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 $\propto M_r^{1.10} \times M_T^{0.5}$, where $M_r$ 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/$M_r$) 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 $M_L \propto M_T^{0.5} \times M_r^{0.5}$, where $M_L$ 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 $M_L + M_r \propto M_T$—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 $M_L \propto M_T$, the typical pattern is $M_L \propto M_T$ in early ontogeny (2, 4, 10, 11).

Finally, Enquist and Niklas assumed that gross photosynthesis, $B \propto M_T^{0.83}$—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 ($P_{\text{area}}$) is stable. $P_{\text{area}}$ 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 $SLA \propto M_T^{-0.22}$ and $M_L \propto M_T$, then leaf area $\propto M_T^{0.32}$ and $B \propto M_T^{0.67}$. Here, as in so many processes in early establishment, SLA plays a fundamental role (13–15).

**References and Notes**

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 $y = a \log x + b$), with $a$ 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 $M_T$, $a = -0.22 \pm 0.024$ ($R^2 = 0.66$); shoot dry mass scaled with root dry mass, $a = 1.02 \pm 0.078$ ($R^2 = 0.83$); $M_L$ scaled with $M_T$, $a = 1.10 \pm 0.085$ ($R^2 = 0.83$); $M_r$ scaled with $M_T$, $a = 0.97 \pm 0.052$ ($R^2 = 0.92$) (17).

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 ear-
plant body mass fits “realistic ontogenetic allometries. . if the area-based photosynthet-
ic 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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References

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