

PLANT ROOTS

THE HIDDEN HALF

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REVISED AND EXPANDED

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Root–Shoot Relations: Optimality in Acclimation and Adaptation or the “Emperor’s New Clothes”?

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I. INTRODUCTION

Differences in the relative sizes and/or function of root and shoot systems can arise due to differences in allocation of biomass, in morphology and chemistry of absorptive root and shoot tissues, and in the turnover rates of those tissues. For as long as the topic has been considered by plant biologists, a consistent theme has prevailed—that, given the relatively opposite roles of shoots and roots in uptake and use of key resources, there should be some kind of balance in size (e.g., biomass) and surface area (or related metric) between the root and shoot systems of individual plants (and perhaps stands). Such a balance should vary in relation to factors such as resource supply and species habitat affinity. For example, this would lead to a proportionally greater root than shoot system when nutrients were in short supply. Although such ideas have been taken as near-paradigm by several generations of physiologists and ecologists, we need to ask: How firmly does the evidence support these ideas?

Historically, the majority of discussion of root–shoot relationships has focused on the relative biomass fractions in roots versus shoots. Scientists have

also focused on the range of components of root and shoot systems (including differences in morphology, chemistry, phenology, metabolism, and longevity), although data on root properties under contrasting environmental conditions are still scarce. In this chapter I revisit the issues raised above, focusing on the existing literature. I will not consider the actual internal communication devices used by plants to signal differential rates of growth or senescence of above-ground versus belowground tissues. Instead I will ask whether root/shoot relationships (1) maintain a so-called functional balance over time; (2) differ phenotypically in relation to differences in supply of light, nutrients, CO₂, or water, or merely differ due to variation in plant size resulting from variation in these factors; (3) differ among plant species differing in habitat affinity; and (4) of aggregations of plants in stands are similar in their behavior to individual plants.

A. Conceptual Considerations

The close coordination of growth of root and shoot systems has long intrigued plant biologists. It led to the functional equilibrium model of coordinated shoot and root growth (Brouwer, 1962a, 1983). It also led to the optimality theory (Wilson, 1988; Bloom et al., 1985; Thornley, 1972, 1998) that argues for preferential partitioning to the part of the plant

Abbreviations: LAR, leaf area ratio; LMF, leaf mass fraction; NAR, net assimilation rate ($\text{mol m}^{-2} \text{h}^{-1}$); RGR, relative growth rate (d^{-1}); RMF, root mass fraction; SLA, specific leaf area ($\text{cm}^2 \text{g}^{-1}$); SRL, specific root length (cm g^{-1}).

which acquires the currently most limiting resource. Such partitioning hypothetically increases the ability of the plant to acquire that most limiting resource. Consistent with the optimality theory is the idea that species will show marked differences in biomass distribution in a fashion related to their differences in habitat affinities. According to such hypotheses, for example, plants adapted to growth in deep shade should tend to display high biomass allocation to leaves (Givnish, 1988), and plants adapted to growth in conditions with limited soil resources (nutrients or water) should tend to display high biomass allocation to roots (Chapin, 1980). Thus, theory suggests that there should be functional balance among root and shoot systems, that this balance should vary with resource supply, and that this balance should vary among species in relation to variation in life history traits and/or habitat affinities.

As demonstrated below, the first point has been shown to be true so far as it has been tested. In fact, the evidence suggests that a tendency toward functional balance may be so pronounced that the second and third points, often taken as paradigm and near-paradigm, respectively, are in fact weak trends compared to the tendency toward individual functional balance. They have been overemphasized in studies of young plants due to failure to account for ontogenetic drift (e.g., Rice and Bazzaz, 1989; Coleman et al., 1994; Reich et al., 1998a). Moreover, differences in morphology, chemistry, and metabolism of roots and leaves are so profound in terms of impact on uptake and use of resources (e.g., Fitter, 1985; Poorter and Remkes, 1990; Poorter et al., 1990; Garnier, 1992, 1998; Lambers and Poorter, 1992; Ryser and Lambers, 1995; Reich et al., 1998b; Poorter and Nagel, 2000) that they exert greater influence on growth than differences in root–shoot biomass fraction in young plants.

B. Terminology

1. Allocation, Partitioning, and Distribution

Although root/shoot ratio has often been criticized for being a static ratio, at least it is defined similarly by most authors, as the ratio of dry mass of belowground [i.e., roots] vs. aboveground plant parts at a given point in time. In contrast, the terms biomass allocation and partitioning (often used similarly) have had diverse uses. These range from narrow definitions in which allocation or partitioning refers only to the short-term transfer and placement of new increments of biomass or specific substances (including carbohydrates,

proteins, lipids, etc.) to broad definitions in which allocation or partitioning refers specifically to the relative distribution of biomass pools among plant parts at a point in time (e.g., Poorter and Nagel, 2000). For purposes of this chapter, I will follow the definitions used by Lutze and Gifford (1998) and refer to *allocation* and *partitioning* as synonyms for the transfer and placement of new increments of biomass. I will refer to the amount of biomass present in any organ system at any comparable time or plant size, relative to the total plant biomass, as the biomass *distribution*. Hereafter I will use the term carbon roughly synonymously with biomass, since carbon represents roughly half of plant biomass. Biomass distribution then is a function of biomass allocation and biomass turnover rate, as shown in this example for root mass fraction (RMF):

$$\text{RMF} = (\text{Biomass allocated to roots} - \text{root biomass turnover}) / (\text{Biomass allocated to roots} - \text{root biomass turnover} + \text{Biomass allocated to stems} - \text{stem biomass turnover} + \text{Biomass allocated to foliage} - \text{foliage biomass turnover})$$

In such a definition, turnover would include biomass lost via respiration as well as by tissue senescence or herbivory. It is clear that biomass distribution (which is frequently measured) is equally a result of turnover as of allocation (both of which are rarely measured), although this important and simple point is often overlooked.

Hence, since turnover rates of roots are still very poorly quantified for the vast majority of species and situations (Eissenstat and Yanai, 1997), we have little reliable data for biomass allocation for whole plants, except during very early rapid growth phases when fine-root turnover is likely to be very low. This lack of empirical data on allocation is further highlighted when we consider our failure to account for carbon allocated to root symbionts such as mycorrhiza in most species and to root nodule bacteria in others, and carbon exuded from roots. Thus, the vast majority of usable, interpretable data are for biomass distribution. Again, for young seedlings, this might largely reflect biomass allocation since turnover has not yet begun in a major fashion. However, for older plants (including older “seedlings”), any conclusions reached in the literature about biomass allocation per se (usually based on biomass distribution) are likely suspect, since the turnover and allocations parts of the equation are generally unknown.

