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# How Increasing CO<sub>2</sub> and Climate Change Affect Forests

*At many spatial and temporal scales, there will be forest responses that will be affected by human activities*

Robin Lambert Graham, Monica G. Turner, and Virginia H. Dale

**T**he strong relationship among climate, atmosphere, soils, biota, and human activities provides a solid basis for anticipating changes in terrestrial biomes in response to changes in the global environment. A major impact of the projected doubling of atmospheric CO<sub>2</sub> and increases in trace gas concentrations is the potential for global climate change (e.g., Tangle 1988). Current predictions are for an average rise in global temperature of 1.5° to 4.5° C, with greater warming in winter than summer and increased warming with increased latitude. But the magnitude, rate, and spatiotemporal characteristics of the climatic response remain uncertain. Increased precipitation in high latitudes and decreased summer precipitation and soil moisture in middle latitudes of the northern hemisphere are also predicted.

Global forests are likely to experience dramatic changes as a consequence of elevated CO<sub>2</sub> and climate changes. Predicting these changes is

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## Forest responses will determine the fate of many species

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not only a social and economic necessity, but it is also a scientific challenge because of the many spatial and temporal scales involved. Forests directly affect climate at the global scale by altering the earth's albedo, hydrological regimes, and atmospheric CO<sub>2</sub>. Forests also affect climate at a local scale by altering temperature, humidity, and solar radiation.

Similarly, forest responses occur at many scales. For example, processes that involve exchanges of water, heat, and CO<sub>2</sub> at the leaf surface have fast response times (seconds to days). Forest growth and community composition have intermediate response times (decades to centuries), whereas the geographic distribution of forests is a long-term response (centuries to millennia; Figure 1). Furthermore, all these responses can be altered by human intervention.

How can the fate of forests be predicted in the face of what appears to be an inevitable rise in atmospheric CO<sub>2</sub> and temperature? It requires explicit consideration of the many temporal and spatial scales at which forest responses occur, incorporation of the links between these scales in both models and experiments, and a clear understanding of human impacts on forest responses.

Four levels of biotic organization

(the biosphere, the biome, the ecosystem, and the tree) provide a useful framework for examining forest responses to CO<sub>2</sub> and climate. Each level has a characteristic spatial and temporal scale and set of ecological processes (Table 1). Of course, many forest responses cross scales, and their assignment may be somewhat arbitrary. For example, forest succession, which takes decades or centuries and is generally studied at the ecosystem level of organization, is a function of species-specific responses to environmental variables (measured at the tree level); competitive interactions among individuals for light, nutrients, and water (measured at the ecosystem level); and seed source availability, which may depend on species migration rates (measured at the biome level).

The objective of this article is to examine potential forest responses to elevated CO<sub>2</sub> in conjunction with climate change. For each level of biotic organization (Table 1), we discuss the potential effects of changed climate and elevated CO<sub>2</sub> on key ecological processes, how human intervention can affect those processes, and the role of modeling in elucidating and predicting forest responses. We conclude with a discussion of future research needs.

## Biosphere

Several processes are of interest at the biosphere scale. They are the various feedbacks among atmospheric CO<sub>2</sub> concentrations, climate, and carbon storage in global forests (Figure 2).

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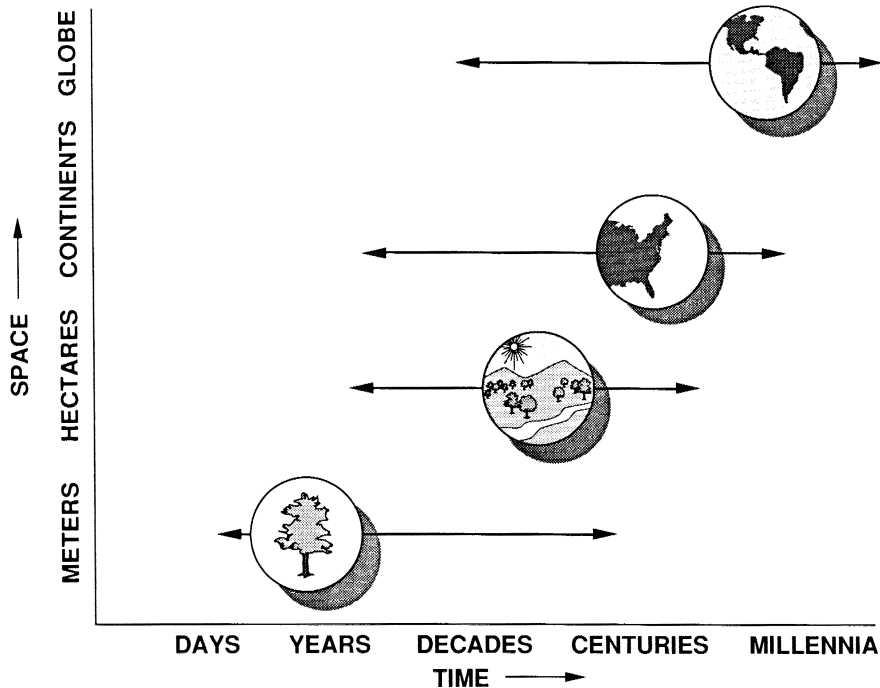


Figure 1. Spatial and temporal scales of biotic levels of organization in forests.

**Carbon cycle.** Carbon, a major constituent of plants, is taken up from the atmosphere as  $\text{CO}_2$  through photosynthesis and released when plant tissue respires or dies and either decomposes or is burned. Because forests contain 90% of the carbon in terrestrial vegetation, the accumulation of forest biomass is a major regulator of atmospheric  $\text{CO}_2$ .

Increased concentrations of atmospheric  $\text{CO}_2$  could increase photosynthesis rates of existing forests, because forests are composed largely of plants with  $\text{C}_3$  photosynthetic path-

ways whose photosynthesis process is not saturated at current atmospheric  $\text{CO}_2$  concentrations (Figure 3). Such an increase might (but not necessarily) result in more carbon storage in forest biomass and thus could serve as a drag on atmospheric  $\text{CO}_2$  rise. Limited tree ring evidence suggests that forest growth in some locations has increased during the past century independent of climate (LaMarche et al. 1984), although this conclusion is open to debate (Kienast and Luxmoore 1988). In addition, global 3-D atmospheric tracer model studies sup-

port the hypothesis that the observed increase in the annual variation of atmospheric carbon, especially in the northern latitudes, is due to an increased growth rate in temperate and boreal forests (Barcastow et al. 1985, D'Arrigo et al. 1987).

The regulation of  $\text{CO}_2$  is but one of the ways global vegetation influences global climate. Vegetation modifies energy fluxes by altering the earth's albedo; vegetation generally has a lower albedo than soil and consequently absorbs more radiant energy, thus warming the earth.

