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Original Research

A theoretical analysis of how plant growth is limited by carbon allocation strategies and respiration

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Abstract. Improving crop yield is essential to meet increasing global food demands. Boosting crop yield requires the coordination of carbon acquisition by leaves and carbon utilization by roots and seeds. Simple modelling approaches may be used to explain how this coordination is achieved within plant growth. Here, the limits to allocation strategies and the influence of maintenance costs are explored by analysing the sensitivity of a simple root–shoot carbon allocation model for vegetative and reproductive growth. The model is formulated based on fundamental constraints on plant growth and therefore can be applied to all plants. This general but quantitative approach shows that the relative costs of root and leaf respiration alter the relationship between carbon allocation and final plant size, enabling a range of allocation strategies to produce a similar total amount of plant material during vegetative growth. This plasticity is enhanced by increasing assimilation rate within the model. Results show that high leaf allocation during vegetative growth promotes early reproduction with respect to yield. Having higher respiration in leaves than roots delays the optimal age to reproduce for plants with high leaf allocation during vegetative growth and increases the restrictions on flowering time for plants with high root allocation during vegetative growth. It is shown that, when leaf respiration is higher than root respiration, reallocating carbon towards the roots can increase the total amount of plant material. This analysis indicates that crop improvement strategies should consider the effects of maintenance costs on growth, a previously under-appreciated mechanism for yield enhancement.

Keywords: Carbon allocation; model; plant growth; reproductive growth; respiration; sink; source; vegetative growth

Introduction

Improving crop yield is considered vital for meeting increasing global food demands (Fischer *et al.* 2009; Beddington *et al.* 2011), and new approaches are needed to break through existing yield barriers. Modern crops have been selectively bred to have increased proportions of biomass in harvestable material in order to maximize yield (Génard *et al.* 2008). Additionally, light interception has been maximized to allow of 80–90 %

of all visible light during growing seasons (Long *et al.* 2015). Out of all plant processes, photosynthesis is the best understood at the mechanistic level, which facilitates the current focus on investigating the efficiency of photosynthesis in crop research. However, the benefits gained from such increases in photosynthetic rates are not only limited by nutrients, temperature and water, but also the energy requirements for growth of non-photosynthetic plant parts (e.g. roots and seeds) and their maintenance.

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Crop yields depend on the accumulation of biomass via growth and its allocation (partitioning of resources) to harvestable plant parts. Environmental trade-offs and metabolic costs can impact the allocation of carbon between leaves and roots. For example, a lack of water or nutrients within the soil can lead to a plant allocating more carbon into roots (Bongarten and Teskey 1987; White *et al.* 2016). Conversely, if there is a lack of light or a loss of leaves, more carbon will be partitioned towards the leaves (Kozłowski 1949; Barney 1951; Nelson 1964; Murthy 1990). A plant's size can impose limitations on carbon acquisition when considering light limitation. Growing surplus leaves per unit ground area (increasing leaf area index [LAI]) leads to self-shading and reduces potential light absorption by the lower leaf layers. Additionally, a large plant requires more energy for respiration and tissue turnover than a small plant. For example, in the case of forest stands, a decline in net primary productivity with stand age and size is thought to arise from high levels of respiration compared with photosynthesis, restrictions on water transport and nutrient limitations on photosynthesis (Hunt *et al.* 1999).

The costs of maintenance respiration may differ between leaves and roots. Johnson (1983) suggests, from a theoretical analysis, that the cost of respiration in the roots is higher than that in the leaves, which is a consequence of nitrogen and anion uptake and assimilation being very expensive within the roots. Conversely, Tjoelker *et al.* (2005) show empirically that leaf respiration varies between 1 and 2.25 times higher per unit mass than root respiration for 39 grassland and savannah species. These examples show that the cost of maintaining a leaf may not always be equal to that required to maintain a root. Amthor *et al.* (2019) argue that respiration should be a focus in optimizing crop productivity. Knowing that there are species where respiration in the leaves is more than twice the cost of respiration in the roots (Tjoelker *et al.* 2005), it becomes important to investigate the limitations on carbon allocation with different ratios of leaf and root maintenance.

Whole plant processes which affect plant growth are well defined in isolation (e.g. photosynthesis (Farquhar *et al.* 1980) and respiration (Amthor 1986)), but there is a lack of knowledge about how such processes defining growth work together to determine the allocation of growth to above- and below-ground biomass. Here, modelling plant growth can be beneficial. Modelling can provide a way of assessing how different mechanisms interact, which can be limited by experiments alone due to a lack of fine control over each process. It also helps to refine the potential range of questions that are addressed with experiments, and allows more targeted hypothesis testing. In particular, it formalizes quantitative

predictions based on the current understanding that can be tested via experimentation. A modelling approach is therefore adopted for the specific research questions in this paper.

It remains unclear what internal mechanisms are responsible for biomass partitioning, since plant growth models use a variety of different assumptions for allocation (Ewel and Gholz 1991; Luxmoore 1991; Weinstein *et al.* 1991; Dewar *et al.* 1994). Some more recent models assume allocation based on a functional balance of resources to leaves and roots and is calibrated to maximize plant relative growth rate (Zerihun *et al.* 2000; Buckley and Roberts 2006; Feller *et al.* 2015). Most carbon allocation or plant growth models investigate the effects of environmental conditions, herbivory, senescence and/or pruning on plant growth (Hogsett *et al.* 1985; Ford and Keister 1990; Luxmoore 1991; Weinstein *et al.* 1991), and ignore the effects of different potential allocation strategies between leaves and roots on growth and how cellular processes such as photosynthesis and respiration alter this. However, any strategy for increasing productivity must balance the allocation of carbon to the growth of source and sink tissues. Here, a carbon source is defined as a net exporter of carbon to the rest of the plant, where carbon is acquired from the environment (i.e. mature leaves via photosynthesis), while sinks are net importers of carbon from internal sources (Doehler 1993), and include young leaves, seeds and roots.

Understanding the developmental stage at which a plant should reproduce can bring insights into optimal strategies that a plant should adopt when faced with environmental or biotic hazards and has a limited amount of time to reproduce before it is killed by an external factor. Equally, when considering crop production in a seasonal climate, development must be completed during a growing season of limited duration. Many have investigated the effects of flowering time on yield (Cohen 1971; King and Roughgarden 1982; Guilbaud *et al.* 2015) and specifically focused on environmental heterogeneity (Paltridge and Denholm 1974; Ledder *et al.* 2004), multiple reproductive phases (Chiariello and Roughgarden 1984) and photosynthetic rates (Schaffer *et al.* 1982). Yet, the effects on yield when varying allocation between leaves and roots during vegetative growth were not addressed.

This paper explores the following questions: (i) How does varying the allocation of carbon for growth between leaves and roots alter total plant biomass during vegetative growth? (ii) How do the processes of respiration and photosynthesis constrain possible strategies of allocation between leaves and roots? (iii) Does increasing allocation towards the roots always lead to a decrease in overall plant size? (iv) How does varying

allocation between leaves and roots during vegetative growth and flowering time alter reproductive output (which is equivalent to seed yield in the case of crops)? These are addressed by analysing the sensitivity of a simple carbon allocation model for vegetative and reproductive growth. All values within this paper are dimensionless in order to look at the general behaviour of the model.

Our model of plant growth dynamics is based on the balance between carbon assimilation rate (photosynthesis) and carbon usage rate (growth and respiration). While the absolute values of these processes vary significantly in different plants, we aim to capture the generic features of the dynamic balance between them. In order to do so, we study our model in dimensionless form. Plant growth depends on many different factors and therefore plant growth models can become extensive and include many parameters which do not necessarily exert strong control over the results. Importantly, the solution of the model may not necessarily depend on all of its parameters independently. Non-dimensionalization allows a model to be simplified by removing those extra parameters that can be combined, and removing the units. This approach has the advantage of identifying the specific combinations of model parameters that control the scaling of model solutions. It results in a model that contains a minimal set of effective parameters, whose solutions depend on the relative magnitudes of different processes. Importantly, the solutions of any dimensional form of the model are obtained from the non-dimensional solutions by scaling. This approach allows the sensitivity of plant growth to changes in allocation, photosynthesis and respiration to be explored in their broadest sense. The model results are described as changes in ratios or relationships between parameters; the inclusion of units does not change these relationships (see [Appendix 1](#) for further detail).

Model description

The model considers only carbon sources and sinks, with no soil or other environmental interactions. Sink or source strength can be defined as the combination of source or sink size and activity, which relates to the uptake or export rate of a particular resource. By combining two alternative, but complementary, perspectives, the model simultaneously accounts for net carbon export rate from the leaves (source strength), internal carbon allocation to leaves for growth (growth of source size) and roots or seeds for growth (growth of sink size), and the development of leaves, roots and seeds ([White et al. 2016](#)).

