Modelling Allocation with Transport / Conversion Processes

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A shoot:root carbon:nitrogen allocation model, based on the two *processes* of transport and chemical conversion, is described and explored. The view is proposed that *all* allocation models, whether built for the purposes of theoretical investigation or practical application, should start with this irreducible framework. In the present implementation, the processes operate according to: for substrate sources, dependence on shoot and root sizes, with possible product inhibition; for transport, movement down a substrate concentration gradient; for substrate sinks or utilization, linear bisubstrate kinetics. The dynamic and equilibrium properties of the model are explored. Failure of this approach to allocation will indicate to the modeller that additional mechanisms to control the processes are needed, and the mode of failure will indicate the type of mechanisms required. Additional mechanisms are discussed which may involve hormones or teleonomic (goal-seeking) controls, and may be added to the irreducible framework. However, these additions should not replace the irreducible framework of transport and chemical conversion, because they do not in reality. Modifications to the basic model to reflect some possibilities such as ontogenesis with the transition from exponential growth towards a steady state or with the scaling of within-plant transport resistances, the influence of hormones, and active transport, are described.

1 Introduction

The objective of this paper is to describe the transport-resistance (TR) model for simulating dry matter allocation in plants, and to explain why this approach provides an irreducible frame-

work for allocation modelling, on to which more elaborate hypotheses may be grafted.

The TR approach was proposed by Thornley (1972) for shoot:root partitioning in relation to the availability of C and N. In this approach substrate sources are connected with transport resistances to substrate sinks where chemical/

biochemical conversions take place. The method is described as 'irreducible' because transport and chemical conversion are processes which must take place in order that allocation is accomplished, although how these processes are controlled is arguable. The TR model has been employed by Wann et al. (1978) and Wann and Raper (1984) for simulating tobacco growth; Mäkelä and Sievänen (1987) have shown that a more aggregated teleonomic allocation model is embedded in the TR model; Rastetter et al. (1991) have used it in a forest and general ecosystem model; Thornley (1991) and Thornley and Cannell (1996) have applied it in a forest plantation model; Dewar (1993) has extended the model to include water transport of N to the leaves and shown that this extension does not significantly change the predictions obtained with the basic formalism; and Minchin et al. (1993) demonstrated that the model can account for a number of experimentally observed source-sink relations. More recently the TR model has been applied to three substrates, carbon, nitrogen and phosphorus (Thornley, 1995), where there is also some discussion of other approaches to allocation. In spite of these developments, the model has not been used extensively in practical applications, although its applications have always been successful. Neither has it been replaced by an alternative mechanistic theory.

Allocation in plants has been the subject of several quite recent and comprehensive reviews by Wilson (1988), Marcelis (1993), and Cannell and Dewar (1994). In his final sentence, Wilson (1988) suggests 'in so far as a working hypothesis is needed, Ockham's Razor indicates that it should be of Thornley's (1972) type.' Marcelis (1993) concludes that 'the approach of potential demand and priority functions is most valuable for simulation ... . However, it requires extensive input data.' He also states that 'transport and sink regulation models are mechanistic and might give valuable results. However, their application is limited due to their complexity and difficulties to determine the parameters.' Cannell and Dewar (1994) state 'although there is much information on the distribution of dry matter in plants, there is surprisingly little understanding of the mechanisms'; 'Progress in understanding ... assimilate allocation in plants may have been ham-

pered by regarding allocation as a single act'; 'Allocation is the outcome of many processes rather than a process in its own right'.

Wilson (1988) proposes that the TR approach is applied initially to these problems, and modified or abandoned when it fails. Cannell and Dewar (1994) give no unequivocal recommendation on the way forward, although they stress the importance of developing methods of measuring the concentrations and fluxes of carbon and other nutrients, and elsewhere, Dewar et al. (1994) state that 'By treating simultaneously the uptake, transport and utilization of carbon, nutrients and water, source-sink models of free growth represent the most promising way forward'. Thus, while many workers see the value of the TR model as an explanatory theory, one main criticism levelled at it concerns the data required to parameterize it for practical applications.

Basically there are only two significant types of process in the plant: transport, and chemical/biochemical conversion. (Morphogenesis can be considered in terms of these two processes also.) Both processes are necessary and are sufficient to accomplish allocation. Allocation is the outcome of the processes of substrate supply, transport and utilization. The mechanisms which determine the rates at which these processes operate may be simple, or complex, and may depend to a greater or lesser extent on hormones, or on constraints which have arisen through evolution and give apparently goal-oriented behaviour ['goal-oriented' responses can be considered as illusory depending on the position of the observer (Monod, 1974); an alternative 'objective' description can always be constructed (e.g. Thornley and Johnson, 1990, pp. 11–12)]. It will be argued here that, within the TR framework, quite simple mechanistic assumptions give rise to a surprising variety of realistic responses, and the formalism is transparent, robust, and easily modified. In addition, it is argued that an indirect parameterization is straightforward, although direct parameter estimates cannot be provided until methods are found of measuring substrate concentrations in the phloem and elsewhere in the plant. Finally, the limitations of purely goal-seeking models not based within a substrate transport/utilization framework are discussed.

2 The Transport-Resistance Model of Allocation

This is shown in Fig. 1. Plant dry matter is considered to consist of structure and of substrates [carbon (C) and nitrogen (N)]. For a shoot:root allocation model, plant structure is divided into shoot (sh) and root (rt). Separate carbon and nitrogen substrate pools exist in the shoot and root. There are therefore six mass state variables, denoted by M + subscript in Fig. 1.

The basic model with the default parameter values (Table 1) simulates *balanced exponential growth (BEG)*: that is, growth where the extensive variables (the M + subscript state variables in Fig. 1) increase exponentially at a constant specific growth rate, and the intensive variables (substrate concentrations, shoot:root ratio) are constant. Balanced exponential growth is often approximately exhibited by young plants and crops, and it provides a valuable idealized situation for exploring the properties of a heuristic model such as this one.

However, in many forest and grassland plant ecosystems, the *steady state (SS)* may be a more appropriate approximation. In the steady state all variables are constant. It is helpful if the model can easily be used to explore allocation in a steady state as well as in balanced exponential growth. In the equations, therefore, a switch σ_{SS} is provided which makes the system eventually

approach a steady-state [see eqns (3), (5) and (6)]. The steady state requires increasing litter fluxes of shoot and root structure, and a ceiling on assimilation of C and N uptake (photosynthesis P, nitrogen uptake U_N: Fig. 1). The model can be used to explore the transition from balanced exponential growth (small plant) to a steady state (state variables constant).

