

# OPT-ing out: Root–shoot dynamics are caused by local resource capture and biomass allocation, not optimal partitioning

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## Abstract

Combining plant growth analysis with a simple model of local resource capture and biomass allocation applied to exemplary experimental data, showed that dynamic changes in allocation to roots when nutrients are scarce is caused by disparities in growth rates between roots and shoots. Whole-plant growth rates also change but are not caused by an adaptive allocation response. Allocation and whole-plant growth rate are interdependent, not independent, traits. Following a switch in nutrient availability or partial biomass removal, convergence of allocation and growth rate trajectories does not reflect goal-seeking behaviour, but the constraints imposed by finite resource availability. Optimal root–shoot allocations are unnecessary to maximise whole-plant growth rate. Similar growth rates are attainable with different allocations. Changes in allocation cannot maintain or restore a superior whole-plant growth rate. Roots and shoots do not have to be tightly coordinated but can operate semiautonomously, as their modular construction permits. These findings question the plausibility of the prevailing general explanation of plants' root–shoot allocation responses, 'optimal partitioning theory' (OPT). Local allocation models, not OPT, explain the origins of variability in root–shoot trade-offs in individuals, the allocation of biomass at global and ecosystem scales and inform selection for allocation plasticity in crop breeding.

## KEYWORDS

balanced growth, *Hordeum*, modularity, *Petunia*, phenotypic plasticity, physiological coordination, plant–environment interaction, plant growth analysis, temporal dynamics

## 1 | INTRODUCTION

Anyone who grows plants for fun, food or funding knows that plant growth is often plastic. Biomass allocation varies with environmental conditions. This is a ubiquitous feature of how plants grow. It is

central to understanding how they work as individuals and interact with neighbours. But we still don't fully understand allocation.

Here I look critically at a familiar aspect of biomass allocation, the trade-off between root and shoot growth in vegetative terrestrial vascular plants. My aims are to clarify, firstly, interpretations of

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dynamic changes in allocation and, secondly, how allocation relates quantitatively to the concurrent growth of whole plants. I review the prevailing model, describe an alternative, and test if it can account for experimental data.

## 2 | OPTIMAL PARTITIONING THEORY (OPT) OF ROOT-SHOOT DYNAMICS

### 2.1 | Background

Reducing the beauty and diversity of plants to two structures, 'root' and 'shoot', is a simplification challenged on anatomical, biophysical, statistical and even philosophical grounds (Groff & Kaplan, 1988; Poorter & Nagel, 2000). But the root-shoot dichotomy reflects a fundamental trade-off: if more resources are allocated belowground, fewer are available simultaneously for aboveground processes, and vice versa; see Wilson (1988), Reich (2002), Weiner (2004), Poorter and Sack (2012) and Wheeldon and Bennett (2021), along with Schneider's (2022) broader review of current thinking about plasticity in plants.

Following seminal experiments (Brouwer, 1962; White, 1937), an appealing model of root-shoot allocation emerged. It has several names: functional equilibrium (Brouwer, 1962, 1963), balanced growth (Iwasa & Roughgarden, 1984), functional balance (Mäkelä & Valentine, 2020; 174) and optimal partitioning (Gedroc et al., 1996), the last conveniently abbreviated to OPT.

OPT says that when starved of nutrients or water, a plant responds by producing relatively more root biomass. This allows greater exploitation of soil to compensate for shortages of those resources. In shade, leaf production or stem extension are favoured to maximise light interception. OPT makes intuitive sense and is widely accepted, often quoted to illustrate how an immobile organism can adapt itself to changing conditions.

OPT features in many plant growth models, many descended from Thornley's (1972) pioneering work. These are process-based models, rich in physiological detail, mathematically describing separate, interconnected root and shoot compartments containing biochemical machinery to convert raw materials (light, nutrients, water) into new biomass plus waste products, and to shuttle materials between compartments, with explicit causal linkages between inputs and outputs. OPT is treated essentially as an engineering problem. These models reproduce the kind of root-shoot responses to light and nutrients seen in meta-analyses of experimental data and field observations (Poorter & Nagel, 2000; Poorter et al., 2012; Reynolds & D'Antonio, 1996).

### 2.2 | Assumptions

#### 2.2.1 | OPT has three key assumptions

**Assumption 1.** Plant growth depends on root-shoot allocation. Changes in allocation change resource capture allowing growth to

return to, or be maintained in, a 'better' state than would be possible otherwise, hence 'optimal' partitioning (whether a real plant ever achieves it is another matter). 'Better' usually means adaptive in some way, such as an allocation that maximises growth-rate or optimises a certain ratio of carbon to nitrogen throughout the plant's tissues (Hilbert, 1990; Kachi & Rorison, 1989; Thornley & Parsons, 2014).

**Assumption 2.** Allocation is controlled by feedback between stimulus (resource availability) and response (resource capture). Allocation adjusts dynamically as if in a goal-seeking way (Thornley & Parsons, 2014) to find the best root-shoot trade-off (as per Assumption 1).

**Assumption 3.** Root responses are coordinated closely with those of shoots. This reflects the idea that roots and shoots work best when 'balanced'. For example, Trewavas (2014; 81): 'Only by optimising root and shoot proliferation, and the balance between and within them, can they maximise the capture of resources', and Muralidhara et al. (2021): 'To ensure optimal plant growth, shoot and root propagation are highly coordinated'.

The net result of these assumptions is the appearance (if not the physiological reality) of integrated control and coordination of allocation in which there is a strong trade-off between root and shoot growth. Many allocation models are structured accordingly.

But closer inspection of OPT shows it to be a weak and problematical theory.

### 2.3 | Eight problems with OPT

**Problem 1.** Experimental results conflict with OPT's predictions (Bernacchi et al., 2000; Gedroc et al., 1996; Harmans et al., 2000; McConaughay & Coleman, 1999; Meier & Leuschner, 2008; Müller et al., 2000). Some results are better explained as allometric covariations between roots and shoots (Farrar & Gunn, 1998; Reich, 2002; Weiner, 2004), although allometry also has its pitfalls (Poorter & Sack, 2012). Real plants are less predictable than theoretical ones. Thornley and Parsons (2014) noted, perhaps with a hint of exasperation, the all-too familiar 'variability and contrariness of measurements of allocation'.

**Problem 2.** OPT does not reflect plants' modular structure. Roots and shoots are not unitary compartments. They are connected populations of meristems (Harper, 1977; 20, 338; de Kroon et al., 2005, 2009; Niklas, 1992; 384; Oborny, 2019; Schneider, 2022; Trewavas, 2014; 78). Phenotypic plasticity is largely the differential development of different modules. Modularity allows repetition, redundancy, resilience, turnover and some independence in how different groups of meristems can respond to their immediate environment, features absent from most OPT-based models.

**Problem 3.** If OPT is correct, it should apply to large plants as well as small. But what might constitute a notional 'optimum' allocation for a massive tree or spatially dispersed clonal plant whose meristems experience many different local microenvironments simultaneously? If OPT applies to a big plant perhaps local stimuli are simply averaged out (unlikely given Problem 2). Or perhaps OPT applies only to modular subsets of a whole-plant, to each ramet rather than genet (Harper, 1977; 24–26). But if OPT can't explain allocation dynamics in big plants, why should it apply to small ones in the first place?

**Problem 4.** Much contemporary plant biology investigates molecular controls of root and shoot development, yet none of it needs OPT. Instead, the focus is on local molecular regulation of development modulated by longer-distance signalling (e.g., Abualia et al., 2022; van den Berg et al., 2021; Rosado et al., 2021). It's revealing that OPT's supposed value as an overarching explanation for root–shoot plasticity conflicts with how easily those who investigate root–shoot development can ignore it.

**Problem 5.** Some root growth is stochastic, an expression of 'developmental instability', rather than resulting from canalised development or a response to identifiable cues (Forde, 2009). Its function might be to allow quasi-random exploration of an unpredictable environment until a favourable gradient of nutrient, water, oxygen or penetrability is encountered, which triggers more specific responses (Hodge, 2004). Developmental instability also influences leaf morphology, and a change in shape usually means corresponding changes in mass (Niklas, 1992; 383); for example, plants with larger leaves need to invest more biomass in supportive petioles. Substantial stochastic growth argues against root and shoot biomasses responding to their environments in the directed ways encapsulated in OPT-based models.

**Problem 6.** A plant's phenotype is not under its sole control. Root development is shaped partly by interactions with rhizosphere microbes including, almost universally, mycorrhiza-forming fungi. Microbial interactions alter a plant's developmental schedule by promoting or suppressing lateral root initiation, extension and turnover (Finkel et al., 2020; Jevon & Lang, 2022; Kosola et al., 1995; Sukumar et al., 2012), all of which influence root biomass and, therefore, allocation relative to the shoot. If a plant doesn't wholly control its biomass allocation, the assumed mechanisms of allocation control embedded in OPT are inappropriate.

**Problem 7.** No one has convincingly demonstrated optimal biomass partitioning in a real plant; nor have the necessary physiological mechanisms been characterised, although many have been hypothesised (e.g., Farrar, 1996; Farrar & Jones, 2000; Hermans et al., 2006; Lambers, 1983; van der Werf & Nagel, 1996). And, just because an optimum allocation can be defined mathematically does not mean that it is biologically realistic.

**Problem 8.** It is not possible to test if OPT quantitatively matches experimental data. In its basic form OPT is not quantitative. OPT says

than allocation to roots generally increases when nutrients are scarce (which is true), but not by how much (which would be more helpful). Ironically, nor is it straightforward to use detailed models. Although these models are quantitative, their many parameters are hard to measure routinely in the same experiment, but it can be done (Feller et al., 2015; van der Werf et al., 1993). Thornley and Parsons (2014) recognised 'certain irreducible difficulties' with OPT-based models, including deciding what goal a plant might be aiming for, but the difficulty of testing them with data wasn't one of them. Models orphaned from data limit the confidence we can have that they reflect reality, or at least some part of it. Consequently, we don't know if the root–shoot trade-off really occurs as OPT assumes, or if it just appears that way.

