

## Optimization of Tissue Nitrogen and Root–Shoot Allocation

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A model is explored which describes the joint optimization of tissue nitrogen and root–shoot allocation in response to variation in nitrogen availability in the environment. The model plant is composed of root and shoot biomass and tissue nitrogen, and relative growth rate is the parameter maximized.

A 'source' (uptake limited) model of joint tissue nitrogen and root–shoot allocation is reviewed (Hilbert, 1990) that optimally balances the uptake of carbon and nitrogen. Modifications including root respiratory costs and fixed root tissue nitrogen are explored. Then the role of tissue nitrogen in regulating 'sink' strength is combined with the balanced source model, and modified by assuming separate tissue nitrogen involved in source *vs.* sink. Generally, the results indicate that as available nitrogen increases, optimal root allocation declines and tissue nitrogen increases. These results appear to be robust for more complicated versions of the model provided that various internal nitrogen compartments 'compete' for the same nitrogen.

**Key words:** Plant growth, RGR, leaf nitrogen, nitrogen productivity, allocation, partitioning, root–shoot ratio.

### INTRODUCTION

Major lines of research have demonstrated that tissue nitrogen correlates well with photosynthetic rates (Mooney and Gulmon, 1979; Field, 1983; Field and Mooney, 1986; Agren and Ingestad, 1987) and with growth rates (Ingestad and Lund, 1979*a*; Ingestad, 1982; Agren 1985; Ingestad and Agren, 1988; Hirose, 1988; Freijon and Veen, 1990; Lambers *et al.*, 1990*b*; Poorter, 1990; Poorter, Remkes and Lambers, 1990; Garnier, 1991). At the same time, variation in nitrogen supply also affects both tissue nitrogen (Ingestad, 1982; Freijon and Veen, 1990) and root–shoot allocation (Mooney, 1972; Chapin, 1980; Troughton, 1980; Wilson, 1988). While it is generally believed that allocation adjustments are active modifications by the plant, it is less clear whether tissue nitrogen changes should be considered controlled adjustments (but see Mooney and Gulmon, 1979; Field, 1983; Field and Mooney, 1986; Hilbert, 1990; Pons *et al.*, 1990). This paper extends the arguments of Mooney and Gulmon (1979) for predicting optimal leaf nitrogen and the work relating tissue nitrogen and root–shoot allocation by Agren and Ingestad (1987), Ingestad and Agren (1988, 1991), Levin, Mooney and Field (1989), Hilbert (1990) and Hilbert, Larigaudrie and Reynolds (1991).

Following Hilbert (1990), this study explicitly seeks a joint optimization of tissue nitrogen and root–shoot allocation as a function of nitrogen supply in order to maximize growth rate. 'Balance' is often used as a component of the solution (Davidson, 1969; Thornley, 1972; Iwasa and Roughgarden, 1984; Agren and Ingestad, 1987) and refers to the adjustment of uptake to balance growth requirements such that all parts of the plant grow at equal rates (with 'parts' defined in any way desired, for

example, leaves *vs.* roots, or N *vs.* C). In addition, this paper will distinguish between two levels of balance, 'uptake balance' and 'source–sink balance'. 'Uptake balance', or equivalently 'source balance', refers to the adjustment of uptake of more than one resource to precisely satisfy demand. 'Source–sink balance' refers to matching the supply of resources (source) with the capacity for utilization (sink). Tissue nitrogen is potentially relevant to both levels of adjustment.

Balanced uptake and growth could be considered an end in itself, but it has no necessary existence. In simple models, the efficiency of physiological and morphological adjustment implied by balanced growth will often lead to maximal growth (Gleeson and Tilman, 1992). In the case considered here, however, allowing both tissue nitrogen and root–shoot ratio to vary results in a set of balanced growth conditions, only one of which is maximal. Thus, while balance is a part of the solution, it is not sufficient. Moreover, in reality excessive uptake of most resources can be accommodated by a plant through storage, accumulation, respiration, or excretion. For these reasons, the concept of balance is most correctly considered a provisional hypothesis, rather than an inevitable condition.

### Overview

First, I will briefly review a model which uses the concept of carbon balance to describe a link between tissue nitrogen, root–shoot allocation, and growth rate (Agren and Ingestad, 1987). This is followed by a review and extension of a model of uptake balance (source balance) of carbon and nitrogen as a function of tissue nitrogen and root–shoot allocation with growth maximization (Hilbert, 1990). This source balance is then used as a basis for considering the relevance

of source–sink balance in growth optimization. Finally, a model assuming separate source and sink tissue nitrogen is explored.

The goal is to predict the patterns of joint adjustment of tissue nitrogen and root–shoot allocation that will produce growth maximization on a gradient of available nitrogen.

### THE CARBON BALANCE MODEL

Agren and Ingestad (1987, see also Levin *et al.*, 1989; Ingestad and Agren, 1991) developed a model that relates tissue nitrogen and root–shoot allocation by assuming that carbon uptake balances growth. They assume that the rate of fixed carbon gain per unit biomass of shoot is a function of tissue nitrogen concentration ( $n$ , units of mass per mass), and call this function  $P(n)$  in units of biomass gained per biomass of shoot. Relative growth rate ( $G = 1/W[dW/dt]$ ,  $W$  = plant biomass) is also assumed a function of tissue nitrogen, in this case a linear function,  $G = an$ , with  $a$  a constant (the ‘nitrogen productivity’). These two functions are brought together through allocation; shoot takes up carbon via  $P(n)$ , and for both functions to produce the same growth rate,  $an = P(n)(S/W)$ . As a result, allocation (here percent shoot, which can be converted to root–shoot ratio) can be derived from nitrogen concentration as

$$S/W = a[n/P(n)]. \quad (1)$$

Agren and Ingestad explain this result as follows, ‘the balance between shoots and roots in plants can be explained as a result of an equilibrium between an internal sink for carbon substrate...and the capacity to supply carbon substrates set by the amount of shoot’. That is, the growth rate determined by tissue nitrogen (the nitrogen productivity) must be matched by carbon gain from photosynthesis. Ingestad and Agren (1991) modify this by replacing  $P(n)$  with gross assimilation. Levin *et al.* (1989) suggest a modified form of the model in order to improve its internal consistency at low levels of tissue nitrogen. Stated somewhat more generally,

$$G(n) = s(n)[P(n)]. \quad (2)$$

Here  $s(n) = S/W$  which is potentially also a function of  $n$ . This equation describes a relation between three variables that are functions of tissue nitrogen.  $G(n)$  and  $P(n)$  are in the same units (biomass gain per unit biomass, or roughly equivalently, fixed carbohydrate gain per unit carbohydrate) and  $s(n)$  a dimensionless fraction that biologically is limited between 0 and 1.

