A Shoot:Root Partitioning Model

J. F. REYNOLDS* and J. H. M. THORNLEY†

Glasshouse Crops Research Institute, Littlehampton, West Sussex BN16 3PU

ABSTRACT

A model for partitioning newly-synthesized structural dry matter between shoot and root is developed. It is based on a postulated partitioning function, which depends upon the relative levels of carbon and nitrogen substrates, with parameters determining the control point and also the degree of control. The model is used to investigate the relationships between plant specific growth rate, shoot:root ratio, and the specific activities of shoot and root (which depend upon environment), during steady-state exponential growth; the transient behaviour of the model is also explored and oscillations in these quantities are obtained.

Key words: Shoot:root ratio, specific growth rate, mathematical model, partition of assimilates.

INTRODUCTION

An integrated understanding of growth behaviour at the whole-plant level requires an assessment of the metabolic activities of each organ in terms of its contribution to the overall balance of growth. The interaction between shoot and root activities in maintaining this balance has been the subject of considerable research (see reviews by Mooney, 1972; Wareing and Patrick, 1975; Russell, 1977; Thornley, 1977; Fischer and Turner, 1978; Novoa and Loomis, 1981).

White (1937) and later Brouwer (1962) proposed a hypothesis, subsequently quantified by Davidson (1969), that a functional equilibrium exists between the size and activity of the shoot (which supplies carbohydrate) and the size and activity of the root (which supplies water and essential nutrients). This may be expressed as

$$\textit{shoot mass} \times \textit{shoot specific activity} \propto \textit{root mass} \times \textit{root specific activity}. \qquad (1)$$

This functional equilibrium has been applied to a large number of plant species (for example, see Hunt, 1975; Boote, 1976; Charles-Edwards, 1976; Edwards and Barber, 1976; Raper *et al.*, 1977; Richards, 1980). In many cases, Eqn (1) often appears to give an acceptable approximate description of experimental data, but a closer scrutiny with high-quality data usually reveals systematic discrepancies.

A major shortcoming in the large number of plant growth models developed in ecology, agronomy and physiology is the highly empirical approach by which the partitioning (and hence balancing) of plant materials between the various organs is usually accomplished (Ledig, 1976; Thornley, 1977). Several modelling efforts have attempted to establish a balance between shoot and root activities by linking shoot growth to water uptake by the roots (de Wit, Brouwer and Penning de Vries, 1970; Borchert, 1973), but lack a sound phenomenology. Thornley (1972*a*, *b*) developed a transport-resistance based model, putting the ideas of White (1937) into mathematical form; this model provides a partitioning of growth between shoot and root by balancing

* Permanent address: Department of Botany, North Carolina State University, Raleigh, North Carolina 27650, U.S.A.
† Present address: Grassland Research Institute, Hurley, Maidenhead, Berks SL6 5LR.

carbohydrate synthesis by the shoot with nitrogen uptake by the root, in terms of the transport between and utilization in the shoot and root compartments of these two substrates. This model has been applied to tomatoes with some success (Cooper and Thornley, 1976), and Thornley (1977) has indicated how the approach can be extended to partitioning problems where uphill or active transport may be involved. However, the approach has been criticized because of its complexity, and also because of the need to measure or estimate resistances to substrate transport (Fick, Loomis and Williams, 1975; Wareing and Patrick, 1975; Ledig, 1976).

In the present paper, a partitioning model is developed which attempts to find a useful compromise between the complex mechanistic approach and the simple highly empirical approach. A main objective is to provide a practical tool for examining and interpreting the relationships between the specific growth rate of a plant, its shoot:root ratio, and the shoot and root specific activities which depend upon the environment. The principal feature of this model is the definition of a partitioning function, which allows for an adaptive response by the plant to changes in shoot or root environment via the relative substrate levels within the plant.

THE MODEL

State variables

The model is shown schematically in Fig. 1. Total plant dry matter (W) is divided into structure (W_G) and storage (W_S) giving

$$W = W_G + W_S. \tag{2}$$

The structural dry matter (W_G) is then sub-divided into the shoot structural dry matter (W_{sh}) and the root structural dry matter (W_r) so that
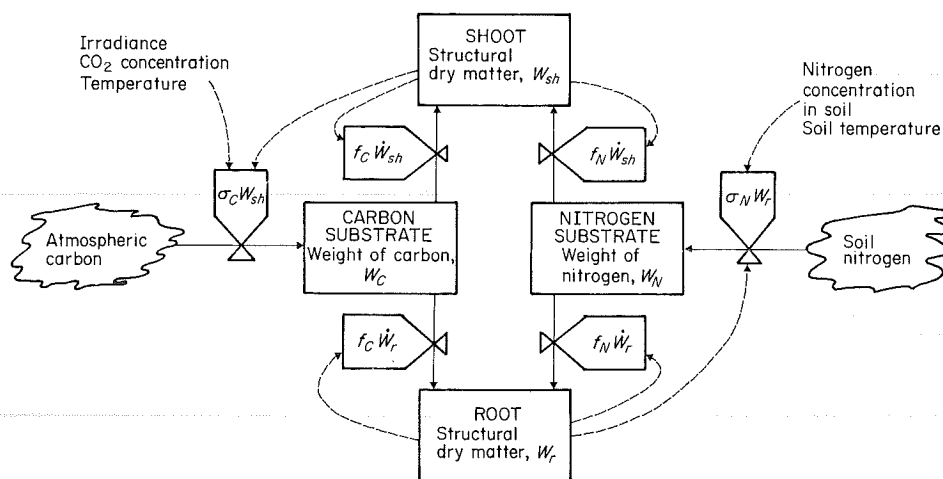
$$W_G = W_{sh} + W_r. \tag{3}$$

