

ORGAN PARTITIONING AND DISTRIBUTION ACROSS THE SEED PLANTS: ASSESSING THE RELATIVE IMPORTANCE OF PHYLOGENY AND FUNCTION

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Understanding how plant biomass is distributed between roots, stems, and leaves is central to many questions in life-history evolution, ecology, and ecosystem studies. Current ecological dogma states that patterns of biomass partitioning result from environmental differences. However, there are methodological issues associated with the role of plant size. In addition, the importance of evolutionary history in biomass distribution is unclear. Here, we assess the relative importance of evolutionary history and growth form on how biomass was not accounted for by plant size is partitioned between plant organs. Our analyses indicate that while growth form was significantly correlated with variation in biomass distribution and partitioning, phylogeny appears to be the strongest factor. Variation in biomass distribution is phylogenetically conserved for leaf mass but not for stems, roots, and annual production, suggesting that these factors may be more plastic. Leaf mass was the only organ with a considerable portion of the residual variation from growth form, which appears to be largely the result of differences in leaf traits. Our results have important implications for ecological studies because partitioning studies must first assess the role of plant size and evolutionary history in order to fully understand variability in biomass partitioning and distribution.

Keywords: plant allometry, residual variation, phylogenetic conservatism, specific leaf area, growth form.

Introduction

Seed plants display great diversity in both form and function. An understanding of the factors that control how plants partition metabolic production has been sought for over a century (Kny 1894) and remains an important focus in many areas of ecology and evolutionary theory (Iwasa 2000). Many studies have emphasized that within and across plant species there is much variability in the partitioning and distribution of biomass between organs. This variation has been largely attributed to factors such as environmental disparity (Davidson 1969; Hunt and Burnett 1973; Bloom et al. 1985; Hunt and Nicholls 1986; Iwasa 2000) and growth form (Monk 1966; Mooney 1972; Tilman 1988). A majority of these studies have focused on optimal partitioning theory, which postulates that plants should allocate biomass to the organ that acquires the most limiting resource (Davidson 1969; Hunt and Burnett 1973; Hunt and Nicholls 1986; Iwasa 2000).

The terms “biomass partitioning” and “biomass allocation” are used interchangeably in the literature. For the purposes of this article, both partitioning and allocation will refer to the residual variation in biomass being added annually to any particular organ from the production available. We will use the term “distribution” to refer to residual variation in the total amount of biomass in stems, roots, and leaves relative to the total mass for a given plant (Reich 2002). It is important to

point out that distribution is explained by both accumulated allocation of annual production and accumulated loss from various factors (Reich 2002), implying that plasticity to environmental heterogeneity may have minimal effect. However, it can also be argued that plant species or different populations should demonstrate distribution patterns that follow optimal partitioning theory, such that plants adapted to particular environmental conditions, such as shade or drought, should demonstrate optimal distribution patterns according to where they live on the resource gradient (Chapin 1980; Givnish 1988; Tilman 1988). However, instead of being a plastic response to environmental variability, this may be both a plastic and adaptive response to the environment. Therefore, although biomass distribution is not identical to biomass partitioning, it is often used to understand partitioning when true allocation data is not available (Reich 2002).

There are a couple of potential problems with interpreting plant organ biomass partitioning in the light of optimal partitioning theory. First, recent studies have indicated variation in biomass partitioning and distribution may often reflect, at least in part, differences in plant size (Coleman et al. 1994; McCaughay and Coleman 1999; Bernacchi et al. 2000; Enquist and Niklas 2002). Thus, variation in biomass partitioning and distribution may not reflect local plastic responses or even recent selective pressures but instead reflect differences in the sizes of the plants being studied. Second, very little emphasis has been placed on the effect of phylogeny on patterns of organ biomass distribution and plasticity of partitioning. Evolutionary history appears to be important to several areas of a plant’s form and function (Antunez et al. 2001; Brouat et al. 1998), and there is evidence of its importance to plasticity in biomass partitioning (Osone and Tateno 2005).

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Consequently, it is unclear whether current patterns of distribution also largely reflect evolutionary history. Additionally, factors such as plant growth form (Monk 1966; Körner 1994) and leaf morphological and physiological traits (Osone and Tateno 2005) may provide additional constraints on plant biomass distribution. Therefore, in order to understand the contributions of environmental variation to variation in biomass partitioning, it is important also to consider the roles of size, phylogeny, and functional differences.

Since the pioneering work of Pearsall (1927), several studies have shown that variation in plant biomass partitioning and distribution can often largely be related to size (Coleman et al. 1994; Bernacchi et al. 2000; Enquist and Niklas 2002). In an extension of metabolic scaling theory, Enquist and Niklas (2002) showed that seed plants, from small herbaceous seedlings to large conifers, appear to be following very similar rules for how their biomass is distributed. Based on constraints relating to the transport of resources from the ground through the plant and the photosynthetic harvesting capacity of the leaves, they predicted that (1) leaf mass, M_L , should scale to the three-fourths power of stem mass, M_S ; (2) M_L should scale to the three-fourths power of root mass, M_R ; and (3) M_S should scale isometrically to M_R (see Enquist and Niklas 2002

for a complete description of the mechanistic constraints due to size). When written in the form of a power law,

$$M_L = \beta_1 M_S^{3/4}, \quad (1)$$

$$M_L = \beta_2 M_R^{3/4}, \quad (2)$$

$$M_S = \beta_3 M_R, \quad (3)$$

where the β terms are normalization constants. The β values reflect differences in biomass distribution not accounted for by size (further details on the model can be found in Enquist and Niklas 2002; Niklas and Enquist 2002; details about metabolic scaling theory in general can be found in West et al. 1999). Extensive data for conifers, monocots, and eudicots spanning six orders of magnitude generally fit the predicted relationships. Plant size explained 97%–99% of the variation in biomass distribution to leaf, stem, and root mass (Enquist and Niklas 2002). However, there existed about one order of magnitude residual variation around these allometric scaling relationships (fig. 1). Thus, while plant size alone explained most of the variation in organ mass distribution,

