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Optimal Allocation Ratios: A Square Root Relationship between the Ratios of Symbiotic Costs and Benefits

Brian S. Steidinger[1,2,*] **and Kabir G. Peay**[1]

1. Department of Biology, Stanford University, Stanford, California 94305; 2. Department of Plant Ecology, University of Konstanz, Konstanz, Germany

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ABSTRACT: All organisms struggle to make sense of environmental stimuli in order to maximize their fitness. For animals, the responses of single cells and superorganisms to stimuli are generally proportional to stimulus ratios, a phenomenon described by Weber's law. However, Weber's law has not yet been used to predict how plants respond to stimuli generated from their symbiotic partners. Here we develop a model for quantitatively predicting the ratios of carbon (C) allocation to symbionts that provide nutrients to their plant host. Consistent with Weber's law, our model demonstrates that the optimal ratio of resources allocated to a less beneficial relative to a more beneficial symbiont scale to the ratio of the growth benefits of the two strains. As C allocation to symbionts increases, the ratio of C allocation to two strains approaches the square root of the ratio of symbiotic growth benefits (e.g., a worse symbiont providing one-fourth the benefits gets $\sqrt{1/4} = 1/2$ the C of a better symbiont). We document a compelling correspondence between our square root model prediction and a meta-analysis of experimental literature on C allocation. This type of preferential allocation can promote coexistence between more beneficial and less beneficial symbionts, offering a potential mechanism behind the high diversity of microbial symbionts observed in nature.

Keywords: coexistence, mycorrhiza, mutualism, overyielding, partner choice, Weber's law.

Introduction

All living things struggle to make sense of their environments—particularly those stimuli that distinguish friend from foe and feast from famine. These stimuli, which include sights, sounds, and chemosensory information from the environment, inform how organisms make life-and-death choices, whether they initiate in the brain of a gazelle avoiding a predator or within a single-celled paramecium swimming toward a patch of light. Formally linking choice with stimuli is essential for predicting how organisms respond to changing environments and how these responses cascade across ecological networks. In this article, we develop novel theory that links how plants choose to allocate resources to different symbiotic partners on the basis of their relative growth-promoting abilities. By availing ourselves of simplifying assumptions, we are able to directly compare model predictions with published experimental data. In so doing, we discover that plant resource allocation to symbionts can be described by the same psychophysical theories for choice originally developed for human subjects (fig. 1).

Research over the past century has emphasized a common psychophysical rule—dubbed Weber's law—that governs choices on the basis of the relative magnitude of two stimuli (Fechner 1860). Weber's law states that an organism's response to a stimulus is proportional to the ratio of its magnitude relative to a neutral background (e.g., the responding jolt of surprise after a stimulating cymbal crash against the background of a quiet library reading room). The scaling of response to stimulus ratios, rather than absolute differences, explains why the same subjects who struggle to tell whether a headlight is on during the daytime can perceive a dim light in the dark (because the intensity of a headlight relative to daylight is much less than that of a dim light relative to the dark). It also explains why humans struggle to perceive differences in lengths and quantities as the ratio of magnitudes approaches 1 (fig. 1*a*–1*d*).

Weber's law has proven to be a remarkably versatile rule, capturing commonality among broad taxa and contexts. The neutral background can be substituted for any sensible reference point, such that Weber's law has been used to predict how often a bird will pick a larger pile of peanuts versus a smaller one (Kelly 2016) or how much a bat will feed from a flower full of sugary nectar versus a flower that is less sweet (Nachev et al. 2013). Because the challenges of responding sensibly to an environment are universal and physiological in nature, the same underlying mechanisms also occur in single-celled organisms (Mori and Koaze 2013) and among superorganisms like slime molds and beehives (Reina et al. 2018). However, to date Weber's law has not been used to

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[*] Corresponding author; email: bsteidi2@gmail.com.

ORCIDs: Steidinger, https://orcid.org/0000-0003-1001-7642; Peay, https://orcid.org/0000-0002-7998-7412.

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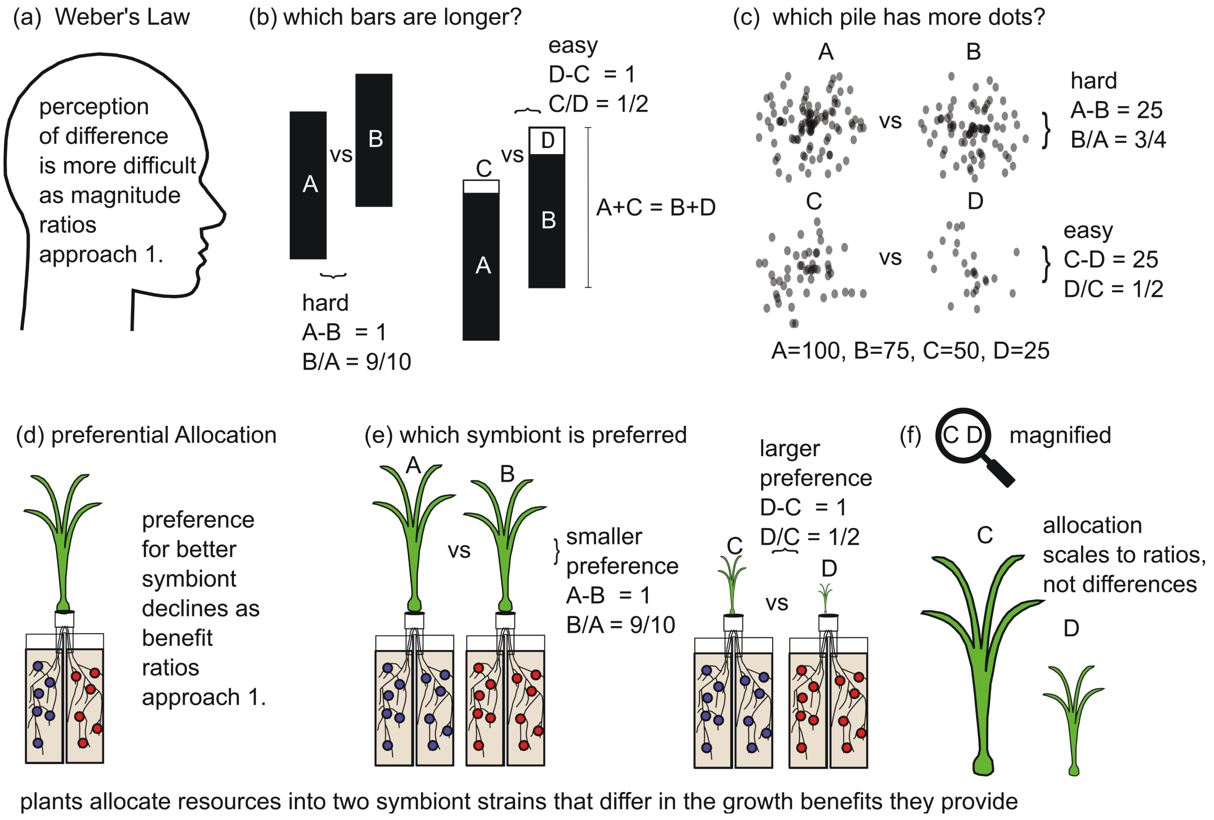


Figure 1: Weber's law as illustrated by limits on human perception (*a–c*) and by the determinant of plant preference for the better of two symbionts (*d–f*). In both cases, differences of equal magnitude are more important when the ratios of those magnitudes deviate farther from 1. For humans, "more important" means easier to perceive. For plants, it forms the basis for fitness-relevant decisions about how to allocate resources to symbionts.

predict how plants make choices about how to allocate resources to their symbiotic partners. Here we argue that the exclusion of Weber's law from the study of plant allocation is arbitrary and has to date fractured synthesis in the study of choice.

