Modeling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stresses[1]

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Summary

The simulation model TREGRO was developed to analyze the response of red spruce saplings to multiple stresses, such as drought, nutrient deficiency, and exposure to pollutants. The model provides a method of identifying changes in structural and non-structural carbon resources in the tree that may become measurable only after many years of exposure. The model is based on the assumption that the ability of plants to take up and use carbon, water, and nutrients depends on the interrelationships in availability among the three resources. Consequently, the model simulates the simultaneous cycling of these resources.

In the model, the tree is divided into the following compartments: a canopy of leaves grouped by age class, branches, stem, and coarse and fine roots in a number of soil horizons. In each of these compartments we track three carbon pools: living structure, dead structure or wood, and total non-structural carbohydrate. The model calculates the photosynthesis of an entire red spruce tree each hour as a function of ambient environmental conditions and the availability of light, water, and nutrients; the daily redistribution of carbon throughout the plant; and the loss of carbon by respiration and senescence. To accomplish this task, the model tracks the flow of carbon dioxide to the sites of fixation within the leaves, the availability of light in the canopy, water and nutrient resources in each of three soil horizons, and the amounts of these resources taken up by the tree. Soil and plant water potentials, photosynthesis, and leaf respiration are simulated on an hourly timestep; nutrient uptake, allocation and growth are computed on a daily timestep.

Through a set of example simulations, we demonstrate how the model can be used to examine the mechanisms by which plants respond to stresses experienced alone and in combination. The model was used to predict the growth decrease and the shifting pattern of carbon allocation expected for an isolated tree exposed to ozone and decreased nutrient availability due to acidic deposition. Decreased nutrient availability resulted in decreased growth and preferential carbon allocation to roots, which helped to alleviate the nutrient stress. Ozone stress also resulted in decreased plant growth but had the opposite effect on allocation patterns, with most of the growth reduction occurring in roots. The effect of simultaneous ozone and nutrient stress on tree growth was less than the sum of the independent single stresses, contrary to our expectation.

This modeling approach can aid in evaluating the long-term effect of stress on resource availability, the potential for gradual deterioration of tree health under long periods of stress, and imbalances in growth accompanying shifts in carbon allocation caused by stress.

Introduction

The simulation model TREGRO was developed to examine the mechanisms by which plants regulate their carbon, water, and nutrient cycles to mitigate damage

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caused by pollutants such as ozone and acid rain (Weinstein and Beloin 1990, 1991). Important processes modeled include: the ability of the plant to utilize resources to fix carbon; the processes by which water and nutrients become available and are taken up for use in photosynthesis, respiration, and growth; the allocation patterns used to maintain resource acquisition; and the ability of the plant to repair pollution damage.

The model has been conceived as three related simulators, each following the flow of one of the three basic plant materials: carbon, water, and nutrients. These three simulators are linked through representations of the mechanisms by which carbon, water, and nutrients influence one another. The ability of the plant to utilize each material is in large part regulated by the availability of the other two. By using the model we can evaluate the long-term effect of pollution on resource availability, the potential for gradual deterioration of tree health under long periods of pollution exposure, and the imbalances in growth accompanying shifts in carbon allocation.

The key role of carbon reserves

Many environmental stresses can adversely affect tree health by affecting the pool of total non-structural carbon (TNC), also referred to as available, or reserve, carbon. Diverse stresses can cause similar symptoms, particularly after tree decline is underway. Inadequate water, light, or nutrients, or impairment of photosynthesis by air pollutants all act to decrease the pool of TNC that can be drawn on to meet immediate growth, maintenance, or repair needs. Therefore, reduced growth may be attributable to any of these initiating causes. The chain of responses exhibited may be identical regardless of cause if the tree is responding to low carbon reserves rather than to the particular stress.

For example, both water stress and nutrient stress cause reductions in photosynthesis, albeit through different pathways. Water stress reduces stomatal conductance, whereas nutrient stress reduces photosynthetic pigments and enzymatic activity. Both stresses can also impair photosynthesis indirectly, if root growth occurs at the expense of the growth of photosynthetic tissue. Both water stress and nutrient stress result in increased carbon allocation to roots, reduced growth, and possibly premature senescence or enhanced susceptibility to disease or other pests. Thus it can be difficult to identify the initiating stress in a sequence of decline symptoms. To understand the chain of events between the initial stress and the eventual plant response, we must keep track of carbon reserves and how they are affected by a wide range of stresses.

Plants survive periodic stress, but they decline when their systems for adaptive response are overwhelmed. Responses that mitigate the effects of stress depend on the availability of carbon reserves that can be mobilized to build or repair tissues. For example, in the case of a tree exposed to ozone, the initial injury slows photosynthesis through either permanent or temporary disruption of the carboxylation sites (Pell 1987). Reduced photosynthesis leads to a reduction in the amount of carbon available

for plant maintenance and growth. Plants tend to mitigate ozone damage by increasing the quantity of new leaf surface. This is accomplished by increasing the proportion of carbon allocated to leaf and branch growth (Oshima et al. 1979). If carbon reserves are sufficient, enough new leaf area may be added to increase net photosynthesis to the pre-stressed rate.

Mitigation of the effects of stress is only achieved at a cost, however. The cost may be decreased allocation of carbon to root production and maintenance (Oshima et al. 1979). Even at sites without severe deficiencies of water or nutrients, loss of root biomass renders plants more susceptible to periodic limitations in belowground resources. When there is insufficient root surface area for water and nutrient uptake to meet the needs of new tissue production, carbon fixation declines. Thus the mitigation of stress of one kind may increase susceptibility to stress of another, the link being the dependence of both processes on the plant's carbon resources.

Trees rely heavily on a reserve pool of carbon (Loach and Little 1973, Holl 1985). Photosynthetis rates vary daily and seasonally; the rate of new fixation is often insufficient to meet all the demands of the plant. At such times, the plant meets its needs by drawing on carbon reserves accumulating during other periods. Under conditions of extended or severe stress, there may be insufficient carbon from the sum of photosynthesis and reserve carbon to satisfy plant requirements. Stunted branches, dense leaf clusters, and decreased leaf area can result.