FIG. 1. Shoot:root partitioning model. The rates are shown within the valve symbols. f_C and f_N are the fractional contents of structural dry matter for carbon and nitrogen respectively. σ_C and σ_N are the specific activities of the shoot for carbon, and of the root for nitrogen. $\dot{W}_{sh}$ and $\dot{W}_r$ are the time derivatives of shoot and root structural dry matter. The continuous lines indicate flow of material; the dashed lines denote control pathways or flows of information.

The storage dry matter (W_S) is of the carbon component is W_C component is W_N so that

where M_C is the molecular ma carbohydrate, $\{CH_2O\}$, then substrate relative to ^{14}N (if the four state variables of the syst

This model does not invoke between shoot and root, which and nitrogen substrates betwee carbon and nitrogen substrates dry matter, whether in shoot of matter is the same as that in t

Specific shoot and root activitie

Carbon and nitrogen substra pools, W_C and W_N of Fig. 1, to the carbon substrate pool is the specific shoot activity (σ_C) structural dry matter, so that

Similarly, the rate of nitrogen

where σ_N is the specific root nitrogen uptake per unit of ro activity (σ_C) is dependent upo concentration and temperatu factors such as soil temperatu

Growth function

The carbon and nitrogen 'c

Following Cooper and Thorn component of the plant, W_G, concentrations, as given by

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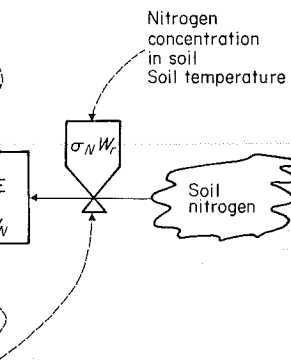
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The storage dry matter (W_S) is also sub-divided into carbon substrate, of which the mass of the carbon component is W_C and nitrogen substrate, of which the mass of the nitrogen component is W_N so that

$$W_S = \frac{M_C}{12} W_C + \frac{M_N}{14} W_N, \tag{4}$$

where M_C is the molecular mass of carbon substrate relative to ^{12}C (if the substrate is carbohydrate, {CH$_2$O}, then $M_C = 30$), and M_N is the molecular mass of nitrogen substrate relative to ^{14}N (if the nitrogen substrate is glutamic acid, then $M_N = 147$). The four state variables of the system are W_{sh}, W_r, W_C and W_N, which are shown in Fig. 1.

This model does not invoke resistances to the flow of carbon and nitrogen substrates between shoot and root, which could give rise to differential concentrations of the carbon and nitrogen substrates between the shoot and the root. It is therefore assumed that the carbon and nitrogen substrates are uniformly distributed with respect to the structural dry matter, whether in shoot or root. Thus, the shoot:root ratio in the total plant dry matter is the same as that in the structural component of the dry matter.

Specific shoot and root activities

Carbon and nitrogen substrates available for growth are contained in the two storage pools, W_C and W_N of Fig. 1, each of which is common to both shoot and root. Input to the carbon substrate pool is a function of the shoot structural dry matter (W_{sh}) and the specific shoot activity (σ_C) which gives the net rate of carbon uptake per unit of shoot structural dry matter, so that the rate of carbon uptake (kg carbon day^{-1}) is

$$\sigma_C W_{sh}. \tag{5}$$

Similarly, the rate of nitrogen uptake by the root is

$$\sigma_N W_r, \tag{6}$$

where σ_N is the specific root activity with respect to nitrogen, and gives the rate of nitrogen uptake per unit of root structural dry matter. The value of the specific shoot activity (σ_C) is dependent upon environmental variables such as light flux density, CO_2 concentration and temperature. Specific root activity (σ_N) might be determined by factors such as soil temperature and soil nitrogen concentration.

Growth function

The carbon and nitrogen 'concentrations' (C and N) are defined by

$$C = \frac{W_C}{W_G} \quad \text{and} \quad N = \frac{W_N}{W_G}. \tag{7}$$

Following Cooper and Thornley (1976, see fig. 1), the growth rate of the structural component of the plant, W_G, is assumed to be a function of the carbon and nitrogen concentrations, as given by

$$\frac{dW_G}{dt} = kCNW_G, \tag{8}$$

where k is a growth rate coefficient. For constant concentrations C and N, this expression gives exponential growth in W_G.

Let f_C and f_N be the fractional carbon and nitrogen contents of plant structural dry matter. These are assumed to be constant (with time), and the same for both shoot and root structural dry matter. The rates at which carbon and nitrogen are being utilized for structural growth are

$$f_C \frac{dW_G}{dt} \quad \text{and} \quad f_N \frac{dW_G}{dt}. \tag{9}$$

Respiration of carbon substrate is ignored here since the specific shoot activity is a net process.

