MODELLING CARBON ALLOCATION—A REVIEW

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ABSTRACT

The problem of allocation of a plant's carbon resources is basically an evolutionary one in which long-term reproductive success is the goal. Analyses of which features maximise seed production have been done on the basis of root:shoot:seed allocation and height growth:seed production. More complex models which focus on many-species interactions along a resource continuum have also been tried. More commonly, however, the problem of allocation is defined in terms of functional (physiological) properties of the plant, with nitrogen availability as a dominant factor. Within this category, some models rely directly on empirical information, others derive root:shoot allocation from various physiological principles such as transport resistance, balance between carbon and nitrogen uptake, or balance between carbon assimilation and consumption. In some cases allocation is calculated from an optimisation scheme. In view of the criteria that should be satisfied by allocation models, we conclude that today there are no allocation models that satisfy all requirements.

Keywords: carbon allocation; competition; functional balance; height growth; root:shoot ratio; seed production.

INTRODUCTION

The regulation of the allocation of the resources of a plant to its different organs is a problem that has been receiving increasing attention in recent years. It is of considerable interest not only as a purely scientific problem in plant physiology and ecology but also in agricultural economy as harvests are normally directed only towards parts of the plant. In addition, a future global climatic change may change the current allocation patterns through the couplings with the nutrient and water cycles at the ecosystem level (Ågren *et al.* 1991).

The problem of allocation is, of course, basically an evolutionary one in which long-term reproductive success is the goal. The obvious approach is to calculate how the seed production of a plant depends on its use of acquired resources. However, such an approach involves a large number of complications only marginally related to the question of allocation (e.g., seed dispersal or seed survival); for many plants the investment in reproduction is also small or comes late in the life cycle. It is, therefore, of interest to look at closer goals that can be expressed in terms of the growth processes as such and also reflect short-term variability in resources.

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The external factors that dominate the controls of the allocation are normally nutrient and water availability, light conditions, and temperature. To this list should, perhaps, be added carbon dioxide availability. When modelling allocation, these external factors should be translated into internal states of the plant (e.g., nutrient and soluble carbon concentrations, or water potential). At a still higher level of physiological resolution it might be necessary to introduce hormones, but so far no one has attempted this.

There is abundant empirical information about the presumed effect of varying external conditions. A good example of how nitrogen nutrition controls root:shoot partitioning has been supplied by Ingestad (1991). His example shows clearly the strong effect of nutrition. For this reason much of the empirical information available in the literature must be regarded with suspicion as nutrition has not been controlled or recorded in many studies (Ingestad & Ågren 1991, 1992). There is also mounting evidence that the generally accepted rule that plants allocate more to roots with decreasing availability of the limiting nutrient is too simple. It holds for some elements (nitrogen, phosphorus, sulphur) but with others the reverse is true (manganese, magnesium) and for still others (potassium, iron) the direction of change of the allocation pattern varies with the nutrient status of the plant (Ericsson 1990).

It is the purpose of this paper to review approaches to modelling the allocation of a plant's carbon resources. A complementary review with a different focus has been given by Wilson (1988). We will use a uniform system of notation throughout even when this deviates from that used in the original citation.

EVOLUTIONARY APPROACHES

In this section we will consider models that address evolutionary success of plants explicitly. The evolutionary strategies of allocation in plants have attracted relatively little attention from modellers. In the three different approaches discussed here, plant physiological properties are defined in general terms in two and the implications of the assumptions can be examined analytically. In the third approach, some details about plant physiology and explicit functions for resource acquisition are provided but at the expense of requiring computer simulations for the analysis.

Shoot / Root / Reproduction

Iwasa & Roughgarden (1984) analysed a plant model consisting of a shoot biomass (W_S), a root biomass (W_R), and reproductive biomass (R). The growth of the plant components was assumed to depend on the shoot and root biomasses through some function $f(W_S, W_R)$ and with time-dependent allocation coefficients (u_i, $i = 0, 1, 2$; $u_0 + u_1 + u_2 = 1$):

$$dW_S/dt = u_1(t)f(W_S, W_R) \tag{1a}$$

$$dW_R/dt = u_2(t)f(W_S, W_R) \tag{1b}$$

$$dR/dt = u_0(t)f(W_S, W_R) \tag{1c}$$

Their problem was then to find the functions u that by the end of the growth period produced the maximum reproduction. With a few weak assumptions about the form of $f(W_S, W_R)$, they showed that it was possible to find the required function u.

