

Plant energetics and population density

Enquist *et al.*¹ present data from 37 plant species showing that the use of resources by individual plants scales approximately as the 3/4 power of plant mass, as predicted previously from a model of resource use in fractal-like branching structures². Thus, $Q \propto M^{3/4}$, where Q is the resource use, estimated as xylem transport, and M is the plant mass. In addition, their re-analysis of data from 251 populations¹ showed that the 'thinning law' between maximum plant population density (N_{\max}) and plant mass also obeys 3/4-power scaling, with $N_{\max} \propto M^{-3/4}$. From these two data sets, they inferred that population resource use per unit area is approximately independent of plant mass, with $N_{\max}Q \propto M^0$, a relation termed energy equivalence³.

Conversely (and more generally), the thinning law (with exponent $-y$, say) can be viewed as the consequence of energy equivalence and allometric scaling of individual resource use (with exponent y). This resource-based interpretation of the thinning law has been proposed previously for both plant⁴ and animal⁵ populations, but the theoretical derivation² of $y=3/4$ is an important new insight. Energy equivalence itself cannot be explained in any mechanistic sense by allometric scaling of individual resource use, despite apparent claims to the contrary¹, and remains to be accounted for as an empirical observation³.

I suggest that, for plant populations, energy equivalence reflects the facts that: (1) once plant canopies have reached closure, most of the incident radiation per unit area is intercepted^{6,7}; and (2) for well-watered plants, growth rate per unit of intercepted radiation (that is, the light utilization efficiency, or LUE) is approximately independent of plant mass⁸⁻¹⁰. There is now a mechanistic explanation for the latter observation in terms of leaf photosynthetic acclimation to light¹¹. It follows that, for closed canopies not subject to water limitation, population energy use for growth is roughly independent of plant mass, but may vary with incident radiation and LUE. An analogous argument, involving mass-independent population resource capture and utilization efficiency, might also explain energy equivalence in animal populations.

However, a word of caution is needed here. An important counter-example to energy equivalence is given by the well-documented observation that the growth rate per unit area of evenly aged forests eventually declines as individual trees become larger^{12,13}. Above-ground net primary productivity typically reaches a maximum in

young forest stands and then decreases by up to 76%, with an average reduction of 34% according to 13 studies of forest age sequences¹⁴. The rate of decline has important implications for sustainable forest management and the role of forests in the global carbon budget. This apparently universal phenomenon has been attributed, at least in part, to height-dependent hydraulic limitations on leaf stomatal conductance^{14,15}, implying that leaf photosynthetic rate and LUE may not always be independent of plant mass, particularly under water-limited conditions.

In summary, it is probably more appropriate to consider energy equivalence — like the thinning law — as an approximate rule of thumb, rather than as a fundamental law applicable to all plant types under all growth conditions.

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Enquist *et al.*¹ present an interesting analysis of the link between plant size, allometry and mortality. But I believe that their claim that it has a functional basis is misleading when it is scaled up to whole populations.

Transpiration in plants is strongly driven by environmental conditions². It is therefore difficult to compare the transpiration rate per plant among different species unless these plants are exposed to the same environment. This does not apply here, as Enquist *et al.* derived their transpiration rates from a re-analysis of data from the literature. The confounding effect is negligible at the scale of individual plants, given the wide range of rates and dimensions reviewed. But when scaling up to the whole canopy, environmental driving variables such as radiation, water availability and site fertility predominate and tend to obscure any effects of plant size on the function of stands of species. This is clear from a comparison of maximum conductances and

assimilation rates among biomes across the world³.

The transpiration rates that have been scaled up to the level of populations by Enquist *et al.*¹ (see their Fig. 4) seem surprisingly high: rates of about 100 l m⁻² per day (that is, millimetres per day) far exceed the maximum values of 3–12 mm per day derived from a global comparison of plant canopies all over the world⁴. Another meta-analysis of evapotranspiration in coniferous forests and grasslands gave maximum values of 6–7 mm per day (ref. 5).

What is most important, however, is that the conclusions drawn by Enquist *et al.* from their upscaling to whole populations are misleading. It is debatable whether "total energy use or productivity of plants in ecosystems is... invariant with respect to body size": stand chronosequences in forest tree species⁶ indicate that, after canopy closure at the polestage, the leaf-area index tends to decline (as a result of self-thinning, among other processes). In mature canopies, this has a marginal effect on the interception of radiant energy and gross primary production⁷. Net assimilation and above-ground allocation, however, are further reduced by increasing respiratory costs, nutrient immobilization in soil litters and hydraulic constraints⁷⁻¹⁰, which are all a direct result of increasing body size, contributing to the well-known decline in forest growth with tree dimensions and age^{6,8}.

Even the conservative nature of forest evapotranspiration on the regional scale¹¹ seems to be true more at the community than at the population level, resulting from interaction among overstorey and understorey processes³. On the contrary, there are considerable changes in transpiration with stand development¹². The results of Enquist *et al.* do not seem to alter this picture.

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