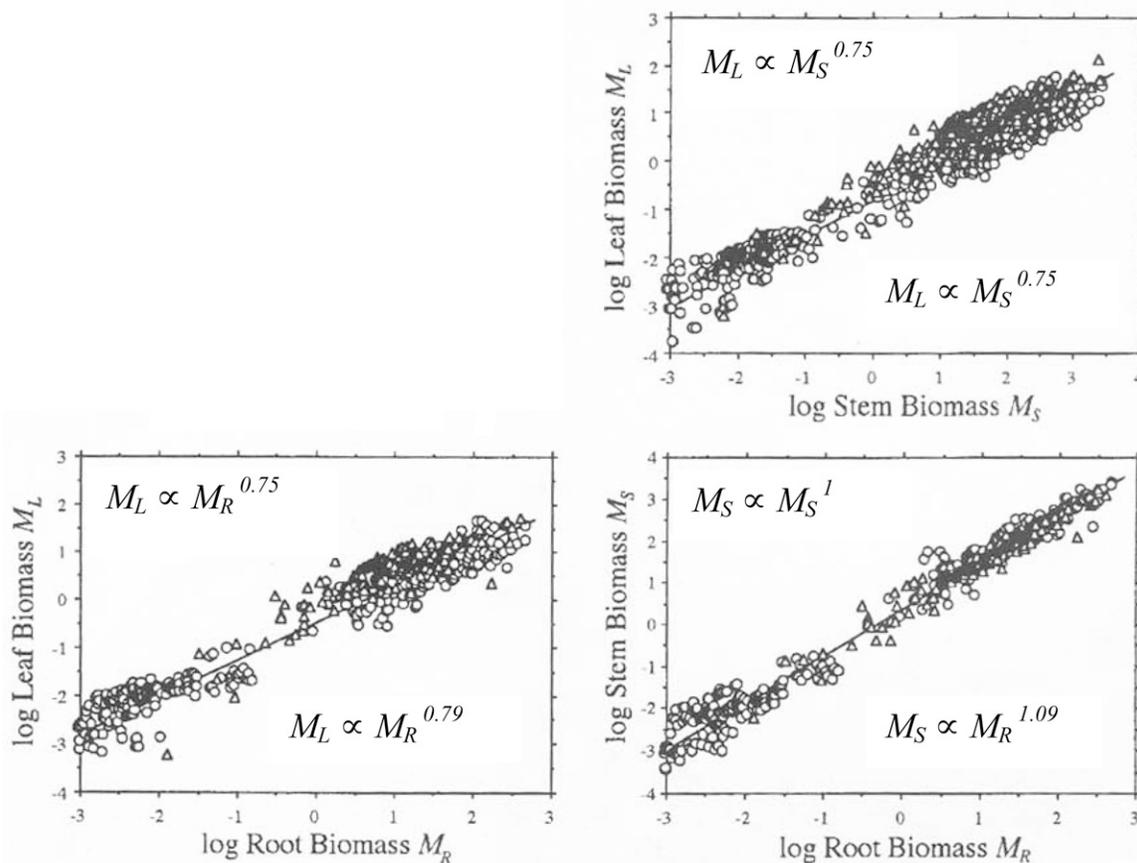


Fig. 1 Biomass allometric relationships between leaf, stem, and root mass for conifers, monocots, and dicots from a global compilation of seed plants. Predicted relationships are in the upper left corner and actual allometries are in the lower right corner of each graph. Graphs are from Enquist and Niklas (2002).

there still remains significant unexplained residual variation. In this article we focus on some of the processes that may be driving this residual variation.

The seemingly great differences between the studies that show biomass partitioning to be extremely variable and studies that show biomass partitioning to be largely attributed to size are explained by the approaches of the studies. First, one difference in the approach is the role of scale. Scaling studies look over enormous size ranges. As a result, variation in biomass partitioning, once size is controlled for (i.e., residual variation in allometric plots), is usually much less than the variation explained by size (fig. 2*a*). In comparison, many studies may look across only half an order of magnitude variation in size, so most of the variation may appear to be related to other factors (fig. 2*b*). Second, many biomass partitioning studies have used root-to-shoot ratios to assess differences in allocation. However, as shown in equations (1)–(3), organ ra-

tios (i.e., the root-to-shoot ratio, $M_L + M_S/M_R$) must vary just from changes in plant size. This is because the exponent that governs the scaling of root and shoot mass is not isometric (i.e., 1). Therefore, an exponent <1 , which is the case for the global data set, will lead to a decrease in the root-to-shoot ratio with increases in size. Interestingly, many optimal partitioning studies have found that root-to-shoot ratios decrease with increases in water and nutrients (Davidson 1969). In short, in examining the role of environment and evolutionary history on biomass partitioning or distribution, one must remove the influence of plant size.

Here we unify the perspectives used in biomass partitioning and distribution studies by examining how phylogeny and growth form (i.e., evergreen trees, deciduous trees, shrubs, forbs, and graminoids), as well as leaf trait differences that may largely explain leaf mass differences between angiosperms and gymnosperms, influence the residual variation in biomass partitioning and distribution once plant size is controlled for. Specifically, we were able to address (1) the relative importance of phylogeny versus growth form in residual biomass partitioning and distribution, (2) whether biomass partitioning and distribution patterns in leaf, stem, and root mass are phylogenetically conserved, and (3) the role of leaf traits such as specific leaf area, photosynthetic rate, and leaf life span in the distribution of leaf biomass.

Methods

Data Sets

A global database containing arboreal conifers, monocots, and dicots, in addition to herbaceous species and seedlings, was used to examine the effects of phylogeny, growth form, and leaf traits on biomass partitioning and distribution. The bulk of these data were from Cannell (1982), which contains organ mass and annual production rates for arboreal monocots, dicots, and conifers, with additional data from the primary literature on organ biomass for seedlings and herbaceous species to broaden the size range (Enquist and Niklas 2002; Niklas and Enquist 2002).

The Cannell data (1982) are standardized to 1.0 ha and contain plant density, total basal stem diameter, standing biomass, and annual production rates of stem, bark, foliage, roots, and fruits as well as latitude, elevation, and age of dominant species. Organ mass and production rates per individual were computed using total standing organ mass, total organ production, and plant density. Data used for analyzing biomass partitioning were generally from even-aged conspecific stands, and production was often an average of several years, which would reduce variance in organ biomass and production. The full data set contains more than 200 species from ca. 600 sites worldwide.