The physiological perspective defines growth by the acquisition and loss of carbon via photosynthesis and respiration, respectively ([Lambers et al. 1990](#)). This expresses carbon gain as the difference between carbon acquired via photosynthesis (source strength) and the loss of carbon through respiration:

$$\text{Net carbon gain} = Al - R_1l - R_2r, \quad (1)$$

where Al represents the rate of carbon assimilation (A is assimilation rate per unit leaf tissue and l is the amount of leaf tissue) and R_1l and R_2r is the rate of use of carbon for maintaining plant material (R_1 and R_2 are leaf and root respiration and r is the amount of root tissue [dimensionless]). This formulation accounts for the fact that not all carbon assimilated is used for the growth of new plant tissue; some is used for the maintenance of existing tissue and other metabolic processes.

The second perspective is the development of source and sink tissues. Here, plants are conceptualized as modular structures, where a module is one of the repeating units from which a plant is constructed (e.g. leaves, roots or cells) and growth is assumed to be a function of module initiation rates (the rate at which each module is constructed). Growth in this case is defined as the development of individual leaves and roots ([Pritchard et al. 1999](#)), which can be expressed as the combination of organ initiation rates:

$$\text{Growth} = \mu_1 M_l + \mu_2 M_r, \quad (2)$$

where μ_1 and μ_2 are the module initiation rates of leaves and roots, and M_l and M_r are the sizes of leaf and root modules, respectively. Individually, these perspectives bring limited insights. The physiological approach is resource driven and the developmental perspective is driven by the carbon requirements for the growth of new organs. By combining these perspectives, the model simulates plant growth based on fundamental constraints ([White et al. 2016](#)), allowing the exploration of how physiological rates, allocation and developmental rates interact to control growth.

Assumptions

Simplifying assumptions mean that the model is best interpreted as a simulation of monocarpic species growing in warm, fertile conditions, with strong competition for light within a closed leaf canopy. This is closest to the situation for annual crops. Although the developmental pattern of these plants means that the limits simulated by the model are never reached in nature, these limits set boundaries that development cannot exceed. Roots are modelled as carbon sinks, which account for all non-photosynthetic plant parts. The model does not simulate soil nutrient limitations or capture other environmental

limitations such as temperature or drought. This allows the effects of carbon allocation on growth to be directly analysed.

Photosynthesis The rate of carbon assimilation by photosynthesis is assumed to be the sole mechanism of carbon acquisition and is modelled as the average canopy photosynthetic rate, which is a decreasing function of the total leaf area. As LAI increases, the average unit rate of photosynthesis (per unit of leaf area) decreases due to self-shading (Pury and Farquhar 1997). Assimilation rate is chosen to be

$$A(l) = \frac{\theta A_0}{\theta + l}, \quad (3)$$

where θ is the shading coefficient, A_0 is the unit rate of photosynthesis for an unshaded leaf and l is the amount of leaf tissue. When $l = \theta$, the rate of photosynthesis per unit leaf area is half of its maximum (unshaded) value. Increasing the shading coefficient (θ) reduces the effect of shading on the assimilation rate.

Determinate growth Acquired carbon can either be allocated for growth and its associated cost (growth respiration) or used for maintenance respiration, where the cost of maintenance is linearly dependent upon the size of the plant (Ryan 1991) (Eq. (9)). The carbon allocated towards growth encompasses the cost of growth respiration since this is a dimensionless system. A necessary condition for growth is that the assimilation rate must always be greater than the respiration rate. This provides a natural constraint on appropriate parameter values. In the model, plants grow until canopy photosynthesis is exactly counterbalanced by total plant respiration, which sets a final plant size. Once this size is reached, no further growth occurs. Although a maximum size set by source–sink balance has been hypothesized for forest trees (Hunt et al. 1999; Day et al. 2001), this idea has been superseded by hypotheses relating to water and nutrient limitation of growth in tall trees and reductions in photosynthetic efficiency (Gower et al. 1996; Murty et al. 1996). However, despite being inappropriate for trees, this approach may be suitable for plants which do not grow indefinitely (determinate growth) such as monocarpic, herbaceous species, including annual crops, where plants reproduce once before dying and can be assumed to maximize reproductive output (i.e. seeds) using available resources. For many crops, the harvestable plant parts are the roots; therefore, within this framework, seeds are used to describe any reproductive organ that stores carbon.

For annual crops, the cessation of vegetative growth is brought about through a pre-determined developmental

pattern. However, a useful approximation for this is when resource uptake and use become balanced (due to self-shading), given that there is no senescence of leaves or roots in the model. It can be argued that the decline in plant relative growth rates is caused by plants becoming less efficient as they grow due to self-shading and tissue ageing (Evans 1972; Rees et al. 2010), while others suggest it is due to increased allocation of growth towards non-photosynthetic plant compartments (roots and stems) and reductions in soil nutrients (Paine et al. 2012; Philipson et al. 2012). Simulating steady-state plant growth is commonly used for plant growth models (Thornley 1972; Charles-Edwards 1976; Reynolds and Thornley 1982; Hirose 1986; Yin and Schapendonk 2004) and it can be argued that they can be applied to non-steady-state conditions (Hirose 1986; Agren and Ingestad 1987; Hirose et al. 1988; Van Der Werf et al. 1993).

Reproductive growth Roots are the only sink organ modelled during vegetative development, and roots and leaves both stop growing after a plant transitions from vegetative to reproductive growth. During reproductive development, the only sinks are seed growth and the respiration required to maintain existing roots and leaves. This transition to reproductive growth is imposed at numerous stages of a plant's life. These assumptions approximately replicate what happens during the development of annual crops such as wheat and rice (Atwell et al. 1999).

Senescence There is no turnover or senescence of plant tissues in the model, and source strength is maintained during reproductive development. This is a simplification that ignores the decline in source activity that occurs in annual crops during seed growth, which is linked to the remobilization of nitrogen from leaves to seeds (Masclaux et al. 2001).

Resource allocation The balance of carbon allocation between sources and sinks is assumed to be fixed such that the model simulates one allocation strategy throughout determinate growth. This ensures easy analytical comparisons between allocation strategies, but ignores ontogenic drift in allocation. Allocation strategy is dependent upon module initiation rates of leaves and roots, where the root module initiation rate is a fixed proportion of leaf initiation rate:

$$\mu_2 = \alpha \mu_1, \quad (4)$$

where α is the allocation coefficient. For example, when $\alpha = 2$, twice as much carbon is allocated to roots than leaves and when $\alpha = 1/2$, twice as much carbon is allocated to leaves than roots.

Model behaviour

Vegetative growth

Leaf and root growth can be individually expressed as

$$\frac{dl}{dt} = \mu_1 m_l, \quad (5)$$

and

$$\frac{dr}{dt} = \mu_2 m_r, \quad (6)$$

where m_l and m_r are leaf and root module size, respectively. Using Eq. (4), root and leaf growth are related by

$$\frac{dr}{dt} = m\alpha \frac{dl}{dt}, \quad (7)$$

where $m = m_r/m_l$.

Therefore, growth trajectories are given by

$$\frac{dr}{dl} = \frac{dr/dt}{dl/dt} = m\alpha \quad (8)$$

As a consequence of assuming a constant allocation strategy, the growth trajectories are straight lines with gradient $m\alpha$. Each growth trajectory represents the duration of plant growth from a seedling to the point, in which plant material reaches steady state as a function of leaf and root tissue and varies dependent upon initial seedling size.

The physiological perspective (Eq. (1)) defines the growth rate as the difference between the rates of photosynthesis and respiration. Carbon assimilated by the plant via photosynthesis is distributed between maintenance respiration and growth (including growth respiration):

$$A(l)l = R_1 l + R_2 r + \frac{dl}{dt} + \frac{dr}{dt}, \quad (9)$$

Substituting from Eq. (7):

$$A(l)l = R_1 l + R_2 r + [1 + m\alpha] \frac{dl}{dt}, \quad (10)$$

and therefore

$$\frac{dl}{dt} = \frac{1}{1 + m\alpha} (A(l)l - R_1 l - R_2 r) \quad (11)$$

Using Eq. (7) again gives

$$\frac{dr}{dt} = \frac{m\alpha}{1 + m\alpha} (A(l)l - R_1 l - R_2 r) \quad (12)$$

The model is given by Eqs (11) and (12). Steady states of the model satisfy the equation

$$r = \frac{A(l)l - R_1 l}{R_2}, \quad (13)$$

which corresponds to a continuous curve in the (l, r) phase space. The function $A(l)$, which represents the

effect of self-shading on photosynthesis, is a decreasing function of l . Using the functional form given in Eq. (3), the general form of the steady-state curve is illustrated in Fig. 1. The curve has a peak at $l = \theta (\sqrt{A_0/R_1} - 1)$, $r = (\theta R_1/R_2) [\sqrt{A_0/R_1} - 1]^2$ and maximum leaf tissue is determined by $l = \theta(A_0 - R_1)/R_1$. Therefore, the qualitative shape of the blue curve is independent of R_2 , which determines only the height of the curve. The location of the peak of the curve is determined by A_0/R_1 ; therefore, optimizing the ratio between the unshaded rate of photosynthesis and leaf respiration increases final plant size within this framework, which is to be expected. The steady-state curve (black line) begins with a steep increase, which is the ratio of root tissue to leaf tissue increasing because a much higher quantity of carbon is required for root respiration to balance out assimilation from the leaves. As leaf tissue increases, the level of self-shading increases. Once assimilation rate reaches its maximum, additional leaves are costly and less root tissue is required for respiration to balance the canopy assimilation rate. This explains the decline in the steady-state curve. For the purposes of behaviour illustration, the following default parameters: $A_0 = 10$, $\theta = 10$, $m = 1$, $\alpha = 1$, $R_1 = 2$, $R_2 = 2$, with initial conditions of $l = 0.01$ and $r = 0$ will be used.

