Tree responses to CO₂ enrichment: CO₂ and temperature interactions, biomass allocation and stand-scale modeling

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Summary In this review, I focus on modeling studies of tree responses to CO₂ enrichment. First, I examine leaf-scale models of assimilation with respect to the interaction between low temperature and CO₂ enrichment. Second, because changes in allocation within a tree may be significant in determining the growth response of trees to CO₂ enrichment and low temperatures, I review models of the control of allocation in plants. Finally, models of stand-scale processes are discussed with respect to their ability to make reliable estimates of likely vegetation responses to predicted climate change. I conclude that our ability to make reliable predictions is hindered by our lack of understanding of several processes, namely: the interaction between increased atmospheric CO₂ concentration and low temperatures; the control of allocation in plants; and the modeling of stand-scale processes.

Keywords: carbon assimilation, growth, leaf-scale models.

Introduction

Atmospheric CO₂ concentrations are increasing at approximately 1.8% per annum. It is predicted that this increase will have a significant impact on the physiology and growth of trees. The short- and long-term responses to increases in atmospheric CO₂ concentration have been extensively reviewed. In this review, therefore, I focus on the models that are being developed to study tree responses to CO₂ enrichment. I examine leaf-scale models of assimilation with respect to the interaction of low temperature with CO₂ enrichment. Because changes in allocation within a tree may be significant in determining the growth response of trees to CO₂ enrichment, I review models of the control of allocation in plants. Finally, models of stand-scale processes are discussed with respect to their ability to make reliable estimates of likely vegetation response to predicted climate change.

Leaf-scale models of assimilation

The response of assimilation to changes in temperature, and the influence of temperature both on the solubilities of CO₂ and O₂ and on the specificity of Rubisco to CO₂ and O₂ are well known. Similarly, the short-term influence of CO₂ concentration on assimilation is well documented. The response of maximum assimilation rate to increasing leaf temperature at different CO₂ concentrations has also been documented (Long 1991, Eamus et al. 1995). As temperature rises, the stimulation of assimilation resulting from any given increase in CO₂ concentration is increased. For example, in response to a doubling in atmospheric CO₂ concentration, CO₂ assimilation at saturating PPFD, A_sat, is predicted to increase by 54% and 73% at 20 and 30 °C respectively (Long 1991), and the optimum temperature for photosynthesis is also predicted to increase (Eamus et al. 1995). However, Rubisco activity declines by 20 to 40% in response to CO₂ enrichment (Sage et al. 1989). As the percentage decline in activity increases, the ratio of A_sat at 700 µmol mol⁻¹ to A_sat at 350 µmol mol⁻¹ declines, and this affects the temperature at which CO₂ enrichment has a positive effect on A (Long 1991). Thus, when Rubisco activity declines in response to CO₂ enrichment, the temperature threshold at which CO₂ enrichment can have a positive impact on assimilation increases. For example, this temperature increases from about 14 to 24 °C as Rubisco activity declines from 80 to 60% of control values (Long 1991). At temperatures below the threshold, typically less than 16–19 °C, CO₂ enrichment has a negative impact on assimilation rate.

Based on these simulations, it has been concluded that CO₂ enrichment will have a larger impact on assimilation at high temperatures than at low temperatures (Jones et al. 1985, Baker et al. 1989). In several studies it has been shown that CO₂ enrichment has a negative impact on plant growth at temperatures below 18 °C (cf. Idso et al. 1987, Kimball et al. 1993, Rogers and Dahlman 1993, Rozema et al. 1993). However, CO₂ enrichment does not always have a negative impact on growth at low temperatures suggesting that C fixation may not be the only process underlying the response of CO₂-enriched plants to low temperatures (Stitt and Schulze 1994). For example, Sionit et al. (1981) showed that okra was able to grow at lower temperatures when supplied with CO₂-enriched air than when supplied with ambient air. Similarly Potvin and Strain (1985) found a C₃ grass was more responsive to CO₂ enrichment at low temperatures than at high temperatures. Potvin (1994) observed that CO₂ enrichment had a significant impact on the biomass increment of two C₃ species and two C₄ species and the effect was not influenced by temperature. In an Arctic tundra study, Grulke et al. (1990) showed that rates of canopy uptake were significantly increased by CO₂ enrich-
ment, despite the low temperatures of the Arctic tundra.

