1 **Natural Migration Rates of Trees: Global Terrestrial Carbon Cycle Implications**
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10 INTRODUCTION
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12   Migration of populations or species of trees ("tree migration") in response to climate change
13 is of interest both to paleoecologists who assess past vegetational responses to climate change,
14 and to global ecologists concerned with future climate change induced by increasing greenhouse
15 gases (GHGs). A major difference between climate-driven tree migrations in prehistory and
16 those expected in the future is the high speed of the latter climate change. The 4-6 km which
17 temperate-zone July isotherms are predicted to move northward annually (Solomon et al. 1984)
18 are about an order of magnitude more rapid than prehistoric rates deduced from paleoecological
19 evidence. Assuming prehistoric rates of warming matched the rate of tree migration (T. Webb
20 1986; Prentice et al. 1991), fossil pollen data allow inference of 400 m/yr (Davis 1983) to 800
21 m/yr (Gear and Huntley 1991) of climate change and tree migration at most. The rate may be
22 even slower if tree migration includes the establishment and maturity of the tree population
23 (Bennett 1986) as well as the processes of seed transport, establishment, growth and seed
24 production, normally defined as migration (e.g., Davis, 1989; MacDonald et al. 1993).
25   The difference in definition is important for predicting the amount of carbon (CO_2 is the
26 most important of the GHGs) that will reside in the atmosphere in the future. The oceans
27 provide the ultimate long-term control on atmospheric carbon concentrations (e.g., Sundquist
28 1985; Prentice et al. 1993). However, the terrestrial biosphere modulates the shorter-term
29 changes in carbon content, measured over a few decades or centuries (Gammon et al. 1985;
30 Keeling et al. 1995; Denning et al. 1995). Forests store about 2/3 of above-ground terrestrial
31 organic carbon and over half of the carbon present in the world's soils (Dixon et al. 1994). The
32 presence of a few trees on the landscape (e.g., MacDonald et al. 1993), indicated by
33 establishment and reproductive maturity of seed trees, contributes little carbon to terrestrial
34 stocks. Instead, closed-canopy stands of mature mixed or pure species provide the dense
35 carbon stocks of interest. These are associated with mature, stable populations.
36   Projections of global terrestrial carbon cycle dynamics under warmer climates of a doubled
37 GHG concentration have used static vegetation models (Prentice and Solomon 1990). These
38 projections hinge on the critical assumption that the migration of trees and the formation of
39 mature, stable populations at new locations proceeds at the same rate as the climate change to
40 which it is responding (Sedjo and Solomon 1989; Leemans, 1989; Prentice and Fung 1990;

1   Smith, et al. 1992a, b; Smith and Shugart, 1993a, b; Solomon et al. 1993). To date, these static
2   model exercises have projected increased global terrestrial carbon storage under future
3   warming, because large new land areas suitable for forest growth are created either by warming
4   of high latitude treeless tundra, or by increased hydrologic cycle intensity in treeless steppe.

5   Yet, unchanged or decreased rather than increased carbon storage may result if forests
6   cannot migrate and establish in the time required to attain the doubled GHG benchmark. The
7   objective of the current paper is to estimate the time required for forests to develop in regions
8   new to them, to estimate the time required for forests to die out where they become climatically
9   obsolete, then to calculate the impacts of those times on future terrestrial carbon stocks.

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12   MIGRATION RATE LIMITS

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14   For our purposes, three time-variable steps may be distinguished in the migration process:
15   seed transport, coupled with establishment of seedlings; reproductive maturation of individuals;
16   and, forest, i.e., maturation of populations in closed canopy forests.

17   Seed Transport. Tree seed transport, whether by wind, animals or running water, requires
18   little more than a day. Establishment of tree seeds (seed germination and growth of a taproot
19   into mineral soil) requires one to two growing seasons. Taken together, transport and
20   establishment are instantaneous compared with the multiple decades required for warming.
21   However, transport and establisment is not a singular process but rather, must be repeated
22   multiple times, each consisting of several time-variable processes.

