



Effects of CO₂ and Climate Change on Forest Trees

EXECUTIVE SUMMARY

INTRODUCTION

Concentrations of carbon dioxide (CO₂) and other trace gases such as methane are increasing in the atmosphere due to human activities. Evidence suggests that increased levels of these gases will produce increases in global temperatures and associated changes in precipitation patterns and amount, cloudiness, and other atmospheric factors which are collectively known as "climate change."

The U.S. Environmental Protection Agency (EPA) has created the Global Climate Research Program (GCRP) to provide integrated research on all aspects of the trace gases and climate change. An important focus of the GCRP at the EPA's Environmental Research Laboratory in Corvallis, Oregon (ERL-C), is to understand how CO₂ and climate change will affect vegetation in North America. A crucial goal of this research is to provide information to policy makers who must make decisions about forest resources. Answers are needed for these key policy issues:

- What are the effects of elevated CO₂ and climate change on the growth and productivity of forest trees?
- Will elevated CO₂ and climate change alter the carbon sequestration potential of forest trees?



- What is the magnitude of elevated CO₂ and climate change impacts on forest trees and will the impacts be widely distributed?

Existing data are not adequate to provide defensible scientific answers to the above policy issues, at either the level of an individual tree or a forest stand. Thus, ERL-C has begun the study called *Effects of CO₂ and Climate Change on Forest Trees*, to help determine how trees are influenced by elevated CO₂ and climate change. The focus will be on Douglas fir, a key Pacific Northwest forest species, which is ecologically and economically important and adapted to the current local climate conditions.

GENERAL APPROACH

To evaluate the qualitative and quantitative effects of climate change on forest trees, four separate but interacting research activities will be undertaken; scoping studies, experimental tasks, modeling tasks, and integration and inference activities (Figure 1).

SCOPING STUDIES

CO₂ and Climate Analysis

To establish experimental conditions, CO₂, temperature, and moisture records were examined for past and present trends. It was established that in 1990 the atmospheric concentration of CO₂ was 353 ppm, or 25% higher than in pre-industrial times. At a moderate rate of increase, the CO₂ concentration in the atmosphere may double to about 700 ppm by the year 2059. However, other trace gases are increasing along with CO₂, and will contribute to global warming over this same period of time. Thus, realistically concentrations of CO₂ alone will be in the range of only 450-500 ppm when global temperatures increase to a level equivalent to that associated with a doubling of CO₂ concentrations.

To predict the impacts of increased CO₂ levels on future temperatures in the Pacific Northwest, we reviewed the output of four atmosphere/climate models. The models projected a significant

