

Root : Shoot Ratios, Optimization and Nitrogen Productivity

GÖRAN I. ÅGREN* and OSKAR FRANKLIN

Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences, PO Box 7072,
SE-750 07 Uppsala, Sweden

Received: 25 April 2003 Returned for revision: 21 July 2003 Accepted: 3 September 2003 Published electronically: 17 October 2003

Plants respond to nitrogen availability by changing their root : shoot ratios. One hypothesis used to explain this allocation is that plants optimize their behaviour by maximizing their relative growth rate. The consequences of this hypothesis were investigated by formulating two models for root : shoot allocation, with and without explicit inclusion of maintenance respiration. The models also took into account that relative growth rate is a linear function of plant nitrogen concentration. The model without respiration gave qualitatively reasonable results when predictions were compared with observed results from growth experiments with birch and tomato. The explicit inclusion of maintenance respiration improved considerably the agreement between prediction and observation, and for birch was within the experimental accuracy. Further improvements will require additional details in the description of respiratory processes and the nitrogen uptake function. Plants growing under extreme nutrient stress may also optimize their behaviour with respect to other variables in addition to relative growth rate.

© 2003 Annals of Botany Company

Key words: Birch, *Betula pendula*, tomato, *Lycopersicon esculentum*, respiration, nitrogen.

INTRODUCTION

It is a standard assumption in plant ecology that plants respond to their environment in such a way as to optimize their resource use (e.g. Bloom *et al.*, 1985). One expression of such an optimization is the allocation between shoots and roots in response to nutrient availability. In general, when nutrient availability increases, plants allocate relatively less to their roots, which is consistent with a resource optimization hypothesis as increasing nutrient availability means that less effort is required to acquire this resource. Exceptions to this rule, when K, Mg or Mn are limiting (Ericsson, 1995), can be recast into the resource optimization hypothesis. Deficiencies of these elements lead also to a shortage of carbohydrates, which signifies to the plant that the allocation to light acquisition is sub-optimal.

Several models have been developed to explain the mechanisms behind the root : shoot allocation (see reviews by Wilson, 1988; Ågren and Wikström, 1993; Cannell and Dewar, 1994). All models are based on a carbon balance, but some additional constraints are required. Two general routes can then be followed. First, some plant property is optimized, which, in practise, always turns out to be the relative growth rate (Johnson and Thornley, 1987; Hilbert, 1990; Thornley, 1995). Secondly, a sink strength depending either on nitrogen concentration (Ågren and Ingestad, 1987; Ingestad and Ågren, 1991) or on carbon and nitrogen substrate concentrations (Thornley, 1972, 1995, 1998) is added. The problem with the latter group of models is that they require phenomenological formulation of plant properties (nitrogen productivity, substrate utilization rates or transport rates) and, therefore, only show consistency

between plant properties without explaining them in terms of some underlying principle. Formulations derived by maximizing the relative growth rate give, in general, qualitatively satisfactory results but quantitative tests seem to be lacking. One reason for this is the problem of independently estimating all the necessary parameters required for testing the predictions; in particular the relationship between net assimilation rate and plant nitrogen concentration has to be specified.

In this paper, a relationship between the shoot fraction (f_s) and plant nitrogen concentration (c_N) will be derived by maximizing the relative growth rate. The problem of the arbitrariness in the relationship between assimilation rate and plant nitrogen concentration will be avoided. Instead the strong empirical, linear relationship between relative growth rate and plant nitrogen concentration (Ågren and Wikström, 1993) will be used to derive the assimilation rate as a function of plant nitrogen concentration. The final relationship, $f_s(c_N)$, will then have only one or two free parameters that will be adjusted when comparing predictions with experimental results.

MATERIALS AND METHODS

For simplicity, a plant consisting of only a shoot biomass and a root biomass will be considered. The total dry mass of the plant is W , its nitrogen content N , the shoot fraction f_s , the carbon assimilation rate per unit shoot mass A , and the uptake rate of nitrogen per unit root mass U . Due to the constancy of carbon concentration in plant biomass, dry weight increase equals carbon assimilation \times a constant factor included in A . It is further assumed that respiratory losses are proportional to plant nitrogen content (Ryan *et al.*,

* For correspondence. E-mail Goran.Agren@eom.slu.se

1996; Cannell and Thornley, 2000). The growth rate and the nitrogen uptake rate are then

$$\frac{dW}{dt} = Af_S W - rN \quad (1)$$

$$\frac{dN}{dt} = U(1 - f_S)W \quad (2)$$

where r is the respiration rate per unit of nitrogen. A list of symbols is given in Table 1.