23   Some shifting populations possess sharp boundaries which resemble a slowly moving wave
24   (Davis, 1987). These depend upon the regular transport of seeds 10-100 m, followed by a few
25   decades to centuries of tree maturity before another 10-100 m "step" is taken. Other population
26   boundaries consist of "infection sites," located well beyond of the main population, surrounded
27   by population voids (Davis, 1987, 1990), and derived from irregular transport events. The
28   latter pattern results from migration comprised of rare long-distance transport and establishment
29   events, and is followed by local population growth via transport and establishment between
30   founder seed sources (Bennett 1984, Davis 1987). This migration form probably produces the
31   most rapid migration rates (Leishman et al., 1992; Collingham et al., 1996). Multiple rare
32   events, by definition, form a (long) time-ordered process. Jumps of 100-200 km have been
33   detected in the Holocene at about 1000 year intervals (S. Webb, 1986; Davis et al., 1986).

34   Tree Maturation. The time required to complete tree life cycles varies considerably. Most
35   evergreen and deciduous conifers can reproduce within 10 years of seed germination and
36   deciduous hardwoods, within 15 years (Harlow et al. 1979). Yet, these times apply to trees
37   growing in full sunlight (i.e., without other trees nearby), and to reproduction by trees still the
38   size of saplings (i.e., 2-5 meters tall). Annual seed production in this case is very small (1000s
39   instead of 100,000s of seeds per tree; Burns and Honkala 1990), and transport distances may
40   be quite small because of the low stature of the seed sources (e.g., <50 m for trees <5 m tall,

1   according to experiments by Greene and Johnson 1989). The short life cycling times occur
2   when tree populations invade treeless areas and form clumped seed sources (with low carbon
3   densities), rather than when populations expand to form areas of continuous forest between
4   seed sources, or grow rapidly within stands already populated by mature forests.

5   Forest Maturation. The development of scattered individuals and stands of trees into closed
6   canopy forests containing maximum carbon densities takes considerably longer than maturation
7   of isolated trees. First, the areas between trees and stands must be occupied. If 10-15 year-old
8   trees each generation produce seedlings 50-100 m away, even a founder population of one
9   tree/km^2 (not a rare event distribution but one calculated by Greene and Johnson, 1995, as rare
10   enough to constrain metapopulation expansion) requires 5-10 generations to plant seeds in all
11   parts of the square kilometer. The sequential completion of 5 or 10 generations could require
12   50-100 years in conifers and 75-150 years in deciduous hardwoods from dense populations,
13   and a millennium from sparse tree densities (ibid.). The minimum number of life cycles
14   obviously depends on the distances between seed sources, but would usually exceed the 5-10
15   generations exemplified at distances beyond about 2-10 km from the original forests (ibid.).
16   This is consistent with estimates of mid-Holocene hemlock occupation of northern lower
17   Michigan in about 500 years (Davis et al., 1986) and documentation of periods exceeding 1000
18   years for local forest development during the forestation of the British Isles (Bennett 1986).

19   Second, closed forests must develop. Tree growth rates are much slower in the shade than in
20   the open. In closed forests, trees must grow to reach the canopy surface before producing
21   significant numbers of seeds (Daubenmire, 1959; Waring and Schlesinger, 1985). This
22   requires a minimum of 25-50 years in most temperate and boreal regions in which closed
23   canopy forests exist (Harlow et al. 1979). Certain shade-tolerant species may require 150 (*Acer*
24   *saccharum*, Canham 1988) to 450 years (*Tsuga canadensis*, Godman and Lancaster 1990) to
25   reach the canopy and complete the cycle. Even the 25-50 years for life cycle completion in
26   closed canopy forests presumes optimum rates of height and diameter growth. Yet, warming is
27   likely to slow growth rates, as it has in the past (e.g., Fritts 1976; Briffa et al. 1995).

28   In sum, the minimum time required for development of mature forests by tree species that
29   originate elsewhere is between 100 years (conifers that spread from initial seed sources in an
30   arbitrary five 10-year generations and grow to canopy height in 25 years) and 200 years
31   (deciduous hardwoods that spread from initial seed sources in ten 15-year generations and
32   grow to canopy height in 50 years). This "transient response" to climate changes is consistent
33   with forest maturity rates measured in the past and simulated by mechanistic gap models (e.g.,
34   Solomon 1986; Bugmann 1993). The latter models exclude the time needed for development of
35   isolated tree seed sources but include crude effects of chronic climate change on tree growth. In
36   reality, the rate will probably be much slower, perhaps approaching the >1000 yr period
37   inferred by Bennett (1986, 1988) in prehistoric data describing forest initiation and maturation.