**Hydrologic regime.** Evapotranspiration from vegetation is a major component of the global hydrologic regime (Shuckla and Mintz 1982). As vapor pressure deficit increases exponentially with temperature, a warmer climate will increase evaporative demand if air moisture is not greatly increased. Although laboratory studies have shown that increased  $\text{CO}_2$  generally reduces stomatal conductances and thus water losses from transpiration, it does not necessarily follow that elevated atmospheric  $\text{CO}_2$  will reduce global evapotranspiration.

The impact of stomatal conductance on transpiration water losses depends on the degree to which the foliage is coupled to the atmosphere (Jarvis and McNaughton 1986). In laboratory tests, there is good airflow over the foliage. Consequently, the foliage is tightly coupled to the atmosphere, and transpiration is sensitive to  $\text{CO}_2$ -mediated changes in stomatal conductance. However, at the regional scale, foliage is poorly coupled to the atmosphere. As a result, regional evapotranspirational water losses are mostly a function of the radiation balance. Thus it has been hypothesized that regional or larger scale water losses will probably be insensitive to changes in atmospheric  $\text{CO}_2$  (Jarvis 1989).

In addition, the absolute amount of water returned to the atmosphere via evapotranspiration is a function of leaf area. If climate change or elevated  $\text{CO}_2$  alters leaf area, this change would have a profound effect on hydrologic regimes and river flows (Wigley and Jones 1985).

**Human impacts.** Recent human activ-

Table 1. Four biotic levels of organization that participate in forest response to climate and  $\text{CO}_2$  change.

Level of organization	Spatial scale	Temporal scale	Major processes	Human activities
Biosphere	Globe	Years to millennia	Energy, carbon, water fluxes	Deforestation, fossil fuel burning
Biome	Subcontinental	Centuries to millennia	Evolution/extinction, migration, disturbance	Plant breeding, land management, conservation
Ecosystem	10 to $10^4$ ha	Years to centuries	Disturbance, nutrient cycling, production, water use, succession, competition	Pollution, exotic pests, fire suppression, flood control, forest management, soil management
Tree	$10^{-2}$ to $10^3$ $\text{m}^2$	Minutes to decades	Phenology, reproduction, physiological processes, death	Fertilizing, watering, weeding, breeding

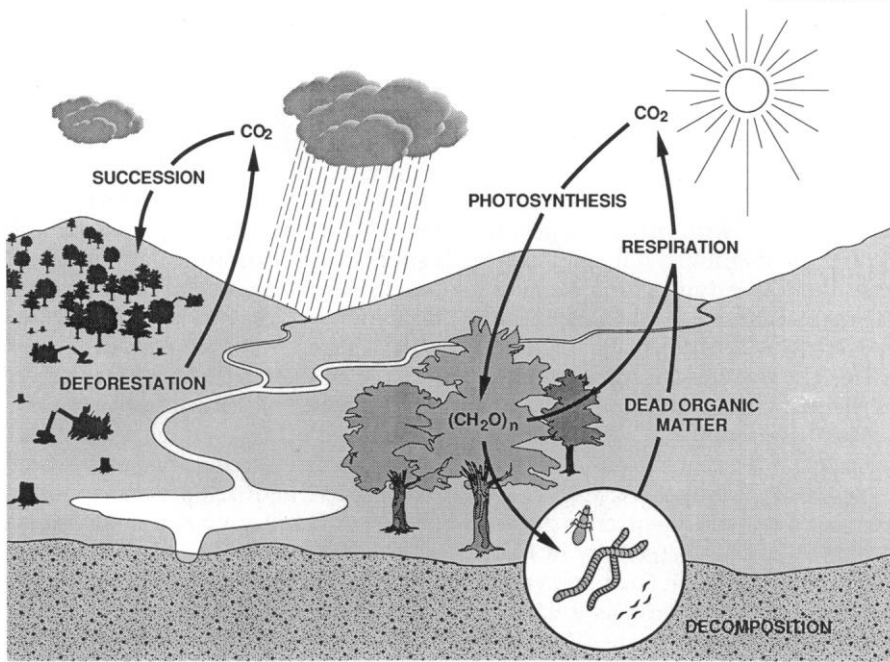


Figure 2. The complex relationships between atmospheric CO<sub>2</sub> and the forest.

ities are affecting the feedbacks among CO<sub>2</sub> concentrations, global climate, and global vegetation. The largest global net fluxes of carbon from 1800 to the present are from fossil fuel burning ( $150$  to  $190 \times 10^{15}$  grams; Rotty 1987) and land use changes, in particular the conversion of forest land (high carbon storage) to agriculture (low carbon storage;  $135$  to  $228 \times 10^{15}$  grams of carbon; Houghton et al. 1983).

The use of fossil fuel for energy is heaviest in the temperate zone of the northern hemisphere, whereas current land-use changes are most dramatic near the equator, where large areas of tropical forests are being cleared or degraded. However, human activities within any region that cause increases in atmospheric CO<sub>2</sub> concentrations can affect global climate patterns.

Extensive planting of intensively managed forests or tree plantations has been discussed as a method for recapturing this "excess" atmospheric CO<sub>2</sub> and thus slowing down the increase in CO<sub>2</sub> and consequently climate change (Marland 1988). However, as Jarvis (1989) pointed out, it would take a new plantation with an area twice the size of Europe to absorb the current global fossil fuel emissions. Furthermore, after 80

years, the carbon uptake ability of such a plantation would begin to decrease due to stand maturity, a new plantation would have to be initiated, and the wood from the previous one would be stored in perpetuity.

Switching from fossil fuels to biomass-based fuels is a much more effective approach for using forests to slow down the buildup of excess atmospheric carbon. The net release of carbon from a biomass fuel is close if not equal to zero. The US Congress Office of Technology Assessment (OTA 1980) estimated that biofuels could potentially generate 6–17 quads of energy annually in the United States. In 1988, the most recent data available, US fossil fuel energy use was approximately 71 quads.

### Biome

The major ecological processes of interest at the biome level are species migration, evolution, and extinction. Disturbances, such as introduced blights, occur at both the biome and the ecosystem level. To avoid duplication, we will review these disturbances in the discussion of ecosystems.

**Migration.** The migration of species

and the redistribution of forest types in response to global change are complex issues (c.f. Brubaker 1986, Davis and Botkin 1985, Pennington 1986). Some organisms track climate change closely, reacting to conditions each year, whereas others respond so slowly that only long-term climatic trends have any observable effect (Davis 1984). Tree species are expected to migrate gradually to track hospitable environments as climate changes. However, although the average rate of tree species migration in Europe and North America during the Ice Ages was approximately 300 m/year (Woodward 1987), future migration rates are difficult to predict, because the projected rate of climate change is an order of magnitude greater than previous climate changes.

Davis (in press) suggests that the spatial displacement of habitats can be visualized if one assumes the same general configuration of climate as today. With a latitudinal lapse rate in the Great Lakes region of approximately 100 km/°C, isotherms would be displaced northward 300 km in the next 100 years. This rate is ten times greater than the documented range extensions for trees in a similar time interval. Furthermore, there are now new barriers to migrations (e.g., cities, agriculture, and roads) and new modes of migration (e.g., cars, trains, transplants for horticulture, forestry, and agriculture.)