Taxonomic information was added to the database from the division to the species level. Taxonomic classifications were used as a proxy for phylogenetic relatedness in some analyses. This approach appears reasonable because all of the taxa used are considered monophyletic by recent molecular analyses. Taxonomic information was obtained from the Angiosperm Phylogeny Web site (Stevens 2002) for angiosperms,

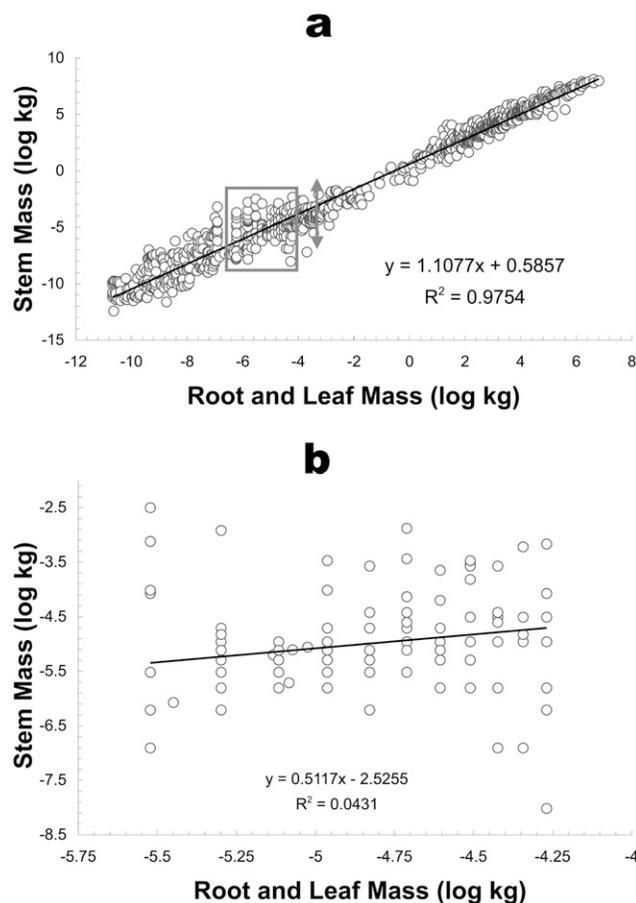


Fig. 2 Allometric relationship between stem mass and total mass minus stem mass viewed across two different size ranges. *a*, Allometric relationship between stem mass and root plus leaf mass (or total mass minus stem mass). Residual variation (variation on the Y-axis [arrow]) around the relationship appears to be very small when examined over 20 orders of magnitude. *b*, Enlargement of the square in *a*. The residual variation in stem mass is similar to and even greater than the variation in body size. Therefore, it appears that size does not play as important a role in biomass distribution in this figure as in the figure above, which encompasses a broader size range.

which bases phylogenies on the most recent molecular analyses of angiosperms with nodes having substantial support (>80% bootstrap values). Phylogenetic information for gymnosperms was obtained from the national plants database (USDA, NRCS 2002). In addition, these analyses and their results were backed up with phylogenetic analyses based on node ages instead of taxonomic levels (see analyses).

An additional data set was used to examine the relationship between leaf traits and biomass distribution. GLOPNET is a database containing multiple leaf traits such as leaf mass area (g cm^{-2}), maximum photosynthetic rate, leaf life span, and dark respiration rate (Wright et al. 2004). Species in this data set that overlapped with the biomass distribution data set were used in the analyses.

Statistical Analyses

Residual variation. Residual variation from the fitted allometric scaling relationships was used in all of our analyses. The residuals were saved from the biomass distribution and allocation regressions for leaf, stem, and root mass and production as well as total annual production. The regressions for leaf, stem, and root mass were performed against total mass minus the response variable to create independence, while the regressions for annual production were performed against the total mass. The residuals for all of the biomass partitioning and distribution data are completely independent of size, and therefore, all further analyses are looking at the variation in partitioning and distribution after the effects of size are considered.

Phylogenetically structured variation. This analysis was adapted from an analysis examining phylogenetically structured environmental variation (Desveves et al. 2003). A series of multiple regressions were used to determine the amount of residual variation in biomass and production explained by phylogeny, growth form, and both phylogeny and growth form. The variation due to phylogeny is measured using a patristic distance matrix, a matrix of distances between all of the tips in the phylogeny, which was produced in Phylocom (<http://www.phylodiversity.net/phylocom/>; Webb et al. 2004). The node ages are determined from the fossil record, and the phylogenetic relationships are determined using recent molecular analyses (Stevens 2002). Given that phylogenetic relationships are based on molecular analyses, the risk of homoplasy should be reduced. In addition, simulations suggest that error in branch lengths and the tree structure should have little effect on phylogenetic analyses (Martins and Garland 1991; Diaz-Uriarte and Garland 1996).

The mean residuals for stem, root, and leaf mass and production were used for each species. The first multiple regression looks at the effects of growth form on the trait of interest (in this case, stem, root, and leaf mass and production residuals). The next multiple regression assesses the effect of phylogeny on the trait of interest. The variation due to phylogeny is determined with a phylogenetic distance matrix produced in Phylocom, which is then put into a principal components analysis (PCA) to determine the axes of variation. The multiple regression then assesses the effect of all the principal components (PCs) on the trait of interest. The third multiple regression looks at the effects of growth form and phylogeny on biomass residuals, using the phylogenetic PCs that had a significant effect

from the previous analysis. The variation because of growth form is equal to the R^2 from the third analysis minus the R^2 from the second. The variation from phylogeny is equal to the R^2 from the third analysis minus the R^2 from the first. And the variation from both is equal to the R^2 from the plus R^2 from the second minus the R^2 from the third. The residual variation, not accounted for by phylogeny or growth form, is equal to 1 minus the sum of the previous three computations (Desveves et al. 2003).

Phylogenetic trait conservatism. Two separate analyses were used to examine trait conservatism in biomass distribution and allocation. The first method was a nested ANOVA performed in R. The nested ANOVA partitions variance into each taxonomic level, where variation at each level subtracts out variation at the next higher level. Taxa used in these analyses were all considered monophyletic (Stevens 2002). Traits in which a large amount of the variation is contained within higher taxonomic levels indicate that the trait is phylogenetically conserved (Promislow et al. 1992; Niklas 1994; Nealen and Ricklefs 2001; Guo et al. 2003). The nested ANOVA was performed on leaf, stem, and root mass and production residual variation using the nested taxonomic levels as the explanatory variables.