## 2.4 | Alternatives

A model without assumptions of integrated control of biomass allocation, yet which reproduced OPT's root–shoot dynamics, was proposed by Cheeseman (1993). Dynamics emerged from roots and shoots operating under local rules reflecting the uptake, assimilation and transport of carbon and nitrogen. More recently, Ledder et al. (2020) theorised that local resource allocation can explain high-level behaviour in any interconnected system whose component parts depend on each other for resources, such as the roots and shoots of the same plant or the parts of mutualistic organisms: corals, sponges, lichens and so on.

Focusing on local processes suggests an alternative approach to OPT. Can a model assuming locally determined allocation and lacking mechanisms to enable optimal root–shoot growth, describe experimental data? If it can, that would undermine OPT's credentials as the best general explanation of root–shoot allocation. Such a model is described next.

## 3 | A LOCAL ALLOCATION MODEL (LAM) OF ROOT–SHOOT DYNAMICS

### 3.1 | Root and shoot growth analysis

Plant growth analysis converts discrete biomass measurements into continuous growth trajectories. We'll meet the trajectories and the model which produces them later, but firstly a reminder of some familiar concepts. Here, these are applied separately to roots and shoots of the same individuals as if they are independent entities, an approach used also by Van der Werf & Nagel (1996).

The absolute growth-rate (AGR) is, instantaneously,

$$\text{AGR} = \frac{dY}{dt} \quad (1)$$

Y is root (R), shoot (S) or total mass, and t is time. In practice, mean AGR is estimated over an interval such as between successive harvests,  $t_2 - t_1$ , as

$$\text{AGR} = \frac{Y_{t_2} - Y_{t_1}}{t_2 - t_1} \quad (2)$$

If  $t_2 - t_1$  is short and there are many sequential intervals, Equation (2) approximates AGR defined by Equation (1).

Whole-plant AGR is the sum of the growth-rates of root ( $\text{AGR}_R$ ) and shoot ( $\text{AGR}_S$ ).

Related to AGR, relative growth-rate (RGR) is computed by analogous equations. Instantaneously,

$$\text{RGR} = \frac{\text{AGR}}{Y} = \frac{1}{Y} \frac{dY}{dt} \quad (3)$$

and mean RGR

$$\text{RGR} = \frac{\ln Y_{t_2} - \ln Y_{t_1}}{t_2 - t_1} \quad (4)$$

Whole-plant RGR is not the sum of  $\text{RGR}_R$  and  $\text{RGR}_S$ , but their mass-weighted mean.

Root-shoot allocation is the root mass fraction, RMF:

$$\text{RMF} = \frac{R}{R + S} \quad (5)$$

RMF lies between 0 and 1. An increase in RMF means the plant becomes more 'rooty'; a decrease, more 'shooty'.

Equation (5) is essentially static. To rewrite it in terms of growth-rates rather than biomasses we need identities for  $R$  and  $S$  implied by Equation (1) and (3):

$$Y = \frac{1}{\text{RGR}} \frac{dY}{dt} = \frac{\text{AGR}}{\text{RGR}} \quad (6)$$

$Y$  is either  $R$  or  $S$ . Substituting root- and shoot-specific versions of Equation (6) into Equation (5) clarifies the dynamic connection between instantaneous root-shoot allocation and simultaneous root and shoot growth-rates:

$$\text{RMF} = \frac{\text{AGR}_R}{\text{AGR}_R + \frac{\text{RGR}_R}{\text{RGR}_S} \text{AGR}_S} = \frac{\text{AGR}_R}{\text{AGR}_R + \alpha \text{AGR}_S} \quad (7)$$

For convenience,  $\text{RGR}_R/\text{RGR}_S$  is replaced in Equation (7) by  $\alpha$ .

Not used for computation, Equation (7) is nevertheless important. It shows explicitly that changes in root-shoot allocation (RMF) arise from differential changes in root and shoot growth-rates (Brouwer, 1962; van der Werf & Nagel, 1996).

Equation (7) also links allocation to allometry. In the standard allometric equation (Niklas, 1994; 15)  $\ln R = \ln \beta + \alpha \ln S$ ,  $\beta$  is a scaling coefficient,  $\alpha$  is the slope of a linear regression of  $\ln R$  on  $\ln S$  and is, by mathematical definition, equal to  $\text{RGR}_R/\text{RGR}_S$  (Hunt et al., 1987).

### 3.2 | Generating root and shoot trajectories

Continuous root and shoot trajectories are needed to visualise how allocation and whole-plant growth change over time and relative to

one another. There are several possibilities. (1) Just use appropriate data, but data are usually too sparse and noisy to themselves generate continuous trajectories and accurate growth-rates. The standard way to fill the gaps and smooth the noise is by (2) fitting to the data a standard equation such as the logistic (Paine et al., 2018), a single-equation polynomial (first-order, second-order and so on, as appropriate: Hunt, 1982; 69; Warton, 2022; 181), or a more elaborate spline function (Hunt, 1982; 154; Warton, 2022; 182).

Another option is to (3) use a physiologically detailed, multi-equation model (see Section 2.1), but these are difficult to use routinely with data, as I mentioned earlier (Problem 8, Section 2.3).

The last possibility, which I use here, is to (4) fit to the data a nonmechanistic, phenomenological model that reduces a complex system to its essentials. This approach is familiar to modellers of animal populations (Lawton, 1991), but perhaps less so to modellers of plant growth.

### 3.3 | LAM

LAM (because it is a local allocation model) describes root and shoot growth as if they depend, to a first approximation, only on resources that each organ captures locally and allocates into new biomass. This has similarities to Brouwer's, (1962, 1963) original working explanation for OPT. Obviously, plants don't really work like that. LAM is, deliberately, not a mechanistic model. It's a tool designed for one purpose: to derive from experimental data continuous root and shoot growth trajectories from which root-shoot allocations and whole-plant growth-rates can be calculated.

LAM assumes, first, that the change in root mass,  $R$ , over an interval  $t$  to  $t+1$  depends on the fraction,  $\varphi_R$ , of belowground resources,  $B_t$ , captured by the root system over that interval, and not on any resources captured by the shoot. You can think of  $\varphi_R$  as the efficiency with which the whole root system captures resources. Resource capture also depends on the current root system mass,  $R_t$ .

Over the interval  $t$  to  $t+1$ ,

$$R_{t+1} = R_t + (B_t \cdot R_t \cdot u_t \cdot \varphi_R) \quad (8)$$

$u_t$  is a coefficient modifying  $\varphi_R$  in response to resource availability. Of many possible ways of describing this response, one minimal version is

$$u_t = \left[ B_0^2 - (B_0 - B_t)^2 \right]^{1/2} / B_0 \quad (9)$$

$B_0$  is the initial availability of belowground resources;  $B_t$  is calculated below. The numerator of Equation (9) describes the arc of a circle of radius  $B_0$  passing through zero, and computes  $u_t$  using Pythagoras's Theorem (a more conventional approach might use a Michaelis-Menten equation, but that would mean finding values for its parameters).  $u_t$  varies from 1 when resource is initially available to zero if resource becomes totally depleted. To ensure Equation (8) is dimensionally balanced  $u_t$  is assumed to apply per unit root mass.

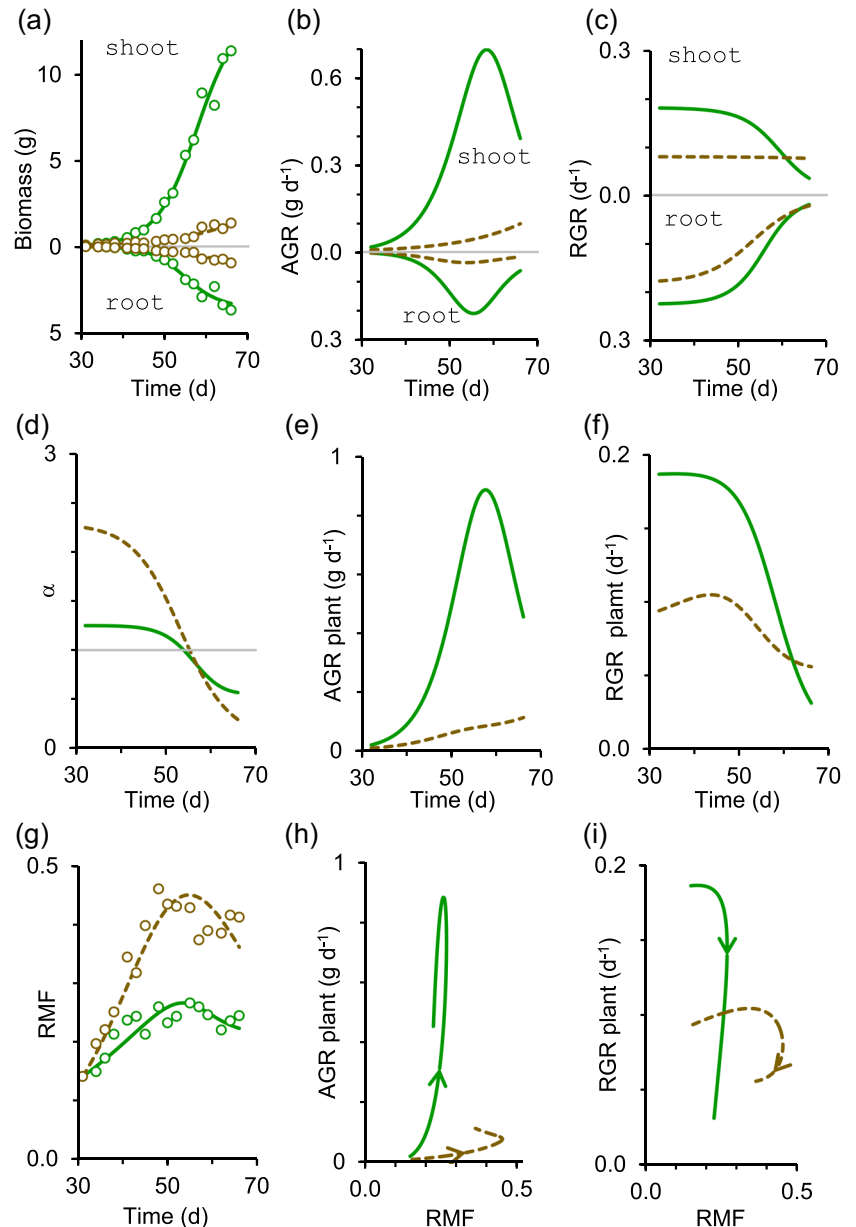
For convenience, the units of  $B$  are assumed to be biomass-equivalents, that is, the biomass produced from a given mass of resource. A value cannot be given to  $B$  solely from measurements of soil nutrient concentrations or water potentials. That's because the effective availability of resources also depends on the root system's size, geometry and physiology, and on soil structure, factors not reflected in measurements of soil nutrient concentrations or water potentials. Identical plants in the same soil could have different  $B$  values if one plant is shaded and the other not, if the shaded plant's roots grow less vigorously and are unable to access as much resource as the roots of the unshaded plant. Likewise, the same resource availability can produce plants with different biomasses if they differ in their efficiency of biomass production per unit resource available. It is logical, though, to expect positive correlations between estimates of  $B$  and measurements of nutrient and water availabilities.