We hypothesize that the ability of trees to withstand stress is closely related to their carbon reserves. The response systems of trees depend on mobilizing carbon to rebuild injured tissue or to increase resource collecting area. In plants with low carbon reserves, increased carbon allocation to one tissue can occur only at the expense of reduced allocation to other tissues, and the resulting imbalance may increase the sensitivity of the plant to other stresses. The principal focus of this modeling effort was to estimate the status and dynamics of the carbon balance of a tree under a variety of pollutant exposure scenarios and to predict the implications of a given carbon status on tree survival.

Goals of the TREGRO model

The goal of the TREGRO model was to test the consequences of proposed mechanisms of air pollution stress on plant growth through modification of the carbon budget. We wished to test the hypothesis that one stress can increase susceptibility to another stress by altering the plant's carbon budget and subsequent allocation. For example, ozone stress, by decreasing root growth, could increase the susceptibility of the tree to nutrient stress caused by leaching of soil cations by acid rain. We hypothesized, therefore, that the effect of simultaneous ozone stress and nutrient stress would be greater than the sum of the effects of the stresses acting alone. This paper demonstrates how the model was used to predict the growth decrease and shifting pattern of carbon allocation expected for an isolated tree exposed to ozone and to decreased nutrient availability caused by acidic deposition.

Model description

Relation to experiments

The TREGRO model was developed in conjunction with field experiments at the Boyce Thompson Institute. In brief, sapling red spruce trees were collected in Maine and brought to Ithaca, NY, where they were established in large pots and exposed in open-topped chambers to precipitation at three acidities and ozone at four concentrations for four growing seasons (Kohut et al. 1988, Amundson et al. 1991*b*). Collaboration between modelers and plant physiologists permitted integrated design of the experiment and the model. The coordinated project provided extended opportunities to collect model parameters, to compare simulations to experimental observations, and to improve on both measurements and modeled processes.

Carbon balance

In the model, the tree is divided into compartments representing four age classes of leaves (current-year, 1-year-old, 2-year-old, and $\geq$ 3-year-old), branches, stem, and coarse and fine roots in each of three soil horizons (Table 1). The carbon stored in branches, stem, and coarse roots is divided into pools of TNC, living structure, and wood or dead structure. Needles and fine roots do not build wood in the model. A single TNC pool is shared by all roots. Dynamics of all the carbon pools are calculated on a daily timestep.

Simulating the carbon balance of the tree requires calculating gross photosynthesis, growth and maintenance respiration, and senescence. The size of the whole-plant simulated carbon pool each day is equal to the accumulated total amount of carbon fixed into plant structure plus that available as non-structural carbon reserves. The daily change in carbon in the whole plant is the sum of photosynthesis of all leaf classes minus the sum of the maintenance respiration and the growth respiration of each tissue type, each calculated hourly and summed over the entire day, and minus the tissue lost daily to senescence. Thus,

$$\frac{dC}{dt} = \sum_{i=1}^{4} P_{g_i} - \sum_{j=1}^{12} R_{m_j} - \sum_{j=1}^{12} R_{g_j} - \sum_{j=1}^{12} S_j \,, \tag{1}$$

where C is the sum of carbon in all plant tissue pools, t is time, P_g is gross photosynthesis, R_m is maintenance respiration, R_g is growth respiration, S is senescence, i is leaf class, and j is compartment (four leaf classes, branch, stem, and two root classes in three soil layers).

Allocation to growth and storage moves carbon within the plant, not directly affecting the total carbon balance, but indirectly influencing photosynthetic capacity and respiration losses. The more structure contained in a tissue, the larger will be its maintenance respiration.

Photosynthesis

The photosynthesis module is based on concepts developed in the models of
Lohammar et al. (1980) and Running (1984). The module uses environmental input
data (daily rainfall and hourly light, temperature, humidity, and ozone) to calculate
gross photosynthesis each hour by each age class of leaf tissue which is then summed
for daily allocation. The rate of fixation is proportional to the conductance to carbon
dioxide flow into the leaf at the stomata and at the cell membrane:

$$\text{Photosynthesis} = \frac{k_s k_m}{k_s + k_m} \, \Delta CO_2 \, , \tag{2}$$

where k_s is stomatal conductance to CO_2, k_m is mesophyll conductance to CO_2 and
ΔCO_2 is the CO_2 concentration gradient from the atmosphere to the carboxylation
site.

The calculated stomatal conductance of a leaf class during each hour depends on
the maximum stomatal conductance possible under optimal growing conditions, the
leaf water potential (which reflects soil water availability), and the water vapor
pressure deficit:

$$k_s = k_{s_{max}} \frac{\Psi_{leaf} - \Psi_{thresh}}{\Psi_{min} - \Psi_{thresh}} - s_{cr} \, \text{VPD}, \tag{3}$$

where $k_{s_{max}}$ is maximum leaf conductance, Ψ_{leaf} is leaf water potential, Ψ_{thresh} is
stomatal closure threshold, Ψ_{min} is the minimum leaf water potential, s_{cr} is the slope
of the k_s reduction with VPD, and VPD is the absolute water vapor pressure deficit.

Increases in VPD cause a decrease in stomatal conductance. Leaf water potential
is given the value of root water potential, which is simulated by the hydrology
submodel, GAPS (Buttler and Riha 1988). Stomatal conductance decreases as a
function of leaf water potential only after the potential falls below the stomatal
closure threshold (Running 1984). Below this threshold, declining leaf water poten-
tial causes stomatal conductance to decrease linearly. In the simulations of well-wa-
tered conditions discussed below, leaf water potential was maintained at its maxi-
mum value and never influenced photosynthesis.

Simulated mesophyll conductance depends on a maximum possible conductance
(measured under light-saturated conditions), the influence of temperature (a skewed
normal curve with a maximum at approximately 15 °C), and solar irradiance. The
relationship between irradiance and mesophyll conductance reflects the half satura-
tion and compensation points (measured from trials of assimilation at different
irradiances):

$$k_m = \frac{I - I_0}{I + I_{1/2}} \, k_{max} f(T) \, , \tag{4}$$

where I is incident shortwave radiation, I_0 is the light compensation point, $I_{1/2}$ is the

irradiance at which k_m is half of k_{max}, k_{max} is the maximum mesophyll conductance, T is air temperature, and $f(T)$ is a function relating k_{max} to air temperature.