One other option is provided: our experience with these and other models (e.g. Thornley, 1995) has shown that the dynamic responses of the system are highly responsive to the presence or absence of product inhibition (PI) of assimilation or uptake: that is, the shoot C concentration C_{sh} inhibits photosynthesis, and the root N concentration N_{rt} inhibits N uptake. These mechanisms are included with the default values of the parameters J_C and J_N [eqns (5), (6)], and with the default value of a product inhibition switch σ_{PI} ($\sigma_{PI} = 1$). By making $\sigma_{PI} = 0$, product inhibition is switched off, both for balanced exponential growth and the steady state. See below for more discussion of product inhibition of carbon assimilation and nitrogen uptake.

2.1 Shoot and Root Structure

Variables and parameters are listed in Table 1. The differential equations for the two state variables M_{sh} and M_{rt} are
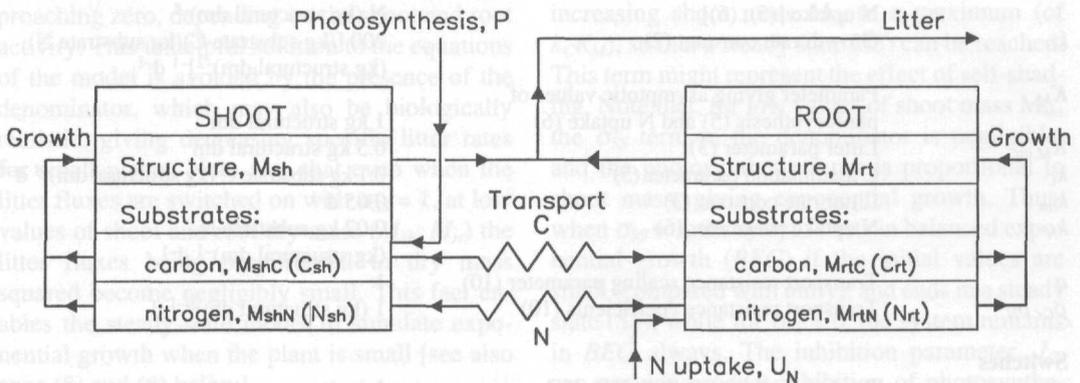
Fig. 1. Transport-resistance model of allocation with C, N substrates. The six state variables of the model are shown (M with subscript); the four substrate concentrations are in brackets (after Thornley 1972).

Table 1. Definitions of symbols, units and numerical values. C, N, dm denote carbon, nitrogen, dry mass. The number of the equation where the symbol is introduced or explained is given.

Symbol	Definition	Units
State variables		
M_{rt}, M_{sh}	Structural dm in root, shoot (1)	kg structural dm
M_{rtC}, M_{shC}	Substrate C in root, shoot (4)	kg C substrate
M_{rtN}, M_{shN}	Substrate N in root, shoot (4)	kg N substrate
Principal other variables		
C_{rt}, C_{sh}	C substrate concentrations in root, shoot (9)	kg C substrate (kg structural dm)$^{-1}$
$\bar{C}, \bar{N}$	Mean C,N substrate concentrations in plant (17)	kg C, N substrate (kg structural dm)$^{-1}$
$f_{G,rt}, f_{G,sh}$	Growth fractions allocated to root, shoot (13)	
f_{rt}, f_{sh}	Fractions of plant structural dm in root, shoot (14)	
G_{rt}, G_{sh}	Growth rates of root, shoot (2)	kg structural dm d^{-1}
$I_{P,shC}$	Input of substrate C from photosynthesis into shoot substrate C pool (5)	kg substrate C d^{-1}
$I_{T,rtC}, I_{T,shN}$	Input by transport of substrate C, N to root C, shoot N substrate pools (8)	kg substrate C, N d^{-1}
$I_{U,rtN}$	Input of substrate N from N uptake into root substrate N pool (6)	kg substrate N d^{-1}
L_{rt}, L_{sh}	Litter fluxes from root, shoot (3)	kg structural dm d^{-1}
M	Plant structural dm (12)	kg structural dm
N_{rt}, N_{sh}	N substrate concentrations in root, shoot (9)	kg N substrate (kg structural dm)$^{-1}$
$O_{G,rtC}, O_{G,shC}$	Outputs to growth of substrate C from root, shoot substrate C pools (7)	kg substrate C d^{-1}
$O_{G,rtN}, O_{G,shN}$	Outputs to growth of substrate N from root, shoot substrate N pools (7)	kg substrate N d^{-1}
$O_{T,shC}, O_{T,rtN}$	Outputs to transport of substrate C, N from shoot C substrate, root N substrate pools (8)	kg substrate C, N d^{-1}
$r_{C,shrt}, r_{N,rtsh}$	Resistances between shoot and root for substrate C, N transport (11)	(kg structural dm)$^{-1}$ d
$r_{C,rt}, r_{C,sh}$, $r_{N,rt}, r_{N,sh}$	Resistances associated with root, shoot for substrate C, N transport (10)	(kg structural dm)$^{-1}$ d
μ	Plant specific growth rate (15)	d^{-1}
Parameters		Numerical value and units
f_C, f_N	Fractions of C, N in structural dm (7)	0.5, 0.25 kg C, N (kg structural dm)$^{-1}$
J_C, J_N	Inhibition constants of C assimilation and N uptake [(5), (6)]	0.1, 0.01 kg substrate C, N (kg structural dm)$^{-1}$
k_G	Growth rate constant (2)	200 [(kg substrate C)(kg substrate N) (kg structural dm)$^{-2}$]$^{-1}$ d^{-1}
K_M	Parameter giving asymptotic values of photosynthesis (5) and N uptake (6)	1 kg structural dm
$K_{M,litt}$	Litter parameter (3)	0.5 kg structural dm
k_C	C assimilation parameter (5)	0.1 kg substrate C (kg structural dm)$^{-1}$ d^{-1}
k_{litt}	Litter rate constant (3)	0.05 d^{-1}
k_N	N uptake parameter (6)	0.02 kg substrate N (kg structural dm)$^{-1}$ d^{-1}
q	Transport resistance scaling parameter (10)	1
ρ_C, ρ_N	Transport resistance coefficients (10)	1 (kg structural dm)$^{q-1}$ d
Switches		
σ_{PI}	Product inhibition switch [(5), (6)]	1 (on)
σ_{SS}	Steady-state growth switch [(3), (5), (6)]	0 (off)

$$\frac{dM_{sh}}{dt} = G_{sh} - L_{sh}, \quad \frac{dM_{rt}}{dt} = G_{rt} - L_{rt} \quad (1)$$

t (d) is the time variable. The input functions G_{sh} and G_{rt} are from growth. Growth is assumed simply proportional to the product of the substrate concentrations (cf. equation 1 of Thornley 1972):

$$G_{sh} = k_G M_{sh} C_{sh} N_{sh}, \quad G_{rt} = k_G M_{rt} C_{rt} N_{rt} \quad (2)$$

$$k_G = 200 \text{ [(kg substrate C)(kg substrate N)}$$
$$\text{(kg structure}^{-2})]^{-1} \text{ d}^{-1}.$$

k_G is a growth parameter, which is assumed to be the same for shoot and root. The substrate concentrations, C and N, subscripted sh for shoot and rt for root, are defined in eqns (9).