Range extension in the future may be less efficient than in the past, because advance disjunct colonies have been extirpated by human disturbances, and propagule sources have

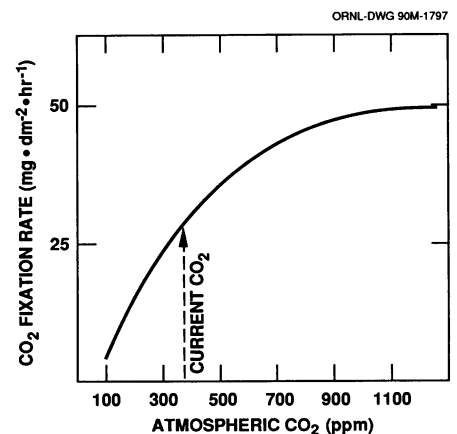


Figure 3. Typical photosynthesis response of a C<sub>3</sub> plant (sugar beet) to increasing atmospheric CO<sub>2</sub>.

often been reduced (Davis 1989a). The current spatial distribution and abundance of a species is expected to influence its ability to migrate successfully to regions of suitable climate and soils (Peters and Darling 1985).

The rate of habitat displacement and the rate of species dispersal and migration will influence the composition and structure of forested landscapes, especially if time lags occur (e.g., Davis 1984, Pennington 1986, Webb 1986). Time lags in species responses to historical climatic changes have been well documented. For example, beech (*Fagus grandifolia*), which has animal-dispersed seeds and tends to move as a front, showed a time lag of 500 to 1000 years in crossing from the eastern to the western shore of Lake Michigan (Davis 1989a). In contrast, hemlock (*Tsuga canadensis*), whose wind-dispersed seeds can travel 100 km beyond the main species front, showed no time lags attributable to crossing the Great Lakes.

Davis (1989a) also proposes that time lags in the adjustments of species abundances to climate will be small (approximately 10–20 yrs) in the heavily disturbed communities that cover most of the landscape. The most common species will be dispersed to new habitats by humans, but time lags will be a problem for unmanaged forests, natural areas, and preserves. The climate change during the next century may not be enough to kill dominant species directly. Thus forested landscapes may appear superficially unchanged even though a different community is becoming established in the understory.

**Evolution.** Evolution or extinction of tree species may be affected by climate change or increasing concentrations of atmospheric CO<sub>2</sub>. The genetic resilience of most tree species to climate change must be inferred from the current climatic conditions within their natural ranges (Johnson and Sharpe 1982). However, the boundaries of a species' range may reflect competitive ability rather than climatic constraints (Woodward 1987, c.f. Michaels and Hayden 1987) or climatic restraints that are only significant during the reproductive phase. Many northern tree species grow quite well in noncompetitive situa-

tions (e.g., city parks) far south of their natural range. Common garden tests, widely used with both tropical and temperate domesticated tree species, could provide more specific information on genetic variability in the climate response (Kellison and Weir 1987).

Tree species with broad ranges, including most commercial species, are most likely to survive climate change. The many tree species that are rare or restricted in occurrence, including 115 of the 679 native tree species in the United States (Little 1979), will likely be at greater risk of extinction.

The evolutionary response of trees to increasing atmospheric CO<sub>2</sub> is unknown. The within-species genetic variability of CO<sub>2</sub> sensitivity in CO<sub>2</sub>-responsive traits such as photosynthesis and stomatal control is unknown also. However, short-term differences in physiological responsiveness of seedlings and leaves of different tree species have been documented (e.g., Tolley and Strain 1984).

Tree species are likely to have high variability in CO<sub>2</sub> sensitivity, because natural tree populations have shown high variability in other characteristics, genetic variability in CO<sub>2</sub> sensitivity has been demonstrated in herbaceous agricultural species, and early evolution of hardwood tree species took place in the Cretaceous era when atmospheric CO<sub>2</sub> concentrations were three to ten times higher than today (Gammon et al. 1985). Positive changes in individual tree water-use efficiency (increase in biomass per unit of water taken up), as a result of stomatal and photosynthesis responses to elevated CO<sub>2</sub> concentrations, could also extend some species' ranges into warmer, drier climates than are acceptable under current CO<sub>2</sub> conditions.

**Modeling.** Several different modeling approaches have predicted biome-level responses to changes in climate and to increased atmospheric CO<sub>2</sub>. Biome changes at the scale of 0.5-degree by 0.5-degree grid cells were simulated by using the Holdridge life zone classification and the current and predicted temperature conditions under a doubling of CO<sub>2</sub> (Emanuel et al. 1985a, 1985b). The simulations predicted biome type changes throughout 34% of the world's land-

mass. Boreal forest decreased by 37%, tundra decreased by 32%, subtropical forest decreased by 22%, subtropical thorn woodland increased by 37%, and subtropical deserts increased by 26%.

In addition to temperature effects, CO<sub>2</sub> and soil moisture effects were included in a model that predicted the ranges of eight commercial northwest North American tree species under a doubling of CO<sub>2</sub> (Leverenz and Lev 1987). The model combined a projected positive effect of elevated CO<sub>2</sub> on the water-use efficiency and photosynthesis of individual trees, with regional-scale calculations of site water-balance and temperature conditions predicted under a doubling of atmospheric CO<sub>2</sub>. The ranges of lower-elevation species were projected to expand to higher elevations at the expense of the current high-elevation species. The requirements for chilling in several of the species, rather than their physiological tolerance to drought and heat, determined their low-elevation and southern-range limits. As in the Emanuel model, migration, succession, and competition are not included.

The usefulness of both these models lies in their ability to provide insight into the range of possible consequences of climate change. As the authors themselves have pointed out, the actual predictive value of each model is quite limited.

The effects of temperature and precipitation change were predicted for forests across eastern North America by using FORENA, an individual-based forest stand model (Solomon 1986). The ability of the model to project successional shifts in response to climate has been corroborated with historic pollen records (Solomon and Webb 1985). The effects of climate change on forest growth of mixed-aged, mature forests were simulated for 21 sites across boreal, deciduous, and tundra biomes. The FORENA model predicted slower growth rates of most deciduous tree species throughout much of their range; a universal but centuries-long dieback of the original forest; an invasion of the southern boreal forest by temperate deciduous trees; a shift in the general pattern of forest biomes similar to the pattern obtained by Emanuel et al. (1985a, b); and, most inter-

esting, time lags in shifts of community species and biome boundaries of up to 1000 years from the initial change in climate. Species migration is not considered in FORENA, and none of the models included the potential effects of natural disturbances or human activities.

**Human impact.** Human activities are expected to influence many forest responses. Activities with biome-level impact include breeding programs, land management, and active conservation. Breeding programs, a viable option for many commercial species, may permit certain species to maintain their current ranges (Kellison and Weir 1987).