For plants with balanced growth (constant exponential rates), the relative growth rate $R_W = (dW/dt)/W$ and the relative nitrogen uptake rate $R_N = (dN/dt)/N$ must be equal. Applying this to eqns (1) and (2) gives

$$f_S = \frac{rc_N^2 + U}{Ac_N + U} \quad (3)$$

where $c_N = N/W$ is the whole-plant nitrogen concentration. Equation (3), for $r = 0$, is identical to the expression derived by Hilbert (1990). We can use eqns (1) and (3) to express the relative growth rate in terms of assimilation rate, uptake rate and plant nitrogen concentration

$$R_W = U \frac{A - rc_N}{U + Ac_N} \quad (4)$$

However, the assimilation rate is also a function of the plant nitrogen concentration (e.g. Field and Mooney, 1983). On the other hand, the uptake rate of nitrogen can be expected to be more dependent on the environmental supply of nitrogen than on plant properties and it will, therefore, be assumed that it is independent of the plant nitrogen concentration. For a plant that optimizes its performance by maximizing its relative growth rate through adjustment of its nitrogen concentration, and thus also its root : shoot ratio, the result is

$$\frac{dR_W}{dc_N} = \frac{U}{(U + Ac_N)^2} \left[U \frac{dA}{dc_N} - rU - A^2 + rc_N^2 \frac{dA}{dc_N} \right] \quad (5)$$

or at optimum

$$U = \frac{A^2 - rc_N^2 \frac{dA}{dc_N}}{\frac{dA}{dc_N} - r} \quad (6)$$

which gives

$$R_{Wopt} = \frac{A^2 - rc_N^2 \frac{dA}{dc_N}}{A + \frac{dA}{dc_N} c_N} \quad (7)$$

To proceed, some relationship between A and c_N could be assumed. However, such assignments would be rather arbitrary (e.g. Ågren and Ingestad, 1987). Instead A will be calculated by utilizing the strict relationship between relative growth rate and nitrogen concentration that exists through the nitrogen productivity, P_N (e.g. Ågren, 1985, 1996).

$$R_W = P_N(c_N - c_{Nmin}) \quad (8)$$

where c_{Nmin} is the minimum nitrogen concentration in the plant required for growth. Equation (8) is only valid for nitrogen-limited plants, but this is the only domain of interest in this paper.

Combining eqns (7) and (8) gives

$$A^2 - rc_N^2 \frac{dA}{dc_N} = P_N(c_N - c_{Nmin}) \left(A + \frac{dA}{dc_N} c_N \right) \quad (9)$$

Equation (9) can be solved exactly for two special cases: (A) $r = 0$ and (B) $c_{Nmin} = 0$. In case (A), the differential equation in eqn (9) can be solved with the substitution $y = Ac_N$ to give

$$A = \frac{P_N(c_N/c_A)c_A}{((c_N/c_A)^2) - \frac{c_N/c_A}{c_{Nmin}/c_A} - \left(\frac{c_N/c_A}{c_{Nmin}/c_A} \right) \ln \left(1 - \frac{c_{Nmin}/c_A}{c_N/c_A} \right)} \quad (10A)$$

where $c_A > 0$ is an integration constant. The integration constant c_A , which also has absorbed a P_N , plays the role of a scale factor for the concentration. It should be noted that the integration constant depends on external factors such as light and temperature and will change when factors that alter P_N change. Finally

$$f_S = \frac{P_N(c_N - c_{Nmin})}{A} = \left(1 - \frac{c_{Nmin}/c_A}{c_N/c_A} \right) \left[\left(\frac{c_N}{c_A} \right)^2 - \frac{c_N/c_A}{c_{Nmin}/c_A} - \left(\frac{c_N/c_A}{c_{Nmin}/c_A} \right)^2 \ln \left(1 - \frac{c_{Nmin}/c_A}{c_N/c_A} \right) \right] \quad (11A)$$