Their solution was what has been called a "bang-bang" strategy. During an initial growth phase all effort goes into the plant becoming as large as possible ($u_0 = 0$), and then at some specific time all efforts are switched into reproduction ($u_0 = 1$). During the vegetative growth phase the plant allocates resources to shoots and roots in a balanced way, which is defined as $\delta f/\delta W_S = \delta f/\delta W_R$. The analysis can be extended to cover examples where the plant has several organs as well as those where the external resource levels are explicitly included. The latter analysis requires, however, that the function f is given explicitly.

Height Growth / Reproduction

Iwasa & Roughgarden (1984) have allowed for no explicit competition between plants. In contrast, Mäkelä (1986) analysed the plant's allocation problem by searching for an evolutionary stable strategy among trees with different allocations between height growth and reproduction. To simplify the problem, she assumed that it is the crown size (productive part in her terminology) of the tree at maturity, which occurs at a given time T, that determines the reproductive success. The problem a given tree has to face is to balance the reduction in specific growth rate caused by taller neighbours, which shadow the tree, against the cost of investing resources in its own height growth. The problem is summarised in the following three equations:

$$dW_S/dt = a(t)Q(t)W_S - mW_S \tag{2a}$$

$$a(t) = 1 - ch(t) \tag{2b}$$

$$Q(t) = Q_0 + b[h(t) - H(t)] \tag{2c}$$

where $Q(t)$ is the specific growth rate, a fraction $a(t)$ of which is allocated to new crown growth. The specific growth rate depends linearly on the difference in height between the subject tree, $h(t)$, and the average tree height in the stand, $H(t)$; b, c, and m are parameters. The solution is again a "bang-bang" strategy, where the tree starts by investing all its resources on height growth up to some point in time when there is a switch to no height growth and all resources are invested in reproduction. The particular time depends on the parameters b, c, Q_0, and the maximum height growth rate but not on the specific mortality, m. The switch between the two growth stages occurs when the tree has become so tall that further height growth would imply a greater decrease in crown growth than would occur due to increased shading from the neighbours, even if the rest of the stand continued to grow.

Tilman's Allocate

While most models treat allocation patterns as an adaptation to different resource levels, the model of Tilman (1988, 1991) treats changes in species composition along resource gradients due to differences in the allocation pattern between species. The focus is directed on competition between species with different allocation patterns rather than allocation within single plants.

The plant is divided into three fractions: leaves that produce photosynthate for biomass production, a stem that increases the competitiveness for light, and roots that compete for nutrients. The proportions of these fractions remain fixed from the germination of the seed to death. All photosynthate produced is used for vegetative growth until the plant reaches its maximum height, after which all photosynthate goes into seed production. Seeds vary in size and numbers among species. Loss rate, i.e., mortality and herbivory, is also included.

Each combination of allocation, seed production, and loss rate will result in a superior competitor at a point along the gradients of soil resources and light. For example, on nutrient-poor sites, species with high allocation to roots will dominate over species with lower allocation to roots but higher growth rate potential. The model simulates plant growth for several generations for a number of species simultaneously, and has been used to explain changes in species composition during successions.

The model consists of a number of equations that are solved numerically. No analytical solutions of plant behaviour along resource gradients are possible.

FUNCTIONAL APPROACHES

A large class of models can be classified as functional approaches as they define the problem of allocation explicitly in terms of functional (physiological) properties of the plant. However, this group of models is far from uniform and contains a variety of approaches ranging from empirical to detailed mechanistic ones. Many of them can, however, be described schematically as in Fig. 1. The most commonly used factor for changing allocation in these models is nitrogen availability.