An additional analysis was used to determine trait conservatism to correct for taxonomic levels comparing clades of different ages, which is a shortcoming of using taxonomy as a proxy for phylogeny (Martins and Garland 1991). The program Phylocom (Webb et al. 2004) was used to determine which traits were phylogenetically conserved. The measure of trait conservatism is essentially determined by examining the magnitude of contrasts across the tree (<http://www.phylodiversity.net/phylocom/>; Webb et al. 2004). If most of the divergences between related species have similar trait values, then the phylogenetic signal is stronger and indicates a more conserved trait. A nonconserved trait should have large trait differences near the tips of the tree and smaller trait differences in the vicinity of the root. The phylogenetic megatree used in this analysis (fig. 3) was generated using Phylomatic (<http://www.phylodiversity.net/phylomatic/>; see also Webb et al. 2004), with branch lengths added in Phylocom. As the backbone of its phylogenies, Phylomatic uses the Angiosperm Phylogeny Web site, which uses recent molecular phylogenetic analyses and nodes with >80% bootstrap support (Stevens 2002). The use of recent molecular data should reduce the risk of homoplasy. In addition, it is important to note that error in branch lengths and minor error in phylogenetic relationships appear to have negligible effects on phylogenetic analyses (Martins and Garland 1991; Diaz-Uriarte and Garland 1996). Significance testing for trait conservatism is based on 1000 randomizations of the trait values across the tips. The average trait residuals for each species were used in the analyses.

Angiosperm/gymnosperm divergence. Based on the results of the trait conservatism and phylogenetically structured variation analyses, variation between angiosperms and gymnosperms were investigated. Differences were examined for leaf mass, leaf annual production, total annual production, and production per unit leaf mass using an ANOVA on the mean residuals for each species.

Leaf trait analyses. Angiosperms and gymnosperms diverge in a number of respects. In addition to these clades

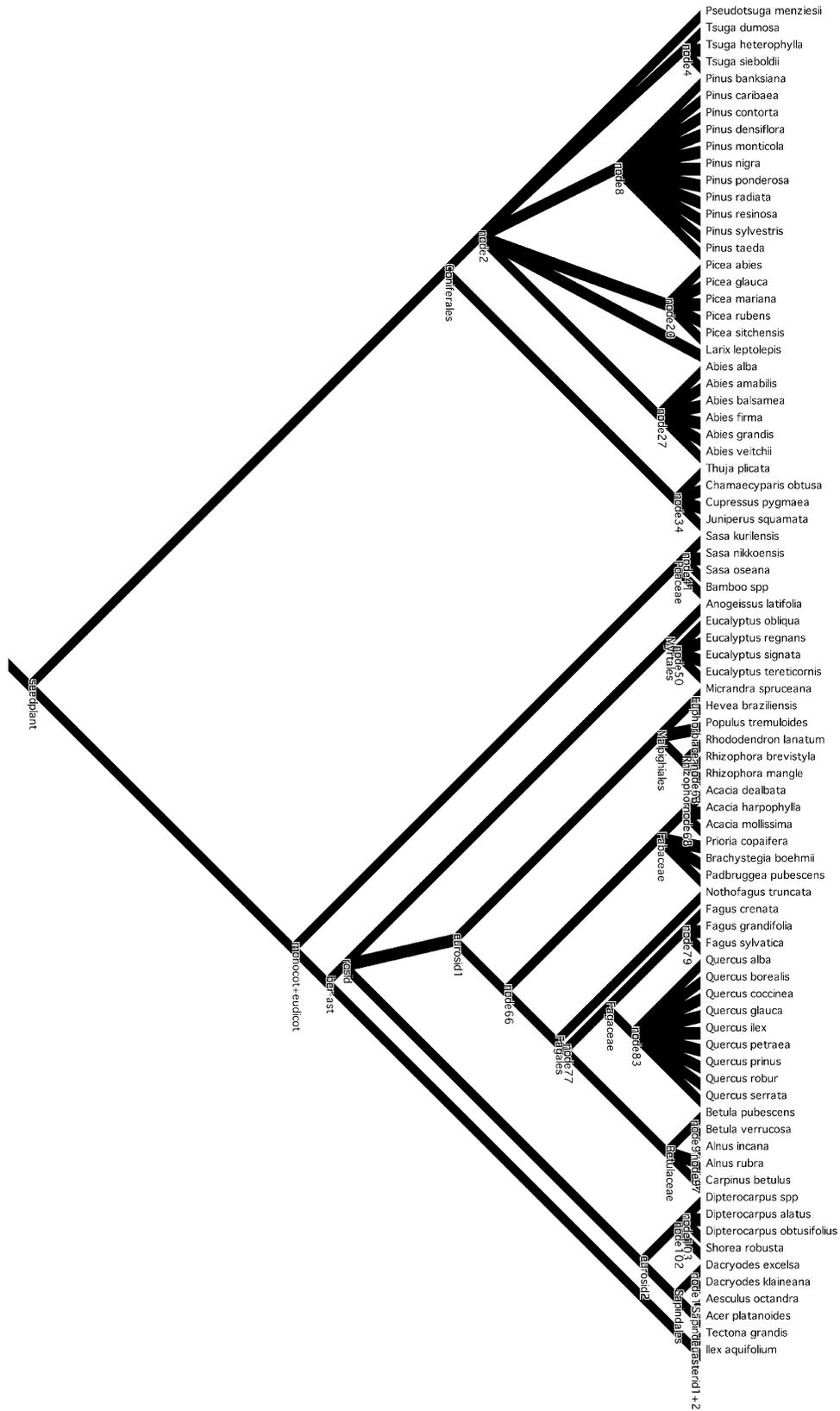


Fig. 3 Phylogenetic supertree of seed plant species generated using Phylocom. Branch lengths are based on fossil data and are not drawn to scale. The relationships in this tree are used in the phylogenetic analyses.

having different evolutionary histories, they possess dissimilar leaf morphologies and experience differing ecological habitats (Givnish 2002). Given that our data set consists of primarily evergreen conifers and deciduous angiosperms that experience similar environmental conditions, the most notable difference between these clades in our data set is their leaf morphology. We examined the relationship between leaf mass distribution and leaf traits to determine whether leaf traits may contribute to the divergence between angiosperms and gymnosperms. This was done by pairing the matching species in the GLOPNET data set (Wright et al. 2004) and the biomass data set. There were multiple measures for each measurement of each species, and therefore, the mean leaf mass residuals and mean leaf trait data were used. The \log_{10} of specific leaf area (SLA), maximum photosynthetic rate (A_{\max}), leaf life span (LL), and the first principal component axis from these three highly correlated traits (Reich et al. 1997; Wright et al. 2004) were used to explain variation in \log_{10} leaf mass residuals using an ordinary least squares (OLS) regression. An OLS regression was used because leaf traits and leaf mass residuals have different units of measurement, and error is expected to be dissimilar (Sokal and Rohlf 1995). SLA and associated traits can vary within a species or even an individual depending on the micro-environment, and therefore, using the average for a species adds error to the analysis. Additionally, the individuals from the data sets and their locations were different. Consequently, any presence of a relationship between leaf mass and leaf traits may signify a much stronger relationship than what actually appears in the analyses.