The output functions L_{sh} and L_{rt} are litter fluxes with

$$L_{sh} = \frac{\sigma_{SS} k_{litt} M_{sh}}{1 + K_{M,litt} / M_{sh}}, \quad L_{rt} = \frac{\sigma_{SS} k_{litt} M_{rt}}{1 + K_{M,litt} / M_{rt}} \quad (3)$$

$\sigma_{SS} = 0$ (BEG), 1 (SS);
$k_{litt} = 0.05 \text{ d}^{-1}$, $K_{M,litt} = 0.5$ kg structure.

The litter fluxes are switched on by setting the parameter $\sigma_{SS} = 1$ to give a steady state (SS). If $\sigma_{SS} = 0$, then there are no litter fluxes and balanced exponential growth (BEG) occurs. k_{litt} is a rate constant. The denominator in the litter function ensures that the litter flux decreases at low values of shoot or root structure quadratically and a steady state is always attained. Without the denominator present (i.e. with $K_{M,litt} = 0$), the plant may 'die', with all the state variables approaching zero, depending on the shoot and root activity. This unhelpful solution to the equations of the model is avoided by the presence of the denominator, which may also be biologically realistic, giving decreasing specific litter rates for small plants. Note also that even when the litter fluxes are switched on with $\sigma_{SS} = 1$, at low values of shoot and root dry mass (M_{sh}, M_{rt}) the litter fluxes being proportional to dry mass squared become negligibly small. This fact enables the steady-state model to simulate exponential growth when the plant is small [see also eqns (5) and (6) below].

2.2 Carbon and Nitrogen Substrates

The differential equations for the masses of C and N substrates in shoot sh and root rt are

$$\frac{dM_{shC}}{dt} = I_{P,shC} - O_{G,shC} - O_{T,shC}$$

$$\frac{dM_{rtC}}{dt} = I_{T,rtC} - O_{G,rtC}$$

$$\frac{dM_{shN}}{dt} = I_{T,shN} - O_{G,shC} \quad (4)$$

$$\frac{dM_{rtN}}{dt} = I_{U,rtN} - O_{G,rtN} - O_{T,rtN}$$

The notation on the right side of these equations is: I = input, O = output; with subscripts: P = photosynthesis, G = growth, T = transport, U = uptake. The right side terms are defined below. Substrate loss with the litter fluxes [eqns (3)] is assumed to be negligible.

2.2.1 Photosynthesis

The input of C from photosynthesis is

$$I_{P,shC} = \frac{k_C M_{sh}}{(1 + \sigma_{SS} M_{sh} / K_M)(1 + \sigma_{PI} C_{sh} / J_C)} \quad (5)$$

$k_C = 0.1$ kg C (kg shoot structure)$^{-1}$ d^{-1},
$K_M = 1$ kg structure, $\sigma_{PI} = 1$,
$J_C = 0.1$ kg substrate C (kg structure)$^{-1}$.

k_C is a photosynthetic parameter. The term in the denominator switched on by $\sigma_{SS} = 1$ [default value 0, see eqn (3)], limits photosynthesis with increasing shoot mass M_{sh} to a maximum (of $k_C K_M$), so that a steady state (SS) can be reached. This term might represent the effect of self-shading. Note that, for low values of shoot mass M_{sh}, the σ_{SS} term in the denominator is negligible, and the photosynthetic input is proportional to shoot mass, giving exponential growth. Thus, when $\sigma_{SS} = 1$, the system starts in balanced exponential growth (BEG) if the initial values are small (compared with unity), and ends in a steady state (SS), while for $\sigma_{SS} = 0$, the system remains in BEG always. The inhibition parameter, J_C, can provide product inhibition of photosynthesis. Although the evidence for product inhibition of photosynthesis is much argued (e.g. Geiger

1976, Sharkey 1985, Blechschmidt-Schneider et al. 1989), the effect of product inhibition of photosynthesis [or N uptake: eqn (6)] on dynamic responses is so great that it is included as the default option in the model. Product inhibition could operate indirectly, e.g. via other processes such as increased respiration or exudation, rather than directly as assumed here. Setting the switch σ_{PI} to zero makes it inoperative. With $J_C = 0.1$, product inhibition of photosynthesis becomes significant when the shoot C substrate concentration is ~0.1 or larger.

2.2.2 Nitrogen Uptake

The input of N from root uptake is

$$I_{U,rtN} = \frac{k_N M_{rt}}{(1 + \sigma_{SS} M_{rt} / K_M)(1 + \sigma_{PI} N_{rt} / J_N)} \quad (6)$$

$k_N = 0.02$ kg N (kg root structure)$^{-1}$ d^{-1},
$K_M = 1$ kg structure,
$J_N = 0.01$ kg substrate N (kg structure)$^{-1}$

k_N is a nitrogen uptake rate parameter. The maximum N uptake rate is $k_N K_M$ for the steady-state scenario ($\sigma_{SS} = 1$) when M_{rt} is large. For low values of root mass M_{rt}, the σ_{SS} term in the denominator is negligible, and the N uptake rate is proportional to root mass, giving exponential growth. J_N provides for inhibition of N uptake depending on the internal concentration of N in the root; the inclusion of this mechanism reduces oscillatory/overshoot effects in the model. The default value of the switch σ_{PI} is 1 [eqn (5)]; setting $\sigma_{PI} = 0$ removes product inhibition from the model. To-date there appears to be no experimental work that addresses the question of possible product inhibition of N uptake in plants. An analysis of an active-transport mechanism across a membrane suggests that product inhibition will occur at some product concentration (e.g. Thornley and Johnson, 1990, equation (S4.6a), p. 592, exercise 4.6, p. 118). Leakage of ions from the root may also be important at higher concentrations of internal substrates (Bouma and De Visser, 1993). Root exudation is another possible mechanism of substrate loss, which is ignored.