Partitioning function

By differentiation of Eqn (3)

$$\frac{dW_G}{dt} = \frac{dW_{sh}}{dt} + \frac{dW_r}{dt}, \qquad (10)$$

where the term on the left side of this equation is given by eqn (8). Partitioning coefficients, λ_{sh} and λ_r, with

$$\lambda_{sh} + \lambda_r = 1, \qquad (11)$$

are defined to describe the division of newly synthesized structural dry matter between the shoot and the root, so that

$$\frac{dW_{sh}}{dt} = \lambda_{sh}\frac{dW_G}{dt} \quad \text{and} \quad \frac{dW_r}{dt} = \lambda_r\frac{dW_G}{dt}. \qquad (12)$$

From eqns (12) it may be deduced that

$$\lambda_{sh} = \frac{dW_{sh}}{dW_G} \quad \text{and} \quad \lambda_r = \frac{dW_r}{dW_G}, \qquad (13)$$

and that

$$\frac{dW_{sh}}{dW_r} = \frac{\lambda_{sh}}{\lambda_r}. \qquad (14)$$

It is convenient to define a partitioning function $\mathscr{P}$ in terms of the relative rate of specific shoot growth to specific root growth, namely

$$\mathscr{P} = \frac{dW_{sh}/W_{sh}}{dW_r/W_r}. \qquad (15)$$

It is assumed that $\mathscr{P}$ is determined by the ratio of carbon:nitrogen in the storage pools according to

$$\mathscr{P} = \left(\frac{N/\eta_N}{C/\eta_C}\right)^q, \qquad (16)$$

where η_N, η_C and q are parameters. Since the ratio of η_N to η_C is the quantity of importance in Eqn (16), it is assumed that

$$\eta_C + \eta_N = 1. \qquad (17)$$

As shown graphically in Fig. 2, Eqn (16) adjusts the shoot:root partitioning depending upon the nitrogen:carbon ratio (N/C) in the storage pools, and the extent to which this departs from the reference value η_N/η_C. The parameter q determines the degree of control that the plant may exhibit over partitioning. For example, if $q = 0$, there is no control over partitioning, the shoot:root ratio is fixed by the initial conditions of W_{sh} and W_r, and the partitioning pattern does not change. If $q > 1$, partitioning is controlled by the levels of carbon and nitrogen as shown in Fig. 2. Note that as $q \to \infty$, Eqn (16) reduces to an on–off control, and partitioning between shoot and root becomes threshold-controlled.

Note that when

$$\frac{N}{\eta_N} = \frac{C}{\eta_C}, \qquad (18)$$

then

$$\mathscr{P} = 1 \quad \text{and} \quad \frac{dW_{sh}}{W_{sh}} = \frac{dW_r}{W_r}. \qquad (19)$$
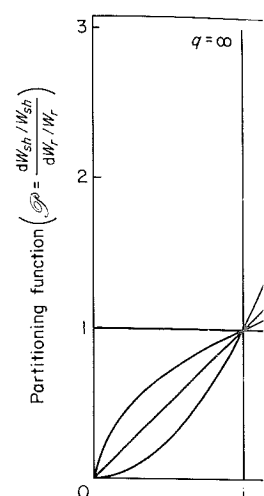

FIG. 2. Partitioning function ($\mathscr{P}$) ‹
carbon:nitrogen ratio for various va
partitioning of newly synth‹

Eqns (18) and (19) describe a st‹
Combining Eqns (11), (14)–(1

$$\lambda_{sh} ‹$$

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$$\lambda_r ‹$$

Dynamic equations

Using the foregoing definition
the four state variables of the s‹

Eqns (3), (7), (8) and (20) are req
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the model, σ_C, σ_N, f_C, f_N, η_C, η_N‹
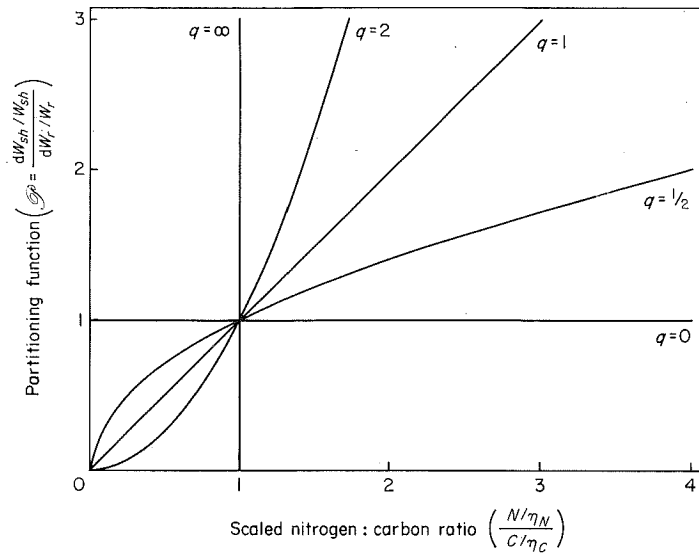and $W_r(0)$ at time $t = 0$, must b‹

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FIG. 2. Partitioning function ($\mathscr{P}$) defined by Eqns (15) and (16), is plotted against the scaled carbon:nitrogen ratio for various values of q giving different levels of control over the proportional partitioning of newly synthesized structural dry matter to the shoot and the root.