Predictions were made for the relationship between leaf mass residuals and leaf traits based on the assumption that leaf mass residuals should scale isometrically with LL. A plant with leaves having a life span of 2 yr should have twice as much leaf mass as a plant with a LL of 1 yr, all else being equal. Further predictions were easily made based on the relationships between LL and the other leaf traits. LL span is negatively related to the SLA with an exponent of -1.34 and negatively related to the photosynthetic potential of the leaf, A_{\max} , with an exponent of -1.71 (Wright et al. 2004). Based on the prediction that leaf mass residuals should scale isometrically with LL and the relationships between leaf traits, the following predictions were made between leaf mass residuals and leaf traits:

$$\text{Leaf mass residuals} \propto \text{LL}^{1.00}, \quad (4)$$

$$\text{Leaf mass residuals} \propto A_{\max}^{-1.34}, \quad (5)$$

$$\text{Leaf mass residuals} \propto \text{SLA}^{-1.71}. \quad (6)$$

Results

Phylogenetically Structured Variation

A series of multiple regressions were used to determine how much of the residual variation in biomass distribution was the result of phylogeny, growth form, and both phylogeny and growth form. This analysis was performed for only stem mass, leaf mass, and leaf production residual variation (table 1). Both

Table 1

Variation for Stem Mass, Leaf Mass, and Leaf Annual Production due to Growth Form, Phylogeny, and Phylogenetically Structured Growth Form

Characteristic	Phylogeny and growth form			Residual
	Related to growth form	Related to growth form and phylogeny	Related to phylogeny	
Stem mass	.016	.089	.440	.455
Leaf mass	.129	.098	.345	.428
Leaf production	.004	.129	.181	.686

Note. The phylogenetically structured growth form variation is the variation that is explained by both growth form and phylogeny. The residual is the variation that is not explained by either phylogeny or growth form.

growth form and phylogeny were significant for stem mass ($R^2 = 0.11$, $P = 0.0298$ and $R^2 = 0.53$, $P < 0.0001$, respectively), leaf mass ($R^2 = 0.23$, $P = 0.0002$ and $R^2 = 0.44$, $P < 0.0001$, respectively), and leaf production ($R^2 = 0.13$, $P = 0.0326$ and $R^2 = 0.31$, $P = 0.0092$, respectively). The analysis was not used on root mass and stem, root, and total production residuals because growth form was not significant. However, it is important to note that phylogeny was significant for root mass ($R^2 = 0.38$, $P < 0.0001$) and total annual production ($R^2 = 0.26$, $P = 0.0436$), and there was a trend for root mass production ($R^2 = 0.21$, $P = 0.0922$).

For stem mass residuals, most of the variation was the result of phylogeny. Only 1.6% of the variation was related strictly to growth form; 44% was from phylogeny, and 8.9% of the variation in stem mass residual variation was because of both phylogeny and growth form. Almost half of the residual variation, 45.5%, was left to be explained by other factors. For leaf mass residuals, the largest fraction of variation was still explained by phylogeny. However, growth form explained a larger amount of the variation in leaf mass residuals, 12.9%, than it had for stem mass, 1.6%. Phylogeny explained 34.5% of leaf mass residual variation, and 9.8% of the variation was explained by both growth form and phylogeny. A large fraction of the variation, 42.8%, was residual. Interestingly, leaf mass production residuals varied from the leaf mass residuals in that very little variation was related to growth form, 0.4%, and the variation due to phylogeny, 18.1%, was similar to that due to both phylogeny and growth form, 12.9%. Most of the variation was residual, 69.6% (table 1).

Phylogenetic Trait Conservatism

A nested ANOVA was used to determine whether biomass distribution and allocation is phylogenetically conserved for seed plants. Most of the variation in leaf, stem, and root mass residuals was explained by the lower taxonomic levels (fig. 4a). However for leaf mass residuals, almost one-fourth of the variation was explained by the division level, or the split between the angiosperms and gymnosperms, indicating that leaf mass is more conserved. Conversely, most of the variation in stem and root mass was at the species level or below, with no variation explained above the family level. While none of the annual production residuals were explained

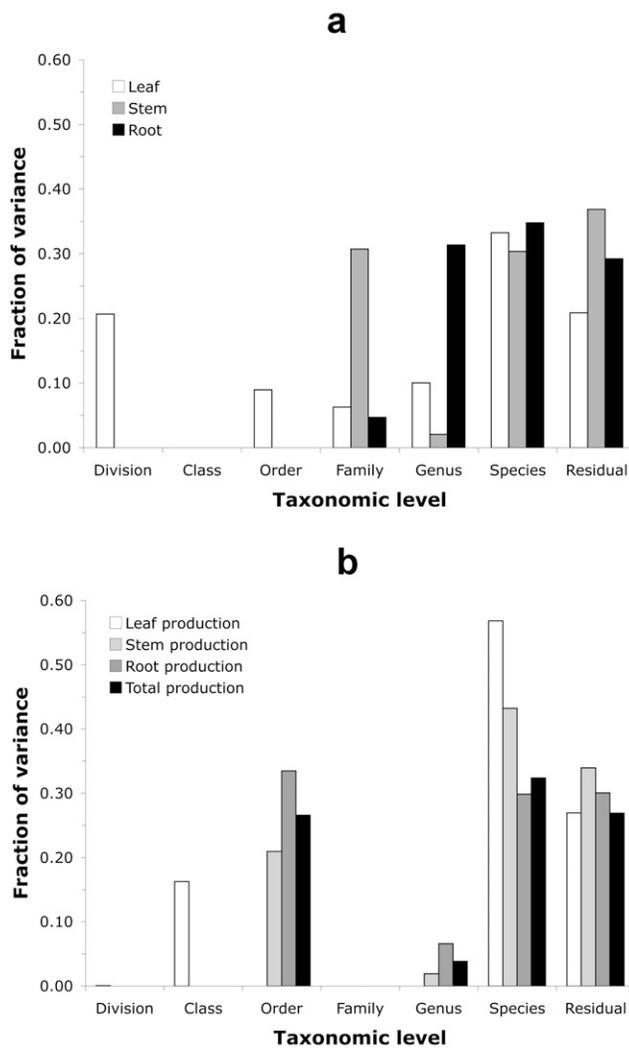


Fig. 4 Amount of variation in distribution and partitioning explained by each taxonomic level. Fractions of variation for each taxonomic level of each component are all significant, mostly $P < 0.0001$, but all $P < 0.05$. *a*, Most of the variation in leaf, stem, and root mass residuals is explained by the species and below the species (residual) level. Only leaf mass residuals have variation explained above the family level. *b*, The majority of the variation in leaf, stem, root, and total annual production residuals is explained by the species and below the species (residual) level. A small portion of the variation in leaf, stem and root production is explained above the family level; however, no variation is explained at the division level.

by the division level (fig. 4*b*), a small amount of leaf mass production was explained by class, and some stem and root mass production was explained by order. However, the majority of leaf, stem, and root production was explained by the species level or below.

