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Allocation within a generic scaling framework

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ABSTRACT

Barnes and Roderick [Barnes, B., Roderick, M.L., 2004. An ecological framework linking scales across space and time based on self-thinning. *Theoret. Popul. Biol.* 66, 113–128] developed a generic ecological framework for scaling from individuals to ecosystems. Their approach is general and can be applied to predict above-ground, or total (above- and below-ground), dry mass. In practice, the most common situation is to measure above-ground dry mass, and apply an allometric relationship to estimate the below-ground component. In this paper we develop a general theory for incorporating the dynamics of plant partitioning into the generic framework. We consider the inclusion of allometric relationships between components (such as between roots and shoots), as well as process driven relationships, and illustrate the application of each case. Through this approach, local scale measurements and individual-based dynamic relationships pertaining to plant partitioning can be applied to an understanding of partitioning at the patch (or ecosystem) scale. Moreover, we also demonstrate that the empirically based allometric relationships have, in some circumstances, a physical explanation, providing biological meaning to empirically established allometric constants.

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1. Introduction

For many ecological applications, such as carbon accounting, estimates of total system mass, or carbon, are required. However, in practice, only above-ground measurements for individual plants are commonly available, and thus research effort has been directed towards predicting below-ground characteristics based on those above ground.

At the scale of an individual, plants allocate resources to different components in different quantities during growth. For example, in the initial stages of germination, or in times of a scarcity of nitrogen, a significant proportion of the resources available may be directed to the roots (Thornley and Johnson, 1990). Plants also use resources in different ways; for growth that results in increasing mass, or metabolism that does not,

for example. Thus, greater allocation of resources to a particular component need not result in a greater stock of dry mass within that component, raising the distinction between stocks and fluxes. In any model concerned with the dynamics of allocation and partitioning, these stocks and fluxes should vary, but it is important to recognise that they are not interchangeable.

Modelling approaches typically applied to partitioning and allocation are at the scale of an individual, and may be phenomenological (Enquist et al., 1998; Niklas, 1994; Niklas and Enquist, 2002) or process driven (Thornley, 1972; Thornley and Johnson, 1990; Bijlsma and Lambers, 2000; Yang and Midmore, 2005); however, owing to their simplicity, the use of empirically derived allometric relationships is most common in applications. In this paper we demonstrate how individual-based

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relationships between plant components, derived through either means, can be incorporated into the dynamical systems modelling framework developed by Barnes and Roderick (2004). That framework allows a scaling up from the level of individuals to patches (groups of interacting individuals), and hence ecosystems that may be at continental scales. (By ecosystem, in this context, we denote an aggregation at any level.)

Typical approaches to scaling up from the level of individuals to patch scale community dynamics are those adopting empirically derived allometric relationships (for example, Niklas et al., 2003) and those that are process driven (for example, Zavala and de la Parra, 2005). The latter approach commonly models individual dynamics, simulating over time water and energy balances, heat flux, leaf temperature and conductance, carbon assimilation, transpiration and so on. In Zavala and de la Parra (2005), these results are provided to a second level model describing the mechanics of tree interactions through resource dynamics, inter-tree shading effects, stand structure and environmental gradients. Similarly, Schwalm and Ek (2004) formulate a process driven simulation model based on tree physiology, but driven by meteorology. Many models include a spatial component, as in Nuttle and Haefner (2007) for forests and in Raventós et al. (2004) for grasslands, and include a mix of allometric growth relationships and community processes. Such simulation models provide a valuable means of tracking specific characteristics within communities of vegetation, although they often require detailed data to generate sensible output. Our approach subsumes these processes in a generic self-thinning mechanism and community carrying capacity, not requiring the many underlying assumptions of large simulation models, or detailed and often unavailable data. However, as we show in this paper, the individual scale processes (or allometric relationships) can be incorporated into our framework in a straightforward manner. And further, the community level dynamics of competing species, as well as the notion of the intermediate disturbance hypothesis, are also integral to our approach (Barnes et al., 2004). As our framework does not capture specific details of each process, we consider that micro-simulation and the approach adopted here complement each other.

Further, we note that while empirical allometric and process driven approaches have developed more or less separately, in some cases a direct relationship can be established between the allometric constants and system processes as, for example, derived in Roderick and Barnes (2004) for self-thinning. In this paper, we show that empirically derived allometric relationships pertaining to plant components, can, under certain circumstances, be related directly to physically meaningful processes.

In Section 2 we outline the generic framework of Barnes and Roderick (2004) and develop the theory to incorporate plant partitioning for an arbitrary number of components. We then consider the model application to two examples; one empirical (Section 3) partitioned into two components, roots and shoots, and the other process driven (Section 4) partitioned into four components, root and shoot structural dry masses and carbon and nitrogen substrates. In each case we illustrate how the individual based partitioning can be

incorporated into the framework and partitioning at the patch scale described. Finally, we relate the empirical allometric and process driven approaches in Section 5, providing physical meaning to the phenomenological model, before drawing some conclusions.

2. A theoretical framework for partitioning

2.1. The general theoretical model

We commence with an outline of the modelling framework developed by Barnes and Roderick (2004), and the assumptions underlying the incorporated self-thinning mechanism, as this forms a basis for our approach to partitioning. Our formulation here is in terms of total above- and below-ground dry mass, as the examples we use to illustrate our approach are in terms of these quantities. (We note, however, that derivations in terms of above-ground dry mass, volume, total mass, or any other such system characteristic, follow similarly.)