The orange line in Fig. 1 is the vegetative growth trajectory, which represents the growth of a plant from seedling to a steady state at which the rates of photosynthesis and respiration are equal. The growth

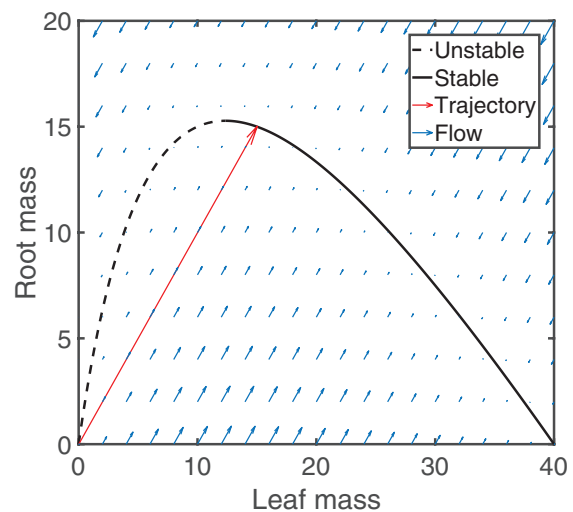


Fig. 1. The range of steady-state solutions (Eq. (13)) (given by values of l and r for which the ratio of respiration and photosynthesis are equal) (black line) with a plot of the vector field $[(dl/dt, dr/dt)]$ showing the local direction of growth trajectories. An example trajectory is also shown (orange line). Using $A_0 = 10$, $\theta = 10$, $R_1 = R_2 = 2$, $\alpha m = 1$ with an initial seedling size of $l = 0.01$, $r = 0$. Assumes vegetative growth only (no reproduction). All model parameters are dimensionless.

trajectories are straight lines in the l, r plane with gradient αm . Allocation is a combination of balance between allocation and module size. The straight line signifies a constant ratio of root to leaf tissue allocation as the plant grows. The root to leaf ratio at steady state depends on αm , initial leaf and root tissue, and the black steady-state curve. Fig. 1 also shows the vector field in blue $[(dl/dt), (dr/dt)]$. This illustrates the fact that only the portion of the steady-state curve with a negative gradient (solid line) corresponds to steady states that are stable. Biologically, this represents plants in which the roots account for the majority of total plant material with very few leaves. These situations are unrealistic given the assumption that roots are only considered as carbon sinks. The maximum stable allocation strategy is defined as

$$\alpha_{\max} = \frac{R_1}{R_2} \left(\sqrt{A_0/R_1} - 1 \right). \quad (14)$$

Fig. 2a shows several growth trajectories for different allocation strategies (α) when the cost of leaf and root maintenance respiration is equal ($R_1 = R_2$). The choice of allocation strategy determines the point at which the growth trajectory intersects the steady-state curve. This determines the ratio of root and leaf material and total plant size at steady state. These final plant sizes can be related to yield as a larger plant produces a greater yield than a smaller one. For these parameters, steady-state total plant size is a decreasing function of allocation strategy. In other words, strategies which favour leaf growth result in larger steady-state total plant size than those favouring root growth, when roots are

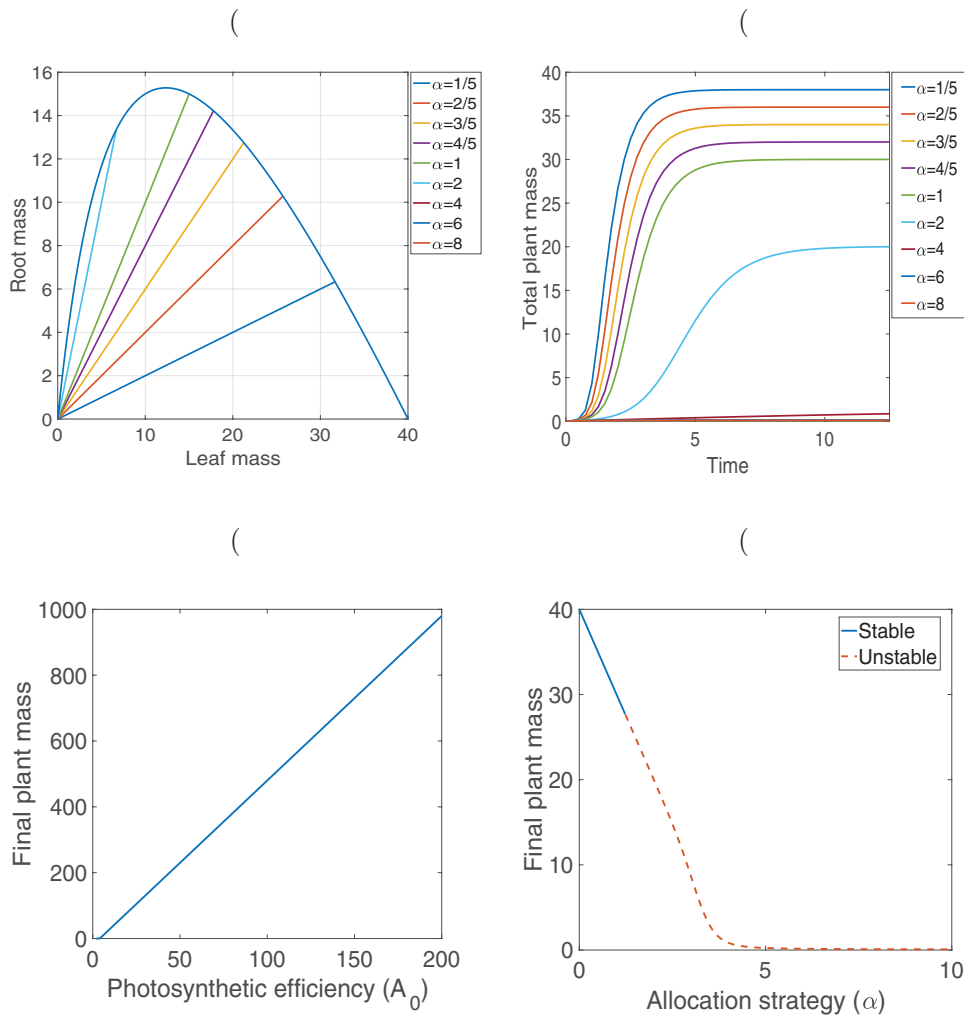


Fig. 2. (A) The range of steady-state solutions (blue line) with multiple growth trajectories for different allocation strategies. (B) Growth curves for multiple allocation strategies when $A_0 = 10$, $\theta = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 2$. (C) The relationship between photosynthetic efficiency (A_0) and final plant size when $\theta = 10$, $m = 1$, $\alpha = 1$, and leaf and root respiration is equal ($R_1 = 2 = R_2 = 2$). (D) The relationship between allocation strategy and final plant size when $A_0 = 10$, $\theta = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 2$. All simulations were performed with initial conditions of $l = 0.01$ and $r = 0$, and all model parameters are dimensionless.

only considered as sinks. The same effects also apply to growth rates (Fig. 2b). The constant allocation ratio implies that the intersection between the vegetative growth line and the steady-state curve (final plant size) is dependent upon the choice of initial seedling size and the steepness of the growth trajectory (allocation strategy). Varying the allocation strategy can alter the point at which the growth trajectory reaches the steady-state curve.

The effects of shading are a decreasing function of the shading coefficient θ ; thus, steady-state total plant size is a decreasing function of θ , since both the peak of the steady-state curve and maximum leaf tissue depend on shading. Increasing A_0 has a positive impact on final plant size as expected (Fig. 2c). As the shading coefficient tends towards infinity, the assimilation rate becomes unconstrained and plant material continuously increases. Conversely, imposing a very small shading coefficient highly constrains assimilation rate and leads to a very small final plant material.

