Models to Assess the Response of Vegetation to Global Change

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The two mathematical simulation models developed by the response of plants to interacting stresses (ROPIS) study can be utilized to address environmental questions related to global change. Utilities and government agencies can use these models to assess ecological effects of global change and to analyze various policy and mitigation options.

BACKGROUND

Forests are subjected to a number of potential anthropogenic stresses (for example, ozone) and natural stresses (such as drought). To understand the effects of any one stress, that stress needs to be incorporated into an analytic framework that includes all stresses. Hence, in the ROPIS study (project RP2799), EPRI developed a general, theoretical, mechanistic framework to analyze plant response to interacting stresses. By approaching the subject mechanistically, that is, by explicit consideration of processes that govern plant allocation of resources and growth, and processes by which a plant interacts with the soil and atmosphere, a framework was developed that could be applied to a broad range of environmental issues, including global change. This framework consists of two computer simulation models, the TREGRO and PGSM models.

OBJECTIVES

To describe the conceptual basis of the ROPIS models; to illustrate how the ROPIS models can be applied to questions related to global change; to identify modifications that can be made to the ROPIS models to enhance their applicability.

APPROACH

The authors describe how the ROPIS models simulate an individual plant's response to factors related to global changes in atmospheric CO2 and climate. They explain how other factors considered by the model, such as nutrient availability, mediate a plant's response and how growth response of a single tree species can eventually alter the composition of a forest composed of several species.

RESULTS

The ROPIS models can be used to address questions of global change, such as the capacity of plants to increase their rate of growth and sequester more carbon under conditions of changing climate and increasing atmospheric CO2. At the biochemical level, for plants possessing the C3 photosynthetic pathway, the models predict photosynthesis to increase with increasing atmospheric CO2, unless nutrients or moisture are limiting or air pollutants interfere with carbon fixation. A plant's response to increasing temperature depends upon the combination of its effects on photosynthesis and respiration. Results from the ROPIS models can be extrapolated using stand models to predict the effects of global change on plant competition and to evaluate the likelihood of ecosystem disruption and changes in the geographic distribution of species.
EPRI PERSPECTIVE  Global climate change will be a major emerging issue for the electric power industry during the coming decade. The industry advisors of EPRI's Environment Division have rated it third in priority among environmental issues. EPRI has developed an integrated program to address global climate. The application of the ROPIS models is part of an effort undertaken by the Ecological Studies Program to assess and predict ecological responses and to evaluate ecological approaches to mitigation. The models can be used not only to predict effects of global change but also to predict growth and carbon sequestering of forests maintained for mitigative objectives. The further enhancement of the ROPIS models and their applications will be carried out under a new project, global change ecological response models (EPRI project RP3316). It is anticipated that current working versions of the new models will be distributed this year. The models will also have applicability to issues of ozone and nitrogen deposition effects, prevention of significant deterioration in park and wilderness areas, and wetlands management.

PROJECT
RP2799-1
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EN-7366
Research Project 2799-1
Topical Report, August 1991

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ABSTRACT

The ROPIS models, which were initially developed to analyze the response of plants to interacting stresses, can be modified to address questions of global change, such as the capacity for plants to increase their rate of growth and sequester more carbon under conditions of changing climate and increasing atmospheric carbon dioxide. The ROPIS models calculate the detailed dynamics of carbon fixation and allocation and are capable of analyzing the degree to which moisture and nutrient availability and pollutant load can restrict the capacity for increased growth.

At the biochemical level, for plants possessing the C₃ photosynthetic pathway, the models predict photosynthesis to increase with increasing atmospheric CO₂, unless nutrients or moisture are limiting or air pollutants interfere with carbon fixation. At the whole-plant level, changes in plant structure resulting from the allocation of carbon for growth can affect the ability of the plant to acquire light, water and nutrients, and thus affect the plant's capacity to increase growth under increasing CO₂. A plant's response to increasing temperature depends on the combination of the effects on photosynthesis which may increase carbon gain and respiration which will accelerate carbon loss at higher temperatures. The models can also incorporate the effects of predicted changes in precipitation on plant growth.

