negligible effect on the useful life of the material coated. Preliminary results of current studies have indicated a statistically significant effect of O_3 and relative humidity on latex house paint, but the final results of those studies are needed before conclusions can be drawn.

A number of artists' pigments and dyes have been found to be sensitive to O_3 and other oxidants. Many organic pigments in particular are subject to fading or other color changes when exposed to O_3. While most, but not all, modern fine arts paints are more O_3 resistant, many older works of art are at risk of permanent damage due to O_3 induced fading. Museums and private collectors should take steps to ensure that susceptible artwork is protected from O_3 exposure.

For a number of important reasons, the estimates of economic damage to materials are problematic. Most of the available studies are now outdated in terms of the O_3 concentrations, technologies, and supply-demand relationships that prevailed when the studies were conducted. Additionally, little was (and is) known about the physical damage functions, and cost estimates were simplified to the point of not properly recognizing many of the scientific complexities of the impact of O_3. Assumptions about exposure to O_3 generally ignored the difference between outdoor and indoor concentrations. Also, analysts have had difficulty separating O_3 damage from other factors affecting materials maintenance and replacement schedules. For the most part, the studies of economic cost have not had the resources to marshal factual observations on how materials manufacturers have altered their technologies, materials, and methods in response to O_3. Rather, the analysts have been forced to rely on assumptions in this regard, most of which remain unverified through the present time.

It is apparent that a great deal of work remains to be done in developing quantitative estimates of materials damage from photochemical oxidant exposures. This is not meant to deprecate the years of research reported in this document, for much has been gained in refining the initial methodologies used for assessing damage. To date, the current state of knowledge can still be summarized by the following quote from Yocom et al. (1985):

"We have learned that some costs may be difficult to quantify either because they are minimal or because they are overshadowed by other factors, such as wear or obsolescence. We have learned that damage functions are complex and are influenced by the presence of other pollutants and by weather. We have learned that more accurate estimates of materials in place may be obtained using selective sampling and extrapolation. And we have learned that a mere cost-accounting of damage does not present a true estimate of economic cost if it does not account for the welfare effects induced by shifts in the supply-demand relationship."

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APPENDIX 5A

COLLOQUIAL AND LATIN NAMES

Alder	*Alnus serrulata* (Aiton) Willdenow
Alfalfa	*Medicago sativa* L.
Ash, green	*Fraxinus pennsylvanica* Marsh.
Ash, white	*Fraxinus americana* L.
Aspen	*Populus tremuloides* L.
Avocado	*Persea americana* Mill.
Azalea	*Rhododendron* spp.
Barley	*Hordeum vulgare* L.
Basswood (linden)	*Tilia americana* L.
Bean, broad	*Vicia faba* L.
Bean, kidney, pinto, snap, white	*Phaseolus vulgaris* L.
Beech, American	*Fagus quadrifolia* Ehrh.
Beech, European	*Fagus sylvatica* L.
Begonia	*Begonia* sp.
Birch, paper	*Betula papyrifera* Marsh
Cabbage	*Brassica oleracea capitata* L.
Celery	*Apium graveolens* L. var. *dulce* Pers.
Cherry, black	*Prunus serotina* Ehrh.
Citrus (lemon)	*Citrus volkameriana* Ten. and Pasq.
Clover, ladino, white	*Trifolium repens* L.
Clover, red	*Trifolium pratense* L.
Corn	*Zea mays* L.
Cotton	*Gossypium hirsutum* L.
Cottonwood (poplar)	*Populus deltoides* Marsh
Cress, garden	*Lepidium sativum* L.
Cucumber	*Cucumis sativus* L.
Dock	*Rumex obtusifolius* L.
Geranium	*Pelargonium* x *hortorum* Bailey
Fescue, tall	*Festuca arundinacea* Schreb..
Fir, Douglas	*Pseudotsuga menziesii* (Mirb.) Franco.
Fir, Fraser	*Abies fraseri* (Pursh) Poir.
Golden-rain	*Koelreuteria paniculata* Laxm.
Grape	*Vitis labruscana* Bailey
Honey locust	*Gleditsia triacanthos* L.
Ivy	*Hedera helix* L.
Kenaf	*Hibiscus cannabinus* L.
Juniper, shore	*Juniperus conferta* Parl.
Lettuce	*Lactuca sativa* L.
Lilac	*Syringa vulgaris* L.
Mangel	*Beta vulgaris* L.

Maple, red	*Acer rubrum* L.
Maple, sugar	*Acer saccharum* Marsh
Milkweed	*Asclepias* spp.
Mint	*Mentha piperita* L.
Oak, white	*Quercus alba* L.
Oak, red	*Quercus rubra* L.
Oats	*Avena sativa* L.
Onion	*Allium cepa* L.
Pea	*Pisum sativum* L.
Pepper	*Capsicum annuum* L.
Petunia	*Petunia hybrida* Vilm.
Pine, Jeffrey	*Pinus jeffreyi* Grev. and Balf.
Pine, loblolly	*Pinus taeda* L.
Pine, pitch	*Pinus rigida* Mill.
Pine, ponderosa	*Pinus ponderosa* Laws.
Pine, Scots	*Pinus sylvestris* L.
Pine, shortleaf	*Pinus echinata* Mill.
Pine, slash	*Pinus elliotti* Englem.
Pine, white	*Pinus strobus* L.
Plane, London	*Platanus* x *acerifolia* (Ait.) Willd.
Poplar	*Populus nigra* L.
Poplar, hybrid	*Populus maximowiczii* x *P. trichocarpa*
Poplar, yellow	*Liriodendron tulipifera* L.
Potato	*Solanum tuberosum* L.
Radish	*Raphanus sativus* L.
Rape, spring	*Brassica napus* L. var. *napus*
Sequoia, giant	*Sequoiadendron giganteum* Buchholz
Sorghum, hybrid	*Sorghum bicolor* (L.) Moench x *Sorghum* x *drummondii* (Steudel) Millsp. and Chase
Soybean	*Glycine max* (L.) Merr.
Spinach	*Spinacea oleracea* L.
Spruce, red	*Picea rubens* Sarg.
Spruce, Norway	*Picea abies* (L.) Karst.
Spruce, sitka	*Picea sitchensis* (Bong.) Carr.
Strawberry, cultivated	*Fragaria* x *ananassa* Duch.
Strawberry, wild	*Fragaria virginiana* Duch.
Sunflower	*Helianthus annuus* L.
Timothy	*Phleum pratense* L.
Tobacco	*Nicotiana tabacum* L.
Tomato	*Lycopercicon esculentum* Mill.
Wheat	*Triticum aestivum* L.