These behaviours imply that the model represents the growth of a plant in a reasonable manner reproducing well-known phenomena.

Reproductive growth

Formulated in terms of the current model, a plant undergoes vegetative growth from an initial seedling size using Eqs (11) and (12) with a pre-determined allocation strategy. The plant can then decide to reproduce at any developmental stage. Once the plant has made the life history decision to reproduce, no further vegetative growth occurs, total leaf and root mass become fixed at this point in time and the reproductive sink increases in size until the steady state is reached. Since the growth of leaves and roots is set to zero, all carbon made available from the plant minus respiratory costs at its chosen developmental stage is invested into seed production. Leaf and root biomass from the chosen developmental stage are the new initial conditions for the reproductive stage of growth. Within this framework, the seeds themselves have the same respiratory cost as roots and simply represent an additional sink. The model then becomes

$$\frac{ds}{dt} = A(l)l - R_1l - R_2r - R_2s, \quad (15)$$

where s is the amount of seed material, A is assimilation rate, l is leaf tissue, r is root tissue, and R_1 and R_2 are maintenance respiration for leaves and roots and seeds, respectively. Within this framework, there are two decisions that a plant can make which alter potential seed yield: (i) The allocation strategy during vegetative growth; (ii) The developmental stage at which a plant reproduces.

How do maintenance costs limit carbon allocation?

Within the model, growth depends on the allocation of carbon to plant compartments, the assimilation of carbon via photosynthesis and loss of carbon via maintenance respiration. How these processes interact together can provide insight into the limitations on growth. In particular, how do maintenance costs limit the range of carbon allocation strategies which alter final plant size?

When leaf and root maintenance costs are equal, unshaded assimilation rate reduces limitations to carbon allocation

In the circumstances when the costs of leaf and root maintenance respiration are equal, increasing allocation towards the leaves increases final plant size. Fig. 2d shows the effect of varying allocation strategy on final plant size. With default parameters, final plant size decreases as α increases, until $\alpha = 4$, then the plant does not have enough carbon to grow when allocation favours the roots. The maximum allocation strategy for stable steady-state solutions is $\alpha_{max} = 1.2361$. This implies that carbon allocation is limited by an upper bound on root strategies; therefore, only plants which allocate up to 1.2361 times more carbon to root growth than leaves are realistic given the parameter set. A sensitivity analysis shows how this upper bound is changed by alternative model parameterizations (see Appendix 2).

There are two parameters within the model that vary the effect of assimilation rate; the unshaded assimilation rate and the shading coefficient. Increases in the unshaded assimilation rate cause both the maximum final plant size and the upper bound of root allocation to increase. For example, when increasing unshaded assimilation to $A_0 = 20$, the limit to root allocation is reached approximately when $\alpha_{max} = 2.1623$. Fig. 3 shows the relationship between allocation strategy and final plant size with multiple unshaded assimilation rates. The gradients of these lines are not altered when varying A_0 . Therefore, the model behaves reasonably, confirming that, having a higher unshaded assimilation rate ensures that the plant has more carbon available to allocate towards new modules, enabling a plant to allocate more towards the roots.

In contrast, increasing the effect of shading on growth has no effect on the limits to carbon allocation. Increasing the shading coefficient (i.e. reducing the effect of shading) increases the maximum final plant size but the upper bound on root allocation remains the same. This is because α_{max} is independent of θ (Eq. (14)). The shading coefficient (θ) simply delays the effect of shading on assimilation rate; therefore, the cost is not applied until the total leaf canopy size is high (small α).

This means that canopy architecture does not constrain the allocation of growth to roots within this framework. Further to this, using different initial conditions would alter the limits to carbon allocation since they alter the rates of photosynthesis and respiration.

When leaf respiration costs more than root respiration, increasing carbon allocation to the roots can increase final plant size

When leaf and root respiration are equal, increasing allocation towards the leaves increases final plant size

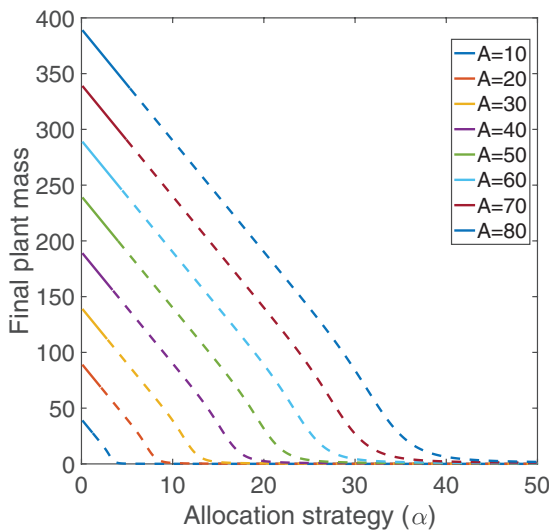


Fig. 3. The relationship between allocation strategy and final plant size with multiple unshaded assimilation rates (A), when maintenance respiration is equal in the roots and leaves ($R_1 = 2, R_2 = 2$), $m = 1$, $\theta = 10$, and initial conditions $l_0 = 0.1$ and $r_0 = 0$. When $\alpha < 1$, more carbon is allocated to the leaves and when $\alpha > 1$, more carbon is allocated to the roots. All model parameters are dimensionless.

and increasing allocation to the roots decreases final plant size. Only the negative slope of the steady-state curve has stable solutions during vegetative growth (Fig. 1b). The gradient of this curve defines the relationship between the allocation strategy and final plant size. If the gradient of the curve is less than -1 , then when α is large (i.e. allocation favours roots over leaves), the trajectory intersects the steady-state curve at a higher point (Fig. 4a). At this point, a larger plant is produced compared with the point of intersection for a smaller α . This is the opposite effect to when the gradient of the curve is greater than -1 , when intersecting a higher point on the curve produces a smaller plant when compared with having a smaller α (Fig. 4b).

When the cost of leaf respiration is higher than the cost of root respiration, decreasing leaf allocation reduces the amount of carbon lost via respiration, enabling a larger plant with a smaller leaf allocation strategy. When increasing allocation to a much larger root production strategy, there would be insufficient carbon assimilated to produce a larger plant. This means that, in the instance where the gradient of the steady-state curve is less than -1 , increasing allocation to the roots increases final plant size. But are there any realistic scenarios where this would happen? In order for this effect to occur within the model, the gradient of the steady-state curve (differentiated Eq. (13)) must be less than -1 , which is equivalent to

$$-\frac{R_1}{R_2} \left(1 - \frac{R_1}{A_0} \right) < -1, \tag{16}$$

therefore,

$$\frac{R_1}{R_2} \left(1 - \frac{R_1}{A_0} \right) > 1. \tag{17}$$

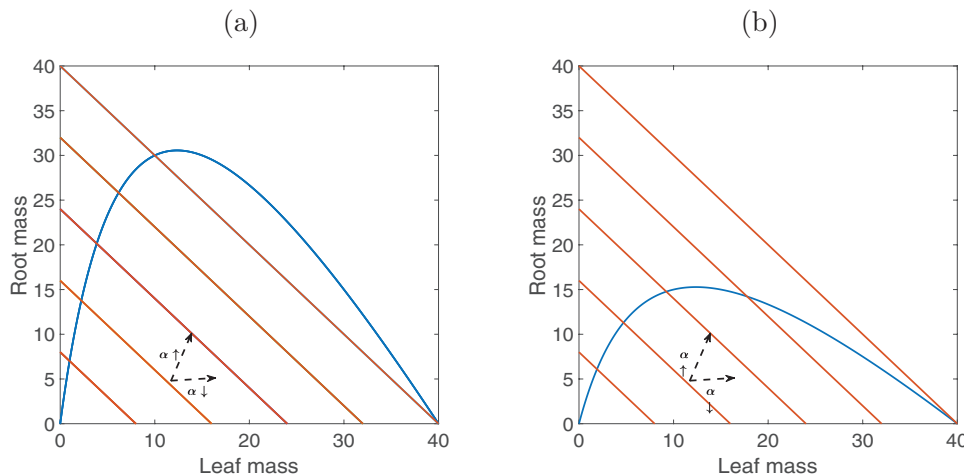


Fig. 4. (A) Curve of steady states (blue line) when the gradient is less than -1 with lines of constant plant size (orange lines) when $A_0 = 10$, $\theta = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 1$. (B) Curve of steady states (blue line) when the gradient is greater than -1 with lines of constant plant size (orange lines) when $A_0 = 10$, $\theta = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 2$ (dimensionless).

A necessary condition for growth is that $A_0 > R_1$; therefore, the cost of leaf respiration must be greater than the cost of root respiration.