38   Forest Tree Mortality. The other half of the migration question for calculating carbon
39   stocks is the concomitant mortality of trees which have become climatically and fatally
40   "obsolete" (i.e., after climate variables exceed their climate tolerances). Stress induced by

1 warming and drought may directly slow growth of individual trees and thereby, induce
2 mortality, usually in less than a decade (Nichols, 1968; Franklin et al., 1987; Auclair, 1992),
3 especially among seedlings and saplings (Peet and Christiansen, 1987). However, climate
4 stresses more commonly predispose trees to succumb to other mortality agents (Waring, 1987),
5 such as air pollutants (Hinrichsen, 1987), wildfire (Payette 1992), insect infestations (Holling
6 1992) and windthrow (Webb 1989). Such direct and indirect stress-induced mortality can be
7 viewed as chronic decline over several decades if it is measured at the scale of a large region,
8 where new individuals, populations and stands are dying each year (Mueller-Dombois, 1992).

9 The amount of time required to extirpate populations from regions in which they have
10 become climatically obsolete is exceedingly complex to predict. The fatal obsolescence itself is a
11 non-linear time-transgressive property of the rate and spatial distribution of climate change.
12 Trees growing in areas undergoing the most rapid climate changes, growing near limits of their
13 distribution and growing in stressed habitats may die in only a few years, while others may just
14 begin to sense stress by the time GHGs have doubled. Following mortality, release of carbon
15 from dead trees may require additional decades. Harmon et al (1986) cite 50% volume loss
16 times of 14-172 years for log mineralization of softwoods under temperate climates inducing
17 slow decomposition, and 2-24 years for hardwoods.

18 Although seedlings and saplings should disappear quickly, the loss of mature trees which
19 store most of the carbon is more relevant. Increased, climate-induced mortality of mature trees,
20 and carbon losses to mortality greatly exceeding carbon gains from new growth (Kirschbaum
21 and Fischlin 1996), is expected to generate a future pulse of increased atmospheric CO_2
22 (Solomon, 1986; King and Neilson, 1992; Smith and Shugart 1993a,b). Epidemics of
23 pathogens and insects, mortality agents through which climate change may act, have required
24 about 50 years in eastern North America to kill most individuals of American chestnut (Odum,
25 1969) and American elm (Gibbs, 1978) in the 20th century and eastern hemlock in mid-
26 Holocene time (Davis, 1981). Based on the foregoing, I assumed that trees would be extirpated
27 from areas of fatal obsolescence in the 60-70 years required to reach climate of doubled GHGs.
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30 MIGRATION RATES APPLIED
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32 The minimum of 100 to 200 years required to develop forests composed of new species in a
33 given region *following* the imposition of a changed climate can be compared to the expected
34 time climate will take to change. Frequently, the time needed to impose the climate of doubled
35 concentrations of CO_2 or of all GHGs (e.g., Houghton et al. 1995) is used, currently expected
36 to occur in 60 to 70 years or by about the year 2050 (Greco et al. 1994). At that rate, forest
37 migration would be very incomplete at best, even if the forest development began when climate
38 change began, rather than following sometime after initiation of the climate change.

39 This lag is incompatible with the assumption of instant migration and forest maturity
40 incorporated by the static models discussed in the introduction, above. Consider that the static

1   vegetation models utilize a half-degree latitude and longitude grid (one degree by Prentice and

2   Fung 1990), with a latitudinal resolution of about 55 km at the equator. Measurement of any

3   tree migration which sequesters carbon by the 70 year doubling of GHGs is highly unlikely, if

4   not impossible, even at the normal 150-400 m/yr migration rate Davis (1983) estimated from

5   fossil pollen data (producing tree migration of only 11-28 km during the 70 yrs). A more

6   realistic assumption is that no forest migration occurs in the 70-year time span needed to reach a

7   doubling of CO_2 or GHGs, although migration would occur eventually. Belotelov et al. (1996)

8   applied this model condition to the Holdridge Life Zone System to define the absolute range of

9   carbon values possible for specified future climate scenarios in the former Soviet Union.

10   Solomon and Kirilenko (1996) modified the Biome 1.1 model (Prentice et al. 1992, 1993)

11   to reflect this "delayed migration" condition. They assumed that tree functional types (TFTs)

12   which were incompatible with doubled GHG climates would disappear during the 60 or 70

13   years from areas acceptable under the initial climate, but that TFTs could not appear in areas in

14   which they were absent under the initial climate. Nonarboreal plant functional types (shrubs,

15   grasses; NAFTs) were modeled as migrating instantly, on the assumption that they are able to

16   produce seed as quickly as their first or second growing seasons, greatly reducing lags in

17   response to rapid climate change.