2.2.3 Growth

The outputs of substrate C and N for utilization in the growth processes in the shoot and root are

$$O_{G,shC} = f_C G_{sh}, \quad O_{G,riC} = f_C G_{rt};$$
$$O_{G,shN} = f_N G_{sh}, \quad O_{G,rtN} = f_N G_{rt}; \quad (7)$$

$$f_C = 0.5, \quad f_N = 0.025, \text{ kg C, N (kg structure)}^{-1}.$$

The fractional C, N contents of structure are denoted by f_i, $i = $ C, N. The growth rates G_{sh} and G_{rt} are defined in eqns (2).

2.2.4 Transport

The transport fluxes are

$$O_{T,shC} = I_{T,rtC} = \frac{C_{sh} - C_{rt}}{r_{C,shrt}},$$
$$I_{T,shN} = O_{T,rtN} = \frac{N_{rt} - N_{sh}}{r_{N,rtsh}} \quad (8)$$

Transport of both C and N substrates is proportional to the concentration difference divided by a resistance. The resistances between shoot and root for C and N substrate transport, $r_{C,shrt}$ and $r_{N,rtsh}$, are obtained by summing components associated with the shoot and root as stated in eqn (11) below. Balanced exponential growth can only occur if the resistances are proportional to the reciprocal of plant mass. This is because a plant of twice the size, growing at the same specific rate, requires transport fluxes that are twice as large with the same concentrations in the shoot and root. Thus transport resistances which are proportional to the reciprocal of plant mass are needed.

2.3 Definitions

The C, N substrate concentrations are

$$C_{sh} = \frac{M_{shC}}{M_{sh}}, \quad N_{sh} = \frac{M_{shN}}{M_{sh}},$$
$$C_{rt} = \frac{M_{rtC}}{M_{rt}}, \quad N_{rt} = \frac{M_{rtN}}{M_{rt}} \quad (9)$$

The transport resistances, with units of (kg structural dry mass)$^{-1}$ d, associated with root and shoot, and C and N substrates are

$$r_{C,rt} = \frac{\rho_C}{M_{rt}^q}, \quad r_{C,sh} = \frac{\rho_C}{M_{sh}^q},$$

$$r_{N,rt} = \frac{\rho_N}{M_{rt}^q}, \quad r_{N,sh} = \frac{\rho_N}{M_{sh}^q} \qquad (10)$$

$$\rho_C = \rho_N = 1 \text{ (kg structural dm)}^{q-1} \text{ d}, \ q = 1$$

ρ_C, ρ_N are specific transport resistances for C and N substrate transport. q is a scaling parameter which depends on architecture. The default value of unity is needed if balanced exponential growth is to be possible. Dewar (personal communication) commenting on an early version of this manuscript suggested this interpretation which associates transport resistances with each organ as in eqns (10) and gives an easy method of calculating a transport resistance between organs [eqns (11)].

The transport resistances between shoot and root for the C, N substrates are

$$r_{C,shrt} = r_{C,sh} + r_{C,rt}, \quad r_{N,rtsh} = r_{N,rt} + r_{N,sh} \qquad (11)$$

The total structural mass M is

$$M = M_{sh} + M_{rt} \qquad (12)$$

The fractions of new structural growth [eqn (2)] allocated to the shoot and root are

$$f_{G,sh} = \frac{G_{sh}}{G}, \quad f_{G,rt} = \frac{G_{rt}}{G} \qquad (13)$$

where $G = G_{sh} + G_{rt}$

The actual shoot and root structural fractions are

$$f_{sh} = \frac{M_{sh}}{M}, \quad f_{rt} = \frac{M_{rt}}{M} \qquad (14)$$

The specific growth rate of the plant, μ is [with eqns (1) and (12)]

$$\mu = \frac{dM/dt}{M} \qquad (15)$$

where $\dfrac{dM}{dt} = \dfrac{dM_{sh}}{dt} + \dfrac{dM_{rt}}{dt}$

For balanced exponential growth with $\sigma_{SS} = 0$, and no product inhibitions of C and N inputs, it can be shown that the shoot and root fractions (f_{sh}, f_{rt}), the specific growth rate (μ), the C, N contents of structure (f_C, f_N), and the mean plant substrate concentrations ($\overline{C}, \overline{N}$) are related by

$$f_{sh}k_C = \mu(f_C + \overline{C}), \ f_{rt}k_N = \mu(f_N + \overline{N}) \qquad (16)$$

The mean plant substrate concentrations are

$$\overline{C} = f_{sh}C_{sh} + f_{rt}C_{rt}$$

$$\overline{N} = f_{sh}N_{sh} + f_{rt}N_{rt} \qquad (17)$$

Elimination of μ between eqns (16) gives

$$\frac{f_{sh}k_C}{f_C + \overline{C}} = \frac{f_{rt}k_N}{f_N + \overline{N}} \qquad (18)$$

This equation represents the much-discussed 'functional equilibrium' hypothesis of Davidson (1969), in which shoot activity and root activity *may be* proportional to each other. Note that shoot activity equals shoot fraction (f_{sh}) times shoot specific activity (k_C).

3 Simulations and Discussion

The heuristic model presented above needs exploration by means of simulation, to illustrate the type and scope of its responses, and to determine whether this type of approach may be suitable for forest growth and ecosystem models. Dynamic behaviour is the first part of this evaluation, followed by consideration of the equilibrium responses.

The equations were programmed in the continuous system simulation language, ACSL (Mitchell and Gauthier 1993). Euler's method was used for integration with an interval of 0.02 d in most cases.