Land use and ownership will affect not only the migration rate of species but also their ultimate range and abundance. For example, the predicted range of loblolly pine (*Pinus taeda*) under a warmer climate would extend well into Indiana and Ohio (Solomon 1986). However, the actual range is not likely to extend that far, because the northern land would still be used for agriculture (Miller et al. 1987). Furthermore, the spatial displacement of forest types may alter their ownership and thus their commercial productivity (Wallace and Newman 1986). Human use of forests for fuel wood could also change with a warmer climate, thereby altering rates of forest degradation in some areas.

The effectiveness of parks and wilderness areas in preserving rare species may change if the spatial distribution of a biome shifts. Humans may need to assist the migration of some species if those species are to survive (Peters and Darling 1985). Active conservation is most likely to be necessary if the range of a species occurs at the edge of a biome, if the species has limited dispersal ability, or if the habitat of the species is disjointly distributed within the biome.

## Ecosystem

Several ecological phenomena are of special interest within the ecosystem level of organization. These include disturbance, nutrient cycling, competition and succession, production, and water use.

**Disturbance regimes.** The interaction between climatic change and disturbance regimes, which can rapidly alter forest structure, potentially could be as important as the direct effects of global warming in controlling shifts in species distributions and local extinctions. Global warming may result in an increased frequency of dry years and a consequent increase in the risk of large fires (Sandenburgh et al. 1987), perhaps increasing the likelihood of fires of the magnitude observed in the northern hemisphere in 1987 (e.g., China and North America) and 1988 (e.g., Yellowstone National Park and elsewhere in North America; Turner and Romme in press). Fire regimes may be more sensitive to climate change than some forest processes, because fire is responsive to fuel moisture, which depends in turn on precipitation and relative humidity. The direct effects of climate change on forest production and decomposition might be overshadowed by more drastic effects of climate on fire regimes (Clark in press).

Past climatic changes of small magnitude have caused significant changes in fire regimes (e.g., Clark 1988, 1990). In northwestern Minnesota, for example, fire was most frequent (approximately 8.6-year return interval) during the warm, dry fifteenth and sixteenth centuries and less frequent (approximately 13.2-year return interval) during the cooler, moister periods from 1240–1440 A.D. and during the period (1640–1840 A.D.) called the Little Ice Age (Clark 1990). Almost all major forest fires in Mt. Rainier National Park, Washington, since 1300 A.D. corresponded with major droughts that were reconstructed for regions east of the Cascade Range (Hemstrom and Franklin 1982).

Fire regimes are sensitive to the average climate over decades to centuries, as well as the interannual variability of water balance (Clark 1990). In northwestern Minnesota, fires were clustered during times of extended low effective precipitation and soil moisture storage in the 1880s and 1910s (Clark 1989). Similarly, the duration of dry periods is one of the best predictors of the area burned in contemporary Canadian forests (Flannigan and Harrington 1988).

However, the projection of changes in fire frequency, intensity, and severity with a changing climate remains challenging because of the complex relationship among weather, fuel availability, and ignition (Turner and Romme in press).

Biotic disturbances such as forest pests and pathogens may also change. Because of their short reproductive cycles, such organisms may be able to adapt or evolve much more quickly than forests. Furthermore, the ranges of forest pests and pathogens are often limited by climatic factors, and species distributions may change with climate. For example, spruce budworm populations may increase with a warmer climate because they are favored by warm, dry, early spring conditions (Haynes 1982). Insect herbivory may also increase because of CO<sub>2</sub>-induced changes in plant tissue quality. In controlled tests, leaf-eating insects that fed on agricultural plant tissue grown under elevated CO<sub>2</sub> generally had higher consumption rates per individual because of the poorer plant tissue quality (high C:N ratio) (e.g., Butler et al. 1986). Trees experiencing stress due to climate change may also have lower resistance to pests such as bark beetles (e.g., reduced resin exudation). Possible shifts in the range and relative competitiveness of weedy plants may be important to managed forests and nature reserves (Peters and Darling 1985).

Because long-lived trees may survive short-term climatic fluctuations, forest species that are best adapted to the current climate may only be able to become established in open habitats after disturbance events. Thus forest composition may respond to climatic changes primarily after disturbance (Dunwiddie 1986). For example, although the ultimate cause of postglacial vegetation change in the Pacific Northwest was climate change, the proximate cause of some vegetation changes was an altered fire regime (Cwynar 1987). It is likely that a small change to a drier climate triggered a relatively large change in the disturbance regime (Cwynar 1987). The implications for the present are extremely important, because an altered disturbance regime may be one of the earliest signals of climate change.

**Competition and succession.** Experimental and paleoecological studies that indicate that competitive abilities of species will shift as a result of species-specific physiological responses to climate change and elevated  $\text{CO}_2$ . In a microcosm study of bottomland and upland tree communities, seedlings of different tree species were grown together for 90 days under elevated  $\text{CO}_2$  and two levels of light. Elevated  $\text{CO}_2$  had no effect on the overall growth of seedlings in either simulated community, although there were differential species responses to  $\text{CO}_2$  within the communities (Williams et al. 1986). In another growth chamber study with seedlings, a fast-growing pioneer tree species showed a 79% increase in biomass under an enriched  $\text{CO}_2$  atmosphere, whereas a slower-growing climax species showed only a 30% increase (Oberbauer et al. 1985).

Such studies suggest that successional paths may change and new community types may evolve under conditions of elevated atmospheric  $\text{CO}_2$ , just as they have in areas subjected to chronic ozone air pollution (Taylor 1984). However, the specific results of such studies with seedlings cannot be interpreted as reliable predictions of future stand responses, because other factors, such as temperature and evaporative demand, that will change concurrently with elevated  $\text{CO}_2$  were not considered in the designs of the experiments, nor were the studies designed to consider effects on seedling establishment or ecosystem feedbacks.

Paleoecological studies also strongly support the hypothesis that individual species response to climate change and elevated  $\text{CO}_2$  and seed source availability will work to create completely new community types (Davis 1989b). For example, such studies have identified community types such as a spruce-oak woodland in North America that existed in the past but cannot be found now. The rate at which communities will change is difficult to predict, because it depends on not only competitive differences but also species longevity, changes in disturbance patterns, and seed source availability.