The productivity of whole assemblages of plants, not just the growth of individuals, is important to the global carbon balance and to changes in plant distributions. The results from physiological models can be used to predict the implications of the effects of CO₂ on plant competition. The consequences of changes in plant competitive success can be used to evaluate the likelihood that ecosystems will be disrupted and their distribution across the landscape altered. Using the relationship between temperature and growth identified by the ROPIS models in a stand-level model, we can predict the susceptibility of forests to invasion by new species under warming temperatures.

The models should be modified to improve their capability of assessing global change questions. Proposed modifications include extending to a variety of species and to types within species, including a more biochemically detailed representation of photosynthetic processes, refining the representation of canopy light regimes, making organic matter decomposition sensitive to litter quality, and accounting for greenhouse gases emitted by the plant-soil system. With these improvements, the ROPIS models can better evaluate plant response to changes in temperature, precipitation, and CO₂ concentration under long-term environmental change.
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Introduction

The carbon dioxide (CO₂) content of the atmosphere has risen dramatically since the Industrial Revolution (Keeling et al. 1989). Anthropogenic activities release approximately six gigatons of carbon into the atmosphere per year and this quantity is increasing annually (Post et al. 1990). Increasing atmospheric CO₂ could cause a change in global climate. Increases in global temperature could occur. Patterns of storm tracks could be altered, changing the input of precipitation to large regions.

Biological processes could be affected by any or all of these changes. Since photosynthesis is commonly limited by CO₂ concentration, increased global CO₂ might be expected to increase plant growth. On the other hand, the ability of plant communities to increase carbon absorption through accelerated growth may be limited by the availability of other resources (light, water, or nutrients) or the dynamics of inter-plant competition. Increases in temperature could increase plant respiration, leading to vegetation growth declines (Warrick et al. 1986). High CO₂ concentrations could also contribute to increased plant respiration (Tolbert and Zeitlich 1983). Changes in the abundance of water could increase or decrease plant growth across whole regions, and could change the pattern of transpiration through which water is returned by plants to the atmosphere. Dramatic shifts in the growth of species might alter the competitive balance in plant communities, causing movement of ecosystem boundaries across landscapes and changes in wildlife habitat.

The global carbon circulation system contains feedbacks that may absorb much of the increases in CO₂ added to the atmosphere by human activities, preventing or delaying anthropogenically induced climate change. Increased plant growth could tie up the excess CO₂ in biomass, preventing atmospheric CO₂ increases and their consequences (Warrick et al. 1986). The terrestrial ecosystems of the world annually absorb 62 gigatons of carbon, ten times the amount generated anthropogenically (Post et al. 1990). However, a nearly equivalent amount of carbon is returned to the atmosphere annually through decomposition. An uncertain amount is sequestered into long-term storage in soils and slowly decomposing wood, effectively removing this carbon from circulation.

What is the capacity of plants to take up additional CO₂? Will this capacity be altered by changes in global temperature and precipitation? Will these changes have profound effects on plants and plant communities? The net effect of the simultaneous interactions between global change and plants and ecosystems is difficult to assess. There is a need for tools that can evaluate the effects of global changes on trees and ecosystems in the context of other stress agents co-occurring in the environment, such as exposure to ozone, acidic deposition, nutrient deficiency, and drought. There is also a need to calculate the fluxes of greenhouse gases from the plant-soil system to the atmosphere. Simulation models of the physiological processes controlling carbon accumulation and models of the consequences of changes in carbon accumulation on the competitive balance in plant communities are our best tools for evaluating the net result of these plant-climate interactions at the biochemical, whole plant, ecosystem, and biome levels.

The modeling tools developed in the ROPIS (Response of Plants to Interacting Stresses) program are well-suited to be extended to study interactions between stress factors and plant responses to increases in global CO₂ and climate change. TREGRO (Weinstein and Beloin 1990, Weinstein et al. in press), a ROPIS model of the physiological and growth response of a single plant to multiple stresses, has been developed at Cornell University from funds supplied by the Electric
Power Research Institute. PGSM (Chen and Gomez 1990a, b, c), a ROPIS model of the interactions between pollutants, environmental stresses, and tree growth, has been developed at Systech Engineering, Inc. from funds supplied by EPRI, the National Council of Paper Industries for Atmosphere and Stream Improvement, and the Southern California Edison Company. In combination with a stand simulator such as a gap-succession model, physiological predictions made by these single-species models can be applied to the dynamics of mixed-species stands.