3.1 Dynamic Behaviour

3.1.1 Balanced Exponential Growth

Balanced exponential growth (*BEG*) is the term used to describe the situation where all extensive variables (e.g. mass variables, Fig. 1) of the system are increasing exponentially at a constant specific growth rate [eqn (15)], and all intensive variables [e.g. concentrations, fractions, eqns (9), (14)] are constant. Figure 2 shows the approach to *BEG*, obtained by using eqns (3), (5) and (6) with the switch $\sigma_{SS} = 0$: this gives no litter fluxes and no asymptotic ceiling on photosynthesis or
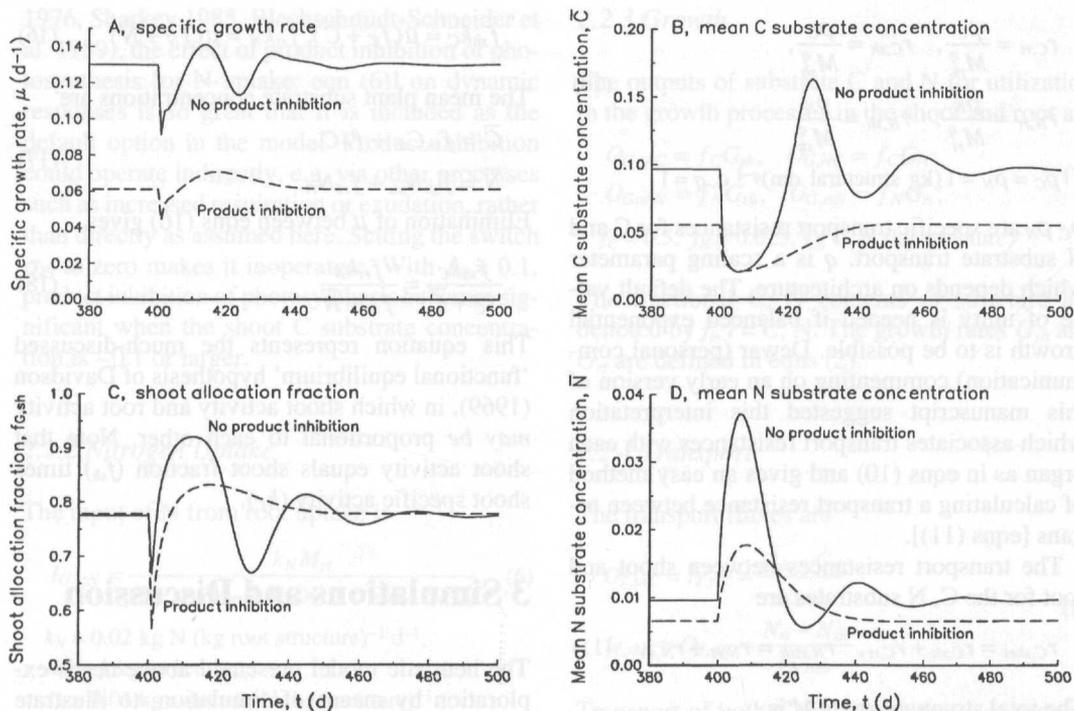
Fig. 2. Dynamics of perturbed balanced exponential growth, obtained with $\sigma_{SS} = 0$ in eqns (3), (5) and (6). 75 % of the shoot is removed at time $t = 400$ d. The responses are shown for without and with product inhibition, obtained by using $\sigma_{PI} = 0$ or 1 in eqns (5) and (6). A, specific growth rate, μ [eqn (15)]; B, mean plant C substrate concentration [eqns (17)] [kg C substrate (kg structural dry matter)$^{-1}$]; C, shoot growth allocation fraction [eqn (13)]; D, mean plant N substrate concentration [eqns (17)] [kg N substrate (kg structural dry matter)$^{-1}$].

N uptake. Although *BEG* can be simulated for a time with the switch $\sigma_{SS} = 1$ (which gives a steady state approached asymptotically as time t proceeds) by integrating the equations at very low mass values when the terms switched out by taking $\sigma_{SS} = 0$ are negligibly small, it is more convenient to use the switch $\sigma_{SS} = 0$ so that the system stays always in *BEG*. These model runs were performed with and without product inhibition of photosynthesis and N uptake, obtained by using the product inhibition switch σ_{PI} in eqns (5) and (6). The initial state is obtained by taking the equilibrium state for balanced exponential growth and scaling down the shoot components by a factor of 0.25, equivalent to a 75 % defoliation. The equilibrium specific growth rate (Fig. 2A) is decreased by the presence of product inhibition of photosynthesis and uptake, as expected. More striking is the effect of product

inhibition on allocation of new growth to the shoot [eqn (13)], drawn in Fig. 2C: when product inhibition occurs [eqns (5), (6)], the highly oscillatory behaviour produced with no product inhibition is replaced by well-damped behaviour with a single overshoot, which is realistic (Fick et al. 1971). The C and N substrate concentrations exhibit similar behaviour (Figs. 2B, D) but move out-of-phase. It seems possible that the highly oscillatory behaviour of the model without product inhibition of assimilation or uptake may be a result of the lumped representation of transport; a more distributed transport model with several substrate reservoirs in series would behave in a more damped manner. The numerical difficulties that are sometimes encountered with the transport-resistance model of allocation can have their origin in these oscillatory characteristics with an inappropriate integration interval.
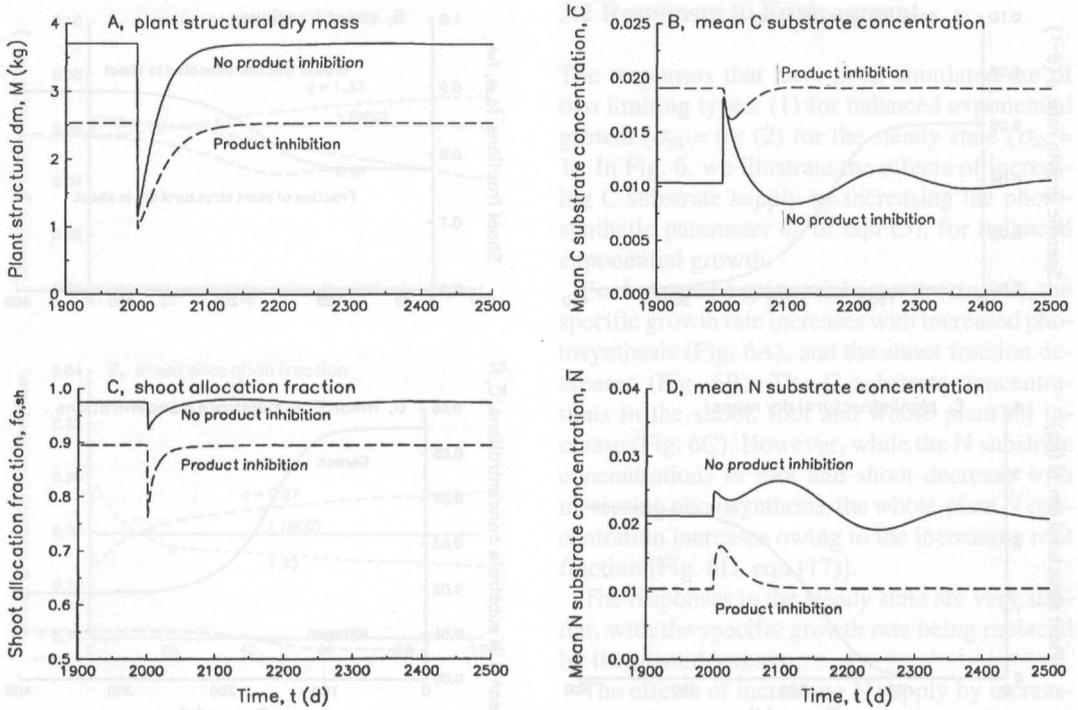
Fig. 3. Dynamics of perturbed steady-state growth, obtained with $\sigma_{SS} = 1$ in eqns (3), (5) and (6). 75 % of the shoot is removed at time $t = 2000$ d. The responses are shown without and with product inhibition, obtained by using $\sigma_{PI} = 0$ or 1 in eqns (5) and (6). A, plant structural dry mass, M [eqn (12)]; B, mean plant C substrate concentration [eqns (17)] [kg C substrate (kg structural dry matter)$^{-1}$]; C, shoot growth allocation fraction [eqn (13)]; D, mean plant N substrate concentration [eqns (17)] [kg N substrate (kg structural dry matter)$^{-1}$].