Let $Y = n\bar{m}$ be the total dry mass of all individuals within a patch of vegetation, with n the number of individuals and $\bar{m}$ the average dry mass of individuals within that patch. The dynamics of Y are given by

$$\frac{dY}{dt} = n \frac{d\bar{m}}{dt} + \bar{m} \frac{dn}{dt}.$$

We assume sigmoidal growth for the patch, with a carrying capacity κ defined in terms of total system dry mass, and self-thinning through

$$-\frac{1}{n} \frac{dn}{dt} = \frac{n\bar{m}}{\kappa} \left(\frac{1}{\bar{m}} \frac{d\bar{m}}{dt} \right). \quad (1)$$

We note here that this equation can be written equivalently as

$$-\frac{\kappa}{n^2} = \frac{d\bar{m}}{dn} \Rightarrow -\frac{\kappa}{n^2} \frac{dn}{d\bar{m}} = 1 \quad (2)$$

as we will make use of this below. Incorporating this self-thinning mechanism (1) into dY/dt leads to the generic model:

$$\frac{dY}{dt} = \left(\frac{1}{\bar{m}} \frac{d\bar{m}}{dt} \right) Y \left(1 - \frac{Y}{\kappa} \right). \quad (3)$$

Like the standard logistic equation, positive values for $(1/\bar{m})(d\bar{m}/dt)$ result in a stable steady-state at $Y = \kappa$ and an unstable steady-state at $Y = 0$. However, this expression differs from the standard logistic equation in that the 'growth rate', $(1/\bar{m})(d\bar{m}/dt)$, is time dependent and nonlinear.

2.2. Incorporating partitioning into the theoretical model

Subsumed in model (3) are the rates of change of the vegetation components, such as roots, stems and leaves, each of which may change at different rates compared with each other, or compared with the total mass of the individual. Our aim here is to incorporate the dynamics of these components into this model. To do so, we first formulate the problem in the most general sense, by partitioning each individual into an arbitrary number of components, s . Subsequently, we

apply our theoretical results to an example with two components, $s = 2$ for roots and shoots (equivalently below- and above-ground dry masses), as well as an example with four components, $s = 4$ for root and shoot structural dry masses and carbon and nitrogen substrates.

Suppose total dry mass is comprised of s components. With m_i the dry mass of the i th individual, $m_i = \sum_{k=1}^s m_{ik}$, from which it follows that

$$Y = n\bar{m} = n \sum_{k=1}^s \bar{m}_k,$$

where $\bar{m}_k$ is the average dry mass of the k th component, taken across all individuals within the patch. We can write the rate of change of the total dry mass in terms of the rates of change of the individual components as follows:

$$\begin{aligned} \frac{dY}{dt} &= \sum_{k=1}^s \frac{d(n\bar{m}_k)}{dt} = \sum_{k=1}^s \left(n \frac{d\bar{m}_k}{dt} + \bar{m}_k \frac{dn}{dt} \right) \\ &= \sum_{k=1}^s \left[\left(\frac{1}{\bar{m}_k} \frac{d\bar{m}_k}{dt} \right) (n\bar{m}_k + \bar{m}_k^2 \frac{dn}{d\bar{m}_k}) \right] \\ &= \sum_{k=1}^s \left[\left(\frac{1}{\bar{m}_k} \frac{d\bar{m}_k}{dt} \right) n\bar{m}_k \left(1 - \frac{n\bar{m}_k}{\kappa} \left[\frac{-\kappa}{n^2} \frac{dn}{d\bar{m}_k} \right] \right) \right] \\ &= \sum_{k=1}^s \left[\left(\frac{1}{\bar{m}_k} \frac{d\bar{m}_k}{dt} \right) n\bar{m}_k \left(1 - \frac{n\bar{m}_k}{\kappa} \left[\frac{-\kappa}{n^2} \frac{dn}{d\bar{m}_k} \right] \frac{d\bar{m}}{d\bar{m}_k} \right) \right]. \end{aligned}$$

Then, incorporating our self-thinning assumption Eq. (1) (equivalently, Eq. (2)), we have

$$\frac{dY}{dt} = \sum_{k=1}^s \frac{d(n\bar{m}_k)}{dt} = \sum_{k=1}^s \left[\left(\frac{1}{\bar{m}_k} \frac{d\bar{m}_k}{dt} \right) n\bar{m}_k \left(1 - \frac{n\bar{m}_k}{\kappa} \frac{d\bar{m}}{d\bar{m}_k} \right) \right].$$

Splitting this single differential equation into a system of s equations, one for each component, results in the system:

$$\begin{aligned} \frac{d(n\bar{m}_1)}{dt} &= \left[\left(\frac{1}{\bar{m}_1} \frac{d\bar{m}_1}{dt} \right) n\bar{m}_1 \left(1 - \frac{n\bar{m}_1}{\kappa} \frac{d\bar{m}}{d\bar{m}_1} \right) \right], \\ \frac{d(n\bar{m}_2)}{dt} &= \left[\left(\frac{1}{\bar{m}_2} \frac{d\bar{m}_2}{dt} \right) n\bar{m}_2 \left(1 - \frac{n\bar{m}_2}{\kappa} \frac{d\bar{m}}{d\bar{m}_2} \right) \right], \\ &\vdots \\ \frac{d(n\bar{m}_s)}{dt} &= \left[\left(\frac{1}{\bar{m}_s} \frac{d\bar{m}_s}{dt} \right) n\bar{m}_s \left(1 - \frac{n\bar{m}_s}{\kappa} \frac{d\bar{m}}{d\bar{m}_s} \right) \right]. \end{aligned} \quad (4)$$

These equations describe the changing dry mass, or stock, of the system, with the fluxes between the various components subsumed in the expressions on the right-hand sides. For example, the fluxes between the vegetation components are embodied in the rates of change, $d\bar{m}_k/dt$ and $d\bar{m}/d\bar{m}_k$, for $k = 1, \dots, s$. Each equation describes a logistic type of growth with steady states at $n\bar{m}_k = 0$ and $n\bar{m}_k = \kappa(d\bar{m}_k/d\bar{m})$. The latter steady state is stable in the case $d\bar{m}_k/dt > 0$, that is, when the average mass of the component is increasing with time. Further, it is dependent on how the component varies with respect to the total dry mass and, in the case that no components are decreasing in mass with time, the steady state attained by each component is less than κ , as would be expected.

Typically, ecologists do not measure how each component varies with respect to the whole plant, but rather how one component varies with respect to the others; how roots vary with respect to shoots, for example. Thus, we replace expressions $d\bar{m}/d\bar{m}_k$, $k = 1, \dots, s$ in system (4) with expressions relating the components, $d\bar{m}_k/d\bar{m}_j$ for $k, j \in [1, s]$, $k \neq j$.