Because the expression in eqns (1) and (2) is presented in those papers as a necessary relation, little discussion is provided as to its meaning, which produces problems in interpretation. As argued above, it is preferable to view the idea of balance eqns (1) and (2) as a falsifiable hypothesis. An uncertainty in their model is whether the tissue nitrogen is presumed to function primarily in source (carbon acquisition), or both in source and sink. The quote above suggests that nitrogen productivity is a sink concept, that the tissue nitrogen measures the capacity to grow when supplied with resources. In this case,  $G(n)$  and  $P(n)$  are independent functions (sink and source, respectively) and there is no necessary relation or balance between the two. At

the same time, the assumption that the same tissue nitrogen is involved in both uptake and growth becomes questionable. Alternatively, eqns (1) and (2) could refer to source limited growth, which would mean that these equations should be interpreted as a definition of  $G(n)$  or perhaps  $P(n)$  (as argued by Levin *et al.*, 1989). Under this assumption, however, it would be unjustified to choose unrelated functions [e.g. linear for  $G(n)$  and saturating for  $P(n)$ ] to predict  $s(n)$ . In either interpretation, tissue nitrogen is assumed to be given empirically, and therefore cannot be predicted. In order to predict tissue nitrogen, nitrogen availability and uptake need to be modelled explicitly.

### THE CARBON AND NITROGEN BALANCE MODEL

Mooney and Gulmon (1979) assume that the photosynthetic benefit of leaf nitrogen,  $P(n)$ , is a decelerating function of leaf nitrogen, and that the costs of acquisition (total root respiration) are more linear. As a result, they predict that optimal leaf nitrogen increases with increasing nitrogen availability. Hilbert (1990) extended this reasoning to whole plant allocation of carbon and tissue nitrogen for growth rate maximization. Here I review and extend this source (uptake) limited growth model and further explore a model combining nitrogen-dependent sink strength with a source of balanced nitrogen and carbon uptake.

#### Source (uptake) balance

One description of uptake balance was formulated by Davidson (1969) as

$$\frac{\text{shoot biomass} \times \text{shoot activity}}{\text{root biomass} \times \text{root activity}} = \text{constant}$$

where ‘activity’ refers to rate of uptake of limiting resource per unit biomass. ‘Activity’ implicitly incorporates resource availabilities as well as physiology, and could be replaced by an explicit function of availability. This balance of shoot and root uptake can be considered optimal if the constant is defined as the plant demand ratio for limiting shoot and root resources (Rapport, 1971; Tilman, 1982, 1988). Even if that demand changes during growth (Johnson and Thornley, 1987) and/or reproduction, the principle of balance can still be retained so long as uptake corresponds to demand (Gleeson and Tilman, 1992). This formulation has been primarily used to study root–shoot biomass ratios in response to changed resource levels (Wilson, 1988), although Davidson (1969) altered activity in one study through temperature rather than resources.

In this paper, as in Agren and Ingestad (1987) and Hilbert (1990), I assume that fixed carbon ( $C_p$ , plant carbohydrate) gain per unit of shoot biomass ( $S$ ) is a function of tissue nitrogen,  $n$  ( $n = N_p/W$  where  $N_p$  is the nitrogen in the plant), of some form  $P(n)$ . While carbon gain is also a function of many other factors (e.g. light), throughout this discussion all resource variation will result from nitrogen availability, i.e. all other factors will be assumed constant. In addition, I assume explicitly that soil nitrogen is taken up by allocation

to root biomass (Hilbert, 1990). This uptake is a result of root biomass ( $R$ ) and nitrogen availability in the soil ( $N$ ). The uptake per unit root is described by some increasing function of availability,  $U(N)$ , and total uptake is the product of  $U(N)$  and root biomass ( $R$ ). Throughout the rest of this paper, for simplicity this function will be referred to as  $U$  since  $N$  is never an explicit variable, and thus  $U$  is equivalent to the root activity (Davidson, 1969; Hilbert, 1990). Root uptake is assumed independent of tissue nitrogen, which may be roughly the case for diffusion limitation (Chapin, 1980).

Source limited growth rate is a result of the uptake of carbon and nitrogen at rates that satisfy requirements for growth (demand). This plant demand for nitrogen *vs.* carbon can be understood as the ratio of materials required to build new plant, and so is closely approximated by the nitrogen concentration ( $N_p/C_p \cong N_p/W$  when  $N_p$  is small relative to  $C_p$ ). Alternatively,  $n$  can be defined as the  $N_p/C_p$  ratio, avoiding the approximation. Efficient uptake of nitrogen and carbon is defined as uptake that satisfies demand, or 'balanced' uptake. At balanced growth, all components of the plant are increasing at the same rate, which is the same as the overall growth rate. If the plant is made up of only carbon ( $C_p$ ) and nitrogen ( $N_p$ ), the relative growth rates of those two components will be equal at optimal allocation,

$$1/N_p(dN_p/dt) = 1/C_p(dC_p/dt) = G. \quad (3)$$

To solve the model for balanced allocation, uptake equations must be specified. The basic model described is as follows

$$1/C_p(dC_p/dt) = P(n)[S/W] \quad (4)$$

$$1/N_p(dN_p/dt) = [RU]/[Wn]. \quad (5)$$

Note that the carbon gain equation is identical to that used in the carbon balance model interpreted as source limitation, i.e.  $G(n)$  defined by  $P(n)$ . Here, the nitrogen uptake is explicit.