Plant carbon component 1 Structural carbon Labile carbon	**Plant nitrogen component 1** Structural nitrogen Labile nitrogen
Plant carbon component 2 Structural carbon Labile carbon	**Plant nitrogen component 2** Structural nitrogen Labile nitrogen
⋮	⋮
Plant carbon component n Structural carbon Labile carbon	**Plant nitrogen component n** Structural nitrogen Labile nitrogen

FIG. 1–Schematic representation of functional approach models. The resolution in terms of carbon and nitrogen components varies greatly among models.

Empirical

In many instances the modelling of the plant occurs in a larger context. It is then often necessary to model the carbon allocation in the plant in order to have an appropriate description of the sizes of the organs of the plant, e.g., root biomass to estimate water and nutrient uptake or canopy size to estimate photosynthetic rates and transpiration, but this can be done without any pretension to explanation. The common feature of these models is that they start from some calculation of photosynthesis, *P*, either a net photosynthesis or a gross photosynthesis from which respiration is subtracted. The growth of the different plant components, W_i, is then simply described by some empirically obtained partitioning coefficients, η_i (cf. the evolutionary approaches which attempt to calculate these coefficients):

$$dW_i/dt = \eta_i P \tag{3}$$

with $\Sigma\eta_i = 1$.

The difference between the models lies in how the partitioning coefficients are determined. In the simplest case (e.g., McMurtrie *et al.* 1989) the partitioning coefficients are constant. In more complicated cases the partitioning coefficients are made functions of plant nutrient concentration (e.g., Hirose 1986) or of plant phenological development (e.g., Eckersten & Ericsson 1989).

Transport Resistance

The first mechanistic models of allocation were based on transport and utilisation of carbon and nitrogen compounds (Thornley 1972a, b). Both carbon and nitrogen are divided into two classes of substances: labile and structural. Labile substances can move easily within the plant whereas structural materials are unavailable for further use once they have been allocated to a plant component. The distinction between the two classes is not absolute but should reflect rather large differences in turnover rates of the two classes, with turnover times for labile compounds of the order of hours. The idea is that carbon enters the plant through the shoots where labile carbon compounds accumulate. Some of these compounds are used for construction of new structural shoot material. A continued accumulation of labile carbon in the shoot will create a concentration gradient which will cause a flow towards the roots thereby supplying them with carbon for their growth. A similar situation prevails for nitrogen but with the roots as the entrance point.

Given a nitrogen uptake rate per unit of root, σ_N, and a carbon assimilation rate per unit of shoot, σ_C, combined with a constant nitrogen:carbon ratio, λ, in the structural material, Thornley (1972b) derived the following from a set of non-linear equations:

$$\sigma_N f_R = \lambda\sigma_C f_S \tag{4}$$

where f_R and f_S ($f_R + f_S = 1$) are the root and shoot fractions, respectively, of the plant. This relationship plays an important role in some other approaches to be discussed below, but in them is assumed rather than derived.

A very different approach, based on water transport resistance and which does not conform to Fig. 1, was independently suggested by Valentine (1985) and Mäkelä (1986). Plant roots are connected to the foliage through a number of "pipes" in the coarse roots, stem, and branches. These pipes are assembled in the sapwood of the tree, corresponding to observations of constant ratios between foliage biomass and sapwood area within a species. An expanding foliage biomass will require an increasing sapwood biomass with its associated costs for production and maintenance. The major consequence of this pipe model theory is, however, that the height growth of the tree increases the length of the pipes and every new pipe that is produced and connected to the top of the tree will therefore be more costly in production and maintenance than those lost when the lower part of the canopy dies.

The pipe model theory can describe the demand on allocation to woody tissues, the main function of which is to connect the resource-capturing fine roots and the canopy. The growth of the fine roots and the canopy has, therefore, to be described by some other means. Mäkelä (1986) did this through the use of a functional balance approach.

Functional Balance

One of the most commonly used approaches to modelling carbon allocation is through the use of the "functional balance" of the plant, implying that a functional equilibrium exists between the size and activity of the shoot (which supplies carbon) and the size and activity of the root (which supplies water and nutrients). Mathematically this relationship is expressed in Eq. (4). Carbon and nitrogen are, on the one hand, incorporated into structural biomass (with a carbon concentration f_C and nitrogen concentration f_N) and, on the other hand, kept in labile form (sometimes denoted substrate carbon and nitrogen with concentrations c_{Cl} and c_{Nl}, respectively) from which the structural material is built. The plant nitrogen concentration, c_N, is therefore the sum of the structural nitrogen concentration and the concentration of labile nitrogen.