For the case $k = 1$ (and for all other cases $k = 2, \dots, s$, similarly),

$$\frac{d\bar{m}}{d\bar{m}_1} = \frac{d(\sum_{k=1}^s \bar{m}_k)}{d\bar{m}_1} = 1 + \frac{d\bar{m}_2}{d\bar{m}_1} + \dots + \frac{d\bar{m}_s}{d\bar{m}_1}. \quad (5)$$

Thus, in general, we can establish an expression for $d\bar{m}/d\bar{m}_k$ in terms of the rates of change of $\bar{m}_k$ with respect to all other components. Similarly, an alternative form for $d\bar{m}_k/dt$, $k = 1, \dots, s$, is given by

$$\frac{d\bar{m}_k}{dt} = \frac{d\bar{m}_k}{d\bar{m}} \frac{d\bar{m}}{dt} = \frac{d\bar{m}}{dt} \left(\frac{1}{d\bar{m}/d\bar{m}_k} \right) \quad (6)$$

and we can substitute in expression (5) derived above. Further, we note that for two components that vary with respect to one another, $d\bar{m}_k/d\bar{m}_j$ (for $k, j \in [1, s]$, $k \neq j$) may be expressed in terms of the mass flux:

$$\frac{d\bar{m}_k}{d\bar{m}_j} = \frac{d\bar{m}_k/dt}{d\bar{m}_j/dt}.$$

We use the above substitutions in the application of system (4) below, although which are used is determined by the available relationships between components.

3. An example with an empirically derived relationship between roots and shoots

To apply the approach proposed, we consider as an example a patch of vegetation comprised of two components, roots and shoots. In this case we make use of an empirically derived relationship between the components to model the system over time; that is, an allometric relationship linking roots and shoots. Our technique is to develop dynamical expressions at the patch scale in terms of shoot dry mass, and then to incorporate the individual level allometric relationship into the patch scale dynamics to determine patch scale root dry mass from our results. We illustrate the approach by comparing the theoretical output with collected data.

3.1. Incorporating root:shoot relationships into the theoretical model

Let $\bar{m}_1$ be the average dry mass of all roots across the patch (below-ground dry mass), and $\bar{m}_2$ be the average dry mass of all shoots (above-ground dry mass). With these two components system (4), including substitutions (5) and (6), becomes:

$$\begin{aligned} \frac{d(n\bar{m}_1)}{dt} &= \left(\frac{1}{\bar{m}_1} \frac{d\bar{m}}{dt} \left[\frac{1}{1 + d\bar{m}_2/d\bar{m}_1} \right] \right) n\bar{m}_1 \left(1 - \frac{n\bar{m}_1}{\kappa} \left[1 + \frac{d\bar{m}_2}{d\bar{m}_1} \right] \right), \\ \frac{d(n\bar{m}_2)}{dt} &= \left(\frac{1}{\bar{m}_2} \frac{d\bar{m}}{dt} \left[\frac{1}{1 + d\bar{m}_1/d\bar{m}_2} \right] \right) n\bar{m}_2 \left(1 - \frac{n\bar{m}_2}{\kappa} \left[1 + \frac{d\bar{m}_1}{d\bar{m}_2} \right] \right). \end{aligned}$$

Suppose now we make use of an empirical allometric relationship established between root and shoot dry mass for forest

and woodland, of the form $\bar{m}_1 = \beta \bar{m}_2^\alpha$ (Enquist and Niklas, 2002; Robinson, 2004; Mokany et al., 2006). Then, the above system can be expressed in terms of the shoot dry mass as

$$\begin{aligned} \frac{d(n\bar{m}_1)}{dt} &= \left[\left(\frac{1}{\beta \bar{m}_2^\alpha} \frac{d\bar{m}_2}{dt} [\alpha \beta \bar{m}_2^{\alpha-1} + 1] \left[\frac{\alpha \beta \bar{m}_2^{\alpha-1}}{\alpha \beta \bar{m}_2^{\alpha-1} + 1} \right] \right) n \beta \bar{m}_2^\alpha \left(1 - \frac{n \bar{m}_2}{\kappa} \left[\frac{\alpha \beta \bar{m}_2^{\alpha-1}}{\alpha \beta \bar{m}_2^{\alpha-1} + 1} \right] \right) \right], \\ \frac{d(n\bar{m}_2)}{dt} &= \left[\left(\frac{1}{\bar{m}_2} \frac{d\bar{m}_2}{dt} [\alpha \beta \bar{m}_2^{\alpha-1} + 1] \left[\frac{1}{1 + \alpha \beta \bar{m}_2^{\alpha-1}} \right] \right) n \bar{m}_2 \left(1 - \frac{n \bar{m}_2}{\kappa} [1 + \alpha \beta \bar{m}_2^{\alpha-1}] \right) \right], \end{aligned}$$

which reduces to

$$\frac{d(n\bar{m}_1)}{dt} = \alpha \beta \bar{m}_2^{\alpha-1} \left(\frac{1}{\bar{m}_2} \frac{d\bar{m}_2}{dt} \right) n \bar{m}_2 \left(1 - \frac{n \bar{m}_2}{\kappa} \left[\frac{1 + \alpha \beta \bar{m}_2^{\alpha-1}}{\alpha} \right] \right),$$

The second differential equation of (7) can, with $Y_2 = n\bar{m}_2$, be written as

$$\frac{dY_2}{d\bar{m}_2} = \frac{Y_2}{\bar{m}_2} \left(1 - \frac{Y_2}{\kappa} [1 + \alpha \beta \bar{m}_2^{\alpha-1}] \right)$$

and solved analytically (Appendix A) to give,

$$Y_2(t) = \frac{\bar{m}_2(t) Y_2(0) \kappa}{\bar{m}_2(0) (\kappa - Y_2(0)) + Y_2(0) (\bar{m}_2(t) + \beta [\bar{m}_2^\alpha(t) - \bar{m}_2^\alpha(0)])}, \quad (8)$$

where $Y_2(0) = Y_2(\bar{m}_2(0))$ and $\bar{m}_2(0)$ are the initial values for the total shoot dry mass of the patch and the average shoot dry mass of an individual, across the patch of vegetation, respectively. To establish the dynamics of the root dry mass ($Y_1 = n\bar{m}_1$) from that of the shoots, instead of a solution to the first differential equation of system (7) we make use of the nonlinear relationship between $\bar{m}_1$ and $\bar{m}_2$, from which it follows that