A second reason for casting resource availability as biomass equivalents is that it allows below- and aboveground resources to be compared directly with each other. A third reason is explained later.

As the root system captures resource, the available pool  $B$  is depleted accordingly (unless renewed from an external source):

$$B_{t+1} = B_t - R_t \tag{10}$$

If an initial value of  $R$  ( $R_0$ ) is provided by appropriate data, for modelling purposes  $R$  (Equation (8)) depends on evaluating two unknowns,  $B_0$  and  $\varphi_R$  ( $u_t$  is defined by Equation (9)). A continuous trajectory of root biomass is derived by adjusting  $B_0$  and  $\varphi_R$  in Equation (8) to find  $R$  values that maximise the goodness-of-fit with data. There is no expectation that unique combinations of  $B_0$  and  $\varphi_R$  will provide that fit; many combinations could do so, but not all will



**FIGURE 1** Root and shoot trajectories of *Petunia hybrida* grown under two nutrient regimes (Feller et al. 2015): 10  $\mu\text{M}$  inorganic phosphorus ( $\text{P}_i$ ; broken curves) or 100  $\mu\text{M}$   $\text{P}_i$  (solid curves). (a) Root and shoot fresh weights of plants harvested between 31 and 66 days after germination. Data from Figure 1b and Supporting Information: Table S4 of Feller et al. (2015). Symbols are means ( $n = 5$ ). Curves show the local allocation model (LAM; Equations 8 and 11) fitted to ln-transformed data,  $r^2 > 0.96$ . Adjusted parameter values, 100  $\mu\text{M}$   $\text{P}_i$ :  $B_0 = 3.80$  g,  $\varphi_R = 0.0664$ ,  $A_0 = 14.6$  g,  $\varphi_S = 0.0139$ ; 10  $\mu\text{M}$   $\text{P}_i$ :  $B_0 = 0.938$  g,  $\varphi_R = 0.286$ ,  $A_0 = 15.9$  g,  $\varphi_S = 0.0055$ . Horizontal line denotes zero fresh weight. (b) Root and shoot absolute growth rates (AGR, Equation 2). Horizontal line denotes zero AGR. (c) Root and shoot relative growth rates (RGR, Equation 4). Horizontal line denotes zero RGR. (d)  $\alpha$  (root RGR/shoot RGR, see Equation 7), derived from panel (c). Horizontal line denotes  $\alpha = 1$ . (e) Whole-plant AGR. (f) Whole-plant RGR. (g) Root mass fractions (RMF, Equation 5); data points are derived from those in (a). (h) AGR-RMF co-trajectories derived from (e) and (g). (i) RGR-RMF co-trajectories derived from (f) and (g).

be valid. 'Valid' means that  $B_0$  must exceed the maximum measured root biomass, and  $\varphi_R$  must be smaller than 1 ( $\varphi_R \sim 1$  implies near-instantaneous resource depletion, and values of  $\varphi_R > 1$  are impossible).

Analogous equations, procedures and arguments are used to calculate shoot mass,  $S$ , over time based on the capture of aboveground resources:

$$S_{t+1} = S_t + (A_t \cdot S_t \cdot v_t \cdot \varphi_S) \quad (11)$$

where  $v_t$  is a coefficient modifying  $\varphi_S$  in response to resource availability:

$$v_t = \left[ A_0^2 - (A_0 - A_t)^2 \right]^{1/2} / A_0 \quad (12)$$

$$A_{t+1} = A_t - S_t \quad (13)$$

$A$  is the availability of aboveground resources. As for  $B$ ,  $A$  is an effective availability, not a certain radiation flux measured by a quantum sensor. Obviously, it is silly to think of a shoot system 'depleting' its environment of light or  $\text{CO}_2$ , but Equations (12) and (13) describe the typical slowing of productivity per unit shoot mass over time as, for example, in Figures 1c and 2c in Hunt (1975), without specifying any mechanism.

A continuous trajectory of shoot biomass is derived by adjusting  $A_0$  and  $\varphi_S$  in Equation (11) to find values of  $S$  that again provide the best match with appropriate data.

From the root and shoot trajectories produced from Equations (8) and (11), absolute and relative growth-rates of whole plants, and their simultaneous root-shoot allocations, are calculated using Equations (2), (4) and (5). Characterising the dynamic relationships between root-shoot allocations and whole-plant growth under different environmental conditions, these trajectories depend only on data, and not on any assumed mechanisms for adaptive, goal-seeking behaviour.

## 4 | APPLYING LAM

Five arguments are usually marshalled to support OPT. These are stated below as questions. To answer them I apply LAM to specific datasets, as follows.

### 4.1 | Does root biomass increase relative to shoot biomass when nutrients are scarce?

Yes, this does occur, as meta-analyses confirm (Poorter et al., 2012). That evidence comprises numerous, multispecies comparisons of root and shoot biomasses measured after plants were grown under different conditions of resource supply, although many provide only a static view. The risks of inferring function from 'snapshot' estimates of dynamic processes are well known but often ignored.

To understand how root-shoot allocation happens, and how it relates to whole-plant growth-rate, we must look at the dynamic interplay between roots and shoots as they grow under different environmental conditions. The data provided by Feller et al. (2015) are an excellent starting point for this.

Feller et al. grew *Petunia × hybrida* (common garden petunia) plants supplied with inorganic phosphorus ( $\text{P}_i$ ) at concentrations of 10 or 100  $\mu\text{M}$  added repeatedly to the rooting medium. They harvested replicate plants about every other day from 31 to 66 days after sowing, and measured root and shoot fresh weights.

Fitted to ln-transformed data by adjusting the unknowns in Equations (8) and (11), LAM described the trajectories of root and shoot growth,  $r^2 > 0.96$ , even for plants grown at 10  $\mu\text{M}$   $\text{P}_i$  yet to reach their final sizes. Values of  $B_0$ ,  $\varphi_R$ ,  $A_0$  and  $\varphi_S$  defining those trajectories (Figure 1a) are valid, as defined above. All that follows flows from those trajectories.

Predictably, plants grown at 100  $\mu\text{M}$   $\text{P}_i$  were bigger than those at 10  $\mu\text{M}$  (Figure 1a). At 100  $\mu\text{M}$ , roots and shoots formed sigmoid trajectories and, therefore, had unimodal root and shoot AGRs (Figure 1b), a pattern scarcely evident in the slower-growing plants at the lower  $\text{P}_i$  concentration.

Root and shoot RGRs declined throughout (Figure 1c), as did their ratio,  $\alpha$  (Figure 1d).  $\alpha$  was initially larger at the lower  $\text{P}_i$  concentration, but eventually matched that at 100  $\mu\text{M}$ .

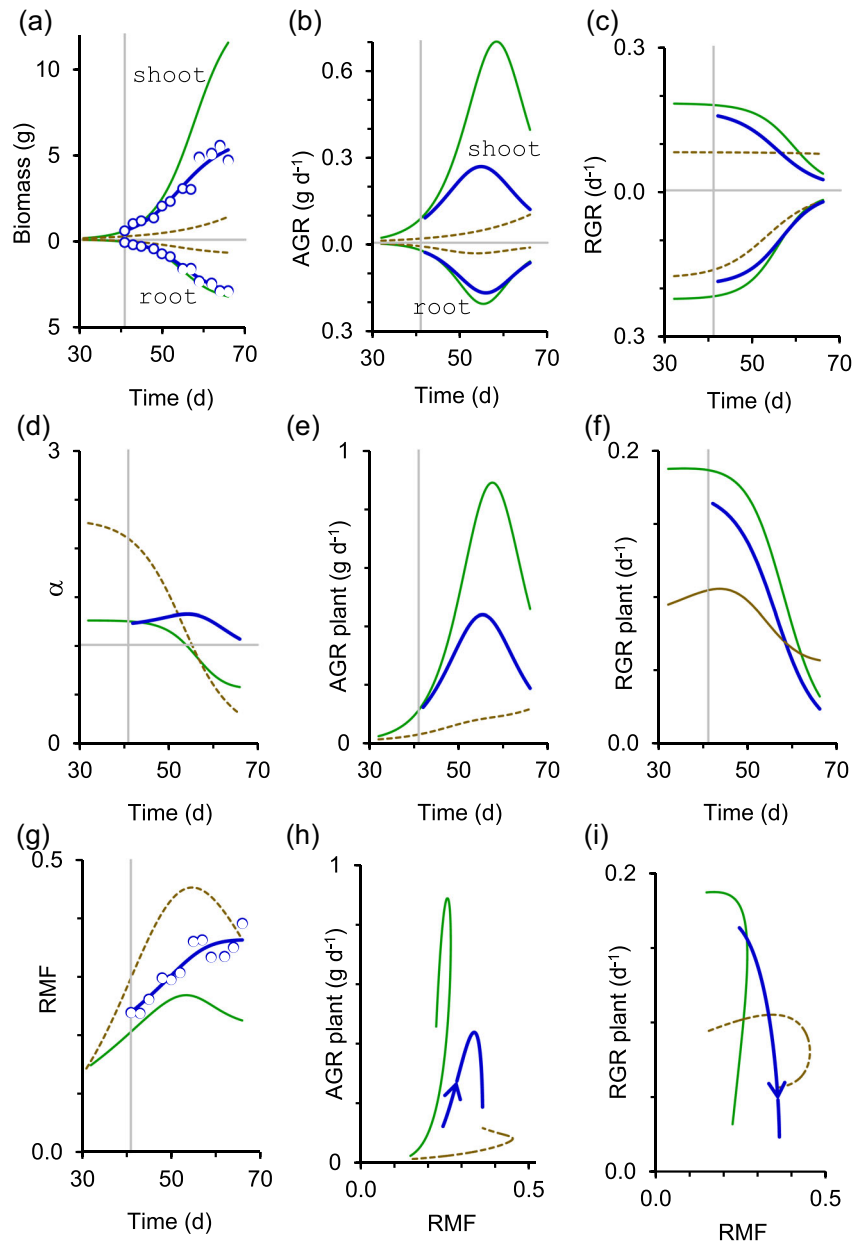
Whole-plant AGR at 100  $\mu\text{M}$  always exceeded that at 10  $\mu\text{M}$ , the maximum disparity being an order of magnitude in favour of plants at 100  $\mu\text{M}$  between 54 and 59 days (Figure 1e).