In this paper we will explore the capacity of the ROPIS models to evaluate the effects of global change. We will first identify the important factors that can influence plant response to climate. We will then examine the ways in which physiological models can be employed to predict the capacity of plants to utilize increased atmospheric CO₂ and thereby influence the global carbon budget. We will then discuss the ways such models can be used to predict the effect on plants of rising global temperatures. We will identify the changes that can be made to these models to permit them to better evaluate the responses of plants to elevated CO₂ and climate change. Since it is the productivity of whole assemblages of plants, not just the growth of individuals, that is important to the global carbon balance and to changes in ecotones, we will demonstrate how the results from physiological models can be used to predict the implications of the effects of CO₂ on plant competition. The consequences of changes in plant competitive success can be used to evaluate the likelihood that ecosystems will be disrupted and their distribution across the landscape altered.

**Factors influencing plant response to elevated CO₂**

Whether a plant will be capable of increasing its accumulation of carbon in response to increasing atmospheric CO₂ depends on the plant's internal condition, its response to the environment, and the health of its competitors. Therefore, biochemical, whole plant, and community or stand levels must be considered in predicting plant response (Figure 1).

**The Biochemical Level**

At the biochemical level, a plant's carbon accumulation capability is determined by the photosynthetic process. The photosynthetic process is comprised of a physical component, in which the molecules of CO₂ diffuse through the stomates and across the mesophyll membrane, and a chemical process, in which fixation into carbon compounds is catalyzed by enzymes. Increases in atmospheric levels of CO₂ will increase the gradient between air and internal leaf spaces, accelerating the physical movement of molecules into the leaf (Lohammer et al. 1980). By providing more CO₂ molecules to the chemical reaction, the photosynthetic rate can thus be increased.

Since the photosynthetic pathway is different in C₃ and C₄ plants, there are differences between these plants in their ability to take up additional CO₂. Unlike C₃ plants, the fixation processes of C₄ plants are normally saturated at present CO₂ levels (Tolbert and Zeihl 1983). Consequently, there is little likelihood that these types of plants can fix CO₂ at a faster rate in a CO₂-enriched atmosphere. Changes in water availability caused by shifts in rainfall patterns could permit greater photosynthetic rates, although these plants tend to be extremely efficient with respect to water use.

Most plants depend on C₃ metabolism and are often observed to grow faster when provided with additional CO₂ in controlled laboratory settings (Warrick et al. 1990). Many environmental conditions can modify this simple response to elevated CO₂. Both the stomates and the mesophyll membrane add resistances to free molecule movement into the leaf. The stomatal resistance can be increased by soil water deficiency or by water vapor pressure deficits between the leaf and the atmosphere. Thus dryness of soil or air can inhibit photosynthesis from increasing with increased CO₂.

Many steps in the biochemical process of CO₂ fixation into glucose molecules are vulnerable to disruption or interference stemming from limitations of available resources or the presence of interfering compounds within the plant. At each step, many conditions can limit the rate at which the photosynthetic process can proceed under elevated CO₂.

Biochemical constraints on photosynthesis include the regulation of enzyme activity and feedback from
Feedback processes at the biochemical level

Carbon fixation may not increase if the rubisco enzymes become saturated, inactivated by other stresses, or their synthesis is repressed. Other biochemical mechanisms may also suppress carbon fixation.

Information feedbacks between levels

Does the rate of fixation in the mesophyll cells increase?

Can the tree adapt its structure to provide resources necessary to utilize additional CO₂?

Feedback processes at the whole-tree level

Carbon may not be fixed if the plant root system is too small to provide necessary water and nutrient resources.

Information feedbacks between levels

How much light and nutrient can the plant access?

Will stand dynamics change the availability of resources?

Feedback processes at the stand level

Carbon may not be utilized if the competitive position of the plant in the canopy prevents it from acquiring necessary resources.