3.1.2 Steady State

A steady state is reached by integrating the equations with the switch $\sigma_{SS} = 1$ which gives rise to litter fluxes [eqn (3)] and puts a ceiling on the assimilation and uptake rates [eqns (5), (6)]. The steady state with a 75 % shoot defoliation is taken as the initial value for examining the dynamics with which the system returns to the steady state. These simulations are given in Fig. 3. The effect of product inhibition is not as marked as for balanced exponential growth (Fig. 2). The steady state is generally better damped than the balanced exponential growth state: overshoot effects and oscillations are smaller (*cf.* Figs 3B, 3C, 3D to Figs 2B, 2C, 2D).

3.1.3 Ontogenesis

A difficulty in investigating shoot:root allocation is the importance of ontogeny (see Wilson 1988). Within the framework of the vegetative allocation model without any explicit representation of development, there are two possibilities for considering 'ontogenetic' effects. The first is to examine the transition from balanced exponential growth to the steady state. The second is to examine the effects of scaling the transport resistances differently, remembering that only if the transport resistances scale inversely with plant size [$q = 1$ in eqn (10)], does an exponential growth solution exist.

In Fig. 4 the shift from balanced exponential growth (*BEG*) to a steady state is illustrated, obtained by running the model with $\sigma_{SS} = 1$ [eqn (3)] starting from a very low mass in *BEG*, with prod-
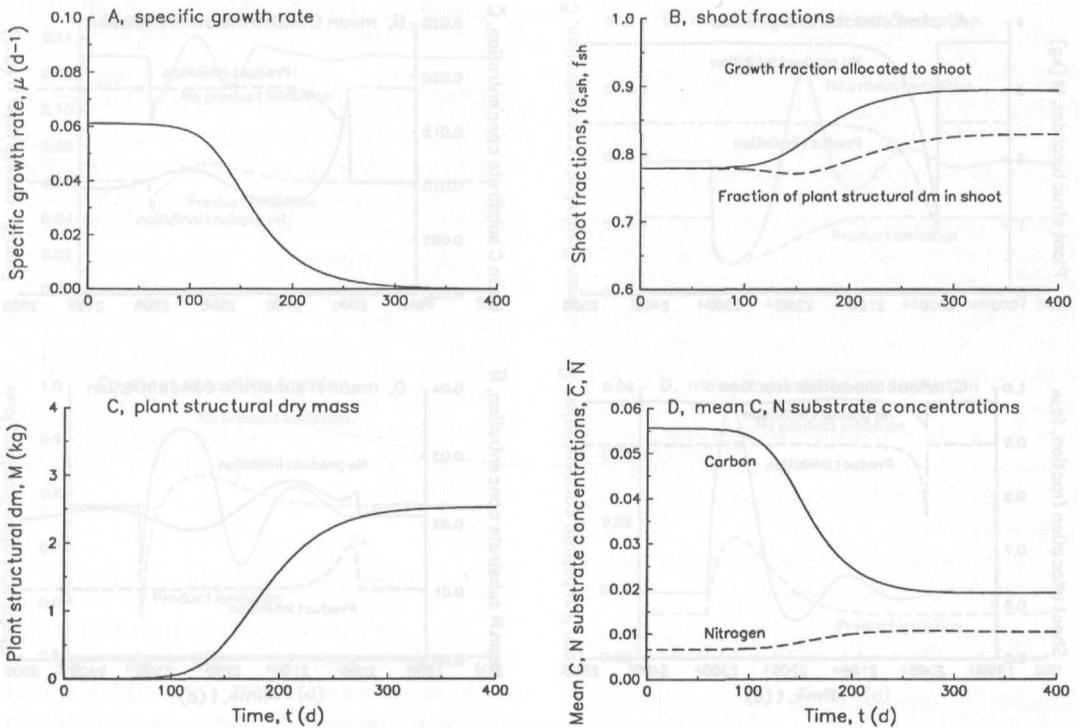
Fig. 4. The transition from balanced exponential growth to the steady state with product inhibition [$\sigma_{PI} = 1$ in eqns (5) and (6)]. The model is simulated with the default parameter values and initial values corresponding to balanced exponential growth and structural dry mass of 0.0001 kg. A, specific growth rate [eqn (15)]; B, allocation of current growth to the shoot [eqn (13)] and fraction of plant structure in the shoot [eqn (14)]; C, plant structural dry mass [eqn (12)]; D, mean plant C and N substrate concentrations [eqn (17)] [kg C, N substrate (kg structural dry matter)$^{-1}$].

uct inhibition. The specific growth rate, initially constant, falls to zero while the dry mass, increasing exponentially, approaches an asymptote (Fig. 4A, C). Total structural dry mass, M, follows a typical sigmoidal growth trajectory (Fig. 4C), similar to the logistic or Gompertz functions (e.g. pp. 80–85 of France and Thornley 1984). Allocation to the shoot [eqn (13)] increases to a higher value (Fig. 4B), whereas the shoot fraction [eqn (14)], which equals the shoot allocation fraction in balanced exponential growth, falls slightly before increasing to a value which in the steady state is lower than the shoot allocation fraction. This is due to the different litter rates in shoot and root. The shoot is larger than the root; its specific litter rate is greater than that in the root [eqn (3)]; and therefore the shoot needs a higher allocation fraction in the steady state. The C and N substrate con-

centrations move in opposite directions as the plant adjusts from exponential growth where carbon is relatively abundant to a steady state where nitrogen is relatively abundant (Fig. 4D).

