Global Allocation Rules for Patterns of Biomass Partitioning

Enquist and Niklas proposed global rules for plant biomass allocation allometry (*1*). However, early plant ontogeny (from emergence to ~5 g plant dry mass) follows different rules than they propose, and this early stage constitutes a crucial period for establishment, with plant size ranging across six orders of magnitude. At this crucial stage, their model falls short in a number of important respects.

Enquist and Niklas first suggested that total leaf area $\propto M_L \propto M_T^{3/4}$, where M_L is standing leaf dry mass and M_T is total plant dry mass. In other words, specific leaf area (*SLA*), defined as total lamina area/M_L, remains constant. After producing their first true leaves, however, plants commonly decline dramatically in *SLA* (*2–4*). For juveniles of seven woody species ranging in M_T from 9 mg to 27 g, we found that $SLA \propto M_T^{-0.22}$ (*4*). This scaling may change in later ontogeny, but *SLA* declines further from saplings to trees (*5*, *6*).

Enquist and Niklas also proposed that $M_L \propto M_S^{3/4} \propto M_R^{3/4}$, where M_S is stem dry mass and M_R is root dry mass (*1*). For small plants, however, their model produces up to a tenfold error. The data for early ontogeny actually support $M_L + M_S \propto M_R$—a constant shoot-to-root ratio (*2*, *4*, *7*, *8*)—as is predicted by the coordinated growth of shoot and root meristems (*7*, *9*). Given $M_S \propto M_R$, the typical pattern is $M_L \propto M_T$ in early ontogeny (*2*, *4*, *10*, *11*).

Finally, Enquist and Niklas assumed that gross photosynthesis, B, $\propto M_T^{3/4}$—an analogy with Kleiber's Law—but data are insufficient to support this assumption for early ontogeny. That pattern does fit realistic ontogenetic allometries, however, if the leaf-area-based photosynthetic rate (P_{area}) is stable. P_{area} sometimes increases ontogenetically with plant size, but only slightly, as the leaf mesophyll thickens (*5*, *6*), because fewer photons penetrate additional mesophyll layers (*12*). If $SLA \propto M_T^{-1/4}$ and $M_L \propto M_T$, then leaf area $\propto M_T^{3/4}$ and $B \propto M_T^{3/4}$. Here, as in so many processes in early establishment, *SLA* plays a fundamental role (*13–15*).

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4. For seven species of woody broad-leaved evergreens, we excavated plants in a range of sizes in the understories of three forests in southern Spain (for six of the species, n = 20 to 40; for the seventh, n = 10). We determined allometries relating variables x and y (i.e., log y = α log x + β), with α calculated as the reduced major axis slope (*16*). For each allometry, different species typically had the same slope with different intercepts; we calculated common slopes. 95% confidence intervals and R^2 values were determined as for least-squares regression (*16*). *SLA* scaled with M_T, α = -0.22 ± 0.024 (R^2 = 0.66); shoot dry mass scaled with root dry mass, α = 1.02 ± 0.078 (R^2 = 0.83); M_S scaled with M_R, α = 1.10 ± 0.085 (R^2 = 0.83); M_L scaled with M_T, α = 0.97 ± 0.052 (R^2 = 0.92) (*17*).
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Response: Sack *et al.* draw much-needed attention to the difference between the allometry of early plant ontogeny and the allometry of interspecific comparisons using data from mature individuals. Using intraspecific data for a few species from closed canopy forests, where light is likely limiting, Sack *et al.* claim that leaf properties (specifically *SLA*) change during early ontogeny, such that our model obtains inaccurate estimates of above-ground biomass.

We agree that *SLA* is an important factor in plant ecophysiology. However, the scaling differences noted by Sack *et al.* can be explained in other, equally effective ways. For example, our theory (*1*, *2*) assumes that plants are mature and that leaves are the sole photosynthetic organs. For most of the data we analyzed, that assumption is reasonably accurate; however, it is often violated during early ontogeny, when stem tissues may significantly contribute to photosynthesis. If stems do contribute significantly to photosynthesis, our model predicts that the sum of leaf and stem biomass will scale in a near-isometric way with respect to root biomass, as noted by Sack *et al.*

Similarly, as we stated (*1*), our model assumes that maternal effects (such as metabolites stored in endosperm or megagametophytes and used in early plant development) are negligible. If this assumption is violated, as it may be in the case of seedling or juvenile establishment, observed standing biomass relations will differ from those predicted by our model. Therefore, a variety of factors other than changes in *SLA* can account for the differences in juvenile versus mature plant biomass partitioning patterns observed by Sack *et al.* That these differences evoke a "tenfold error" in the predictions of our model for extremely small, juvenile plants is hardly surprising, but it is also somewhat misleading. Our model identifies the functional allometric relations among standing leaf, stem, and root biomass (across rather than within species) based on Model Type II regression analyses. Therefore, the magnitude of "error" in one variable must be placed in the context of the magnitude of "error" in the other variable against which it is regressed. In this regard, the "errors" referred to by Sack *et al.* are comparable across 12 orders of magnitude of body size.

Sack *et al.* also attribute to us statements that we did not make. We explicitly stated that according to allometric theory, "the surface areas over which resources are exchanged with the environment (e.g., leaf surface area, which correlates with M_L) are proportional to the 3/4 power of the total plant biomass" [see also (*3*)]. It cannot escape attention that the resource exchange "surface areas" of leaves include internalized mesophyll surface areas in contact with the air. Further, as noted above, these exchange surfaces might also include stems during early ontogeny. Thus, total exchange surface areas may not be equivalent to total leaf surface area as defined by Sack *et al.* Unfortunately, these and other inaccurate statements detract from many of the valuable points that Sack *et al.* make.

We are nonetheless gratified that Sack *et al.* agree that the 3/4 scaling relation we proposed for gross photosynthesis and total

plant body mass fits "realistic ontogenetic allometries. . .if the area-based photosynthetic rate. . .is stable," noting that such rates sometimes increase "ontogenetically with plant size, but only slightly." Clearly, these observations only bolster the predictions of our model. Indeed, our recent data compilations support a 3/4 scaling of whole plant resource use for both adult and juvenile plants (*4*, *5*).

We agree with Sack *et al.* that allometric relationships for early ontogeny may be very different as a result of a variety of factors, some of which we outlined in (*1*). Neverthe-less, our model accurately predicts the scaling relations among standing leaf, stem, and root biomass across 12 orders of magnitude of body size for monocot, dicot, and conifer species growing under remarkably different environmental conditions. To our knowledge, no other analytically based treatment of vegetative biomass partitioning is as statistically, conceptually, or mechanistically robust.

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