The relationship between the allocation strategy and final plant size changes substantially when making leaf respiration larger than root respiration. Fig. 5b shows multiple trajectories intersecting the steady-state curve with different allocation strategies. Higher allocation strategies (large α) intersect a higher point on the steady-state curve and lower allocation strategies (small α) intersect a lower point on the curve. Towards the top of the steady-state curve, the gradient is less steep than -1 . Thus, as α increases, the point of intersection moves further along the steady-state curve, declining in plant size until the gradient reaches zero. This can be seen in Fig. 5a. It shows the increase in final plant size as allocation tends towards favouring the roots. Once the α reaches 1.2, the final plant size decreases. Therefore, there is only a small region along the steady-state curve, where increasing allocation strategy increases the final plant size. This graph implies that allocating more carbon towards the roots when $\alpha < 1.2$ would improve yield. It is also important to note the small range of final plant size in Fig. 5a—i.e. when varying allocation between two times more carbon to the leaves and two times more carbon to the roots, there is only a change of 4% in the final plant size when $A_0 = 10$, $\theta = 0.1$ and $m = 1$ (Fig. 5a). This implies that steady-state plant size can be plastic with respect to allocation strategy, such that over a range of α , any allocation strategy can be implemented and achieve the same final plant size. This identifies two key questions: what range of parameter

values defining carbon uptake (shading coefficient θ and unshaded assimilation rate per leaf A_0) allows this plasticity of final plant size to occur? Can altering these values limit or extend this plasticity within the model?

Varying the shading coefficient has no effect on the range of plasticity within the model The scenario in which leaf respiration costs twice the amount of root respiration is fairly common across different plant species (Hansen and Jensen 1977; Reich et al. 1998; Loveys et al. 2003; Tjoelker et al. 2005). This implies that there is a large range of parameter values which allow plasticity to occur with minimal change in final plant size. In the following sensitivity analysis, all parameters are varied within the model, while leaf and root respiration remain constant.

Increasing the shading coefficient has no effect on the region of allocation strategies which do not alter final plant size. For plasticity to occur, Eq. (16) must be satisfied. Since this equation is not dependent upon θ , it cannot have any effect on the range of plasticity. When the shading coefficient is 0.5 (high shading), a plant can have any strategy of α between 0.5 and 1.5 (Fig. 6a). Within this framework, the range of allocation strategies which produce similar final plant biomass is not altered by shading as increasing shading only reduces the availability of carbon for allocation.

As assimilation increases, there is more available energy to grow; therefore, much more carbon needs to be allocated to the roots when growth stops in the model. This means that the range over which final plant size increases and then decreases (parabola-like curve shown

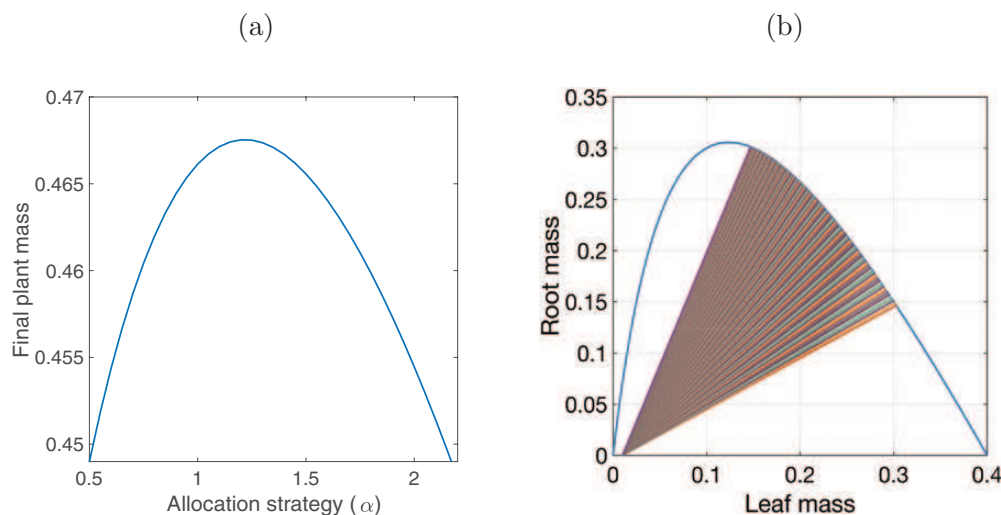


Fig. 5. (A) The relationship between allocation strategy and final plant size when the cost of leaf maintenance respiration is twice the cost of root maintenance respiration. (B) The ratios of leaf and root tissue at steady state with growth trajectories for a range of allocation strategies. Both produced with $A_0 = 10$, $\theta = 0.1$, $m = 1$, $R_1 = 2$, $R_2 = 1$ and initial leaf and root tissue of $l_0 = 0.01$ and $r_0 = 0$. $\alpha_{max} = 2.4721$; therefore, all solutions are stable within the range of alpha plotted. All model parameters are dimensionless.

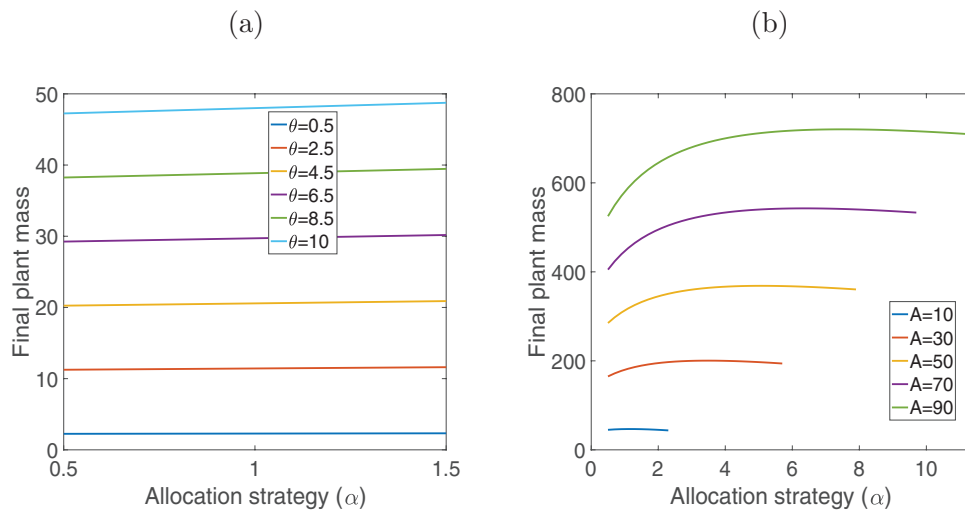


Fig. 6. The relationship between allocation strategy and final plant size (A) whilst varying shading coefficient (θ) when leaf and root maintenance respiration is equal. Allocation strategy is varied from $\alpha = 0.5$ to the maximum stable α with $A_0 = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 1$. (B) whilst varying unshaded assimilation rate (A) when leaf and root maintenance respiration is equal. Allocation strategy is varied from $\alpha = 0.5$ to the maximum stable α with $\theta = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 1$. Using initial leaf and root tissue of $l_0 = 0.01$ and $r_0 = 0$. All model parameters are dimensionless.

in Fig. 5a) is much larger. Though this is the case, there is a much larger change in final plant size under these scenarios. Fig. 6b shows the relationship between final plant size and a range of allocation strategies which produce a stable steady-state when varying A_0 . When unshaded assimilation rate is $A_0 = 10$, plasticity occurs when α is between 0.5 and 2.47 (Fig. 6b), while as assimilation increases, this range shifts to root-favoured strategies. When $A_0 = 70$, plasticity occurs when α is between 4 and 9.83 (Fig. 6b). Therefore, increasing assimilation rate increases the parameter space which allows plasticity of final plant size to occur and promotes a root-favoured allocation strategy.

How does the timing of reproduction influence yield?

The steady-state condition when photosynthetic carbon gain is exactly balanced by respiratory carbon loss is a special case that may not be commonly achieved in nature. One situation when this may occur is in mature forest stands, as size becomes a limiting factor on growth. This balance of the rate of photosynthesis and respiration rate is one mechanism proposed to explain why forest biomass does not increase indefinitely, but tends to approach a plateau (Hunt et al. 1999; Day et al. 2001). The general problem with such a steady state is that, once this point is reached, the system is essentially ‘stuck’ unless tissues turn over. One biological situation where this is not a problem is at the end of life in a monocarpic plant. Monocarpic species reproduce once at the

end of their lives (Harper and White 1974), and thus it might be assumed that they invest all remaining photosynthetic carbon into seed production at this point, so that growth approaches a steady-state situation. If this argument is accepted, this is an interesting case to consider because many crop species are annuals (i.e. monocarpic), including all cereal and grain legume crops.

Seed production depends on allocation strategy and developmental stage

Vegetative growth is simulated with a variety of allocation strategies. This produces multiple growth trajectories with different gradients. An initial root tissue of 0.1 is used for each trajectory, and initial leaf tissue is determined by $r = \alpha ml$. This sets the initial seedling size for each vegetative growth trajectory. Reproductive growth is then simulated by taking a point along the growth trajectory with a distinct amount of leaf and root tissue as the initial conditions to solve Eq (17) (Fig. 7a). The time taken to produce seed can be solved analytically using Eq. (17) for a range of allocation strategies and developmental stages. The amount of seed produced is calculated and compared.