Figure 1. Possible feedbacks in response to elevated CO₂.
glucose accumulation. Photosynthesis is limited by the quantity of rubisco enzymes available to pick up the CO2 molecules and carry them to the site of fixation (Warrick et al. 1986). If these enzymes become inactive or their synthesis is repressed, the enzymes remaining will quickly become saturated with CO2 and will be unable to carry additional molecules. For example, exposure to gaseous pollutants such as ozone may cause enzyme inactivation or repression. If enzymes are limiting, the plant may be unable to utilize any of the extra CO2 to which it is exposed.

Under conditions of nutrient stress, enzymes lost through natural deterioration cannot be replaced because resources necessary for their manufacture are in short supply. The quantity of rubisco enzyme manufactured is regulated by the amount of nitrogen available to the plant for the construction of amino acids. If nitrogen availability is limited, the plant will be unable to manufacture the additional enzyme necessary to carry extra CO2 and will be unable to respond to elevated CO2 by raising photosynthesis rates.

It has been postulated that if photosynthesis manufactures glucose molecules faster than they can be removed to the translocation stream in the phloem, the accumulation of glucose may inhibit further photosynthesis. Unless phloem loading accelerates as much as photosynthesis with elevated CO2, this feedback may eventually suppress photosynthesis and limit the quantity of extra CO2 that can be fixed by the plant.

The Whole Plant Level

Increases in carbon uptake at the leaf level may lead to increased growth at the plant level, provided the supply of other essential resources can be increased. In order to increase this supply, the plant could alter its structure by building more root tissue to increase the uptake of nutrients or water or by expanding the canopy to reach more sunlight. If carbon fixation increases due to increased atmospheric CO2, additional carbon will be available to construct the needed tissue, which can in turn increase the plant’s capacity for accelerated fixation.

Environmental conditions can prevent plants from utilizing ever-greater supplies of CO2. If resources are extremely limited, no amount of reallocation will supply the plant with sufficient resource quantities to permit increased growth.

Some limiting conditions can be circumvented through increases in the efficiency of resource use. Limiting water conditions might be circumvented through the gains in water use efficiency that may accompany elevated atmospheric CO2. At higher atmospheric concentrations, more CO2 molecules can pass a given stomatal opening in a unit time. Since water loss is related to the amount of stomatal opening, more molecules of CO2 will be taken up for each molecule of water lost. This additional efficiency in the amount of water used in fixing each new carbon molecule can permit the plant to increase overall carbon accumulation even when water uptake would otherwise limit growth.

The Stand Level

Interactions between plants in communities or forest stands can also limit plant response to elevated CO2. The water and nutrient status of an individual plant, discussed above, can be limited by competition from its neighbors. Even a plant with access to abundant water and nutrients may be unable to increase carbon fixation if competing plants are blocking access to light.

To predict the dynamics of plants in forest stands requires consideration of the regeneration dynamics, longevity, photosynthesis, respiration, growth allocation, water, and nutrient-use patterns of co-occurring species.

Modeling the capacity of plants to Increase CO2 fixation

There are clearly many factors affecting the response of plants to elevated CO2. The simple tendency of CO2 fixation to increase with CO2 concentration can be overridden by other conditions, such as limitation by light, water, or nutrients. To alter rates of acquisition of these resources, the plant can change its carbon allocation patterns, thereby changing the limits to growth. Other interactions can also affect plant growth; for example, increased CO2 may reduce water loss, permitting improved growth under water-stressed conditions. Because there are so many variables affecting plant response to elevated CO2, models are necessary to evaluate their complex interactions.

The two ROPIS models are tools with which the status of carbon, nutrient, and water limitations of growing
trees can be analyzed and the resulting ability of trees to utilize higher carbon dioxide concentrations can be estimated. The models calculate the detailed dynamics of carbon fixation and allocation in greater detail and would be capable of analyzing feedbacks between moisture availability, pollutant load, and carbon dioxide levels (Figure 2).

Photosynthesis
One of the ROPIS models is already capable of simulating the effect on photosynthesis of changes in atmospheric CO2 and other environmental factors. The TREGRO model predicts hourly gross photosynthesis, the total amount of CO2 fixed each hour, based on the concentration gradient between the atmosphere and the site of carbon fixation within the leaf and the resistances to the flow of carbon to this point of fixation. Increases in the gradient of CO2 between the atmosphere and the internal spaces of the leaves will cause increases in the flow as long as the resistance to flow does not change. Using this simple relationship and assuming that the photosynthetic enzymes will not become saturated as more CO2 becomes available for fixation, the model can calculate the expected increase in the rate of fixation under elevated CO2 levels when no other factors are limiting.

