

Modelling whole-plant allocation in relation to carbon and nitrogen supply: Coordination versus optimization: Opinion

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Abstract

One of the few integrating theories related to allocation is the hypothesis of optimization. While optimization theory has great heuristic appeal and has been used to describe a range of physiological and ecological phenomena, it has major limitations. Optimization is necessarily based on a definite time integral and an optimal control strategy must be specific to the same patterns exhibited by the driving variables over this same period of time. Optimization tends to employ the use of oversimplifications in order to facilitate analytical solutions to the optimal control strategy, i.e. the mechanism governing the response of plants, which is the critical issue of interest. It is difficult to define objective criteria that can account for the natural variability in plants and testing the quantitative predictions of optimality models is also difficult. Thus, we suggest that optimization theory is too limited for practical use in modelling whole plant allocation. In this paper, we introduce the use of coordination theory as a practical alternative. We develop a simple plant growth allocation model using both coordination and optimization approaches and show that coordination theory is easily applied, produces results that are quantitatively similar to optimization, and overcomes the inherent limitations of optimization theory.

Introduction

A major uncertainty in modelling the effects of elevated atmospheric [CO₂] and climate change on plant function and growth is our lack of understanding of the mechanisms of whole-plant allocation (Reynolds et al., 1996). The allocation of carbon and inorganic nutrients, particularly nitrogen (N), is in response to a complex of competing demands, e.g. plant defenses, symbionts, storage, fluxes to the rhizosphere, and vegetative vs. reproductive growth (see review by Friend et al., 1994). As a result, patterns of allocation are observed to be highly integrated, vary temporally, are plastic, may be determined at early stages of plant development, and are regulated by a complex network of competing "sources" and "sinks."

The concept of balanced activity has been successfully used to model whole plant allocation (e.g. Charles-Edwards, 1976; Hilbert and Reynolds, 1991;

Johnson and Thornley, 1987; Luo et al., 1994; McMurtrie and Wolf, 1983; Reynolds and Thornley, 1982; Thornley, 1995). This concept is consistent with empirical evidence showing that plants maintain a balance between the rate of supply of carbon from leaves and the rate of supply of nutrients from roots (Chapin, 1980; Davidson, 1969; Field and Mooney, 1986; Friend et al., 1994; Schulze et al., 1983). Many of these models are based on optimization principles, whereby a plant is viewed as allocating biomass in order to maximize its rate of growth (see Hilbert, 1990; Iwasa and Roughgarden, 1984; Makela, 1986; Schulze et al., 1983). While optimization theory has great heuristic appeal and has been used to describe a range of physiological and ecological phenomena, it has major limitations. Optimization is necessarily based on a definite time integral (e.g. 24 hours or a total growing season) and the optimal control strategy must be specific to the same patterns exhibited by the environmental variables over this period of time. It is meaningless to argue that plants can "foresee" what the environment will

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be like over a growing season (see Kastner-Maresch and Mooney, 1994, for discussion of local vs. global optimization). In most cases, optimization theory must rely on major simplifications in order to facilitate analytical solutions to the optimal control strategy, i.e. the mechanism governing the response of the plant to its environment, which is the critical issue of interest. Lastly, it is extremely difficult to define objective criteria that can be used to test the quantitative predictions of optimality models and that can account for natural variability in populations (Orzack and Sober, 1994).

In a previous paper (Chen et al., 1993), we introduced coordination theory as a practical alternative to optimization theory for explaining how plants allocate N within canopies in order to optimize total canopy photosynthesis. We hypothesized that the allocation is a balance between two processes, each of which is dependent on leaf N content and each of which potentially limits photosynthesis: 1) W_c , the Rubisco-limited rate of carboxylation, and 2) W_j , the electron transport-limited rate of carboxylation. Do plants allocate N differentially to leaves in different canopy layers in such a way that W_c and W_j remain roughly balanced? Coordination theory predicts that the driving force for the allocation of N within a canopy is the difference between the leaf N content required to bring W_c and W_j into balance. We demonstrated that daily carbon assimilation of a canopy with a N distribution resulting from an internal coordination of W_c and W_j was identical to results obtained using optimization theory. Due to its simplicity, we think coordination theory can be easily applied to study other problems.

In this paper we present a simple plant growth allocation model based on coordination theory. Two versions of the model – with and without the capacity to store carbon and N – are presented, along with steady-state and dynamic solutions. The model predicts allocation based on the imbalance principle and we compare the results to an equivalent allocation model based on optimal control theory.

Model overview

The total dry weight of the plant (W_G) is given by:

$$W_G = W_{sh} + W_r \quad (1)$$

where W_{sh} is the shoot and W_r is the root structural dry weights, respectively. In many allocation models (e.g. Reynolds and Thornley, 1982; Johnson and Thornley, 1987), plant growth is considered analogous

to an overall chemical reaction of two main substrates, carbon and nitrogen. The growth rate of the plant is proportional to C and N concentrations, i.e.:

$$\frac{dW_G}{dt} = \alpha CNW_G \quad (2)$$

where $C = W_C/W_G$, $N = W_N/W_G$, α is a constant of proportionality, and W_C and W_N are the dry weights of non-structural carbon and nitrogen, respectively. This approach emphasizes the importance of carbon and nitrogen storage since growth will cease if either substrate goes to zero. Here, we present two versions of our model, one where C and N are treated as "inventories," that is, they are treated as supplementary rather than essential terms, and another version where C and N are not explicitly included.