The dependence of seed production on the developmental stage of reproduction is shown in Fig. 7b for a range of allocation strategies when leaf and root respiration are equal. Each developmental stage represents the total amount of leaf tissue as a percentage of the total amount of leaf tissue reached at steady state during vegetative growth (percentage of total age) or in other words, various stages along a plant’s lifespan if it did not

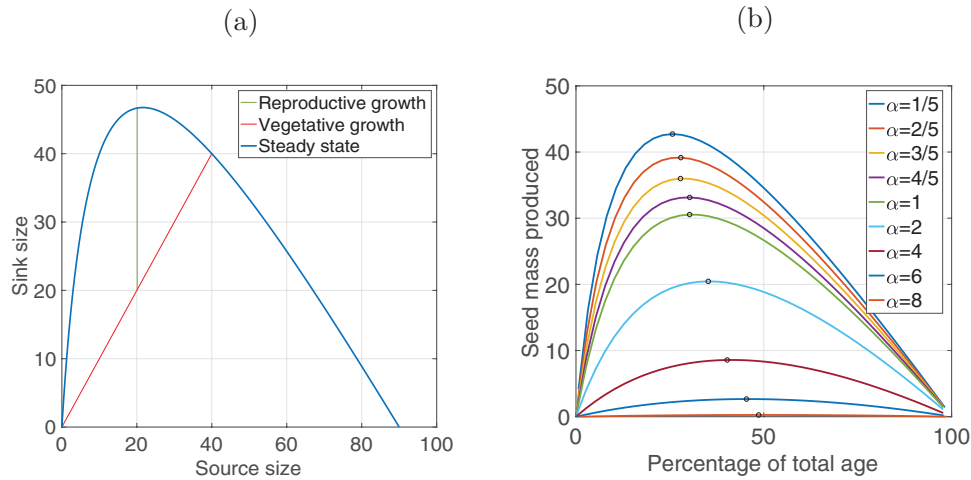


Fig. 7. (A) The range of root to leaf allocation patterns when growth stops (blue line) with a vegetative growth trajectory (orange line) starting from an initial leaf and root tissue of $l = 0.1$, $r = 0.1$ and a reproductive growth trajectory (green line) starting from half of its total possible vegetative size ($l = 20$, $r = 20$), when $A_0 = 10$, $m = 1$, $\alpha = 1$, $\theta = 10$ and leaf respiration is equal to root respiration ($R_1 = 1 = R_2 = 1$). Sink size includes the combined tissues of roots and seeds, while source size is the amount of leaf tissue. (B) The relationship between transition to reproduction at different percentages of total age (percentage of the amount of total plant material at vegetative steady state) and seed production, comparing multiple allocation strategies with an amount of initial root tissue of 0.1, and when $A_0 = 10$, $m = 1$, $\theta = 10$, $R_1 = 1$ and $R_2 = 1$. The data points (circles) represent the maximum amount of seed tissue produced for each allocation strategy. Developmental stage is a percentage of the amount of total plant material at vegetative steady state. All model parameters are dimensionless.

reproduce. As the amount of leaf tissue increases during growth, the amount of energy available to produce seed increases and so does the level of self-shading. Once the plant produces a certain amount of leaf tissue, assimilation per unit leaf tissue begins to decrease (due to shading costs) while the cost of maintaining the plant is still increasing. This leads to a decline in the amount of seed tissue. A plant with an allocation strategy favouring leaf growth should reproduce at 25–31 % of its total potential vegetative age to produce the maximum seed. A plant with an allocation strategy favouring root growth, should reproduce at 35–49 % of its potential vegetative age. A plant favouring leaf growth can reproduce at an earlier ontogenic stage as it has already invested more energy into leaf growth whereas a plant favouring root growth would need more time to develop enough leaves to create the most seed. High leaf allocation therefore promotes early reproduction. Although the timing of reproduction is affected by factors such as day length, temperature and stress, the balance of carbon between leaves and roots during vegetative growth imposes limits that all potential reproductive scenarios sensitive to these factors must stay within.

The optimal strategy for maximizing reproductive output is defined by the maximum vertical distance between the vegetative growth trajectory and the steady-state curve. This difference is the potential energy available to synthesize seed material. This potential energy (ΔE) can be expressed as

$$\Delta E = \frac{A(l)l - R_1l - R_2r}{R_2}, \quad (18)$$

where A is assimilation rate, l is the amount of leaf tissue, r is the amount of root tissue, and R_1 is maintenance respiration for leaves and R_2 is maintenance respiration for roots and seeds. Equation (18) states that the potential energy for reproduction available at a given time is equivalent to the difference between the energy produced via photosynthesis and the energy required to maintain the leaves and roots.

With the largest potential energy producing the maximum yield, allocation strategies with the least steep trajectories have the largest potential energy. This implies that allocation strategies favouring leaves will have the largest potential energies for reproduction. Fig. 7b confirms this, where it is clear that allocation strategies which favour leaves produce the largest amount of seed tissue. The strategy which allocates the largest amount of carbon to the leaves produces the most seed and as allocation towards the roots increases, yield decreases.

During vegetative growth, leaf favoured allocation strategies promote early reproduction

The time taken to produce seed can be calculated by integrating Eq. (17) and rearranging to yield:

$$t = \frac{r_{ss} - r_0}{A(l)l - R_1l - R_2r}, \quad (19)$$

where t is the time taken to produce seed, r_{ss} is the total sink size (seed + root tissue) at steady state and r_0 is initial root tissue (amount of root tissue at the end of vegetative growth).

The time taken to produce seed decreases with the developmental stage for plants favouring leaf allocation strategies during vegetative growth, implying that a plant reproducing later along the vegetative trajectory takes less time to reproduce. Fig. 8a shows that there is a positive linear relationship between the amount of seed tissue and the time taken to produce seed. The time taken to reproduce decreases as allocation towards the roots increases. This is because less carbon has been invested in leaf growth, so there is less energy available from photosynthesis to produce seed and it is exhausted more rapidly. For plants with a root favoured strategy during vegetative growth, the relationship between developmental stage and time taken to produce seed is much weaker (Fig. 8b). This is due to root allocation strategies ($\alpha > 1$) creating a much steeper vegetative trajectory, reducing the variation in potential seed production for the range of developmental stages along the trajectory. This suggests that there is a trade-off between the time taken to reproduce and yield. For a plant in a hazardous environment creating a reduced growing season, it may be beneficial to reproduce earlier and not obtain the maximum possible yield. For plants without constraint on the length of the growing season, the optimal age to reproduce can be chosen based on the total seed produced as shown in Fig. 7b.

Higher leaf maintenance costs delay reproduction for plants allocating more carbon to the leaves

When increasing the cost of leaf maintenance, there is a reduction in seed production and therefore also in the time taken to produce seed. The maximum sink size (at the peak of the steady-state curve) is equivalent to

$$r_{\max} = \frac{\theta}{R_2} (\sqrt{A_0 R_1} - R_1)$$

Therefore, as the cost of respiration tends towards the amount of carbon assimilated via photosynthesis, the maximum sink size decreases. Not only does the maintenance cost affect yield, but it also affects the optimal age to reproduce in order to maximize yield. When maintenance costs are equal and $A_0 = 20$, for high leaf allocation strategies, it is beneficial to reproduce between 20 and 23 % of the potential vegetative age if it did not reproduce. In contrast, for high root allocation strategies, it is beneficial to reproduce within 27–41 % of the potential vegetative age for default parameters. However, when maintenance costs are unequal ($R_1 = 2R_2$), for high leaf allocation strategies it is beneficial to reproduce between 25 and 28 % of the potential vegetative age and for high root allocation strategies, it is beneficial to reproduce within 30–38 % of the potential vegetative age. This change in maintenance costs shifts the optimal region for leaf allocation strategies by 5 % towards later reproduction and reduces the optimal region for root allocation strategies by 6 %. This implies that having a higher maintenance cost for leaves than the roots, whilst allocating more carbon to the leaves,