#### Root-shoot adjustment at constant tissue nitrogen

Setting the component relative growth rates equal and solving gives

$$R/S = [nP(n)]/U. \quad (6)$$

For constant  $n$  (which is the demand ratio of nitrogen to fixed carbon in this model), if uptake of nitrogen increases monotonically with the amount available, then as  $N$  increases, optimal root allocation declines as expected. This is the classic model of optimal root-shoot allocation assuming fixed demand (Davidson, 1969; Wilson, 1988). The equation could also be used to predict  $n$  if  $R/S$  were fixed.

#### Joint optimization of tissue nitrogen and allocation

If  $N$  increases in the environment, and the plant can alter  $R/S$ , does the optimal nitrogen concentration change? Intuitively it seems that optimal  $n$  might go up, but it is not obvious why or how much. If it is good to reduce  $n$  in poor soils, why is it not equally good in rich soils? Further,

changes in  $n$  and  $R/S$  have the potential to counteract each other. If the plant increases  $n$  with increasing  $N$ , since this  $n$  increase will increase demand for nitrogen, does optimal root allocation increase or decrease?

The same eqn (6) is still relevant,

$$R/S = [nP(n)]/U,$$

but since both  $R/S$  and  $n$  are now variables, this equation no longer specifies the optimum, but rather the set of pairs of values that will lead to balanced growth. Only one of these will maximize growth. Because both parameters can vary, balanced uptake is no longer a sufficient criterion. To find the maximum relative growth, the component growth equations above ( $1/C_p \cdot dC_p/dt$ ,  $1/N \cdot dN_p/dt$ ) are written in terms of  $R/S$  ( $S/W = [(R/S) + 1]^{-1}$ , and  $R/W = 1 - [S/W]$ ) and then, since at the optimum  $R/S$  is determined by  $n$ ,  $R/S$  is replaced by  $[nP(n)]/U$  for balanced growth, eqn (6). When this is done, both growth rates are equal and

$$G(n) = [P(n)U]/[nP(n) + U]. \quad (7)$$

Using the notation  $f'(n) = df(n)/dn$ , eqn (7) is locally maximized [ $G'(n) = 0$ ] when,

$$U = [P(n)]^2/P'(n)$$

or,  $P(n)/U = P'(n)/P(n) = d[\ln P(n)]/dn \quad (8)$

provided that the second derivative  $G''(n) < 0$  at the maximum, or,

$$P''(n) < 2[P'(n)]^2/P(n). \quad (9)$$

Since the term on the right in eqn (9) is positive, this condition is always satisfied if  $P(n)$  is a decelerating function [ $P''(n) < 0$ ], but  $P(n)$  may also be linear or even accelerating within limits.

If  $P(n)$  is an increasing function, for increasing available  $N$ , optimal  $n(n^*)$  increases. This can be shown by implicit differentiation (I am grateful to A. Sih, S. Foege, and a reviewer for this result) as follows: let

$$z[U, n] = \log[UP'(n)] - \log[P(n)^2].$$

If the condition of eqn (9) applies, it follows that

$$\partial z(U, n)/\partial n < 0.$$

By the implicit function theorem,  $n$  is a function of  $U$  and  $z(U, n) = 0$  can be solved locally for  $n(U)$ . By solving

$$dz[U, n(U)]/dU = \partial z[U, n(U)]/\partial U + (\partial z[U, n(U)]/\partial n) \cdot [dn(U)/dU] = 0$$

for  $dn(U)/dU$ , it follows that the condition of eqn (9) is sufficient for

$$dn(U)/dU > 0.$$

If eqn (9) applies then  $n^*$  will increase with  $U$ , which will increase with  $N$  available by assumption.

What is the cause of this shifting optimum with increasing  $N$  availability? Note that the  $G(n)$  is the product of carbon uptake per unit shoot [ $P(n)$ ] and percent shoot [ $S/W$ ; see eqn (4) for  $1/C_p \cdot dC_p/dt$ ]. The percent shoot at balanced uptake, i.e.  $s(n)$  for a given  $n$  value, is given by  $U/[nP(n) + U]$ . This is an explicit solution for the  $s(n)$  function, and it requires knowledge of  $U$  and  $N$ . By inspection, it can be seen