The models contain simplifications of the photosynthetic process, such as “mesophyll resistance”, which describes molecule movement across the membrane into the mesophyll cells, into linkage with enzymes, and into fixation in carbon compounds. This simplification of complex biochemical steps prevents the models from being used to evaluate the influence of some factors on plant response to elevated CO2. For example, the presence of oxygen can interfere with electron transport and decrease assimilation rates (Meyer et al. 1973), yet this interaction is not included in the models. The models could be equipped with the capability of examining the effects of such processes by calculating mesophyll resistance from biochemical relationships, as in the model of Farquhar et al. (1980).

Environmental Factors
The response of photosynthesis to changes in the CO2 gradient must be modified in response to humidity and to limitations of light, water, or nutrients. In the ROPIS models, these alterations are made through adjustments of the stomatal and mesophyll resistances, both of which are sensitive to various environmental conditions. For calculation purposes, the term “conductance”, the inverse of resistance, is used to describe movement of CO2 into the leaf (stomatal conductance) and its movement across and into the mesophyll cells (mesophyll conductance). As the concentration gradient increases, the flow of CO2 molecules into the internal spaces in the leaf will increase. Increases in the rate of either stomatal conductance or mesophyll conductance will lead to increases in photosynthesis. Any decrease in conductance will hinder the ability of the plant to utilize additional atmospheric CO2. In one of the models, TREGRO, stomatal conductance is regulated by both plant water potential and the vapor-pressure deficit between the interior leaf spaces and the atmosphere. A low water potential deficit or a high vapor pressure deficit will decrease stomatal conductance and cause a decline in the rate of movement of CO2 molecules into leaf cavities. If this decline occurs simultaneously with an increase in CO2 concentrations in the atmosphere, the net effect might not be increased photosynthesis.

A plant receiving more CO2 molecules per unit of stomatal opening may improve water-use efficiency by partially closing the stomates, decreasing transpiration losses. Over time this reduction in water use could maintain higher water potentials in the soil and, subsequently, in the plant. The net result of this improved water status could be longer periods of the growing season when stomates can remain open and utilize CO2.

The models can presently evaluate whether conditions of insufficient light or nitrogen will limit photosynthesis and prevent utilization of higher concentrations of CO2. In the models, photosynthesis proceeds at a maximum rate under full sunlight and declines as light decreases below a critical "saturation" level that varies among species. The models will calculate a lower photosynthesis rate during each hour that light availability is below this critical level.

Since photosynthesis is proportional to the quantity of rubisco enzyme, which, in turn, is proportional to the nitrogen concentration in the plant that has not been immobilized in the manufacture of structural tissue, it is assumed in one model that photosynthesis is proportional to this nitrogen concentration. This concentration
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**Processes at the biochemical level**
- Leaf photosynthesis is proportional to the gradient of CO$_2$ from outside the leaf to internal leaf spaces. As CO$_2$ increases, photosynthesis will increase unless otherwise limited.
- However, CO$_2$ movement is slowed if stomates close.
- The rate of fixation slows if enzyme construction and maintenance is impaired because of insufficient nutrient supplies.

**Inter-level information to be exchanged**
*Will the rate of fixation be increased by higher atmospheric concentrations or will photosynthesis be saturated with CO$_2$?*

*Can the tree provide resources necessary to utilize additional CO$_2$?*

**Processes at the whole-tree level**
- Carbon fixation will be slowed if the plant cannot provide sufficient nutrients to maintain enzymes.
- Carbon will accumulate in the leaves if it cannot be utilized elsewhere in the plant. The rate of fixation slows as carbon compounds accumulate in the leaf.
- Respiration will increase under higher temperatures.

**Inter-level information to be exchanged**
*Does the plant have room to grow?*

*Will growth deplete the nutrient supply?*

*Will the plant continue to have access to light?*

**Processes at the stand level**
- Carbon may not be utilized if the competitive position of the plant in the canopy prevents it from acquiring necessary resources.

\[\text{Figure 2. Processes in the ROPIS model to evaluate the response to elevated CO}_2.\]
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is proportional to the availability of nitrogen in the soil for uptake. To estimate nutrient availability, the model calculates the quantity of essential nutrients and water available in the soil and the amount of these resources taken up by the plant each hour. Equipped with the capability of making these calculations, the model can serve to assess light and nitrogen limitations to the ability of the plant to utilize increased CO₂ in photosynthesis and growth.