We employ the following major assumptions:

1. Since the model is integrated on a daily basis, carbon assimilated and nitrogen taken up by the plant is readily available throughout the plant, ignoring the problem of transportation.
2. Stored forms of non-structural carbon and nitrogen are equivalent to those currently acquired. Conversion between insoluble and soluble forms is ignored.
3. The growth rates of the shoot and root are limited only by the supply of carbon or by the supply of nitrogen. Practically, both shoot and roots have a maximum growth rate that is determined by the size and activity of the meristems in the shoot and root.
4. The fractions of carbon (f_C) and nitrogen (f_N) of the plant structure are constant.
5. The carbon and nitrogen supply functions are proportional to the structural dry weights of the shoot and roots, respectively. Of course, as a plant grows, other factors (e.g. self-shading) will eventually affect carbon and nitrogen uptake.

These assumptions allow us to keep the model presented in this paper as simple as possible in order to demonstrate the nature of the coordination theory and to compare it with optimization theory. These assumptions can be relaxed to make the model more realistic (discussed below).

Version with no storage terms

In this formulation of the model we ignore storage and focus on growth allocation based only on the variables, W_{sh} and W_r . The growth rate of the whole plant, G , is

assumed to be directly related to the supplies of carbon and nitrogen:

$$G = \frac{dW_G}{dt} = \min\left\{\frac{S_C}{f_C}, \frac{S_N}{f_N}\right\} \quad (3)$$

in which S_C and S_N are supply rates of carbon and nitrogen. The underlying assumption of Equation (3) is that for every unit increment of the structural biomass, W_G , a fixed portion of carbon, f_C , and a fixed portion of nitrogen, f_N , are needed, and G will be limited by either of carbon or nitrogen supply whenever these two supply rates are not in some required proportion or balance.

The supply of carbon is assumed to be proportional to the shoot structural dry weight, and the supply of nitrogen is assumed to be proportional to the root structural dry weight:

$$S_C = \sigma_C W_{sh} \quad (4)$$

$$S_N = \sigma_N W_r \quad (5)$$

where σ_C and σ_N are the specific shoot and root activities, respectively. Then, Equation (3) becomes:

$$G = \frac{dW_G}{dt} = \min\left\{\frac{\sigma_C W_{sh}}{f_C}, \frac{\sigma_N W_r}{f_N}\right\} \quad (6)$$

and G is the sum of the growth rate of the shoot, dW_{sh}/dt , and the growth rate of the root, dW_r/dt :

$$G = \frac{dW_{sh}}{dt} + \frac{dW_r}{dt} \quad (7)$$

Allocation coefficients to the shoot (λ_{sh}) and to the root (λ_r) are defined as:

$$\lambda_{sh} = \frac{dW_{sh}}{dt} / G \quad (8a)$$

$$\lambda_r = \frac{dW_r}{dt} / G \quad (8b)$$

where

$$\lambda_{sh} + \lambda_r = 1. \quad (8c)$$

Following Chen et al. (1993), we assume that the plant can respond to whatever process – carbon supply or nitrogen supply – is limiting growth by "coordinating" these processes. In this paper, we are specifically interested in the allocation of growth between the shoot and root as the means of coordination; hence, we assume that the plant can respond to an imbalance in the carbon or nitrogen supply (Equation 3) by modifying the allocation coefficients, λ_{sh} and λ_r . In mathematical

form, we define an imbalance, Im , between these two processes as:

$$Im = \frac{S_C}{f_C} - \frac{S_N}{f_N} \quad (9)$$

To eliminate an imbalance, the supply rates of carbon and nitrogen must be modified to satisfy:

$$\frac{\Delta S_C}{f_C} - \frac{\Delta S_N}{f_N} = -Im \quad (10)$$

Changes of S_C and S_N due to the growth of W_{sh} and W_r can be expressed as:

$$\begin{aligned} \Delta S_C &= \frac{\delta S_C}{\delta W_{sh}} (\lambda_{sh} \Delta W_G) + \frac{\delta S_C}{\delta W_r} (\lambda_r \Delta W_G) \\ &= \left\{ \frac{\delta S_C}{\delta W_{sh}} \lambda_{sh} + \frac{\delta S_C}{\delta W_r} \lambda_r \right\} G \Delta t \end{aligned} \quad (11)$$

$$\begin{aligned} \Delta S_N &= \frac{\delta S_N}{\delta W_{sh}} (\lambda_{sh} \Delta W_G) + \frac{\delta S_N}{\delta W_r} (\lambda_r \Delta W_G) \\ &= \left\{ \frac{\delta S_N}{\delta W_{sh}} \lambda_{sh} + \frac{\delta S_N}{\delta W_r} \lambda_r \right\} G \Delta t \end{aligned} \quad (12)$$

where Δt is the time step used in integration, which here we set $\Delta t = 1$ day. Thus, substitution of Equations (11) and (12) into Equation (10) gives:

$$\left(\frac{\delta S_C}{\delta W_{sh}} - \frac{\delta S_N}{\delta W_{sh}} \right) \lambda_{sh} - \left(\frac{\delta S_N}{\delta W_r} - \frac{\delta S_C}{\delta W_r} \right) \lambda_r = -\frac{Im}{(G \Delta t)} \quad (13)$$