**Productivity.** Site-specific ecosystem productivity will change as a conse-

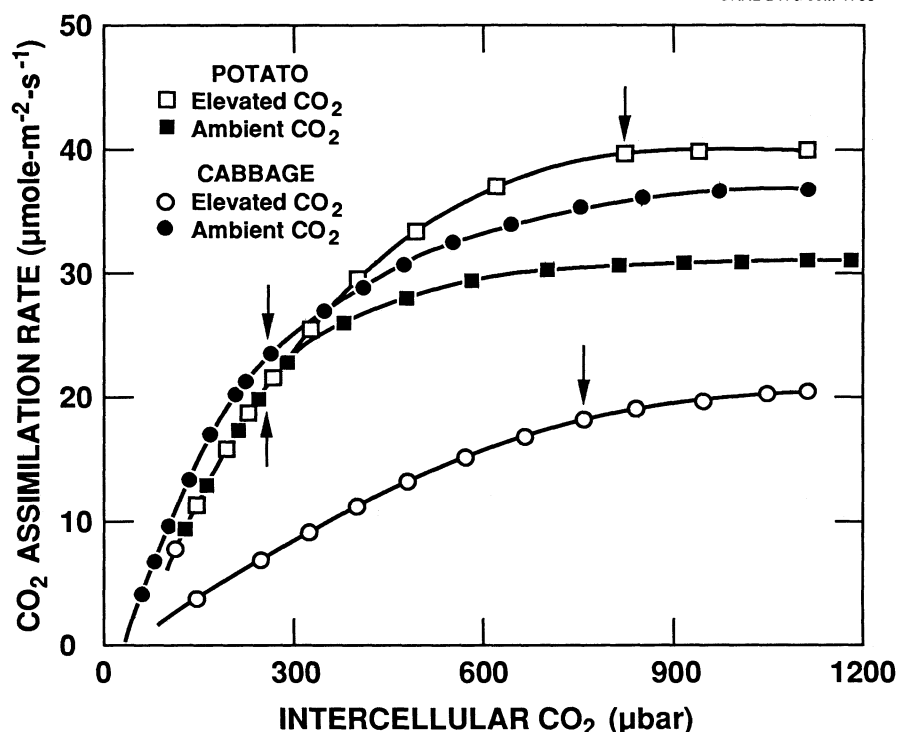


Figure 4. The relationship between photosynthesis and intercellular  $\text{CO}_2$  partial pressure in two  $\text{C}_3$  species grown at atmospheric  $\text{CO}_2$  partial pressure of 300  $\mu\text{bar}$ s (filled symbols) or 900–1000  $\mu\text{bar}$ s (open symbols) (300  $\mu\text{bar}$ s is the normal partial pressure of  $\text{CO}_2$  in the atmosphere in Reno, Nevada, where the experiments took place). The arrows indicate the intercellular partial pressure of  $\text{CO}_2$  when the experimental atmospheric  $\text{CO}_2$  was set equal to the partial pressure of  $\text{CO}_2$  at which the plants were grown. Note that the adaption to elevated  $\text{CO}_2$  resulted in a greatly reduced rate of photosynthesis in the cabbage plant (*Brassica oleracea*) but an increased rate of photosynthesis in the potato plant (*Solanum melongena*). (Adapted from Sage et al. 1989 with permission.)

quence of changes in multiple factors, such as species composition, altered climate conditions for growth, and/or  $\text{CO}_2$  fertilization effects (Leverenz and Lev 1987). Furthermore, the direction of the change may shift over time. For example, if ecosystem change is initiated by catastrophic disturbance, productivity will undoubtedly first decrease and then increase. In the short term, ecosystem productivity will be a function of the responses of the trees currently present and of the abundance and growth rates of invading individuals. Thus the short-term response is not necessarily indicative of the long-term condition.

Long-term positive increases in productivity are likely where current growth is strongly limited by length of the growing season. The correlation between warmer climate and an increase in stem wood productivity in

the boreal forest during the past century is evidence of this type of relationship (Josza and Powell 1987). Long-term decreases in productivity will occur in ecosystems where the current most limiting environmental factor becomes even more limiting. Forest ecosystems in the southeastern United States appear to be quite vulnerable to a warming, because there is currently a delicate balance between potential evapotranspiration and actual precipitation (Neilson et al. 1989).

The degree to which elevated  $\text{CO}_2$  will directly alter forest responses is the wild card in all climate change scenarios. Species adapt to elevated  $\text{CO}_2$  in different ways. Some species display high assimilation rates at twice ambient  $\text{CO}_2$ , regardless of the  $\text{CO}_2$  concentrations under which the individuals have been grown (e.g., the potato plant in Figure 4). In other



species, the positive assimilation response to elevated CO<sub>2</sub> is lost if the individuals have been grown under elevated CO<sub>2</sub> (e.g., the cabbage plant in Figure 4). For an increase in productivity in response to elevated CO<sub>2</sub>, not only must the species be responsive to elevated CO<sub>2</sub> even if adapted, but there must also be a carbon sink for the extra photosynthate, that is, the ecosystem must be environmentally capable of increasing its biomass (Drake et al. in press).

The complexities of the CO<sub>2</sub> response are apparent in the published reports of two long-term ecosystem-level studies on the impact of elevated CO<sub>2</sub>. Arctic tussock tundra, an exceptionally environmentally limited ecosystem, showed no increase in productivity during three years of in situ exposure to double ambient CO<sub>2</sub> (Oechel and Reichers 1986, Tissue and Oechel 1987). Furthermore, laboratory studies with tundra species have shown no positive growth responses to elevated CO<sub>2</sub>, even with the addition of nutrients (Billings et al. 1984, Oberbauer et al. 1986). Thus, in the arctic tundra ecosystem, both species characteristics and environmental limitations appear to keep ecosystem productivity from responding positively to elevated CO<sub>2</sub>.

In contrast, a salt marsh dominated by a C<sub>3</sub> species showed increased productivity during each of the three contiguous years that it was subjected in situ to elevated CO<sub>2</sub> (Curtis et al. 1989a,b, Drake et al. 1989, in press). Both above-ground and below-ground productivity were higher under elevated CO<sub>2</sub>. Quite interestingly, the increase in productivity was not only a consequence of increased assimilation rates but also of decreased respiration rates (Drake et al. in press). These two studies suggest that potential forest ecosystem responses to elevated CO<sub>2</sub> are also likely to be complex.

Even if all other things were constant (which, of course, will not be the case under a changed climate), it is quite doubtful that forest productivity responses to elevated CO<sub>2</sub> would be uniform. Young or aggrading forests would be more likely than mature forests to display increased productivity in response to elevated CO<sub>2</sub>, because younger stands should provide more of

a carbon sink for extraphotosynthate.

**Water use.** It is difficult to predict how water use will change in specific ecosystems. Although water-use efficiency of individual seedlings subjected to elevated CO<sub>2</sub> generally increases due to stomatal and photosynthesis effects, total ecosystem water use may stay the same or increase, because water use is a function of many factors in addition to efficiency.

Leaf area is positively correlated with stand water use; thus a CO<sub>2</sub>-induced increase in stand leaf area would increase water use, all other factors being equal (Jarvis 1989). Water use is also strongly related to evaporative demand, which will increase under a warmer climate. In addition, water use is a function of precipitation and timing of precipitation. If climate change alters either, then forest water use will change, and this change could have profound consequences on stream flow (Wigley and Jones 1985). Finally, if the forest canopy is dense and deep, and thus poorly coupled with the atmosphere, water use will be largely a function of net radiation absorbed by the canopy rather than of canopy conductance (Jarvis and McNaughton 1986).

**Nutrient cycles.** Climate change and elevated CO<sub>2</sub> will affect forest nutrient cycles by altering litter decomposition rates, plant nutrient uptake, and/or internal cycling. Decomposition rates will change in response to alterations in the physical environment, litter quantity and quality, or abundance and types of decomposers. A warmer climate would tend to increase the rate of decomposition by enhancing fungal and bacterial growth (Meentemeyer 1978), but a drier climate would tend to retard decomposition. Forest arthropods, a key component of the decomposition process, could have their ranges altered and their activity levels affected by changing plant tissue or litter quality (Kimball 1985).