Air pollution exposure is another environmental factor that could decrease mesophyll conductance, limiting the ability of a plant to use additional CO₂. For example, in the models, ozone that passes through the stomates reduces mesophyll conductance based on the assumption that it impedes the operation of the CO₂ fixation enzymes. This relationship is complicated by the presence of environmental conditions that reduce stomatal conductance, such as low soil water potentials. By reducing the stomatal opening, low soil water potentials restrict the amount of ozone that can penetrate to the mesophyll. Increased CO₂ may also allow the plant to reduce stomatal opening. The models can give an estimate of the amount of interference that these effects have on one another and, most importantly, on the ability of the photosynthetic mechanism to respond to elevated CO₂.

Carbon Allocation
The pattern of allocation of the carbon fixed through photosynthesis can affect the responsiveness of the plant to elevated CO₂. In the models, following the calculation of the net daily carbon gain from photosynthesis and respiration, the carbon is allocated to various plant organs where it is made into structure or used in maintenance and respired. The quantity of carbon moved to each tissue type depends on the need for more tissue of a particular type to be made and on the phenology of plant development. As a result, some tissue types will act as strong sinks for carbon at certain times of the year and only weak sinks at others. The models can help identify the expected magnitudes of the carbon sinks at different points during each growing season.

Even if photosynthesis does increase, the amount of the new carbon that is retained in the canopy for leaf construction instead of stem or root manufacture will determine the degree to which the plant can maintain the increased photosynthesis rate. For example, in the later part of the summer in certain species most photosynthate is allocated to building stem and coarse root structure. Since these types of tissues have a large respiration cost, their expansion occurs at the expense of continuing canopy construction. The models can be used to estimate whether the pattern of allocation exhibited by a particular species will cause it to accelerate respirational losses of carbon in response to increased fixation.

Stress-related alterations in the typical pattern of carbon allocation can influence the plant’s ability to respond to elevated CO₂. For example, in the models, under conditions of nutrient deficiency or water stress, newly fixed carbon and available carbon stores of the plant are allocated to root growth, giving the plant increased nutrient and water uptake capacity. Unless this reallocation towards root growth alleviates the nutrient deficiency rapidly, however, continued root growth may exhaust carbon stores that normally would be used for canopy expansion. If carbon is being diverted from the canopy, insufficient resources may remain to build leaf area, repair enzymes, and otherwise maintain or increase the capacity of the plant to utilize increased concentrations of CO₂. On the other hand, increased carbon uptake under conditions of elevated CO₂ could delay the exhaustion of the carbon supplies available for allocation. Simulating carbon allocation is essential to predicting when various plant processes will begin to be deprived of carbon and when carbon reserves will become depleted.

Because the ROPIS models include the dynamics of carbon allocation and the influence of multiple environmental stresses, they can be used to examine plant response to elevated CO₂ even where low nutrient availability, water stress, and elevated atmospheric pollutant concentrations may all co-occur.

Modeling the response of plants to elevated temperatures
To predict the response of plants to global change, the models must be capable of accurately representing the response of whole-plant photosynthesis to temperature changes. Increases in temperature permit higher rates of mesophyll conductance because of increased rubisco
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The geographic distributions of species are not limited with annual average temperatures of more than 6°C. Currently, red spruce is rarely found in environments with annual average temperatures of more than 6°C. The geographic distributions of species are not limited only by temperature, but also by other factors. Based on the physiological considerations represented in the models, we expect that northern species may be capable of good and perhaps improved growth under the higher temperatures associated with global warming.