Instead of directly using the allocation coefficients λ_{sh} or λ_r and Equation (13), we define an allocation parameter, P , as:

$$P = \left(\frac{\delta S_C}{\delta W_{sh}} - \frac{\delta S_N}{\delta W_{sh}} \right) \lambda_{sh} - \left(\frac{\delta S_N}{\delta W_r} - \frac{\delta S_C}{\delta W_r} \right) \lambda_r \quad (14)$$

and assume that P is responding to Im as:

$$P = \kappa (-Im / G) \quad (15)$$

where κ is a coordination parameter that specifies how rapidly the plant can adjust the allocation coefficients in response to the imbalance. κ has a units of day^{-1} . At one extreme, where $\kappa = 1$, the plant can "correct" the imbalance completely in the next day; at another extreme, $\kappa = 0$, the plant maintains a constant allocation to shoot and root, regardless of the imbalance between carbon and nitrogen supplies. Thus, a reasonable value of κ should be between 0 and 1 and is likely to be species specific. Below, we conduct a theoretical analysis to estimate the magnitude of κ and show that

while a large κ slightly favours growth, it results in large fluctuations in allocation coefficients that are not consistent with experimental observations.

It is not clear which physiological processes affect κ , but κ must remain fairly constant for a given species. If κ changes dramatically on a daily basis, coordination theory would have little practical use. We have to distinguish, however, the allocation parameter, P , from the time constant parameter, κ . While κ is constant, P changes on a daily basis since P also depends on the magnitude of the imbalance, Im . According to Equation (9), the imbalance depends on carbon supply, S_C , and nitrogen supply, S_N , which change on a daily basis. The functions determining S_C and S_N are highly simplified (Equations 4 and 5); however, modifications to Equations (4) and (5) will only affect the magnitude of the imbalance, Im , not the value of κ (Chen and Reynolds, unpubl.), and the essential features of the coordination model presented here are not affected.

After P is determined from Equation (15), λ_{sh} and λ_r can be obtained from P as:

$$\lambda_{sh} = \frac{\frac{\frac{\delta S_N}{f_N}}{\delta W_r} - \frac{\frac{\delta S_C}{f_C}}{\delta W_r} + P}{\frac{\frac{\delta S_C}{f_C}}{\delta W_{sh}} - \frac{\frac{\delta S_N}{f_N}}{\delta W_{sh}} + \frac{\frac{\delta S_N}{f_N}}{\delta W_r} - \frac{\frac{\delta S_C}{f_C}}{\delta W_r}} \quad (16a)$$

$$\lambda_r = \frac{\frac{\frac{\delta S_C}{f_C}}{\delta W_{sh}} - \frac{\frac{\delta S_N}{f_N}}{\delta W_{sh}} - P}{\frac{\frac{\delta S_C}{f_C}}{\delta W_{sh}} - \frac{\frac{\delta S_N}{f_N}}{\delta W_{sh}} + \frac{\frac{\delta S_N}{f_N}}{\delta W_r} - \frac{\frac{\delta S_C}{f_C}}{\delta W_r}} \quad (16b)$$

In this simple model, S_C and S_N are defined by Equations (4) and (5). Hence, Equations (14), (16a) and (16b) become:

$$P = \frac{\sigma_C}{f_C} \lambda_{sh} - \frac{\sigma_N}{f_N} \lambda_r \quad (17)$$

$$\lambda_{sh} = \frac{\frac{\sigma_N}{f_N} + P}{\frac{\sigma_C}{f_C} + \frac{\sigma_N}{f_N}} \quad (18a)$$

$$\lambda_r = \frac{\frac{\sigma_C}{f_C} - P}{\frac{\sigma_C}{f_C} + \frac{\sigma_N}{f_N}} \quad (18b)$$

Steady state, balanced growth

In the special case where the environmental conditions are constant and the plant eventually succeeds in coordinating the two supply rates of carbon and nitrogen (i.e. where $Im = 0$), then the growth rate will be:

$$G = \frac{dW_G}{dt} = \frac{\sigma_C W_{sh}}{f_C} = \frac{\sigma_N W_r}{f_N} \quad (19)$$