If hourly irradiance data are not available, they can be calculated from the time of day, time of year, and probability of cloudiness. The fraction of leaves exposed to full sunlight depends on the time of day and the position of the leaf in the crown, which depends on its age class. The amount of light available to leaves in the shade depends only on the time of day. The proportion of each leaf class in the sun and the degree of light attenuation with shading are determined from field observations of trees.

Respiration

Simulated respiration by each tissue depends on temperature, tissue mass, and the tissue's base respiration rate at 20 °C. Rates of maintenance respiration at 20 °C were initially assumed to be the same for all tissues: 0.5% of carbon mass lost per day, a value at the low end of the range of 0.5 to 2.0% suggested by Waring and Schlesinger (1985). Initial simulations predicted slightly more carbon fixation than was measured by whole canopies in the field, suggesting that respiration was too low. To force the model to simulate the measured carbon gain, the respiration of all tissues was increased to 0.65%. This value was consistent with field data for leaf tissue. Stem, coarse root, and fine root respiration could not be independently assessed from the field measurements. Accurate values for the respiration of each tissue are critically needed.

Carbon allocation

Each simulation day, the model calculates the allocation of newly synthesized carbohydrate and TNC reserves to various tree compartments for respiration, growth, and TNC storage.

Respiration needs must be satisfied before C can be allocated to growth or TNC storage. The respiration needs of each leaf class are always met first, from carbon fixed by that leaf class during the day, from new net fixation by other leaf classes, or from TNC stores, in that order. Daily respiration needs of non-leaf living structural tissue are met from daily excess of newly fixed carbon over leaf respiration needs or, if more is needed, from TNC stores. Some net photosynthate is available during most of the year to meet the respiration needs of other tissues. If the supply of net photosynthate fixed during the day is exhausted and TNC is needed to satisfy respiration, carbon is extracted from the tissues with TNC proportionately closest to saturation. The TNC saturation level of each tissue is a function of the structural mass of the tissue. More saturated compartments will donate proportionately more TNC.

Structural tissue is constructed in any plant part only if all the necessary resources of carbon and nutrients are available to that plant part in the required stoichiometric relationship. Only structural tissue requires nutrients for formation; TNC and wood construction are not limited by nutrient availability. Growth is limited by: (1) the amount of carbon available; (2) the amount of nutrients available, where structure is concerned; or (3) the maximum possible growth rate of each plant part at the ambient

temperature. When carbon availability limits growth, allocation follows rules of tissue priority, described below under "Growth partitioning." If the supply of newly fixed carbon is exhausted and demands for growth still remain, TNC pools will be utilized to meet these demands. Carbon will be withdrawn from the seven TNC pools according to their saturation, as explained above.

If the day's supply of photosynthate exceeds the demand for respiration and growth, excess carbon will be allocated as TNC among the seven TNC pools. Each simulation day, after leaf TNC has increased to saturation, excess carbon is distributed to branch, stem, and coarse root TNC pools in proportion to the TNC deficit for each tissue. The deficit is calculated as the difference between the TNC content of a tissue and its TNC saturation content.

Growth partitioning

When carbon or nutrients are insufficient to permit all tissues to grow at their maximum rates, the priority of the various tissues for carbon and nutrients becomes important. Growth partitioning in this model is mechanistically, not empirically, defined. There is no explicit ratio in the model for partitioning carbon among different tissues. Instead, carbon for growth is allocated on a daily timestep according to simple rules of priority and the limits of maximum growth rates and nutrient availability.

Carbon is acquired by leaves, and in the model, when plant phenology permits needle growth, needle structure has first priority for carbon use. Needle TNC stores have second priority for carbon. Only needle TNC has higher priority than any structural carbon pools. When phenology permits them to grow, the remaining tissues have the following priority: branches, stem, coarse roots, and lastly fine roots, in order of their proximity to the source. This order of priority never changes, but some tissues are not allowed to grow during certain growth periods or times of year, as described below under "Phenology of carbon allocation." After the growth of all tissues is satisfied, any remaining carbon is allocated to the other TNC pools, as described above under "Carbon allocation."

Although the tissue highest on the priority list is given the first opportunity to use available carbon, its growth is limited by a maximum daily growth rate obtained from measured allometric relationships. Therefore, it is rare in practice that this tissue will use all the carbon fixed in the one-day timestep. In fact, when resources are abundant, the tissue that will garner the largest supply of available carbon will be that with the highest potential growth rate, i.e., the one representing the greatest carbon sink, even if it is low on the priority list. However, when carbon is in short supply, a tissue with a high maximum growth rate that is low on the priority list may not grow as fast as tissue above it on the priority list even though it represents a stronger sink, as carbon will be utilized by other growth processes before it reaches this sink. However, even when carbon availability is low, it is possible for a low priority tissue to grow more than tissues higher on the priority list if the higher priority tissues have very low growth rates.

Carbon use and growth can also be limited by mineral nutrients: even if carbon is

available, maximum growth rates of high-priority tissues may not be achieved. This is because nutrient allocation follows a scheme that opposes that of carbon allocation: nutrients are obtained by fine roots, which have first priority at nutrient utilization for growth. Thus in the case of nutrient limitation, where much of the nutrient available is utilized by root growth, shoot growth will be limited by lack of nutrients. Carbon not used by the shoot is available to roots, permitting their continued growth. Increased carbon allocation to roots results until such time as the increased root mass is sufficient for nutrient uptake to support shoot growth again.

This method of simulating carbon allocation requires that empirical data be used to set the maximum growth rate allowed for each tissue and to establish the order of priority in allocation during each growth period. However, the realized growth rate of tissues is not predetermined by empirical data, but reflects the pattern of available resources.