Charles-Edwards (1976) analysed a simple version of the general model in Fig. 1 by only including shoot and root biomasses under balanced exponential growth. Under these conditions the relative uptake rate of carbon and nitrogen must be equal, which can be expressed as:

$$dW/dt = \sigma_C W_S / f_C = \sigma_N W_R / f_N \qquad (5)$$

where $W = W_S + W_R$. Rearranging Eq. (5) to get W_S and W_R and summing gives:

$$\frac{dW}{dt} = \frac{\sigma_N \sigma_C}{f_N \sigma_C + f_C \sigma_N} W \qquad (6)$$

which combined with Eq. (5) directly gives the root and shoot fractions. It should be noted that the specific activities, σ_C and σ_N, do not correspond to the total carbon fixation and nitrogen uptake respectively as only the structural components are considered. For carbon this is probably no major problem but the contribution from the labile nitrogen pool to the total plant nitrogen is too important to be neglected.

Reynolds & Thornley (1982) provided a more complete model in which labile carbon and nitrogen concentrations are also explicitly included, but with a constant ratio and not influenced by external conditions. This ratio also serves as a partitioning function for the root:shoot allocation. From this analysis they found that a relationship such as Eq. (4) can only be approximately valid over a large range of environmental conditions. To overcome some of the problems with the Reynolds & Thornley model, Johnson (1985) suggested a different partitioning function where a relationship similar to Eq. (4) is assumed to apply under balanced exponential growth

$$c_{Cl} f_S = \xi c_{Nl} f_R \qquad (7)$$

where ξ is a partitioning parameter. The concentrations of labile carbon and nitrogen no longer have a constant ratio. The dynamic behaviour of Johnson's model is also more stable than the one by Reynolds & Thornley. An extensive comparison of the model by Reynolds & Thornley and the transport resistance models made by Mäkelä & Sievänen (1987) shows that the Reynolds & Thornley model can be seen as a subset of the transport resistance models. A further extension of these models was suggested by Hilbert & Reynolds (1991) who also included a compartment for leaf protein. Dewar (1993) provided still another extension by allowing a fraction of the nitrogen taken up to be directly transported to the shoots through the xylem and later transported back to the roots through the phloem (Münch flow).

As an alternative to the use of a rather arbitrary partitioning parameter, one can add an equation requiring that some property attains an extreme value. In view of the previous discussions about evolutionary behaviour, the maximum plant growth rate in the vegetative growth phase is a desirable goal. However, since maximising absolute growth rate is not a simple problem, it has been preferred to maximise relative growth rate, R_W, which has a constant value during an exponential growth phase. Johnson & Thornley (1987) replaced the partitioning parameter ξ of Johnson (1985) and could derive optimal solutions for the allocation which qualitatively had the appropriate behaviour. The results have, however, been criticised by Ingestad & Ågren (1991) for being inconsistent with empirical evidence on the relationship between relative growth rate and internal nutrient status.

Kachi & Rorison (1989) employed a model with root and shoot carbon and nitrogen as state variables. The nitrogen concentrations in roots and shoots were assumed to be linearly related to each other. With a σ_C that increased linearly with shoot nitrogen concentration up to some critical concentration and was constant above that level, they found that the optimal behaviour of the plant corresponded to a constant root:shoot ratio when shoot nitrogen concentration was below the critical one. Once the nitrogen concentration had reached the critical level it would remain at that point, but increasing the nitrogen uptake rate led to an increasing shoot fraction.

Hilbert (1990) combined the functional balance equation, Eq. (4) with λ equal to the whole plant nitrogen concentration, and the carbon assimilation equation:

$$dW/dt = \sigma_C W_S \tag{8}$$

He could then find optimal root:shoot ratios with changing nitrogen availability and, in contrast to Johnson & Thornley (1987), also a reasonably linear relationship between relative growth rate and plant nitrogen concentration. It is worth noting that when shoot and root nitrogen concentrations are set equal in Kachi & Rorison's (1989) model, it becomes formally equal to Hilbert's.