Whole-plant RGR at 100  $\mu\text{M}$  was never more than double that at 10  $\mu\text{M}$ , and then only initially (Figure 1f). RGR always declined at 100  $\mu\text{M}$  and, until the final 10 days, exceeded RGR at the lower  $\text{P}_i$  concentration. At the lower concentration, whole-plant RGR did not decline throughout. It increased slightly up to 46 days before falling. Even if root and shoot RGRs decline over time, whole-plant RGR does not necessarily do likewise; its trajectory depends on the dissimilarity between root and shoot RGRs.

The effects of low  $\text{P}_i$  on root and shoot growth-rates caused RMF to increase more rapidly and to a greater extent than at the higher concentration (Figure 1g), but RMF changed in both  $\text{P}_i$  treatments. In Figure 1g, the root-shoot allocation response to  $\text{P}_i$  availability is the difference between the two RMF trajectories. Temporal changes in each RMF trajectory constitute 'ontogenetic drift' in allocation (Gedroc et al., 1996; McConnaughay & Coleman, 1999).

The inflexion points on the RMF trajectories in Figure 1g occurred when  $\alpha$  fell below 1, when  $\text{RGR}_S$  exceeded  $\text{RGR}_R$ .  $\alpha$  determines whether RMF increases or decreases. Whether RMF is large or small depends more on the disparity between root and shoot AGRs. If  $\text{AGR}_R > \text{AGR}_S$ , RMF tends towards 1, as deduced from Equation (7); if  $\text{AGR}_R < \text{AGR}_S$ , RMF declines. But the control of RMF by root and shoot growth-rates is more subtle than Equation (7) suggests because AGR and RGR are not independent: a change in one rate automatically means a change in the other (Equation (3)).

**FIGURE 2** (a–i) As for Figure 1, but with  $P_i$  supply switched at 41 days (vertical lines), from 100 to 10  $\mu\text{M}$   $P_i$ . Data from Feller et al. (2015). In (a) the bold curves are the local allocation model (LAM) fitted to ln-transformed data ( $r^2 > 0.96$ ). Fine solid and broken curves are those from Figure 1 describing trajectories under constant  $P_i$  concentrations of 10 or 100  $\mu\text{M}$   $P_i$  superimposed for comparison. Adjusted parameter values:  $B_0 = 0.94$  g,  $\phi_R = 0.062$ ,  $A_0 = 5.87$  g,  $\phi_S = 0.029$ . [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



A change in RMF is not by itself evidence for an allocation response. So, while the answer to Question 4.1 is affirmative, it is a qualified yes.

Whole-plant AGR peaked at single but different RMFs in the two  $P_i$  treatments (Figure 1h). Even though whole-plant AGR reached a maximum in each, those maxima were transient points. There was no possibility of a plant adjusting its RMF to remain at or close to those points. Nor was there any evidence that certain RMFs allowed faster whole-plant AGRs. What promoted faster AGR was more  $P_i$ , not a particular root–shoot allocation. Similarly, there was no indication that whole-plant RGR was maximised at any optimum RMF. The same RMF was associated with a wide range in RGR (Figure 1i). For example, plants with an RMF of 0.22 had RGRs of 0.18, 0.10 or 0.03  $\text{day}^{-1}$  depending on time and treatment.

To contrast allocation dynamics under nominally constant  $P_i$  availability, we can ask what happens when a plant's  $P_i$  supply is

switched from a low to high availability or from high to low? Resource switching experiments provide deep insights into the responsiveness of root–shoot allocation.

**4.2 | When nutrients are partly withheld from a well-fed plant does root biomass increase relative to shoot biomass, and does the opposite happen after nutrients are resupplied to a nutrient-starved plant?**

Yes. Feller et al. (2015) compared the allocation responses of *Petunia* plants grown with 10 or 100  $\mu\text{M}$   $P_i$ , as described above, with those of plants switched after 41 days from 10 to 100  $\mu\text{M}$ , or from 100 to 10  $\mu\text{M}$ . Fitting LAM to data collected after 41 days ( $r^2 > 0.96$ ), we can see what happened before and after  $P_i$  supply was switched by

comparing those trajectories with the unswitched controls in Figure 1.

Reducing  $P_i$  from 100 to 10  $\mu\text{M}$  slowed the AGR and RGR of shoots more than roots (Figure 2b,c).  $\alpha$  remained relatively constant after the switch (Figure 2d), in contrast to the large changes in both controls after 41 day. By the end of the experiment, whole-plant AGR had dropped to almost one-third that of plants grown at 100  $\mu\text{M}$  (Figure 2e). The effect on whole-plant RGR of switching  $P_i$  was weaker, one so small I doubt it would have been detectable from experimental data alone (Figure 2f).

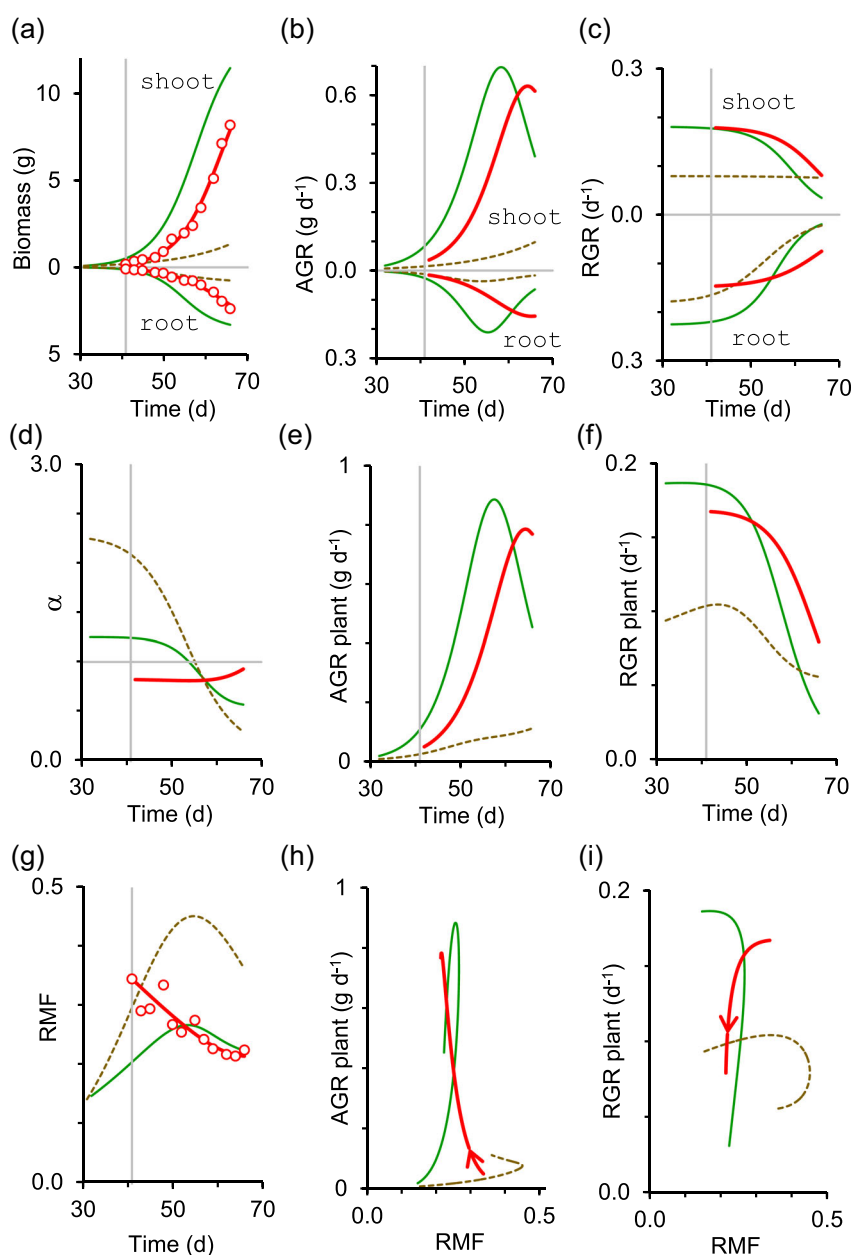
Reducing  $P_i$  from 100 to 10  $\mu\text{M}$  was followed by a continued increase in RMF (Figure 2g), in contrast to the 100  $\mu\text{M}$  controls where RMF peaked before falling (Figure 1g). Root-shoot allocation in switched plants changed entirely within the envelope defined by the RMF trajectories of the unswitched controls. By the end of the

experiment the RMF in switched plants matched that of plants grown on 10  $\mu\text{M}$  throughout.