General Approach

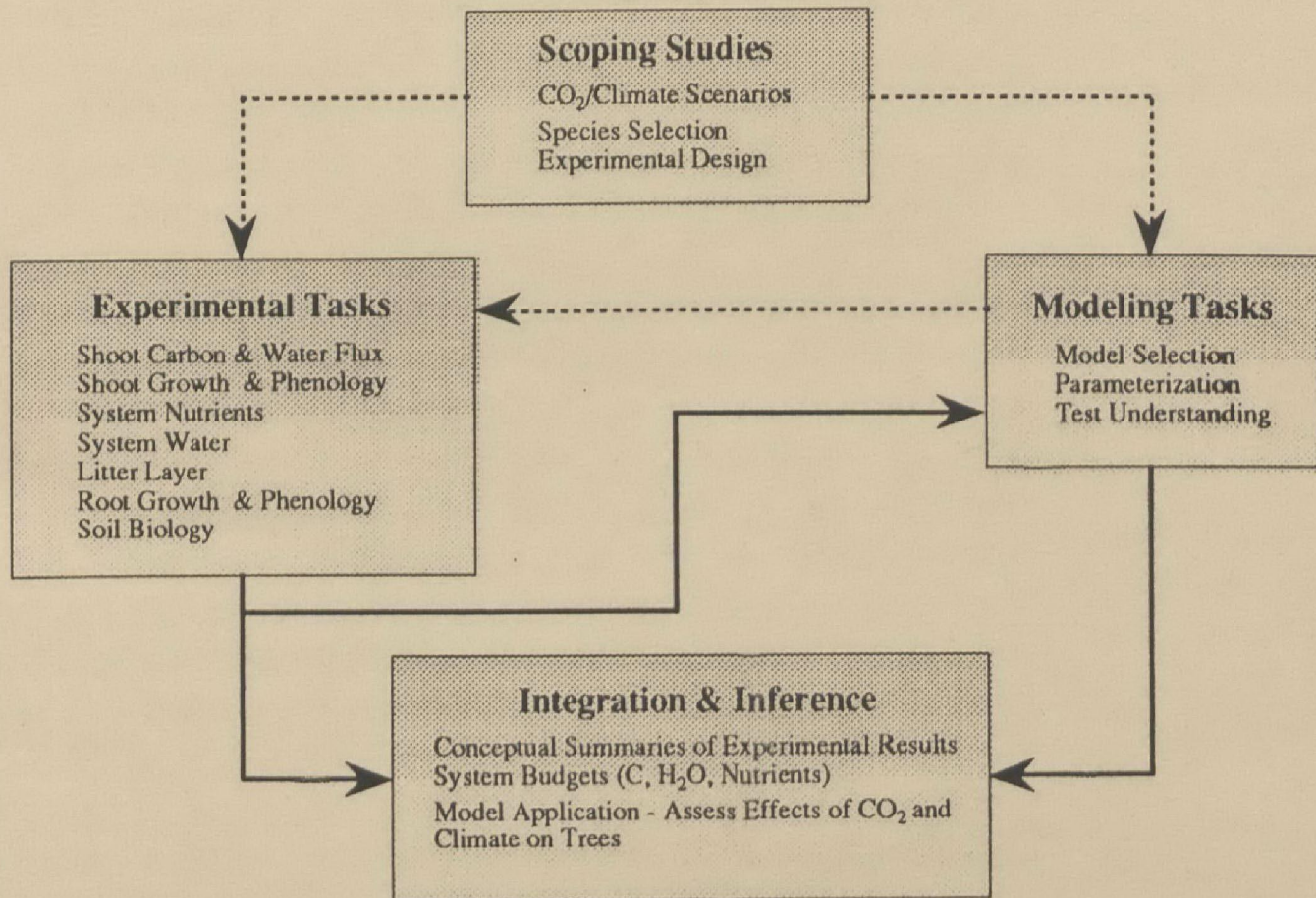


Figure 1. General research approach and relationship among the various tasks. The dotted lines indicate information flow, and the solid lines indicate data flow.

warming and drying of the climate in the Pacific Northwest using a scenario which included a doubling of atmospheric CO₂ concentrations. For example, in the Willamette Valley temperatures could increase for all months resulting in a mean from 2.3 to 5.1°C, depending on the model used. Also, growing degree-days are projected to increase significantly by 27% to 171% from current conditions, with greater percentage increases in growing-degree days at higher elevations.

The model-based projections for precipitation under double CO₂ concentrations did not show the same consistent trend as temperature. Model outputs ranged from essentially no change to 27% increase in annual precipitation. All models projected that the current seasonal pattern of relatively dry summers and wet winters will persist, but the proportion of rain vs. snow from current conditions may change because of the increase in temperature.

Overall, the future climates projected from the climate models represent a significant change from present conditions. When viewed in a south-to-north transect, the projected temperature changes were equivalent to shifting current climates from 200 to 500 km north, i.e., moving the climate of northern California into northern Oregon. However, strict geographical analogues of future climate were difficult to define since projected precipitation may remain unchanged. Similarly, from an elevational perspective, the climate projections suggested a 500 to 1000 m upward movement of temperature regimes.

Species Selection

Douglas fir (*Pseudotsuga menziesii*), currently the most important timber species in the Pacific Northwest, was selected as the experimental plant material. Douglas fir is widely distributed, growing under a variety of climatic conditions. Seedlings were grown from "woods run" seed lots, rather than half-sib or full-sib seed lots, to ensure that the seedling's genetic variability reflects that of the natural forest. Seed lots were selected from five low-elevation seed zones (<600 m) on the western side of the Oregon Cascade Mountains in the Willamette Valley. Seedlings were provided by the Weyerhaeuser Company as 1+1's, i.e., grown for one year in a seed bed, then one year in a nursery bed, and then transplanted into terracosms as bare-root, 2-year-old stock.