2. Root-Shoot Ratios, Biomass Fractions, and Allometric Analyses

Given historic use of the root-shoot ratio I will repeatedly refer to it in this chapter, although I prefer the term biomass fraction to refer to the fraction of total plant mass in a given plant component. The term biomass fraction is preferred for statistical reasons over root/shoot ratio, although they convey the same information. In addition to evaluating patterns of biomass fractions, I shall also discuss the use and value of allometric relationships in which the log-transformed biomass of the shoot is plotted against the log-transformed biomass of the roots or of the whole plant (Pearsall, 1927; Evans, 1972). This enables the separation of differences in biomass distribution due to differences in size from those due to true shifts in partitioning. Although allometry is not perfect, it is "the only routine method of showing an effect of treatment on net partitioning" (Farrar and Gunn, 1998). When allometry is performed to relate roots to shoots, the allometric slope constant k is the ratio of the relative growth rate (RGR) of the shoot versus the RGR of the root, and hence a precise measure of relative net change in biomass for the shoot vs. the root. It is useful to evaluate whether k is less than or greater than unity, since this directly defines the direction of the ontogenetic drift in partitioning.

Although k is useful as typically defined, it does not distinguish among stems, leaves, and roots, which may limit its usefulness (Poorter and Nagel, 2000). However, one can determine a k for any specific pair of tissues. Additionally, nonlinearities in the allometric relationships are problematic and the slopes of allometric relationships do not fully account for differences in the overall elevation of the allometric lines. Apparently, plants might allocate proportionally less to one component (roots, for example) as they grow larger under a given treatment A as compared to another treatment B (i.e., have a lower slope under treatment A if roots are the Y-axis variable). Yet they still might have a greater proportion of total biomass in that tissue component at any plant size because of differences in intercept. Hence, allometric relationships should consider the slopes and intercepts to adequately interpret potential differences in allocation and distribution. Finally, allometry provides some information on the outcome of partitioning, not the process itself. Despite these limitations it is far more appropriate as a means of addressing questions of partitioning than comparing plants in different treatments at the same time (Evans, 1972; Coleman et al., 1994; Lutze

and Gifford, 1998). A number of authors have also compared leaf mass fraction (LMF) or RMF to plant size (Peace and Grubb, 1982; McConnaughay and Coleman, 1999; Poorter and Nagel, 2000), which accomplishes roughly the same purpose as the direct allometric approach.

C. Evidence

In evaluating the published data in support of or against the idea of optimality in acclimation and adaptation of biomass allocation or distribution, I used all my reprints plus 675 articles gleaned from an electronic search for "root" and "shoot" using the database Agricola. Roughly 200 citations met the criteria needed to be relevant to the topic at hand. Although not an exhaustive search, it is likely relatively comprehensive. Moreover, when I refer to papers that did not account for ontogenetic drift and yet arrived at conclusions regarding shifts in biomass allocation, there is no attempt to denigrate these authors. To demonstrate this, I point out here that my own work (e.g., Reich et al., 1987; Walters and Reich, 1989) has suffered from the failure to account for ontogenetic drift.

II. FUNCTIONAL BALANCE AND RESPONSES OF ROOT VERSUS SHOOT SYSTEMS TO VARIATION IN RESOURCES

A. Functional Balance, Optimality Theories, and Ontogenetic Drift

The relative differences in response of root versus shoot systems to variation in resources such as light, water, nutrients, or CO₂ has long been a central question in plant biology. Brouwer (1962a,b) performed several pioneering investigations that showed that leaf- or root-pruned seedlings rapidly regained their original root-shoot biomass balance and that the pruned plants were then on the same line in the allometric analysis as the control plants; i.e., when compared to a (younger) control plot with a similar dry mass, they had the same proportion of that mass in roots and shoots. Surprisingly few studies were ever made to validate this finding, although work by Caloin et al. (1991), Farrar and Gunn (1998), and Poorter and Nagel (2000) demonstrate the same result for herbaceous plants. Indirect evidence in this same vein has been seen for woody plants by Eissenstat and Duncan (1992), Reich et al. (1993), Kruger and Reich (1993), and Vanderklein and Reich (1999) for lightly to

moderately shoot-pruned or defoliated woody plants. Hence I will presume that this is a general process until proven otherwise. If true, this is remarkable, in that the control and conservation of biomass distribution occurs only due to plastic variation in the allocation or partitioning of new carbon (Farrar and Gunn, 1998). The recovery of root–shoot balance in partially defoliated plants comes at a cost, such as of fruit production in citrus (Eissenstat and Duncan, 1992).

Even if we accept that all plants behave in such a fashion, many possible mechanisms may be involved, and understanding of this process is surprisingly limited to this date (Farrar and Gunn, 1998; Poorter and Nagel, 2000). Building conceptually on earlier studies that showed greater shoot fraction in low light or root fraction under low soil resource supply (which one should note were typically based on root–shoot ratios of plants of different sizes), Brouwer (1983) synthesized his own work to develop the “functional equilibrium” theory. In a simplified framework this can be stated as (Poorter and Nagel, 2000): plants shift their allocation toward shoots if the carbon gain of the shoot is limited by a low level of aboveground resources, such as light or CO₂. Allocation is shifted toward roots if belowground resources, such as nutrients or water, are at low levels. Optimal partitioning theory further suggests that plants respond to variation in the environment by partitioning biomass among various plant organs to optimize the acquisition of nutrients, light, water, and carbon in a manner that maximizes plant growth (Thornley, 1969; Bloom et al., 1985). For example, plants experiencing low levels of nutrient supply would be predicted to shift resources toward root growth and to processes associated with nutrient capture rather than those associated with carbon uptake. In this sense we can think of the optimal partitioning theory as an extension of the “functional equilibrium” model.

Both functional equilibrium and optimal partitioning models explain the recovery of a stable root–shoot biomass distribution following pruning or nutrient starvation. They also explain shifts toward higher root biomass fraction under low soil resources and higher shoot biomass fraction under high soil resources believed to be a common whole-plant behavior. Moreover, these shifts could be considered adaptive, since they might lead toward enhanced capture of the resources most limiting to plant growth. However, optimality may not be a good explanation. Instead, one could argue that the plant is reestablishing a functional equilibrium selected for over time for reasons unrelated to optimality and determined genetically.

Since the mechanisms controlling functional equilibrium are still at best partially known, and other aspects of the “optimal allocation vis-à-vis resource supply” theory are only weakly supported, I propose that functional equilibrium may be as much or more a case of plants maintaining homogeneity rather than responding optimally to variation in resource supply.