Plants have important choices to make, particularly when it comes to divvying up available resources in a way that maximizes their performance. Most plant species rely on microbial root symbionts to perform essential functions, from acquiring water and growth-limiting nutrients to defending against pests and disease (Hoeksema et al. 2010; Smith and Read 2010; Brundrett and Tedersoo 2018; Steidinger et al. 2019). Single plant host species can interact with hundreds of species of microbial symbionts both locally and across their ranges (Bahram et al. 2011; Talbot et al. 2014), with microbes differing in the extent to which they provide services that increase plant performance (Koziol and Bever 2016). Plants that fail to sense and respond to this variability in symbiont quality face a potential fitness shortfall—a lower return of nutrients required to grow and reproduce, leading to failure in the struggle for existence.

It is clear from experiments that plants do respond to variability in symbiont quality. Thus, plants associating with different strains of mycorrhizal fungi preferentially allocate carbon to the most beneficial strains (Bever et al. 2009; Kiers et al. 2011; Zheng et al. 2015; Ji and Bever 2016). Likewise, plants preferentially allocate resources to symbiotic bacteria that are able to fix atmospheric N_2 versus bacteria that are unable to do so (Kiers et al. 2003, 2006). However, it remains unclear whether the magnitude of preferential allocation follows the same general pattern as that predicted by Weber's law in other systems (fig. 1), with preference tracking ratios in symbiont quality rather than absolute differences. Furthermore, it is currently not possible to quantitatively compare experimental demonstrations of preferential allocation with model predictions.

Comparing experimental studies of preferential allocation with model predictions requires tailoring existing generalized models with simplifying assumptions. Biological market theory, which is one such generalized model, qualitatively predicts optimal allocation based on the verbal analogy between symbionts exchanging commodities (C exchanged for nutrients) and different classes of human traders exchanging goods (Noë and Hammerstein 1994). Mathematical formalizations of these models explain how plants can maximize their return on investment by seeking the highest possible marginal rates of return offered by different symbiont strains, either via plant-directed choice of C investment (Kummel and Salant 2006; Cowden and Peterson 2009) or collective plant/symbiont bargaining (Akçay and Simms 2011). However, the generality of these models is a double-edged sword, as they can be initiated with a wide range of different assumptions and parameter values (e.g., Kummel and Salant 2006). This flexibility allows market theory to simulate virtually as many outcomes in biological markets as are realized in human ones, leaving it unclear what specific predictions should apply in the experimental settings where preferential allocation is actually studied.

At present, one market theory model clearly predicts the ratio of C allocation from the ratio of benefits provided by different symbiont strains (specifically, arbuscular mycorrhizal fungi, which trade phosphorus for C; Wyatt et al. 2014). The model predicts that plants should follow a linear proportional allocation rule, such that if symbiont B provides 50% as much nutrients as symbiont A, it should get 50% as much C. Such a prediction conforms to an intuitive sense of fairness: linear proportional allocation results in pay equity (symbionts providing equal P get equal C) and avoids overcompensating partial symbiotic contributions (all symbionts face the same marginal return of C for P). Moreover, linear proportional allocation re-creates the predictions of Weber's law, such that preferential C allocation tracks ratios rather than absolute differences in symbiotic benefits. However, Wyatt et al. (2014) do not demonstrate that linear proportional allocation is evolutionarily stable among all possible allocation strategies. Thus, it remains unclear whether a host with an alternative allocation strategy could invade and displace plants using linear proportional allocation.

The success or failure of linear proportional allocation is not just a matter of accurately predicting C allocation—it also has implications for the coexistence of symbionts. Preferential allocation of host resources to beneficial symbiont strains has the potential to exclude nonbeneficial or less beneficial strains. For example, in game-theoretical models where symbionts can abstain from symbiotic services, only nonlinear, saturating, and logistic (or step function) models of plant allocation with symbiotic services lead to coexistence (Archetti and Scheuring 2011; Steidinger and Bever 2016; Jandér and Steidinger 2017). Steidinger and Bever (2016) found that coexistence is contingent on the relative amount of resources a host allocates when symbiotic services are halved. If plants respond by reducing allocation by less than 50%, then models predict that beneficial and less beneficial symbiotic strains can coexist. By contrast, if plant allocation declines by 50% or more, then either beneficial or nonbeneficial strains dominate, with no coexistence (Steidinger and Bever 2016). A formal model of optimal allocation can answer how plants should respond when symbiotic services are halved, bridging optimal resource use and symbiotic population biology.

Here we develop a model based on the reciprocal exchange of resources between a plant and its symbiotic partners (e.g., carbon for phosphorus or nitrogen). While solving for optimal allocation ratios, we reveal that most model terms can be ignored when plant resources are superabundant and the growth benefits from multiple symbionts are equal to the average growth offered by each symbiont. To justify one of our assumptions, we conducted a meta-analysis of whether growth benefits of multiple symbionts are equal to the average offered by each single symbiont (a key model assumption). Finally, we compared our model predictions with published experimental data on resource allocation from plant-mycorrhizal and plant-rhizobia symbioses.