18   Figure 1 illustrates a Biome 1.1 model run using climate output from the UKTR coupled

19   ocean-atmosphere GCM for climate of current and of doubled GHG concentration (Solomon

20   and Kirilenko 1996). Note that differences between instant migration and no migration are

21   present at all latitudes. Reduced temperature constraints on tree growth in high latitudes permit

22   occupation of latitudinal bands of nonarboreal tundra by boreal forests under instant migration

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38   Figure 1. Global distribution of land occupied by forest, projected by the BIOME 1.1
39   model (Prentice et al., 1993) under the UKTR climate scenario (Murphy and Mitchell
40   1996). Areas in black show differences between assuming instant migration and absent
41   migration and areas in grey are forested under either instant or absent migration.

1 assumptions. Similarly, increased soil moisture and instant tree migration produces forest
2 occupation of longitudinally-oriented steppe and savanna areas by dry temperate forests in
3 North and South America and by tropical forests in Africa, India and Asia. In part the patterns
4 reflect the great difference in sensitivity of temperature to GHGs at high latitudes compared to
5 that at low latitudes which undergo little warming (Greco et al 1995).

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8 RESULTS AND DISCUSSION
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10 The paper is written to estimate the time required to form closed canopy, mature forests by
11 immigrating species and the time required to eliminate trees which have become fatally obsolete.
12 The objective is to define the implications of this lagged climate response to the global carbon
13 cycle. Prentice et al (1993) have transformed biome areas into carbon stocks by appying carbon
14 density estimates for aboveground and belowground carbon.
15 Table 1 compares terrestrial carbon storage under future climate with migration versus no-
16 migration assumptions. Like other static models, this exercise with instant migration generated
17 more terrestrial carbon under doubled GHG climate than under modern climate. Simulated
18 tropical forests invade large areas of grassland and savanna due to the positive moisture balance
19 this particular GCM projects for the tropics. The difference between modern and future carbon
20 with instant migration is considerably less than others have projected (Prentice and Fung 1990;
21 Leemans, 1989; Smith et al, 1992a, b; Smith 1993; Solomon et al. 1993). The UKTR coupled
22 ocean-atmosphere GCM is considerably less GHG-sensitive than those used in the past.

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24 TABLE 1. Above ground (AG)[1], below ground (BG)[2] and total (TOTAL) biomass in Petagrams
25 (Pg) under modern and doubled GHG climate, with and without tree migration
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BIOMES	MODERN CLIMATE[3]			DOUBLED GHG CLIMATE[4]					
				WITH MIGRATION			NO MIGRATION		
	AG	BG	TOTAL	AG	BG	TOTAL	AG	BG	TOTAL
Boreal Forests	170	300	470	179	298	477	165	292	457
Temperate Forests	169	360	529	174	343	517	147	336	483
Tropical Forests	300	289	589	346	330	676	287	281	568
Boreal Nonforest	11	177	188	8	127	134	12	151	163
Temperate Nonforest	22	189	211	25	191	216	33	261	294
Tropical Nonforest	52	144	196	51	132	183	49	128	177
Forest Biomass	639	949	1588	699	971	1670	599	909	1508
Total Biomass	723	1459	2177	783	1420	2203	693	1449	2142