Optimal partitioning theory is generally accepted—in fact, it is loosely used as a paradigm in plant ecology, based on concept and empirical evidence (Bloom et al., 1985; Chapin, 1991; Reynolds and D’Antonio, 1996), although there is no consensus about the mechanisms involved. This idea still merits partial support, but a variety of studies have indicated that some significant fraction of the evidence taken as support for such theory is actually due to failure to account for ontogenetic drift (Evans, 1972; Rice and Bazzaz, 1989; Walters et al., 1993a,b; Coleman et al., 1994; Reich et al., 1998a; Farrar and Gunn, 1998; McCaughay and Coleman, 1999). Such allometric evidence suggests that the plasticity of allocation in response to resource variation is often relatively muted (and differentially dependent on the resource involved). The large differences reported in the literature and attributed to plasticity sometimes reflect large differences in plant size, rather than true differences in allocation. In fact, failure to account for ontogenetic drift can cause authors to misjudge the magnitude, duration, and even direction of many of the adjustments in biomass allocation patterns found for many species (McCaughay and Coleman, 1999). Those investigators noted that a surprisingly small number of studies have explicitly distinguished between biomass distribution differences that result as a natural consequence of ontogenetic drift (i.e., plant growth and development) and “true” adjustments in biomass distribution (i.e., those that require an adjustment in biomass allocation). The numbers of such publications are small as compared to the much larger number of papers on plant responses to nutrients, light, water, or CO₂ published in the past several decades without considering ontogenetic drift.

Poorter and Nagel (2000) have argued that root–shoot differences that occur among treatments at a point in time due only to differences in prior growth rate, and hence in plant size at that time, are nonetheless meaningful. This is because the plants actually co-occur in time and differences in biomass fractions may influence their response to current conditions. Although this latter possibility may be true, the hypothetical plants are also likely to differ in many other ways (leaf or root chemistry, metabolism, plus

overall plant size) that may influence their functions. Hence, Evans (1972), Coleman et al. (1994), and Lutz and Gifford (1998) have argued, and I agree, that the comparison of biomass distribution in plants, that are of widely differing sizes because of microenvironmental differences, sheds no light on the actual process of allocation, or of plasticity in allocation. If plants of a given species under low light conditions actually shifted their proportional allocation of new biomass toward leaves (which I define as a plastic response), they would have a higher k and likely a higher LMF at the same size as high light plants. If the plants make absolutely no change in allocation, high light will cause faster overall growth and hence over time the plants diverge along the same developmental trajectory and with exactly the same partitioning patterns, and yet have divergent LMF at the same time.

B. Responses to Resource Gradients

1. Light

Optimal partitioning theory hypothesizes increased allocation to leaf production should be a phenotypic response of plants to lower light environments (e.g., Givnish, 1988). The vast majority (in fact, every test I could find) of studies that compared plants under varying light conditions reported higher leaf mass fraction in low-light-grown plants when plants were harvested at a common time (cf. Olff et al., 1990; Callaway, 1992; Latham, 1992; Lei and Lechowicz, 1998) and a meta-analysis of such studies also reports a significant shift toward leaves and stems and away from roots under low light (Poorter and Nagel, 2000). This evidence of differences in biomass *distribution* of plants of widely different size that grew under differing light conditions led to the common paradigm that plants shift *allocation* toward leaves when grown at low light. However, most of the studies that addressed this issue examined plants only at a common time. In contrast, the vast majority of the smaller set of studies that explicitly tested for allocation by accounting for ontogenetic drift, have *not* found increasing allocation to leaf mass in low light. This is the case for 23 species (of 26 tested) as disparate as herbs (Evans and Hughes, 1961; Hughes and Evans, 1962; Peace and Grubb, 1982; Rice and Bazzaz, 1989; Philippot et al., 1991; Casper et al., 1998; McConnaughay and Coleman, 1999), crop plants (Terry, 1968; Corre, 1983), and woody plant seedlings (Ledig et al., 1970; Steinbrenner and Rediske, 1964; Walters et al., 1993a; Stoneman and Bell, 1993; Chen, 1997; Chen and Klinka, 1998; Reich et al., 1998a). Thus, most

studies that accounted for ontogenetic drift found no evidence of allocation shift toward leaf production at low light. Using an alternative approach, Ingestad and Agren (1991) also concluded that there is no effect of irradiance on allocation if a plant is at steady-state nutritional conditions. Thus the preponderance of evidence suggests that plastic allocational shifts in biomass in response to light gradients predicted by optimality theory are the exception rather than the rule.

As an example of the evidence regarding biomass allocation patterns under contrasting light environments, I present data for seedlings of nine woody species that were summarized in a condensed fashion in Reich et al. (1998a). It is evident (Fig. 1; Table 1) that there is no consistent difference in the allometric coefficient k (here defined as the change in leaf RGR versus root RGR, ignoring stem mass) in contrasting light treatments. Only one of the nine species had a significant shift in k , and many species even had lower k in lower light. The intercepts were generally not significantly different either. Only *Larix* had a significantly different intercept, showing for this species that even for a given root size, low-light plants had greater leaf mass despite a similar k . Using these data, we also see no significant differences between light treatments if LMF is regressed against plant size.

One alternative way of examining allocational shifts bears mention. Some studies which reported an effect of light on biomass allocation and attempted to adjust for plant size, did so using analysis of covariance (ANCOVA), wherein the relationship between leaf fraction and light environment was statistically adjusted for plant size (cf. Veneklass and Poorter, 1998; Poorter et al., 1999). For our data set (Fig. 1; Table 1), ANCOVA results were often substantially different from those from a strictly allometric analysis, and the range of plant size occupied by each treatment was quite distinct, so that the statistical adjustment using ANCOVA may not adequately account for ontogenetic drift. Therefore, until such data are examined using both allometry and ANCOVA, studies that use only ANCOVA should be considered weak evidence as a test of plasticity.

When analyzed allometrically, for woody plants there was no shift toward higher LMF at lower light for 12 species (Walters et al., 1993a; Reich et al., 1998a), but there was a consistent shift toward stems and away from roots. This was also seen earlier for etiolated peas (Pearsall, 1927) and for the woodland herb *Impatiens* in studies by Evans and Hughes (1961), Huges and Evans (1962), and Peace and