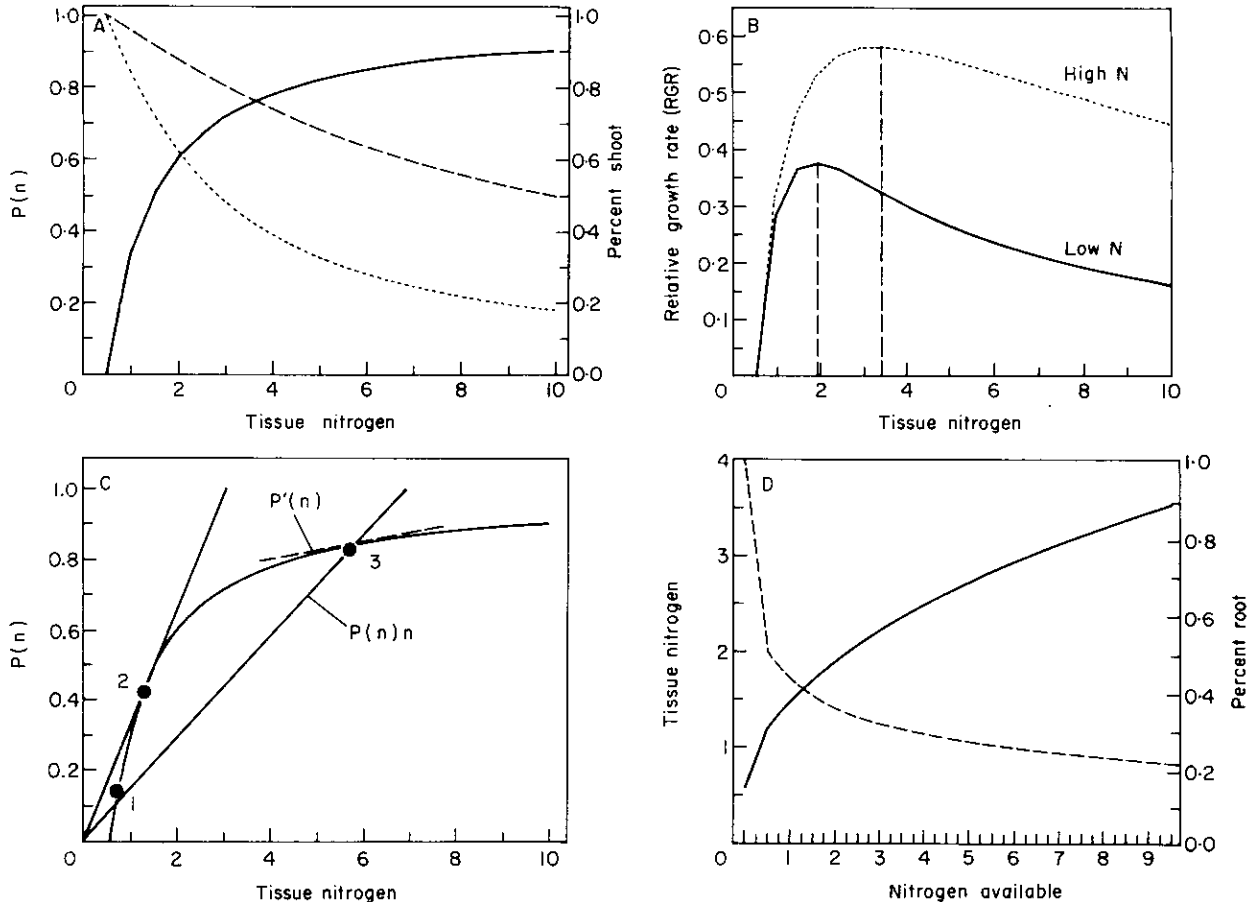


FIG. 1. Results of the basic source model. A, Carbon gain curve,  $P(n)$ , as a function of tissue nitrogen (—) and the percent shoot allocation that balances uptake for two fixed levels of available nitrogen, high (---) and low (·····). An hyperbolic function,  $P(n) = a \cdot (n - n_0) / (K + n - n_0)$ , with  $a = K = 1$  and  $n_0 = 0.5$ .  $U(N) = N$ , low  $N = 2$  and high  $N = 9$ . B, Effects of variation in tissue nitrogen on relative growth rate at two fixed levels of available nitrogen (as in A). Tissue nitrogen that maximizes growth corresponds to the peak in the growth curve. C, Graphical depiction of the optimal root-shoot ratio as a function of the optimal tissue nitrogen ( $n$ ). The  $R/S$  is given by the ratio of the slope of  $P(n)$ ,  $P'(n)$ , and the slope of a line from  $P(n)$  to the origin,  $P(n)/n$  [see text, eqn (11)]. As optimal  $n$  increases,  $R/S$  declines. At point 1  $R/S > 1$ , at point 2  $R/S = 1$ , at point 3  $R/S < 1$ . D, Optimal tissue nitrogen (—) and percent root (---) across a gradient of nitrogen availability (parameters as in A).

that this curve declines as  $n$  increases at a given  $N$  (Fig. 1A). When  $n$  is at a minimum and carbon gain is zero, the plant is all carbon and no root is required (but note that growth is also zero), and as  $n$  increases,  $nP(n)$  becomes positive and increasing and percent shoot declines (eventually to zero). The product of the two curves,  $P(n)$  and  $s(n)$ , may go through a peak, which is the maximum growth rate. As  $U$  increases with increasing  $N$  available, the effect of increasing  $nP(n)$  in the denominator is diminished which reduces the rate of decline of the percent shoot function. The result is that the peak of the curve of the product of the two functions shifts to the right, and so optimal  $n$  increases with increasing available  $N$  (see Fig. 1B). The intuitive concept is essentially the same as Mooney and Gulmon (1979), that as  $N$  becomes scarce, the root costs of nitrogen increase requiring a higher marginal carbon gain per unit nitrogen (Hilbert, 1990). More simply, if increases in  $n$  are beneficial, then more is used when it is cheaper. The cost in the present model of increasing tissue nitrogen is higher root allocation at a given  $N$  availability (Hilbert, 1990), rather than respiration as in Mooney and Gulmon (1979).

The relationship between  $R/S$  and  $n$  at balanced uptake is obtained by substituting eqn (8) into eqn (6) giving

$$R/S = nP'(n)/P(n) = d[\ln P(n)]/d[\ln(n)]. \quad (11)$$

This expression describes allocation on the basis of tissue nitrogen and carbon gain only, as in the carbon balance model, but in this case we know the conditions for  $n^*$  as a function of available nitrogen (particularly the conditions for an increase in  $n^*$  with  $N$ ). This result in eqn (11) can be expressed graphically as in Fig. 1C. In the figure,  $P(n)$  is assumed to be a decelerating function with positive  $x$ -intercept. The  $R/S$  function in eqn (11) can be rewritten  $P'(n)/[P(n)/n]$ , which graphically is the ratio of the slope of the function at  $n^*$  divided by the slope of a line from the origin to  $P(n)$ . In this example as optimal  $n$  increases, the  $R/S$  can be seen to decrease from some number greater than one to some number less than one.