In Fig. 5 the consequences of assigning different values to the transport resistance scaling factor, q [eqn (10)], are illustrated, with the model otherwise running in the balanced exponential growth mode with $\sigma_{SS} = 0$ and with product inhibition ($\sigma_{PI} = 1$). Transport fluxes become increasingly limiting for values of $q < 1$ [eqn (10)] because they do not increase proportionately to plant size: this causes specific growth rate to decrease with time (Fig. 5A), allocation to the shoot to increase (Fig. 5B), and the difference between the shoot and root C substrate concentrations to widen (Fig. 5C). The opposite trends occur if the resistances decrease faster

A, specific growth rate

Specific growth rate, μ (d^{-1})

0.10
0.08
$q = 1.33$
0.06
1 (BEG)
0.04
0.67
0.02
0.00
0   20   40   60   80   100

B, shoot allocation fraction

Shoot allocation fraction, $f_{G,sh}$

0.84
0.82
0.80
$q = 0.67$
0.78
1 (BEG)
1.33
0.76
0.74
0   20   40   60   80   100

C, carbon substrate concentrations

C substrate concentration

0.10
$q = 0.67$
0.08
Shoot
1 (BEG)
0.06
1.33
0.04
$q = 1.33$
1 (BEG)
0.02
Root
0.67
0.00
0   20   40   60   80   100
Time, t (d)
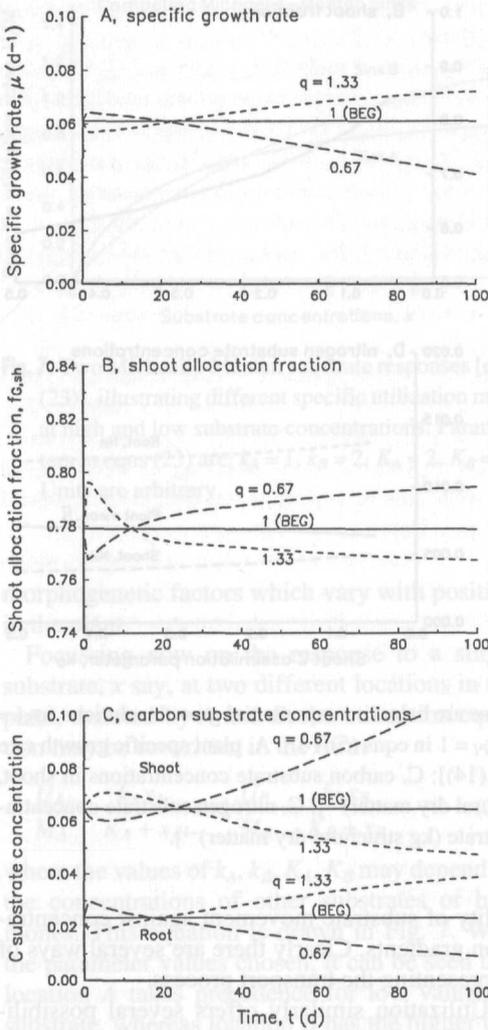
Fig. 5. Effect of scaling transport resistances [eqn (10)] on balanced exponential growth (*BEG*, $\sigma_{SS} = 0$) with product inhibition of inputs of both substrates [eqns (5), (6)]. The scaling parameter q [eqn (10)] is assigned the values given. A, plant specific growth rate [eqn (15)]; B, allocation fraction of growth to shoot [eqn (13)]; C, shoot and root C substrate concentrations [eqns (9)] [kg C substrate (kg structural dry matter)$^{-1}$].

than plant mass increases [$q > 1$ in eqn (10)].

A further possible simulation, not reported here, is to combine the ontogenetic effects of approaching a steady state (Fig. 4) with an allometric scaling of the transport resistance (Fig. 5).

3.2 Responses to Environment

The responses that have been simulated are of two limiting types: (1) for balanced exponential growth ($\sigma_{SS} = 0$); (2) for the steady state ($\sigma_{SS} = 1$). In Fig. 6, we illustrate the effects of increasing C substrate supply by increasing the photosynthetic parameter k_C of eqn (5), for balanced exponential growth.

For balanced exponential growth ($\sigma_{SS} = 0$), the specific growth rate increases with increased photosynthesis (Fig. 6A), and the shoot fraction decreases (Fig. 6B). The C substrate concentrations in the shoot, root and whole plant all increase (Fig. 6C). However, while the N substrate concentrations in root and shoot decrease with increasing photosynthesis, the whole-plant N concentration increases owing to the increasing root fraction [Fig. 6D, eqn (17)].

The responses in the steady state are very similar, with the specific growth rate being replaced by the plant dry mass.

The effects of increasing N supply by increasing the N uptake parameter k_N of eqn (6) are analogous to the increases in the photosynthetic parameter k_C in Fig. 6, both for balanced exponential growth and the steady state: root fraction *versus* k_N is similar to Fig. 6B; nitrogen substrate concentrations *versus* k_N are similar to Fig. 6C interchanging shoot and root; and carbon substrate concentrations *versus* k_N are similar to Fig. 6D interchanging shoot and root.

3.3 Transport Mechanisms; Sink Utilization Functions; Priorities

An allocation model based on the two essential processes of transport of substrates and the subsequent utilization of those substrates at their destination, allows allocation priorities to be represented in terms of these two processes. Differing resistances with the same substrate utilization functions will produce differing allocation patterns, just as will similar resistances with differing utilization functions.

Mason and Maskell (1928) studied carbohydrate transport in cotton plants. The transport processes of eqns (8) conform to the general type observed by these authors, namely
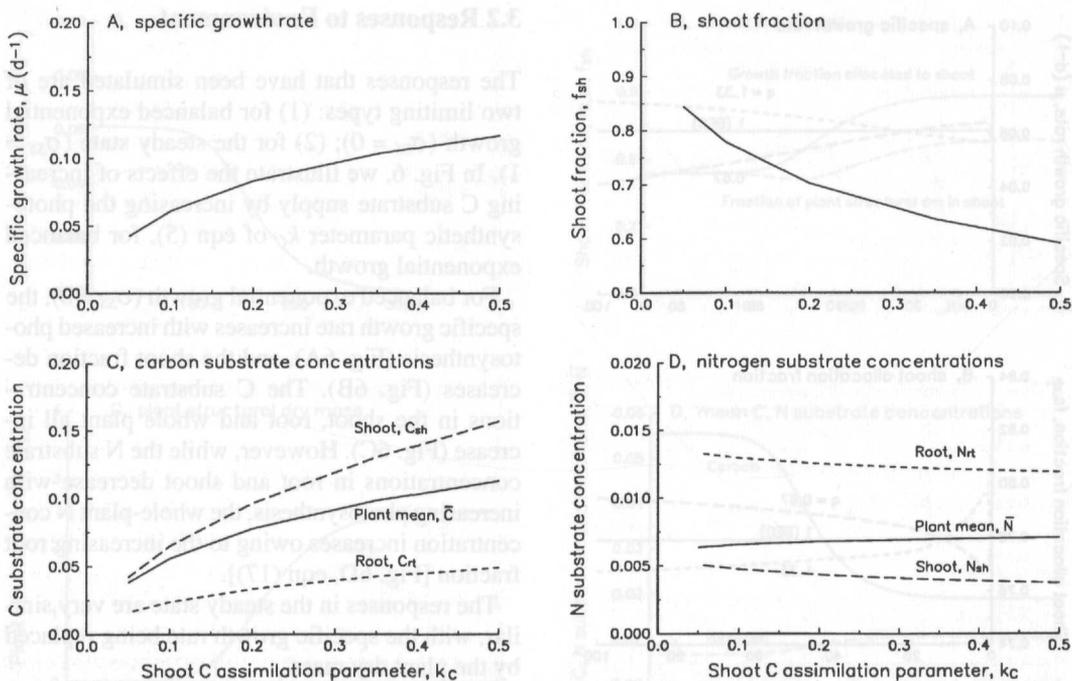
Fig. 6. Response to shoot activity parameter k_C [eqn (5)]. These are balanced exponential growth solutions (σ_{SS} = 0) with product inhibition of inputs of both substrates [σ_{PI} = 1 in eqns (5), (6)]. A, plant specific growth rate [eqn (12)]]; B, shoot structural dry mass fraction [eqn (14)]; C, carbon substrate concentrations in shoot, root and plant [eqns (9), (17)] [kg C substrate (kg structural dry matter)$^{-1}$]; C, nitrogen substrate concentrations in shoot, root and plant [eqns (9), (17)] [kg N substrate (kg structural dry matter)$^{-1}$].