EXPERIMENTAL DESIGN

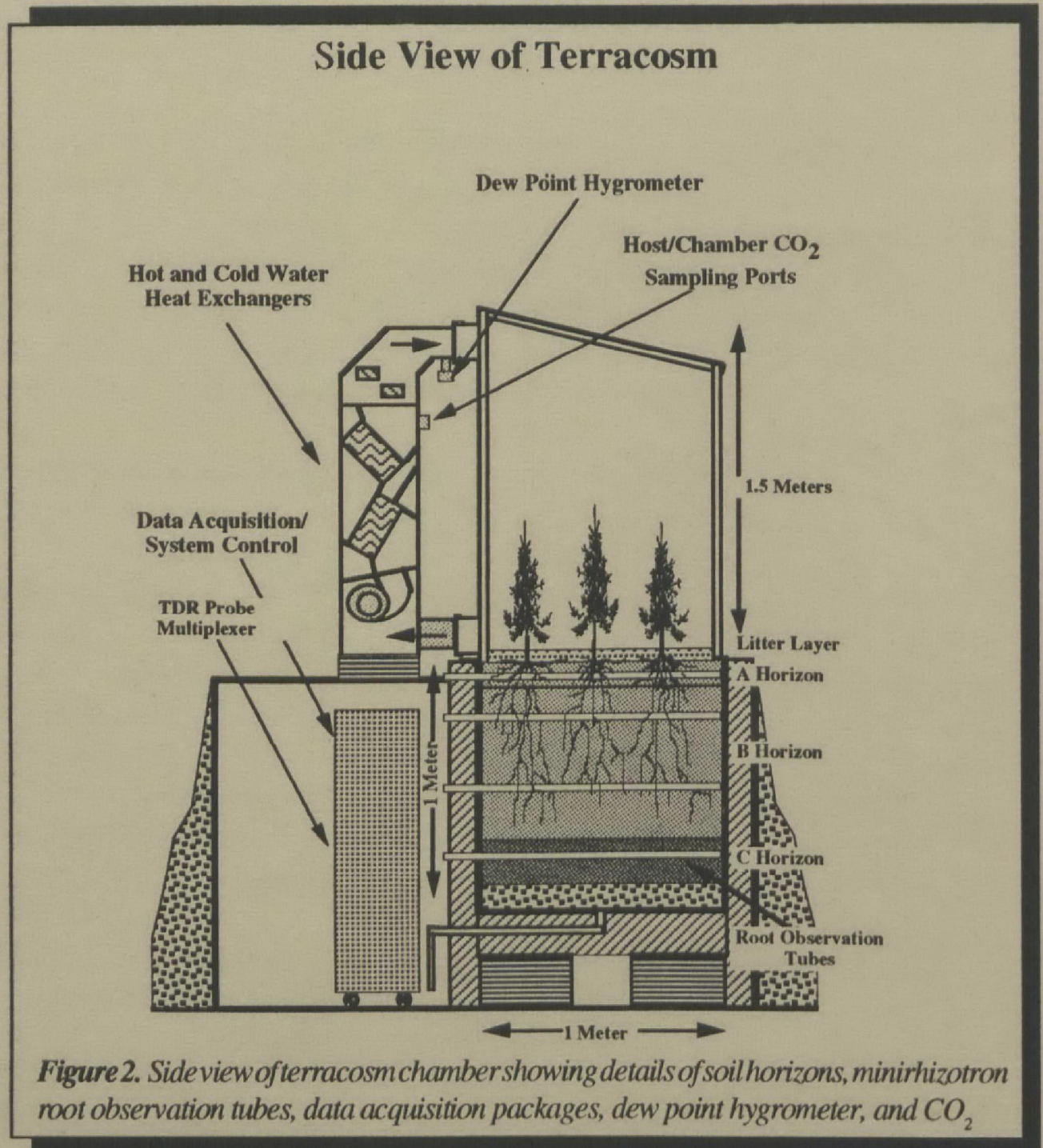
Experimental Facilities: The study uses twelve 1.0 x 2.0 meter surface area and 1.2 x 1.5 meter high "terracosms" built at ERL-C (Figure 2). Terracosms are closed systems including a sun-lit upper chamber where atmospheric and climate conditions are controlled and measured, and a lower soil lysimeter where soil water content is controlled and soil parameters are monitored. The terracosms allow researchers to achieve control of the environment and provide a mechanistic understanding of the effects of elevated CO₂, temperature and drought on above- and belowground tree and soil processes.

While the overall study will focus on the long-term effects of increasing CO₂ and climate change on Douglas fir seedlings growing in the terracosms, supporting experiments also will be conducted in pots, large soil lysimeters, and at field sites. These studies will provide additional data necessary for modeling activities and for comparison between responses of trees grown in the terracosms and trees growing under native conditions.