Methods

Model

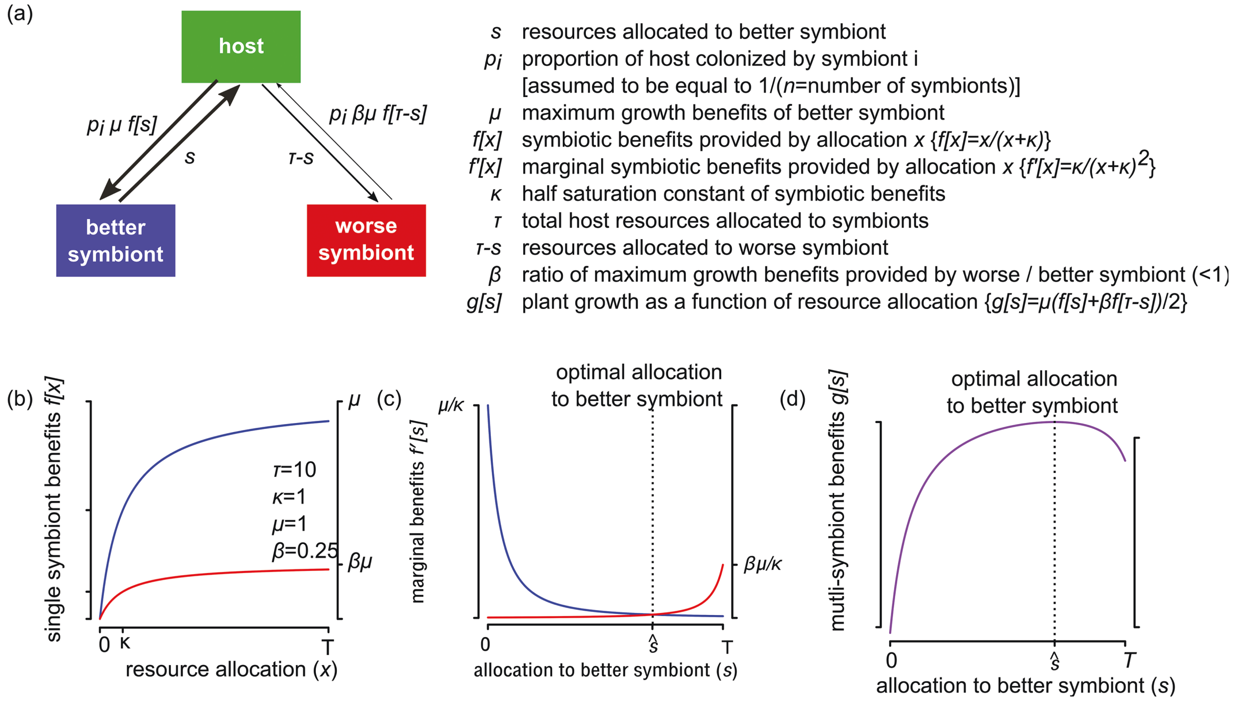
We built a simple model of optimal allocation where plant growth is maximized. This model is a specific case of the more general biological market framework used by Kummel and Salant (2006), and it uses assumptions identical to those of the Wyatt et al. (2014) model for preferential allocation (although it differs from the latter in solving for an evolutionarily stable strategy of allocation among all possible strategy sets). Like these previous models, ours assumes that plants accurately perceive the benefits of their symbionts; thus, it describes how plants would optimally allocate resources under perfect information.

Let total plant growth equal g, such that

$$g = \bar{g} = \sum_{i=i}^{n} p_i \mu_i f[s_i], \tag{1}$$

where n is the total number of symbionts, p_i is the proportion of roots occupied, μ_i is the maximum benefits provided by the ith symbiont, and $f[s_i]$ describes the resource-dependent (s-dependent) growth benefits of the ith symbiont (fig. 2 provides a glossary of all model terms). Thus, equation (1) states that growth with multiple symbionts is equal to the sum of each of the constituent symbiotic growth benefits weighted by their relative abundances.

At present we assume that a host associates with equal fractions of all of its symbionts, such that $p_i = 1/n$. This is certainly initially the case in experiments where different symbiont strains are introduced to the plant host in equal amounts (Bever et al. 2009; Kiers et al. 2011; Zheng et al.



s	resources allocated to better symbiont
p_i	proportion of host colonized by symbiont i [assumed to be equal to 1/(n=number of symbionts)]
μ	maximum growth benefits of better symbiont
$f[x]$	symbiotic benefits provided by allocation x $\{f[x]=x/(x+\kappa)\}$
$f'[x]$	marginal symbiotic benefits provided by allocation x $\{f'[x]=\kappa/(x+\kappa)^2\}$
κ	half saturation constant of symbiotic benefits
τ	total host resources allocated to symbionts
τ-s	resources allocated to worse symbiont
β	ratio of maximum growth benefits provided by worse / better symbiont (<1)
$g[s]$	plant growth as a function of resource allocation $\{g[s]=\mu(f[s]+\beta f[\tau\text{-}s])/2\}$

Figure 2: *a*, Conceptual model of preferential allocation to a better versus a worse symbiont (blue and red, respectively), where growth benefits are additive. Model terms and functions are defined on the right. *b*, Monod model for the benefits from the better and worse symbiont as a function of resource allocation (x) from zero to the total plant resources available (τ). *c*, First derivative of the Monod curves from *b* drawn antiparallel such that the curves intersect the optimal allocation to the better symbiont, $\hat{s}$. *d*, Growth benefits to the plant host as a function of allocation to the better symbiont, s, which peaks at the value $\hat{s}$ from *c*.

2015; Ji and Bever 2016). It also is somewhat more appropriate to split-root experiments, where symbionts introduced to half of the root system cannot spread to the other half. However, the assumption that $p_i = 1/n$ ignores the potential for host allocation to alter the proportions of the symbiont strains in mixture (e.g., Werner et al. 2018). Alternatively, preferential allocation could promote the spread of the most beneficial symbiotic strains in the root system, such that they would dominate the plant's growth response to the whole symbiont community. These possibilities are interesting but would complicate the search for a clear model prediction by requiring some representation of C allocation × symbiont population feedbacks.

Taken together, the assumption of additive growth benefits (eq. [1]) and equal proportions of each symbiont strain imply that plant growth with multiple symbiont strains is the linear average of growth with each individual strain. An alternative model could include synergy among symbionts, such that the benefits are more than expected by their additive contributions to plant performance. However, previous studies have shown that synergy is relatively rare even in cases where symbiont strains perform complementary functions (Larimer et al. 2010; Van Nuland and Peay 2020). Furthermore, growth benefits from arbuscular mycorrhizal fungi are most often bound within a range set by the least- to most-growth-promoting symbiont in isolation (Hoeksema et al. 2010). Later we will test this assumption by quantifying differences between actual growth and expectations from equation (1) experimental literature (fig. 3).

We describe the benefits a plant derives from its symbionts as a function of resource allocation using the Monod model, such that

$$\mu f[s] = \mu\left\{\frac{s}{s+\kappa}\right\}, \tag{2}$$

where μ is the maximum growth rate and κ is the half-saturation constant (fig. 2*a*). The derivative of this function with respect to s gives the marginal growth benefit, such that

$$\mu f'[s] = \kappa\mu\left\{\frac{1}{(s+\kappa)^2}\right\}. \tag{3}$$

The Monod model has the following properties: (1) growth is always a positive function of resource allocation (e.g., carbohydrates sent to roots via phloem) and (2) the marginal growth rate is highest at low s and then diminishes in a nonlinear, concave-down function (fig. 2*b*).