A separate program, Phylocom, was used as a second, more robust measure of trait conservatism. This analysis works similarly to the taxonomic nested ANOVA, except instead of using taxonomic level to determine the spread of variation, node ages are used. Leaf mass residuals were significantly conserved ($P = 0.004$); however, stem and root mass residuals in addition to leaf, stem, root, and total an-

nual production were not ($P = 0.36$, $P = 0.86$, $P = 0.64$, $P = 0.30$, $P = 0.35$, and $P = 0.29$, respectively), lending support to what was found by the nested ANOVA.

Angiosperm/Gymnosperm Divergence

The considerable divergence in leaf mass between angiosperms and gymnosperms, in addition to variation in leaf mass having a large component explained by growth form and phylogenetically structured growth form, compels further investigation. Differences between angiosperms and gymnosperms were investigated by performing a *t*-test on the residual variation of leaf mass. Gymnosperms have higher leaf mass residuals than angiosperms ($P < 0.0001$, $R^2 = 0.49$). Despite the higher leaf mass residuals of gymnosperms, angiosperms had higher residuals in annual leaf production ($P = 0.0002$, $R^2 = 0.07$). Similarly, angiosperms have higher residuals for total annual production than gymnosperms ($P = 0.0188$, $R^2 = 0.03$). The combination of these factors lead to angiosperms having a much higher amount of production for a given leaf mass ($P < 0.0001$, $R^2 = 0.61$).

Leaf Trait Analyses

SLA, LL, and A_{\max} were compared with leaf mass residuals to determine whether these factors explain the differences between angiosperms and gymnosperms. The predictions based on the assumed relationship between variation in leaf mass and LL and the relationships among the leaf traits were given in equations (4)–(6). LL was positively related to the leaf mass residuals with the confidence interval (CI) of the slope including the prediction of 1 (fig. 5*a*) ($\beta = 0.84$; 95% CI: 0.48, 1.20; $R^2 = 0.45$; $P < 0.0001$). The A_{\max} and SLA were both negatively related to the leaf mass residuals (fig. 5*b*, 5*c*). The relationship between A_{\max} and leaf mass residuals included the predicted exponent of -1.34 ($\beta = -1.49$; 95% CI: -0.91 , -2.06 ; $R^2 = 0.51$; $P < 0.0001$). The relationship between SLA and leaf mass residuals was less than the prediction of -1.71 but followed the predicted direction ($\beta = -0.82$; 95% CI: -0.19 , -1.46 ; $R^2 = 0.12$; $P = 0.0125$). Leaf mass residuals were also compared with the first principal component from a PCA of the leaf traits since LL, A_{\max} , and SLA are highly correlated. The first PC of the three leaf traits was also negatively related to the leaf mass residuals ($\beta = -0.83$; 95% CI: -0.55 , -1.11 ; $R^2 = 0.63$; $P < 0.0001$). This matches what was found with the previous regressions, such that plants with higher LL and lower SLAs and A_{\max} values fall out higher in the leaf mass residuals, and plants with lower LLs but higher SLAs and A_{\max} values have lower leaf mass residuals (fig. 5*d*).

Discussion

There have been numerous studies examining the effects of different ecological and evolutionary factors on plant biomass allocation and distribution (Monk 1966; Davidson 1969; Hunt and Burnett 1973; Bloom et al. 1985; Hunt and Nicholls 1986; Tilman 1988; Iwasa 2000). However, recent studies have shown that some of the variation in biomass allocation can be attributed to changes in size (McConaughay and