If the higher C:N ratio found in plant tissues grown under elevated CO<sub>2</sub> results in higher C:N ratios in litter, then decomposition may be slowed because decomposition rates are negatively correlated with litter C:N ratios. However, there is experi-

mental evidence that tree litter lignin:N ratios, which are also negatively correlated with decomposition rates and generally a better indicator of decay rates than C:N ratios, remain the same or decrease under elevated CO<sub>2</sub> (Norby et al. 1986). The interaction of all these positive and negative effects and the difficulties in extrapolating results across ecosystems limits current ability to predict the overall impact of climate change and elevated CO<sub>2</sub> on decomposition processes.

The effect of elevated CO<sub>2</sub> on many aspects of internal nutrient cycling is largely unknown for forest ecosystems. No studies have followed the effect of elevated CO<sub>2</sub> on woody plant nutrition for longer than one growing season. Limited data suggest that the return of nitrogen through litter fall may remain constant or decrease due to an observed increase in nutrient-use efficiency (Norby et al. 1986). Species shifts associated with climate change may also change ecosystem nutrient cycling patterns and rates at specific sites (Pastor and Post 1988).

**Modeling.** Experimental studies of the impact of climate change and elevated CO<sub>2</sub> on forest ecosystems are limited by inability to easily manipulate climate and atmosphere at the spatial scale of a forest ecosystem. There are no experimental studies exposing intact forests ecosystems to elevated CO<sub>2</sub> with or without warmer climate conditions. Thus predicting forest ecosystem response to changes in CO<sub>2</sub> concentrations and climate requires extrapolating results from finer to broader scales, probably through modeling (Johnson and Sharpe 1982, Solomon 1986).

The effects of climatic change on processes such as net primary production and decomposition may be elucidated by ecosystem simulation models. Individual-based stand simulation models, which incorporate climatic factors as driving variables for tree growth, have been widely used to predict the response of forest stands to climate change (e.g., Davis and Botkin 1985, Pastor and Post 1988). Model results have supported paleoecological evidence that species abundances are not always in equilibrium with climate (Woodward 1987), and



competitive interactions can strongly influence community response (Solomon 1986). Simulations also suggest that there may be a transition period of up to 200 years during which time stand biomass drops (often later to recover) as the forest developed under the original climate is replaced by species better suited to the modified climate (Solomon 1986). Empirical models of the relationship between climate and ecosystem processes such as decomposition (e.g., Meentemeyer 1978) may also be useful, particularly at broad spatial scales.

The combined impact of climate change and elevated CO<sub>2</sub> on forest stand structure and growth has been simulated using individual-based models by incorporating hypothetical effects of elevated CO<sub>2</sub> on individual tree growth. For example, Solomon and West (1987) modified FORENA by increasing the maximum potential growth by 20% for deciduous species and 11% for coniferous species and by decreasing deciduous-tree water use by as much as 18%. These modifications were designed to account for possible productivity and water-use efficiency effects associated with a doubling of CO<sub>2</sub>.

Three forest types were simulated: boreal forest, coniferous-deciduous transition forest, and southern deciduous forest. Temperature was assumed to increase by 6° to 9° C in the winter and 4° to 5° C in the summer, and precipitation was assumed to decrease by 25% in all but the boreal site. The incorporation of CO<sub>2</sub> effects modified the projected forest responses to climate by shortening the transition period, decreasing the associated decline in biomass, and increasing the projected equilibrium stand biomass by 50% in the water- and heat-stressed southern deciduous forest and by 16% in the coniferous-deciduous transition forest.

Because understanding of ecosystem responses to CO<sub>2</sub> is so limited, the simulation results must be regarded as highly speculative and useful largely for their heuristic value. Nonetheless, if reliable information becomes available, these models will help us examine the potential ecosystem implications of climate change under conditions of elevated CO<sub>2</sub>.

The impact of elevated CO<sub>2</sub> on

short-term carbon assimilation in *Picea sitchensis* plantations was modeled by using MAESTRO, a physiologically based canopy model (Jarvis 1989). Although the stand structure, soil respiration, and leaf area parameters of the model were not modified for the elevated CO<sub>2</sub> simulation, the photosynthesis and stomatal parameters were altered on the basis of physiological data collected from seedlings adapted to elevated CO<sub>2</sub> concentrations. Such seedlings display somewhat lower photosynthesis rates than unadapted seedlings at a given level of CO<sub>2</sub>. Nonetheless, the model still predicted an increase in carbon assimilation at the stand level under elevated CO<sub>2</sub>. The modeling exercise demonstrated the importance of considering CO<sub>2</sub> adaption effects in modeling even at the larger scale of the canopy.

Models at different spatial or temporal scales can be linked in various ways. For example, ecosystem models can be joined with stand models, with the ecosystem model defining available resources and the stand model allocating resources and growing individual trees. Pastor and Post (1988) explored the impact of climate change on mature forests of eastern North America on a variety of soils with an individual-based stand simulation model in which the nitrogen cycle and water balance were explicitly modeled. In the simulations, productivity and biomass increased on soils that retained adequate water but decreased on soils with inadequate water. The model results illustrate the importance of spatial heterogeneity of soils in predicting forest responses to climatic change at the ecosystem scale.

**Human impact.** Humans influence forest ecosystems primarily through forest management activities, although local air and water pollution, poor soil management (erosion or compaction), introduction of new pests, and human modifications of natural disturbance regimes through activities such as fire suppression and flood control can also be important. Silvicultural tools such as planting stock, density of planting, mulch, fertilization, and thinning regimes may be used in managed stands to counteract negative effects of climate change or to augment positive effects

(Sandenburgh et al. 1987).

Forest response to elevated CO<sub>2</sub> and climate change may be easier to manage in mixed-species stands under uneven-aged management than in monospecific stands under even-aged management. Individual trees will respond to climate change on a gradual basis and at uneven rates. Uneven-aged management allows harvesting in accordance with the differential timing of those responses. In stands under even-aged management, species composition and genotype can be switched only at planting time. In short-rotation, intensive-culture plantations, where genotypes and/or cultural regimes can be easily changed every 10 to 20 years, the risk may be minimal. However, even-aged stands having longer rotation times will require decisive management with much more risk. Already there is concern within the United States timber industry about the fate of loblolly pine stands planted to the south and west of their natural range if the climate in that region becomes even drier and hotter (Graham et al. 1986).

Regional land-use changes will also influence forest ecosystem responses (e.g., Turner 1987). Hierarchy and landscape ecology theory suggest that an ecosystem's response to disturbance may be a function of the system's setting in the larger landscape (e.g., Turner et al. 1989b).

