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Allocation of new growth between shoot, root and mycorrhiza in relation to carbon, nitrogen and phosphate supply: Teleonomy with maximum growth rate

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HIGHLIGHTS

- Expressions allocating new dry matter to shoot, root and mycorrhiza are derived which maximize growth rate.
- These demonstrate several key intuitive phenomena concerning resource sharing between plant components and associated mycorrhizae.
- The approach offers a methodology for introducing resource sharing between species into ecosystem models.
- Such teleonomic (optimal response) models may provide a valuable means of simulating allocation.
- This can avoid the circularity of empirical models and circumvent the complexities and uncertainties inherent in mechanistic approaches.

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ABSTRACT

Treating resource allocation within plants, and between plants and associated organisms, is essential for plant, crop and ecosystem modelling. However, it is still an unresolved issue. It is also important to consider quantitatively when it is efficient and to what extent a plant can invest profitably in a mycorrhizal association. A teleonomic model is used to address these issues. A six state-variable model giving exponential growth is constructed. This represents carbon (C), nitrogen (N) and phosphorus (P) substrates with structure in shoot, root and mycorrhiza. The shoot is responsible for uptake of substrate C, the root for substrates N and P, and the mycorrhiza also for substrates N and P. A teleonomic goal, maximizing proportional growth rate, is solved analytically for the allocation fractions. Expressions allocating new dry matter to shoot, root and mycorrhiza are derived which maximize growth rate. These demonstrate several key intuitive phenomena concerning resource sharing between plant components and associated mycorrhizae. For instance, if root uptake rate for phosphorus is equal to that achievable by mycorrhiza and without detriment to root uptake rate for nitrogen, then this gives a faster growing mycorrhizal-free plant. However, if root phosphorus uptake is below that achievable by mycorrhiza, then a mycorrhizal association may be a preferred strategy. The approach offers a methodology for introducing resource sharing between species into ecosystem models. Applying teleonomy may provide a valuable short-term means of modelling allocation, avoiding the circularity of empirical models, and circumventing the complexities and uncertainties inherent in mechanistic approaches. However it is subjective and brings certain irreducible difficulties with it.

1. Introduction

There continue to be difficulties modelling dry matter allocation in plant growth and plant ecosystem models. The latter are becoming increasingly important with the growing concern with climate change and carbon sequestration. The problem is sufficiently challenging that many crop and plant ecosystem models use simple “outcome-level” empiricism, an approach that is unlikely to give useful insights and often leads to circularity. While mechanistic models represent the “holy grail”, they may be unattainable at the present time. Arguably, an approach that could provide progress is to use “functionality” – assuming a goal which the system attempts to attain via means which exist because of adaptation. Apparent goal-seeking behaviour can only be obtained through mechanisms, which may or may not exist for that purpose. However, postulating goals

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and assuming that the means have evolved to fulfil those goals provides an alternative (but arguably short-term) approach to the allocation problem. It leads to models which are sometimes dubbed teleonomic or functional, or optimal response.

While here we develop teleonomic approaches, one should not forget the importance of mechanism and the many successes achieved by traditional scientific reductionism, although this approach can require great persistence and a long time horizon, both of which may not be easy to obtain. This situation is highlighted by a recent review of allocation (Poorter et al., 2011), which appears to be devoid of hypotheses or synthetic mathematical statements (Warren Wilson et al., 1986). To misquote Rutherford: “all real science is reductionist; the rest is just stamp collecting”. Nevertheless, teleonomic relationships can contribute to the investigation of complex systems when too little may be known for reductionism to proceed confidently.

Some reviews of modelling allocation are by Franklin et al. (2012, who omit mechanistic methods), Dewar et al. (2009, they discuss teleonomic models of forest response), Thornley and France (2007,, pp. 8–9, 326–341), Lacointe (2000) (an excellent review), Thornley (1998a), Cannell and Dewar (1994), Mäkelä (1990, covers functional balance and pipe theory) and Wilson (1988). Early work in the area is often described by the term functional equilibria, e.g. White (1937), Brouwer (1962) and Davidson (1969). Functionality can equally well be described as goal-seeking or as teleonomy (Monod, 1974): we decide the function or goal, possibly guided by experimental data, or ideas about fitness or evolution. Indeed, much of allocation modelling straddles uneasily the fault line between mechanistic approaches and functional or teleonomic approaches, attempting to make progress in this difficult but important area. Hopefully the present teleonomic study can contribute to this debate. The particular teleonomic approach applied here was first suggested by Reynolds and Thornley (1982), and has been further discussed by Johnson and Thornley (1987) and Thornley and France (2007), pp. 328–333). The method adjusts allocation fractions so as to maximize growth rate. An important paper by Mäkelä and Sievänen (1987) gives a detailed comparison of the (mechanistic) transport-resistance and teleonomic approaches to C, N allocation in a shoot–root model, concluding significantly that the teleonomic model essentially is embedded in the mechanistic model. This is important because it demonstrates that apparently goal-seeking predictions can be generated by an objective mechanistic model. Dewar et al. (2009) review “optimal function” (or teleonomic) modelling in forests, and make recommendations for further work to progress this approach to modelling.

In this paper we revisit and extend a teleonomic model which maximizes proportional growth rate while allocating carbon (C) and nitrogen (N) to shoot and root. The extension includes phosphorus (P) as a third nutrient and mycorrhiza as a third possible compartment. Our objectives are first to develop teleonomic methodology for an extended system, second to see if it can provide new insights into plant-mycorrhizal associations, and last to sharpen up (make more quantitative) the questions in this area. The method may help provide submodels suitable for including in larger crop and ecosystem simulators.