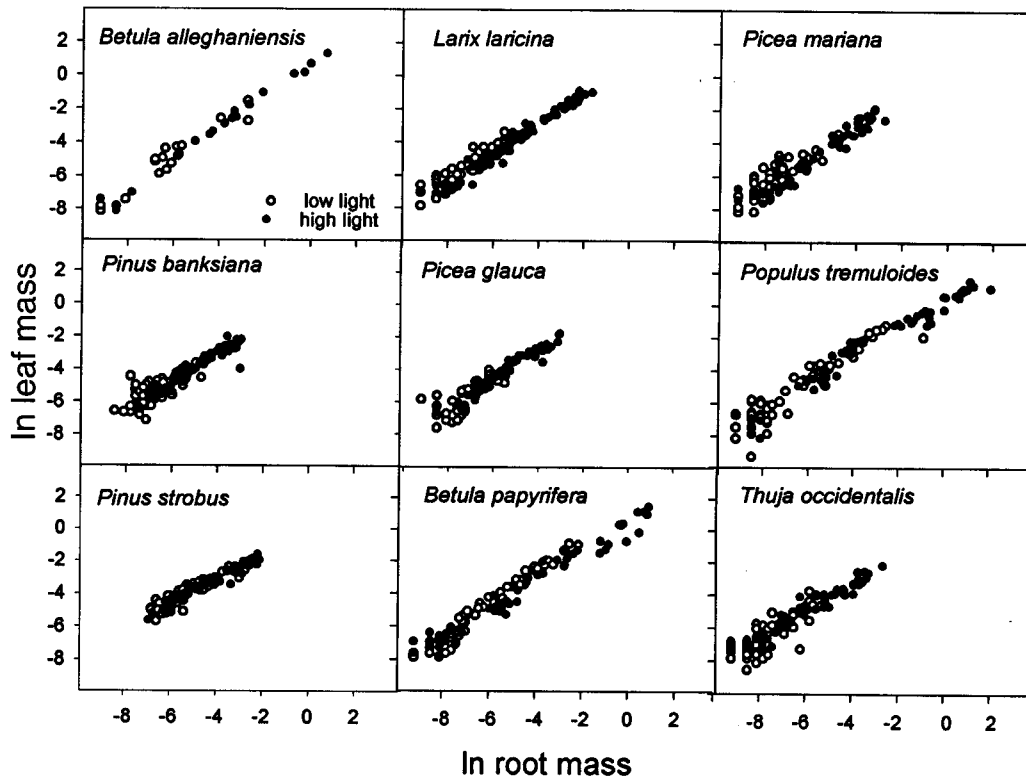


Figure 1 Variation in leaf mass versus root mass, shown on a logarithmic scale, for young seedlings of nine woody plant species grown at low and high light (5% and 25% of full sunlight, respectively) ($n = 59$ plants on average per light level per species). Statistical summaries of slope and intercept differences across light treatments are provided in Table 1. Individual data points are individual plants harvested at nine different times over the course of the growing season. (Expanded from data summarized in Reich et al., 1998a.)

Table 1 Summary of Values of the Allometric Constant (k) for the Relationship Between Leaf Mass and Root Mass for Each of Nine Woody Species in Two Contrasting Light Environments—Low (5% of full sunlight) and High (25% of full sunlight).

Species	Shade tolerance classification	Low light	High light	$P(k)$	$P(\text{intercept})$
<i>Populus tremuloides</i>	Intolerant	0.92 ± 0.05	0.84 ± 0.02	ns	ns
<i>Betula papyrifera</i>	Intolerant	1.07 ± 0.03	0.89 ± 0.02	*	—
<i>Larix laricina</i>	Intolerant	0.91 ± 0.04	0.93 ± 0.02	ns	*
<i>Pinus banksiana</i>	Intolerant	0.76 ± 0.07	0.87 ± 0.03	ns	ns
<i>Betula allegheniensis</i>	Intermediate	0.96 ± 0.07	0.97 ± 0.02	ns	ns
<i>Pinus strobus</i>	Intermediate	0.73 ± 0.04	0.73 ± 0.02	ns	ns
<i>Picea glauca</i>	Tolerant	0.89 ± 0.08	0.94 ± 0.03	ns	ns
<i>Picea mariana</i>	Tolerant	0.90 ± 0.08	0.96 ± 0.03	ns	ns
<i>Thuja occidentalis</i>	Tolerant	0.89 ± 0.08	0.81 ± 0.03	ns	ns

Mean is followed by 1 SE. Species are arrayed from least to most shade tolerant.

Probabilities (P) contrast the two light levels and are those for the slope (the allometric constant k) and for the intercept of the allometric relationship (not testable for *Betula papyrifera* since there were significant slope differences).

Source: Expanded from data summarized in Reich et al. (1998a).

Grubb (1982). These patterns could be construed as indirect support for the optimal allocation model, since stems and leaves collectively are needed to harvest light and fix carbon, while roots acquire water and nutrients. If both leaf fraction and stem fraction increase under low-light conditions then one could argue that these changes supported the optimality theory, since immediate resource gain would occur. However, if only stem fraction increases, as commonly observed, it suggests a strategy to improve the likelihood of future potential resource gain and perhaps to increase the likelihood of survival. Moreover, since the plants in these experiments were growing as isolated individuals, with shade coming from high above the plant, increased carbon gain would have come directly from more leaves or leaf area but not from more stem mass or stem length. Hence, the observed shift toward stems rather than leaves must represent an acclimation that has been selected for because of its value in natural environments, rather than a plastic response to increase carbon gain in the near term.

In contrast to the weak evidence for optimal biomass partitioning with respect to light—or, in fact, any consistent shift in LMF—dramatic shifts in leaf morphology were routinely shown, e.g., with leaves in low light having lower density, lower thickness, or both. This was demonstrated by higher SLA values, even when accounting for ontogenetic drift in SLA with plant size (Hughes, 1965; Peace and Grubb, 1982; Walters et al., 1993a; Reich et al., 1998a). There are few data available examining shifts in root properties (such as specific root length) under differing light conditions, but the data are consistent with leaf responses. Plants of nine species grown under low-light conditions had lower specific root lengths and higher SLA than plants of the same size grown under higher light conditions (Fig. 2; Reich et al., 1998a). Although all nine species showed shifts in SRL with light environment, these are not easily explained simply by differences in the slope of the change in root length with root dry mass or whole plant mass. The initial differences between light levels (in the smallest, youngest plants measured) were sometimes so large that SRL was higher in high-light than in low-light plants across their common range of plant sizes. This is despite a steeper slope of root length versus root mass for low light plants.

Acclimation of tissue morphology appears to represent a greater means of plasticity than shifts in biomass allocation in response to variation in light (Evans, 1972; Walters et al., 1993a; Reich et al., 1998a). Moreover, greater SLA and lesser SRL at low light

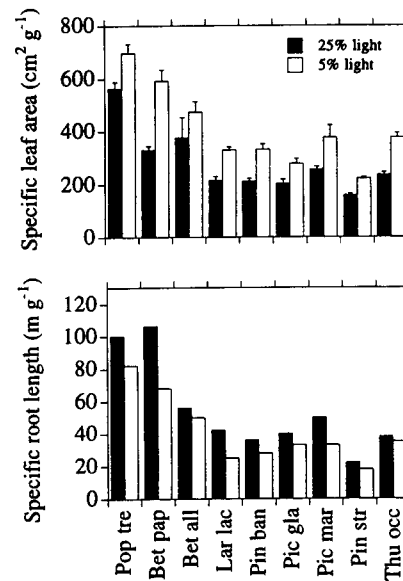


Figure 2 Specific leaf area (cm² foliage per g foliage) and specific root length (m root length per g root) for seedlings of nine species grown at low and high light (5% and 25% of full sunlight, respectively). See Fig. 1 or Table 1 for species names. (From Reich et al., 1998a.)

are consistent with the idea of improving the uptake of the most limiting resource (Givnish, 1988), assuming that uptake of resources is related to high surface area or length of the tissue in question (Reich et al., 1998b). Hence, optimality theory might be better supported if it were considered using models that incorporate the full constellation of plant traits and responses, including morphological ones that result in changes in the relative area or length of absorptive tissues.