**Direction of changes.** Although ecosystem phenomena are likely to change in response to elevated CO<sub>2</sub> and climate change, the direction of the changes will depend on highly specific circumstances. The prediction of the impact of these changes on forest resources will depend on integrating experimental results from a finer scale and linking them through concepts of ecosystem function (Woodward 1987). The most significant long-term effect of elevated CO<sub>2</sub> and climate change on forest ecosystems is likely to be changes in disturbance regimes (Turner and Romme in press) and in successional patterns in the unmanaged, mixed-species stands that dominate global forest resources (Solomon et al. 1984). The role of elevated CO<sub>2</sub> in these changes is highly uncertain because of our inability to predict whole, mature tree responses to elevated CO<sub>2</sub> and the

many feedbacks between CO<sub>2</sub> and ecosystem function and structure. Both current modeling results and paleoecological evidence suggest that during times of climate change, the response of natural forests in the absence of disturbance is delayed because of the longevity of the individual trees. Thus we may not perceive climate effects on community composition until long after the climate has changed. Managed mixed-species stands and plantations will also be sensitive to elevated CO<sub>2</sub> and climate change, but with foresight, human intervention can potentially mitigate many of the economically and socially detrimental responses.

## Tree

Processes of interest when considering individual trees are phenology, life-cycle events (e.g., reproduction and death), and physiological processes (e.g., photosynthesis, transpiration, respiration, carbon allocation, nutrient uptake, and nutrient allocation). The key challenge is to identify the whole-tree effects of climate factors and/or atmospheric CO<sub>2</sub> with and without other stresses (e.g., drought, flooding, cold, shade, poor soil, and pollution).

**Climate.** Current understanding of the effect of climate variables on trees is based largely on qualitative observations of mature trees and short-term (minutes to days) experiments on leaves or seedlings. Experimental studies on whole, mature trees have been limited because of tree size and longevity. Mature-tree responses to climate are generally inferred by relating observed growth responses to past weather patterns (e.g., Holdaway 1988). Field data on growth responses to climate are often qualitative, and growth data are generally lacking from the tropics (Solomon et al. 1984). In particular, there is little information on how the frequency of extreme climatic events affects tree-level processes. This lack is especially important, because after the predicted climate change trees may be exposed more frequently to extreme events. Trees may survive an infrequent extreme event such as a severe drought but experience deleterious effects—even death—if the fre-

quency of such events increases.

Information on the effect of elevated CO<sub>2</sub> on trees is limited primarily to leaf-level studies, a 3-week exposure of the canopy of 12-year-old trees (Wong and Dunin 1987), and short-term (two growing seasons) studies on seedlings or young saplings of less than 30 tree species (Eamus and Jarvis 1989). The results from the few longer-term studies are confounded by experimental artifacts (Jarvis 1989). Under well-watered and fertilized conditions, nearly all C<sub>3</sub> species, including trees, show significantly greater growth with elevated CO<sub>2</sub> (Kramer and Sionit 1987).

The usefulness of this information is limited, however, because trees generally grow under less than ideal conditions and for many years. Thus data on the long-term response of trees to CO<sub>2</sub> under conditions of nutrient stress, water stress, and light deprivation are needed. These data will be difficult to obtain and will likely be limited to a few species.

Although initially some of the ecological literature invoked Liebig's Law of the Minimum to suggest that CO<sub>2</sub> will have no beneficial effect if other environmental factors are limiting, short-term seedling studies have repeatedly found that elevated CO<sub>2</sub> enhances growth even under conditions of nutrient, soil moisture, or light deprivation (e.g., Tolley and Strain 1984). In many cases, the relative response of stressed plants to elevated CO<sub>2</sub> exceeds that of unstressed plants. Whether this enhancement can be maintained over a longer period is, however, unknown.

Several long-term field studies currently under way should help resolve this most important issue. Elevated CO<sub>2</sub> can also induce in seedlings subtle morphological changes such as increased branching, increased ratio of fine to coarse roots, and greater nodule mass on nitrogen-fixing species (e.g., Norby 1987). Tissue quality also changes with elevated CO<sub>2</sub>; C:N ratios increase, and lignin content decreases (e.g., Williams et al. 1986).

The combined effect of elevated CO<sub>2</sub> and other environmental factors, such as temperature, humidity, or air pollution, have only been studied at the individual leaf level in trees. Agricultural studies suggest that elevated CO<sub>2</sub> may partially mitigate negative

responses to these factors (Kramer and Sionit 1987). The lack of long-term studies precludes much data on the impact of elevated CO<sub>2</sub> on tree life-cycle events or phenology.

**Modeling.** Even at the much finer spatial and temporal scale of the tree, modeling is essential for understanding and predicting response to CO<sub>2</sub> and climate. Tree size, longevity, and the large number of species preclude taking an exclusively experimental approach to evaluating individual tree responses. Models of physiological processes such as photosynthesis and respiration (e.g., Farquhar et al. 1980) can be used to test hypotheses about the interactions of temperature, CO<sub>2</sub>, radiation, and moisture on a leaf. These models may help elucidate the mechanisms of whole-tree responses to climate change and allow prediction of tree responses under conditions beyond those of the experiments.

**Human impact.** Humans can influence individual trees by modifying either the immediate environment of the tree (e.g., watering, fertilization, weed control, or pollution abatement) or the genetic makeup of the tree (e.g., breeding or genetic engineering). Of the four levels considered in this article, the individual tree seems most amenable to experimental study. Currently, long-term data and data on life-cycle events and phenological responses are especially needed.

## Implications for future research

Predicting and detecting forest responses to the projected changes in CO<sub>2</sub> and the global climate present significant challenges that require creative solutions. Major issues include changes in the areal distribution of forests and forest types, changes in productivity or other functions of interest, and the influence of landscape heterogeneity on these responses. The challenges arise primarily from the broad-scale nature of the questions, the projected rate of change, and the many environmental interactions that must be considered. The types and combinations of experiments that can be conducted become increasingly limited as one goes to successively

**Table 2.** Timing of forest responses to global climate change and elevated CO<sub>2</sub>.

Feature	Likely response
<b>Early changes (years to decades)</b>	
Disturbance regimes	Changes in the frequency, intensity, and extent of disturbances such as fire, pest or pathogen outbreaks, and storm events may lead to rapid changes in forested landscapes.
Seedling establishment	Changes in the relative abundance of seedlings of different species (i.e., failed or decreased recruitment) suggest the initiation of a long-term change in species composition.
Ecotone movement	Biome-level changes in the location of boundaries between forested and nonforested systems may be observed early, because species at the edges of their ranges are likely to be less tolerant of climatic changes.
Hydrologic regimes	Changes in precipitation, temperature, and stand water use will alter runoff patterns, although potential regional-level changes in water use efficiency are not well understood.
<b>Intermediate to long response time (decades to centuries)</b>	
Productivity rates	Forest productivity over large spatial areas will change slowly, because changes in species composition may reduce the rate of change in productivity. Increased water use efficiency in trees may help mitigate potential productivity losses due to drought.
Changes in pools of carbon and other essential elements	As productivity, decomposition, and nutrient cycling change with climate, storage of essential elements in forests will also change.
Species composition in interior biomes	Tree migration will be a long-term response because of time lags in the responses of mature trees. Mature individuals may persist for decades, even though the composition of the understory changes.

larger spatial and temporal scales. Future research should include monitoring, experimentation, and modeling.