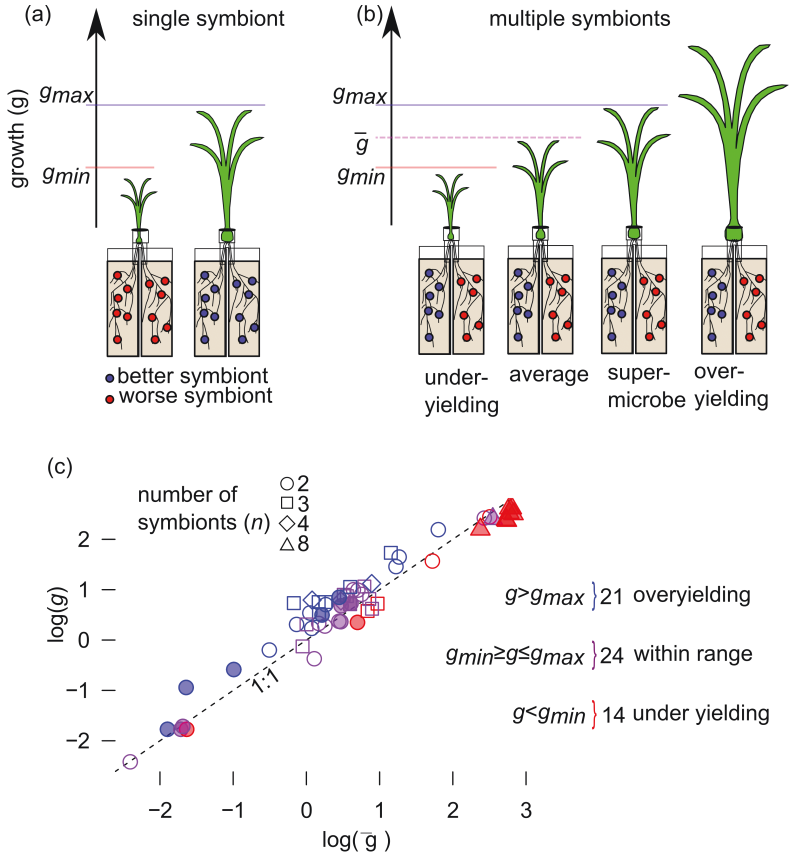


Figure 3: Graphical representation of the growth benefits of a plant host with either a single symbiont (*a*) or multiple symbionts (*b*), including a better and worse growth-promoting strain. For *a* and *b*, growth is visualized as plant height against the *y*-axis. *c*, Meta-analysis of published growth experiments, with $x = \log$(growth averaged over single symbionts) plotted against $y = \log$(actual plant growth with multiple symbionts). Separate studies used either total plant mass (open points) or aboveground mass only (filled points). The dashed line gives the 1∶1 expectation where $g = \bar{g}$.

The justification for using the Monod equation is as follows. First, the symbioses described here are based on an exchange of C for nutrients. Growth as a function of the nutrients is frequently modeled using the Monod equation (Grover 2012), which captures the diminishing marginal returns nutrients provide when they are abundant relative to plant needs. For mycorrhizal fungi, the Monod model correctly predicts that the symbiotic benefits are maximized when the plant's growth is strongly nutrient limited (Van Nuland and Peay 2020). Additionally, the Monod model captures the diminishing benefits of foraging for a finite resource. For example, mycorrhizal fungi use plant-acquired C to build nutrient-absorptive hypha, which forage within a finite volume of soil. When resources within this volume are depleted, there should be a diminishing marginal benefit of allocating more resources to mycorrhizal fungi. The Monod model also captures the substrate-dependent rates of enzymatic reactions (where the same equation is dubbed the Michelson-Menten equation). For a N-fixing rhizobium, plant resource allocation fuels the activity of an enzyme—nitrogenase—which fuels the reaction that coverts N_2 gas into a plant-usable form.

We consider a case where a plant has a choice between two symbiont strains. This is explicitly the condition for a plant whose roots have been split into two compartments, each inoculated with a different mycorrhizal strain (e.g., Bever et al. 2009). As we shall see when we calculate optimal allocation ratios, the simplification when $n = 2$ can be used without any loss of generality—it allows us to calculate optimal allocation ratios to any pair of symbionts even when the plant associates with more than two symbionts. In a two-symbiont model (where $p_1 = p_2 = 1/2$), equation (1) is written as

$$\begin{aligned} g_{n=2} &= \left(\frac{\mu}{2}\right)\{f[s] + \beta f[\tau - s]\} \\ &= \frac{\mu}{2}\left\{\frac{s}{s+\kappa} + \frac{\beta(\tau - s)}{\tau - s + \kappa}\right\}, \end{aligned} \tag{4}$$

where τ is the total amount of resources allocated to all symbionts,

$$\tau = \sum_{i=1}^{n} s_i, \tag{5}$$

and β describes the relative growth benefits of the less-growth-promoting fungi ($\beta < 1$).

Optimal Allocation Ratios

Using the pairwise plant benefit equation (4), we can solve for the ratio of resource allocation to the two strains that is optimal for the plant, meaning the allocation ratio that results in maximum plant growth. To do this, we take the derivative of the plant growth function $g[s]$ (given by eq. [4]),

$$\bar{g}'[s]|_{n=2} = \frac{\kappa\mu}{2}\left\{\frac{1}{(\kappa + s)^2} + \frac{\beta}{(\kappa - s + \tau)^2}\right\}, \tag{6}$$

and set it equal to zero (such that the difference inside the brackets is equal to zero). Rearranging this equation, we can then solve for parameters τ and/or s, describing the allocation into each strain. This occurs when the allocation in the more-growth-promoting symbiont, s, equals

$$\hat{s} = \frac{\tau + \kappa(1 + \beta) - \sqrt{\beta(2\kappa + \tau)^2}}{1 + \beta}. \tag{7}$$

Let the ratio of allocation to the lesser versus the better growth-promoting symbiont be equal to α, such that

$$\alpha = \frac{\tau - \hat{s}}{\hat{s}} = \frac{-\kappa - \beta(\kappa + \tau) + \sqrt{\beta(2\kappa + \tau)^2}}{\kappa - \beta\kappa + \tau - \sqrt{\beta(2\kappa + \tau)^2}}. \tag{8}$$

For example, if a total of $\tau = 12$ resource units are allocated and $s = 8$ go to the better symbiont, then the ratio would be $\alpha = (12 - 8)/8 = 1/2$.

There is an interesting possibility hidden in equation (8). Whenever $\tau < \kappa(1 - \sqrt{\beta})/\sqrt{\beta}$, optimal allocation ratios are negative. For the worse symbiont, this implies that the normal direction of resource exchange is inverted, such that the arrows on the left-hand side of figure 2*a* change in direction. In the plant-mycorrhizal mutualism, this could occur if the plant acquires C from one of its fungal symbionts—a phenomenon that has been observed both in mycoheterotrophic interactions and across common mycorrhizal networks. We will address this potential further in the discussion section. For the present, we will consider cases where the total amount of resources (τ) is much greater than κ.