In the second expression for f_S , the explicit dependence on P_N has disappeared and all effects of other variables, apart from plant nitrogen concentration, are included in the integration constant c_A . When $c_{Nmin}/c_A < 0.1$, eqn (11A) can be simplified with an error of less than 10 % for most values of c_N to

$$f_S \approx \frac{1}{2} + \left(\frac{c_N}{c_A} \right)^2 \quad (12A)$$

In case (B), the substitution $A = yc_N$ leads to the solution

$$A = \frac{(2P_N + r)c_N}{1 + \left(\frac{c_N}{c_B} \right)^{\frac{2P_N+r}{P_N+r}}} = \frac{(2P_N + r)(c_N/c_B)c_B}{1 + \left(\frac{c_N}{c_B} \right)^{\frac{2P_N+r}{P_N+r}}} \quad (10B)$$

where c_B is another integration constant, which also, in this case: enters a scale factor, and

$$f_S = \frac{P_N + r}{2P_N + r} \left[1 + \left(\frac{c_N}{c_B} \right)^{\frac{2P_N+r}{P_N+r}} \right] \quad (11B)$$

which for $r/P_N < 1/4$ can be approximated with an error of less than 10 % with

$$f_s \approx \frac{1}{2} \left[1 + \left(\frac{c_N}{c_B} \right)^2 \right] \quad (12B)$$

In the limits of $r = 0$ and $c_{Nmin} = 0$, cases (A) and (B) are the same, except that the integration constants are slightly different.

The net assimilation rate per unit shoot mass (NAR_W) is related to A through

$$A = NAR_W + r \frac{c_N}{f_s} \quad (13)$$

Examples of net assimilation rates and shoot fractions as functions of plant nitrogen concentrations are given in Fig. 1. These figures show that the qualitative behaviour of the results agrees with general knowledge. The lack of an effect of increasing light on allocation for case (A) and the increasing allocation to shoots with increasing P_N in case (B) in Fig. 1 have to be interpreted with caution because the same value for the integration constants has been used for all curves.

TABLE 1. List of symbols and units

A	Dry weight assimilation rate per unit shoot biomass, d^{-1}
c_A, c_B	Integration constants, $g\ N\ (g\ d.\ wt)^{-1}$
c_N	Plant nitrogen concentration (N/W), $g\ N\ (g\ d.\ wt)^{-1}$
c_{Nmin}	Minimum plant nitrogen concentration for growth, $g\ N\ (g\ d.\ wt)^{-1}$
f_s	Shoot fraction, dimensionless
N	Plant nitrogen content, $g\ N$
NAR_W	Net assimilation rate per unit shoot mass, d^{-1}
P_N	Nitrogen productivity, $g\ d.\ wt\ (g\ N)^{-1}\ d^{-1}$
r	Maintenance respiration per unit plant nitrogen, $g\ d.\ wt\ (g\ N)^{-1}\ d^{-1}$
R_N	Relative rate of nitrogen uptake, d^{-1}
R_W	Relative growth rate, d^{-1}
t	Time, d
U	Uptake rate of nitrogen per unit root biomass, $g\ N\ (g\ d.\ wt)^{-1}\ d^{-1}$
W	Plant biomass, $g\ d.\ wt$

COMPARISON WITH DATA

The prediction of allocation was tested against growth data for tomato (*Lycopersicon esculentum*) (Ingestad *et al.*, 1994a; de Groot *et al.*, 2002) and birch (*Betula pendula*) (Ingestad *et al.*, 1994b). These studies were performed at different light intensities and using different relative addition rates of nitrogen, but otherwise under constant environmental conditions. This led to a time series of steady-state growth. For any given light intensity and relative addition rate of nitrogen, the plant nitrogen concentration and shoot fraction remained stable during the whole experimental period, in spite of increases in plant size by more than a factor of 20. From the experiments of Ingestad *et al.* (1994a, b) we used P_N and c_{Nmin} calculated by Ågren and Bosatta (1998) and estimated c_A and c_B such that f_s agreed with the experimental values when $c_N = 0.03$