43 1. from table converting area to biomass in Prentice et al. 1993, based on Olson, et al. 1983.
44 2. from table converting area to biomass in Prentice et al. 1993, based on Zinke et al. 1984.
45 3.from data of Leemans and Cramer (1990).
46 4. from temperature and precipitation differences between 2 X CO2 and 1 X CO2 of Murphy and
47 Mitchell (1996) applied to data of Leemans and Cramer (1990).
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1   In contrast to carbon increases associated with instant migration, the amount of carbon
2   stored in terrestrial vegetation and soils declines under GHG-induced climate when one assumes
3   that trees do not migrate (Table 1). All forests decline in biomass and do so both above (40 Pg)
4   and belowground (40 Pg). Nonarboreal biomass that replaced forest biomass (9 Pg above
5   ground, 30 Pg below ground) does not make up for the forest carbon loses. Despite the
6   moderate future climate scenario used, and hence, the moderate amount of forest response
7   projected, the difference in forest biomass between the two assumptions is significant. The
8   above-ground forest biomass difference is 100 Pg or about 16% of the initial 639 Pg, and the
9   total forest biomass difference is 162 Pg, or 10% of the initial 1583 Pg.
10   The foregoing values, for vegetation composition responses to climate change alone, exceed
11   the calculated amount of carbon sequestered in terrestrial vegetation from carbon fertilization, as
12   hypothesized from lab experiments (Melillo et al. 1993; Schimel et al. 1995), or calculated by
13   difference from ocean uptake (Denning et al. 1995). Although the global difference for all
14   biomes is considerably less (61 Pg), it is the forests, especially those at high latitudes, which are
15   suspected of increasing storage of the carbon not accounted for in ocean-atmosphere models.
16   Clearly, where this view depends on the future distribution of forests (e.g., Melillo et al. 1993;
17   VEMAP Participants 1996), it needs to be reexamined. In any case, the amount of carbon
18   tabulated under the traditional instant-migration assumption should be recalculated based on a
19   concept of imperceptibly slow forest immigration response to climate change in the 21st century.
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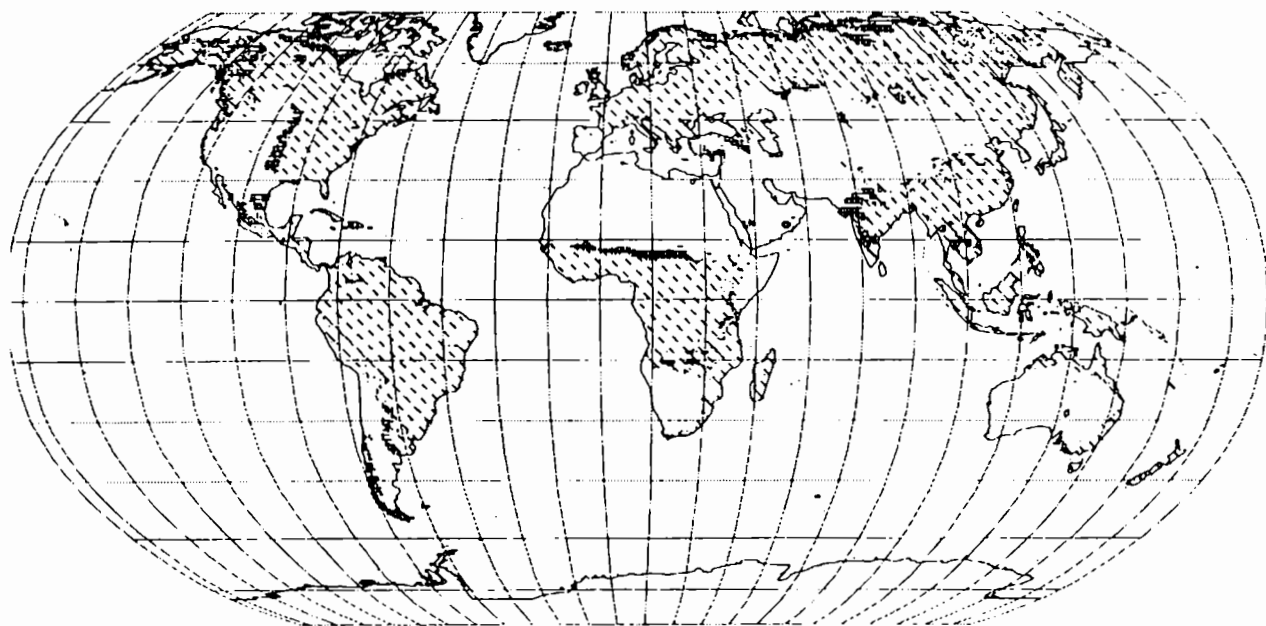22   ACKNOWLEDGEMENTS
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33   REFERENCES CITED
34
35
36   Auclair, AND (1993) Extreme climatic fluctuations as a cause of forest dieback in the Pacific
37   Rim. Air Water and Soil Pollut. 66:207-229
38   Bennett KD (1984) The post-glacial history of *Pinus sylvestris* in the British Isles. Quat. Sci.
39   Rev. 3:133-155.
40   Bennett KD (1986) The rate of spread and population increase of forest trees during the
41   postglacial. Philos. Trans. R. Soc. London B134:523-531.
42   Bennett KD (1988) Modeling changes in beech populations: A reply to Dexter et al. (1987).
43   Rev. Palaeobot. Palynol. 56:361-364.