**Detection.** Attempts to detect changes in forests should focus on sensitive processes and areas, recognizing the different time scales over which responses will be observed (Table 2). One of the earliest indications of forest response to global change may be alterations in the frequency and intensity of disturbances. Therefore, particular emphasis should be placed on increasing ability to predict the occurrence and effects of disturbances and on monitoring disturbance-prone forests. Seedling establishment may be particularly sensitive to climate change. Thus tracking tree recruitment in natural stands may provide an earlier indication of forest response than monitoring changes in the overstory composition, which may exhibit substantial time lags.

Efforts to predict changes and monitor the distribution and boundaries of major ecosystem types should con-

tinue. In the absence of disturbance, the first perceptible changes in global vegetation patterns may be at the transitions between major life zones (e.g., Nielson et al. 1989). The boreal forest transition zone and its alpine counterpart may be particularly sensitive. It is also critical that the effects of changes on the variance in temperature and precipitation be considered. Mean values may not be meaningful, because extreme events may affect forested areas even though the mean remains unchanged.

**Experimental research.** Experimental research needs include quantitative data on the water use, productivity, nutrient uptake, and phenological responses of mature trees to long-term exposure to elevated CO<sub>2</sub>, the sensitivities of tropical species to climate, and the interactions between exposure to elevated CO<sub>2</sub> and other environmental stresses. We need to know if the adaption and acclimation responses observed in seedlings are characteristic of mature trees and, if

they are not, why. More information on below-ground responses to elevated CO<sub>2</sub> is also needed, as is information on tropical forest responses.

It may be prudent to focus experimental work on tree species that are economically important or characteristic of particular forest ecosystem types. Research on water use and CO<sub>2</sub> response is particularly relevant for species that reside in regions such as the southeastern United States that are likely to be water limited under global warming. Experimental work should also focus on variables that provide linkages between spatial scales and biotic levels. For example, Norby et al. (1986) focused on parameters linking tree-level physiological phenomena with ecosystem-level decomposition processes. Because of the increased likelihood of drought in some of the major temperate forest areas and the societal importance of water availability, the interactions between CO<sub>2</sub> and water use and forests at larger spatial scales needs particular exploration.

**Scaling.** Research is especially needed on the scaling problems that permeate the entire discussion of forest responses to climate change and elevated CO<sub>2</sub>. Methods to extrapolate information from site-specific studies to the regional scale must be developed if the broad-scale questions are to be answered.

Changes in the importance of the variables controlling ecological processes at different scales should be used to our advantage in developing hypotheses and designing experiments (Turner et al. 1989a). Ecological responses differ with the temporal and spatial scale at which they are studied, and the controlling variables at each scale are likely to be different. As spatial extent increases, for example, the level of discernible detail, the number of important variables, and the potential for experimental manipulation all decrease (Meentemeyer and Box 1987).

Important variables at the broad scale tend to be abiotic rather than biotic, and the variance of parameters in the landscape may increase with scales (Meentemeyer and Box 1987). For example, the rates of litter decomposition at a particular site can be predicted knowing the chemical/

physical properties of litter species, but at broad spatial scales, climatic variables are sufficient to predict rates (Meentemeyer 1978, 1984). Thus we may be able to substantially simplify experiments if we can identify a priori the key controlling variables at a particular scale. The development of good correlative relationships between abiotic and biotic variables, for example, could significantly reduce the number of parameters that must be measured through time to predict forest responses.

**Large-scale studies.** The dynamics of heterogeneous landscape must be understood to predict regional forest responses. Global change is likely to have substantial effects on the structure and function of forested landscapes, yet the implications of spatial heterogeneity over large areas are only beginning to be understood (Turner 1989). The traditional process-oriented view of ecosystems must be complemented with other approaches as we seek to understand forest responses at larger and larger spatial scales. For example, manipulation of the factors that constrain a species distribution or an ecological process may be more insightful than obtaining a more detailed view of all factors that influence the phenomenon of interest.

Cross-site research is essential to understanding forest responses to global change. Observations or manipulative experiments can be conducted in forests across a globally significant gradient (e.g., temperature or precipitation gradients in North America) to test hypotheses about the mechanisms controlling ecological processes at broad scales. For example, studies conducted along a climatic gradient might use a variety of carefully chosen sites as surrogates for climatic change. One might test hypotheses about the ability of particular tree species to withstand different climates, the time for recovery from disturbances, or changes in the variance of biological or physical parameters. Identical perturbations could be imposed in different forests across a major temperature or precipitation gradient in the United States and responses compared. Experiments can also be conducted along altitudinal gradients across which climate

changes rapidly in response to elevation. Comparative studies of the same phenomena at different scales would aid in the development of extrapolation rules.

**Modeling.** Current modeling capabilities should continue to be used to explore hypotheses about ecological responses, identify sensitive parameters that should be monitored, and provide a means to extrapolate local responses to regional scales. Modeling is particularly important because of the time lags in forest responses. Because of the potential economic consequences of climate change, it is also important to predict forest effects that are relevant to management actions. From the perspective of the forest industry, information must be geographically and temporally specific.

A comprehensive research program should avail itself of current capabilities in remote sensing. The extrapolation of empirical results and simulation studies to large spatial scales requires methods to measure and track changes in broad patterns of vegetation (Iverson et al. 1989a) and processes (e.g., gas flux, evapotranspiration, and production; Luvall and Holbo in press, Running et al. 1989). Remote sensing holds great promise as a means of gathering synoptic information on forest composition, structure, and processes at landscape, biome, and global scales (Iverson et al. 1989b). Remote-sensing data may be invaluable in addressing questions regarding the effect of landscape heterogeneity on forest responses. A variety of indices may be used to quantify landscape patterns (Turner 1989). By repeating such measurements through time with satellite imagery, changes in the spatial pattern of forests can be quantified at broad scales. Remote sensing should also be combined more frequently with empirical studies so that measured values of processes can be correlated with the spectral data (Cook et al. 1989).

Humans influence forests across all spatial and temporal scales. In turn, forest resources are critical for humans. Forests influence the availability of water, serve many recreational purposes, and provide fiber, timber, and fuel. National economies may be

altered by the displacement of forests at the biome scale, and local economies will certainly be affected. Forest responses to climate change and elevated CO<sub>2</sub> will determine the fate of many of the species dependent on them, including humans.

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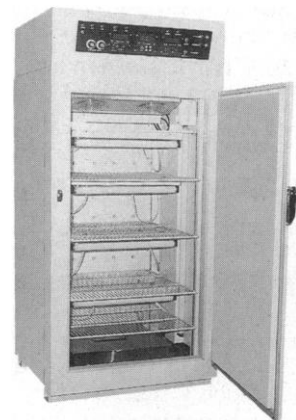


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