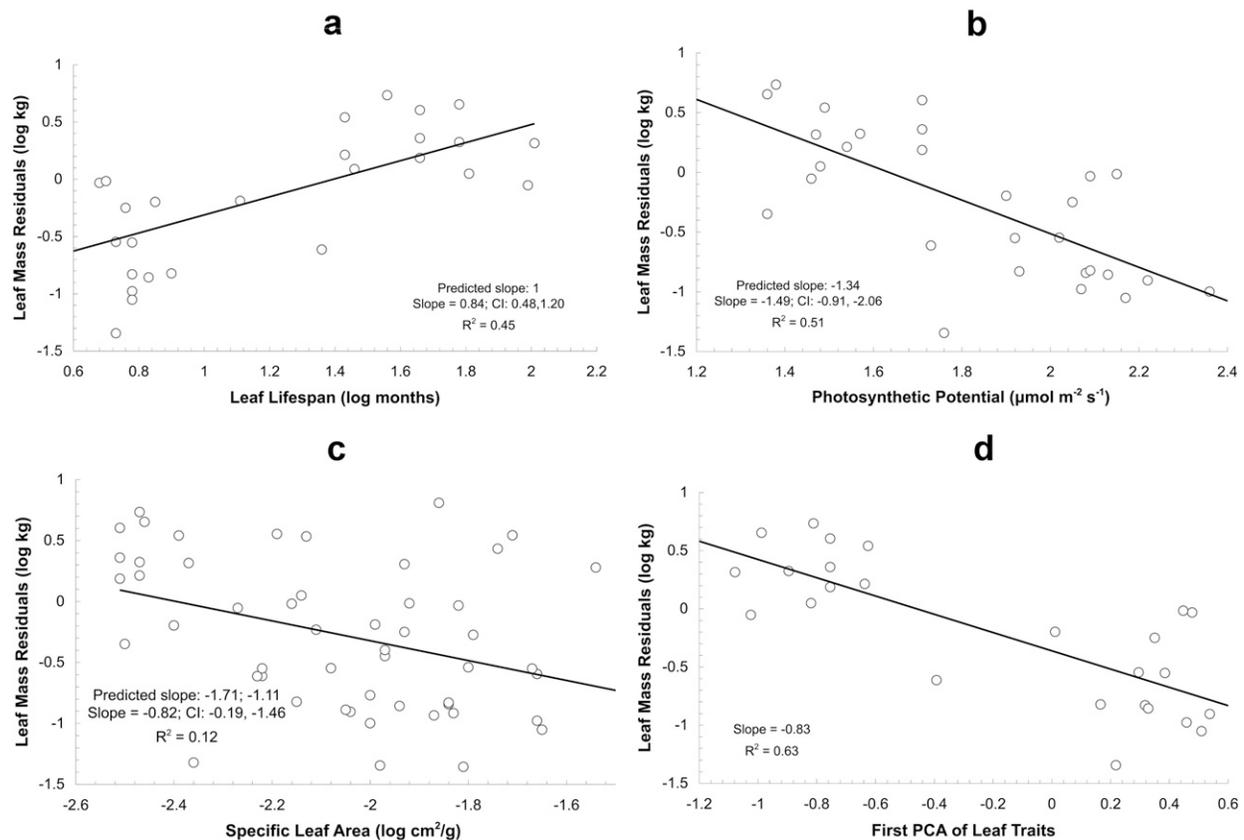


Fig. 5 Relationships between the mean leaf mass residuals and leaf traits for seed plant species. *a*, Leaf mass residuals are positively related to leaf life span (LL). The predicted slope, actual slope with confidence intervals (CIs), and the R^2 value are in the bottom right corner. The CIs overlap with the predicted slope of 1. *b*, Variation in leaf mass is negatively correlated with maximum photosynthetic rate (A_{max}) ($\mu\text{mol m}^{-2} \text{s}^{-1}$). The predicted slope, actual slope with CIs, and the R^2 value are in the bottom left corner. The CIs overlap with the predicted slope of -1.34 . *c*, There is a negative relationship between leaf mass residuals and specific leaf area (SLA). The predicted slope based on the RMA leaf trait relationships and ordinary least squares (OLS) leaf trait relationships, actual slope with CIs, and the R^2 value are in the bottom left corner. The CI does not overlap with the predicted slope of -1.71 ; however, it does with a slope of -1.11 , based on the OLS relationship between SLA and LL. *d*, Variation in leaf mass is negatively related to the first principal components axis from a PCA of LL, A_{max} , and SLA. There is no predicted slope for this relationship; however, the predicted direction is negative. The slope and R^2 values are listed in the bottom left corner.

Coleman 1999; Bernacchi et al. 2000; Enquist and Niklas 2002). Based on the constraints of transporting resources and the photosynthetic harvesting capacity of leaves, an allometric analysis made several predictions concerning how much biomass should be distributed to a particular component relative to other components (Enquist and Niklas 2002). These predictions were supported by the empirical evidence, with 97%–99% of the variation in biomass distribution being explained by size with about one order of magnitude residual variation. These allometric models and the variation surrounding them provide the basis to understand how other evolutionary and ecological factors affect biomass distribution.

Phylogenetically Structured Variation

Phylogeny has been shown to be important to several areas of plant form and function (Brouat et al. 1998; Antunez et al. 2001); however, most biomass distribution and partitioning studies have failed to take evolutionary history into consideration. We attempt to determine how much of the var-

iation in biomass allocation and distribution is constrained by phylogeny. Because the two dominant clades in our study differ both morphologically and phylogenetically, we first try to partition out the variation due to phylogeny from that due to growth form, specifically, the evergreen versus the deciduous habit.

While many studies have overlooked the effects of phylogeny on biomass allocation and distribution, our results indicate that phylogeny alone can explain a significant fraction of biomass partitioning and distribution not explained by plant size. Importantly, phylogeny explains more of the residual variation in stem mass, leaf mass, and leaf production than growth form and growth form related to phylogeny (table 1). In addition, growth form was not even a significant factor in root mass and production variation and total annual production variation, unlike phylogeny. The combination of phylogeny and growth form leave less than half of the variation in stem and leaf mass to be explained by other more proximate sources such as local environmental variation. Interestingly, a much larger portion of the variation was residual for leaf

production than for leaf mass, suggesting that proximate factors, particularly environment, may be a much more important factor for variability in biomass allocation to leaves than for leaf mass distribution. Additionally, neither phylogeny or growth form explained significant variation in stem annual production, again suggesting that biomass allocation to stems is more plastic than stem mass distribution. The combination of these results suggests that while there is some phylogenetic constraint on biomass partitioning, there is still a large portion available to plastic responses to environmental variability. Additionally, the distribution of biomass, which incorporates both allocation and loss over time, is further constrained by evolutionary history.

Phylogenetic Trait Conservatism

In the nested ANOVA, the location of taxonomic variation in biomass distribution and allocation is used to indicate the conservativeness of the trait being examined (Niklas 1994). If most of the variation in the trait is contained in the higher taxonomic levels, this indicates that the trait is conserved, while variation in the species or the residual level indicates more plasticity in that trait. Our analysis showed that about 30% of the variation in leaf mass is explained above the family level, with 20% of the variation explained by the divergence between angiosperms and gymnosperms (fig. 4a). Conversely, neither stem nor root mass had any variation explained above the family level. While all three organ masses had significant fractions of variation explained at the lowest taxonomic levels, suggesting considerable plasticity, the large fraction of leaf mass variation explained by the division level also demonstrates a reasonable amount of phylogenetic conservatism. In addition, previous analyses have shown a strong trade-off between stem and root mass residuals existing even within species (M. C. McCarthy, B. J. Enquist, and A. J. Kerkhoff, unpublished manuscript), further indicating that these traits may be more plastic in order to adjust to microenvironmental variation. While leaf, stem, and root production had a small amount of variation explained above the family level, these traits contained most of the variation (60%–83%) at the lowest taxonomic levels (fig. 4b), with no variation explained by division. A small amount of variation in leaf annual production was within class; however, more than 50% of leaf production variation was contained in the species level, and about a third of the variation in leaf production was residual. The production results suggest that biomass partitioning may demonstrate considerable plasticity. Additionally, leaf partitioning appears to be much more plastic than leaf mass distribution.

This analysis was supported by an additional analysis in Phylocom. Phylocom (Webb et al. 2004) bases the measure of trait conservatism on the amount of variation explained by older nodes in the phylogeny compared with younger nodes instead of different taxonomic levels. Not surprisingly, the results from Phylocom showed that leaf mass residuals were significantly phylogenetically conserved ($P = 0.004$). However, stem and root mass were not ($P = 0.36$ and 0.86 , respectively). Variation in leaf, stem, root, and total annual production was also not phylogenetically conserved ($P = 0.64$, 0.03 , 0.35 , and 0.29 , respectively).