The AGR-RMF co-trajectory of the switched plants diverged gradually from that of the 100  $\mu\text{M}$  controls and curved towards, but didn't quite reach, that of the 10  $\mu\text{M}$  controls (Figure 2h). The same was true for the RGR-RMF co-trajectories (Figure 2i).

The story for plants switched the other way, from 10 to 100  $\mu\text{M}$  at 41 days, is virtually a mirror image. Unsurprisingly, increasing  $P_i$  at 41 day boosted subsequent growth, particularly of the shoot (Figure 3a-c). A near-constant  $\alpha$  resulted (Figure 3d).

Having access to more  $P_i$  after 41 days allowed the AGR and RGR of previously  $P_i$ -limited plants to follow trajectories like those of plants grown throughout on 100  $\mu\text{M}$ , albeit delayed by several days (Figure 3e,f). Likewise, the RMF trajectory shifted from that of the 10  $\mu\text{M}$  controls to track that of the 100  $\mu\text{M}$  controls (Figure 3g), again



**FIGURE 3** (a–i) As for Figure 1, but with  $P_i$  supply switched at 41 days (vertical lines), from 10 to 100  $\mu\text{M}$   $P_i$ . Data from Feller et al. (2015). In (a) the bold curves are the local allocation model (LAM) fitted to ln-transformed data ( $r^2 > 0.99$ ). Fine solid and broken curves are those from Figure 1 describing trajectories under constant  $P_i$  concentrations of 10 or 100  $\mu\text{M}$   $P_i$  superimposed for comparison. Adjusted parameter values:  $B_0 = 4.25$  g,  $\varphi_R = 0.037$ ,  $A_0 = 14.2$  g,  $\varphi_S = 0.001$ . [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



remaining within the envelope bounded by those controls. And, as in Figure 2, the co-trajectories of AGR-RMF and RGR-RMF (Figure 3h,i) gradually converged on those of the 100  $\mu$ M controls.

The convergence in RMF trajectories (Figures 2g and 3g) is unmistakable, evidence perhaps of an 'adaptive' allocation response, which is what you'd expect from OPT. But LAM assumes no such mechanism. So, what's going on? What causes convergence?

### 4.3 | When roots or shoots are pruned, does root–shoot biomass allocation converge towards that of unpruned plants?

Yes, but not for the reason you might think. OPT was inspired largely by Brouwer's (1962) renowned experiment on beans (*Phaseolus vulgaris*, presumably, species unspecified in the original). Brouwer removed parts of the root or shoot systems and measured how the plants responded. Within days the pruned plants' growth had changed to match that of intact controls (see Figure 7 in Brouwer, 1962). That experiment was repeated by Farrar (1996), on the grass *Dactylis glomerata* L. (cocksfoot), and by Poorter and Nagel (2000) using cultivated barley (*Hordeum vulgare* L.), both with similar results. Here I will use data from this last experiment.

Poorter and Nagel (2000) grew barley in hydroponics for 28 days. After 7 days, they removed about half the root mass or about half the shoot mass. Controls remained intact. Root and shoot dry weights were measured every 1–4 days (Hendrik Poorter, personal communication, 2020). Fitted to Poorter & Nagel's In-transformed data ( $r^2 > 0.97$ ), LAM captured the dynamics of roots and shoots of intact controls (Figure 4), and of shoot- (Figure 5) or root-pruned (Figure 6) plants.

Perhaps surprisingly, clipping had small effects on whole-plant growth-rates (Figures 5e,f and 6e,f). But, as in Brouwer's (1962) experiment, the most striking feature is the convergence in root–shoot allocation during regrowth of pruned plants towards the allocations of intact controls (Figures 5g and 6g). Consequently, the AGR-RMF and RGR-RMF co-trajectories of pruned plants also converged on those of the controls (Figures 5h,i and 6h,i).

The trajectories in Figures 4–6 are LAM reconstructions of those in Figure 2 of Poorter and Nagel (2000) who concluded, quite reasonably, that their data vindicated OPT's qualitative predictions. In terms of OPT, the pruned plants restored their growth-rates via appropriate, responsive adjustments in root–shoot allocation. Convergent trajectories are taken as de facto evidence of adaptive, goal-seeking behaviour.

But does convergence have another explanation? To answer this, we need to understand what determines the start and end points of a trajectory within the RMF-RGR space, and what controls a trajectory's direction across that space. LAM can provide some answers.

The start of the trajectory along the RMF axis depends, obviously, on the plant's initial root and shoot masses,  $R_0$  and  $S_0$ . So, the initial RMF is defined as  $R_0/(R_0 + S_0)$ . The starting position

along the RGR axis depends on initial resource availabilities,  $B_0$  and  $A_0$ , and on their capture efficiencies,  $\varphi_R$  and  $\varphi_S$  (Equations (8) and (11)). Those equations say that the bigger the absolute values of these variables, the larger the initial changes in  $R$  and  $S$  are likely to be, and the further up the RGR axis the trajectory will start (Equation (4)).

The end of an RMF trajectory is determined solely by the initial below- and aboveground resource availabilities,  $B_0$  and  $A_0$ . This is because these define, respectively, the maximum possible root and shoot masses. This is the third reason for couching resource availability in terms of biomass equivalents: it allows the terminus of a growth trajectory to be characterised. The terminal RMF is  $B_0/(B_0 + A_0)$ . In Figure 4i, for example, the values of  $B_0$  and  $A_0$  estimated from the data are 1.44 and 5.11 g, respectively. Therefore  $B_0/(B_0 + A_0)$  is 0.22. That's the RMF towards which the trajectory in Figure 4i is heading. The same argument also explains the convergences in Figures 2, 3, 5 and 6.

The RGR towards which a plant ultimately tends is zero. RGR might never reach zero, but that's its destination (e.g., Figs. 2.1, 5.15, 8.6 in Hunt, 1982). RGR inevitably falls because it is physically impossible to sustain proportional mass increases as a plant grows, just as a bacterial colony can't grow indefinitely at an exponential rate. RGR can be negative if respiration and senescence exceed production, which happens diurnally as part of normal physiology (Hunt, 1980). Even so, and even if there is an initial transient increase in RGR, as in Figures 1f and 5f, the general direction of whole-plant RGR is downwards.

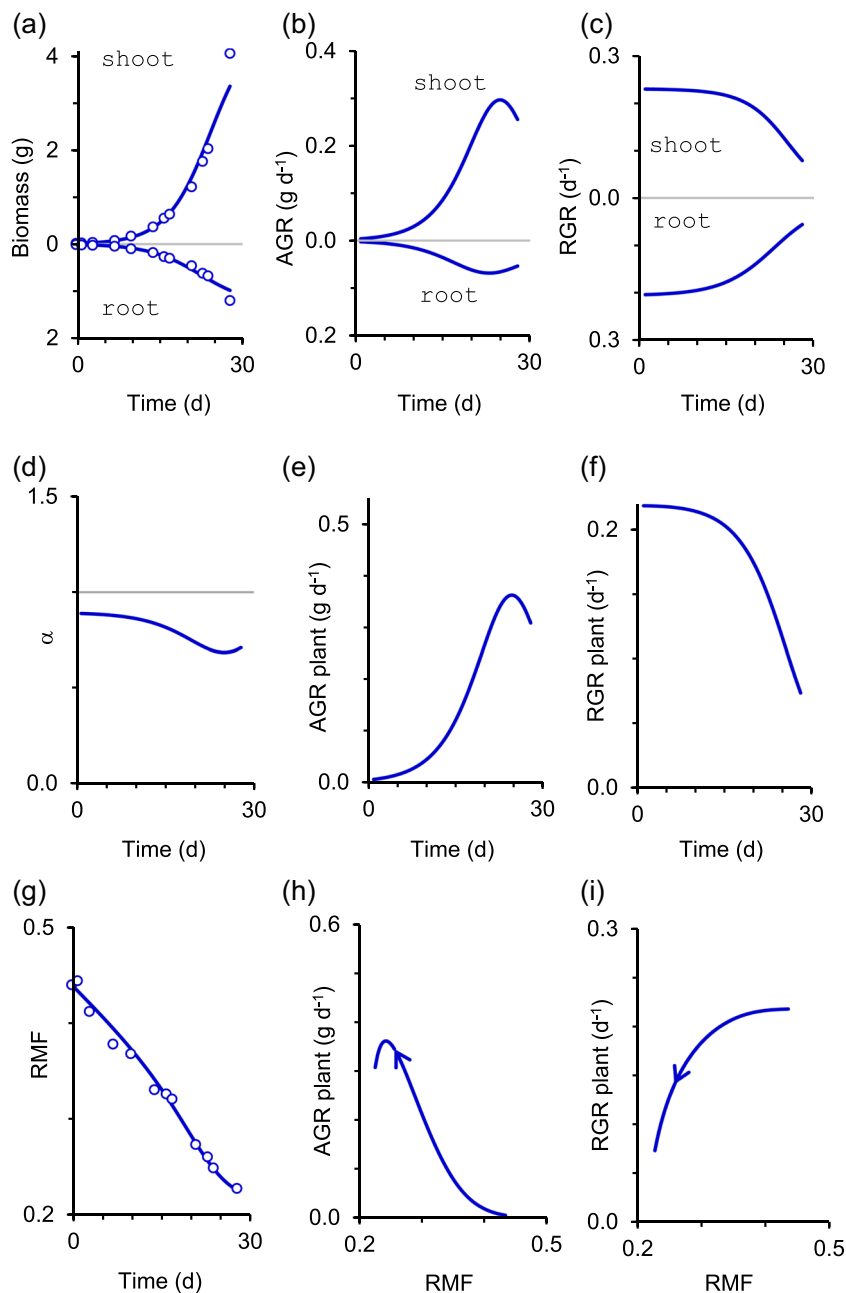
What causes RMF and whole-plant RGR to vary in some directions as opposed to others as growth proceeds (compare Figures 1i, 2i, and 3i, for example)? To explore this, I use as a convenient control the trajectory of intact barley in Figure 4i from which different 'virtual' trajectories are generated as follows.