This special case is identical to the one obtained by Charles-Edwards (1976), in which the plant achieves a balanced growth, with the specific growth rate, μ :

$$\mu = \frac{1}{\frac{f_C}{\sigma_C} + \frac{f_N}{\sigma_N}} \quad (20)$$

The allocation coefficients λ_{sh} and λ_r and the root weight ratio, RWR, under balanced exponential growth are given by:

$$\lambda_{sh} = \frac{\frac{f_C}{\sigma_C}}{\frac{f_C}{\sigma_C} + \frac{f_N}{\sigma_N}} \quad (21a)$$

$$\lambda_r = \frac{\frac{f_N}{\sigma_N}}{f_C/\sigma_C + f_N/\sigma_N} \quad (21b)$$

$$RWR = \frac{W_r}{W_{sh} + W_r} = \frac{f_N/\sigma_N}{f_C/\sigma_C + f_N/\sigma_N} \quad (22)$$

Dynamic solutions

In balanced growth, in a constant environment, the plant achieves a steady state as a function of the "coordination power" of the plant, which is specified by parameter κ . We illustrate this dynamic behavior using numerical examples. The following parameter values from Johnson and Thornley (1987) are used:

$$f_C = 0.45 \text{ kg carbon} \quad (\text{kg structure})^{-1} \quad (23a)$$

$$f_N = 0.03 \text{ kg nitrogen} \quad (\text{kg structure})^{-1} \quad (23b)$$

$$\sigma_C = 0.10 \text{ kg carbon} \quad (\text{kg shoot structure})^{-1} \text{ day}^{-1} \quad (23c)$$

$$\sigma_N = 0.05 \text{ kg nitrogen} \quad (\text{kg root structure})^{-1} \text{ day}^{-1} \quad (23d)$$

with initial conditions:

$$W_{sh} = 0.1 \text{ kg structure} \quad (23e)$$

$$W_r = 0.1 \text{ kg structure} \quad (23f)$$

The dynamic behaviours of the allocation coefficient, λ_{sh} , the root weight ratio, RWR, and the specific growth rate of the plant, μ , for $\kappa = 0.05$ and 0.5 are shown in Figures 1A–1C, respectively. The initial values of W_{sh} and W_r (Equations 23e and 23f) are chosen to represent a situation where carbon supply is limiting growth. This initial imbalance between carbon and

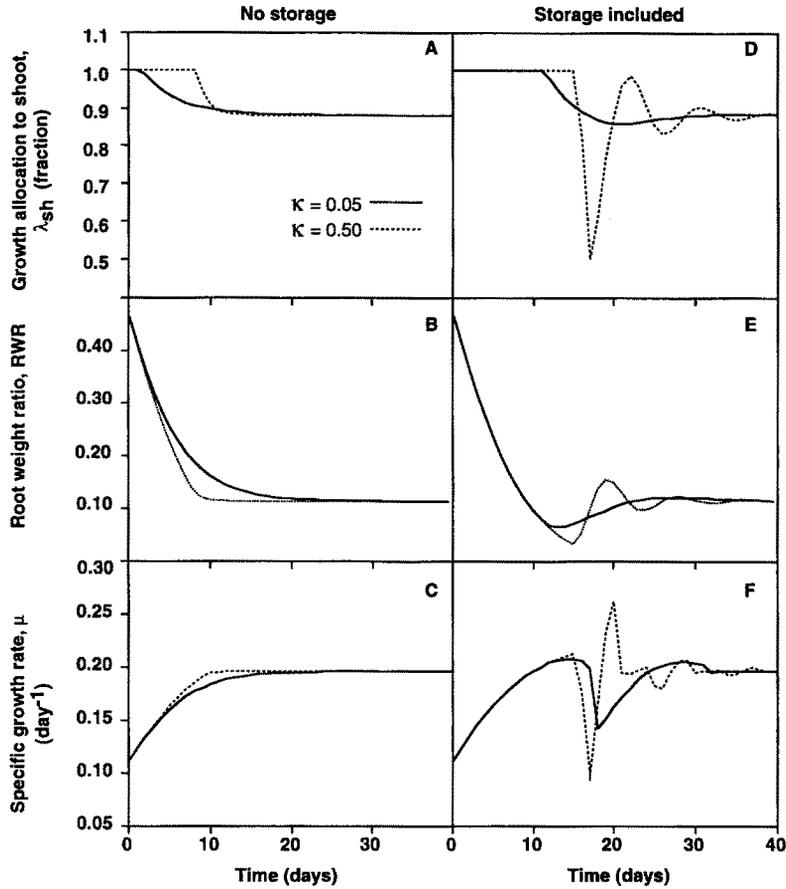


Figure 1. Dynamic solutions from the model with and without storage terms, illustrating the effects of the coordination coefficient κ (Equation 15).

nitrogen supply might result from a sudden decrease in shoot size such as clipping or grazing, or from a sudden change in environmental conditions. For example, a plant which grows in a low nitrogen availability environment, where carbon and nitrogen supply is balanced, is transferred to a high nitrogen availability environment, where carbon supply becomes relatively too small. The plant responds to this imbalance by allocating all growth to the shoot (Figure 1A). The response is rapid with $\kappa = 0.5$ compared to when $\kappa = 0.05$, although the two curves eventually approach the same steady state value, $\lambda_{sh} = 0.882$, specified by Equation (21a). The root weight ratio (Figure 1B), and the specific growth rate of the plant structural dry weight (Figure 1C), approach steady state values of RWR = 0.118, and $\mu = 0.196$, respectively (see Equations 22 and 20), but at different rates depending of the value of parameter κ .