$$Y_1(t) = Y_2(t) \beta (\bar{m}_2(t))^{\alpha-1}. \quad (9)$$

In the case of a linear relationship between the dry mass of the roots and shoots, that is, the above case with $\alpha = 1$ (Mokany et al., 2006), system (7) reduces to

$$\begin{aligned} \frac{d(n\bar{m}_1)}{dt} &= \beta \left(\frac{1}{\bar{m}_2} \frac{d\bar{m}_2}{dt} \right) n \bar{m}_2 \left(1 - \frac{n \bar{m}_2}{\kappa} [1 + \beta] \right), \\ \frac{d(n\bar{m}_2)}{dt} &= \left(\frac{1}{\bar{m}_2} \frac{d\bar{m}_2}{dt} \right) n \bar{m}_2 \left(1 - \frac{n \bar{m}_2}{\kappa} [1 + \beta] \right) \end{aligned} \quad (10)$$

with analytical solution (Appendix A):

$$Y_1(t) = \beta Y_2(t), \quad Y_2(t) = \frac{\bar{m}_2(t) Y_2(0) \kappa / (1 + \beta)}{\bar{m}_2(0) (\kappa / (1 + \beta) - Y_2(0)) + Y_2(0) \bar{m}_2(t)}. \quad (11)$$

3.2. Application to data from forests

We now apply the results from the previous section to data from a variety of forest types. For each dataset, we consider a patch size of an hectare, as data measurements are provided for this unit.

To apply the model above we require empirically determined allometric constants for the relationship between average root dry mass and average shoot dry mass across the hectare patch. Below, we consider two alternatives. Mokany et al. (2006) established relationships between total root dry mass and total shoot dry mass (Fig. 1). In the case of a linear relationship, $\sum_i m_{1i} = \beta (\sum_i m_{2i})$ (where the sum is taken over

all individuals within the hectare patch), they established $\beta \approx 0.26$ across the extensive group of forests and woodlands considered. This implies that $\bar{m}_1 = \beta \bar{m}_2 \approx 0.26 \bar{m}_2$. Alternatively,

$$\frac{d(n\bar{m}_2)}{dt} = \left(\frac{1}{\bar{m}_2} \frac{d\bar{m}_2}{dt} \right) n \bar{m}_2 \left(1 - \frac{n \bar{m}_2}{\kappa} [1 + \alpha \beta \bar{m}_2^{\alpha-1}] \right). \quad (7)$$

they established an allometric relationship for the total dry mass for the hectare, $\sum_i m_{1i} = \beta (\sum_i m_{2i})^\alpha$ ($\alpha \neq 1$), where they estimated $\beta \approx 0.49$ and $\alpha \approx 0.89$; however, this does not imply that $\bar{m}_1 = \beta \bar{m}_2^\alpha$ for the same α and β , since, for a patch of n individuals ($i = 1, \dots, n$)

$$\bar{m}_1 = \frac{\sum_i m_{1i}}{n} = \frac{1}{n} \beta \left(\sum_i m_{2i} \right)^\alpha = (n^{\alpha-1}) \beta \bar{m}_2^\alpha.$$

From above, since $n > 1$, positive and variable, and typically $0 < \alpha < 1$, thus $n^{\alpha-1} \beta < \beta$ and we expect the allometric coefficient relating $\bar{m}_1$ and $\bar{m}_2$, for the same exponent α , to be less than β .

Alternatively, Enquist and Niklas (2002) and Robinson (2004) have established individual-based allometric relationships between $\bar{m}_1$ and $\bar{m}_2$; that is, $\bar{m}_1 = \beta \bar{m}_2^\alpha$, based on the data for average individuals from Cannell (1982). To ascertain the allometric constants (α and β), we have plotted the average data ($\ln \bar{m}_2$ against $\ln \bar{m}_1$) from five forest and woodland sites considered by Mokany et al. (2006); that is, those that included records of the number of individuals. The resulting estimates of the allometric constants were $\beta \approx 0.19$ and $\alpha \approx 0.84$ (Fig. 1(b)). While the value for α is of similar magnitude to that of Mokany et al. (2006) (given above), the value for β is smaller, as expected (see above). We note that a linear relationship for these data estimates $\beta \approx 0.26$ (Fig. 1(a)), which is in agreement with that of Mokany et al. (2006) (see above). (Moreover, from Enquist and Niklas, 2002 the best fit was for $\alpha \approx 1$ and $\beta \approx 0.26$, and from Robinson, 2004, $\alpha \approx 1$ and $\beta \approx 0.37$.)

The model application also requires an estimate of the carrying capacity κ , the approximate upper limit attainable by the system. This quantity may be available directly, established from mature sites where the conditions and vegetation are similar. Alternatively, it can be estimated from the data; either from a plateau in the time sequence, or approximated from the location of the maximum rate of increase of total dry mass, at which point the level of vegetation can be approximated by $\kappa/2$ (see Barnes et al., 2006). Both methods were used in the estimates below, the former when data were available, and, alternatively, the latter. While this parameter is not simple to estimate, the results are not highly sensitive to small variation in κ , as discussed in Barnes et al. (2006).

We now compare datasets with our model output, incorporating these empirical parameter values into the framework formulated in the previous section; model (7) in the case of an allometric relationship, and model (10) in the linear case.

Fig. 1 – Relationships between roots ($\bar{m}_1$) and shoots ($\bar{m}_2$) are plotted using data (dark points) from a collection of forest ecosystems (Mokany et al., 2006). Regression estimates (a) the linear model as $\bar{m}_1 \approx 0.26\bar{m}_2$ (solid line) with $R^2 = 0.87$, and (b) the nonlinear model as $\ln \bar{m}_1 \approx 0.84(\ln \bar{m}_2) - 1.65$ (solid line) with $R^2 = 0.89$.

3.2.1. Mixed forest (Fig. 2(a))

Uhl (1987) and Saldarriaga et al. (1988) reported the dry mass of vegetation components and plant numbers from 23 tropical forest sites in the Upper Rio Negro region of Colombia and Venezuela. The sites had been subjected to slash-and-burn agriculture in the near and distant past, and together comprised a long-term chronosequence. These data provide a record of dry mass for a mixed forest comprised of many species, and includes some data for older (greater than 180-year old) forests. For a comparison between data and model predictions see Fig. 2(a). We note that root crowns were not measured at the time of sampling, leading to a probable under-

estimate of total root dry mass. However, in spite of this, as well as the fact that the data at each time derive from different sites, the model adheres reasonably closely to the data.