Belotelov NV, Bogatyrev BG, Kirilenko AP, and Venevsky SV (1996) Modelling time-dependent biome shifts under global climate changes. Ecological Modeling (in press).

Briffa KR, Jones PD, Schweingruber FH, Shiyatov SG, and Cook ER (1995) Unusual twentieth-century summer warmth in a 1,000-year temperature record from Siberia. Nature 376:156-159.

Bugmann HKM (1993) On the ecology of mountainous forests in a changing climate: A simulation study. Ph.D. Dissertation, Swiss Federal Institute of Technology, Zürich.

Burns RM and Honkala BH (eds) (1990) Silvics of North America. Volume 1, Conifers; Volume 2, Hardwoods. Agr. Hndbk. 654. USDA Forest Service, Washington D.C.

Canham CD (1988) Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69:786-795

Collingham YC, Hill MO and Huntley B (1996) The migration of sessile organisms: a simulation model with measureable parameters. J. Veg. Sci. (in press)

Daubenmire RF (1959) Plants and environment. J. Wiley and Sons, Inc., NY

Davis MB (1981) Outbreaks of forest pathogens in Quaternary history. Proc. IV Int. Palynol. Conf., Lucknow (1976-1977) 3:216-227

Davis MB (1983) Quaternary history of deciduous forests of eastern North America and Europe. Ann. Mo. Bot. Gard. 70:550-563.

Davis MB (1987) Invasions of forest communities during the Holocene: Beech and hemlock in the Great Lakes Region. 373-393 IN Gran AJ, Crawley MJ and Edward PH (eds) Colonization and stability. Blackwell Scientific Publications, Oxford UK

Davis MB (1989) Lags in vegetation response to greenhouse warming. Clim. Change 15:75-82

Davis MB (1990) Climatic change and the survival of forest species. 99-110 IN Woodwell GM (ed) The earth in transition: Patterns and processes of biotic impoverishment. Cambridge Univ. Press, Cambridge UK

Davis MB, Woods KD, Webb SL and Futyma R (1986) Dispersal versus climate: Expansion of *Fagus* and *Tsuga* into the Upper Great Lakes region. Vegetatio 67:93-103

Denning AS, Fung IY and Randall D (1995). Latitudinal gradient of atmospheric CO_2 due to seasonal exchange with land biota. Nature 376:240-243.

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC and Wisneiwski J (1994) Carbon pools and flux of global forest ecosystems. Science 263:185-190.

Franklin JF, Shugart HH and Harmon ME (1987) Tree death as an ecological process. BioScience 37:550-556

Fritts HA (1976) Tree rings and climate. Academic Press, NY

Gammon RH, Sundquist ET and Fraser PJ (1985) History of carbon dioxide in the atmosphere 25-62 IN Trabalka JR (ed) Atmospheric carbon dioxide and the global carbon cycle. DOE/ER-0239, US Dept. of Energy, Washington DC.

Gear A J and Huntley B (1991) Rapid changes in the range limits of scots pine 4000 years ago. Science 251:544-547.

Godman RM and Lancaster K (1990) *Tsuga canadensis* (L) Carr., Eastern Hemlock. 604-612 IN Burns RM and Honkala BH, (eds) (1990a) Silvics of North America. Volume 1, Conifers. Agr. Hndbk. 654, USDA Forest Service, Washington D.C.

Greco S, Moss RH, Viner D and Jenne R (1995) Climate Scenarios and Socioeconomic Projections for IPCC WG II Assessment. Material assembled for Lead Authors by IPCC WG II TSU, Washington, D.C.

Greene DF and Johnson EA (1989) A model of wind dispersal of winged or plumed seeds. Ecology 70:339-347.