Version with storage terms

Although ignoring carbon and nitrogen storage does not prevent us from obtaining the essential features of growth allocation, it is an over-simplification. Next, we include storage terms for carbon and nitrogen substrates. The differential equations describing the growth of shoot and root are the same as in the model without storage, i.e.:

$$\frac{dW_{sh}}{dt} = \lambda_{sh}G \quad (24a)$$

$$\frac{dW_r}{dt} = (1 - \lambda_{sh})G \quad (24b)$$

but Equations 6 and 9 are now:

$$G = \min\left\{\frac{S_C + W_C}{f_C}, \frac{S_N + W_N}{f_N}\right\} \quad (25)$$

$$I_m = \left\{\frac{S_C + W_C}{f_C} - \frac{S_N + W_N}{f_N}\right\} \quad (26)$$

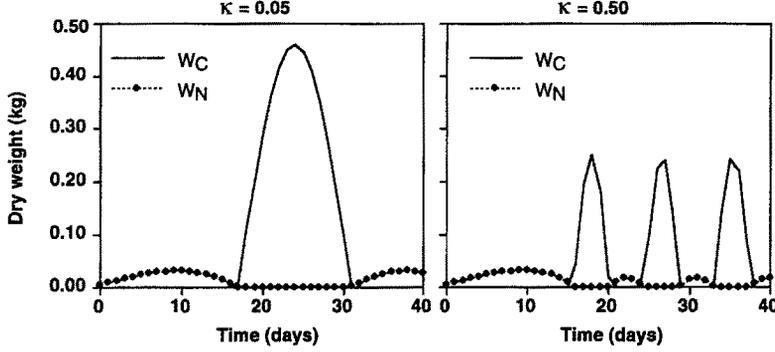


Figure 2. Dynamic solutions to the non-structural carbon and nitrogen (W_C and W_N) with κ set to 0.05 and 0.50.

respectively. The dynamics of W_C and W_N are given by:

$$\frac{dW_C}{dt} = \begin{cases} S_C - f_C G & \text{if } \frac{S_C + W_C}{f_C} > \frac{S_N + W_N}{f_N} \quad (27a) \\ -W_C & \text{if } \frac{S_C + W_C}{f_C} < \frac{S_N + W_N}{f_N} \quad (27b) \\ 0 & \text{if } \frac{S_C + W_C}{f_C} = \frac{S_N + W_N}{f_N} \quad (27c) \end{cases}$$

$$\frac{dW_N}{dt} = \begin{cases} S_N - f_N G & \text{if } \frac{S_C + W_C}{f_C} < \frac{S_N + W_N}{f_N} \quad (28a) \\ -W_N & \text{if } \frac{S_C + W_C}{f_C} > \frac{S_N + W_N}{f_N} \quad (28b) \\ 0 & \text{if } \frac{S_C + W_C}{f_C} = \frac{S_N + W_N}{f_N} \quad (28c) \end{cases}$$

The remaining Equations (14, 15, 16a, 16b, 17, 18a, 18b) describing the coordination remain the same. (Note that in Equations 25–28, W_C and W_N should be written as W_C/T_C and W_N/T_N , respectively, where T_C and T_N are time constants, in order to achieve the correct units. For simplicity, we assume that T_C and T_N equal 1, which implies that all storage is used for growth at the next time step.)

Dynamic solutions

The parameter values and initial conditions are specified by Equations (23a–23f) and $W_C(0) = W_N(0) = 0$. The results are shown in Figures 1D–1F. As before, results are presented for $\kappa = 0.05$ and $\kappa = 0.5$. The incorporation of the carbon and nitrogen storage terms brings about some interesting phenomena (compare to Figures 1A–1C). The steady state values (i.e. $\lambda_{sh} = 0.882$, $RWR = 0.118$, and $\mu = 0.196$) are not altered by the inclusion of the storage terms, but they are reached later in the simulation and show greater variability. These dynamics are more pronounced with $\kappa = 0.5$ than with $\kappa = 0.05$ (Figures 1D–1F). This can be explained as follows. The initial shoot size is relatively small compared with the root size, and initially

the growth is limited by the carbon supply. Nitrogen is in surplus and thus accumulates into the storage until (see Equation 28a):

$$S_N - f_N G = 0 \quad (29a)$$

Since growth is limited by carbon supply and $W_C = 0$ initially, the growth rate, $G = S_C/f_C$, and the above condition becomes:

$$S_C/f_C = S_N/f_N \quad (29b)$$

When there is no storage (i.e. Figures 1A–1C), this represents a threshold from carbon- to nitrogen-limiting conditions. With storage, this threshold signifies that the non-structural nitrogen ceases to accumulate, while the growth is still limited by the carbon supply as long as:

$$S_C/f_C < S_N/f_N + W_N \quad (30a)$$

and the growth allocation will still favour the shoot. When the threshold

$$S_C/f_C > S_N/f_N + W_N \quad (30b)$$

is reached, growth is limited by nitrogen supply. The non-structural nitrogen decreases to zero, and the non-structural carbon starts to accumulate (from zero). The decreasing W_N and increasing W_C around this threshold magnifies the sensitivity of the system to the growth allocation coefficient, λ_{sh} , as shown in Figure 1D.