Taking the values  $B_0 = 1.44$  g,  $\varphi_R = 0.164$  g,  $A_0 = 5.11$  g, and  $\varphi_S = 0.051$  which define the trajectory in Figure 4i and flexing each by fixed amounts, up or down, singly or in combination, or holding them constant, produces 81 (=  $3^4$ ) virtual trajectories including the control trajectory itself. To keep the 80 virtual trajectories anchored reasonably close to reality, their parameters are flexed by only modest amounts, 1, 5 or 10%.

With a 1% flex, only 1 trajectory out of 81 has an initial increase in RGR, and none an increase in RMF (Figure 7a). Predictably, such small variations in parameter values generate trajectories hardly distinguishable from the original. They all converge towards final RMFs near 0.22, as defined by  $B_0/(B_0 + A_0)$ .

A 5% flex means that almost 40% of trajectories start with an increase in RGR and 6% an increase in RMF (Figure 7b). The spread of trajectories across RMF-RGR space is wider than before, but all converge onto RMFs between 0.20 and 0.24.

An even wider spread of trajectories is produced by a 10% flex (Figure 7c). Now, 43% of the trajectories have an initial increase in RGR and 19% an increase in RMF. Yet, despite occupying much of the available RMF-RGR space as they unfold, all trajectories still converge towards a narrow RMF range, 0.19–0.26.



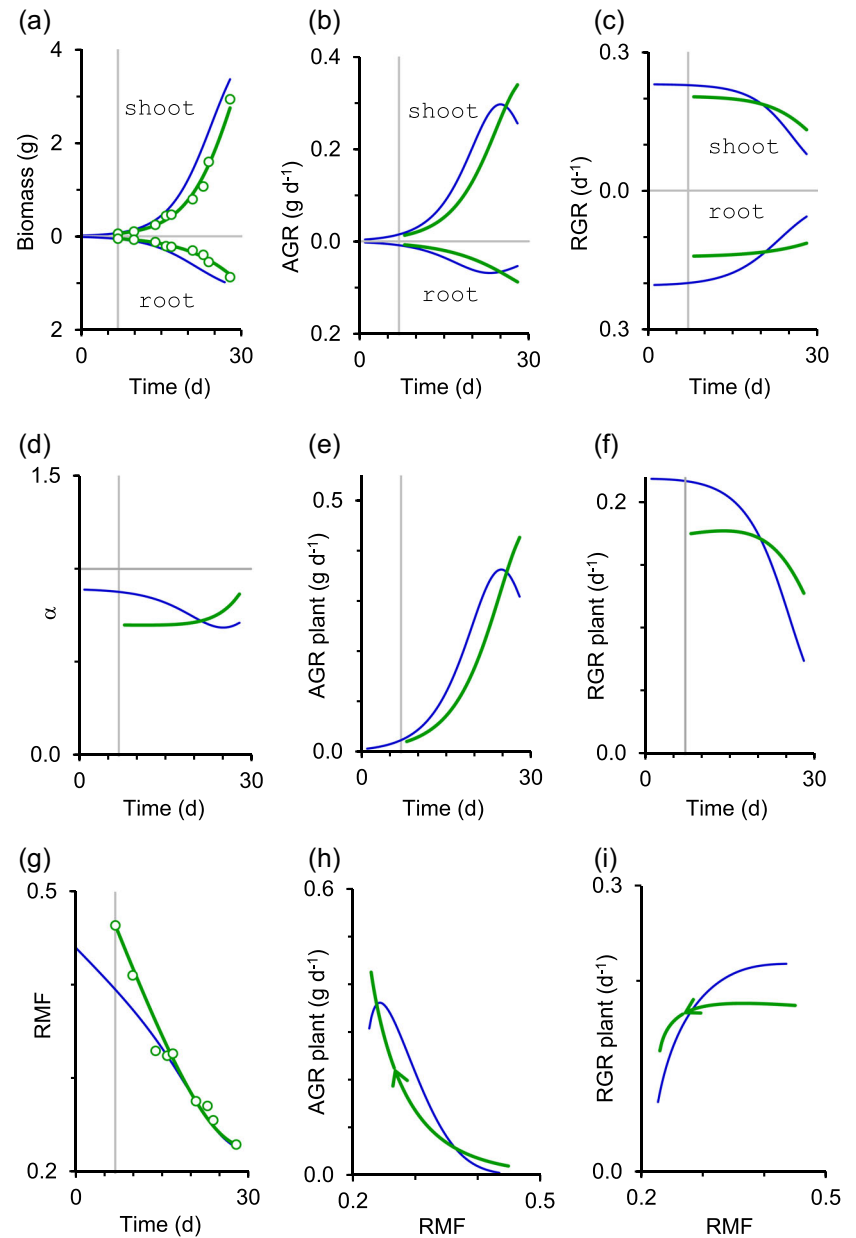
**FIGURE 4** Root and shoot trajectories of *Hordeum vulgare* (cultivated barley) in which root and shoot systems remained intact (Poorter & Nagel, 2000). (a) Root and shoot dry weights of plants harvested between 0 and 28 days after the start of the experiment. Symbols are means ( $n = 8$ ). Curves are the local allocation model (LAM) fitted to ln-transformed data,  $r^2 > 0.99$ . Adjusted parameter values:  $B_0 = 1.44$  g,  $\varphi_R = 0.164$ ,  $A_0 = 5.11$  g,  $\varphi_S = 0.051$ . (b–i) As for Figure 1. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pce.14470)]

This exercise shows that the dynamic relationship between root–shoot allocation and whole-plant growth-rate is constrained at the ends of its trajectory. Between those extremes considerable plasticity in allocation and growth-rate is possible even with only modest variation in resource availability and capture, as in Figure 7. To hit a certain trajectory commensurate with OPT a plant would have to orchestrate its physiology with intricate precision (involving, in LAM, just four variables,  $\varphi_R$ ,  $\varphi_S$ ,  $B_0$ ,  $A_0$ ; in a real plant, mechanisms and molecules too numerous to enumerate). Even small imprecisions would risk shifting growth onto an entirely different trajectory, although it turns out that wouldn't necessarily jeopardise whole-plant growth-rate (see Section 4.4). The precise trajectory taken by a plant depends, in terms of LAM, on the relative sizes of, and disparities

between, resource capture efficiencies of roots and shoots,  $\varphi_R$  and  $\varphi_S$ . But that dependency is also conditioned by initial resource availabilities,  $B_0$  and  $A_0$ .

Resource capture efficiencies can influence allocation and growth-rate when plenty of resources are available and dwindle in influence as resources are consumed. The window in which a plant can modify its root–shoot allocation might be narrow if resource capture is rapid and supply sluggish. When resources are finite and growth-rates fall as demand outstrips supply, root–shoot allocation necessarily becomes more constrained, forced into a progressively narrower range of RMFs as defined by  $B_0$  and  $A_0$ . Initially different RMF-RGR co-trajectories will then inevitably converge towards each other, into a 'phenotypic bottleneck', as Gedroc et al. (1996) discovered.

**FIGURE 5** As for Figure 4, but at 7 days (vertical lines) about half the shoot biomass was removed by clipping. (a) Root and shoot dry weights of shoot-pruned plants harvested between 7 and 28 days after the start of the experiment. Symbols are means ( $n = 8$ ). Bold curves are the local allocation model (LAM) fitted to ln-transformed data,  $r^2 > 0.98$ . Adjusted parameter values:  $B_0 = 3.52$  g,  $\phi_R = 0.043$ ,  $A_0 = 6.99$  g,  $\phi_S = 0.032$ . (b–i) As for Figure 4. Fine curves are those for intact controls (Figure 4) superimposed for comparison. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



According to LAM, convergence of different allocation-growth-rate trajectories reflects the availabilities of locally available resources and the variable capacities of roots and shoots to capture resources and turn them into new biomass. Convergence need have nothing to do with allocation responses taking the plant closer to an optimum state.

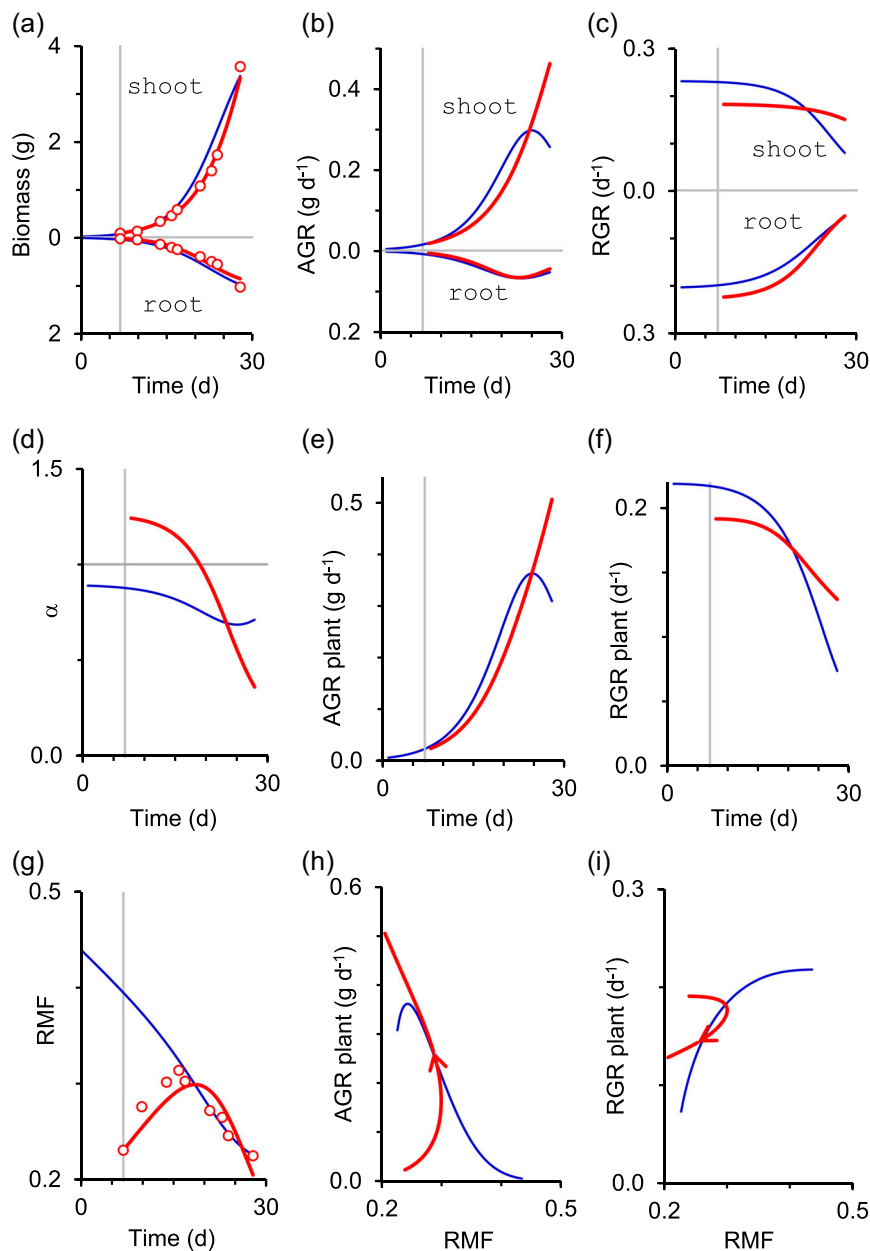
We don't normally have access to full growth trajectories from experiments, and so remain largely unaware of constraints imposed on phenotypic expression as available resources are consumed. As mentioned previously, many contemporary datasets offer static measurements of allocation orphaned from their parent trajectories. But with access to full trajectories, we can see that roots and shoots are not necessarily free to do what theory—OPT, that is—says they should.