2. Nutrients and Water

The evidence for phenotypic shifts in partitioning is stronger for nutrients than any other resource, but still is not universal. The predominant response noted in studies that did not account for ontogenetic drift was a large shift toward roots and away from shoots at low nutrient supply (Poorter and Nagel, 2000). Most studies that adjusted for plant size also found shifts in allocation across varied nitrogen supply, as reported by Ryser and Lambers (1995), Volin and Reich (1996), Gedroc et al. (1996), Lutze and Gifford (1998), Baxter et al. (1997) and McConnaughay and Coleman (1999) (Fig. 3). The relative magnitude of the shift was typically smaller when examined ontogenetically rather than at a single

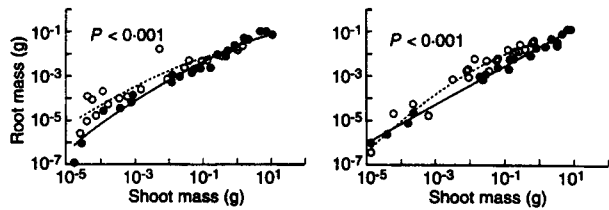


Figure 3 Variation in root mass versus shoot mass, shown on a logarithmic scale, for young seedlings of the annual herbaceous plant species *Abutilon theophrasti* (left) and *Chenopodium album* (right) grown at low (open circles) and high (closed circles) nutrient regimes ($n = 22$ plants per nutrient regime per species). Individual data points are individual plants harvested at different times over the course of the growing season. (From Gedroc et al., 1996.)

point in time. Evidence in response to supply of P and other nutrients is less clear. Eissenstat et al. (1993) found shifts toward decreasing RMF with increasing P supply in sour orange, even when comparing plants at a common size. However, using data from a study of common bean plants (Nielsen et al., 1998), there is no evidence of decreasing RMF with increasing P supply, and in fact, the evidence suggests the opposite (Fig. 4). Ryser and Lambers (1995) found declining RMF with increasing P supply in one grass species (*Brachypodium pinnatum*) but not in another (*Dactylis glomerata*). Using a different experimental approach, several authors concluded that there is a systematic shift in allocation for variable P and N supply, but not for K (Ingestad and Agren, 1991; see also Van der Werf et al., 1993a,b).

Similar to the limited database on root traits across light gradients, there are few data for root traits across nutrient gradients. Ryser and Lambers (1995) found that in the grass species *Dactylis glomerata*, SRL decreased with increasing N supply at various levels of P supply, but in the grass species *Brachypodium pinnatum* there was no decline in SRL with increasing N supply. In neither species was there a consistent shift in SRL with variation in P supply. In contrast, Eissenstat et al. (1993) found a decrease in SRL with increasing P supply in sour orange.

Only scant data on plastic allocation responses to water availability are available in experiments where ontogenetic drift was accounted for in the design. Of those data, increased allocation toward roots, when water was in low supply, have been reported for some woody plants (Ledig et al., 1970; Tomlinson and Anderson, 1998) and during certain phenotypical phases in different woody seedlings (McMillan and

Wagner, 1995). However, it was not observed for annual herbs (McConnaughay and Coleman, 1999). This database is too scant and inconsistent to provide a basis for reaching firm conclusions. Moreover, with regard to water acquisition, optimality theory may not apply in cases of uncertainty (Lerdau, 1992; Lerdau and Gershenzon, 1997). If plants were to develop roots after water shortage occurred, it would be too late. Therefore they may have been selected to invest in excessive amounts of roots in habitats that may be subjected to periodic and unpredictable drought.

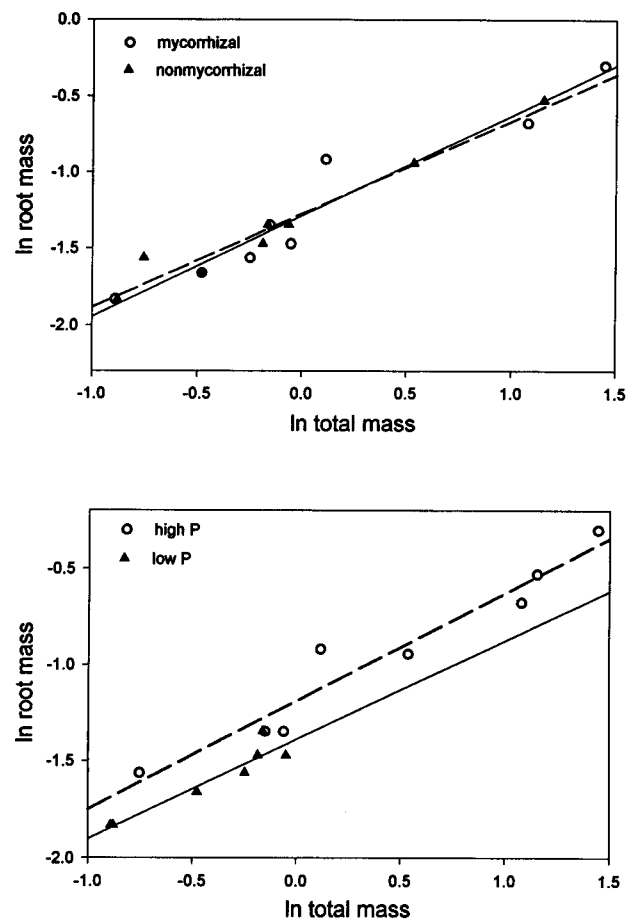


Figure 4 Variation in root mass versus total plant mass, shown on a logarithmic scale, for young common bean plant seedling grown (lower panel) at low and high phosphorus supply rates and (upper panel) with or without mycorrhizal infection. Individual data points are average values for plants harvested at four dates over the time course of the experiment, pooled across the other treatment. (From Nielsen et al., 1998.)