$$T = \frac{x_A - x_B}{r} \qquad (19)$$

where T is the transport flux, r is the resistance and x_A and x_B are the concentrations of substrate x at the locations A and B in the plant. This is the simplest and most widely used assumption. Dewar (1993, equation 7) made use of the expression

$$T = g\bar{x}(x_A - x_B) \qquad (20)$$

where $\bar{x}$ is the mean substrate concentration [cf. eqn (17)], and a similar quadratic expression was suggested by Thornley (1976, equation 2.45). Thornley (1977, equation 18) proposed that an equation of the type

$$T = \frac{c_1 x_A - c_2 x_B}{r} \qquad (21)$$

could be used to combine passive and active transport mechanisms, thereby giving the possi-

bility of substrate movement against concentration gradients. Clearly there are several ways of representing the transport process.

Utilization similarly offers several possibilities. Here in eqn (2) a bilinear form is employed for the specific utilization rate. This is a simplification of an equation borrowed from enzyme kinetics, namely

$$\frac{U}{M} = \frac{k}{1 + K_C / C + K_N / N + K_{CN} / CN} \qquad (22)$$

where the specific utilization rate U/M of say C substrate depends on the local C and N concentrations in an organ of mass M, with asymptote k and Michaelis-Menten constants K_C, K_N and K_{CN} (equation 1, Thornley 1972). This equation has been extensively investigated by Mäkelä and Sievänen (1987, their equation 14). The asymptote and other parameters of eqn (22) may be influenced by hormones, growth factors or other
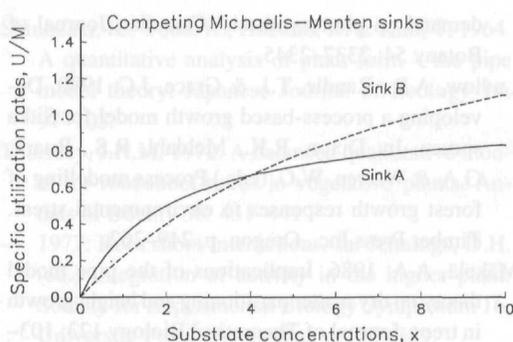
Fig. 7. Two Michaelis-Menten substrate responses [eqn (23)], illustrating different specific utilization rates at high and low substrate concentrations. Parameters in eqns (23) are: $k_A = 1$, $k_B = 2$, $K_A = 2$, $K_B = 8$. Units are arbitrary.

morphogenetic factors which vary with position in the plant.

Focussing now on the response to a single substrate, x say, at two different locations in the plant, denoted by A and B, the utilization equation may be re-written in the form

$$\frac{U_A}{M_A} = \frac{k_A x_A}{K_A + x_A} \text{ and } \frac{U_B}{M_B} = \frac{k_B x_B}{K_B + x_B} \quad (23)$$

where the values of k_A, k_B, K_A, K_B may depend on the concentrations of other substrates or hormones. This equation is drawn in Fig. 7. With the parameter values chosen, it can be seen that location A takes precedence for low values of substrate, whereas location B has the higher utilization rate at high values of substrate concentration. Thus, traditional enzyme-kinetic expressions allow quite complex utilization or sink responses to be readily simulated.

Comparing eqns (22) and (23) with the bilinear forms used for growth in eqns (2), because the root N concentration N_{rt} is greater than the shoot N concentration N_{sh}, the slope with respect to carbon substrate of G_{sh}/M_{sh} is less than that of G_{rt}/M_{rt}. This means that a given increment in carbon substrate applied equally to shoot and root gives a greater increment in specific root growth than in specific shoot growth. This causes the allocation responses of the transport-resistance model.

4 Conclusions

A summary of the present logical position is as follows. Transport and chemical conversion are the only two significant processes occurring in plants. Allocation is the result of these processes. As illustrated here, these two processes alone, with the simplest of phenomenological assumptions for the rates of the processes, are sufficient to predict a wide range of allocation responses. There are several possibilities for modifying the assumed phenomenology for the transport and conversion processes in order to obtain different allocation responses. These include, for example, scaling of transport resistances [eqn (10)], non-linear transport fluxes [eqn (20)], active transport [eqn (21)], integrating substrate transport with water transport (Dewar 1993), and more complicated substrate utilization responses [eqn (22)] in which the effects of hormones, growth factors or water status are incorporated [see eqn (23) and Fig. 7].

The pipe-model hypothesis (Shinozaki et al. 1964) is based on water transport. It has been used and developed further by Valentine (1985), Mäkelä (1986, 1990) and Ludlow et al. (1990). To recast this into a transport-utilization framework could involve: taking account of the role of water transport in substrate transport (Dewar 1993), taking account of the effects of plant water status on utilization and transport processes (e.g. Thornley 1996), or possibly taking a route from water stress to hormone production to modifying utilization functions according to local hormone concentrations.

Teleonomic (apparently goal-seeking) models can have the allure of a siren: simplicity, a useful range of realism, and an evolutionary interpretation. However, this allure is deceptive. The approach is a cul-de-sac. There are many possible goals. The choice of goal is inevitably subjective. The parameters can only be obtained by fitting responses at the system level. When the teleonomic model fails, as all models invariably do, there is nowhere to go, nowhere to seek the cause of failure in other than the most superficial terms. This is not to deny the importance of evolved constraints, or the value of a teleonomic viewpoint. Only if the teleonomic criteria are

built into a mechanistic framework can they be properly considered in a progressive modelling endeavour.

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