When the total amount of resources available is much greater than the half-saturation constant of symbiotic benefits ($\tau \gg \kappa$), the expression for α (eq. [8]) can be simplified to a single term. This becomes clear when we assess the limit for α when τ approaches infinity:

$$\lim_{\tau\longrightarrow\infty}\alpha = \sqrt{\beta}. \tag{9}$$

Equation (9) states that the optimal ratio of resource allocation to the lesser versus the better symbiont is equal to the square root of the ratio of growth benefits derived from these two strains. For example, if the lesser symbiont provides one-fourth the benefit of the better symbiont, it will receive $\sqrt{1/4} = 1/2$ the amount of resources.

Whereas $\alpha = \sqrt{\beta}$ when τ is infinite (eq. [9]), clearly this is biologically unreasonable. Hosts have finite resources to allocate to their symbionts. The longer expression for α from equation (8) is more realistic, as it avoids the infinite resources assumption. However, equation (8) also requires specifying the parameters τ and κ, which are often unmeasured. Here we consider how similar the predictions from the simplified $\alpha = \sqrt{\beta}$ and the more realistic equation (8) are. Both equations (8) and (9) predict strict pay equity among symbionts: when $\beta = 1$ (symbionts do equal work), $\alpha = 1$ (symbionts get equal pay). However, when symbionts do not do equal work ($\beta < 1$), the two equations differ in their predictions, such that $\alpha < \sqrt{\beta}$ so long as τ is finite. However, in practice τ need not be infinite for $\alpha = \sqrt{\beta}$ to approximate allocation ratios. We find that $\alpha = \sqrt{\beta}$ is a good approximation for α from equation (8) so long as $\tau \geq 19\kappa$. For example, when $\tau = 19\kappa$ and $\beta = 0.25$, $\alpha = 0.46$ (compared with $\alpha = \sqrt{\beta} = 0.50$). Thus, when we generalize $\alpha = \sqrt{\beta}$ when $\tau \gg \kappa$, we mean that τ must be approximately 20 times the value of κ (fig. 4*a*).

A virtue of this approach is the ability to solve for all pairwise allocation ratios. Under the simplifying assumptions that led to equation (9), the square root relationship holds for any two symbionts in a multiple inoculum. The total allocation can be expressed as

$$\tau = s_1(1 + \alpha_{1,2} + \alpha_{1,3} + +\alpha_{1,4} + \cdots + \alpha_{1,n}),$$

where s_1 goes to the single best symbiont and $\alpha_{1,i}$ is equal to s_i/s_1. Thus, the allocation to each symbiont can be solved by calculating values of α for all pairwise comparisons with a single reference strain (in this case, we specified this as the strain that provides the most benefit in single inoculum). For example, let a hypothetical plant associate with three symbionts: A, B, and C (where A is the best, B is intermediate, and C is the worst growth-promoting strain). Let symbiont B provide one-fourth and symbiont C provide one-sixteenth the benefit of symbiont A. The model would then predict the following allocation ratios: B gets one-half as much resources as A, and C gets one-half as much resources as B and one-fourth as much resources as A.

Meta-analysis

We conducted two related meta-analyses in order to (i) validate a key simplifying assumption in the model and (ii) test whether empirical data fit our model predictions. First, we evaluated the model assumption that the growth benefits with multiple symbiont strains are equal to the linear average of growth with each of the constituent single symbionts. Confirming this assumption would allow us to reasonably ignore interactions among symbionts—for example, one symbiont strain providing a more or less favorable rate of trade to its plant host in the presence of another symbiont strain (Akçay and Simms 2011; Argüello et al. 2016). Crucially, the assumption of additive growth benefits enabled us to prune higher-order interactions from our model (fig. 2*a*), enabling the simplified solution of $\alpha = \sqrt{\beta}$ (eq. [9]).

To test whether growth benefits with multiple symbiont strains are equal to the linear average of growth with each of the constituent single symbionts, we evaluated articles from the MycoDataBase, which was published to evaluate the context dependency of plant response to inoculation with mycorrhizal fungi (Hoeksema et al. 2010). We subset a supplemental file of all studies included in MycoDataBase that included only those studies that fit the following two criteria: (1) they quantified the growth benefit to the plant of associating with multiple symbionts in pure culture and (2) they quantified the growth benefit to the plant when inoculated with multiple strains. Because only a small number of studies in MycoDataBase matched our criteria for meta-analysis, we expanded our search using Google Scholar and the terms "plant growth" and "multiple inoculum." We recorded for each study evaluated why it was or was not included in the meta-analysis; a frequent reason for non-inclusion was that multiple-strain inoculation treatments included some strains that were not provided to the plant as a single-inoculum treatment.

For the first meta-analysis, we compared the actual growth (g) with multiple symbionts strains to the expectation using simple linear averaging ($\bar{g}$). The goodness of fit was evaluated by manually computing the coefficient of determination (c.o.d.) using the following equation: $\text{c.o.d.} = 1 - \text{SS}_{\text{res}}/\text{SS}_{\text{tot}}$, where SS_{tot} is the total sum of squares and SS_{res} is the residual sum of squares using $\bar{g}$ as the model prediction. To assess the percentage error of the model (%error), we calculated the mean of the residual growth over the predicted growth using the following equation: $\%\text{error} = 100 \times (g - \bar{g})/\bar{g}$. Although the meta-analysis results were plotted on a log scale, both c.o.d. and %error were calculated on untransformed data.

For the second meta-analysis, we evaluated studies that measured resource allocation to different strains that colonized a single root system. For these studies we quantified both the value of β (the ratio of growth benefits) and the value of α (the ratio of allocation) as follows: (1) $\beta = \mu_B/\mu_A$, or the ratio of plant biomass when inoculated with the lesser versus the greater growth-promoting symbiont strain in isolation, and (2) $\alpha = C_B/C_A$, where C_B and C_A are the carbon allocation to the lesser versus the greater growth-promoting symbiont strain.

Because MycoDataBase does not include resource allocation to symbionts, we searched for studies that fit these criteria using Google Scholar and the following terms: "carbon allocation," "partner choice," "split root," and "symbiosis." Studies included in our meta-analysis had to fit the following criteria: (1) they quantified the growth benefit to the plant of associating with each of the multiple symbionts in pure culture (same as criterion 1 from the first analysis) and (2) they presented data on resource allocation to symbionts in a way that made it possible to compute the ratio of allocation to the different strains.

We made a single exception for these two criteria, including in our meta-analysis one study from the legume/N-fixing rhizobium mutualism that quantified the benefit ratios, β, in terms of the potential percentage N-fixing capacity (Kiers et al. 2006). The reduction in potential N fixation was accomplished by substituting a percentage of N_2 gas with ArO_2. In this case, rather than measure C allocation directly, the authors measured the fitness of rhizobia as the number of bacteria that emerged from leguminous nodules. Although this study uses a different methodology than the others in our meta-analysis, it was able to stratify its treatments along a gradient of symbiotic benefit ratios β in a manner ideal for comparison with our model. In the meta-analysis results, this study is plotted using a different aesthetic (triangles rather than circles; fig. 4*b*).