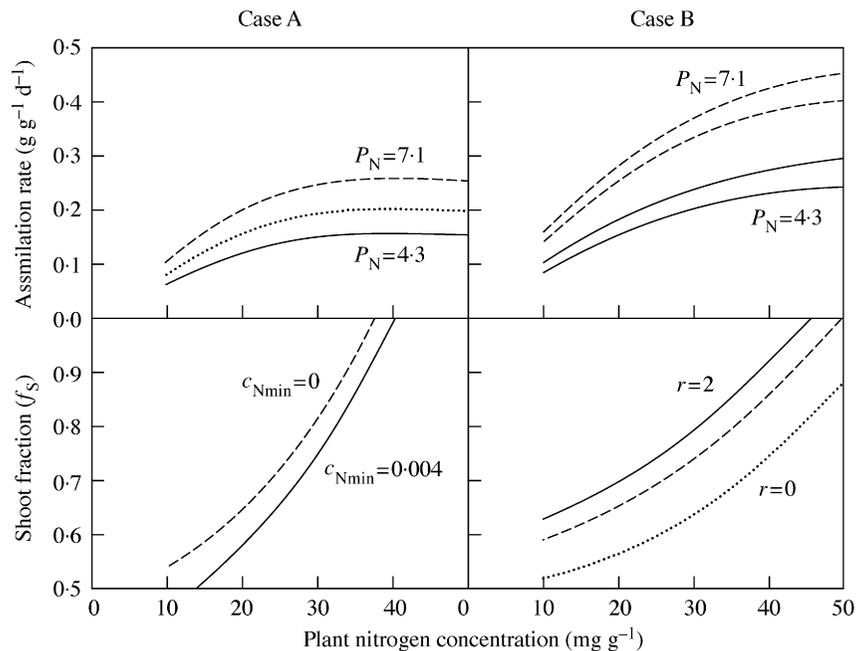


FIG. 1. Assimilation rate (A) and shoot fraction (f_s) as functions of plant nitrogen concentrations (c_N) for different values of nitrogen productivity (P_N). Case A: $c_A = 0.0534\ g\ N\ (g\ d.\ wt)^{-1}$. For A, $c_{Nmin} = 0.004\ g\ N\ (g\ d.\ wt)^{-1}$ and $P_N = 4.3, 5.5$ and $7.1\ g\ d.\ wt\ (g\ N)^{-1}\ d^{-1}$ corresponding to quantum fluxes of 5, 14 and $30\ mol\ m^{-2}\ d^{-1}$, respectively, in the experiments with birch by Ingestad *et al.* (1994b). For f_s , $c_{Nmin} = 0$ and $0.004\ g\ N\ (g\ d.\ wt)^{-1}$. Case B: $c_B = 0.0511\ g\ N\ (g\ d.\ wt)^{-1}$, $P_N = 4.3$ and $7.1\ g\ d.\ wt\ (g\ N)^{-1}\ d^{-1}$, and $r = 0$ and 2 . The lower curve for each P_N for A correspond to $r = 0$. The curves for f_s with $r = 0$ coincide for the two values of P_N (dotted line).

TABLE 2. Plant parameters for comparison with experiments

	P_N g d. wt (gN) ⁻¹ d ⁻¹	c_{Nmin} gN (g d. wt) ⁻¹	c_A gN (g d. wt) ⁻¹	c_B gN (g d. wt) ⁻¹	r g d. wt (gN) ⁻¹ d ⁻¹
Birch ¹	6.3	0.004	0.0534	0.0575	2
Tomato ²	11.0	0.015	0.0698	0.0746	2
Tomato ³	7.1	0.00817	0.119	0.065	2
Tomato ⁴	12.51	0.00738	0.069	0.043	2

Data from ¹ Ingestad *et al.* (1994b); ² Ingestad *et al.* (1994a); ³ de Groot *et al.* (2002) at low light; ⁴ de Groot *et al.* (2002) at high light.

for birch and 0.05 g g⁻¹ for tomato, respectively (Table 2). Ideally, c_A and c_B should have been estimated from measurements of the $A - c_N$ curve, but such data were not available. In all cases a parameter value of $r = 2$ g d. wt (gN)⁻¹ d⁻¹ was chosen, which was somewhat higher than Cannell and Thornley (2000) estimated from the work of Ryan *et al.* (1996).

RESULTS

The comparison between experimental results and predictions is shown in Fig. 2. It is clear that case (A) fails to give a satisfactory agreement for both species. The agreement between experimental data from Ingestad *et al.* (1994a, b) and predictions using eqn (11B) is good for birch, while the observed root : shoot ratio is less flexible than predicted for tomato. The importance of the intercept c_{Nmin} is also much smaller for birch than for tomato. Another observation is that at the lowest nitrogen concentrations, corresponding to low relative growth rates (less than 0.05 d⁻¹ for birch and 0.10 d⁻¹ for tomato), the experimental root : shoot ratios respond differently to plant nitrogen concentration than at higher nitrogen concentrations. Moreover, birch and tomato behave differently. Birch shows a rapid decrease in the shoot fraction whereas tomato, contrary to expectations, shows an increase in the shoot fraction. With birch, there is also a region of high nitrogen concentration with no response in root : shoot ratio. A part of this region is possibly involved in the uptake and storage of excess nitrogen not required for immediate physiological use. The increasing allocation to shoots in tomato at the lowest plant nitrogen concentrations is, at least partly, associated with an increased allocation to stem growth at the expense of leaves.