3. Elevated Atmospheric CO₂

Consistent with optimality theory, it was hypothesized (e.g., Reynolds and Thornley, 1982) and often empirically observed (e.g., Eamus and Jarvis, 1989; Ceulemanns and Mousseau, 1994; among many such publications) that growth in elevated CO₂ results in increased dry-mass partitioning to roots. However, few if any of these reports accounted for ontogenetic drift in biomass fraction with plant size. In contrast, opposite results were reported by researchers who made explicit tests with woody and herbaceous species of the role of ontogenetic drift vis-à-vis biomass allocation under elevated CO₂ (Tjoelker et al., 1998; Gunn et al., 1999; Lutze and Gifford 1998). They found that the strong size dependence of partitioning of dry mass among plant parts resulted in "apparent" differences in root and shoot dry mass partitioning, that in fact were the result of differences in plant size and not a functional adjustment to CO₂ environment (e.g., Table 2, Fig. 5). Recent meta-analyses that did not account for plant size (Curtis and Wang, 1998; Poorter and Nagel, 2000) also indicated that these earlier suggestions of optimality in root-shoot partitioning in response to elevated CO₂ are not supported by critical evidence.

C. Conclusions Regarding Experimental Tests of Allocation Across Resource Gradients

A better understanding of acclimation of biomass distribution under variable environmental conditions is critical to our ability to comprehend plant growth, or the responses of plants to multiple resource scenarios (McConnaughay and Coleman, 1999). Optimal partitioning theory has often been the basis for models which attempt to predict plant responses to global environmental changes. If the assumption that plants shift biomass partitioning in response to environmental cues is untrue, or much more limited in degree than previously believed, the predictions of such models must be questioned.

Some studies show pronounced shifts in allocation as hypothesized, but others do not. What can we therefore conclude? If optimality allocation theory holds for all plant resources, we should see predicted shifts in response to variation in light, CO₂, water, and nutrients. There is strong evidence against such claims for light and CO₂, strong evidence in favor of these claims for N, and variable evidence for P or water.

Table 2 Allocation of Dry Mass to Roots Among Five Boreal Species (*Populus tremuloides*, *Betula papyrifera*, *Larix laricina*, *Pinus banksiana*, and *Picea mariana*) Grown as Seedlings Under Ambient (370 μmol mol⁻¹) and Elevated (580 μmol mol⁻¹) Concentrations of CO₂ in Combination with Five (day/night) Growth Temperatures

Genus	CO ₂	Growth temperature (°C)				
		18/12	21/15	24/18	27/21	30/24
<i>Populus</i>	370	1.19 ± 0.04	1.10 ± 0.02	1.11 ± 0.02	1.04 ± 0.02	1.11 ± 0.02
	580	1.18 ± 0.05	1.08 ± 0.02	1.21 ± 0.02	1.08 ± 0.02	1.12 ± 0.01
	<i>P</i> > <i>F</i> ^a	ns	ns	.001	ns	ns
<i>Betula</i>	370	1.07 ± 0.02	1.05 ± 0.01	1.15 ± 0.03	1.05 ± 0.01	1.08 ± 0.02
	580	1.07 ± 0.01	1.05 ± 0.01	1.09 ± 0.02	1.05 ± 0.01	1.04 ± 0.01
	<i>P</i> > <i>F</i>	ns	ns	ns	ns	ns
<i>Larix</i>	370	0.93 ± 0.01	1.03 ± 0.02	1.02 ± 0.01	0.99 ± 0.01	1.04 ± 0.01
	580	0.96 ± 0.01	0.99 ± 0.02	1.01 ± 0.01	1.01 ± 0.01	1.05 ± 0.01
	<i>P</i> > <i>F</i>	0.09	ns	ns	ns	ns
<i>Pinus</i>	370	1.05 ± 0.02	1.01 ± 0.02	0.98 ± 0.02	0.99 ± 0.01	1.00 ± 0.02
	580	1.07 ± 0.02	1.05 ± 0.02	1.02 ± 0.01	0.99 ± 0.01	0.99 ± 0.01
	<i>P</i> > <i>F</i>	ns	ns	0.05	ns	ns
<i>Picea</i>	370	1.01 ± 0.01	0.97 ± 0.02	1.00 ± 0.01	0.97 ± 0.01	0.99 ± 0.02
	580	1.01 ± 0.01	0.94 ± 0.01	1.00 ± 0.01	0.98 ± 0.01	1.04 ± 0.02
	<i>P</i> > <i>F</i>	ns	ns	ns	ns	0.08

Mean (±SE) allometric coefficients relating change in root mass to change in plant mass are shown. Slope values determined from individual plant dry mass data using the linear regression equation: $\ln(\text{root}) = \text{slope} \times \ln(\text{plant}) + b$, all $R^2 \geq 0.97$. Values > 1.0 indicate an increased partitioning of dry mass to roots for a given change in plant mass.

^a*P* values for test of separate slopes for CO₂ treatment in analysis of covariance; ns indicates *P* > .1.

Source: Tjoelker et al. (1998).

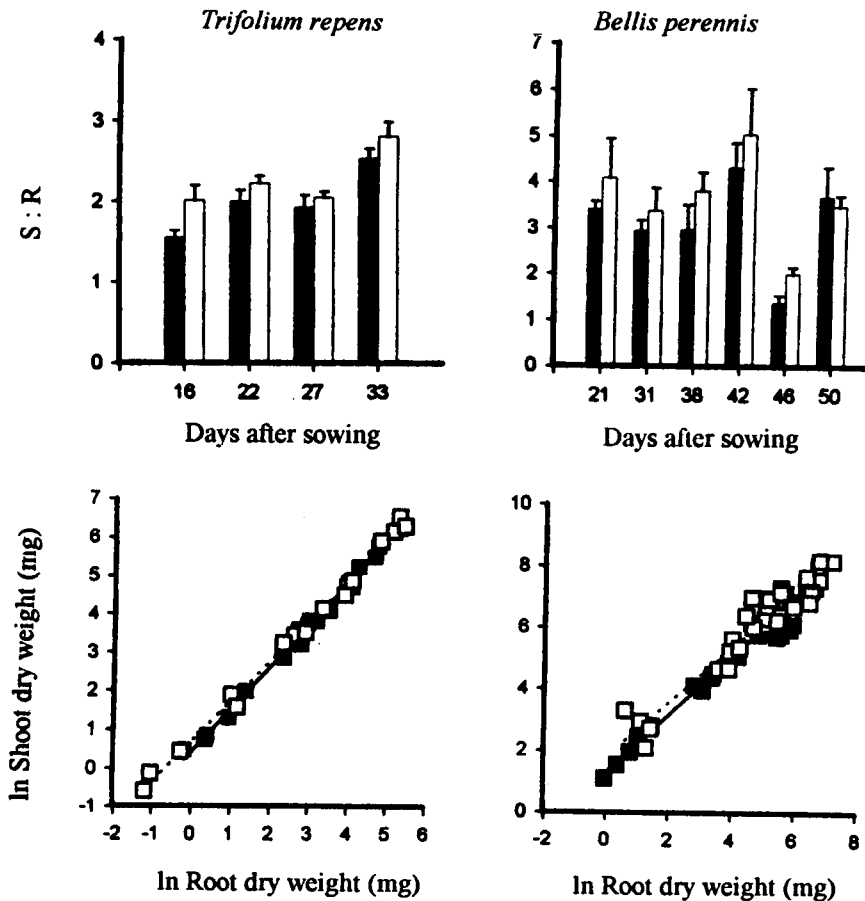


Figure 5 The effect of atmospheric CO₂ concentration on (A) shoot–root ratio at a number of harvest dates, and (B) the allometric relationship between shoot and root, for *Bellis perennis* and *Trifolium repens*. Plants were grown hydroponically in controlled environments of either 350 or 700 μmol CO₂ μmol⁻¹. Open bars of each pair (above) represent elevated CO₂ levels. Open squares (below) represent elevated CO₂ levels. (From Gunn et al., 1999.)