Experimental Treatments: The experimental design is a 2 x 2 factorial with two CO₂ treatments, two temperature treatments, and three replicate terracosms per treatment combination. The two CO₂ levels are ambient and ambient plus 200 ppm (a possible CO₂ increase in approximately 50 years). The two temperature levels are ambient and ambient plus 4°C (a predicted temperature over the same period of time). The increased CO₂ and increased temperature treatments are added continuously to the current ambient levels to preserve natural diurnal, seasonal and yearly variability. Ambient conditions are based on continuous measurements from a meteorological tower at the research site.

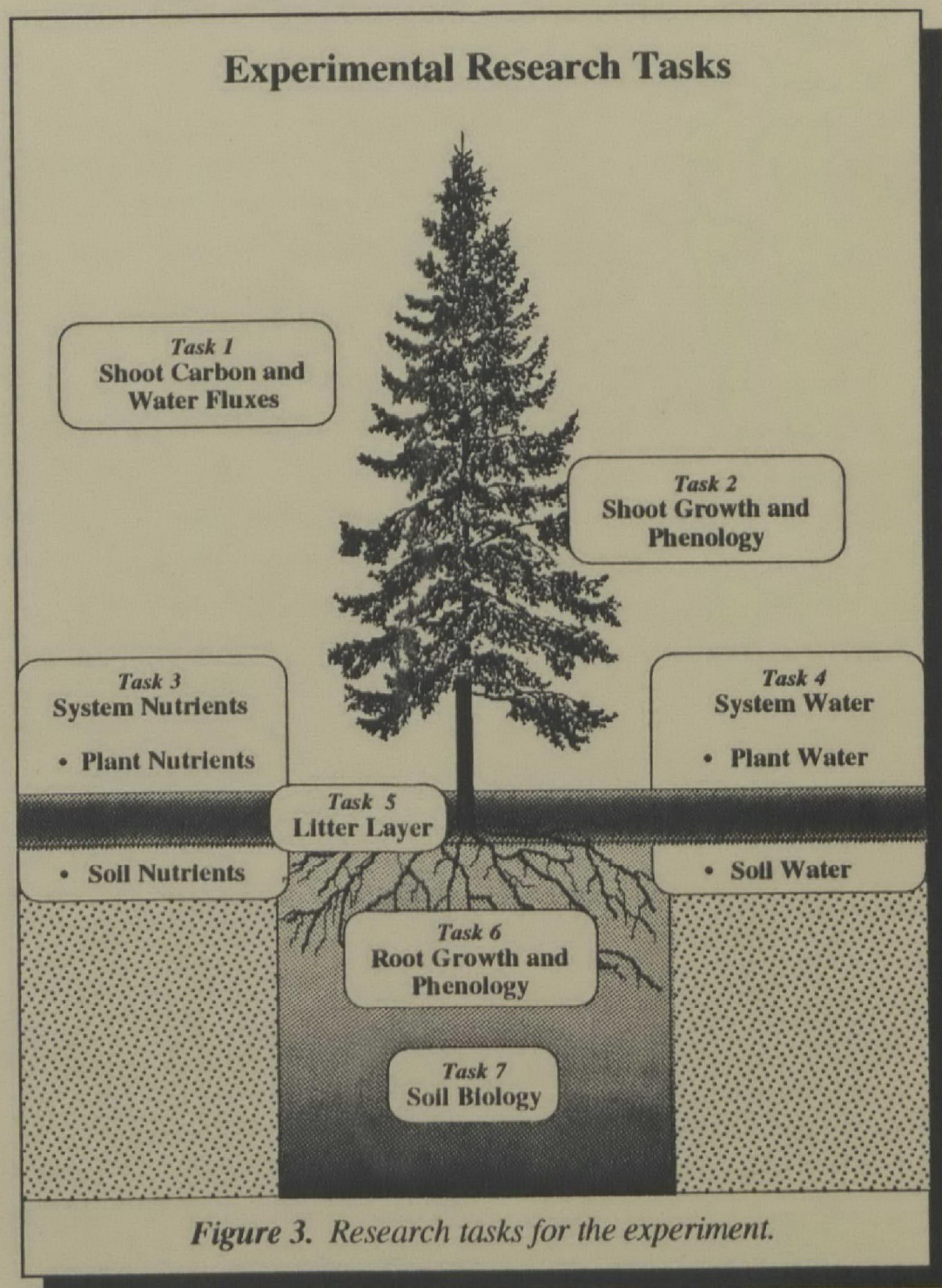
Soil Selection: Douglas fir is found primarily on two kinds of soils in the Cascade Mountains of Oregon. Roughly 30% grows in high-elevation sandy loam derived from volcanic ejecta and glacial till. The other 70% grows in a heavy-textured soil derived from colluvium and residuum. The sandy loam soil was chosen