Eqns (18) and (19) describe a steady-state situation with a stable partitioning pattern. Combining Eqns (11), (14)–(16), λ_{sh} and λ_r can be obtained, giving

$$\lambda_{sh} = \frac{W_{sh}(N/\eta_N)^q}{W_{sh}(N/\eta_N)^q + W_r(C/\eta_C)^q}$$

and

$$\lambda_r = \frac{W_r(C/\eta_C)^q}{W_{sh}(N/\eta_N)^q + W_r(C/\eta_C)^q}. \qquad (20)$$

Dynamic equations

Using the foregoing definitions and Fig. 1, the four differential equations governing the four state variables of the system can now be written down, giving

$$\frac{dW_C}{dt} = \sigma_C W_{sh} - f_C \frac{dW_G}{dt}, \qquad (21a)$$

$$\frac{dW_N}{dt} = \sigma_N W_r - f_N \frac{dW_G}{dt}, \qquad (21b)$$

$$\frac{dW_{sh}}{dt} = \lambda_{sh} \frac{dW_G}{dt}, \qquad (21c)$$

and

$$\frac{dW_r}{dt} = \lambda_r \frac{dW_G}{dt}. \qquad (21d)$$

Eqns (3), (7), (8) and (20) are required in order that dW_G/dt, λ_{sh} and λ_r can be calculated from the four state variables, W_C, W_N, W_{sh} and W_r. Values for the eight parameters of the model, σ_C, σ_N, f_C, f_N, η_C, η_N, k and q, and four initial values, $W_C(0)$, $W_N(0)$, $W_{sh}(0)$ and $W_r(0)$ at time $t = 0$, must be supplied before Eqns (21) can be integrated.

Steady-state exponential growth

It is assumed that the plant and its component parts are growing exponentially at a specific growth rate μ. For the extensive variables therefore

$$\mu = \frac{1}{X}\frac{dX}{dt} \quad \text{where} \quad X = W_C, W_N, W_{sh} \text{ or } W_r. \tag{22}$$

Eqns (21) become

$$\mu W_C = \sigma_C W_{sh} - f_C \mu W_G, \tag{23a}$$

$$\mu W_N = \sigma_N W_r - f_N \mu W_G, \tag{23b}$$

$$\mu W_{sh} = \lambda_{sh} \mu W_G, \tag{23c}$$

$$\mu W_r = \lambda_r \mu W_G. \tag{23d}$$

Note that Eqns (23c) and (23d) are now equivalent. The fractions of the plant dry matter in the shoot (f_{sh}) or the shoot (f_r) are defined by

$$f_{sh} = \frac{W_{sh}}{W_G} \quad \text{and} \quad f_r = \frac{W_r}{W_G}, \quad \text{with} \quad f_{sh} + f_r = 1. \tag{24}$$

Dividing through Eqns (23a–c) with W_G, and using Eqns (7) and (24), therefore

$$\mu C = \sigma_C f_{sh} - \mu f_C, \tag{25a}$$

$$\mu N = \sigma_N f_r - \mu f_N, \tag{25b}$$

$$\mu f_{sh} = \mu \lambda_{sh}. \tag{25c}$$

Also, Eqn (8) becomes

$$\mu = kCN. \tag{25d}$$

With $f_r = 1 - f_{sh}$, these four equations are to be solved for the four unknowns C, N, f_{sh} and μ.

Elimination of C, N and f_{sh} yields a cubic equation for μ:

$$\mu^3 \frac{1}{k}\left(\frac{1}{\sigma_C^2}\frac{\eta_C}{\eta_N} + \frac{2}{\sigma_C \sigma_N} + \frac{1}{\sigma_N^2}\frac{\eta_N}{\eta_C}\right) - \mu^2\left(\frac{f_C}{\sigma_C} + \frac{f_N}{\sigma_N}\right)^2 + 2\mu\left(\frac{f_C}{\sigma_C} + \frac{f_N}{\sigma_N}\right) - 1 = 0. \tag{26}$$

This equation may be written more simply as

$$\mu^3\left(\frac{\alpha}{k}\right) - \left(\frac{\mu}{\mu_m} - 1\right)^2 = 0, \tag{27}$$

where the two derived parameters, α and μ_m are given by

$$\alpha = \frac{1}{\sigma_C^2}\frac{\eta_C}{\eta_N} + \frac{2}{\sigma_C \sigma_N} + \frac{1}{\sigma_C^2}\frac{\eta_N}{\eta_C} \quad \text{and} \quad \mu_m = \left(\frac{f_C}{\sigma_C} + \frac{f_N}{\sigma_N}\right)^{-1}. \tag{28}$$

The solutions of Eqn (27) may be examined by considering the intersection of the cubic

$$y = \mu^3\left(\frac{\alpha}{k}\right) \tag{29a}$$

with the parabola

$$y = \left(\frac{\mu}{\mu_m} - 1\right)^2. \tag{29b}$$

There is always (for all positive real parameter values) at least one real root for μ. For some parameter values, there are three real roots for μ, but in the cases presented in this paper, it appears that only the lowest root is a stable, physiologically meaningful solution.