Angiosperm/Gymnosperm Divergence

The large amount of variation in leaf mass residuals explained by the angiosperm/gymnosperm divergence was followed up by examining the difference in residuals for leaf mass and production between these clades. Gymnosperms had greater amounts of leaf mass for a given body size than angiosperms. However, this greater amount of leaf mass was not because gymnosperms produce more leaf mass each year. Angiosperms have higher annual leaf production, indicating that the higher leaf mass that gymnosperms have results from retaining leaf mass from previous years instead of adding more leaf mass per year. It may also be expected that because of the higher amounts of leaf mass, gymnosperms should be able to achieve higher total annual production rates. This also does not occur. Although gymnosperms have more leaf mass to photosynthesize with, angiosperms have higher total yearly production. These differences in leaf mass and production between angiosperms and gymnosperms lead to angiosperms having an order of magnitude higher production for a given leaf mass.

Because angiosperms and gymnosperms differ in many ways besides organ partitioning, it is difficult to determine whether the divergence in leaf mass is the result of phylogeny or general growth form and functional differences. Angiosperms and gymnosperms possess diverse leaf morphologies and physiologies, occupy dissimilar ecological niches, and have different evolutionary histories (Midgley 1991; Givnish 2002). While the bulk of the variation in leaf, stem, and root mass appears to be the result of phylogeny, leaf mass is the only factor that also has a substantial portion of the variation due to growth form. In fact, almost a quarter of the variation in leaf mass can be attributed to growth form and phylogenetically structured growth form, which suggests that the differences in leaf morphology between these clades may pose additional constraints to the evolutionary history.

Leaf Trait Analyses

Work on leaf traits by Reich et al. (1997) provides an understanding of how gymnosperms can have greater leaf mass while adding less leaf mass per year and how angiosperms can have higher annual production with less leaf mass. SLA, which is leaf area divided by leaf mass, is positively correlated with A_{\max} . In addition, SLA is negatively correlated with LL (Wright et al. 2004). A leaf with smaller SLA will therefore have lower photosynthetic rates for a given leaf mass and a longer life span than a leaf with higher SLA. Because gymnosperms tend to have lower SLAs than angiosperms, these patterns would lead to gymnosperms having higher leaf masses because of accumulation of long-lived leaves and lower production rates per unit leaf mass.

The relationships between leaf mass and leaf traits can be incorporated into the allometric coefficient of the leaf mass allometric regression such that $M_L = \beta M_T^{3/4}$, where $\beta = LL^1$. This demonstrates that variation in leaf mass is a function of the life span of leaves and therefore the number of cohorts of leaves contained at any one time. Several predictions were made based on this assumption and the relationships between the leaf traits.

We tested the predictions by comparing the SLA, LL, and A_{\max} to the leaf mass residuals. The relationship between LL

and the leaf mass residuals was close to the prediction of unity, 0.84, with the CIs including 1 and 0.49–1.20 (fig. 5a). The R^2 was relatively high for this relationship, 0.45, with LL accounting for almost half of the variation in leaf mass residuals. Similarly, the relationship between the potential photosynthetic rate and leaf mass residuals (fig. 5b) was very close to the prediction of -1.34 (slope = -1.49 ; 95% CI: $-0.91, -2.06$), with potential photosynthetic rate explaining slightly more than half of the variation in leaf mass residuals ($R^2 = 0.51$). The slope of the relationship for SLA and leaf mass residuals (fig. 5c) was greater than the prediction of -1.71 (slope = -0.82 ; 95% CI: $-0.19, -1.46$) with a much lower R^2 value ($R^2 = 0.12$). The lack of fit for this relationship is not surprising. First of all, the measurements for the leaf traits were not from the same individuals as the measurements the leaf mass was taken from. Because SLA can vary from individual to individual depending on the microenvironment, this is most likely adding large amounts of error to these analyses. Additionally, the relationship between SLA and LL, which was used to generate the predicted exponent of -1.71 between SLA and leaf mass residuals, contains much more variation than the other relationships between leaf traits because it is affected by precipitation (Reich et al. 1997; Wright et al. 2004). This extra variation leads to a lower R^2 value, leading to an increase in the reduced major axis slope, which is equal to the OLS slope divided by r (Sokal and Rohlf 1995). The least squares slope between SLA and LL is -1.11 , which is included in the CI between SLA and the leaf mass residuals, $-0.19, -1.46$.

To further support the strength of the relationship between leaf mass residuals and the leaf traits, the first principal component axis of the leaf traits is highly correlated with leaf mass residuals (fig. 5d) (slope = -0.83 , $R^2 = 0.63$, $P < 0.0001$). Plants with higher LL and lower SLA and photosynthetic potential, such as conifers, fall out higher in the leaf mass residuals, as would be expected, and plants with lower LL and higher SLA and photosynthetic potential, like many deciduous angiosperms, have lower leaf mass residuals. The strength of the relationships between leaf traits and leaf mass residuals is extremely impressive given the amount of error expected from pairing data sets with different individuals and using the mean leaf mass residuals and leaf traits. These relationships may largely explain the differences between angiosperms and gymnosperms in their leaf mass distributions. Additionally, these patterns suggest that leaf morphology may constrain leaf mass distribution.

Conclusions

It has become increasingly apparent that body size governs much of form and function for both animals (West et al.

1999) and plants (Niklas 1994; Enquist and Niklas 2002; Niklas and Enquist 2002). While the majority of biomass partitioning and distribution studies have concentrated on environmental effects (Davidson 1969; Hunt and Burnett 1973; Hunt and Nicholls 1986; Iwasa 2000), most have ignored the importance of body size and phylogenetic and growth form constraints. The biomass partitioning patterns found by Enquist and Niklas (2002) were used as a baseline to understand how other factors may constrain biomass distribution and allocation after the effect of size is accounted for.

Our results indicate that phylogeny seems to explain a significant fraction of the variation in biomass partitioning when looking globally across a wide range of body sizes. Also, angiosperms and gymnosperms show important differences in leaf mass and production rates that appear to be related to leaf morphology and physiology. Thus, by using the allometric models as a baseline to understand residual variation in biomass partitioning and distribution, in addition to incorporating differences due to leaf phenology and other factors into the allometric coefficients of the biomass distribution model, we can obtain a more detailed understanding of processes influencing variation in organ partitioning across the spermatophytes.

Our results have important implications for ecological studies. Understanding interspecific differences in organ distribution must first assess constraints due to plant size, evolutionary history, and growth form. Furthermore, plant biomass partitioning studies need to consider constraints due to allometry and perhaps growth form. For example, a species that displays limited variation in leaf morphology may also be less plastic in biomass partitioning. We suspect that future studies that incorporate phylogeny, size, function, and environmental conditions together will likely provide insight into the ecological and evolutionary processes that shape differences in botanical biomass partitioning and distribution.

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