Is the interpretation suggested by LAM any more believable than that offered by OPT? A test is straightforward: do a pruning

experiment while varying resource availabilities before and after pruning to guarantee different  $B_0$  and  $A_0$  values. If LAM-like logic applies, the trajectories will change as predicted by the new resource regime. If OPT is true, the stronger influence on regrowth trajectories will be the root–shoot allocations of unpruned controls towards which the regrowing plants should converge.

#### 4.4 | Are certain optimal root–shoot allocations necessary for maximal growth?

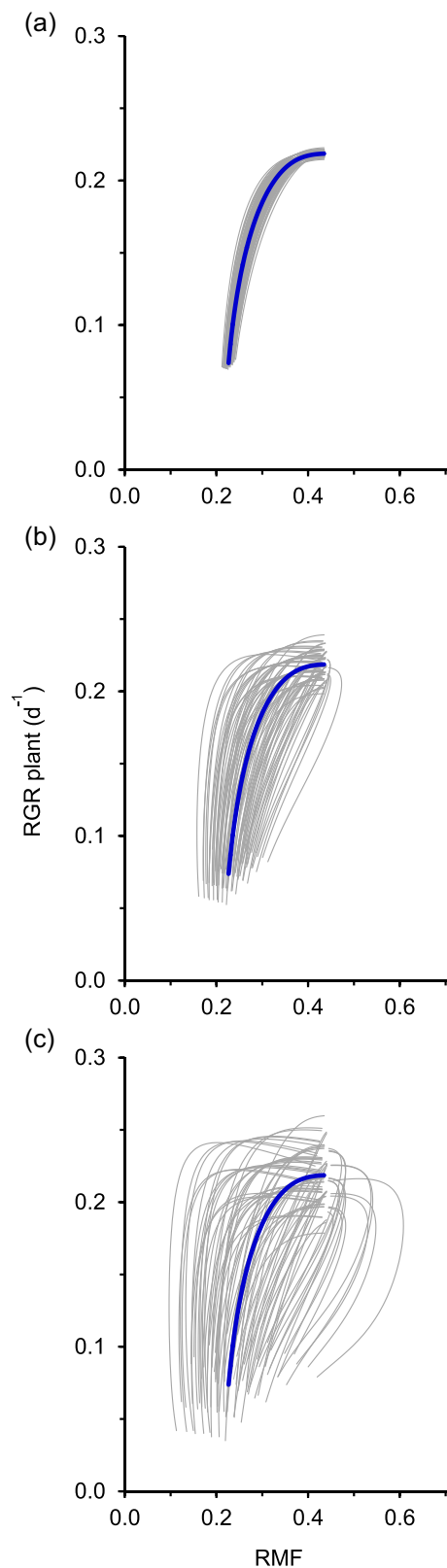
No. You might argue that the trajectory taken by plants in Figure 4i, for example, is in fact the optimal one, as dictated by OPT, and that others that were not taken would have been less optimal. But that would be incorrect.



**FIGURE 6** As for Figure 4, but at 7 days (vertical lines) about half of the root biomass was removed by clipping (Poorter & Nagel, 2000). (a) Root and shoot dry weights of shoot-pruned plants harvested between 7 and 28 days after the start of the experiment. Symbols are means ( $n = 8$ ). Bold curves are the local allocation model (LAM) fitted to ln-transformed data,  $r^2 > 0.97$ . Adjusted parameter values:  $B_0 = 1.14$  g,  $\phi_R = 0.222$ ,  $A_0 = 15.8$  g,  $\phi_S = 0.013$ . (b–i) As for Figure 4. Fine curves are those for intact controls (Figure 4) superimposed for comparison. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pce.14470)]

Certain root–shoot allocations are not necessary for a faster whole-plant growth-rate. The evidence is in Figure 7c: in intact barley plants expressing modest physiological plasticity (in terms of LAM, at least), an RGR of, for example,  $0.2 \text{ day}^{-1}$  is possible, transiently and at different times, with RMFs anywhere between 0.1 and 0.6. Only in the trivial cases of extreme allocations (RMF  $\sim 0$  or  $\sim 1$ ) preventing any growth are some RMFs genuinely inferior to others. Consistent with this, large net primary productivities at ecosystem scales are not associated with certain biomass allocations between above- and belowground (McNickle et al., 2016). There is nothing a plant can do in terms of adjusting its root–shoot allocation to achieve a superior growth-rate. There is no magic combination that can allow a faster growth-rate and which is consistent with the growth trajectory of a real plant.

The curves in Figure 7 also question another feature of OPT, the assumed causality between root–shoot allocation and whole-plant growth-rate. RMF and whole-plant RGR have no unique relationship with one another, as may be deduced from Equation (7): any change in allocation almost always means a change in growth-rate. Root–shoot allocation cannot determine whole-plant growth-rate because they are interdependent traits; like a circle's area and radius, one can't change without the other. This explains why plants with different root–shoot allocations can have similar growth-rates, and why there is no strong trade-off between allocation and whole-plant growth-rate (Reynolds & D'Antonio, 1996). It also explains the 'variability and contrariness of measurements of allocation' referred to earlier (see Section 2.3).



**FIGURE 7** 'Virtual' RGR-RMF co-trajectories (grey curves) derived from that of the intact control plants (Figure 4i), the bold curve in each panel. The 80 'virtual' trajectories were produced by flexing the parameters which define that curve ( $B_0 = 1.44$  g,  $\varphi_R = 0.164$ ,  $A_0 = 5.11$  g,  $\varphi_S = 0.051$ ), singly or in all 80 combinations, up or down, by (a) 1%, (b) 5% or (c) 10%. RGR, whole-plant relative growth-rate; RMF, root mass fraction. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

#### 4.5 | Does close coordination between roots and shoots ensure 'balanced' growth?

Not necessarily. 'Balance' is intuitively a virtue, exemplified for roots and shoots by Trewavas's quotation (see Section 2.2), and in common usage: 'balanced economy', 'balanced diet', 'balance of nature' (Reynolds, 2022), but is rarely defined unambiguously. Johnson (1985), however, was helpfully explicit: 'balanced exponential growth solutions, defined mathematically as when the specific growth-rates of the shoot, root and substrate components are constant and equal...' Growth is 'balanced' when root and shoot RGRs (specific growth-rates in Johnson's terminology) match and do not change, that is, when  $\alpha$  ( $= RGR_R/RGR_S$ ; Equation (7)) equals, or at least hovers around, 1.

Balanced growth emerges as a stable condition in simulation models (Cheeseman, 1993; Feller et al., 2015; Johnson, 1985; Reynolds & Thornley, 1982), is a general prediction of metabolic scaling theory (Niklas & Enquist, 2002), and is implied by allometric analysis. Applying the standard allometric equation (Section 3.1) to data often produces  $\alpha$  values near 1 on average (e.g., in the combined allometric data reported by Hunt et al. (1987), Shipley and Peters (1990) and Shipley and Meziane (2002) for numerous species, mean  $\alpha = 1.02$ , range 0.47–1.90, 95% CI: 0.99–1.04,  $n = 224$  ln-transformed values).

But an individual plant doesn't necessarily grow 'on average'. During the growth of *Petunia* and barley plants,  $\alpha$  values near 1 occurred only transiently and inconsistently (Figures 1–6). Shipley and Meziane (2002) found the same thing (see their Figure 2), concluding this to be reasonable evidence for balanced growth, a conclusion I don't share.  $\alpha$  does converge on 1 when root and shoot RGRs finally approach zero, but that isn't the sort of 'balance' meant by OPT.

Looking at root–shoot allocation in terms of its temporal dynamics, as in Figures 1–6, rather than through the lens of conventional allometry (which masks temporal variation in  $\alpha$ ) or OPT-based models (often structured to ensure root and shoot RGRs can eventually match), suggests that balanced growth is not a physiological necessity. Root–shoot growth is more often unbalanced than not. Lohier et al. (2014) struggled to explain deviations from balanced growth in physiological terms, and with some success, but their working assumption was that optimum allocations exist. I don't think they do.