In Figure 2, we plot W_C and W_N to illustrate switches between carbon- and nitrogen-limiting conditions. With $\kappa = 0.05$ there are only two switches between carbon and nitrogen limitations, and with $\kappa = 0.5$ there are six (Figure 2). Due to Equations (27b) and (28b), there is only 1 day lag between $W_C = 0$ and $W_N = 0$ (Figure 3). In this example, both C and N concentrations approach zero in the steady state (Figure 3).

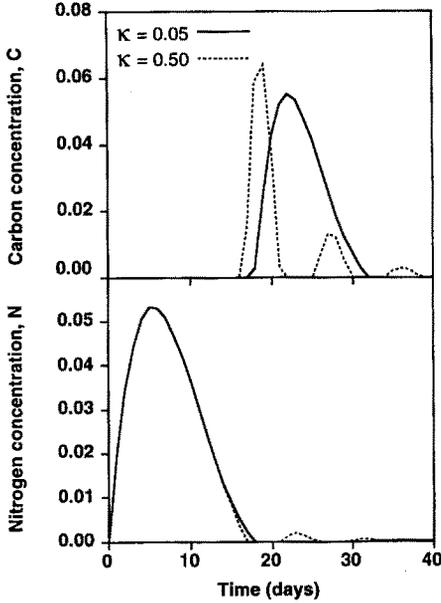


Figure 3. Dynamic solutions to the concentration of non-structural carbon and nitrogen with $\kappa = 0.05$ and 0.50 .

As κ increases from 0.05 to 0.5 , fluctuations in allocation coefficients, root weight ratio, and specific growth rate increase substantially (see Figures 1D, 1E, 1F), results that are rarely observed experimentally. This suggests that the value of κ should be relatively small, i.e., the time constant for adjusting allocation coefficients might be in the order of a few weeks.

An equivalent model based on optimal control theory

In this section we formulate an equivalent model based on optimization theory. Our objective function, J , is:

$$J = W_{sh}(t = T) + W_r(t = T) \quad (31)$$

where T is the length of the growing period. The control variable is $\lambda_{sh}(t)$. We try to find an optimal trajectory of the control variable, $\lambda_{sh}^*(t)$, that maximizes J (the total structural dry weight of the plant at the end of the growing period), under the constraints described by Equations (24, 25, 27a, 27b, 27c and 28a, 28b, 28c). The state variables W_{sh} , W_r , W_C , and W_N , and the control variable λ_{sh} , are constrained by:

$$W_{sh}, W_r, W_C, W_N \geq 0 \quad (32a)$$

$$0 \leq \lambda_{sh} \leq 1 \quad (32b)$$

From the Hamiltonian, H :

$$H = z_{sh}\lambda_{sh}G + z_r(1 - \lambda_{sh})G + z_C\Psi_C + z_N\Psi_N \quad (33)$$

where z_{sh} , z_r , z_C and z_N are Lagrangian multipliers, and Ψ_C and Ψ_N represent the functions on the right-sides of Equations (27a, 27b, 27c) and (28a, 28b, 28c), respectively. Rearranging Equation (33):

$$H = [(z_{sh} - z_r)\lambda_{sh} + z_r]G + z_C\Psi_C + z_N\Psi_N \quad (34)$$

from which we can see that the optimal control trajectory $\lambda_{sh}^*(t)$ will contain a singular arc when $z_{sh} - z_r = 0$. To find the analytical solution, we have to find this singular arc and solve the joining problem of the singular arc with the non-singular ones (see Chen and Wang, 1988). In the case of the system with two state variables and the non-linearity introduced by Equation (26), an analytical solution for the optimal control is extremely difficult to obtain. Thus, we must rely on a numerical method to obtain the optimal control. We tried various algorithms, e.g. the gradient, the modified conjugate gradient, parallel tangent, and others (Aleksiev et al., 1987; Rao, 1984) and eventually selected the simplest gradient method, although it converges rather slowly.

The parameter values and the initial conditions are still specified by Equations (23a–23f). The growth allocation to shoot and root weight ratio are shown in Figure 4, which compares the optimization results to those obtained using coordination. The final structural dry weight of the plant obtained with optimization was 226.9 kg, compared to 210.1 kg and 218.0 kg using coordination with $\kappa = 0.02$ and $\kappa = 1$, respectively.

The dynamic solutions to non-structural carbon and nitrogen obtained from optimization are given in Figure 5. W_C is nearly zero throughout the simulation and W_N approaches zero at the end of the simulation. Since the objective is to maximize the structural dry weight of the plant at the end of the period, it makes sense to convert all of the non-structural carbon and nitrogen into structural biomass. The accumulation of nitrogen early in the simulation is a result of the initial conditions, which represent a large surplus in nitrogen supply. The problem is how to allocate growth between shoot and root to use up the W_N just at the end of the period. In terms of W_C , there is no surplus in the beginning and it is economic to convert it as soon as possible to the structure, since the non-structural carbon makes no contribution to the carbon assimilation.