2. Model and methods

2.1. Basic analysis

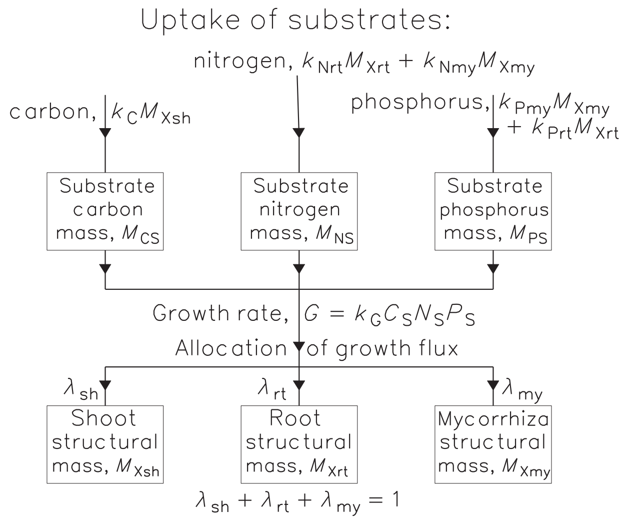

Fig. 1. Model scheme for carbon, nitrogen and phosphorus uptake, growth and allocation in a plant-mycorrhizal system. This comprises shoot (sh), root (rt) and mycorrhiza (my). There are six state variables as indicated by the boxes. Uptake fluxes of C, N, P substrates are associated with shoot, root, and mycorrhiza as shown [Eq. (1)]. Total structural dry matter growth rate, G [Eq. (6)], is allocated according to fractions, λ_{sh}, λ_{rt} and λ_{my} to shoot, root and mycorrhiza [Eq. (10)]. See Eq. (2) for substrate concentrations, C_{S}, N_{S} and P_{S} and Eq. (3) for total structural dry matter, M_{X}.

The model scheme is drawn in Fig. 1. Substrate C is taken up by the shoot, substrates N and P are taken up by both root and mycorrhiza. The five k shown in Fig. 1 are uptake parameters [Eq. (1)]. We study teleonomic allocation between shoot, root and mycorrhiza, maximizing overall growth rate of the association. This optimization, which determines allocation, is performed for particular values of the uptake parameters. The procedure is carried out for the model system in “steady-state” exponential growth, when all parts of the system, shoot, root and mycorrhiza, grow at the same proportional rate. Exponential growth is assumed for three reasons: first it permits a thorough algebraic analysis; second, arguably, early exponential growth is important for “fitness” or survival, partially justifying our particular teleonomic assumption; and last, empirical data indicate that early plant growth can be approximately exponential before processes such as self-shading, root competition and respiration set in (e.g. Causton and Venus, 1981, p. 39). The model is constructed so that exponential-growth solutions exist.

State variables, other variables and parameters with default values are listed in Table 1. There are six mass (M) state variables, shown in Fig. 1: three for the structural components (X) for shoot M_{Xsh}, root M_{Xrt} and mycorrhiza M_{Xmy}, with units of kg structural dry matter; and three for the substrate pools (S), M_{CS}, M_{NS} and M_{PS}, with units of kg carbon (C), nitrogen (N) and phosphorus (P) substrates. The substrates are assumed to be equally accessible to all parts of the system.

The uptake rates of C, N and P substrates, U_{C}, U_{N} and U_{P} (units: kg substrate C, N, P d^{-1}) are

$$\begin{aligned}
&U_{\mathrm{C}} = k_{\mathrm{C}}M_{\mathrm{Xsh}}, \quad U_{\mathrm{N}} = k_{\mathrm{Nrt}}M_{\mathrm{Xrt}} + k_{\mathrm{Nmy}}M_{\mathrm{Xmy}}, \quad U_{\mathrm{P}} = k_{\mathrm{Pmy}}M_{\mathrm{Xmy}} + k_{\mathrm{Prt}}M_{\mathrm{Xrt}},\\
&k_{\mathrm{C}} = 0.2 \text{ kg substrate C (kg shoot structural dry matter)}^{-1}\ \mathrm{d}^{-1},\\
&k_{\mathrm{Nrt}} = 0.05 \text{ kg substrate N (kg root structural dry matter)}^{-1}\ \mathrm{d}^{-1},\\
&k_{\mathrm{Nmy}} = 0.025 \text{ kg substrate N (kg mycorrhiza structural dry matter)}^{-1}\ \mathrm{d}^{-1},\\
&k_{\mathrm{Pmy}} = 0.02 \text{ kg substrate P (kg mycorrhizal structural dry matter)}^{-1}\ \mathrm{d}^{-1},\\
&k_{\mathrm{Prt}} = 0.01 \text{ kg substrate P (kg root structural dry matter)}^{-1}\ \mathrm{d}^{-1}, \qquad (1)
\end{aligned}$$

with uptake parameters k_{C}, k_{Nrt}, k_{Nmy}, k_{Pmy} and k_{Prt}. Note that here $k_{\mathrm{Nrt}} > k_{\mathrm{Nmy}}$ and $k_{\mathrm{Pmy}} > k_{\mathrm{Prt}}$: the root is better than the mycorrhiza at N uptake, and vice versa for P uptake so that the optimum system for growth comprises root and mycorrhiza. These are illustrative values, not based directly on empirical evidence, except that they support acceptable rates of plant growth. In the simulations a range is k values is considered.