for use in the terracosms because of the ease with which it could be excavated and reconstituted and its resiliency to disturbance. The soil was collected by horizon from the perimeter of a 500-600 year-old Douglas fir stand in the Oregon Cascade Mountains and then reconstructed by horizon in the terracosms (Figure 2). Sensors, samplers and minirhizotron tubes were placed in the soil during the reconstruction process.



EXPERIMENTAL TASKS

Seven research tasks were chosen to answer fundamental science questions of this project (Figure 3). For each task specific objectives and experimental approaches were identified. Outputs will be in the form of data to address the science questions, and as specific inputs for a physiological process-based tree growth model.



TASK 1

Shoot Carbon & Water Fluxes

Science Questions:

- *Will the net carbon flux for plants change in response to elevated CO₂ and climate change?*
- *Will plant water-use efficiency (WUE) increase in response to elevated CO₂ and climate change, and will this WUE increase occur on a vegetated area basis as well as on a single plant basis?*

Objectives:

- To measure at the whole plant canopy level photosynthetic, respiration, and transpiration rates in response to the individual and combined effects of increased CO₂ and increased temperature.
- To measure at the needle/branch level photosynthetic, respiration and transpiration rates, and stomatal conductance changes in response to elevated CO₂ and climate change. These measurements will be made with different photosynthetically active radiation (PAR) levels, temperatures, and CO₂ concentrations, and will be made for different needle age classes and leaf nitrogen levels.
- To measure at the canopy and needle/branch levels, diel and seasonal patterns in photosynthetic, respiration, and transpiration rates, and stomatal conductance in response to elevated CO₂ and climate change.
- To measure at the needle/branch and whole plant level the influence of leaf water potential (WP), and air vapor pressure deficit (VPD) on stomatal conductance and transpiration. These measurements will be made with different photosynthetically active radiation (PAR) levels, temperatures, and CO₂ concentrations; and for different needle age classes and leaf nitrogen levels.
- To derive photosynthesis, respiration and stomatal conductance input variables for the TREGRO model based on the above measurements and literature values.

Approach: Photosynthesis will be measured at two scales: 1) total plant canopy using the terracosm upper chamber, and 2) needle/branch using a portable gas-exchange system. Measurements may also be made on a whole plant level to assist in scaling from the needle/branch to canopy levels. Canopy level measurements will be made in the terracosms and needle/branch (and possibly whole plant) measurements will be made primarily in supporting studies. A limited number of needle/branch measurements will be made in the terracosms to determine how the CO₂ and temperature treatments affect the shoot responses characterized in the supporting studies. Respiration rates will be measured throughout the duration of the experiment to quantify net carbon flux to characterize metabolic rates and energy consumption. Respiration will be measured on the needle/branch and canopy scale, using a darkened chamber during the day, and/or under natural darkness at night, as necessary, to obtain accurate measurements. Respiration will be partitioned, as feasible, between growth and maintenance components. Transpiration will be measured at the following three scales: 1) plant canopy in the terracosms, 2) whole plant in the terracosms, and 3) needle/branch in supporting experiments. Stomatal conductance will be derived from transpiration and leaf temperature measurements on both the needle/branch and whole plant scale.

Outputs:

- Characterization of net carbon flux for Douglas fir shoots in response to elevated CO₂ and climate change.
- Characterization of WUE for Douglas fir shoots in response to elevated CO₂ and climate change.
- Characterization of diel and seasonal patterns of carbon and water fluxes for Douglas fir shoots in response to elevated CO₂ and climate change.
- Characterization of relationships among photosynthesis, respiration, tissue C/N ratios, and total nonstructural carbohydrates (TNC).
- Evaluation of potential for changes in plant canopy temperature induced by transpiration reductions.