For both meta-analyses, we either transcribed data from tables directly into a .csv file or used WebPlotDigitizer to estimate mean or median responses from published figures (point, bar, or box-and-whisker plots). For some studies plant biomass was measured in roots, stems, and leaves separately, whereas in others only stem or overall biomass was recorded. We used either the whole biomass or only stem biomass, depending on data availability. The data underlying the meta-analysis results (figs. 3, 4) have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.vt4b8gts7; Steidinger 2021).

Results of Growth Meta-analysis

We extracted data on plant growth with multiple strains of arbuscular mycorrhizal fungi from 58 experiments, representing 17 plant species from 13 genera and seven

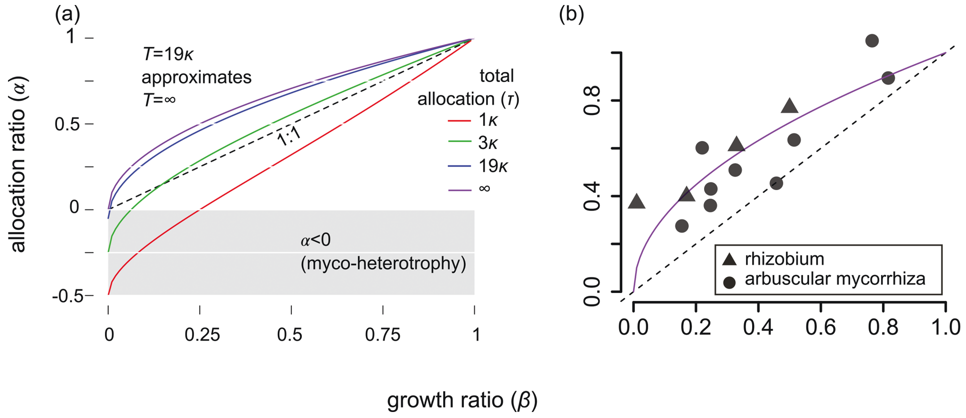


Figure 4: *a*, Relationship between the ratio of growth benefits, β, and the ratio of resource allocation, α, as function of total resource allocation (T). When $T \geq 19\kappa$, α is approximated by $\sqrt{\beta}$. When τ is low relative to κ, it is possible to have negative allocation to the worse symbiont, a condition described as mycoheterotrophy when carbon is withdrawn from mycorrhizal fungi. *b*, Meta-analysis of the experimental literature on the relationship between α and β. The square root line is shown in purple, and a one-to-one line is dashed and black. The square root line approximates the actual allocation patterns, with a coefficient of determination of 0.66.

families (including Poaceae, Anacardiaceae, Fabaceae, and Solanceae) as well as 28 different fungal strains (including the genera *Glomus*, *Gigaspora*, and *Scutelospora*; Steidinger 2021). Of these 58 total data points, 21 studies reported only stem mass. Consistent with our meta-analysis criteria, for each of the 58 growth experiments with multiple fungal strains, investigators also reported plant growth for each of the constituent single strains. This allowed us to compare actual plant growth with multiple strains to the mean value from the single-strain experiments ($\bar{g}$).

We found that 91% of the variability in plant growth with multiple-strain inoculum was explained by our model's predicted 1∶1 relationship with mean plant growth with each of the constituent single strains ($\bar{g}$). Visual inspection of residuals suggested that they were approximately normally distributed, with a median %error of 16%. Approximately equal proportions of plants grew above the single best symbiont ($g > g_{\max}$), within the range of single symbionts ($g_{\max} \geq g \geq g_{\min}$), and below the growth of the single worst symbiont ($g < g_{\min}$; fig. 3*c*).

Results of Square Root Law Meta-analysis

We were able to extract values of β and α for a total of 14 different plant-symbiont combinations. We plotted the results against both a 1∶1 line, which is the model prediction for linear proportional allocation, and our own model expectation that $\alpha = \sqrt{\beta}$ (fig. 4*b*). In a single case we omitted an outlier where the plant allocated more C to the less beneficial symbiont (which occurred under a high phosphorus fertilizer treatment, where overall C allocation was low and small differences in allocation between strains lead to highly skewed allocation ratios; Ji and Bever 2016).

There is a clear pattern of increasing ratios of allocation to the lesser symbiont as the ratio of growth benefits approaches 1. Moreover, every single data point occurs above the 1∶1 line for the ratio of benefits to allocation. The square root relationship is a good approximation, explaining 66% of the variability among 13 plant-symbiotic treatments using a manually computed coefficient of determination (fig. 4*b*).

Discussion

Plants in multiple mutualisms preferentially allocate resources to more beneficial symbionts relative to less beneficial ones. We used biological market theory to quantitatively predict these allocation patterns. We found that when hosts allocate excess by-product resources to symbionts, the optimal ratio of allocation to a worse versus a better growth-promoting symbiont (α) approaches the square root of the ratio of growth benefits of those symbionts (β), or $\alpha = \sqrt{\beta}$. In other words, a worse symbiont providing only $\beta = 1/4$ as much services should get $\alpha = \sqrt{1/4} = 1/2$ as much resources as a better symbiont. Our model links plant preferential allocation with Weber's general psychophysical model of choice and makes quantified predictions we compared with published data. These model-data comparisons provide strong support for our model and its accompanying assumptions.

Optimal Allocation and Weber's Law

The square root relationship between the ratios of symbiotic costs and benefits is an optimal physiological analog to Weber's law. This represents a new frontier for Weber's law, which originally described the insensitivity of test subjects to perceive differences in sights, sounds, and quantities that can be detected by a finely tuned instrument (Fechner 1860; fig. 1*a*, 1*b*). More recently, Weber's law has been invoked to describe (nonhuman) animal insensitivity to measurable differences in quantity (Gómez-Laplaza and Gerlai 2011; Nachev et al. 2013; Kelly 2016). Our study highlights how Weber's law could additionally describe how plants, like humans, slime molds, and single cells, do not behave like finely tuned instruments.

Thus, for plants inoculated with single symbiont strains, a finely tuned balance could easily measure the three order of magnitude differences in growth from the following pairwise symbiont contrasts: 1 versus 4, 10 versus 40, and 100 versus 400 grams. By contrast, our model suggests that plants inoculated with both symbiont strains from each of these contrasts should behave the same, allocating twice as much C to the better symbiont. This solution does not emerge by invoking perceptional limitations for the plants; instead, the plants make fitness-relevant decisions by accurately gauging the marginal utility of their symbionts. Plants obey Weber's law because there is no benefit to breaking it.