This allocation scheme causes the relative growth rate of different tissues to remain approximately constant throughout a given growth period when resources needed for growth are abundant, but deviates from this pattern when essential resources become limiting. Thus environmental conditions influence carbon partitioning whenever a resource is in short supply.

Phenology of carbon allocation

In the allocation scheme described above, shoots have first priority for carbon and roots have first access to nutrients for growth. This pattern is necessarily restricted by tree phenology, which is also simulated in the model. Many activities are restricted to certain developmental stages. The model allocates new photosynthate and TNC according to distinct seasonal growth periods (Figure 1). Before growth begins in the spring, newly fixed carbon that is not respired can only be used to increase TNC stores. An early spring period of root growth and bud swelling is followed in late spring by leaf flushing and branch elongation. Carbon fixed in midsummer is used to increase the mass of the coarse root system and, to a lesser degree, to increase branch and stem material. In the fall, carbon is used for root structural development. In the winter, the plant is dormant; only respiration is allowed. Though some root growth could occur during warm periods in the winter, we assume that ignoring growth between mid-November and early March does not introduce a large error in our estimates of root biomass or respiration. Transitions between these growth periods are determined by the environment (accumulated growing degree days) or by tree status (TNC content). The model contains this amount of detail on the seasonality of growth patterns because the timing of nutrient depletion or ozone exposure may have a significant effect on the response of the tree to stress.

Senescence

The only tissues allowed to senesce during the simulation are fine roots and leaves. Fine roots die at a constant rate currently set at 0.5% per day. Leaves are dropped when they become unproductive. When TNC reserves in a given age class of needles
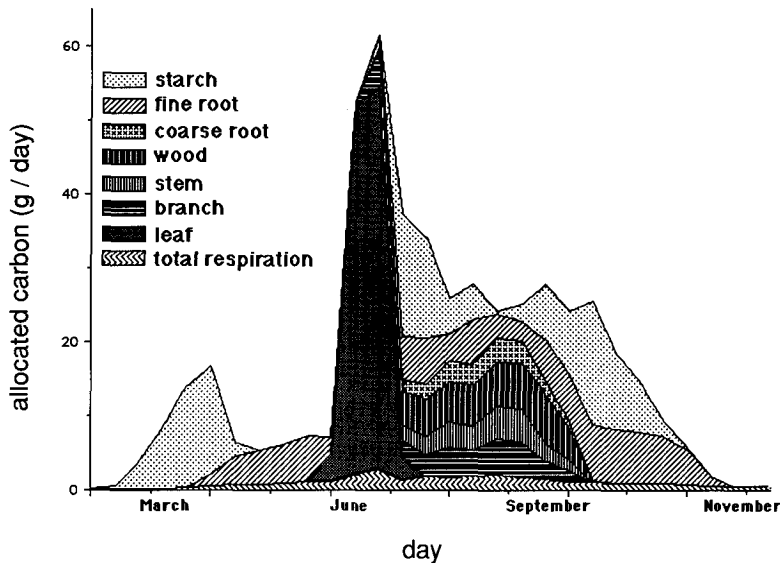
Figure 1. Phenology of carbon allocation in TREGRO.

fall below a minimum level (currently set at 1%), a fraction (currently 10%) of that needle class is dropped. The tree is considered dead if it has lost all its needles and fails to grow a new leaf class the following growing season.

Formation of needle primordia

One of the major uncertainties in the model lies in predicting the annual increase in tree leaf mass. Since the modeled ability of trees to survive stress is tied to the pool of internal non-structural carbon, the predicted behavior of stressed trees depends on the rate at which carbon can be acquired. The greater the leaf mass of the tree, the greater the potential for carbon fixation. In conducting longer simulations (such as the 10-year scenarios discussed below), the formation of needle primordia was a critical process.

The size of each year's needle class is determined by the number of primordia established the previous year. This number increases as the tree enlarges. Little carbon is required to make the primordia; we assume that they are made at negligible cost to the tree and that their construction is not limited by the availability of carbon. In the model, the number of primordia formed is a function of temperature. The maximum rate of daily production is defined by the user. For the simulations presented here, we assumed that the number formed increased by 50% each year (a number empirically derived from the experimental trees). In fact, the rate of increase probably changes over time, reflecting the stage of development of the tree. The model results were clearly dependent on this value, indicating the need for better information about the control of primordium formation.

Soil nutrient availability

In the current version, concentrations of essential nutrients in soil and soil solution available for plant uptake must be fixed for each model run. Because soil nutrient availability is constant, the process of soil nutrient depletion cannot be simulated. However, the effect of nutrient stress on plant growth can be simulated by specifying low soil nutrient concentrations. The next version of TREGRO will simulate the concentrations and quantities of nutrient ions in soil and soil solution taking into account rainfall inputs, weathering rates, equilibrium chemistry, hydrologic fluxes, and root uptake properties.

Water and nutrient uptake

In the model version used for these simulations, water uptake was fixed at a constant rate per gram of fine root per day. Nutrient uptake was calculated as the product of water uptake and soil solution concentrations. With only passive nutrient uptake, the contribution of new root growth is underestimated, particularly for a non-mobile ion such as phosphate, and the values of solute concentrations are unrealistic. However, nutrient uptake does reflect changes in fine root biomass, because of the dependence of water uptake on root mass. The next version of TREGRO will calculate nutrient uptake by active uptake, diffusion, and depletion of a zone around the root. The next version will also include a more sophisticated hydrologic model based on the model GAPS (Buttler and Riha 1988), which will calculate plant water uptake and soil water availability and movement.

Comparison to experimental data

We compared the annual carbon fixation and partitioning simulated by the model to that of a red spruce tree in the experiment with which the model was associated. The model was initialized using the average mass of compartments of five non-treatment trees harvested in the fall of 1986. The simulated biomass of tree compartments was compared to that of the actual tree harvested at the end of the 1987 growing season. Records of actual hourly radiation and temperature for the 1987 growing season were used along with actual intervals of applied precipitation.