Greene DF and Johnson EA (1995) Long-distance wind dispersal of tree seeds. Can. J. Bot. 73:1036-1045

Gibbs JN (1978) Intercontinental epidemiology of Dutch elm disease. Ann. Rev. Phytopath. 16:287-307

Harlow WM, Harrar ES and White FM (1979) Textbook of dendrology, 6th edn. McGraw-Hill, NY

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SO, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, and Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15:133-302

Hinrichsen D (1987) The forest decline enigma. BioScience 37:542-546

Holling CS (1992) The role of forest insects in structuring the boreal landscape. 170-191 IN

1   Shugart, HH, Leemans R and Bonan GB (eds) A Systems Analysis of the Global Boreal
2   Forest. Cambridge University Press, NY.
3 Houghton JT, Meira-Filho LG, Bruce J, Lee H-S, Callander BA, Haites E, Harris N and
4   Maskell K (eds) (1995) Climate change 1994: Radiative forcing of climate change and an
5   evaluation of the IPCC IS92 emission scenarios. Cambridge Univ. Press, Cambridge, UK
6 Keeling CD, Whorf TP, Wahlen M and van der Plicht J (1995) Interannual extremes in the rate
7   of rise of atmospheric carbon dioxide since 1980. Nature 375:666-670.
8 King GA and Neilson RP (1992) The transient response of vegetation to climate change: A
9   potential source of CO_2 to the atmosphere. Water, Air and Soil Pollut. 64:365-383
10 Kirschbaum M and Fischlin A (1996) The impacts of climate change on forest ecosystems,
11   IPCC WG II Second Assessment Report, Chapter 1. (in press)
12 Leemans R (1989) Possible changes in natural vegetation patterns due to a global warming 105-
13   122 IN Hackl A (ed.) Der Treibhauseffekt: Das Problem-Mögliche Folgen-Erforderliche
14   Massnahmen. Akadamie für Umwelt und Energie, Laxenburg, Austria.
15 Leemans R and Cramer WP (1991) The IIASA database for mean monthly values of
16   temperature, precipitation and cloudiness on a global terrestrial grid. Research Report
17   RR91-18. Internat. Inst. for Applied Sys. Anal. Laxenburg, Austria.
18 Leishman MR, Hughes L, French K, Armstrong D and Westoby M (1992) Seed and seedling
19   biology in relation to modeling vegetation dynamics under global climate change. Aust. J.
20   Bot. 40:599-613
21 MacDonald GM, Edwards TWD, Moser KA, Pienitz R and Smol JP (1993) Rapid response of
22   treeline vegetation and lakes to past climate warming. Nature 361:243-246.
23 Melillo JR, McGuire AD, Kicklighter DW, Moore B, Vorosmarty CJ and Schloss AL (1993)
24   Global climate change and terrestrial net primary production. Nature 363: 234-239.
25 Mitchell JFB, Johns TC, Gregory JM and Tett SFB (1995) Climate response to increasing
26   levels of greenhouse gases and sulphate aerosols. Nature 376:501-504
27 Mueller-Dombois D (1992) Potential effects of the increase in carbon dioxide and climate change
28   on the dynamics of vegetation. Water, Air and Soil Pollut. 64:61-79
29 Murphy JM and Mitchell JFB (1996) Transient response of the Hadley Centre coupled ocean-
30   atmosphere model to increasing carbon dioxide. Part II: Spatial and temporal structure of the
31   response. Jour. of Climate (in press)
32 Nichols JO (1968) Oak mortality in Pennsylvania: A ten-year study. J. For. 66:681-694
33 Odum EP (1969) Fundamentals of Ecology, WB Saunders Co, Philadelphia PA
34 Olson JS, Watts JA and Allison LJ (1983) Carbon in Live Vegetation of Major World
35   Ecosystems. ORNL/TM-5862, Oak Ridge National Laboratory, Oak Ridge, TN.
36 Payette S (1992) Fire as a controlling process in the North American boreal forest. 144-169 IN
37   Shugart HH, Leemans R and Bonan GB (eds) A Systems Analysis of the Global Boreal
38   Forest. Cambridge Univ. Press, Cambridge, UK.
39 Peet RK and Christiansen NL (1987) Competition and tree death. BioScience 37:586-595
40 Prentice K and Fung IY (1990) The sensitivity of terrestrial carbon storage to climate change.
41   Nature 346:48-50.
42 Prentice IC and Solomon AM (1990) Vegetation models and global change. 365-383 IN
43   Bradley RS (ed) Global Changes of the Past. OIES, UCAR, Boulder, CO
44 Prentice IC, Bartlein PJ and Webb T III (1991) Vegetation change in eastern North America
45   since the last glacial maximum: A response to continuous climatic forcing. Ecology
46   72:2038-2056.
47 Prentice IC, Cramer WP, Harrison SP, Leemans R, Monserud RA and Solomon AM (1992) A
48   global biome model based on plant physiology and dominance, soil properties and climate.
49   J. Biogeogr. 19:117-134.
50 Prentice IC, Sykes MT, Lautenschlager M, Harrison SP, Denissenko O and Bartlein PJ (1993)
51   Modelling global vegetation patterns and terrestrial carbon storage at the last glacial
52   maximum. Global Ecol. and Biogeogr. Let. 3:67-76.
53 Schimel D, Enting IG, Heimann M, Wigley TML, Raynaud D, Alves D and Siegenthaler U
54   (1995) CO_2 and the Carbon Cycle. 39-71 IN Houghton JT, Meira-Filho LG, Bruce J, Lee
55   H-S, Callander BA, Haites E, Harris N and Maskell K (eds) Climate change 1994:
56   Radiative Forcing of Climate Change and an Evaluation of the IPCC IS92 Emission
57   Scenarios. Cambridge Univ. Press, Cambridge, UK
58 Sedjo RA and Solomon AM (1989) Climate and forests. 105-119 IN Rosenberg NJ, Easterling
59   WE, Crosson PR and Darmstadter J (eds) Greenhouse Warming: Abatement and