From the experiment of de Groot *et al.* (2002) P_N and c_{Nmin} were estimated from observations on relative growth rate and plant nitrogen concentration. The integration constants (c_A and c_B) have then been adjusted to meet the observed values of NAR_W (Table 2). The comparisons between experimental results and predictions are shown in Fig. 3. The fit to the observed assimilation rate is quite good for case (A) but for case (B) there is a tendency towards too high values at low plant nitrogen concentrations. The predictions for this experiment with tomato also show too high a flexibility in allocation, except for case B at low light.

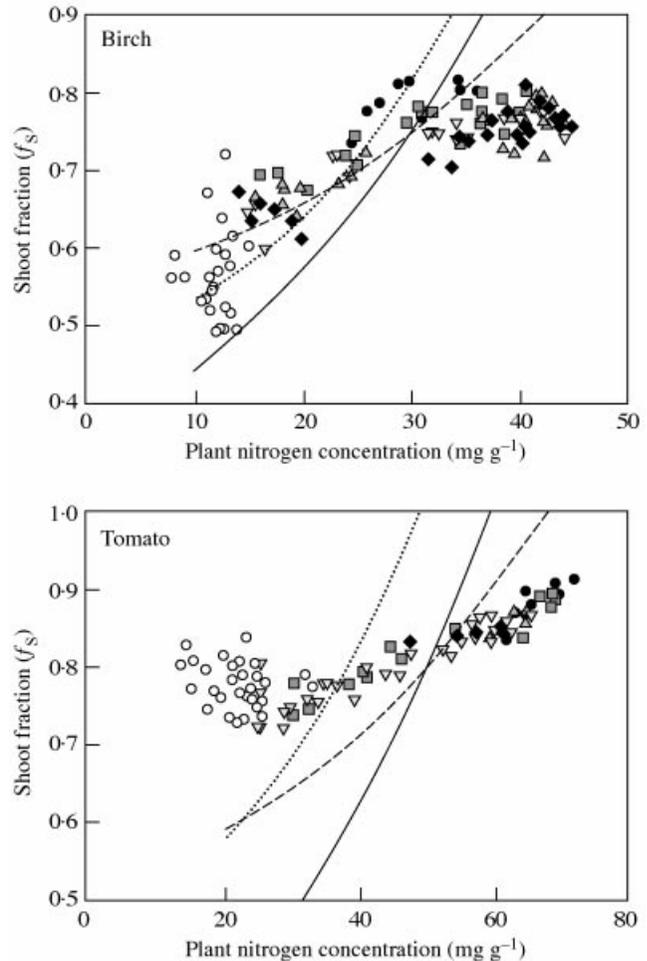


FIG. 2. Shoot fraction as a function of plant nitrogen concentration. Solid line, $c_{Nmin} > 0$, eqn (11A); dotted line, $c_{Nmin} = 0$, eqn (12A); broken line: $r = 2$, eqn (11B). Other parameters as in Table 1. Symbols are data from experiments with birch (Ingestad *et al.*, 1994b) and tomato (Ingestad *et al.*, 1994a). Open symbols represent experiments with low relative addition rates of nitrogen. Solid symbols (circles, squares, triangles, inverted triangles and diamonds) represent faster growing plants at five different light intensities (5, 11, 22, 30 and 39 mol m⁻² d⁻¹) for birch and (3, 6, 10, 18 and 23 mol m⁻² d⁻¹) for tomato.