Maximum growth rates were established by identifying the fastest daily growth per gram of tissue carbon achieved at any time during the growing season by the chosen tree in the field. In the model, this maximum is only achieved when all resources are abundant. During most periods of the year, carbon supplies will be inadequate to maintain this maximum growth rate, and the actual growth rate predicted by the model will be lower. This maximum growth rate was then adjusted until the predicted annual weight increase of each tissue type approximated that observed in the representative test tree.

The growth of individual tissue types was predicted within 10% of the measured growth of the tree, with total growth only 2% in error (Figure 2). This comparison does not constitute an independent test of the model, because maximum growth rates were calculated from the same experimental tree. However, it shows that the rules of
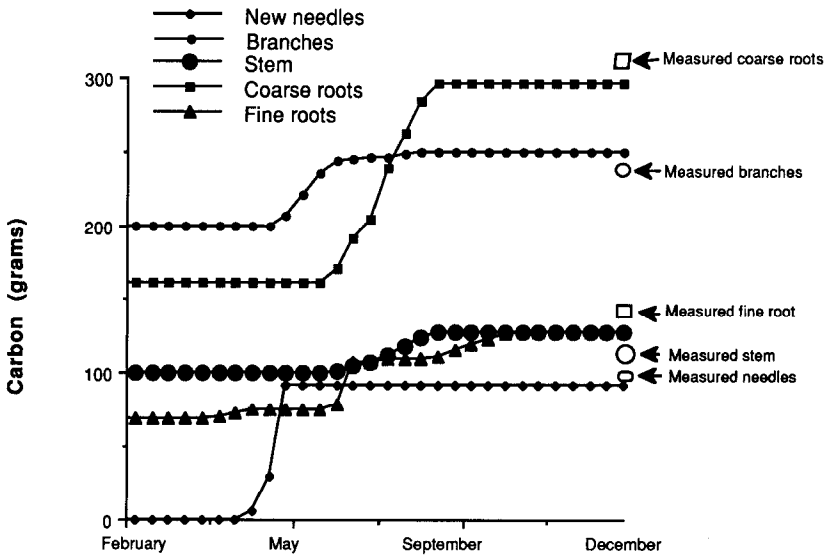
Figure 2. Comparison of the simulated growth with the actual growth of an untreated tree for the 1987 season.

allocation and responses to resource availability contained in the model can produce a tree with reasonable proportions of carbon in its various tissues.

Stress scenarios used for simulations

Ten-year scenarios were simulated, beginning with trees nominally 10 years old, using hourly environmental data from 1987 for each year of the simulation. To evaluate plant response to acidic precipitation and ozone exposure, two processes were represented: the effect of reduced nutrient availability associated with accelerated leaching of soil cations from the rooted zone, and the direct interference of ozone with photosynthesis.

Acid rain or nutrient stress

We simulated the effect of acid rain on spruce growth by reducing the availability of nutrients. In the experimental pots, after two years of treatment, Ca and Mg were significantly reduced in the O_a horizons in the most acidic treatments (Sherman and Fahey, 1991). We did not simulate any direct effect of acid rain on the tree canopy, nor of aluminum mobilization on tree roots. Nutrient depletion was simulated by reducing the rate of solute uptake per unit of fine root (g C). From repeated simulations we found that an uptake rate of 0.18 mg Ca (g fine root)$^{-1}$ day^{-1} produced a tree that was never nutrient limited in the 10-year simulation; this tree represented the unstressed "base case." An uptake rate of 0.12 mg Ca (g fine root)$^{-1}$ day^{-1} made the tree sometimes nutrient limited; the more severe nutrient stress scenarios had uptake rates of 0.09 mg Ca (g fine root)$^{-1}$ day^{-1} and 0.06 mg Ca (g

fine root)$^{-1}$ day^{-1}. On the assumption that the rate of Ca uptake required for adequate nutrition was about 0.15 mg Ca (g fine root)$^{-1}$ day^{-1}, we refer to the 0.12, 0.09, and 0.06 mg Ca (g fine root)$^{-1}$ day^{-1} uptake rate scenarios as 20%, 40%, and 60% nutrient reductions, respectively. Because the amount of nutrient acquired by the tree depended also on the amount of fine root mass, these rates do not translate directly into differences in nutrient uptake.

Ozone

Many mechanisms have been proposed to explain the effect of ozone exposure on net photosynthesis; several mechanisms may act simultaneously. The evidence is at present inconclusive. For example, a relationship between damage and cumulative ozone dose could be the result of either a slow accumulation of irreparable damage to the photosynthetic system or a complete repair of instantaneous damage leading to a gradual depletion of the carbon reserves of the plant because of associated carbon costs. We have equipped the model with the ability to examine the consequences of a variety of these hypotheses. The TREGRO model can simulate instantaneous or cumulative effects, or both, on gross photosynthesis, with or without a respiration cost for repair.

For these simulations, we assumed that ozone exerts its influence on growth through instantaneous damage to the mesophyll cells, with no cost of repair. We assumed no ozone effect on maximum mesophyll conductance at less than 40 ppb ozone (hourly mean), followed by a linear decrease such that conductance would fall by 30% if ozone exposure reached 200 ppb. According to this hypothesized mechanism, growth reductions under ozone are caused by impaired instantaneous carbon gain, not by cumulative damage to the leaf or by increased respiration.

Because of the strong diurnal pattern in ozone concentration, simulation at an hourly time step was essential to implementing the hypothesized mechanism of damage. Ozone concentrations were commonly highest at midday or early in the afternoon when irradiances are also high. Thus ozone prevented simulated mesophyll conductance from reaching its potential maximum. Hourly ambient ozone records for Ithaca for the 1987 growing season were used as input to the model. Approximately 10% of the measured hourly ozone concentrations exceeded 60 ppb; 40% exceeded 40 ppb, and concentrations during several hours approached 100 ppb.

Two ozone simulations are reported here. For the 1-year simulation, ozone was set at twice the ambient concentration in Ithaca. The 10-year simulation used a linear rise from ambient ozone to 45% above ambient (increasing 5% annually). This scenario approximated the expected rise in ambient ozone concentrations.