In general, optimal root allocation will decline as  $n^*$  increases (i.e., with increasing  $N$ ) when  $d(R/S)/dn^* < 0$ , which is given by

$$P''(n) < [P'(n)]^2/P(n) - P'(n)/n. \quad (12)$$

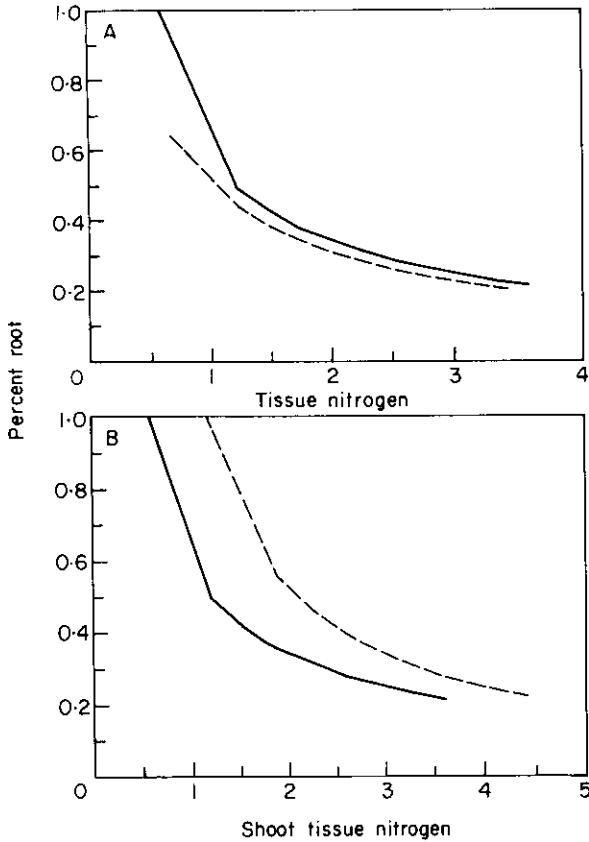


FIG. 2. Modifications of the basic model. A, Comparison of the basic model (—) with the same model with root respiratory costs ( $c = 0.1$ : ----). B, Comparison of the basic model (—) with the same model with fixed root nitrogen ( $n_0 = 0.5$ : ----).

By inspection, it can be seen that this is a more restrictive condition than the condition for  $n$  to increase with  $N$ , eqn (10). As a result, there is some set of functions with  $P''(n) > 0$  that will result in constant or even increasing  $R/S$  with increasing  $n$  (and  $N$ ). In fact, even deceleration of the  $P(n)$  function does not guarantee decreasing  $R/S$ . A useful 'threshold' function is a power function with zero intercept,  $P(n) = an^x$  (which includes linear functions with  $x = 1$ ). The solution is  $R/S = x$ , so that allocation is constant independent of  $n$  even if  $x < 1$  [ $P(n)$  decelerating]. If the power function has a positive  $x$ -intercept [ $n_0$ ;  $P(n) = a(n - n_0)^x$ ], root allocation will decline [ $R/S = nx/(n - n_0)$ , for  $n > n_0$ ]. If  $P(n)$  accelerates faster than a power function [e.g.  $P(n) = e^n$ , or  $P(n) = n^n$ ] then  $R/S$  will actually increase with increasing optimal  $n$  (i.e. with increasing  $N$ ). However, since no data has ever suggested any function more accelerating than linear, this last observation seems of little biological interest. If  $P(n)$  decelerates faster than a power function, e.g., the hyperbola used in these examples  $P(n) = a(n - n_0)/(K + n - n_0)$ , root allocation will decline.

In conclusion, in most plausible cases of this model, increases in nitrogen availability simultaneously favour both increases in tissue nitrogen and decreases in root allocation. Interestingly, in these cases since optimal  $n$  is increasing (and therefore relative nitrogen demand), the

declining trend in  $R/S$  will be reduced relative to the comparable trend with unvarying  $n$ .

*Respiratory costs*

The above model assumes no explicit respiratory costs. Since the  $P(n)$  function could be considered a net carbon gain in excess of shoot respiration, shoot respiration need not be explicitly incorporated. However, root respiration will vary with root allocation, and so could potentially alter the results. Root respiration ( $c$ , rate of fixed carbon lost per unit biomass of root) can be incorporated by modifying the carbon gain equation (the nitrogen uptake is unaltered) as follows:

$$1/C_p \cdot dC_p/dt = P(n) \cdot S/W - c \cdot R/W = [P(n) + c] \cdot s - c \tag{13}$$

and allocation is given by

$$R/S = (U + n \cdot c) / \{n \cdot [P(n) + c] + U\} \tag{14}$$

The effect of respiration is to increase shoot allocation at a given  $n$  since the carbon cost of roots has increased. Growth rate is maximized when

$$P'(n)/P(n) = [P(n) + c] / [U + n \cdot c] \tag{15}$$

Numerical simulation of this model suggests no qualitative differences with the basic model in relation to the form of  $P(n)$ . Increases in root respiration result in lower growth rates and also higher shoot allocation (Fig. 2A). These results are consistent with the interpretation that root respiration increases carbon demand. Interestingly, the effect of changes in  $c$  on optimal  $n$  appears to depend on the level of nitrogen available. When nitrogen is high,  $dn^*/dc < 0$ , but when it is low,  $dn^*/dc > 0$ . The significance of this result is unknown.

*Fixed root tissue nitrogen*

The basic source model assumes that  $n$  doesn't affect root uptake, and yet root  $n$  increases with whole plant  $n$ . This is inefficient, and it would seem that the plant would do better to keep root  $n$  at a minimum. In this section, root  $n$  is assumed fixed at the minimum tissue value ( $n_0$ ). Noting that  $n_s$  refers to shoot  $n$  only, the model then has the form

$$\begin{aligned} 1/C_p \cdot dC_p/dt &= (S/W) \cdot P(n_s) \\ 1/N_p \cdot dN_p/dt &= [R \cdot U] / [(S \cdot n_s) + (R \cdot n_0)] \\ &= [(R/S) \cdot U] / [n_s + (R/S) \cdot n_0] \end{aligned} \tag{16}$$

The plant will be at balanced growth when

$$(R/S)^2 \cdot U + (R/S) \cdot [U - P(n_s) \cdot n_0] - n_s \cdot P(n_s) = 0 \tag{17}$$

The solution to this quadratic expression gives the root allocation that leads to balanced growth. This value can be substituted into either growth rate eqn (16) to solve for the optimal shoot  $n$  [and by eqn (17) for optimal allocation] as done in the basic model.