Likewise, other studies have focused on how perceptional limitations in animals may match the fitness-relevant scales where those animals make decisions. For example, Weber's law correctly predicts that angelfish prefer to join larger shoals over smaller ones but are relatively insensitive to differences in the shoal size among groups that provide equivalent protection against predators (Gómez-Laplaza and Gerlai 2011). Nectar-feeding bats discriminate among the sugar content of different flowers according to Weber's law (or a "near-miss" variant), which is consistent with diminishing metabolic returns of increased sugar consumption (Nachev et al. 2013). In effect, plants, fish, and bats do not fail to sense difference in quantity—they successfully sense equivalence of utility.

Optimal Allocation Promotes Symbiont Coexistence

Given that plants can preferentially allocate resources to the most beneficial arbuscular mycorrhizal fungi and N-fixing rhizobia, it is unclear whether variability in symbiont quality should persist in these mutualisms. In this light, experimental demonstrations that plants choose the best symbionts appear to clash with data showing that those same plants can interact with hundreds of species of microbial symbionts both locally and across their ranges (Bahram et al. 2011; Talbot et al. 2014), with microbes differing in the extent to which they increase plant growth (Koziol and Bever 2016).

Specifying the functional form of preferential allocation can reconcile the diversity of symbioses with the selective pressures of preferential allocation. Theoretical models demonstrate that only saturating models of preferential allocation can promote the coexistence of symbionts that differ in quality (Archetti and Scheuring 2011; Steidinger and Bever 2016; Jandér and Steidinger 2017). For example, Steidinger and Bever (2016) demonstrated that coexistence is contingent on relative host allocation (α) when symbiotic benefits are halved, or $\beta = 1/2$. Specifically, the model demonstrates that if $\alpha|(\beta = 1/2) > 1/2$, then coexistence of beneficial and less beneficial symbionts is possible; by contrast, if $\alpha|(\beta = 1/2) = 1/2$—a model referred to as linear proportional allocation (Wyatt et al. 2014)—coexistence is impossible. In our model, we can plug in $\beta = 1/2$ and solve the square root, $\alpha|(\beta = 1/2) = \sqrt{1/2} = .707$, which is greater than 0.5. Thus, optimal resource allocation strategies can promote symbiont coexistence.

Does Total Resource Allocation Greatly Exceed the Half-Saturation Constant?

The square root relationship between symbiont benefit and host allocation ratios is built on simplifying assumptions. Here we evaluate these assumptions individually, justifying them when possible and describing some of the consequences for situations in which they are violated.

We begin with the assumption that hosts allocate resources well in excess of the half-saturation constant of symbiotic benefits ($\tau \gg \kappa$). This assumption allowed us to ignore differences in total allocation when comparing plant growth with different symbiont strains. However, the assumption strains credulity given that arbuscular mycorrhizal fungi are estimated to consume from 2% to 20% (Douds et al. 1988) and ectomycorrhizal fungi from 7% to 30% of the plant's total C budget (reviewed in Leake et al. 2004). Surely a plant would not part with as much as a third of its C for symbiotic rewards if the majority of these rewards could be purchased for far less. Nevertheless, both empirical work and theoretical work show that plants in high-light, low-nutrient conditions can be so flush with C and starved for nutrients that they can afford to allocate C to their symbiotic partners in the excess required by our model.

Support for the assumption that $\tau \gg \kappa$ follows from the observation that plants obtain benefits from their mycorrhizae not by paying less C for nutrients but by saturating their symbionts with relatively more C in order to obtain nutrients from otherwise unavailable sources (e.g., inside a greater volume of soil or from different chemical pools). Thus, although ecto- and arbuscular mycorrhizal tree seedlings grow faster and obtain more nutrients than nonmycorrhizal controls, they can actually pay a higher C cost per unit nitrogen and phosphorus (Koide and Elliott 1989; Corrêa et al. 2012). Such inefficiency of nutrient acquisition is consistent with plants chasing small marginal returns on nutrition with saturating C allocation ($\tau \gg \kappa$). In fact, biological market theory explicitly predicts such saturating C allocation when nutrient gains from mycorrhizal fungi enhance plant photosynthesis and overall C budgets, which more than compensate for their increased C cost (Tuomi et al. 2001). Crucially, this feedback loop functions only when photosynthetic nutrient use efficiency is high (e.g., under high light) and nutrients are in short supply (low soil P or N, depending on the symbiosis), which are the conditions associated with the greatest mycorrhizal growth benefits.

The observation that C may be inexpensive for the plant would place mycorrhizal mutualism in the company of other by-product mutualisms—defined under conditions where one host is unable (or ill adapted) to completely monopolize a single resource (Connor 1995; Leigh 2010). However, even host C present in superabundance should be invested wisely, just as trillionaires are ill advised to sink their entire fortunes into a single bad investment. For the plants in our model that are flush with excess C, the stakes of choosing how to allocate that C range from a fraction of the benefits offered by the single worst symbiont to the average offered by all symbionts. Given the marked differences in growth offered by different strains of mycorrhizal fungi (Koziol and Bever 2016) and symbiotic N-fixing bacteria, these stakes could make the difference of being among the fittest in the struggle for survival.

Negative Allocation Ratios Re-create Mycoheterotrophy and C Transfer in Hyphal Networks

For plants growing under low-light or high-nutrient conditions, C may cease to be a tradeable by-product and become a commodity as precious as the soil nutrients it can purchase. When total resource allocation reaches a critical point, $\tau < k(1-\sqrt{\beta})/\sqrt{\beta}$, the model appears to "break," predicting optimal allocation ratios that are negative, with hosts acquiring C from their symbionts (eq. [8]; fig. 4*a*). In fact, negative allocation ratios are common in nature—mycoheterotrophy and C transfer in common mycorrhizal networks.

Mycoheterotrophy occurs when plants acquire C from mycorrhizal fungi. A full 10% of plant species are facultatively mycoheterotrophic early in their life cycle, and some 160 plants remain obligately mycoheterotrophic throughout their lives (Leake and Cameron 2010). Our model predicts that when $\tau < k(1-\sqrt{\beta})/\sqrt{\beta}$, plants switch to a mycoheterotrophic game of robbing Peter to pay Paul, with the plant taking C from less beneficial mycorrhizal fungi and trading it for nutrients with more beneficial mycorrhizal fungi. Although this mechanism may not accurately describe obligate mycoheterotrophs, which can specialize to obtain both C and nutrients from a single mycorrhizal fungi (robbing Peter and paying no one; Bidartondo 2005), our model provides insight into the numerically more common facultative and/or partial mycoheterotrophs. The model requires only two criteria to be met, both of which can be supported by literature to date: (1) mycoheterotrophic plants associate with multiple mycorrhizal fungal strains (Hynson et al. 2009) and (2) simultaneous C influx and efflux takes place via a fungal-root interface (Cameron et al. 2008). Moreover, our model predicts that mycoheterotrophy is associated with the most C-limited plants (lowest τ relative to κ), which is consistent with the tendency of mycoheterotrophic plants to disperse via dust seeds (low C during early growth, as in orchids) and grow tissues without chlorophyll (no ability to photosynthesize). Likewise, the transfer of C from fungus to plant via common mycorrhizal networks—itself a form of mycoheterotrophy—has been observed to supplement shaded understory seedlings (low photosynthetic potential) with C fixed by canopy trees (Simard et al. 1997). In each case, our model correctly predicts an inversion of normal resource allocation during conditions that promote C limitation.