Rewriting Eq. (8) as

$$R_W = \sigma_C f_S \tag{9}$$

and differentiating with respect to f_S, Ingestad & Ågren (1991) obtained

$$\frac{dR_W}{df_S} = \sigma_C + f_S \frac{d\sigma_S}{df_S} = \sigma_S + f_S \frac{d\sigma_S}{dc_N} / \frac{df_S}{dc_N} \tag{10}$$

where the right-hand side consists of only positive terms. It should, therefore, not be possible to optimise the relative growth rate with respect to root:shoot partitioning. Hilbert's (1990) result to the contrary seems to come from his assumption of a "specific root activity" that is independent of the plant nitrogen concentration. The way in which the functional balance, Eq. (4), is constructed implies, however, that the specific root activity and the plant nutrient concentration are functions of each other. The argument does not apply to the analysis by Johnson & Thornley (1987) because in that case Eq. (10) should include one more (and negative) term coming from changes in labile carbon.

Consumption / Production

Ågren & Ingestad (1987) (with a later extension by Levin *et al.* 1989) suggested that rather than balancing nitrogen and carbon uptakes one could use the carbon balance of the plant.

Carbon assimilation by the plant is given as in the functional balance approaches by Eq. (8). The utilisation of the carbon is, on the other hand, expressed by the nitrogen productivity, P_N, and the nitrogen amount in the plant, N. The two ways of expressing growth give the following equation:

$$dW/dt = \sigma_C W_S = P_N N \tag{11}$$

from which the root:shoot ratio can be calculated as a function of the plant nitrogen concentration. One of the consequences of Eq. (11) is that for low nitrogen concentrations the root:shoot ratio increases with increasing plant nitrogen concentration, but above some critical value it decreases as normally observed. The position of this critical value depends on how σ_C varies with nitrogen concentration. This strange behaviour for nitrogen at low concentrations could perhaps be useful in explaining the changes in allocation when other mineral nutrients are limiting.

Other Approaches

Hunt & Nicholls (1986) addressed the problem of allocation between roots and shoots by defining artificial stress indices of the root and shoot environment. Plant performance was then expressed in terms of the sum of these two indices (the total stress) and the ratio (the stress ratio).

Robinson (1986), using an argument similar to the functional balance, derived an expression from which he could study the effects of root:shoot ratio and specific root length on relative growth. His conclusions were that adjustments of these two properties could allow a plant to maintain a high relative growth even when the nutrient availability decreased.

Orians & Solbrig (1977) used a cost-income model to qualitatively analyse the allocation problems in terms of root:shoot ratio and leaf morphology of plants under water stress. This is, to our knowledge, the only model that deals with the effects of water. Their results explain some features observed when comparing plants growing in deserts and in soils well supplied with water.

An entirely different aspect of allocation was given by Horn (1971) who studied the mechanical design of plants from the aspect of adaptation to physical stress factors such as wind. His results are more relevant for understanding the shape of stems and branches than the functions of roots or shoots.

DISCUSSION

There are criteria that should be satisfied by allocation models (Table 1). Some of these arise from a theoretical and/or philosophical view whereas others are based on empirical evidence of plant behaviour. Some of these properties are desirable but not necessary for models to encompass, whereas others are such that models not satisfying them should not be used.

Theoretical Desiderata

In a model there should be a clear distinction between internal plant variables and external conditions. A failure to meet this criterion will lead to confusion as changes in external

TABLE 1–Summary of properties of the different classes of models with respect to desired properties of allocation models.

	Theoretical desiderata			Empirical desiderata	
	Based on evolution	Separation of external and internal variables	Simplicity	R_W linear function of c_N	Increasing or decreasing root allocation with c_N
Reproduction models	Yes	Yes	Reasonable	Not applicable	Not applicable
Allocate	Yes	Yes	Complex	Not applicable	Not applicable
Empirical	No	Not applicable	Very simple	Not applicable	Can be chosen
Transport resistance	No	In some models	Not always analytical solutions	Unknown	Increasing
Functional balance	No	In some models	Simple	Not always or unknown	Increasing
Consumption-production	No	Yes	Simple	Yes	Both

conditions will be confounded with changes in internal plant properties. A typical example is the use of "root-specific activity". When used as nutrient uptake rate per unit of root (e.g., Thornley 1972a, b), it is a reflection of the external availability of a nutrient and no problems appear. However, when it is used in functional balance approaches, which do not explicitly contain plant nutrient amounts, it describes not only the external nutrient situation but also the internal plant nutrient status. It is then unclear how these two factors change in relation to each other or whether the "root-specific activity" has to be considered as a function of plant nutrient status.