TASK 2
Shoot Growth,
Morphology,
Allometry,
Phenology, &
Carbon
Partitioning

Science Questions:

- *Will shoot growth change in response to elevated CO₂ and climate change?*
- *Will shoot morphology and allometric relationships change in response to elevated CO₂ and climate change?*
- *Will shoot phenology change in response to elevated CO₂ and climate change?*
- *Will the biochemical partitioning of C in shoots change in response to elevated CO₂ and climate change?*

Objectives:

- To measure, at the individual plant level, effects of elevated CO₂ and climate change on shoot biomass (dry weight) by age class of the main stem, branches, needles, and buds.
- To measure, at the individual plant level, effects of elevated CO₂ and climate change on shoot allometric parameters, i.e., stem diameter, height, and needle elongation.
- To measure, at the individual plant level, effects of elevated CO₂ and climate change on shoot morphology and allometric relationships including numbers, rank, and weights of branches, needles, and buds for all age classes of tissue. Needle areas will be taken to determine specific needle weights.
- To measure, at the individual plant level, effects of elevated CO₂ and climate change on shoot phenology. The dates of key events, such as onset of bud break, secondary bud break, and first frost will be carefully noted.
- To quantify the changes in the biochemical partitioning of C between structural and nonstructural compounds in the various shoot fractions in response to elevated CO₂ and climate change.

Approach: The study will focus on the long-term effects of increasing CO₂ and climate change on Douglas fir seedlings growing in the terracosms. Baseline measurements will be taken at an initial destructive harvest of 50 bare-root seedlings. Interme-

diate measurements will be taken to follow the course of tree growth over time; they will be nondestructive in the terracosms but destructive in the supporting experiments. Final destructive measurements will be made to look at the cumulative effects of the treatments and experimental conditions on overall tree growth.

Outputs:

- Characterization of shoot growth of Douglas fir in response to elevated CO_2 and climate change.
- Characterization of shoot morphology and allometric relationships of Douglas fir in response to elevated CO_2 and climate change.
- Characterization of shoot phenology of Douglas fir in response to elevated CO_2 and climate change.
- Characterization of changes in the biochemical partitioning of C between structural and nonstructural compounds in the various shoot fractions in response to elevated CO_2 and climate change.
- Evaluation of the performance of the CERES device for continuous analysis of seedling growth through stem diameter measurement.

TASK 3

System

Nutrients

Science Questions:

- *Will elevated CO_2 and climate change affect plant nutrient balance?*
- *Will the response of forest trees to elevated CO_2 and climate change alter plant and soil nutrient pools?*

Objectives:

- To monitor changes in inorganic nutrient concentrations in above- and belowground plant tissues, litter material, soils and soil solutions as a function of CO_2 and climate change.
- To evaluate the effects of elevated CO_2 and climate change on inorganic nutrient balance in Douglas fir seedlings.

- To evaluate the physiological significance of nutrient availability in respect to the observed responses to elevated CO₂ and climate change.
- To measure C, N, S, and TNC concentrations in above- and belowground plant tissue, litter material, soil, and soil solutions.

Approach: Chemical analysis will be conducted on plant tissues, litter material, soil samples, and soil solutions to 1) determine C and nutrient concentrations, 2) quantify C and nutrient pools, and 3) monitor changes in these pools over time. Samples will be from Tasks 2, 5, and 6 focused on above- and belowground responses, with the results of the analyses evaluated within the task where the samples originate. Questions on the whole plant and soil nutrient status will be addressed within this task. Analyses will include C/H/N/S, inorganic nutrients, and TNC.

Outputs:

- Characterization of complete soil macro- and micronutrient composition at the beginning and end of the experiment both in the individual terracosms and at the field soil collection site.
- Evaluation of changes in plant nutrient concentration, composition, and relative nutrient ratios to assess differences between experimental treatments.
- Characterization of changes in plant available soil nutrient levels over the period of the study.
- Evaluation of the dynamic relationships between plant and soil nutrient pools as affected by elevated CO₂ and climate change.
- Analysis of C/N and lignin/N ratios in plant tissues (needles and roots), total C and N in soil, and net C and N storage.

TASK 4

System Water

Science Questions:

- *Will elevated CO_2 and climate change affect plant water balance?*
- *Will elevated CO_2 and climate change significantly change the driving forces and resistances that determine water flow in the soil-plant-atmosphere continuum?*

Objectives:

- To measure the effects of elevated CO_2 and climate change on the relationship between plant and soil water potential.
- To measure the effects of elevated CO_2 and climate change on the overall system water balance.
- To measure and monitor volumetric water content in each soil horizon. These data will be used to regulate irrigation scheduling and for calculating system water budgets.