Adaptation. Resources for the Future, Washington, D.C.

Smith TM, Leemans R and Shugart HH (1992a) Sensitivity of terrestrial carbon storage to CO_2-induced climate change: Comparison of four scenarios based on general circulation models. Clim. Change 21:367-384

Smith TM, Shugart HH, Bonan GB and Smith JB (1992b) Modeling potential response of vegetation to global climate change. Adv. Ecol. Res. 22:93-116.

Smith TM and Shugart HH (1993a) The transient response of terrestrial carbon storage to a perturbed climate. Nature 361:523-526.

Smith TM and Shugart HH (1993b) The potential response of global terrestrial carbon storage to a climate change. Water, Air and Soil Pollut. 70:629-642.

Solomon AM (1986) Transient response of forests to CO_2-induced climate change: Simulation experiments in eastern North America. Oecologia 68:567-79.

Solomon AM and Kirilenko AP (1996) Implications for terrestrial carbon stocks of delayed tree species immigration under changed climate (ms. submitted to Nature)

Solomon AM, Tharp ML, West DC, Taylor GE, Webb JW and Trimble JL (1984) Response of Unmanaged Forests to C Dioxide-Induced Climate Change: Available Information, Initial Tests, and Data Requirements. TR-009, United States Department of Energy Washington, DC.

Solomon AM, Prentice IC, Leemans R and Cramer WP (1993) The interaction of climate and land use in future terrestrial carbon storage and release. Water, Air and Soil Pollution 70:595-614.

Sundquist, ET (1985) Geologic analogs: Their value and limitations in carbon dioxide research 371-402. IN Trabalka JR and Reichle DE (eds) The Changing Carbon Cycle: A Global ANalysis. Springer-Verlag, NY

VEMAP Participants (1996) Comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO2 doubling. Global Biogeochem. Cyc. (in press)

Waring RH (1987) Characteristics of trees predisposed to die. BioScience 37:569-574

Waring RH and Schlesinger WH (1985) Forest Ecosystems: Concepts and Management. Academic Press NY

Webb SL (1986) Potential role of passenger pigeons and other vertebrates in the rapid Holocene migrations of nut trees. Quat. Res. 26:367-375

Webb SL (1989) Contrasting windstorm consequences in two forests, Itasca State Park, Minnesota. Ecology 70:1167-1180

Webb T III (1986) Is vegetation in equilibrium with climate? How to interpret late-Quaternary pollen data. Vegetatio 67:75-91.

Zinke PJ, Stangenberger AG, Post WM, Emanuel WR and Olson JS (1984) Worldwide organic soil carbon and nitrogen data, ORNL TM-8857, Oak Ridge National Laboratory.

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16. ABSTRACT

This paper discusses the forest-ecological processes which constrain the rate of response by forests to rapid future environmental change. It establishes a minimum response time by natural tree populations which invade alien landscapes and reach the status of a mature, closed canopy forest when maximum carbon storage is realized. It considers rare long-distance and frequent short-distance seed transport, seedling and tree establishment, sequential tree and stand maturation, and spread between newly established colonies. The universally applied assumption of instant forest migration and development must be replaced by an assumption of no forest migration during the next century. Previously simulated increases in terrestrial carbon stocks become declines under doubled greenhouse gas-induced warming.

17.	KEY WORDS AND DOCUMENT ANALYSIS		
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