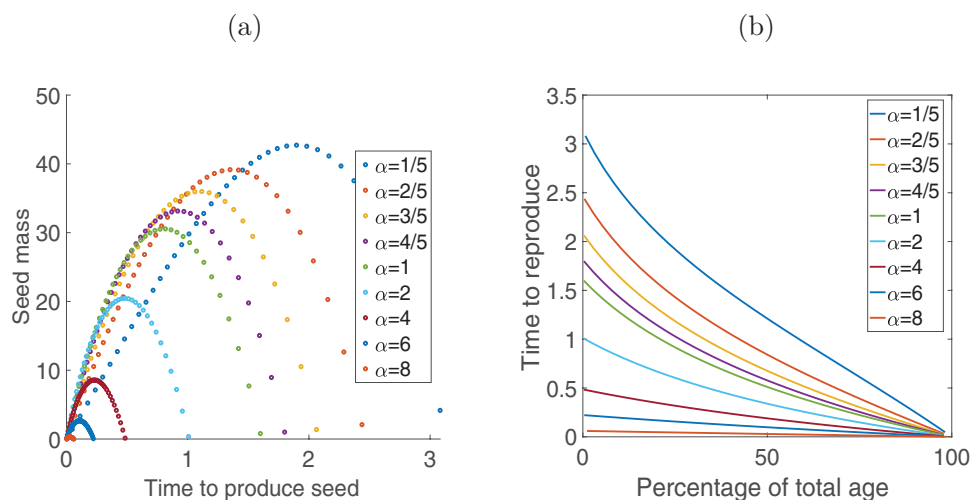


Fig. 8. (A) The relationship between the time taken to produce seed during reproductive growth and the amount of seed tissue for multiple allocation strategies when $A_0 = 10$, $m = 1$, $\theta = 10$ and $R_1 = R_2 = 1$. When $\alpha < 1$, more carbon is allocated to the leaves and when $\alpha > 1$, more carbon is allocated to the roots. Each data point represents a different developmental stage. (B) The relationship between the choice of reproduction at different percentages of total age and the time taken to produce seed for multiple allocation strategies. All model parameters are dimensionless.

delays the optimal age to reproduce and further limits the optimal age to reproduce, when the plant is allocating more carbon towards the roots. This is because having a higher cost of leaf material reduces the amount of energy available to produce seed. A plant must therefore be more established in order to have the maximum energy available to reproduce (data not shown).

Discussion and conclusions

The aims of this paper were to understand the consequences of different allocation strategies and costs of maintenance respiration for plant growth in a general but quantitative manner, and to investigate any possible limitations to carbon allocation. These were addressed by using a simple root–shoot carbon allocation model. The effects of varying the source–sink allocation ratio on plant growth are not explicitly explored in the work of most plant growth models. Typically, these incorporate an allocation assumption and investigate the effects of environmental conditions or perturbations on growth (Hogsett et al. 1985; Ford and Keister, 1990; Luxmoore 1991; Weinstein et al. 1991). Ignoring the effects of environmental conditions made it possible to determine which underlying processes have the greatest influences on plant growth. In particular, the model suggested that maintenance respiration plays a significant role in the effect of allocation strategies on growth.

When maintenance costs are equal between leaf and root tissue, increasing allocation to the leaves increases the growth rate and therefore the final plant size. Many propose that the most efficient means for a plant to maximize its growth rate is to allocate just enough resources to the roots for nutrient assimilation and allocate the majority of resources to the leaves (Mooney 1972; Wareing and Patrick 1975; Russell et al. 1977; Reynolds and Thornley 1982). In the case when maintenance costs are equal, there are limitations on carbon allocation to the roots and high assimilation rates alleviate these limitations. Thus, high rates of photosynthesis enable both large plant size and high root allocation.

However, it is not necessarily the case that leaf and root maintenance respiration are equal, and published data show that leaf respiration can be up to 2.25 times larger than root respiration (Hansen and Jensen 1977; Reich et al. 1998; Loveys et al. 2003; Tjoelker et al. 2005). In the circumstance where leaf respiration is higher than root respiration, increasing root allocation can in theory lead to a larger plant. This effect is especially pronounced when canopy self-shading is high (i.e. the shading coefficient in the model is low), and contradicts the widely held assumption that carbon should be preferentially allocated to the leaves to optimize growth.

Instead, it shows that maintaining a large number of shaded leaves within a canopy can be detrimental for production when those leaves carry a high maintenance cost. When leaves become too inefficient and costly to maintain, plants senesce their leaves.

Long-standing theory in vegetation modelling predicts that plants should add leaf layers until the lowest layers fail to make a positive net contribution to canopy carbon gain (Woodward et al. 1995). However, modern crops such as soybean seem to violate this prediction, producing very dense leaf canopies, especially when supplied with high atmospheric CO₂, and the dense shading of lower leaves means that they contribute little to canopy carbon assimilation (Drewry et al. 2010a, b). Recent modelling and experimental manipulation of soybean crop canopies shows that these plants overinvest in leaves, and that leaf removal can actually improve yields (Srinivasan et al. 2017). Under certain circumstances, crop plants, therefore, produce more leaves than is optimal for growth and yield, and the model shows how this behaviour can arise from the high cost of maintaining leaves and a declining rate of photosynthesis with shading. It has been hypothesized that the overproduction of leaves evolves in wild plants from the benefits of shading out competitors in dense, competitive plant communities (Anten 2005). This may increase the fitness of individual plants but, in the case of crops, breeders and farmers aim to maximize the yield from the whole population of plants within the field, and it is advantageous to reduce competition among individuals (Denison 2012; Anten and Vermeulen 2016). Respiration accounts for a large proportion of carbon loss within the plant (Gifford et al. 1984; Amthor 1989, 2000; Cannell and Thornley 2000), providing a key mechanism which can be manipulated to boost crop productivity. Advances in respiration research identify genes responsible for substrates, enzymes and transporters that are essential for protein turnover and transport, which can be targeted to optimize respiration (Amthor et al. 2019).

In the model, circumstances when leaf maintenance costs are higher than root maintenance costs also introduce a certain level of plasticity with respect to final plant size, such that a range of allocation strategies can lead to similar final plant size (this occurs when the gradient of the steady-state curve is less than -1). When maintenance costs are equal, leaves are much more beneficial for growth than roots, but when leaves cost more to maintain than roots, the benefits of growing leaves and roots become more equal. This allows for a range of root:shoot ratios to produce the same final plant size. Work has been done to investigate the effect of environmental conditions (Ericsson 1995) or competition (Waite and Hutchings 1982) on the plasticity of allocation but not necessarily how maintenance costs

alter the plasticity of allocation. Increasing the shading coefficient has no effect on the range of allocation strategies where this plasticity occurs. However, increasing assimilation rate increases the range of allocation strategies where final plant size does not change.

When looking at reproductive growth, the optimal developmental stage for the plant to reproduce is defined by the carbon available to produce seeds or other reproductive organs such as tubers. Therefore, allocation strategies favouring leaf growth will have the largest potential energies for reproduction, implying that high leaf allocation during vegetative growth promotes early reproduction. This corroborates the work of [Guilbaud *et al.* \(2015\)](#) who suggest that high growth rates correlate with early flowering, since high leaf allocation leads to a higher growth rate. Their work extends that of [Cohen \(1971\)](#) by investigating how nitrogen dynamics alter the decision to flower. [Cohen \(1971\)](#) paved the way for reproductive growth models by investigating the effect of transition to flowering on yield. He determined that one transition which allocates all resources from vegetative growth to reproductive growth is the most beneficial for yield, and that flowering time is dependent upon the length of the growth season. Other models build onto this by including loss terms ([King and Roughgarden 1982](#)) or environmental conditions and hazard rates ([Paltridge and Denholm 1974](#); [Ledder *et al.* 2004](#)). Others investigate the effects of multiple reproductive phases ([Chiariello and Roughgarden 1984](#)) and the effect of photosynthetic rate on reproduction ([Schaffer *et al.* 1982](#)). However, there has been little previous work investigating the effect of varying vegetative allocation strategy on yield. Having higher leaf respiration than roots delays the optimal age to reproduce for leaf allocation strategies and increases the restrictions on flowering time for root allocation strategies.

The model results hinge upon the assumption that growth stops when carbon sources and sinks are balanced. The extent to which this situation arises in natural or crop systems is unclear, and three factors would tend to act so that steady state is not reached. First, new growth is always required to replace tissues as they turnover. Secondly, the requirement for roots (in terms of anchorage, nutrient and water uptake) may be less than the limit imposed by maintenance costs. A model incorporating tissue turnover and functional roots would be required to evaluate the magnitude and consequences of these effects. Finally, the development of short-lived plants, in particular, ensures that the limits imposed by carbon balance are not reached. Nonetheless, these limits set boundaries beyond which development cannot stray.

The model simulates carbon allocation by using a constant allocation ratio throughout the ontogeny of a

plant and, therefore, has only one pre-determined allocation strategy throughout. However, allocation is usually allometric, such that it depends on size, and the proportion of carbon allocated to leaves or roots varies with time ([Weiner 2004](#)). The choice of a simplified assumption of allocation within the model provides a framework to test distinct strategies of allocation and make predictions on how certain behaviours can influence plant growth. Further analysis with this model could consider an allocation strategy that is variable and dependent upon plant size.