Thus, the published data indicate that the growth response to CO₂ enrichment does not increase with increasing temperature in all species, and some species exhibit a positive growth response to CO₂ enrichment at low temperatures. Possible explanations for these results are that, in some species, Rubisco activity or content may not decline in response to elevated CO₂ (cf. Delgado et al. 1994), or that declines in Rubisco activity or content are not correlated with a decline in Aₘax. Other explanations to account for the increase in growth rate at low temperatures include changes in allocation, or changes in efficiency of use of fixed carbon. Alternatively, the flux control for photosynthesis (Kacser and Burns 1973) may change with temperature and CO₂ concentration so that the degree of limitation imposed by Rubisco on carbon fixation may decline under CO₂-enriched conditions at low temperatures (Stitt and Schulze 1994).

Changes in specific leaf area, leaf weight area, shoot weight ratio, carbon content of dry matter, and respiration rates of roots and shoots can all directly influence growth. All of these relationships and processes respond to CO₂ enrichment, but both the magnitude and direction of the response are variable (Poorter 1993, Stulen and den Hertog 1993, Wullschleger et al. 1994). Johnson and Lincoln (1990) concluded that even a decline in the carbon content of plant biomass can result in an increase in growth. Therefore, although the Rubisco model predicts a decrease in the rate of carbon fixation per unit leaf area with decreasing temperature, a change in allocation of carbon within the plant could increase growth rate per plant, if this results in increased photosynthetic area.

Increased efficiency of conversion of fixed carbon to support growth may also contribute to the observed increased growth at low temperatures. Stitt and Schulze (1994) have discussed the concept of wastage of stored carbohydrate based on the observation that changes in response to reduced Rubisco content in Rubisco antisense transformed tobacco cells included a decline in the wastage of stored carbohydrate to compensate for reduced rates of carbon fixation. Wullschleger et al. (1994) concluded that respiration can increase or decrease in response to CO₂ enrichment. Maintenance and growth respiration may respond differently to CO₂ enrichment at low temperatures. A decline in respiration rate in response to CO₂ enrichment at low temperatures and an increase or no change in respiration rate in response to CO₂ enrichment at higher temperatures has been observed (Ziska and Bunce 1994). Thus, at low temperatures, a reduction in respiratory carbon loss could contribute to enhanced growth (Ziska and Bunce 1994).

I conclude that growth of CO₂-enriched plants may increase at low temperatures despite a decline in the rate of carbon fixation. Changes in allocation, efficiency of use of fixed carbon, and changes in flux control for photosynthesis may all contribute to an increase in growth rate at low temperature. The finding that the growth rate can increase in response to low temperatures even though the Rubisco model predicts a decline in the rate of carbon fixation with decreasing temperature implies that either the model is incorrect, or the relationship between carbon fixation rate and growth is complex. Because the Rubisco model appears to be correct, the latter explanation is favored.

**Biomass allocation models**

An understanding of the mechanisms underlying the control of biomass allocation in trees is especially relevant to the development of models for predicting canopy and catchment scale responses to climate change and CO₂ enrichment. Models of the control of allocation in plants can be classified into four groups (Wilson 1988): (a) allometric; (b) functional equilibria; (c) Thomley-type models; and (d) hormone models. Allometric models fit equations to data sets so that the equation is a good description of the data. However, such models are empirical and do not provide insight into mechanisms that may underlie the relationship between shoot and root growth.

Functional equilibria models emphasize the importance of the differential functioning of shoots and roots. A generalized functional equilibrium model can take the form: root mass × root activity = k × shoot mass × shoot activity, where root activity signifies ion (or N) uptake capacity (Givnish 1986, Dewar 1993), shoot activity is the capacity for carbon assimilation, and the proportionality constant, k, represents the amount of nitrogen used in plant material per unit amount of carbon (Makela and Sievanen 1987). Although functional equilibria models are a significant development over allometric models, these models only describe a data set and provide no information about the mechanisms that control the allocation of biomass to roots and shoots.

Thomley developed mechanistic models based on three features. First, root or shoot growth is dependent on the concentrations of carbon and nitrogen in root and shoot; second, the movement of labile C and N between shoots and roots is dependent on the difference between shoot and root in concentrations of labile C and N compounds; and third, structural material and labile compounds are treated as separate pools. Of models developed by Thomley, the transport resistance model (Thomley 1972), which views the allocation of C and N as a means of balancing the functional relationships of roots and shoots, appears to be the most robust and has been incorporated into several forest models (Rastetter et al. 1991, Thomley and Cannell 1992).