3.2.2. Temperate conifer forest plantation (Fig. 2(b))

Ritson and Sochacki (2003) measured root and shoot dry mass in 18 plantations of *Pinus pinaster* in south-west Western Australia. Stands examined ranged in age from 1 to 47 years and in height from 0.4 to 20 m. Stocking varied between 130 and 2200 stems ha^{-1} . A minimum of six trees were sampled per site. Stands were selected to represent a range of tree ages, site quality and planting densities (includ-

Fig. 2 – Patch dry mass (in Mg) for a 1 ha patch is plotted against time, with data for roots (open points) and shoots (filled points), as well as model estimates for roots (dashed lines) and shoots (solid lines). Model (7) output (Eqs. (8) and (9)) is denoted with dark lines, while the output for linear model (10) (Eq. (11)) is denoted with fine lines. The four different forest ecosystems described in the text relate to (a) a mixed forest ($\kappa \approx 300 \text{ Mg}$), (b) a temperate conifer forest plantation ($\kappa \approx 300 \text{ Mg}$), (c) a temperate eucalypt forest plantation ($\kappa \approx 400 \text{ Mg}$), and (d) a temperate broadleaf forest plantation ($\kappa \approx 160 \text{ Mg}$). Initial values were taken from initial data points.

ing close and open spaced). Over the 18 sites, precipitation ranged from 400 to 600 mm year⁻¹. For a comparison between data and model predictions see Fig. 2(b). We note that this example too is not comprised of a sequence of measurements from a single site, but rather measurements taken from different sites, under similar conditions, but of different ages.

3.2.3. Temperate eucalypt forest plantation (Fig. 2(c))

Brand (1999) measured root and shoot dry mass of *Eucalyptus globulus* in 10 plantations in south-west Western Australia. A minimum of six trees were sampled at each site. Plantations ranged in age from 1 to 11 years, with height measuring between 1 and 30 m, and the stocking varied between 561 and 1308 stems ha⁻¹. Mean annual precipitation of the stands examined varied between 600 and 1400 mm year⁻¹, with both high and low productivity sites being sampled. For a comparison between data and model predictions see Fig. 2(c). As with the examples above, the data derive from different sites of different ages, not a sequence of measurements from a single site.

3.2.4. Temperate broadleaf forest plantation (Fig. 2(d))

Ruark and Bockheim (1988) measured root and shoot biomass in five stands of *Populus tremuloides* in north central Wisconsin, USA. Stands ranged in age from 8 to 63 years, and were all even aged and fully stocked, having regenerated naturally following clear-cutting. Stocking varied between 890 and 12,670 stems ha⁻¹. The mean annual precipitation for the stands examined was 800 mm year⁻¹. For a comparison between data and model predictions see Fig. 2(d). Note that, as with the cases above, the measurements are taken from different sites at different stages of development.

3.2.5. Summary

Although the cases considered above are from a variety of plantation species, as well as a mixed forest, the models with generic parameters established here and in Mokany et al. (2006) closely follow the observed system behaviour. However, application of the model requires an input time sequence of the average mass of the shoots, and thus provides predictions at those points and not beyond. Such predictions are highly sensitive to the available data, as discussed in Barnes et al. (2006).

Further, as in Barnes et al. (2006), given an allometric (or some other) growth curve for average or individual shoot dry mass, $\bar{m}_2$, forward predictions can be achieved. Such a growth relationship can be applied to generate a data sequence, and the model can then be used to forward predict the total root and shoot dry mass for the system at a patch scale, requiring only initial conditions and an estimate for κ , the system carrying capacity. Such predictions are not highly sensitive to small variations in the choice of allometric parameters or κ , as discussed in Barnes et al. (2006).

While the examples cited above are for forest systems, we have also applied the model to non-forest vegetation systems, such as swards of clover. The results are similar to those presented here, in terms of model fit, but the data sets were inadequate, particularly concerning initial numbers of individuals, and were thus omitted. Nevertheless, the frame-

work is relevant to both forest and non-forest systems of vegetation.

4. An example with process driven relationships

Thornley (1972) and Thornley and Johnson (1990) have taken a dynamical systems approach to modelling partitioning within an individual plant, based on system mechanisms such as plant specific growth rate, and we illustrate how such an approach can be incorporated into framework (4). We consider again a patch of vegetation comprised of components, although in this case, following Thornley and Johnson (1990), we consider four components comprising total dry mass, and include process driven relationships between these components. Unlike the previous case, this model has no explicit solution; however, we generate a solution through numerical techniques, illustrating the dynamics of the components at the patch scale over time. Furthermore, we relate this process driven model to the approach based on an empirically established allometric relationship of the previous section, providing physical meaning to the allometric constants under certain conditions.

4.1. The Thornley–Johnson model

The Thornley–Johnson model is comprised of equations that describe the rate of change in the structural dry mass and substrate stores within the plant for an individual, where the root and shoot structural dry masses are denoted m_r and m_{sh} , respectively, and the dry mass of substrate is denoted m_C for carbon substrate and m_N for that attributed to nitrogen. The resulting dynamical system is given by

$$\begin{aligned} \frac{dm_r}{dt} &= c g_r(m_C, m_N) m_r, \\ \frac{dm_{sh}}{dt} &= c g_{sh}(m_C, m_N) m_{sh}, \quad \frac{dm_N}{dt} = c_N m_r - f_N \frac{d(m_r + m_{sh})}{dt}, \\ \frac{dm_C}{dt} &= c_C m_{sh} - f_C \frac{d(m_r + m_{sh})}{dt}. \end{aligned} \quad (12)$$

c denotes a constant growth rate coefficient, g_r and g_{sh} are the functions of the substrate, c_N and c_C are the specific root and shoot activities, that is, the rates of nitrogen uptake and photosynthesis, by the roots and the shoots, respectively, dependent on environmental conditions and assumed constant here; and f_N and f_C are the fractional substrate nitrogen and carbon contents of the structure, respectively, and considered constant. (For details of the derivation see Thornley and Johnson, 1990.)