Are Symbiotic Half-Saturation Constants Really Equal?

We assumed that the Monod curves describing the symbiont benefits of strains as a function of host allocation have the same half-saturation constant, κ. Thus, symbiont strains in our model differ only in terms of the maximum benefits they can provide (μ; in the language of enzyme kinematics, enzymes can have different concentrations but must have the same substrate affinity). For example, let a plant associate with two symbionts, A and B, where symbiont A is more beneficial to the plant in single culture ($\mu_A > \mu_B$). If we repeat our analyses (eqq. [1]–[9]) but allow the symbionts to have different κ values (κ_A and κ_B, respectively), then equation (9) describing allocation ratios as a function of benefit ratios becomes the more general

$$\lim_{\tau\to\infty}\alpha = \sqrt{\left(\frac{\kappa_B}{\kappa_A}\right)\beta}. \tag{10}$$

Crucially, adding $\sqrt{(\kappa_B/\kappa_A)}$ as a factor in our calculation of optimal allocation ratios unleashes interesting biological possibilities that could throw our simple result into confusion.

Allowing symbionts to have different κ values while assuming that plant resources are superabundant ($\tau \gg \max(\kappa_A, \kappa_B)$) creates conditions where it pays for symbionts to be withholding. To illustrate, let symbiont B provide only half the benefit of symbiont A in single culture, such that $\beta = 1/2$. Using equation (10) to calculate allocation ratios, it can be shown that the plant should allocate relatively more resources to the less beneficial symbiont B so long as $\kappa_B > 2\kappa_A$. The higher the value of κ_B relative to κ_A, the more resources the model predicts should go to the less beneficial symbiont. Symbionts may be able to adjust their marginal rates of return to manipulate demand from their plant hosts. Consistent with this, experiments have found that arbuscular mycorrhizal fungi can hoard sudden "booms" in soil phosphorus availability (van't Padje et al. 2021*a*, 2021*b*), while theoretical models predict that ectomycorrhizal fungi withhold nitrogen reserves in order to keep their plant hosts dependent on them (Franklin et al. 2014). However, we chose to ignore this complexity, as it would have required us to parameterize κ values—a practical impossibility given available published data. As with the other assumptions, the value of these simplifications is that they yield testable predictions. The proof is in the model fitting.

Can We Ignore Symbiotic Interactions That Give Rise to Interference and Overyielding?

We assumed that symbiont strains do not interact with one another when they share a plant host. This assumption allowed us to calculate the ratios of symbiont growth benefits using published data from single-strain growth experiments (β values from fig. 4*b*). By contrast, if symbionts provide different growth benefits in single- versus multiple-strain inoculum (Vogelsang et al. 2006; Akçay and Simms 2011), then the β values we estimated from single-strain experiments would not match the corresponding allocation ratios from multiple-strain experiments (α). If this assumption is violated, then estimating β would require parsing the contributions of individual symbiont strains when they interact with the plant in a mixed inoculum—a practical difficulty that would undermine our model-data comparison.

We used a meta-analysis to test the assumption that there are no interactions among symbiont strains. In the absence of symbiont interactions, the expected plant growth with multiple strains should equal the weighted sum of plant growth with each individual strain. Published data strongly support this assumption, with 91% of the variability in plant growth with multiple symbiont strains explained by the weighted sum of plant growth over each strain. However, across all of the experiments we did observe cases of both over- and underyielding (growth above the best growth-promoting and below the worst growth-promoting symbiont strain). Thus, the full distribution of multiple symbiont interactions ranges from interference (underyielding) to complementarity (overyielding), with our assumed no interaction among strains emerging as the central tendency.

Does $\alpha = \sqrt{\beta}$?

The best justification for our model assumptions is that they yielded a simple, testable, high-performing model. We found that our $\alpha = \sqrt{\beta}$ model explains approximately 66% of the variability in symbiotic allocation ratios (fig. 4*b*).

A comparison of our model predictions (fig. 4*b*, filled points) and experimental work on quantitative sanctions in rhizobia (Kiers et al. 2006) is particularly noteworthy, as the ratio of symbiotic benefits to the ratio of symbiotic fitness follows the square root relationship with high fidelity. In a series of experiments, Kiers et al. (2006) measured rhizobia reproductive output (a measure of host allocation) as a function of the quantitative capacity of rhizobia to fix N_2 (manipulated by altering the concentration of N_2 gas). Genetically identical rhizobia in nodules fixing at 50% of their potential compared with plants grown under ambient N_2 concentrations had a reproductive output 77% as high (vs. 70.7% expected from a square root relationship), and those fixing at 33% potential had 61% reproductive output (vs. 57.4% expected); with 17% fixing potential, reproductive output was at 40% (vs. 41.2% expected). The experiment-model correspondence breaks down only when rhizobia were limited to 1% of their fixation potential, causing reproductive output to fall to 37% (vs. 10% expected).

Our model fit could be improved if we incorporated the biological basis for a positive y-intercept between benefit (x) and allocation (y) ratios. Plants may have to allocate some resources to symbionts before they can assess their marginal rates of return (Bever 2015; Christian and Bever 2018). Such a symbiotic "start-up" investment would be split equally among all symbionts and thus would increase the relative allocation to symbionts that provide little or no benefit ($\alpha \ll 1$). Whereas ours is currently a more parsimonious model for the maintenance of symbiosis diversity, future studies should focus on measuring allocation between symbionts at very low values of β. If a consistent signal of overallocation to relatively low-performing symbionts is observed, it may be necessary to build a more complex model that quantifies this start-up C investment.

Conclusion

We conclude that the same psychophysical law—Weber's law—that applies to human subjects, vertebrate animals, superorganisms, and single cells has its analog with plants foraging within their own root systems for the best symbiotic return on investment. Just as the reader might struggle to discriminate lengths and quantities (fig. 1), a plant may appear to struggle to discriminate among fungi or rhizobia whose differences in quality are obscured when quality ratios approach 1. Moreover, our model describes how optimal patterns of resource allocation evolve, which can reconcile partner choice in the face of variable partner quality and the observed hyperdiversity in plant-microbial symbioses. Finally, we built a model readily applicable to empirical tests, accurately predicting the relationship between the ratio of symbiotic costs as the square root of symbiotic benefits.

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Statement of Authorship

B.S.S. wrote the initial draft of the manuscript, derived the model, and conducted the data analysis. K.G.P. edited all manuscript drafts and provided key insights into how the model could be applied in real biological systems.

Data and Code Availability

All files required to replicate our meta-analyses, including R code, have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.vt4b8gts7; Steidinger 2021).

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