In another example, a simulation of the response of loblolly pine to elevated temperatures was conducted with the PGSM model. The net effect of warming climate on loblolly pine was evaluated by introducing a 2°C temperature increase to the simulation of diameter at breast height of a permanent sampling plot in the Duke Forest in North Carolina (Chen and Gomez 1990c). The result indicates that a 2°C increase in temperature will lead to slightly smaller tree diameters (Figure 7). In the simulation, photosynthesis did not increase as much as respiration because photosynthesis was more limited by light interception in this closed canopy than by temperature-dependent processes. Since North Carolina is at the northern edge of loblolly pine's current distribution, this result is unexpected, and demonstrates that the effects of climate change cannot be predicted simply on the basis of species's current geographic distributions.

**Modeling the effects of elevated temperature on plant competitive success**

Ultimately, the physiological effects predicted by the ROPIS models must be extended to stand-level models to evaluate the influence of changes in growth patterns on plant success in competition with other individuals. For example, the reason that red spruce trees are not found under temperature conditions warmer than 6°C may be that they are out-competed by faster growing trees. In other words, trees of this species may be absent from warmer sites because their growth rates are low compared to other species capable of growing under those conditions, not because they are intolerant of higher temperatures. To ascertain whether the changes in whole-plant carbon accumulation patterns will alter the success of the plants in a community, stand-level models, such as commonly used gap-succession simulators, can be used to evaluate competitive effects.

Gap-succession models use estimates of the expected growth rates of different tree species to predict the...
Figure 3. Generalized temperature effect on mesophyll conductance.

Figure 4. Generalized effect of temperature on maintenance respiration.
Figure 5. Net effect of temperature on carbon gain.

Figure 6. A TREGRO model prediction of the effect of temperature on annual net carbon gain in single red spruce trees.
effects of competition among individuals of different species. The magnitude of the competitive effect is calculated based on the degree to which each tree's access to light and nutrients is restricted by its neighbors. The relationship between growth rate and temperature is based on current geographical distributions of each species. These models assume that temperature prevents plant growth beyond the northern and southern boundaries of a species's range and that the growth rate is highest at the middle temperature between these boundaries (Botkin et al. 1972, Pastor and Post 1986, Solomon 1986). Since the TREGRO model predicted that red spruce should grow faster outside its current range, this method will not accurately predict changes in stand dynamics if changes in the relative competitive ability of species are important. Consequently, such models cannot be used to examine the effect of a small change in temperature on plant community structure.

Gap-succession models can be modified, however, to accept information from a detailed single-tree physiology model. For example, the relationship of growth and temperature predicted by the ROPIS physiological models can be used to parameterize the competition model. Thus we can assess whether temperature changes will alter the ability of a species to maintain its competitive position in a vegetation community or stand. By applying the physiological models to a wide range of species in changing environmental conditions, we could use a gap-succession model to examine the outcome of simultaneous changes in the ability of all the species in an ecosystem to compete with one another. Finally, we could predict the likelihood of change in the pattern of successional development in neighboring ecosystems and across ecotonal boundaries.

**Figure 7.** A PGSM model simulation of the response of loblolly pine to a 2°C temperature increase.

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**Models to Assess the Response of Vegetation to Global Change**

Modeling the effects of changes in plant competition on movements of ecosystem boundaries

The boundaries between major ecological systems (ecotones) are likely to be highly sensitive to alteration...
of global climate. Climate changes stemming from increases in CO₂ levels could cause ecosystems to be redistributed across landscapes. Our ability to predict whether these redistributions will occur is dependent on our ability to predict the changes at the boundaries between ecosystems, since plant communities can move across the landscape mainly by invading adjacent communities. With the modeling tools outlined above, we can predict the physiological response of species to environmental factors as those factors change at these boundaries and extrapolate these predictions to their implications for community development.

The ecotone is a region where some groups of species are prevented from extending their range by environmental conditions. Our ability to predict what will happen at these ecotones is dependent on our ability to estimate species responses to changes in these conditions. For other groups of species, the ecotone marks the boundary at which certain species can no longer outcompete other species for available resources.

We can use the ROPIS models to help predict the effect of temperature increases on, for example, the northern hardwood ecosystem, the spruce-fir ecosystem, and the ecosystem boundary between these two. We can evaluate whether northern hardwood trees will become established, grow, and outcompete conifers in what is presently the spruce-fir ecosystem as the region is subjected to temperature changes associated with increasing atmospheric greenhouse gases. We can use a gap-succession model, FORNUT (Weinstein et al. 1982, Shugart 1984), in which the relationship between temperature and tree growth has been modified based on results from the TREGRO physiological model described above. We can then examine the ways that the spruce-fir ecosystem might resist changes for a period of time through competitive interactions among individuals and we can evaluate the potential for change in the spruce-fir community at the boundary between the northern hardwood and spruce-fir ecosystems.