Thornley and Johnson (1990) define P as the ratio of specific root and shoot growth rates for an individual:

$$P = \frac{(1/m_r)(dm_r/dt)}{(1/m_{sh})(dm_{sh}/dt)} = \frac{m_{sh}}{m_r} \frac{dm_r}{dm_{sh}}. \quad (13)$$

For balanced exponential growth $P = 1$, we have $g_r = g_{sh} = g$ and

$$\frac{m_{sh}}{m_r} \frac{dm_r}{dm_{sh}} = 1 \Rightarrow m_r = \gamma m_{sh} \quad \text{with } \gamma = \frac{m_r(0)}{m_{sh}(0)}.$$

where $m_r(0)$ and $m_{sh}(0)$ are specified (initial) conditions. (This expression relates directly to the empirically established relationship of Section 3, as is discussed in Section 5 below.)

4.2. Incorporating the Thornley–Johnson relationships into the theoretical model

To incorporate the Thornley–Johnson formulation of growth and partitioning into model (4), we require expressions relating the average masses of the plant components, $\bar{m}_r$, $\bar{m}_{sh}$, $\bar{m}_N$ and $\bar{m}_C$. So as not to complicate the illustration of our approach unduly, we assume the case of an even aged monoculture, so that variances and covariances among individuals within a patch, at any moment in time, are close to zero.

Under these conditions, and for balanced exponential growth, with averages taken over n individuals

$$\frac{1}{\bar{m}_r} \frac{d\bar{m}_r}{dt} \approx \overline{cg(m_N, m_C)} \approx cg(\bar{m}_N, \bar{m}_C) = c\bar{g}.$$

$$\frac{1}{\bar{m}_{sh}} \frac{d\bar{m}_{sh}}{dt} \approx \overline{cg(m_N, m_C)} \approx cg(\bar{m}_N, \bar{m}_C) = c\bar{g}.$$

$$\frac{d\bar{m}_N}{dt} \approx c_N \bar{m}_r - f_N \left(\frac{d\bar{m}_r}{dt} + \frac{d\bar{m}_{sh}}{dt} \right),$$

$$\frac{d\bar{m}_C}{dt} \approx c_C \bar{m}_{sh} - f_C \left(\frac{d\bar{m}_r}{dt} + \frac{d\bar{m}_{sh}}{dt} \right)$$

and then

$$\frac{d\bar{m}_r}{d\bar{m}_{sh}} \approx \frac{\bar{m}_r}{\bar{m}_{sh}} \Rightarrow \bar{m}_r \approx \gamma \bar{m}_{sh},$$

where $\gamma = \bar{m}_r(0)/\bar{m}_{sh}(0)$, the ratio of average initial values.

The above equations define a relationship between the four plant components. To incorporate these components and their relationship into the general ecological framework (4), we define the total dry mass of the patch Y , such that $Y = Y_1 + Y_2 + Y_3 + Y_4$. The patch scale components are $Y_1 = n\bar{m}_r$ and $Y_2 = n\bar{m}_{sh}$, which relate to root and shoot structural dry masses, respectively, and $Y_3 = n(M_N/14)\bar{m}_N$ and $Y_4 = n(M_C/12)\bar{m}_C$ (where M_N and M_C refer to molecular masses), which relate to nitrogen and carbon substrate dry masses, respectively. Inclusion into framework (4) yields:

$$\frac{dY_1}{dt} = c\bar{g} Y_1 \left(1 - \frac{Y_1}{\kappa} \left[1 + \frac{\bar{m}_{sh}}{\bar{m}_r} + \frac{d\bar{m}_N}{d\bar{m}_r} + \frac{d\bar{m}_C}{d\bar{m}_r} \right] \right),$$

$$\frac{dY_2}{dt} = c\bar{g} Y_2 \left(1 - \frac{Y_2}{\kappa} \left[1 + \frac{\bar{m}_r}{\bar{m}_{sh}} + \frac{d\bar{m}_N}{d\bar{m}_{sh}} + \frac{d\bar{m}_C}{d\bar{m}_{sh}} \right] \right),$$

$$\begin{aligned} \frac{dY_3}{dt} &= \frac{1}{\bar{m}_N} \left(c_N \bar{m}_r - f_N \left[\frac{d\bar{m}_r}{dt} + \frac{d\bar{m}_{sh}}{dt} \right] \right) \\ &\times Y_3 \left(1 - \frac{Y_3}{\kappa} \left[1 + \frac{d\bar{m}_r}{d\bar{m}_N} + \frac{d\bar{m}_{sh}}{d\bar{m}_N} + \frac{d\bar{m}_C}{d\bar{m}_N} \right] \right), \end{aligned}$$

$$\begin{aligned} \frac{dY_4}{dt} &= \frac{1}{\bar{m}_C} \left(c_C \bar{m}_{sh} - f_C \left[\frac{d\bar{m}_r}{dt} + \frac{d\bar{m}_{sh}}{dt} \right] \right) \\ &\times Y_4 \left(1 - \frac{Y_4}{\kappa} \left[1 + \frac{d\bar{m}_r}{d\bar{m}_C} + \frac{d\bar{m}_{sh}}{d\bar{m}_C} + \frac{d\bar{m}_N}{d\bar{m}_C} \right] \right), \end{aligned}$$

which reduces to

$$\frac{dY_1}{dt} = \gamma \frac{dY_2}{dt},$$

$$\frac{dY_2}{dt} = c\bar{g} Y_2 \left(1 - \frac{Y_2}{\kappa} \left[(1 + \gamma)(1 - f_N - f_C) + \frac{\gamma c_N + c_C}{c\bar{g}} \right] \right),$$

$$\begin{aligned} \frac{dY_3}{dt} &= \left(\frac{\bar{m}_{sh}(\gamma c_N - (1 + \gamma)f_N c\bar{g})}{\bar{m}_N} \right) Y_3 \\ &\times \left(1 - \frac{Y_3}{\kappa} \left[1 + \frac{c_C + c\bar{g}(1 + \gamma)(1 - f_C)}{\gamma c_N - (1 + \gamma)f_N c\bar{g}} \right] \right), \\ \frac{dY_4}{dt} &= \left(\frac{\bar{m}_{sh}(c_C - (1 + \gamma)f_C c\bar{g})}{\bar{m}_C} \right) \\ &\times Y_4 \left(1 - \frac{Y_4}{\kappa} \left[1 + \frac{\gamma c_N + c\bar{g}(1 + \gamma)(1 - f_N)}{c_C - (1 + \gamma)f_C c\bar{g}} \right] \right). \end{aligned} \quad (14)$$