In Figure 6, we show the structural dry weights of a plant at the end of the growth period obtained from

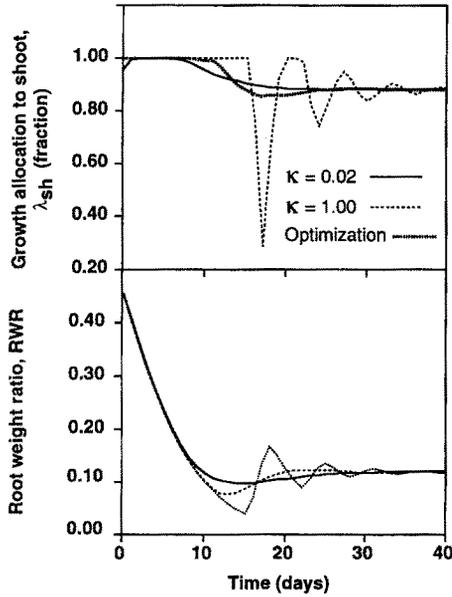


Figure 4. Dynamics of growth allocation coefficient to shoot and root weight ratio based on coordination theory with $\kappa = 0.02$ and $\kappa = 1$ and the model based on optimization theory.

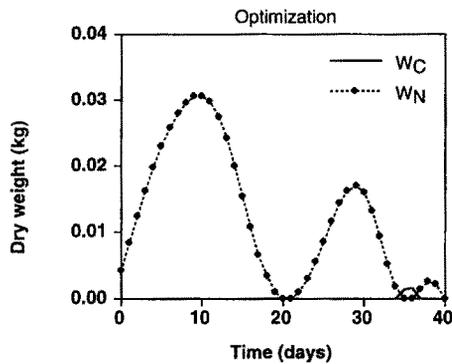


Figure 5. Dynamic solutions to the non-structural carbon and nitrogen (W_C and W_N) based on the optimization model.

coordination using different values of κ ranging from 0.01 to 1 (a hundred-fold change) expressed as a percentage of the results obtained from the optimization model. The curve lies in the range of 90%–95%. For comparison, results are presented where we held the growth allocation coefficient to the shoot, λ_{sh} , constant (from 0.01 to 1) throughout the entire growth period.

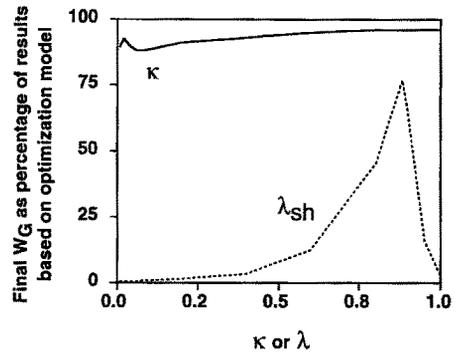


Figure 6. The structural dry weights of plants at the end of the growth period expressed as the percentage of that obtained based on optimization theory. The solid line represents the results from coordination theory with κ ranging from 0.01 to 1, and the dashed line represents the results by setting the growth allocation coefficient λ_{sh} at a constant value, ranging from 0.01 to 1 throughout the whole growth period.

Discussion

Our explanations for interpreting the results of the optimization model are necessarily heuristic since our grasp of mechanism is lost when we must rely on numerical methods. The mechanism can only be obtained with an analytical solution, which is a serious problem because very few optimization problems can be solved analytically. In our example, we can draw the optimal trajectory of the growth allocation coefficient to the shoot, but we can say nothing about how the plant allocates growth between shoot and root in response to what kind of external and internal conditions. If any one of the parameters – or even the length of the growth period – changes, we solve the problem from the beginning. When the environment is not constant, a change of any environmental condition at any time in the growth period will affect the optimal solutions. That is, for obtaining the optimal solutions the environmental conditions during the entire growth period must be explicitly defined beforehand. This not only imposes a constraint on our understanding of the plant response, it also introduces the unrealistic situation where a plant, at the beginning of a growing period, must "know" beforehand the environmental conditions it will experience during the growth period. The latter constraint is necessary since the plant must determine at each time step how much growth should be allocated to the shoot in order to maximize the dry weight of the plant structure at the end of the period. Therefore, while optimization theory is theoretically beautiful and capa-

ble of explaining some results related to plant growth, it has a number of major shortcomings as a tool for modelling allocation.