The transport resistance model (hereafter the TR model) allocates C and N on the basis of C and N labile substrate concentrations in root and shoot, current shoot and root fractions of total plant biomass, and the fractional C and N content of roots and shoots. This allocation coefficient can be constrained to a fixed substrate C/N ratio, irrespective of changes in C and N availability, or set to allow variations in C/N ratio, or set to maximize relative growth rate, RGR. In the latter case, the effects of leaf N content on photosynthesis have been incorporated (Hilbert et al. 1991). The TR model assumes that as plant mass increases, the resistance to sap flow decreases. As a result of these resistances to flow, gradients in C and N concentration in roots and shoots arise whereby the concentration of N is higher in the root and the concentration of C is higher in the shoot. Because growth is assumed to be propor-
tional to C and N concentration, the product of C × N can be used to explain the response of allocation to changes in N or C availability.

The weakness of the TR model is the assumption that allocation of C to the root and allocation of N to the shoot is proportional to the amount of root and shoot biomass, respectively. That is, the model does not attempt to account for the retranslocation of C and N within the plant. This weakness has been addressed in the mechanistic model proposed by Minchin et al. (1993), which is based on a kinetic analysis of substrate unloading from the xylem in sinks. In this model, which is based on the Michaelis-Menten equation, it was shown that if the Michaelis constant, kₘ, and maximum velocity of phloem unloading, Vₘₐₓ, of two sinks differ, and if source loading declines due to a decline in source activity, then partitioning of photosynthate to the two sinks will differ. Consequently, with appropriate values of kₘ and Vₘₐₓ for competing sinks, it was possible to model the observed increase in partitioning to shoots in response to shading of the source leaves without having to invoke changes in allocation of N from the roots (Minchin et al. 1994). An important feature of this model is that the feedback between changes in supply of C from source leaves and allocation of photosynthate between source and sink is explained on the basis of kinetic properties of the sinks, rather than on the basis of shoot and root biomass. The model of Minchin et al. (1993, 1994) deals only with the allocation of C substrates. Whether it can be extended to include the allocation of N remains to be tested. However, uptake of nitrogenous compounds from xylem sap into leaf cytoplasm and loading of nitrogenous compounds into the phloem of leaves for retranslocation to roots with subsequent unloading in roots, provide steps for carrier-mediated transport across membranes. Thus, the idea of differences in kₘ and Vₘₐₓ may be applicable to the allocation of N in plants. Because up to 50% of the N of roots is derived from N retranslocated from leaves, it is possible that, in the absence of active mechanisms for N unloading from the xylem and phloem, the link between changes in N availability in the soil and changes in allocation of C and N to roots could be mediated via the translocation of C from the shoots.

Dewar (1993) has expanded the TR model based on the work of Givnish (1986) to include a role for water uptake by roots. This root–shoot partitioning model simulates the transport of water, labile N and C, and the interaction between these factors in the control of growth. The model assumes that the growth rate of a site (root/shoot) is determined by the availability of labile C and N at that site, and by its water status. It also assumes that a fraction of the total N taken up by roots is transported to the shoot via the xylem, and the remaining fraction is passed to the root phloem, where it joins the N that is moving down the plant from the shoot.

The model has four important characteristics. First, when the fraction of N that is moved to the shoot is less than or equal to the fraction of total plant biomass in the shoot, then the concentration of labile N in the root increases and is available to support increased root growth. Second, the existence of counter-gradients of labile C and N determine the root and shoot responses to changes in the supply of C or N. Third, root and shoot water potentials and biomass are explicitly linked in this model. Finally, unlike the TR model, this root–shoot partitioning model can account for the difference in the response of root/shoot ratio to changes in N supply versus changes in potassium, magnesium and manganese supply.

Luo et al. (1994) have modeled the response of allocation of biomass in plants grown under CO₂-enriched conditions on the basis of specific leaf and plant N concentrations, leaf mass per unit area, and plant N productivity. Generally, N concentrations declined and leaf mass per unit area and plant N productivity increased in response to CO₂ enrichment. They were also able to predict up and down regulation of photosynthesis on the basis of the relative changes in leaf mass per unit area and leaf N concentrations. They then compared two regulatory models, a simple functional balance model and a photosynthesis–growth model, to explain changes in root and shoot allocation. The photosynthesis–growth model is based on the hypothesis that photosynthesis and RGR are mechanistically related, whereas the functional balance model is based on the hypothesis that allocation and physiological activity of roots and shoots are mechanistically linked. The functional balance model was found to be a poor description of the experimental data; however, the photosynthesis–growth model, which predicted root allocation on the basis of relative sensitivities of photosynthesis and relative growth rate to CO₂ enrichment, more closely matched published results. The model predicted that root allocation increases whenever the rate of photosynthesis per unit leaf mass increases more than RGR in response to CO₂ enrichment.