DISCUSSION

The behaviour of the allocation response to nitrogen availability is in good agreement with general observations

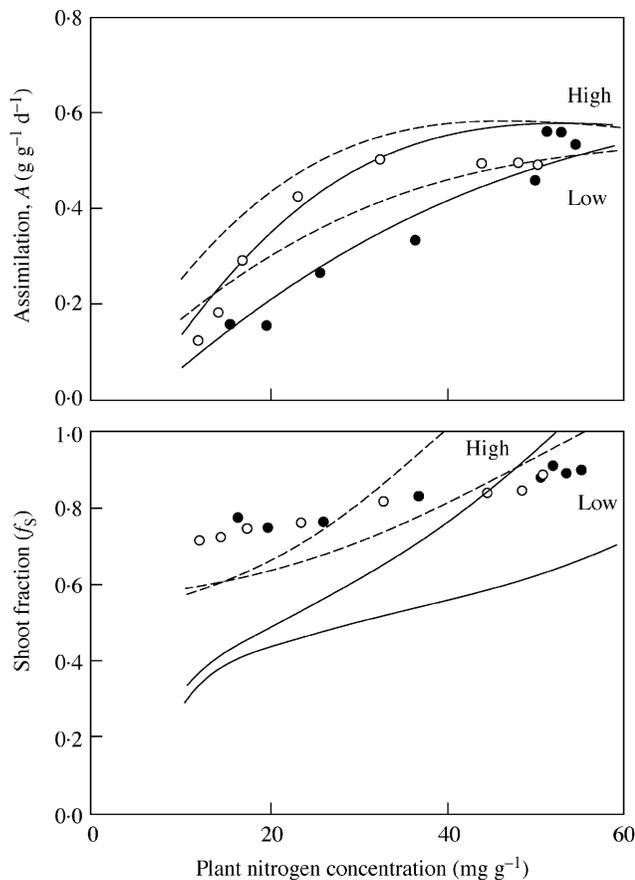


FIG. 3. Simulated and measured assimilation (A) and shoot fraction (f_s). Solid circles, low light; open circles, high light; solid lines, case (A); broken lines, case (B). Data from de Groot *et al.* (2002).

for birch. For tomato, the general behaviour is as expected but not entirely satisfactory quantitatively. It would be easy to adjust the assimilation curve (Fig. 3) to the experimental data by replacing c with $c - c_{Nmin}$ in eqn (10B). This would still leave the relative growth rate as an almost perfectly linear function of plant nitrogen concentration. Such a substitution is, however, contrary to the spirit of this paper as it is pure curve fitting. Moreover, it does not improve the behaviour of f_s .

There are several options for improving the agreement between prediction and observation. It should be noted that the plants are sufficiently small that self-shading is not a problem. The simplification of dividing the plants into only roots and shoots should be acceptable as leaves constitute generally more than 80 % of shoots of fast-growing plants, and changes in allocation in response to light are small. However, in the experiment on tomatoes by Ingestad *et al.* (1994a), there is a large shift in the allocation between leaves and stems where the leaf fraction of the shoot decreases from 85–90 % at high nitrogen concentrations to about 60 % at low nitrogen concentrations. For larger plants, the subdivision into only roots and shoots is an oversimplification.

The considerable improvement when an explicit respiratory term is included indicates that there might be additional

possibilities for improving the models for allocation by adding additional respiratory costs. However, maximizing the relative growth rate may not be the correct optimization criterion. This could explain the problems at the lowest growth rates where plants may be adapted to optimize properties other than relative growth rate. At higher growth rates, this is less likely to be a problem but the assumption of a constant uptake rate per unit root biomass must be challenged. However, replacing the constant U requires a model of the interaction between roots and the nutrient-supplying medium that is lacking. Such a model seems necessary before better descriptions of allocation can be made. Ingredients of such a model must probably take into account the extent to which the nutrient supply is replenishment-limited or concentration-limited (Rastetter and Shaver, 1992).

An interesting aspect of the results is that there seems to be no shift in allocation as a response to light availability, although such results are standard (e.g. Cannell and Dewar, 1994; Canham *et al.*, 1996) but are not always observed (e.g. Shipley, 2000). It is suggested that the explanation for this is that the shoot fraction has been expressed as a function of plant nitrogen concentration and that when analysed in this way there is little effect of light on allocation. Indeed, when Canham *et al.* (1996) plotted root fractions as functions of plant nitrogen concentrations instead of as functions of light intensity, the effects of light disappeared and it turned out that the effect of light was to change the nitrogen concentration. It is expected that most observations of decreased allocation to shoots when light is increased can be explained in this way. An increase in light will increase carbon assimilation and if this is not accompanied by a similar increase in nitrogen supply, the plant nitrogen concentration will decrease along with the allocation to the shoot. However, this is only an indirect effect of a change in light intensity; the driving force for the change in allocation is the change in nitrogen concentration (Ingestad and McDonald, 1989; De Pinheiro Henriques and Marcelis, 2000). Ågren *et al.* (1999) have made a similar observation with respect to the interaction between carbon dioxide and nitrogen.