As an alternative to optimization, we propose the use of coordination theory. We show here that a plant may respond to dynamic environmental conditions by correcting the imbalance between the carbon and nitrogen supplies. We can demonstrate that the results obtained from coordination theory are numerically very similar to those obtained based on optimization theory. We have intentionally kept the allocation model developed here as simple as possible – yet employing the essential features of growth allocation between shoot and root – in order to illustrate the fundamental nature of coordination theory. Although it is very simple, this model provides a basic structure for further development. By relaxing some of the simplifying assumptions, more advanced versions of the model can be easily developed. For instance, assumption (5) is only valid when plants are very small; it permits plants to grow exponentially for an indefinite period. Carbon supply, S_C , depends on many processes, such as photosynthesis, respiration, radiation extinction in a canopy, etc. The simplified carbon supply function (Equation 4) may be replaced by a leaf photosynthesis model with stomatal control, a respiration model that includes both growth and maintenance respiration, and a canopy model that describes light extinction and nitrogen distribution within a canopy. Assumption (4) can be relaxed by assuming that f_N is not a constant, but an additional means of coordination in response to imbalance between carbon and nitrogen supply. Assumption (3) can be relaxed to include equations that describe the relation between maximum growth rate and meristems. Assumption (2) can be relaxed by adding starch as an additional variable and including equations describing the relation between soluble and insoluble carbohydrates. These are examples that will improve model performance and will expand our capability to address problems of allocation that are not very well solved (Chen and Reynolds, unpubl.).

We suggest that coordination theory has potential to be a valuable and practical tool to modelling plant growth allocation and should be further developed. Experimental work is needed to quantify the dynamics of the "coordination" coefficient, κ , which controls how fast a plant can respond to an imbalance.

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References

- Alekseev V M, Tikhomirov V M and Fomin S V 1987 Optimal Control. Consultants Bureau, New York, USA.
- Chapin F S III 1980 The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* 11, 233–260.
- Charles-Edwards D A 1976 Shoot and root activities during steady state plant growth. *Ann. Bot.* 40, 767–772.
- Chen J-L, Reynolds J F, Harley P C and Tenhunen J D 1993 Coordination theory of leaf nitrogen distribution in a canopy. *Oecologia* 93, 63–69.
- Chen J-L and Wang Q 1988 A theoretical analysis of the potential productivity of ryegrass under grazing. *J. Theor. Biol.* 133, 371–383.
- Davidson R L 1969 Effect of root/leaf temperature differentials on root/shoot ratios in some pasture grasses and clover. *Ann. Bot.* 33, 561–569.
- Field C and Mooney H A 1986 The photosynthesis-nitrogen relationship in wild plants. *In* On the Economy of Plant Form and Function. Ed. T G Givnish. pp 25–55. Cambridge Univ. Press, Cambridge, UK.
- Friend A L, Coleman M D and Isebrands J G 1994 Carbon allocation to root and shoot systems of woody plants. *In* Biology of Adventitious Root Formation. Eds. T D Davis and B E Haissig. pp 245–273. Plenum Press, New York, USA.
- Hilbert D W 1990 Optimization of plant root:shoot ratios and internal nitrogen concentration. *Ann. Bot.* 66, 91–99.
- Hilbert D W and Reynolds J F 1991 A model allocating growth among leaf proteins, shoot structure, and root biomass to produce balanced activity. *Ann. Bot.* 68, 417–425.
- Iwasa Y and Roughgarden J 1984 Shoot/root balance of plants: Optimal growth of a system with many vegetative organs. *Theor. Pop. Biol.* 25, 78–105.
- Johnson I R and Thornley J H M 1987 A model of shoot:root partitioning with optimal growth. *Ann. Bot.* 60, 133–142.
- Kastner-Maresch A E and Mooney H A 1994 Modelling optimal plant biomass partitioning. *Ecol. Model.* 75/76, 309–320.
- Luo Y, Field C B and Mooney H A 1994 Predicting responses of photosynthesis and root fraction to elevated $[CO_2]$ (a): Interactions among carbon, nitrogen, and growth: theoretical paper. *Plant Cell Environ.* 17, 1195–1204.
- Makela A 1986 Partitioning coefficients in plant models with turnover. *Ann. Bot.* 57, 291–297.
- McMurtrie R and Wolf L 1983 A model of competition between trees and grass for radiation, water and nutrients. *Ann. Bot.* 52, 449–458.
- Orzack S H and Sober E 1994 How (not) to test an optimality model. *Trends Ecol. Evol.* 9, 265–276.
- Rao S S 1984 Optimization, Theory and Applications. Second edn. Wiley Eastern Limited, New York, USA.
- Reynolds J F and Thornley J H M 1982 A root:shoot partitioning model. *Ann. Bot.* 49, 585–597.

- Reynolds J F, Kemp P R, Acock B, Chen J-L and Moorhead D L 1996 Limitations, uncertainties and challenges in modelling the effects of elevated CO₂ on plants and ecosystems. *In* Carbon Dioxide and Terrestrial Ecosystems. Eds. G Koch and H A Mooney. pp 347–380. Physiological Studies Series, Academic Press, San Diego, USA.
- Schulze E D, Schilling K and Nagarajah S 1983 Carbohydrate partitioning in relation to whole plant production and water use of *Vigna unguiculata* (L.) Walp. *Oecologia* 58, 169–177.
- Thornley J H M 1995 Shoot:root allocation with respect to C, N and P: An investigation and comparison of resistance and teleonomic models. *Ann. Bot.* 75, 391–405.

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