It seems likely that changes in allocation of biomass, resulting from CO₂ enrichment influence water use, nutrient and light capture, and nutrient use efficiency, and hence the functional ecology of catchments. However, without a detailed understanding of the mechanisms controlling biomass allocation, our ability to develop models of such responses is seriously restricted.

**Modeling at the stand scale**

A recent development in forest process modeling has been the G’DAY model of Comins and McMurtrie (1993). In this model, photosynthesis, tree productivity, soil carbon–nitrogen dynamics and allocation are included to generate equilibrium responses of tree stands to changes in specific environmental conditions. Three biomass fractions are included (foliage, wood and fine roots). The soil component has four litter compartments (surface structural, soil structural, surface metabolic and soil metabolic). In addition, the soil has three organic fractions (active, slow and passive). When CO₂ concentrations are doubled, the model predicts a short-term, rapid and large increase in productivity. Consequently, C input to the soil increases and this results in increased sequestration of nutrients in the soil and nutrient availability declines rapidly (within 1 year). As a result, plant C/N ratio increases and productivity is substantially reduced.

The G’DAY model represents a significant advance because...
it incorporates many aspects of tree and forest ecophysiology previously ignored. Thus, N deposition, N release from wood decay, and other processes in the N cycle, as well as the influence of foliar N content on carbon assimilation, are taken into account to a lesser or greater extent. Carbon contents and sequestration into a variety of pools are also explicitly dealt with.

Kirschbaum et al. (1994) tested the effects of varying certain model parameters on model predictions and obtained the following information. (1) When the N/C ratio of wood is proportional to the N/C ratio of foliage, the impact of CO$_2$ enrichment on productivity increases from 1.1 (when the ratio is kept constant) to 14.1%, indicating the importance of experimentally determining the relationship between wood and foliage N/C ratios for trees exposed to ambient and enriched CO$_2$. (2) The relationship between foliar N content and maximum assimilation rate can change under CO$_2$ enriched conditions. Nitrogen use efficiency can increase (Tissue et al. 1993) and decrease (Stitt 1991). Given this uncertainty, the relationship between foliar N and $A_{\text{max}}$ was assumed to be unchanged. (3) The sensitivity of the whole canopy to CO$_2$ concentration was sensitive to the choice of photosynthetic parameters and to the choice of the relationship between foliar N content and assimilation. More information for mature trees growing in a CO$_2$-enriched environment is required. (4) If the allocation ratio for foliage, fine roots and woody parts is fixed at 0.2, 0.2 and 0.6, respectively, productivity increases by 14.1% when CO$_2$ concentration is doubled. When a negative linear response for allocation to roots as a function of foliar N content is incorporated, productivity increases to 14.8%. Interestingly, the sensitivity of wood production to a doubling of the CO$_2$ concentration declines from 14.1 to 10.6%, a decline of approximately 25%, as a result of enhanced allocation to fine roots. Changes in specific leaf area substantially influence the response of productivity to CO$_2$ enrichment. When specific leaf area, SLA, declined by 20%, sensitivity of productivity declined from 14.1 to 8.2%. Thus there is a significant negative feedback between SLA and light interception and responsiveness to CO$_2$ concentration. (5) The data of Mousseau and Enoch (1989) show that leaf longevity increases in response to CO$_2$ enrichment. Similarly, there is experimental and theoretical evidence showing that the light compensation point for photosynthesis is decreased by CO$_2$ enrichment (Long 1991), and consequently, leaf longevity may increase. However, from considerations of the relationship between foliar nitrogen content and leaf longevity, Kirschbaum et al. (1994) showed that productivity increased from 14.1 to 19.3% when leaf longevity increased. The increase was especially noticeable on soils of low N content. Clearly, leaf longevity can have a substantial impact on canopy responses to CO$_2$ enrichment. (6) The model showed that nitrogen limitations do not provide an overriding constraint on the ability of trees to respond to CO$_2$ enrichment. Rather, several interactions between soil, plant and atmosphere determine the final response of trees to CO$_2$ enrichment.

The study by Kirschbaum et al. (1994) revealed the importance of the percentage of N lost from the system through leaching and gaseous emissions. It was the N recycling constraint curve that essentially determined the magnitude of the response of productivity to CO$_2$ enrichment.

I conclude that tree-based mechanistic studies of long-term responses to CO$_2$ enrichment are needed. Vertical integration of these long-term responses at the three major spatial scales, namely leaf scale, whole-plant scale and stand scale, should be possible by the end of the century.

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References