As with the individual-based model of Thornley and Johnson (1990) (Eq. (12)), such a system requires numerical methods for solution. For this, expressions for $\bar{m}_{sh}$, $\bar{m}_N$ and $\bar{m}_C$ over time are required (that can be established from solution to system (12)), and an explicit formulation of function g is also necessary. However, the most important aspect is that a process driven formulation of the relationships between vegetation components can be incorporated into the framework (Eq. (4)), thereby scaling up from the characteristics of an individual to the patch level.

4.3. Model application

Because data were not available with which to compare the model output, we have solved system (12) numerically using parameter values taken from Thornley and Johnson (1990), and used these results in framework (14). In Fig. 3(a), the results from Thornley's individual scale model (12) are given, where we note that, as for the case of the allometric relationship in Section 3, growth is exponential. In Fig. 3(b), the results of (a) are incorporated into the patch scale theoretical framework (14), and the system solved numerically to give the system dynamics at the larger (patch) scale. We note that the framework ensures sigmoidal growth towards the system carrying capacity, although characteristics of the system growth are determined by individual properties and the interactions between components within the individual.

5. Relating the allometric and process driven approaches

While the models from the two cited examples, that of the empirical allometric equation relationships of Erquist and Niklas (2002), Robinson (2004) or Mokany et al. (2006), and that of the process driven system of Thornley and Johnson (1990), were developed separately and derived through very different means, a natural relationship between the two emerges.

Consider the ratio of specific root and shoot growth rates (defined in Eq. (13)), but for an average individual plant:

$$P = \frac{(1/\bar{m}_r)(d\bar{m}_r/dt)}{(1/\bar{m}_{sh})(d\bar{m}_{sh}/dt)}. \quad (15)$$

In the case $P = \hat{\alpha}$ is constant, one particular case considered by Thornley and Johnson (1990), then

$$\frac{1}{\bar{m}_r} \frac{d\bar{m}_r}{dt} = \hat{\alpha} \left(\frac{1}{\bar{m}_{sh}} \frac{d\bar{m}_{sh}}{dt} \right)$$

Fig. 3 – (a) Average individual dry mass (g) is plotted against time (days), applying the individual scale model (12). (b) Total patch dry mass (g) is plotted against time (days), applying model (14) together with the output of model (12). All components are labelled, with solid lines denoting the structural dry mass of roots and shoots, and dashed curves denoting the structural dry mass of carbon and nitrogen substrates. Parameter values were $c = 100 \text{ day}^{-1}$, $c_N = 0.05 \text{ day}^{-1}$, $c_C = 0.15 \text{ day}^{-1}$, $f_N = 0.03$, $f_C = 0.45$ and $\kappa = 1 \text{ kg set arbitrarily for an arbitrary patch size}$. Following Thornley and Johnson (1990), $\bar{g} = 1/2(\bar{m}_N \bar{m}_C)/(\bar{m}_r + \bar{m}_{sh})^2$. Initial values were taken as $\bar{m}_r(0) = 0.1 \text{ g}$, $\bar{m}_{sh}(0) = 0.3 \text{ g}$, $\bar{m}_N = 0.01 \text{ g}$ and $\bar{m}_C = 0.7 \text{ g}$, whence $\gamma = 0.33$, and $M_N = 14 \text{ kg (kg mol)}^{-1}$ and $M_C = 12 \text{ kg (kg mol)}^{-1}$, for illustrative purposes.

and integrating gives:

$$\int \frac{1}{\bar{m}_r} d\bar{m}_r = \hat{\alpha} \int \frac{1}{\bar{m}_{sh}} d\bar{m}_{sh} \Rightarrow \ln \bar{m}_r = \hat{\alpha} \ln \bar{m}_{sh} + C.$$

where C is the constant of integration. Including initial conditions, with $\bar{m}_r(0)$ and $\bar{m}_{sh}(0)$ initial values for $\bar{m}_r$ and $\bar{m}_{sh}$, respectively:

$$\bar{m}_r = \left(\frac{\bar{m}_r(0)}{\bar{m}_{sh}(0)} \right)^{\hat{\alpha}} \bar{m}_{sh}^{\hat{\alpha}} = \hat{\beta} \bar{m}_{sh}^{\hat{\alpha}}, \quad (16)$$

where $\hat{\beta}$ represents the constant ratio $\bar{m}_r(0)/(\bar{m}_{sh}(0))^{\hat{\alpha}}$.

Comparing Eq. (16) with the allometric relationship of Section 3 (that is, $\bar{m}_1 = \beta \bar{m}_2^{\alpha}$), the allometric exponent, α , can be interpreted as the ratio of the relative growth rates of the two components (P), and the coefficient, β , as the ratio $\bar{m}_r(0)/\bar{m}_{sh}(0)^{\alpha}$. The special case of $\hat{\alpha} = 1$, is the case considered in Section 4, and relates to the empirical case of $\bar{m}_1 = \beta \bar{m}_2$ of Section 3.

In this way, for the case of constant P , the allometric exponent α and coefficient β can be related directly to physical dynamics, as derived by Thornley and Johnson (1990). Although Thornley and Johnson (1990) consider the case of balanced exponential growth in their process driven model, we note that, in general, P need not be constant, but may be time dependent, in which case there need not be any generic relationship with these allometric constants. However, in spite of this caveat, it can be seen that empirical estimates of allometric constants can be imbued with physical meaning, and the two approaches, empirical and process driven, related.