If the growth rate coefficient k [Eqn (8)] is large ($k \to \infty$), then from Eqn (27), the specific growth rate μ takes its maximum value at $\mu = \mu_m$, and it does not depend on the partitioning function [Eqn (16)] or its parameters η_C and η_N. For given values of k

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Davidson's functional relations

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Parameter values

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the four unknowns C, N, f_{sh}

μ:

$$\mu\left(\frac{f_C}{\sigma_C}+\frac{f_N}{\sigma_N}\right)-1 = 0.\qquad (26)$$

(27)

$$\left(\frac{f_C}{\sigma_C}+\frac{f_N}{\sigma_N}\right)^{-1}.\qquad (28)$$

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and μ_m, the specific growth rate μ is maximized by minimizing α in Eqn (27); for given values of σ_C and σ_N (these are environmentally determined parameters), this is achieved when

$$\frac{\eta_C}{\eta_N} = \frac{\sigma_C}{\sigma_N},$$

and with Eqn (18), this gives

$$\frac{\eta_C}{\eta_N} = \frac{\sigma_C}{\sigma_N} = \frac{C}{N}.\qquad (30)$$

Thus, a capacity of a plant to adjust its carbon:nitrogen ratio in storage, represented by the parameters η_C and η_N, will enable optimum growth rates to be achieved in a given environment.

Davidson's functional relationship

This hypothesis, concerning the balance between shoot and root sizes and activities, is presented in Eqn (1); in this section, the extent to which the steady-state exponential growth solutions of the current model are compatible with Eqn (1) are examined.

From Eqns (25a and b) elimination of μ gives, in the form of Eqn (1),

$$f_{sh}\,\sigma_C = \left(\frac{C+f_C}{N+f_N}\right) f_r\,\sigma_N.\qquad (31)$$

For Eqn (1) to be valid, this means that

$$\frac{C+f_C}{N+f_N} = \text{constant.}\qquad (32)$$

Eqn (32) implies that one of the following conditions is satisfied:

(i) $C \ll f_C$, $N \ll f_N$ and f_C/f_N constant;

(ii) $C \gg f_C$, $N \gg f_N$ and C/N constant;

(iii) f_C, f_N, C and N are all constant;

(iv) $C \propto f_C$, $N \propto f_N$ and f_C/f_N is constant.   (33)

Conditions (ii) and (iii) seem rather unlikely. Condition (i), that the carbon and nitrogen levels in the storage pools are small relative to the levels of carbon and nitrogen in structure, also does not seem very likely to hold over a wide range of conditions, although this may well provide the reason why Eqn (1) sometimes appears to apply over a restricted range of conditions; condition (i) is identical with the result obtained by Thornley [1972b, Eqn (43)] using a more detailed model. Condition (iv) does not seem very plausible, as it implies that the carbon and nitrogen contents of structural materials such as proteins and cell wall substances vary with substrate availability.

RESULTS

Parameter values

The equations derived above, and especially the steady-state equations, provide a powerful tool for exploring interactions between specific environmental conditions and plant growth strategies. This is readily accomplished by setting the parameters which characterize a particular physiological status of the plant (i.e. k, f_C, f_N, η_C and η_N) to fixed values while varying those parameters which reflect environmental conditions (i.e. specific shoot and root activities, σ_C and σ_N) and observing the resultant growth activity. The unknowns of interest are μ, f_{sh}, f_r, C and N.

The following parameter values were chosen, guided by the data on the tomato plant of Cooper and Thornley (1976, figs 1 and 4).

$$k = 25 \text{ day}^{-1} \text{ (kg carbon kg}^{-1} \text{ structure)}^{-1} \text{ (kg nitrogen kg}^{-1} \text{ structure)}^{-1}, \quad (34a)$$

$$f_C = 0\cdot45 \text{ kg carbon (kg structure)}^{-1}, \quad (34b)$$

and $f_N = 0\cdot03$ kg nitrogen (kg structure)$^{-1}$. $\quad (34c)$

The parameter q only affects the dynamic solutions and the approach to steady-state growth; this is an important control parameter for changing environmental conditions, and values of

$$q = 2 \text{ and } q = 6 \quad (34d)$$

were used. The environmental parameters σ_C and σ_N were varied over a range, but physiologically reasonable reference values are

$$\sigma_C = 0\cdot18 \text{ kg carbon (kg shoot structure)}^{-1} \text{ day}^{-1}, \quad (34e)$$

and $\sigma_N = 0\cdot10$ kg nitrogen (kg root structure)$^{-1}$ day^{-1}. $\quad (34f)$

Finally, the parameters η_C and η_N [Eqns (16) and (17)] were assigned a ratio of one-half the ratio at which the specific growth rate (μ) is a maximum [Eqn (30)], so that

$$\frac{\eta_C}{\eta_N} = 0\cdot5 \frac{\sigma_C}{\sigma_N},$$

giving $\eta_C = 0\cdot474$ and $\eta_N = 0\cdot526$.

Steady-state solutions

These were obtained in two ways: by solving Eqn (26) for μ, and hence obtaining C, N, f_{sh} and f_r from Eqns (25) and (24); or by using the simulation program CSMP (IBM, 1967) to integrate Eqns (21) until steady-state growth was obtained. The two methods yielded identical results.