Since the ultimate driving force for allocation is evolutionary, it seems logical that models of allocation explicitly recognise this. However, most of the models analysed above neglect this aspect entirely. Although it would be more satisfactory to describe allocation from an evolutionary perspective, we believe that much can be learnt even without that. If we assume that plants have certain physiological characteristics, we can study which of these can be combined to provide the appropriate plant behaviour. From this understanding we can, perhaps, ask why evolution has led to these particular combinations of plant properties. It may be simpler to understand the evolution of some physiological properties rather than the allocation patterns, e.g., root:shoot ratios, directly.

We also want to come to the right conclusion for the right reason. Models that can be analysed only through simulations are less satisfactory unless it is possible to reduce them to some simplified version that allows a qualitative or semi-qualtitative analysis. In pure simulation models, it is difficult to know the generality of the model as only single points in the parameter space can be investigated.

Empirical Desiderata

Allocation models that contain plant nutrients must allow for a variable nutrient concentration because variation in plant nutrient status is (perhaps) the most important factor associated with carbon allocation. In the earliest versions of "functional balance" models this was not the case. Moreover, plant nutrient concentration should be approximately linearly related to the relative growth rate for small plants, and this is one of the best-established relationships in plant ecophysiology (Ingestad & Ågren 1992).

Depending on which nutrient we are studying, the carbon allocation pattern can be shifted towards either the roots or the shoots when the nutrient availability increases. Is it therefore desirable that both responses can be included in the model in a natural way.

Missing Features

Two aspects that could be important in terms of carbon allocation but which seem to be missing in all models are exudation and defence substances. The quantitative role of exudation is uncertain but sometimes large amounts of carbon are reported as exudates. Investment in exudation could be a means of increasing nutrient uptake. The quantification of the amounts of carbon allocated to defence substances is also largely unknown. In addition, defence substances might be re-utilised and an allocation to them could therefore mean a temporary allocation of carbon only.

CONCLUSION

There are no allocation models today that satisfy all our requirements. All of the current approaches have their advantages and drawbacks. The best path for the future must be to continue to explore a large variety of modelling approaches. In addition, there are a number of additional features that might have to be included before we can satisfactorily model (explain) carbon allocation. Let a hundred flowers bloom.

REFERENCES

ÅGREN, G.I.; INGESTAD, T. 1987: Root-shoot ratios as a balance between nitrogen productivity and photosynthesis. *Plant, Cell and Environment 10*: 579–86.

ÅGREN, G.I.; McMURTRIE, R.E.; PARTON, W.J.; PASTOR, J.; SHUGART, H.H. 1991: State-of-the-art of models of production-decomposition linkages in conifer and grassland ecosystems. *Ecological Applications 1*: 118–38.

CHARLES-EDWARDS, D.A. 1976: Shoot and root activities during steady-state plant growth. *Annals of Botany 40*: 767–72.

DEWAR, R.C. 1993: A root-shoot partitioning model based on carbon-nitrogen-water interactions and Münch phloem flow. *Functional Ecology 7*: 356–68.

ECKERSTEN, H.; ERICSSON, T. 1989: Allocation of biomass during growth of willow. Pp.65–76 *in* Perttu, K.L.; Kowalik, P.J. (Ed.) "Modelling of Energy Forestry Growth, Water Relations and Economics". Simulation Monographs, Pudoc, Wageningen.

ERICSSON, T. 1990: Dry matter partitioning in birch seedlings—A balance between internal nitrogen and carbon fluxes. Pp.232–3 *in* Werner, D.; Müller, P. (Ed.) "Fast Growing Trees and Nitrogen Fixing Trees". Gustav Fischer Verlag, Stuttgart.