Combined stresses

Because acidic precipitation and ozone exposure can co-occur, the model was designed to simulate simultaneous exposure of the plant to both pollutants. We expected effects on both partitioning and growth. First, we expected ozone damage to cause carbon to be preferentially allocated to aboveground repair and, in opposition, acidic precipitation damage to cause carbon to be preferentially moved

belowground in response to nutrient deficiency. Therefore we hypothesized that the shoot-to-root ratio of a tree subjected to both stresses simultaneously would be intermediate between those of trees subjected to a single stress. Second, because the reduced root mass induced by ozone stress could increase the plant's vulnerability to nutrient stress, we hypothesized that the negative effects of the two stresses on carbon assimilation rates would be more than additive.

Results of simulations

Acid rain or nutrient stress

Figure 3a shows the result of a multi-year simulation of three intensities of nutrient stress on total aboveground biomass. Nutrient reduction resulted in reduced tree growth, as expected. After ten years of simulation, the 20% and 40% nutrient reductions caused 19% and 28% decreases in growth compared to the base case. The 60% nutrient reduction caused a 66% decrease in aboveground growth.

Figure 3b shows the total belowground biomass for the same four simulations. Again, growth was reduced by nutrient stress, most markedly in the most severe scenario, which produced a 46% reduction. In all cases, the reduction in belowground growth was proportionately less than the reduction in aboveground growth. Surprisingly, root growth was greater under 40% nutrient reduction than 20% nutrient reduction, implying a more extreme shift in growth allocation.

The shoot-to-root ratio (Figure 3c) compares growth reductions above- and belowground and is a rough measure of the amount of canopy depending on each unit of root tissue for belowground resources. The base case, with no nutrient stress, consistently had the highest shoot-to-root ratio. Nutrient stress resulted in increased allocation of carbon to root growth. As we will discuss later, increased allocation to roots is not forced by the model whenever nutrient stress occurs. Instead, it is the consequence of nutrient limitation on aboveground growth and the preferential access that roots have to nutrients because of their proximity to the source, permitting the roots to continue to grow while canopy growth slows.

In the base case, without nutrient limitation, aboveground mass accumulated faster than belowground mass in most years, causing an overall increase in shoot-to-root ratio (Figure 3c). It could be supposed that without a need for root system development to explore the soil and increase the rate of nutrient uptake, newly fixed carbon was preferentially used to build the canopy. Toward the end of the simulation the canopy had presumably grown too large for its existing root system, and the direction of preferential carbon distribution reversed to root development. The shoot-to-root ratio declined at this point, but remained higher than in any of the nutrient-stressed trees.

In the case of 20% nutrient reduction, the shoot-to-root ratio fell initially, but recovered several years into the simulation. This behavior is explained by the improved access to nutrients permitted by a proportionately larger root mass. The shoot-to-root ratio never reached that of the base case, suggesting that the tree never
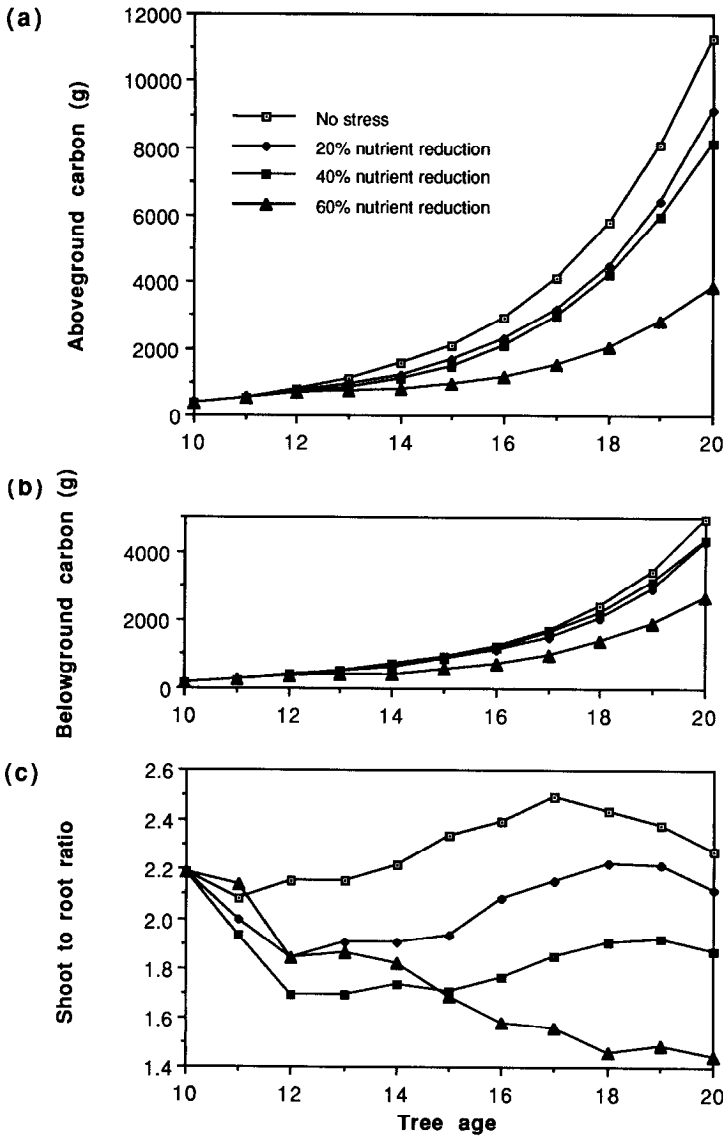
(a)

(b)

(c)

Figure 3. Effects of nutrient limitation on the sum of aboveground carbon pools (a), the sum of belowground carbon pools (b), and shoot-to-root ratio (c) under four scenarios: (1) base case (no nutrient limitation); (2) 20% nutrient reduction; (3) 40% nutrient reduction; and (4) 60% nutrient reduction. The model calculates carbon pools on a daily timestep; here we have graphed only one data point per year to eliminate seasonal variations.

achieved the condition of the base case, in which the canopy was supported by a relatively small root system. Under nutrient limitation the tree had to maintain a proportionately larger root mass at the cost of producing less photosynthetic tissue.