Numerical simulation suggests that the qualitative behaviour of this model is generally similar to the basic model; increases in  $N$  result in increases in  $n_s^*$  and decreases in  $R/S$

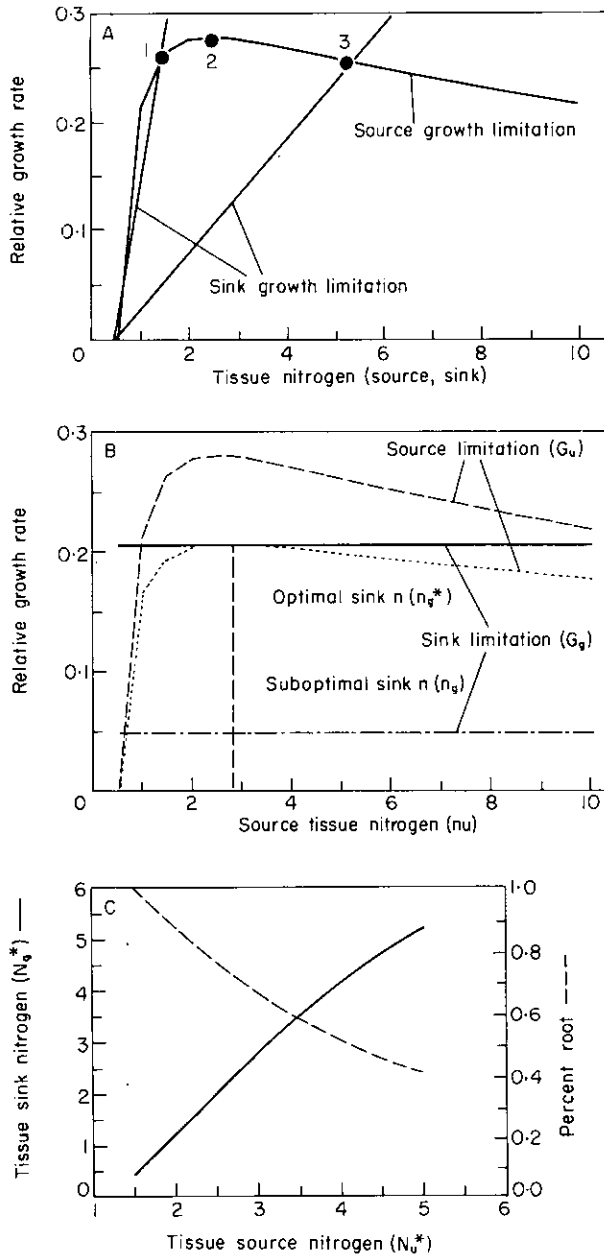


FIG. 3. Source-sink models. A, One tissue nitrogen compartment controlling both source limited growth,  $G_u(n)$ , and sink limited growth,  $G_g(n)$ . Actual growth rate will be the minimum of the two functions, balance the intersection of the two. Two different  $G_g(n)$  functions are illustrated. Point 1 is balanced but not maximized (point 2 is the maximum) for the steeper function, and point 3 is both balanced and maximized for the function of lower slope. B, Separate sink and source nitrogen compartments. Source and sink limited growth rates for two levels of sink nitrogen (optimal and below optimal) across an array of source  $n$  ( $n_u$ ) values. As the suboptimal  $n_g$  is increased sink limited growth increases and source limited growth declines. When the sink limited line intersects with the peak of the source limited growth curve, both  $n_u$  and  $n_g$  are jointly optimized. In B and C,  $P(n)$  is as in Fig. 1 A with  $n_u = n$ , and  $b = 0.1$ . In Fig. 1 B, suboptimal  $n_g = 1$ , and optimal  $n_g = 2.57$ . C, Solution for the joint optimization of  $n_u$ ,  $n_g$ , (—) and percent root (---) across a range of available nitrogen. Note the strong positive correlation between  $n_u$  and  $n_g$ .

(Fig. 2B). A notable exception occurs in the case of a linear or accelerating  $P(n_s)$ ; there is no intermediate optimum  $n_s$ . If  $P(n_s)$  is linear, increases in  $n$  are always favoured (at any  $N$ ) because less carbon is 'wasted' on leaves. That is, a linear gain curve implies that the carbon in the leaf structure plays no role in photosynthesis. If the photosynthesis curve is linear to some threshold (at which the rate is then flat), then the optimal tissue  $n$  would be at the corner. In addition,  $G$  is higher with fixed root  $n$  than the comparable basic model since nitrogen is not wasted on the root.

#### Source-sink balance

The above models assume that plant growth is resource limited, and thus uptake rates and their balance control growth. Alternatively, the plant could potentially be sink limited, one possible interpretation of the concept of 'nitrogen productivity'. In this section, two versions of source-sink adjustment will be explored, including the relevance of 'balance'. In both cases, source (uptake) balance is considered a necessary component of source-sink optimization. First I assume that the same tissue nitrogen controls both source and sink strength, and then I assume that tissue nitrogen must be subdivided into separate source and sink components.