HILBERT, D.W. 1990: Optimization of plant root:shoot ratios and internal nitrogen concentration. *Annals of Botany 66*: 91–9.

HILBERT, D.W.; REYNOLDS, J.F. 1991: A model allocating growth among leaf proteins, shoot structure, and root biomass to produce balanced activity. *Annals of Botany 68*: 417–25.

HIROSE, T. 1986: Nitrogen uptake and plant growth. II. An empirical model of growth and partitioning. *Annals of Botany 58*: 479–86.

HORN, H.S. 1971: "The Adaptive Geometry of Trees". Princeton University Press, Princeton, N.J.

HUNT, R.; NICHOLLS, A.O. 1986: Stress and the coarse control of growth and root-shoot partitioning in herbaceous plants. *Oikos 47*: 149–58.

INGESTAD, T. 1991: Nutrition and growth of forest trees. *Tappi Journal 74*: 55–62.

INGESTAD, T.; ÅGREN, G.I. 1991: The influence of plant nutrition on biomass allocation. *Ecological Applications 1*: 168–74.

———1992: Theories and methods on plant nutrition and growth. *Physiologia Plantarum 84*: 177–84.

IWASA, Y.; ROUGHGARDEN, J. 1984: Shoot/root balance of plants: Optimal growth of a system with many vegetative organs. *Theoretical Population Biology 25*: 78–105.

JOHNSON, I.R. 1985: A model of the partitioning of growth between the shoots and roots of vegetative plants. *Annals of Botany 55*: 421–31.

JOHNSON, I.R.; THORNLEY, J.H.M. 1987: A model of shoot:root partitioning with optimal growth. *Annals of Botany 60*: 133–42.

KACHI, N.; RORISON, I.H. 1989: Optimal partitioning between root and shoot in plants with contrasted growth rates in response to nitrogen availability and temperature. *Functional Ecology 3*: 549–59.

LEVIN, S.A.; MOONEY, H.A.; FIELD, C. 1989: The dependence of plant root:shoot ratio on internal nitrogen concentration. *Annals of Botany 64*: 71–5.

MÄKELÄ, A. 1986: Implications of the pipe model theory on dry matter partitioning and height growth in trees. *Journal of Theoretical Biology 123*: 103–20.

MÄKELÄ, A.A.; SIEVÄNEN, R.P. 1987: Comparison of two shoot-root partitioning models with respect to substrate utilisation and functional balance. *Annals of Botany 59*: 129–40.

McMURTRIE, R.E.; LANDSBERG, J.J.; LINDER, S. 1989: Research priorities in field experiments on fast-growing tree plantations. Pp.181–207 *in* Pereira, J.S.; Landsberg, J.J. (Ed.) "Biomass Production by Fast-growing Trees". Kluwer Academic, Dordrecht.

ORIANS, G.H.; SOLBRIG, O.T. 1977: A cost-income model of leaves and roots with special reference to arid and semiarid conditions. *American Naturalist 111*: 677–90.

REYNOLDS, J.F.; THORNLEY, J.H.M. 1982: A shoot:root partitioning model. *Annals of Botany 49*: 585–97.

ROBINSON, D. 1986: Compensatory changes in the partitioning of dry matter in relation to nitrogen uptake and optimal variation in growth. *Annals of Botany 58*: 841–8.

THORNLEY, J.H.M. 1972a: A model to describe the partitioning of photosynthate during vegetative plant growth. *Annals of Botany 36*: 419–30.

———1972b: A balanced quantitative model for root:shoot ratios in vegetative plants. *Annals of Botany 36*: 431–41.

TILMAN, D. 1988: Plant strategies and the dynamics and structure of plant communities. *Princeton University Press, Monographs in Population Biology 26.*

———1991: Relative growth rates and plant allocation patterns. *The American Naturalist 138*: 1269–75.

VALENTINE, H.T. 1985: Tree-growth models: Derivations employing the pipe-model theory. *Journal of Theoretical Biology 117*: 579–85.

WILSON, J.B. 1988: A review of evidence on the control on shoot:root ratio, in relation to models. *Annals of Botany 61*: 433–49.