Having the roots solely as sinks within the model underpins the finding that minimal allocation to roots maximizes plant growth. However, resources obtained via the roots influence the allocation of carbon to sources and sinks and also overall plant growth ([Running and Gower 1991](#)). Environmental conditions control fluctuations in carbon and nitrogen availability, causing crosstalk between signalling pathways of carbon and nitrogen ([White *et al.* 2016](#)). This crosstalk determines allocation to sources and sinks. When there is ample nitrogen, cytokinins are produced, which increases sink strength ([Kuiper 1993](#); [Ghanem *et al.* 2011](#); [Thomas 2013](#)), and this also increases carbon acquisition. When there is high carbon availability, nitrogen sources are up-regulated ([Stitt and Krapp 1999](#)) and sink activity is increased ([Klein *et al.* 2000](#); [Kaiser *et al.* 2002](#); [Reda 2015](#)). There is a need for a new type of allocation model which includes the interaction of carbon and nitrogen feedback and feedforward mechanisms defining allocation to further understand how allocation can be used to improve growth.

Overall, this quantitative modelling approach has revealed that the maintenance costs of leaves and roots alter the limitations on allocation by increasing the plasticity of final plant size in vegetative growth and restricting the range of optimal developmental stages for reproduction. It has shown that when leaf respiration is higher than root respiration, reallocating carbon away from leaves and towards the roots can improve plant growth. This analysis indicates that crop improvement and management strategies should consider the effects of canopy maintenance costs for improving growth.

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Contributions by the Authors

B.L.H., N.A.M.M., R.H.C. and C.P.O. designed the study. B.L.H. developed the model and carried out the theoretical analysis. B.L.H., N.A.M.M., R.H.C. and C.P.O. interpreted the results.

B.L.H. led the writing of the paper with input from the other authors.

Conflict of Interest

No conflicts of interest.

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Appendix 1. Non-dimensional analysis

The aim of non-dimensionalization is to identify the relevant scales appropriate to the system and to determine the way in which the form of the model (and its solution) depend on these scales. Consider the vegetative growth model (Eqs 11 and 12):

$$\frac{dl}{dt} = \frac{\eta}{1 + m\alpha} (A(l)l - R_1l - R_2r), \quad (\text{A.1})$$

$$\frac{dr}{dt} = \frac{\eta m\alpha}{1 + m\alpha} (A(l)l - R_1l - R_2r), \quad (\text{A.2})$$

where $A(l) = \theta A_0 / (\theta + l)$.

The first step in non-dimensionalization is to determine the dimensions of each variable and parameter. These are given in Table 1.

Note that the parameter η appears multiplicatively in the growth equations, and that the compound parameters ηA_0 , ηR_1 and ηR_2 have dimension time^{-1} . Any one of these can be taken to define a typical time scale for the system.

To non-dimensionalize the system, we define a typical mass scale l_0 (e.g. the dry mass of a single mature leaf) and a typical time scale t_0 (e.g. 1 day). We then define dimensionless variables and parameters as follows:

Table A1. Dimensions of the parameters and variables in the model (Eqs 11 and 12).

Parameter/variable	Dimension
l, r, θ	Mass
t	Time
η	$\text{area} \times \text{carbon}^{-1}$
R_1, R_2, A_0	$\text{carbon} \times \text{area}^{-1} \times \text{time}^{-1}$
m, α	Dimensionless

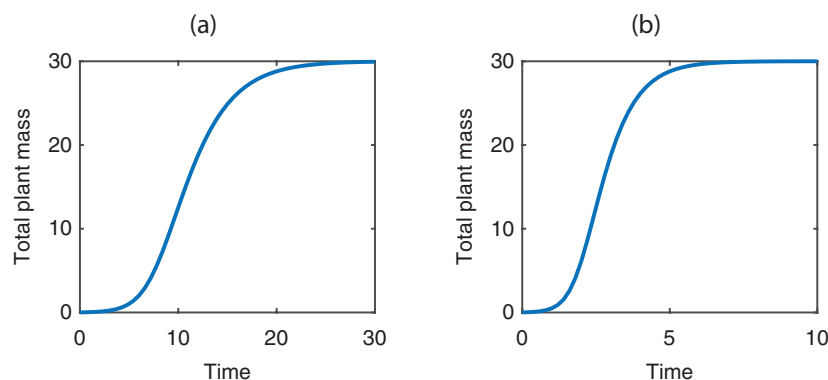


Fig. A1. Total plant mass over time when the model has (A) not been non-dimensionalized using $\eta = 0.25$, (B) been non-dimensionalized without η . Both versions of the model used $A_0 = 10$, $\theta = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 1$ with an initial seedling size of $l = 0.01, r = 0$.

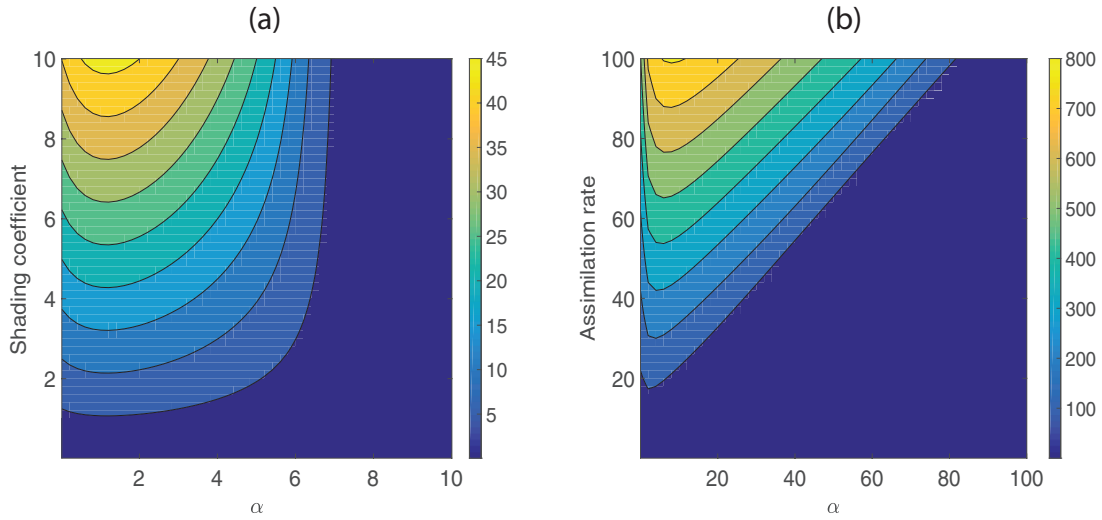


Fig. A2. (A) Sensitivity analysis of final plant material when varying shading coefficient and allocation strategy when $A_0 = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 1$. (B) Sensitivity analysis of final plant material when varying assimilation rate and allocation strategy when $\theta = 10$, $m = 1$, $R_1 = 2$ and $R_2 = 1$. Using initial leaf and root tissue of $l_0 = 0.01$ and $r_0 = 0$. The black lines represent contours of constant final plant material. Colour bar represents different final plant materials. All model parameters are dimensionless.

$$\tilde{l} = l/l_0, \tilde{r} = r/l_0, \tilde{\theta} = \theta/l_0.$$

$$\tilde{t} = t/t_0, \tilde{A}_0 = t_0\eta A_0, \tilde{R}_1 = t_0\eta R_1, \tilde{R}_2 = t_0\eta R_2.$$

The growth equations are then given in non-dimensional form as

$$\frac{d\tilde{l}}{d\tilde{t}} = \frac{1}{1+m\alpha} \left(\frac{\tilde{\theta}\tilde{A}_0}{\tilde{\theta}+\tilde{l}} \tilde{l} - \tilde{R}_1\tilde{l} - \tilde{R}_2\tilde{r} \right); \quad (\text{A.3})$$

$$\frac{d\tilde{r}}{d\tilde{t}} = \frac{m\alpha}{1+m\alpha} \left(\frac{\tilde{\theta}\tilde{A}_0}{\tilde{\theta}+\tilde{l}} \tilde{l} - \tilde{R}_1\tilde{l} - \tilde{R}_2\tilde{r} \right); \quad (\text{A.4})$$

This demonstrates that the only role that the parameter η plays in the behaviour of the model is to regulate the rate of change of plant mass. Neither the relative amounts of leaf or root tissue nor the final plant mass depends on the value of η . This is illustrated in Fig. A1.

Appendix 2.

The black lines represent parameter space where final plant material remains the same and the colours represent different final plant materials (yellow is high plant material and blue is virtually no plant material). For low shading coefficient values, the black lines of constant final plant material are horizontal for the majority of allocation strategies (Fig. A2). As allocation strategy continues to increase after $\alpha = 2.7$, these lines become almost vertical. As the shading coefficient increases, the region where the black line is approximately horizontal for a given shading value decreases in size and is much smaller using $\theta > 7$. This implies that the shading coefficient reduces the level of plasticity within the model by increasing light penetration into the leaf canopy.