Approach: Plant water potential will be measured at the needle level four times a year using destructive sampling and thermocouple psychrometry. Efforts will be made early in the experiment to develop and apply a method for continuous and nondestructive measurement of water status on a whole plant basis. This technique will be based on the application of the CERES Device. Because regular collection and drying of soil samples, to determine soil water, is not practical due to the number of samples and time required to process them, two non-destructive technologies were selected to provide measures of soil water. The first is a relatively new technology called time-domain reflectometry (TDR), and the second is the neutron moisture probe.

Outputs:

- Characterization of the independent and interactive effects of elevated CO_2 and climate change on plant water balance and soil water status.
- Characterization of relationship between short-term seedling stem diameter changes and plant and soil water status.

- Evaluation of the potential for the continuous nondestructive measurement of plant water status and plant water flux through the combined use of the CERES device and stem sap flow gauges.
- Daily characterization of volumetric soil water content by soil horizon and rooting volume to determine seasonal irrigation scheduling.

TASK 5

Litter Layer

Science Questions:

- *Will the rate of litter decomposition change in response to elevated CO₂ and climate change?*
- *Will nutrient cycling through the litter layer change in response to elevated CO₂ and climate change?*

Objectives:

- To measure changes in the rate of litter decomposition with elevated CO₂ and climate change.
- To determine how elevated CO₂ and climate change affect nutrient cycling in the forest floor litter layer.
- To measure changes in litter layer quality (C/N ratio, lignin/N ratio, etc.) throughout the study.
- To determine the effects of elevated CO₂ and climate change on the net storage of carbon in the forest floor litter layer.

Approach: This task focuses on the long-term effects of elevated CO₂ and climate change on decomposition and nutrient cycling in the forest floor of the terracosms. Weight loss and changes in mineral nutrient and organic chemistry of the litter layer will be used as integrative measures of litter processing and carbon storage. Rates of litter layer decomposition and changes in chemistry will be monitored using litter contained in inert mesh bags and needle packs.

TASK 6

Root Growth, Morphology, Phenology, & Carbon Partitioning

Outputs:

- Characterization of litter layer decomposition rates, and carbon and nutrient cycling of Douglas fir litter under elevated CO_2 and climate change.
- Characterization of changes in litter quality while undergoing decomposition under elevated CO_2 and climate change.
- Characterization of net storage of carbon in the litter layer under elevated CO_2 and climate change.

Science Questions:

- *Will root growth change in response to elevated CO_2 and climate change?*
- *Will elevated CO_2 and climate change affect the allometric relationships among coarse roots, fine roots, and mycorrhizae?*
- *Will root phenology be altered by elevated CO_2 and climate change?*
- *Will the biochemical partitioning of root C and N be affected by elevated CO_2 and climate change?*

Objectives:

- To quantify root growth with numbers of roots produced, their distribution and turnover, and the total weight of the standing stock of roots under elevated CO_2 and climate change.
- To quantify dynamics of root production, development, and mortality under elevated CO_2 and climate change, and to determine the effects on root allometries, i.e., distribution of biomass among coarse roots, nonmycorrhizal fine roots, and mycorrhizae.
- To characterize effects of elevated CO_2 and climate change on root phenology.
- To quantify biochemical partitioning of C between structural and nonstructural compounds in the various root fractions.

Approach: Roots will be assessed by two methods, one destructive (cores-to-depth) and one nondestructive (minirhizotrons). Destructive sampling will be limited in the terracosms to avoid destruction of the biological and physical integrity of the belowground component, recognizing that infrequent destructive sampling may be insufficient to characterize root biomass with a high degree of accuracy. Two soil cores (5 cm i.d. x 95 cm) will be collected twice a year and separated into 10-cm segments by depth. Samples will be sorted into four fractions: live coarse roots (> 2 mm), live fine roots (< 2 mm) and mycorrhizae, dead coarse roots, and dead fine roots and mycorrhizae. Besides dry weights, the separated soil and root fractions will be analyzed for C fractions and nutrients. Total C and N will be measured in the root “cellulose”, “extractives”, and “lignin” fractions. Minirhizotrons will be used with miniature video camera system to provide a nondestructive measure of root production and dynamics.