In Fig. 3 the effects of varying the specific shoot activity σ_C or the specific root activity σ_N on the specific growth rate μ and the shoot:root ratio f_{sh}/f_r are shown. The solutions were obtained for two situations. First, the partitioning parameters η_C and η_N were kept constant as σ_C or σ_N were varied, to represent the case where the plant is not able to change its partitioning strategy as the environment changes, and this gives sub-optimal growth. Second, to illustrate an optimal growth strategy, η_C and η_N were varied as σ_C or σ_N vary, so that Eqn (30) is always satisfied, giving a maximum specific growth rate μ for all combinations of shoot and root environments. The difference between the fixed strategy and the optimal strategy can be substantial. With the parameter values assumed, the specific growth rate μ is more sensitive to changes in the shoot environment than the root environment, but changes in either shoot or root specific activity result in proportionally smaller changes in specific growth rate.

The changes in shoot:root ratio in Fig. 3 are similar to many experimental observations of shoot:root ratios of plants in different shoot and root environments; this is also the case for the carbon:nitrogen ratios which satisfy Eqn (18). However, Davidson's hypothesis of Eqn (1) about a balance between the total activities of shoot and root is not obeyed in the solutions of Fig. 3; this is shown by the bottom rows in Tables 1(a) and 2(a), where specific shoot and root activities at the ends of the range are taken, and the parameter values are the same as in Fig. 3. Alternatively, if the carbon:nitrogen ratio in storage (C/N) is made equal to that in structure by choosing
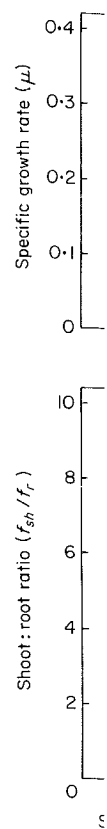
$$\frac{\eta_C}{\eta_N} = \frac{f_C}{f_N},$$

FIG. 3. Dependence of (a) specific
and root activities, σ_C and σ_N. c
Parameters are given by Eqns (34
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TABLE 1. *Steady-state expon*
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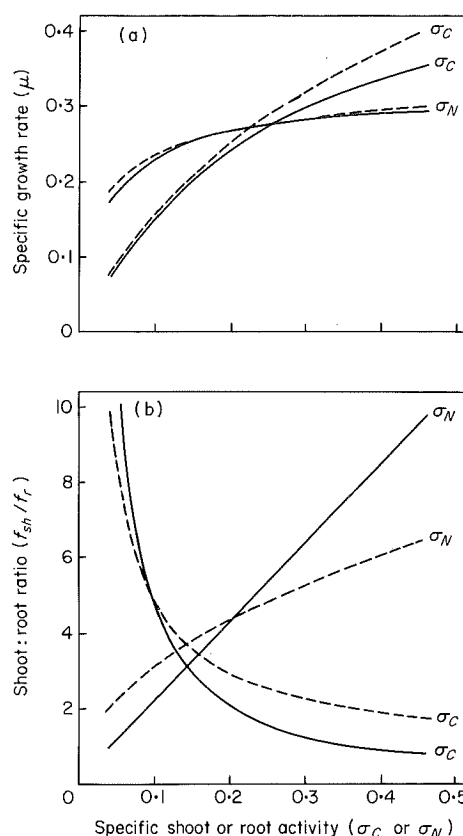... of the range are taken, and
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FIG. 3. Dependence of (a) specific growth rate (μ) and (b) shoot: root ratio (f_{sh}/f_r) on the specific shoot and root activities, σ_C and σ_N. σ_C or σ_N vary over the range shown, while $\sigma_N = 0.1$ or $\sigma_C = 0.18$. Parameters are given by Eqns (34a–c). The continuous lines give the steady-state exponential growth solutions for $\eta_C = 0.474$ and $\eta_N = 0.526$; the dashed lines give optimal growth with η_C and η_N given by Eqns (30) and (17), varying as σ_C or σ_N vary.

TABLE 1. *Steady-state exponential growth solutions: specific shoot activity varied with specific root activity (σ_N) held constant at 0.10. Parameters as in Eqns (34a, b and c)*

(a) $\eta_C = 0.474$ and $\eta_N = 0.526$

σ_C	0.08	0.44
μ	0.132	0.353
$\sigma_C f_{sh}$	0.069	0.199
$\sigma_N f_r$	0.014	0.055
$\dfrac{\text{Total shoot activity}}{\text{Total root activity}}$	4.87	3.63

(b) $\eta_C/\eta_N = f_C/f_N$ gives $\eta_C = 0.938$ and $\eta_N = 0.063$

σ_C	0.08	0.44
μ	0.108	0.369
$\sigma_C f_{sh}$	0.076	0.341
$\sigma_N f_r$	0.0051	0.0226
$\dfrac{\text{Total shoot activity}}{\text{Total root activity}}$	15.00	15.00

TABLE 2. *Steady-state exponential growth solutions: specific root activity varied with specific shoot activity (σ_C) held constant at 0·18. Parameters as in Eqns (34a–c)*

(a) $\eta_C = 0.474$ and $\eta_N = 0.526$

σ_N	0·04	0·24
μ	0·171	0·275
$\sigma_C \, f_{sh}$	0·090	0·151
$\sigma_N \, f_r$	0·020	0·039
$\dfrac{\text{Total shoot activity}}{\text{Total root activity}}$	4·51	3·91