One particular point is that the shoot fraction cannot decrease below 0.5 when $c_{Nmin} = 0$. The value 0.5 is also a lower limit for case (B), which is obtained when $r = 0$. Experimental evidence indicates also that root biomass rarely exceeds shoot biomass (e.g. Ågren and Ingestad, 1987; Baxter *et al.*, 1994; Canham *et al.*, 1996; Bolinder *et al.*, 1997; Ryser *et al.*, 1997; McConnaughay and Coleman, 1998). These studies represent seven tree (coniferous and hardwood) species, three old-field annuals, four cereals and six grass species grown under a range of experimental conditions.

Two models have been used to investigate how different aspects could modify the response of root : shoot allocation to nitrogen availability. Although the two models give quantitatively differing results, qualitative effects are lacking. This indicates that the general approach is robust and that improving the predictability of root : shoot models requires other approaches. It should also be noted that, if we add a respiratory cost for growth of about 25 % of net

growth (cf. Cannell and Thornley, 2000), the total respiration is about 50 % of gross assimilation for birch but somewhat lower for tomato. This is a level that is considered an average value for most plants (Waring *et al.*, 1998).

The approach described here has, compared with other models, the advantage that it requires only a small number of parameters which are relatively easy to estimate experimentally. For this reason, it has been possible to test the predictions of the model against experimental data, which has indicated where improvements in root : shoot models might be required. The linear relationship between relative growth rate and plant nitrogen concentration imposed in eqn (8) closely resembles the slightly curved relationship derived by Hilbert (1990), but seems more difficult to reproduce with other approaches (cf. Ingestad and Ågren, 1991).

In conclusion, it has been shown that a functional equilibrium approach (Brouwer, 1983) where the relative growth rate is maximized can serve as a basis for describing root : shoot allocation. However, this approach may not be valid for plants growing under extreme conditions of high or low nutrient availability. Moreover, to have quantitatively correct root : shoot allocations it seems necessary to have a better understanding and formulation of how plants regulate nitrogen uptake and plant respiration. The focus on the partitioning of mass rather than other functional attributes can also lead to inappropriate optimization criteria (Reich, 2002).

ACKNOWLEDGEMENTS

We thank Bill Shipley and Annikki Mäkelä for helpful comments on the manuscript. This work was supported by the Swedish Council for Forestry and Agricultural Research.