Collectively, the body of evidence suggests that the optimal allocation theory is not a general theory. Why is this so? An idea central to this theory is that plants plastically shift biomass allocation to have a higher resource gain under a new situation than would otherwise occur without such a shift. However, several important issues make this idea untenable:

1. A variety of traits influence plant resource balance, including morphology, metabolism, and chemistry, that are often more biologically significant and influential than biomass allocation (Evans, 1972; Lambers and Poorter, 1992; Reich et al., 1998a,b). For example, a plant can change carbon gain by either changing LAR or by changing the photosynthetic rate

of that leaf area (NAR). A plant can change leaf area by changing either SLA or LMF. In short, there are numerous ways to enhance C gain and RGR, and only few of them require shifts in biomass allocation. Thus, even if plants did routinely phenotypically change to maximize resource gain, they would not necessarily need to shift biomass allocation to do so. Apparently it is a less effective means of doing so as compared to other alternatives.

2. Shifts in allocation, morphology, architecture, chemistry, and metabolism have likely been selected for to simultaneously improve C and N balance and survival, not just to improve C and N balance. For instance, responses to an increase from a very low to a low level of a limiting resource are often inconsistent with optimality arguments. Almost all shifts, such as

decreased SLA (and hence decreased LAR) in higher but still limiting light or CO₂ conditions, should in theory reduce C gain and RGR (Lambers and Poorter, 1992) when compared to a plant that had not shifted SLA or LAR.

3. Traits that enhance resource gain do not necessarily enhance survival and vice versa, especially in resource-poor and/or disturbed habitats (Walters and Reich, 1996, 2000a,b). Thus, shifts that have been selected for to increase survival may in fact work against a shift toward enhanced resource status.

Only a whole-plant model that simultaneously examines shifts in allocation, morphology, chemistry, metabolism, turnover, and architecture, and their interaction, can characterize such changes. Unfortunately, it is easier to propose such a model than to develop it.

III. VARIATION IN ROOT-SHOOT RELATIONSHIPS AMONG SPECIES

Species of differing resource environments have been hypothesized to differ in their root-shoot relations (Grime, 1979; Chapin, 1980; Tilman, 1988; Gleason and Tilman, 1990), especially for resources that either are soil based, such as nutrients and water, or above-ground based, such as light and CO₂. In essence, if it is advantageous to be rootier as an individual when soil resources are poor, all species should phenotypically act this way, and species adapted to poor soils should be intrinsically rootier than those adapted to richer soils. But what do the data show?

Species found in soil resource-poor habitats have been hypothesized to be inherently "rootier" than species from richer habitats (Chapin, 1980). A test of this idea requires comparison of individuals in comparable habitats. Several studies designed to address this question have had conflicting results (Poorter and Remkes, 1990; Garnier, 1991; Fichtner and Schultze, 1992; Van der Werf et al., 1993a,b), and no conclusion can be made in support of the hypothesis. Moreover, the best objects for such test would be of species in natural field settings. However, there are few if any such published data available. Moreover, no clear distinction in root morphological or chemical traits was apparent among species varying in fertility of habitat (cf. Ryser, 1996; Craine et al., 2001).

Optimality theory also suggests that if it is advantageous to allocate proportionally more biomass to leaves when an individual plant is shaded, shade-adapted species should tend to be leafier than shade-

intolerant ones (Givnish, 1988). However, in comparing shade-tolerant versus intolerant species, recent results show opposite patterns vis-à-vis biomass distribution, allocation and tissue traits as long-held hypotheses. Shade-tolerant species actually appear to have equal or higher RMF than intolerant species. This was true in a comparison of tropical woody species considered shade tolerant versus intolerant, (Veneklass and Poorter, 1998) and for winter deciduous temperate broadleaf species (Walters and Reich, 1999). A neutral pattern was observed for evergreen broad-leaved species (Walters and Reich 1999) and for our study species (Table 1; note that k is not different for tolerant vs. intolerant species).

Hence, comparisons among species whose distribution is related to fertility or light gradients do not lend strong support for the optimal allocation or distribution theory. In contrast to the weak evidence for differences in biomass distribution among species in relation to habitat affinity, there is much stronger evidence of differences in tissue morphology, chemistry, metabolism, and turnover rates, increasingly of roots as well as shoots (Walters et al., 1993a,b; Ryser, 1996; Reich et al., 1998a,b; Walters and Reich, 2000b). Plants adapted to low fertility and/or low light may in fact be selected for low turnover of leaf and root tissues, rather than to high allocation to roots or shoots (Aerts, 1990; Reich et al., 1992, 1998a). They are also selected for traits associated with slow tissue turnover that minimize resource losses, such as dense tissues with low respiration rate. These include extended nutrient residence time via long tissue life span, for plants adapted to infertile habitats (Aerts, 1990). They also maintain low carbon losses via the combination of low respiration rates of all tissue types, and low tissue turnover rates, for plants adapted to deep shade (Walters and Reich, 1999, 2000a,b). Generally, species from resource-rich microhabitats have higher concentrations of nutrients, faster photosynthetic and respiration rates, higher SRL and SLA, and faster turnover of leaves than those from resource-poor environments (Chapin, 1980; Reich et al., 1992, 1998a,b, 1999). However, the comparative multispecies database for roots is still weak. Thus, it is uncertain whether root turnover rates are also higher for species from resource-rich microhabitats (Eissenstat and Yanai, 1997). The importance of leaf and root morphology and metabolism, rather than biomass allocation, was shown in contrasts of diverse species (Poorter and Remkes, 1990; Walters et al., 1993a; Reich et al., 1998a; Cornellissen et al., 1996) and among populations within a species (Ryser and Aeschlimann, 1999).