(b) $\eta_C/\eta_N = f_C/f_N$ gives $\eta_C = 0.938$ and $\eta_N = 0.063$

σ_N	0·04	0·24
μ	0·178	0·212
$\sigma_C \, f_{sh}$	0·139	0·172
$\sigma_N \, f_r$	0·0092	0·0114
$\dfrac{\text{Total shoot activity}}{\text{Total root activity}}$	15·00	15·00
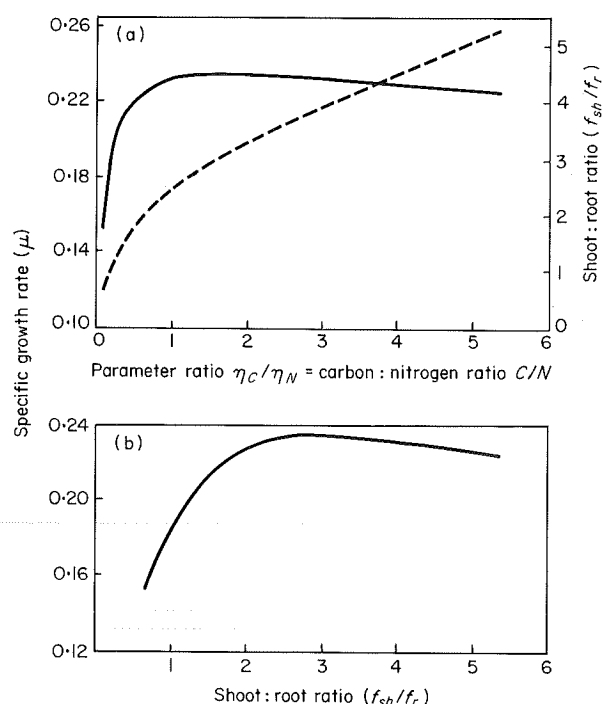
FIG. 4. (a) Dependence of the specific growth rate μ (continuous line) and the shoot:root ratio f_{sh}/f_r (dashed line) on the parameters η_C and η_N and hence on the storage carbon:nitrogen ratio C/N. Parameter values as in Eqns (34a–f). A maximum value of μ is obtained when $\eta_C/\eta_N = \sigma_C/\sigma_N = 1.8$ [Eqn (30)]. In (b), the relationship between the specific growth rate μ and the shoot:root ratio f_{sh}/f_r is shown; this is drawn from the values given in (a).
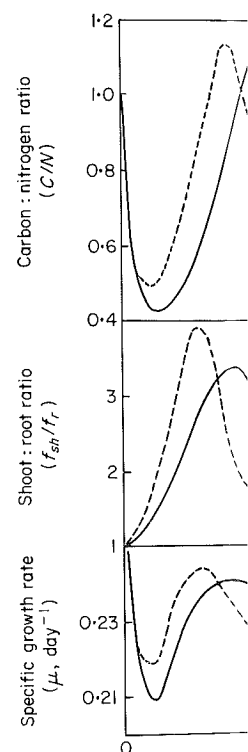
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The effects of maximizing
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Dynamic solutions

The time-dependent behavio
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FIG. 5. Dynamic solutions are sho
(f_{sh}/f_r) and (c) the specific growth
as in Eqns (34a–g); initial condit
Integration by

so that condition (iv) of (33) is satisfied [due to Eqn (18) being true in the steady-state], then the total activities of the shoot and root are in balance. This is illustrated in Tables 1(b) and 2(b).

The effects of maximizing the overall specific growth rate μ by adjusting the carbon:nitrogen balance in storage are further illustrated in Fig. 4. This was accomplished by varying the ratio of the parameters η_C and η_N over a range of values from less than to greater than the ratio of the specific shoot activity to specific root activity. The specific growth rate is maximized when Eqn (30) holds. With the assumed parameter values, a low carbon:nitrogen ratio in storage can be seen to have an important effect on μ. A lowering of the ratio from the level which results in a maximum growth rate sharply reduces μ; on the other hand, large increases in the carbon:nitrogen level can be seen to reduce μ in a more gradual way [Fig. 4(a)]. This response follows that described by Wareing and Partrick (1975): a low carbon:nitrogen ratio indicates a 'source-limiting' condition where the overall utilization of assimilates (hence, growth rate) is limited by carbon availability whereas a high carbon:nitrogen ratio indicates a 'sink-limiting' condition where growth is limited by nitrogen availability.

Dynamic solutions

The time-dependent behaviour of the model is illustrated in Fig. 5, which shows that a steady-state condition is achieved for each of the variables plotted. The oscillations prior