Under the 40% nutrient reduction scenario, the same pattern in the development of the shoot-to-root ratio was exhibited. The initial decline in the ratio during root

system development was even more pronounced than in the slight depletion case. Recovery to the point where canopy development could preferentially occur was delayed for three years. The ratio increased only slightly and never to its initial value.

In the 60% nutrient reduction scenario, a threshold may have been exceeded. The first year response was a slower reallocation to the root system than in the other low nutrient scenarios. After two years the ratio was similar to that achieved in the 20% reduction case. Presumably, there was simply insufficient nutrient with which to build a root system capable of meeting plant demands. As a consequence, the plant was never able to recover. The root system continued to grow faster than the shoot, causing the shoot-to-root ratio to fall throughout the simulation. Only a very small canopy was grown under these conditions. Unlike the trees with less severe nutrient reductions, which could minimize the effects of nutrient deficiency on growth by shifting allocation patterns, the tree under the severe reduction scenario had insufficient nutrients with which to manipulate its carbon resources to alleviate the stress.

Ozone

Figure 4 shows both above- and belowground biomass for a 1-year simulation of twice ambient ozone, compared to the base case of no ozone. The ozone-stressed tree was smaller than the unstressed tree, as expected. A cumulative growth reduction resulted from an instantaneous damage mechanism.

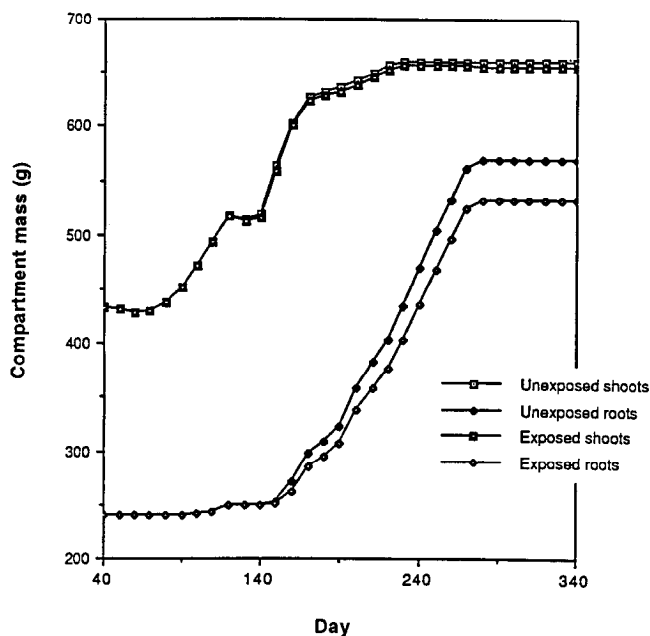**Simulated effect of ozone on root and shoot growth**

Figure 4. The sum of above- and belowground carbon pools for a one-year simulation under no ozone or twice ambient ozone.

Unlike the nutrient-stressed tree, the loss of growth in the ozone-stressed tree was mainly belowground. In other words, the response of the tree to ozone stress was to favor aboveground over belowground allocation. As was the case with the effect of nutrient limitation on allocation, this did not occur because the model is designed to force this preferential allocation whenever ozone damage occurs. Instead, it was the effect of ozone on available carbon and the preferential access of aboveground tissues to carbon, because of their proximity to the source, that permitted the canopy to continue growing while root growth slowed.

Simultaneous acid rain and ozone

The 40% nutrient reduction scenario was chosen for combination with an ozone stress scenario for a multi-year simulation. The simulated ozone increase (beginning at age 10 with 1987 Ithaca ambient concentrations and increasing the concentrations linearly at the rate of 5% each year), applied as a single stress, reduced aboveground growth about half as much as the 40% nutrient reduction alone (Figure 5a). Aboveground growth under the combined stresses was only very slightly less than that under nutrient stress alone. In other words, for these scenarios, the effect of the simultaneous stresses on aboveground growth was less than additive.

In contrast with aboveground growth, belowground growth was more affected by ozone alone than by nutrient stress alone, for the intensities of stress simulated (Figure 5b). Belowground growth under the combined stresses was intermediate between that observed with either of the stresses alone, again demonstrating that multiple stresses can have less than additive effects on growth.

The effect of the ozone stress on allocation was complex (Figure 5c). Initially, as in the one-year simulation, the shoot-to-root ratio of the ozone-stressed tree was higher than that of the unstressed tree, showing that root growth was reduced more than shoot growth. In the middle years of the simulation, the shoot-to-root ratio of the ozone-stressed tree was lower than that of the unstressed tree. This depression of the shoot-to-root ratio is best explained as a delay in the development of the stressed tree, which took longer to achieve increased allocation to aboveground growth than the unstressed tree.