V. PLANT COMMUNITIES AND PLANTS IN COMMUNITIES

Field studies that include whole-plant biomass data are rare. The root–shoot distributions of five conifer species planted in the field did not differ in trenched plots with higher nitrogen and water supply than in untrenched plots (Machado et al., 2001), even for plants of common size. Similarly, naturally grown sugar maple seedlings growing across a soil fertility and soil moisture gradient did not differ in biomass fraction distributed to roots, even when accounting for plant size and light environment (Walters and Reich, 1997), but did differ in other important plant traits such as tissue %N. It is possible that modest natural gradients in soil resource supply have different, or inconsequential, effects, compared to the large gradients observed in experimental studies with very young plants. It is also likely that biomass fractions in older seedlings are markedly influenced by turnover rates of leaves and roots.

Do stands or patches of plants behave similarly vis-à-vis root–shoot relationships as individual plants? Answering this question is difficult since most accounts of individual plants involve small chamber-grown plants, whereas most studies of plant stands involve larger, older, field-grown plants. For forests, both observational and experimental studies show that plants growing under lower nutrient and water availability tend to have a greater RMF and a greater shift toward fine-root than toward foliage production, as compared with plants of high nutrient and water availability (Linder and Axelsson, 1982; Gower et al., 1992). These patterns could result either from shifts toward greater allocation to roots at low resource supply, from lower fine-root turnover rates, or from both. The relative contribution of each is practically impossible to calculate, given the paucity of root turnover data. Across a N gradient that resulted from 32 years of variable experimental fire frequency regimes, a strong gradient in root:foliage fraction was found (Fig. 6; Reich et al., 2001). Oak savanna stands under chronically low N supply have a greater fraction of fine biomass in fine roots rather than in foliage. This pattern is consistent with optimality theory, but it is impossible to know whether it results from variation in dominance of one vegetation type over another, since the low-fertility, frequently burned end of the continuum was dominated more by grasses than trees. Moreover, again we cannot separate allocation from turnover rates in this instance.

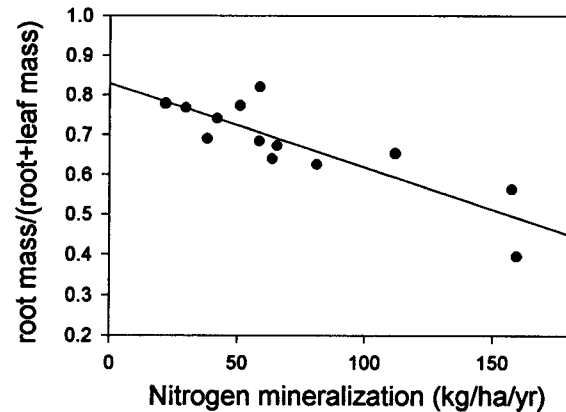


Figure 6 The fraction of total fine root plus leaf mass distributed to fine roots in relation to net nitrogen mineralization rate for 14 oak savanna stands in a fire frequency experiment in Minnesota. Along with the variation in nitrogen mineralization rate are parallel gradients in fire frequency and relative tree versus grass dominance, with frequently burned stands being dominated more by grasses than trees and having low mineralization rates, and vice versa. (From Reich et al., 2001.)

At a very coarse, but very large scale, Jackson et al. (1996) summarized existing data regarding root and shoot biomass for different biomes of the world. Even segregating woody from nonwoody systems (because these two classes vary in root–shoot ratio primarily due to the differences in aboveground woody biomass), there were substantial differences among biomes. For forests, there were differences among boreal (0.32), temperate coniferous (0.18), temperate deciduous (0.23), tropical deciduous (0.34), and tropical evergreen (0.19) forests, but these do not provide any discernible pattern. This could be a result of the confounding of the myriad of differing environmental factors across such broad gradients. One way to separate out genetic from environmental effects would be to compare different species or populations in common gardens, or the same genotype in plantations across environmental gradients. Some such data are available for Scots pine populations, wherein those populations from colder environments show greater biomass fractions in roots, both as stands of trees (Oleksyn et al., 1999) and as individual seedlings. Across this climate of origin gradient, there are strong gradients in temperature, nutrient supply, length of growing season, and day length, so discerning the most responsible factors for such patterns is difficult.

VI. SUMMARY

It is not clear why young plants phenotypically shift biomass allocation in response to gradients in N supply in a manner consistent with optimality theory, fail to do so consistently for light or CO₂, and show mixed patterns for P and water. This may not even be an important question to consider in isolation. It may well be that plants benefit more from shifting morphology, phenology, metabolism, chemistry, tissue longevity, or architecture in response to such factors than from shifting allocation. Only holistic consideration at the whole-plant level can answer such questions.

Knowledge of ontogenetic drift in root-shoot biomass distribution with plant size and age is not at all new. There are now a considerable number of publications calling attention to the possible misinterpretation of root-shoot "snapshots" in time. Nonetheless, despite systematic tests of the role of ontogenetic drift, these have failed to alert plant scientists sufficiently to these patterns. Instead, many authors continue to refer to differences in root-shoot relations as differences in plasticity of allocation that may well be largely the result of ontogenetic drift (e.g., Walters and Reich, 1989; Conroy et al., 1992; Latham, 1992; Graves, 1994; Lusk et al., 1997; Lei and Lechowicz, 1998; Messier et al., 1999; Valladares et al., 2000). For instance, root-shoot ratio was reported to be significantly higher in bean plants under low than moderate P supply and higher in nonmycorrhizal than mycorrhizal plants, based on comparisons of plants at common harvest times (Nielsen et al., 1998). It is difficult to reconcile results of such "snapshots" with those obtained by allometric relationships (Fig. 4) showing that at a common plant size, low P plants had fewer roots, not more. The point of such a specific example for P (Fig. 4), plus an example for CO₂ (Fig. 5), is to provide graphic examples of a persistent problem of inadequate evaluation of whether shifts in biomass allocation are real, or whether we often "see" what we have been trained to "see."

Similarly, many elegant studies have used sophisticated techniques to study the mechanisms involved in the control of allocation, as influenced by resource supply. However, their results may teach us about how plants developmentally adjust biomass allocation as they grow larger and older, rather than teaching us about how resource supply influences allocational processes. Only careful scrutiny of all such studies can help us decide when the right interpretation was made.

Changes in allocation patterns are relatively strong when nutrient supply is varied, but changes in other

aspects of plant morphology or physiology more generally dominate the responses of plants to variation in a wide set of resources, including light, nutrients, water, and CO₂. In essence, rather than adjust allocation of biomass, plants change tissue morphology, chemistry, metabolism, and turnover to alter their capability for resource interception, and to vary the rate of resource capture or resource loss. To the best of our knowledge, evidence for optimality in biomass allocation is even scarcer when examining differences among species that vary in habitat association, along either fertility or light gradients. Again, shifts in other attributes that may positively or negatively affect rates of resource capture or resource conservation appear to be far more important. Hence, it seems timely to suggest the removal of the significance of biomass allocation from its historically premier position, when discussing both how plants respond phenotypically to their environment and how plants have arrived through natural selection at their intrinsic genotypic traits.

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