#### Single tissue nitrogen (source and sink)

The carbon balance model (Agren and Ingestad, 1987) asserts that  $G(n) = P(n) \cdot s(n)$ , which can be interpreted to posit a source-sink balance as a function of tissue nitrogen. In this interpretation,  $P(n) \cdot s(n)$  and  $G(n)$  are two different measures of potential growth rate, depending on whether the plant is source or sink limited. These two potential growth curves as a function of tissue  $n$  are  $G_u(n)$  [uptake, or source, limited;  $P(n) \cdot s(n)$ ] and  $G_g(n)$  (sink limited), and source-sink balance is given by the intersection of the two curves. Assuming the plant is either sink or source limited then the realized growth curve as a function of tissue nitrogen,  $G(n)$ , is the minimum of those two functions

$$G(n) = \text{MIN}[G_u(n), G_g(n)].$$

Assuming uptake is balanced, all the results concerning  $G_u(n)$  developed above can be incorporated here. However, whether or not the maximum of  $G(n)$  will be at the intersection (i.e. balance) of  $G_u(n)$  and  $G_g(n)$  depends entirely on the shapes of the functions. For example, if  $G_u(n)$  exceeds  $G_g(n)$  initially and if  $G_u(n)$  crosses  $G_g(n)$ ,  $G_u(n)$  must have a negative slope at that point, or the balance will not be a local maximum (Fig. 3A). If the curves do result in an intermediate optimal  $n$  that balances source and sink as in Fig. 3A, that  $n^*$  appears to increase with increasing  $N$  available, because of the general increase in the source curve,  $G_u(n)$ . However, it is feasible that no intersection of the two functions may occur, with  $G_u(n)$  entirely above  $G_g(n)$  [in which case  $G(n) = G_g(n)$ ] or vice versa. If a single tissue nitrogen compartment is assumed to control both source and sink limitation by separate functions, the problem of optimal tissue nitrogen is entirely dependent on the functional forms of  $G_u$  and  $G_g$ .

## Subdivided tissue nitrogen (source vs. sink)

The above model assumes that the same tissue  $n$  affects both source and sink. Alternatively, it may be more logical to assume that the tissue nitrogen involved in uptake (photosynthesis) is different to the nitrogen that creates the resource sink for growth. In this case there are two separate internal nitrogen compartments that create an internal tradeoff of nitrogen use, and there are two internal levels,  $n_u$  (source) and  $n_g$  (sink), that need to be jointly optimized for growth. A model that incorporates this is

$$\begin{aligned} 1/C_p \cdot dC_p/dt &= P(n_u) \cdot S/W \\ 1/N_p \cdot dN_p/dt &= R \cdot U/[W \cdot n_u + S \cdot n_g] \quad (18) \\ G_g &= f(n_g) = b \cdot (n_g - n_0). \end{aligned}$$

At source balance,  $G_u = 1/C_p \cdot dC_p/dt = 1/N_p \cdot dN_p/dt$ . Note that the total plant nitrogen is the sum of the two types of nitrogen, and that the total measurable shoot  $n$  is  $(n_u + n_g)$  but  $n_g$  does not contribute to carbon uptake. This model can be analysed by assuming either  $n_g$  or  $n_u$  constant and solving for the optimal value of the other. Here I assume first that  $n_g$  is a constant, and study the relation of  $G_u$  and  $n_u$ . Then I examine the pattern of  $G_u$  and  $n_u$  at a range of  $n_g$  in order to understand the joint optimization of  $n_u$  and  $n_g$ .

This model is similar to the model with fixed root  $n$  ( $n_0$ ) above, and similarly resists simple analytical treatment. Note that the case of  $n_g = 0$  is equivalent to the case of  $n_0 = 0$  in that model. In the present model, the solution for allocation that balances uptake with demand is quadratic

$$[s(n_u)]^2 \cdot n_u \cdot P(n_u) + s(n_u) \cdot [n_g \cdot P(n_u) + U] - U = 0 \quad (19)$$

where  $s(n_u) = S/W$ . This can be solved as the positive root of the quadratic formula and substituted into  $G_u = P(n_u) \cdot s(n_u)$ . Based on numerical study of this model, as in the fixed root nitrogen model it is reasonable to expect a  $G_u$  without a hump (higher values of  $n_u$  yield higher  $G_u$ ) if  $P(n_u)$  is linear or accelerating. Any deceleration in  $P(n_u)$  results in a humped  $G_u$ . As  $n_g$  is increased from a low value, the overall  $G_u$  curve declines as root increases to supply the nitrogen, and the value of  $G_g$  increases as sink strength increases. As a result,  $G$  (the minimum of the two functions) reaches a maximum when  $G_g = G_u$ . This is illustrated in Fig. 3B for an optimal and suboptimal  $n_g$ .

Thus, the tradeoff between the two types of tissue  $n$  leads to an intermediate maximum for both  $n_g$  and  $n_u$  that balances source and sink. Analysis of this model is entirely numerical, but the result seems to be robust. Optimal  $n_u$  and  $n_g$  both increase, and root allocation decreases, with increasing  $N$  available,  $U$ , illustrated in Fig. 3C.

In conclusion, the effect of separating tissue nitrogen into source and sink components can result in an optimum that balances source and sink, but this is only certain if the two forms of nitrogen are exclusive, i.e. the correlation between the two processes is negative (Gleeson and Tilman, 1992). If so, then increases in source nitrogen would be inefficient if the plant is sink limited and vice versa, and optimal subdivision of nitrogen would be that which balances source and sink leading to a positive correlation between the two components.

## DISCUSSION

The most consistent result in these models is that as nitrogen becomes more available in the environment, increases in tissue nitrogen and decreases in root allocation relative to shoot result in maximal growth rates, as predicted by Hilbert (1990). This is consistent with the separate predictions that if increased use of a resource has positive effects on fitness, as the costs for obtaining a resource (nitrogen) go down: (a) allocation directed toward obtaining that resource (root) will decline relative to allocation to obtaining other resources (Davidson, 1969; Thornley, 1972); and (b) the use of that resource will go up (Mooney and Gulmon, 1979). Because of the increase in nitrogen demand with increasing tissue nitrogen, these two predictions have the potential to cancel one another, but the models presented here generally do not show this. In the extreme, increases in tissue nitrogen with increased nitrogen availability may result in no change in optimal root allocation, but increases in root allocation seem very unlikely. No cases were found where adjustment was achieved by only root allocation if tissue nitrogen was allowed to vary. Shifts in the predicted directions are consistent with the empirical results of Ingestad and Lund (1979a, b) illustrated in Fig. 4A.