The 40% nutrient stress produced a low shoot-to-root ratio for the duration of the 10-year simulation (Figure 5c). The combined stress scenario produced a shoot-to-root ratio closer to that of the base case than that of nutrient stress alone. A balanced shoot-to-root ratio implies that each unit of canopy has an adequate supply of resources, which should benefit plant growth over the long term. In this case, however, a benefit should not necessarily be inferred, because the more "balanced" ratio results from a reduction in both above- and belowground growth caused by simultaneous multiple stresses.
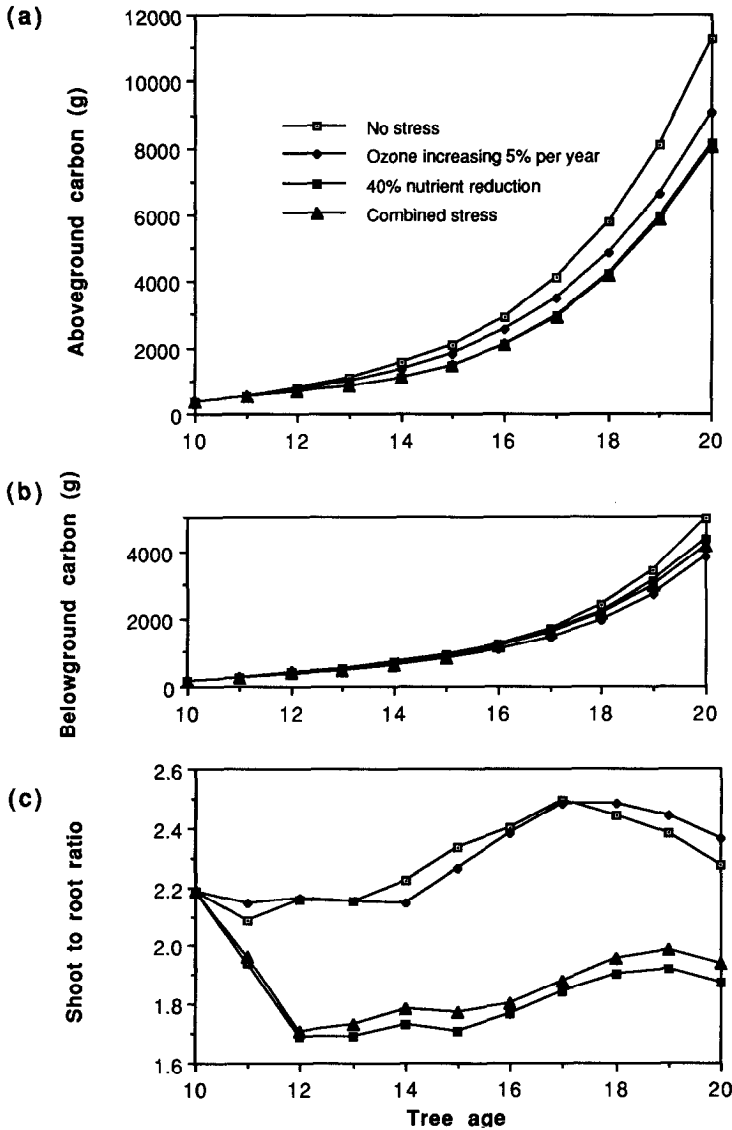
Figure 5. The sum of aboveground carbon pools (a), the sum of belowground carbon pools (b) (note change of scale), and shoot-to-root ratio (c) under four scenarios: (1) base case (ambient ozone); (2) increasing ozone 5% per year; (3) 40% nutrient reduction; and (4) simultaneous ozone exposure and nutrient reduction. The model calculates carbon pools on a daily timestep; here we have graphed only one data point per year to eliminate seasonal variations.

Discussion

The effect of stress on growth partitioning

Both ozone and nutrient stress had important influences on carbon allocation above- and belowground. The model simulated the shift toward root growth under nutrient

stress through a shift in the strength of the sources and sinks for carbon and nutrients, without any explicit or empirical carbon partitioning coefficient. Simply stated, root growth in the model has first priority at using nutrients. When nutrients are limiting, aboveground parts will not be able to use much of their photosynthate for growth. The excess carbon becomes available for root growth, even though roots have last priority for carbon. Thus, the shoot-to-root ratio falls.

Ozone stress had the opposite effect on carbon allocation, reducing root growth. In the model, this occurs because aboveground parts had adequate nutrients for growth and first priority for carbon use. In this simulation, as in the associated experiment, aboveground growth was almost unaffected by the ozone stress (Laurence et al. 1989), suggesting the importance of measuring belowground biomass in experiments designed to assess ozone damage. Because the maintenance of an optimal shoot-to-root ratio is crucial for continued plant resistance to stresses, the shifts in partitioning predicted to accompany pollution exposure are of major concern.

The response of plants to interacting stresses

The results shown here suggest that moderate increases in ozone exposure will likely cause only slight injury to plants already stressed by nutrient deficiencies. This conclusion should not be generalized, however, because the interaction of multiple stresses depends on the action of the particular stresses and the timing of resource use. In investigations currently underway with the model, we are exploring whether higher concentrations of ozone concurrent with nutrient deficiency could have more than additive effects on growth. If intensitites of stress are reached that exacerbate growth reductions, the effects may be severe, because the response of the plant to nutrient deficiency is to place available carbon in structural tissue that exacts a maintenance cost but does not fix additional carbon. Continued allocation of carbon to roots must ultimately strain the limited carbon reserves of the plant, while ozone increases respiratory demands for repair of damaged tissue.

These simulations were conducted in the absence of water stress, which would also affect the strength of sources and sinks that determine growth allocation. A shift toward shoot growth under ozone stress might exacerbate the effect of water stress. Alternatively, water stress might prevent such a shift from occurring. The next version of the model will be capable of examining the interaction of water stress with other stresses.

Interpreting model predictions

The model simulations demonstrated that increases in ozone exposures and decreases in nutrients caused by continuing deposition of acidic precipitation could have significant effects on the growth of red spruce trees over the next 10 years. Although the growth declines predicted are modest, these results may presage more serious changes. If acid deposition reduces the availability of limiting nutrients in the soil, red spruce trees are predicted to have a finite ability to withstand the damage, by expending carbon to increase root tissue. With severe nutrient depletion, however,

the ability to compensate by increased root production may be exceeded. In the short-term, the capacity for such compensation depends on the quantity of non-structural carbon reserves.

In interpreting the magnitude of measured or simulated growth response to ozone, it is important to recognize that young trees may be less susceptible to ozone than mature trees because of their rapid growth rates, high percentage of foliage in the newest age class, and high ratio of source to sink tissues (Amundson et al. 1991a). Mature trees in forests have the additional stress of competition. Any conditions that further lower a tree's TNC reserves would increase its vulnerability to stress above that reported here.

More extensive testing of the model is underway in three arenas: simulating the growth of a larger number of individual red spruce trees, comparing modeled stress responses to those exhibited in the associated field experiment, and applying the model to species with a range of growth strategies. The model is currently being calibrated for a set of control trees grown in filtered air and low acid rainfall in open-top chambers. We will next predict the growth response of trees to different treatments of ozone and acidic precipitation. Comparing simulated and observed responses under different modeled mechanisms of damage and response will help to identify probable causes for the observed stress responses and their interactions. The model is also being parameterized to simulate loblolly pine responses to ozone and acid rain. Similar applications are planned for sugar maple and hybrid poplar.

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