LITERATURE CITED

- Ågren GI. 1985. Theory for growth of plants derived from the nitrogen productivity concept. *Physiologia Plantarum* **64**: 17–28.
- Ågren GI. 1996. Nitrogen productivity or photosynthesis minus respiration to calculate plant growth. *Oikos* **76**: 529–535.
- Ågren GI, Bosatta E. 1998. *Theoretical ecosystem ecology – understanding element cycles*. Cambridge: Cambridge University Press.
- Ågren GI, Ingestad T. 1987. Root:shoot ratio as a balance between nitrogen productivity and photosynthesis. *Plant, Cell and Environment* **10**: 579–586.
- Ågren GI, Wikström JF. 1993. Modelling carbon allocation – a review. *New Zealand Journal of Forestry Science* **23**: 343–353.
- Ågren GI, Shaver GR, Rastetter EB. 1999. Nutrients: dynamics and limitations. In: Lou Y, Mooney HA eds. *Carbon dioxide and environmental stress*. San Diego: Academic Press, 333–345.
- Baxter R, Ashenden TW, Sparks TH, Farrar JF. 1994. Effects of elevated carbon-dioxide on 3 montane grass species. 1. Growth and dry-matter partitioning. *Journal of Experimental Botany* **45**: 305–315.
- Bloom AJ, Chapin III TS, Mooney HA. 1985. Resource limitation in plants – an economic analogy. *Annual Review of Ecology and Systematics* **16**: 363–392.
- Bolinder MA, Angers DA, Dubuc JP. 1997. Estimating shoot to root ratios and annual carbon inputs in soils for cereal crops. *Agriculture, Ecosystems and Environment* **63**: 61–66.
- Brouwer R. 1983. Functional equilibrium: sense or nonsense. *Netherlands Journal of Agricultural Science* **31**: 335–348.
- Canham CD, Berkowitz AR, Kelly VR, Lovett GM, Ollinger SV, Schnurr J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. *Canadian Journal of Forest Research* **26**: 521–530.
- Cannell MGR, Dewar RC. 1994. Carbon allocation in trees: a review of concepts for modelling. *Advances in Ecological Research* **25**: 59–104.
- Cannell MGR, Thornley JHM. 2000. Modelling the components of plant respiration: some guiding principles. *Annals of Botany* **85**: 45–54.
- de Groot CC, Marcelis LFM, van den Boogaard R, Lambers H. 2002. Interactive effects of nitrogen and irradiance on growth and partitioning of dry mass and nitrogen in young tomato plants. *Functional Plant Biology* **29**: 1319–1328.
- De Pinheiro Henriques AR, Marcelis LFM. 2000. Regulation of growth at steady-state nitrogen nutrition in lettuce (*Lactuca sativa* L.): interactive effects of nitrogen and irradiance. *Annals of Botany* **86**: 1073–1080.
- Ericsson T. 1995. Growth and shoot:root ratio of seedlings in relation to nutrient availability. *Plant and Soil* **168/169**: 205–214.
- Field C, Mooney HA. 1983. Leaf age and seasonal effects on light, water, and nitrogen use efficiency in a California shrub. *Oecologia (Berlin)* **56**: 348–355.
- Hilbert DW. 1990. Optimization of plant root: shoot ratios and internal nitrogen concentration. *Annals of Botany* **66**: 91–99.
- Ingestad T, Ågren GI. 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications* **1**: 168–174.
- Ingestad T, McDonald AJS. 1989. Interaction between nitrogen and photon flux density in birch seedlings at steady-state nutrition. *Physiologia Plantarum* **77**: 1–11.
- Ingestad T, Hellgren O, Ingestad Lund AB. 1994a. *Data base for tomato plants at steady state. Methods and performance of tomato plants (Lycopersicon esculentum Mill. cv. solentos) under non-limiting conditions and under limitation by nitrogen and light*. Report 74. Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences.
- Ingestad T, Hellgren O, Ingestad Lund AB. 1994b. *Data base for birch plants at steady state. Performance of birch plants (Betula pendula Roth.) under non-limiting conditions and under limitation by nitrogen and light*. Report 75. Department of Ecology and Environmental Research, Swedish University of Agricultural Sciences.
- Johnson IR, Thornley JHM. 1987. A model of shoot: root partitioning with optimal growth. *Annals of Botany* **60**: 133–142.
- McConaughay KDM, Coleman JS. 1998. Can plants track changes in nutrient availability via changes in biomass partitioning? *Plant and Soil* **202**: 201–209.
- Rastetter EB, Shaver GR. 1992. A model of multiple-element limitations for acclimating vegetation. *Ecology* **73**: 1157–1174.
- Reich PB. 2002. Root–shoot relations: optimality in acclimation and adaptation or the ‘‘Emperor’s new clothes’’? In: Waisel Y, Eshel A, Kafkafi U eds. *Plant roots – the hidden half*. New York: Marcel Dekker, 205–220.
- Ryan MG, Hubbard RM, Pongracic S, Raison RJ, McMurtrie RE. 1996. Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. *Tree Physiology* **16**: 333–343.
- Ryser P, Verduyn B, Lambers H. 1997. Phosphorus allocation and utilization in three grass species with contrasting response to N and P supply. *New Phytologist* **137**: 293–302.
- Shipley B. 2000. Plasticity in relative growth rate and its components following a change in irradiance. *Plant Cell and Environment* **23**: 1207–1216.
- Thornley JHM. 1972. A balanced quantitative model for root: shoot ratios in vegetative plants. *Annals of Botany* **36**: 431–441.
- Thornley JHM. 1995. Shoot: root allocation with respect to C, N and P: an investigation and comparison of resistance and teleonomic models. *Annals of Botany* **75**: 391–405.
- Thornley JHM. 1998. Modelling shoot: root relations: the only way forward? *Annals of Botany* **81**: 165–171.
- Waring RH, Landsberg JJ, Williams M. 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiology* **18**: 129–134.
- Wilson JB. 1988. A review of evidence on the control on shoot: root ratio, in relation to models. *Annals of Botany* **61**: 433–449.