The present results suggest that prediction of real plant behaviour will need to consider the degree to which internal nitrogen compartments must be separated. In the basic model, internal nitrogen is considered to consist of one compartment present in all tissues which is photosynthetic.

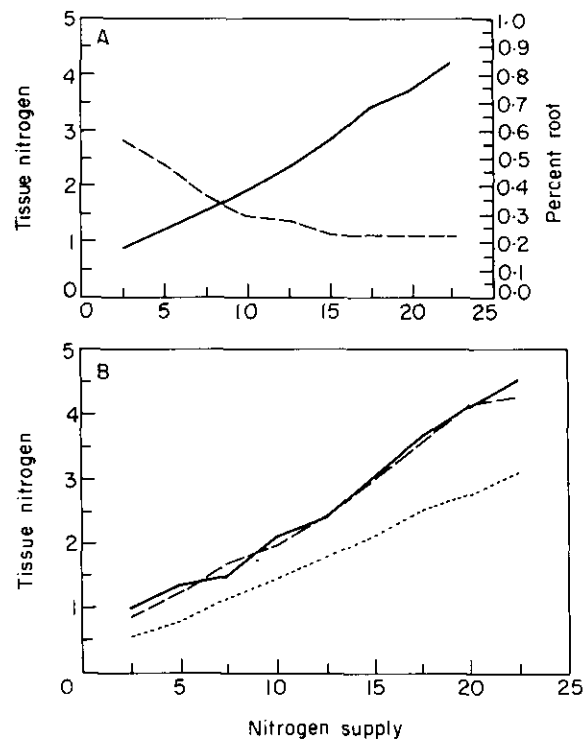


FIG. 4. Data from Ingestad and Lund (1979a, b) for birch seedlings grown at a range of nitrogen supply rates. A, Overall tissue nitrogen (—) and percent root (---) with increased  $N$  supply. B, Trends in tissue nitrogen with increasing  $N$  supply in leaves (—), stems (····), and roots (—) separately.

cally active in the shoot. If root tissue nitrogen can be adjusted separately from shoot, then root tissue nitrogen remains fixed at the structural minimum and only shoot nitrogen responds to N availability. If the physiologically active nitrogen also controls assimilation (sink) then optimal tissue nitrogen is determined by whether the plant is source or sink limited. If a separate compartment of physiologically active nitrogen for assimilation (sink) is included, then this nitrogen is adjusted so that source and sink are balanced. As a result, source and sink nitrogen are positively correlated and both increase with available nitrogen. In general (i.e. if this conclusion persists with further compartmentalization of nitrogen), this may be a useful result, for it suggests that using a single overall plant nitrogen may be a reasonable simplification. Photosynthetic nitrogen then is only one compartment of many in the plant (in both root and shoot) that will increase with increased supply of nitrogen and the resulting increase in carbon uptake, since all compartments will be positively correlated to balance transfer rates. As a result, the simplifications of the initial model (Hilbert, 1990) may be approximately valid. Tissue nitrogen increases in all plant parts may be the norm, as illustrated here by the data in Ingestad and Lund (1979*a, b*) in Fig. 4B.

Many possible aspects of this problem have not been considered explicitly here, including stem cost, nitrogen involvement in nutrient uptake, uptake dependent respiratory costs, more complex interaction of source and sink strength, other resources, etc. Root nitrogen involvement in root uptake is an alternative explanation of whole plant increases in tissue nitrogen—even if sink strength is never limiting. Another possible compartment for nitrogen is an internal reservoir which can increase or decrease with uptake as in the models of Thornley and collaborators (Thornley, 1972; Reynolds and Thornley, 1982; Johnson and Thornley, 1987). Because this nitrogen compartment is very different than those used in this paper, no direct comparison can be made.

These optimization models are 'teleonomic', or goal-directed, in the sense of Thornley and Johnson (1990). The basic model, when driven by a particular root-shoot allocation, will attain balanced growth (Gleeson, unpubl. res.) and could also be thought of as 'mechanistic' in their sense. However, it will balance for any allocation pattern, and thus will never attain the optimal allocation (except by chance) unless competition between allocation patterns is included. Ingestad and Agren (1991) object to the use of the optimization approach. As argued above, the balance approach is most logically considered part of an optimization approach. In addition, their objection that  $d[s(n)]/dn$  must be negative in theory but is positive in practice misunderstands  $ds(n)/dn$ . The negativity of  $d[s(n)]/dn$  refers to the increase in root as tissue  $n$  increases that is required at a fixed nitrogen available in order to maintain balanced uptake. The empirical result that  $s(n)$  and  $n$  are positively correlated is a result of variation in  $n$  in response to a gradient of increasing  $N$ , which as predicted above leads to a positive correlation of  $s(n^*)$  and  $n^*$ . Simply, in theory for a given  $N$ ,  $d[s(n)]/dn < 0$ , but across a gradient of  $N$ ,  $d[s(n^*)]/dn^* > 0$  (usually). Compare Figs 1A and 2A (and see Hilbert, 1990).

The goal of this sort of modelling is to find the simplest model of a plant that can still explain a large amount of observed variation. Simplicity is sought in order to isolate crucial parameters and to maximize the likelihood of solving problems at and above the level of the individual plant. Carbon allocation models by themselves appear to be insufficient (Lambers *et al.*, 1990*b*; Garnier, 1991), but perhaps incorporation of physiology in relatively simple ways such as described in Hilbert (1990; Hilbert *et al.*, 1991) and here will provide improved predictive hypotheses.

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