A simulation of the 300-year development of the spruce-fir forest at the ecosystem boundary under present temperature conditions was compared to its development under a warming climate. The temperature change in the model was begun at simulation year 100, after red spruce abundance reached relative stability, and over the course of the next 60 years the annual temperature was increased by 0.05°C per year, stabilizing at year 160 at 3°C above the base case. Figure 8 plots the simulated basal area of the three most important species in this ecosystem boundary for the base case and for the high temperature case. In the base case, balsam fir slowly declines in importance, for lack of regeneration opportunities; red spruce increases in the third century; sugar maple and other northern hardwood species are nearly absent. In the high temperature case, both red spruce and balsam fir lose basal area relative to the base case, while northern hardwood species such as sugar maple establish in increasing numbers.

Note that the loss of red spruce basal area due to warming climate is slow relative to that of balsam fir. The persistence of red spruce is partly due to the increase in growth rates predicted for this species by the ROPIS model under warming conditions, as described above. Using the relationship between temperature and growth identified by the physiological model, the gap-succession model predicted that red spruce would resist invasion by hardwood stands for many decades after a temperature increase. In contrast, models that use a temperature response relationship based on geographical distributions would predict an immediate deterioration of the red spruce population with warming climate.

The inferences that can be drawn from this simulation are limited because only the temperature response for red spruce was parameterized based on physiological relationships. To correctly simulate the interactions among multiple species, each species should be reparameterized using a ROPIS physiological model.

Summary of proposed improvements to the models

Biochemistry of CO₂ Fixation
To improve the realism of the photosynthesis routine, the mesophyll conductance parameter should be replaced by a more detailed model of biochemical processes. Such a model could include the turnover of the enzyme ribulose biphosphate, which regulates photosynthetic carbon reduction and photorespiratory carbon oxidation; the rate of photosynthetic electron transport; and the production and consumption of NADPH
and ATP (Farquhar et al. 1980). This improvement will also enable us to evaluate the repressive effect of CO₂ on photorespiration.

Variations Among Individuals and Species
The present ability of the ROPIS models to predict the responses of landscapes to global climate changes is limited by the focus of model dynamics on simulating average trees. We need to analyze the variation that stems from differences in photosynthesis, phenology, and allocation patterns between individuals of a species. Further, multiple species must be parameterized if the interactions between trees in mixed-species stands is to be simulated.

Shading In Tree and Forest Canopies
The models’ predictions of plant response to changes in CO₂ depend on empirical estimates of canopy shading within each tree and among trees in a stand. The pattern of distribution of light within the canopy could easily change as a result of CO₂ increases, rendering these empirically derived relationships invalid. To improve their capabilities, the models must include the dynamics of canopy light regimes in even-aged and mixed-age stands. Further, since most forests involve a mix of species of uneven ages, each with its own dynamics of canopy development and response to neighbors, the models should be parameterized for all the species in a forest and equipped with the capability of simulating changes in canopy development.
Models to Assess the Response of Vegetation to Global Change

Organic Matter Decomposition
The potential for changes in decomposition rates with global change is important for predictions of plant response and feedbacks to atmospheric composition. Increased decomposition with increasing temperature is easily simulated in the ROPIS models. Changes in soil moisture also affect decomposition rates. Additional interactions between plants and soil will occur if changing environmental conditions result in changes in litter quality and quantity. These factors should be incorporated in the models' decomposition routines. Changes in decomposition rates not only influence the rate at which CO₂ is released from decaying organic matter back to the atmosphere, but affect the rate at which nutrients become available, thereby affecting the subsequent ability of the plant to utilize CO₂.

Gas Efflux
At present, the models simulate the flux of materials from the environment to the plant and soil. Emissions from plants and soils to the atmosphere are also important influences on future global change. Plants contribute many important greenhouse gases to the atmosphere (water vapor, CO₂, CH₄, N₂O, and organic acids, among others); the models should provide an accurate accounting of such fluxes.
References