Biomass allocation is constrained stoichiometrically, anatomically, mechanically and genetically. Signals and metabolites exchange continually between roots and shoots. Despite these constraints and communications, the resulting coordination of growth can be surprisingly loose. For example, below- and aboveground phenologies are often asynchronous (Abramoff & Finzi, 2015; Albert et al., 2018; Liu et al., 2022; Makoto et al., 2020), suggesting considerable independence in root and shoot responses to local conditions (cool air, warm soil or vice versa). At the opposite spatiotemporal scale, Apelt et al. (2021) found asynchrony in *Arabidopsis* root and shoot transcriptomes, and Hani et al. (2021) heterogeneity in  $P_1$ -triggered transcription among *Arabidopsis* root cells. Using ideas mainly from network theory, Hardwick (1986) argued that some independence among constituent modules is indeed necessary for a plant's developmental stability. Stability is threatened if more than about 15% of modules interact simultaneously via phloem connections,

for example. Growth, gene transcription and other processes in connected roots and shoots are not choreographed as tightly as models assume. Root and shoot growth do not need to be finely balanced for a plant to function.

Another common assumption (Mäkelä & Valentine, 2020; 174) is that root and shoot activities must balance so that surplus photosynthate or nutrients do not accumulate inefficiently. This is countered by plants' remarkable, if underappreciated, capacities to sequester and dispose of excess assimilates, an evolutionary legacy of their colonisation of land (Thomas & Sadras, 2001).

## 5 | DISCUSSION

### 5.1 | Where are we now?

To recap:

1. Biomass allocation to roots changes when nutrients are scarce. That change is caused by disparities in growth-rates between roots and shoots. Whole-plant growth-rates also change. Those changes do not reflect an adaptive response. They occur because root–shoot allocation and whole-plant growth-rate are interdependent.
2. Following a switch in nutrient supplies or defoliation, the convergence of allocation and growth-rate trajectories towards those of control plants does not, according to LAM, reflect an adaptive response to nutrient shortage or defoliation, but the influence of constraints imposed by resource availabilities.
3. Optimal root–shoot allocations are not necessary for a certain whole-plant growth-rate. The same growth-rate is attainable by plants with very different root–shoot allocations.
4. Changes in root–shoot allocation cannot maintain or restore a superior whole-plant growth-rate.
5. Root and shoot growth do not have to be tightly coordinated or balanced.

The idea that optimal root–shoot allocations maximise growth-rate is an illusion arising from the assumption that changes in allocation are potentially adaptive. That illusion disappears if, instead, root and shoot growth dynamics are seen primarily as local responses to local conditions. Those responses have consequences for whole-plant growth-rate that, while in no way optimal, are not catastrophic either. Without an optimum for a plant to aim for, OPT has no *raison d'être*.

Some growth responses to the environment can potentially compensate for nonuniform and unpredictable resource availabilities or for defoliation. These include localised root proliferation in nutrient-rich soil (Hodge, 2004; Robinson, 1994), and leaf and stem expansion into better illuminated gaps (Küppers, 1994). These are the potentially adaptive responses that matter. As they occur, root and shoot growth-rates inevitably change differentially and, therefore, so does root–shoot allocation (Equation (7)). Those changes in biomass allocation will appear as if they are the primary responses, but they aren't.

As well as localised root and shoot growth responding to their immediate environments, root and shoot morphologies and the physiological activities of their parts, also change. These responses also have adaptive potential. In N- or P-rich soil patches, for example, proliferating roots are often more finely branched than in homogeneous soil, and their rates of N or P uptake per unit root increase temporarily compared with other roots on the same plant (Hodge, 2004). Despite occurring locally, such responses involve the systemic transmission of signals and metabolites from root to shoot and vice versa, so in that sense they are certainly whole-plant responses (Trewavas, 2014; 80; Wheeldon & Bennett, 2021). But that shouldn't automatically imply tight whole-plant coordination.

Root–shoot allocation changes whenever *anything*—nutrients, light, water, cold, warmth, hard soil, loose soil, anoxia, toxins, pests, pathogens, trampling, UV radiation, ozone, fungicides, neighbours and so on—differentially alters root and shoot growth-rates. Changes in allocation are unavoidable secondary consequences of some root or shoot meristems encountering and responding locally to new microenvironments. They aren't hallmarks of potentially optimal behaviour.

Thinking of a plant not as an entity comprising two juxtaposed centres of growth ('roots' and 'shoots') that can be modelled from engineering principles, but as populations of dispersed, multiple meristems connected to one another, subsets of which can experience and respond separately to different local conditions, undermines current ideas of potentially optimal whole-plant behaviour. With modularity as a fundamental feature of biomass allocation models (Oborny, 2019), new insights are likely to emerge. The value of such insights will depend on how well they can explain or predict observable reality, that is, data.

OPT stimulated us to think critically about allocation and growth, inspiring much ingenious modelling work. But it has proved a dead-end in terms of explaining how the root–shoot trade-off works in real plants. Optimality can be a powerful guide, but it doesn't always point the right way (Pierce & Ollason, 1987; Railsback, 2022). As a metaphor for root–shoot allocation OPT is inappropriate. As Cobb (2020; 373) observed, metaphors are invaluable for insight and discovery, but 'there will come a point when the understanding they allow will be outweighed by the limits they impose'. OPT has reached those limits.

### 5.2 | Wider relevance

Biomass allocation in terrestrial vegetation is often interpreted in terms of OPT: large RMFs in tundra reflect selection to maximise nutrient foraging in infertile soils; small RMFs in crops indicate weaker selection for foraging in nutrient-rich fields; and so on. In mature vegetation, biomass production is typically in a steady-state; in terms of LAM, root and shoot biomasses are close to  $B_0$  and  $A_0$ , respectively. If that condition applies, can the logic behind LAM predict RMFs in global vegetation?

Lacking the below- and aboveground growth trajectories that we had for *Petunia* and barley, we need another way to estimate global  $B_0$  and  $A_0$ . This is where positive correlations expected between  $B_0$  and  $A_0$  and actual measurements of resource availability come in.

Total dry matter (DM) production is the product of intercepted radiation and radiation use efficiency. Taking as global averages  $3 \text{ GJ m}^{-2} \text{ year}^{-1}$  for the former and  $0.5 \text{ g DM MJ}^{-1}$  for the latter, values falling within extremes for crops at one end of the spectrum and tundra at the other (Jones, 1983; 167), gives a productivity of  $1.5 \text{ kg DM m}^{-2} \text{ year}^{-1}$ . As in LAM, assume all that DM is allocated aboveground, giving this as the global average  $A_0$ .

If N is the belowground resource most influencing productivity (although in many circumstances it will be water or another nutrient), we need the annual N supply. Olff et al. (1994) measured N mineralisation rates of  $6\text{--}18 \text{ g N m}^{-2} \text{ year}^{-1}$  in unfertilised grasslands. Assume a conservative global N supply rate of  $6 \text{ g N m}^{-2} \text{ year}^{-1}$  and all that N is captured ( $\phi_R \sim 1$ ) and used to produce only root biomass. To estimate  $B_0$  we also need the mean global N concentration in plant DM, approximately  $1 \text{ mol N kg}^{-1}$  (Robinson, 2016). So,  $B_0 = 0.44 \text{ kg DM m}^{-2} \text{ year}^{-1}$ .

These  $B_0$  and  $A_0$  estimates suggest a global average RMF of  $0.44 / (0.44 + 1.5) = 0.23$ . This matches values (0.20–0.24) calculated from extensive data, modelling and mapping exercises (Huang et al., 2021; Ma et al., 2021). Analysed in this way, much measured variation in site- or biome-specific RMFs could be quantified in terms of below- and aboveground resource availabilities, an improvement over the vague qualitative interpretations possible with OPT. Obviously, this approach won't always provide the best explanation for ecological variations in RMF. For example, you'd expect the typically large RMFs in grasslands (Ma et al., 2021) to be caused mainly by herbivores repeatedly destroying aboveground biomass than by the resources available for its production.

Another example of LAM's possible relevance is in crop breeding. Future breeding programmes will target belowground traits directly, as opposed to relying on unconscious selection as in the past (Zhu et al., 2019). The main focus is on root system architecture, but root–shoot allocation is also in the spotlight (Brooker et al., 2022; Reynolds et al., 2021). If allocation is a serious breeding target, rather than narrowing RMF towards some theoretical (in practice, nonexistent) optimum, LAM suggests instead maximising plasticity in RMF, an aim supported by experimental evidence (Bacher et al., 2021, 2022). Maximising plasticity in RMF would entail identifying genes giving greater potential for local root proliferation or leaf expansion responses to below- and aboveground environments. Maximising flexibility in root–shoot allocation could improve resource capture under a range of conditions without seriously compromising population productivity (Weiner, 2019).

## 6 | FINAL REMARKS: OPT-ING OUT

Du Noyer (2002; 58) noted, in a very different context, that 'When a theory gets long in the tooth there is a temptation to rubbish it from sheer boredom'. Although OPT is certainly old, my critique was not prompted by boredom. On the contrary, it is because root–shoot allocation is so intriguing and OPT such a familiar, yet unenlightening, explanation that it warrants critical scrutiny. OPT failed that scrutiny because it is incompatible with how real plants grow.

Improving how knowledge of whole-plant functioning is applied demands that experiments and models are appropriate to the task (Passioura, 1996). Here this means ditching an attractive and much-loved, but ultimately misleading, idea about the trade-off between roots and shoots. Alternative models acknowledge the potential for semiautonomous, local responses of roots and shoots to their environments. These have, in my view, more explanatory power and provide greater scope for future theoretical developments and practical applications.

## ACKNOWLEDGEMENTS

I thank Hendrik Poorter, Didier Reinhardt and their coauthors for their excellent data. Hendrik also provided valuable and insightful comments on an earlier version of this paper, as did Ian Bingham, Rob Brooker, John Peterkin and three anonymous reviewers, all of whom improved it significantly. Some of my ideas and text appeared originally in an online preprint: [www.biorxiv.org/content/10.1101/2020.06.29.177824v1](http://www.biorxiv.org/content/10.1101/2020.06.29.177824v1).

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

## ORCID

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**How to cite this article:** Robinson, D. (2023) OPT-ing out: Root-shoot dynamics are caused by local resource capture and biomass allocation, not optimal partitioning. *Plant, Cell & Environment*, 46, 3023–3039. <https://doi.org/10.1111/pce.14470>