6. Conclusion

Through the examples in this paper, we have shown how the framework developed by Barnes and Roderick (2004) can be applied to describe the dynamics at the patch scale of vegetation components, such as, roots and shoots. In particular, our

examples have formulated the problem for roots and shoots, as well as carbon and nitrogen substrates, but the approach is general and can describe any partitioning within vegetation. Furthermore, this approach allows the inclusion of both empirical and/or process driven approaches to modelling at the individual scale, scaling up to the patch level through the embodied self-thinning mechanism of that framework. Thus, this method facilitates an understanding of patch scale partitioning, based on the dynamics and measurements of individuals, the scale typical of data collection.

In general, in terms of the estimates for such larger scale (patch scale) dynamics, there are again two classes of approach: empirical allometric, or dynamical based on physical mechanisms. Our approach is a framework based on the physical mechanism of self-thinning that subsumes all small scale mechanisms. It requires an estimate of system carrying capacity (an environmental characteristic) and individual plant growth functions, empirically derived or process defined. There are many papers to which such an approach can contribute, and we suggest a few.

A model, such as that to predict patch scale dry mass of Niklas et al. (2003), relies on empirically derived constants at the level of individuals as well as the patch/community scale. While establishing such relationships is extremely valuable towards an understanding of plant dynamics, when amalgamating them there are mathematical pitfalls (Welsh et al., 1988; Williams, 1983). Our approach allows, with an estimate of system carry capacity, the ability to use the individual level characteristics to predict, through self-thinning dynamics, the total system mass over time. This avoids the above-noted mathematical difficulties and has been demonstrated to provide robust predictions here and in Barnes et al. (2006).

Alternatively, a growth-density model driven by physical mechanisms predicting total above-ground dry mass, differing in approach to that of Thornley and Johnson (1990), is that of Moorcroft et al. (2001). While the approach has many variables, enabling the tracking of many processes, it is complex and may be impracticable in many circumstances. Further, it also relies on allometric growth relationships. Applied to the same

set of data (Uhl, 1987; Saldarriaga et al., 1988), our approach is in good agreement with that of Moorcroft et al. (2001), when applied to above-ground dry mass. The approach presented here allows an extension to the prediction of below-ground dry mass at a patch scale (as illustrated in Fig. 2(a)) without requiring further variables and parameters.

A third model, based on physical mechanisms, to which this modelling approach could provide a valuable extension is that of Bijlsma and Lambers (2000). Such a model has similar properties to that of Thornley and Johnson (1990), but our methodology would contribute community level estimates of plant components, based on their individual level characteristics.

A key feature of this article is that we have shown that allometric relationships can be related to process driven models, providing allometric constants with physical meaning. Consequently, the dynamics embodied in the constants is understood and theoretical analysis is facilitated.

We note that disturbance has not been dealt with in this paper, although it is integral to such systems. However, it is formulated and discussed in Barnes and Roderick (2004), and can be included into the partitioning model similarly. Annual defoliation, as a disturbance process, is subsumed into the generic total mass loss term in that formulation, and is thus integral to the modelling approach.

Although not discussed here, the formulation can be extended to entire ecosystems, at regional, continental or global scales, following the theory in Barnes and Roderick (2004) and the partitioning approach presented in this paper. Further, although the formulation here was defined in terms of system dry mass, it could just as well have been expressed in terms of system volume, or total mass, thus incorporating individual-based partitioning models based on alternative characteristics.

Appendix A. Solution equation (8)

The second equation of system (7) can, with $Y_2 = n\tilde{m}_2$, be written as

$$\frac{dY_2}{d\tilde{m}_2} = \frac{Y_2}{\tilde{m}_2} \left(1 - \frac{Y_2}{\kappa} [1 + \alpha\beta\tilde{m}_2^{\alpha-1}] \right)$$

and solved explicitly as follows. Rearranging the above equation:

$$\frac{dY_2}{d\tilde{m}_2} - \frac{Y_2}{\tilde{m}_2} = -\frac{Y_2^2}{\kappa\tilde{m}_2} (1 + \alpha\beta\tilde{m}_2^{\alpha-1}).$$

Then, setting $w = 1/Y_2$:

$$\begin{aligned} -\frac{1}{w^2} \frac{dw}{d\tilde{m}_2} - \frac{1}{w\tilde{m}_2} &= -\frac{1}{w^2\kappa\tilde{m}_2} (1 + \alpha\beta\tilde{m}_2^{\alpha-1}) \\ \Rightarrow \frac{dw}{d\tilde{m}_2} + \frac{w}{\tilde{m}_2} &= \frac{1}{\kappa\tilde{m}_2} (1 + \alpha\beta\tilde{m}_2^{\alpha-1}), \end{aligned}$$

and in this form the equation is separable. Thus, with integrating factor $\tilde{m}_2$, the equation can be expressed as

$$\frac{d(\tilde{m}_2 w)}{d\tilde{m}_2} = \frac{1}{\kappa} (1 + \alpha\beta\tilde{m}_2^{\alpha-1})$$

and integrated to give

$$\tilde{m}_2 w = \frac{\tilde{m}_2}{\kappa} + \frac{\beta\tilde{m}_2^\alpha}{\kappa} + C.$$

C is the constant of integration, and in terms of the initial values $\tilde{m}_2(0)$ and w_0 :

$$C = \tilde{m}_2(0)w_0 - \frac{\tilde{m}_2(0)}{\kappa} - \frac{\beta\tilde{m}_2^\alpha(0)}{\kappa}.$$

Substituting this expression for C into the equation above, recalling that $w = 1/Y_2$ and setting $w_0 = 1/Y_2(0)$, and then rearranging the terms, gives the solution:

$$Y_2(t) = \frac{\tilde{m}_2(t)Y_2(0)\kappa}{\tilde{m}_2(0)(\kappa - Y_2(0)) + Y_2(0)(\tilde{m}_2(t) + \beta[\tilde{m}_2^\alpha(t) - \tilde{m}_2^\alpha(0)])}.$$

We note that, in the case $\alpha = 1$, this solution reduces to

$$Y_2(t) = \frac{\tilde{m}_2(t)Y_2(0)\kappa/(1 + \beta)}{\tilde{m}_2(0)(\kappa/(1 + \beta) - Y_2(0)) + Y_2(0)\tilde{m}_2(t)}.$$

This result can also be obtained from integrating the second equation of system (7) without substitutions, as it is in a separable form when $\alpha = 1$.

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