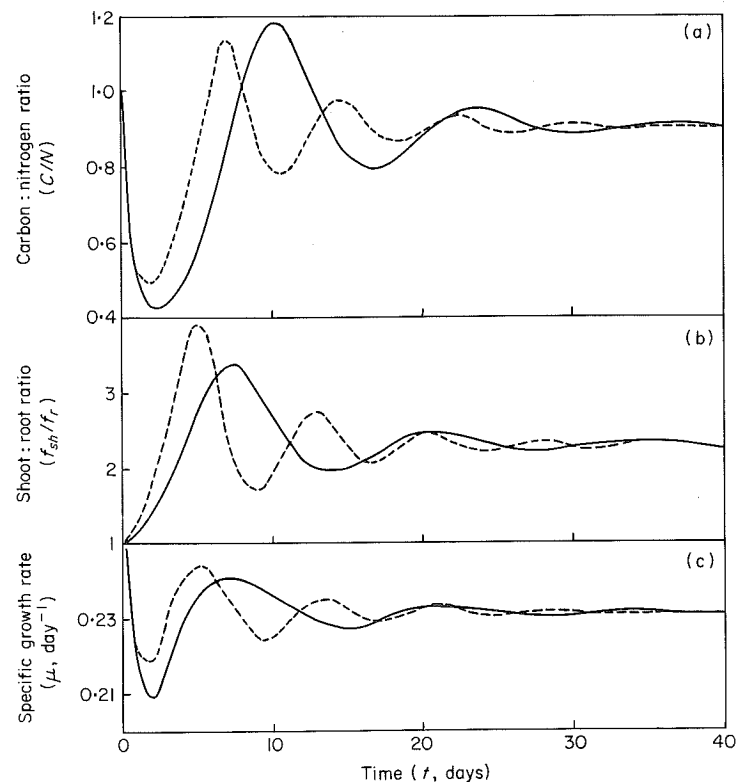FIG. 5. Dynamic solutions are shown for (a) the carbon:nitrogen ratio (C/N), (b) the shoot:root ratio (f_{sh}/f_r) and (c) the specific growth rate (μ). Continuous line, $q = 2$; dashed line, $q = 6$. Parameters as in Eqns (34a–g); initial conditions ($t = 0$) of $W_{sh} = 0.1$, $W_r = 0.1$, $W_C = 0.025$ and $W_N = 0.25$. Integration by Euler's method with a time-step, $\Delta t = 0.05$ day.

to the convergence to the steady-state level are affected by the initial conditions and the value of q in Eqn (16). The larger value of q in Fig. 5 gives more rapid oscillations, and an earlier convergence to the steady-state level. Comparison of figs 7 and 8 of Cooper and Thornley (1976), who used a transport-resistance based partitioning model, with Fig. 5 here, suggests that the resistance model is capable of giving more highly damped behaviour.

DISCUSSION

The model presented here provides another possible approach to the partitioning problem, one which might be useful for certain types of plant, or for plants at particular stages in their growth cycle. It provides, by Eqns (31) and (32) and the conditions in (33), a possible interpretation of the validity (or lack of validity) of Davidson's (1969) functional-balance hypothesis.

Perhaps more important is the attempt, in the partitioning function of Eqns (15) and (16), to parameterize what might be anthropomorphically termed, the partitioning strategy of the plant. It is often suggested that the simplest strategy for a plant to attain a maximum growth rate would be to divert a minimum proportion of its assimilates to roots (in order to provide essential nutrients and water), while using the greatest proportion for shoot growth (Russell, 1977; Wareing and Patrick, 1975; Mooney, 1972). However, the interplay of a variety of factors at the whole-plant level concerning the procurement and utilization of growth substances and the overall balance of plant growth tend to complicate this simple idea. This model enables one to start examining the implications of various growth strategies in relation to different environments. For example, a plant that must survive in a range of environments may not be capable of optimum performance in a given environment [cf. Eqn (30)].

The partitioning function could be extended to take account of additional substrates, growth substances, and more than two compartments.

ACKNOWLEDGEMENTS

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C	carbon concentration
f_C, f_N	fractional carbon and carbon (nitrogen) kg⁻
k	growth rate coefficient kg⁻¹ structure)⁻¹
N	nitrogen concentration
$\mathscr{P}$	partitioning function [
q	parameter in the parti
W_C	mass of substrate carb
W_G	mass of plant structur
W_N	mass of substrate nitr
W_r	mass of root structura
W_{sh}	mass of shoot structui
η_C, η_N	parameters in the part
λ_r, λ_{sh}	partitioning coefficient
μ	specific growth rate [e
σ_C, σ_N	specific activities of sh (nitrogen)⁻¹: kg carbc

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PRINCIPAL SYMBOLS

C carbon concentration [eqn (7)]: kg carbon kg^{-1} structural dry matter

f_C, f_N fractional carbon and nitrogen contents of structural dry matter [eqn (9)]: kg carbon (nitrogen) kg^{-1} structural dry matter

k growth rate coefficient [eqn (8)]: day^{-1} (kg carbon kg^{-1} structure)$^{-1}$ (kg nitrogen kg^{-1} structure)$^{-1}$

N nitrogen concentration [eqn (7)]: kg nitrogen kg^{-1} structural dry matter

$\mathscr{P}$ partitioning function [eqns (15) and (16)]

q parameter in the partitioning function [eqn (16)]

W_C mass of substrate carbon in plant [eqn (4)]: kg carbon

W_G mass of plant structural dry matter [eqn (2)]: kg structural dry matter

W_N mass of substrate nitrogen in plant [eqn (4)]: kg nitrogen

W_r mass of root structural dry matter [eqn (3)]: kg structural dry matter

W_{sh} mass of shoot structural dry matter [eqn (3)]: kg structural dry matter

η_C, η_N parameters in the partitioning function [eqn (16)]

λ_r, λ_{sh} partitioning coefficients [eqns (11) and (20)]

μ specific growth rate [eqn (22)]: day^{-1}

σ_C, σ_N specific activities of shoot (root) with respect to carbon [eqns (5) and (6)] (nitrogen)$^{-1}$: kg carbon (nitrogen) day^{-1} kg^{-1} shoot (root) structure

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