Outputs:

- Characterization of the effects of elevated CO₂ and climate change on root growth.
- Characterization of changes in root phenology caused by elevated CO₂ and climate change.
- Characterization of changes in the distribution of C, nutrients, “cellulose”, “extractives”, and “lignin” in the belowground standing stocks of coarse roots, nonmycorrhizal fine roots and mycorrhizae.
- Characterization of changes in the biochemical partitioning of C between structural and nonstructural compounds in the various root fractions.

TASK 7

Soil Biology

Science Questions:

- *Will bacterial and fungal populations, soil fauna, nematode community structure, and the colonization of tree roots by mycorrhizal fungi, be affected by elevated CO₂ and climate change?*
- *Will soil greenhouse gas production, processing, and emissions be affected by elevated CO₂ and climate change?*

Objectives:

- To quantify the effects of elevated CO₂ and climate change on total and active soil microbial populations (bacteria and fungi), nematode community structure, and soil fauna populations.
- To characterize the carbon transformation rates of the bulk soil microbial population under elevated CO₂ and climate change as indicated by the activities of enzymes processing organic compounds.
- To quantify the effects of elevated CO₂ and climate change on the colonization of roots by mycorrhizal fungi and on the diversity of mycorrhizal fungi colonizing roots.
- To measure trace gas production and loss within the soil profile and the physical, chemical, and environmental factors affecting their production and loss.

Approach: Measures of soil bacteria, fungi, mycorrhizae, nematodes and soil enzymes will be determined using samples from the cores-to-depth collected twice a year. Soil fauna populations will be assessed using separate litter and soil samples collected at the same biennial samplings. Bacterial and fungal total biomass estimates will be performed by direct microscopy on hyphae and bacterial cells. Bacterial and fungal active biomass will be determined by fluorescein diacetate staining followed by direct microscopy. Soil microbial activity will be determined by measuring activity of enzymes such as β -glucosidase, peroxidase, phenoloxidase, phosphatase, and proteinase. Mycorrhizal fungi colonization will be determined by microscopy. Mycorrhizal

fungi diversity will be determined on a limited basis by assessment of nucleic acid “fingerprints” of mycorrhizal fungi. The fate of key soil fauna species, including earthworms, spiders, millipedes, and centipedes, will be assessed by direct observation of litter and soil samples.

Two kinds of soil gas samples will be collected and analyzed for CO_2 , CH_4 , N_2O , and O_2 . Soil gas samplers have been placed at five depths in the terracosm soil. Headspace chambers will be used to measure soil surface emission (litter layer-air interface). Both kinds of samples will be analyzed using gas chromatography.

Outputs:

- Estimates of total and active bacterial and fungal biomass, nematode community structure, and soil faunal populations under elevated CO_2 and climate change.
- Estimates of soil microbial activity as affected by elevated CO_2 and climate change.
- Estimates of root colonization by mycorrhizal fungi under elevated CO_2 and climate change.
- Characterization of the effects of elevated CO_2 and climate change on differentiation of the mycorrhizal fungi community on roots.
- Estimates of annual emissions of greenhouse gases from terracosm soils.
- Characterization of greenhouse gas production and processing in terracosm soils.

MODELING TASKS

The primary goal of these tasks is to parameterize a process-based tree growth model to study the responses of trees to elevated CO_2 and climate change. The TREGRO model was selected because it simulates the growth of both above- and belowground plant components and incorporates fundamental processes likely to be affected by elevated CO_2 and climate change. The model is cur-

rently operational and provides a reasonable simulation of plant growth. Parameterization of the TREGRO model will occur using data from the experimental research tasks from this project, with additional data from the initial biomass values for our population of Douglas fir trees, published literature, and the Ozone and Forest Response Program at ERL-C. The parameterized model will be used to test our conceptual understanding of how Douglas fir responds to elevated CO₂ and climate change by comparing experimental results to model predictions in an iterative fashion. The output from the modeling tasks will be a parameterized and calibrated version of TREGRO for Douglas fir, useful for studying the effects of elevated CO₂ and climate change.

INTEGRATION & INFERENCE

This study will support policy objectives of the U.S. Interagency Committee on Earth and Environmental Sciences (CEES), particularly in the areas of effects of global climate on ecosystems and influences (feedbacks) of ecosystems on atmospheric CO₂ concentrations and climate change processes. The support will be in the form of providing: 1) an integration of the experimental results into a cohesive understanding of the effects of elevated CO₂ and climate change on forest trees and soils, and 2) inference of these effects across time and space through the application of a tree growth model.