

Sizing up life and death

Karl J. Niklas*

Department of Plant Biology, Cornell University, Ithaca, NY 14853

Determining the “rules” that govern the lifespans and birth and death rates of organisms is a central goal of population biology and lies at the heart of understanding a broad range of ecological and evolutionary phenomena (1, 2). Yet, until recently, quantifying these rules and, more importantly, providing a mechanistic explanation for how they operate have eluded biologists. This gap in our knowledge is understandable. Organisms manifest lifespans that range on the order of minutes or hours in the case of bacteria to many hundreds or thousands of years in the case of some tree species. In addition, for organisms like some unicellular algae and plants, which can reproduce asexually, the application of concepts like “birth” and “death” can be problematic or ambiguous. Nevertheless, the work of Marbà *et al.* (3) in this issue of PNAS provides reason to hope that the life and death dynamics of otherwise very dissimilar organisms abide by predictable and explicable rules. Equally important, their work demonstrates that lifespan and birth/death rates scale with respect to body size across aquatic and terrestrial and unicellular and multicellular plant species in ways that accord remarkably well with those predicted by a generalized theory for the metabolic optimization of life history traits (4, 5).

To understand this theory and fully appreciate the significance of the analyses of Marbà *et al.* (3), we must first consider the observation that many biological traits vary with body size in a manner conveniently described by the allometric equation $Y = \beta_0 M^\alpha$, where Y is the variable of interest, β_0 is the normalization “allometric constant” (that can nevertheless vary numerically with the nature of Y , the kind of organism studied, or the environmental conditions attending growth and development), M is total individual body mass, and α is the allometric or “scaling” exponent. Second, numerous studies of organisms ranging from bacteria and algae to terrestrial plants and animals have shown that many important functional traits scale as quarter-powers of total body mass. For example, across ecologically and phylogenetically very different organisms spanning 20 orders of magnitude in body size, α is $\approx 3/4$ for metabolic and growth rates, $-3/4$ for population densities, and $-1/4$ for biomass-doubling times or “birth rates” (5–11) (Fig. 1).

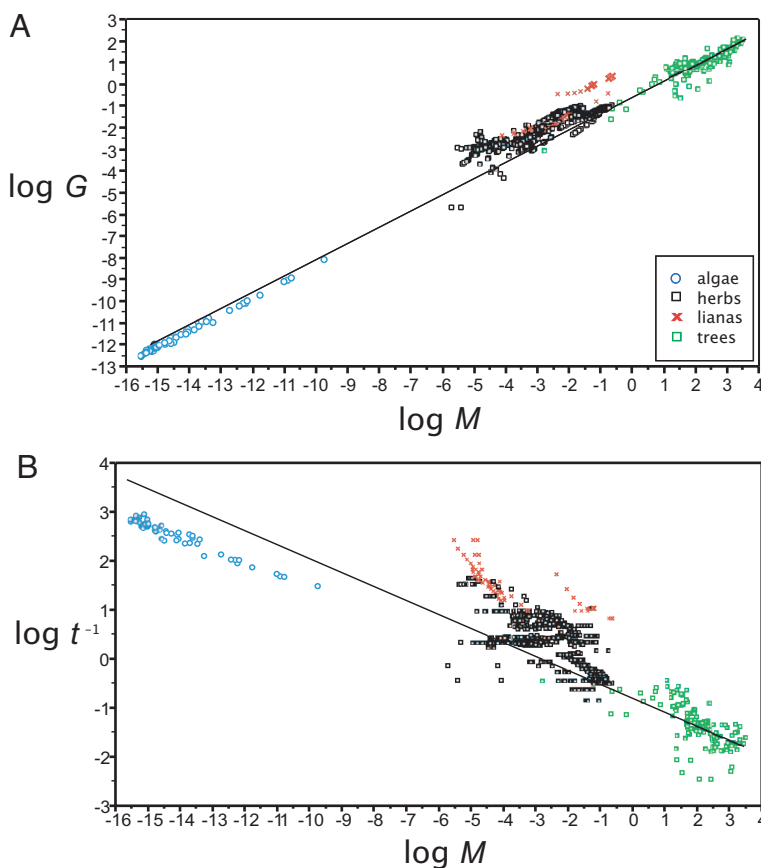


Fig. 1. Total annual growth in dry mass per individual plant (M) and the reciprocal of body-mass-doubling time (t^{-1} or birth rate) plotted as functions of total body mass across algae, herbs, lianas, and trees (see key for symbols). Solid lines are standardized major axis regression curves for all data ($n = 1,176$). The data are from a variety of sources. (A) Growth rates plotted against body mass manifest a scaling exponent of $\approx 3/4$. (B) Reciprocal of doubling times plotted against body mass manifest a scaling exponent of approximately $-1/4$.

Yet, despite many attempts to explain why these and other scaling exponents take on the numerical values that they do, no theory has been entirely successful, that is, perhaps not until the one proposed by Geoffrey B. West, James H. Brown, and Brian J. Enquist (4), which has been transfigured to predict the scaling of life history traits based on the perspective of metabolic optimization (5).

Specifically, this metabolic theory predicts that lifespan, E , should scale optimally as the $1/4$ power of total body mass (i.e., $E \propto M^{1/4}$) and that birth and death rates, B and D , should scale as the $-1/4$ power of body mass (i.e., $B \propto M^{-1/4}$ and $D \propto M^{-1/4}$), from which it follows that population growth rates are predicted to be size-independent across

different kinds of organisms (i.e., $B \propto D$). Some of these scaling relationships have been observed empirically and validated statistically well before the publication of this theory or the work of Marbà *et al.* (3–5). For example, across three very different functional plant-species groups (unicellular algae, herbs–graminoids, and tree species), individual growth in body mass, G , has been shown previously to scale as the $3/4$ power of body mass (i.e., $G \propto M^{3/4}$) (see refs. 12 and 13), from which it follows that the doubling time in body mass will, on av-

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*E-mail: kjn2@cornell.edu.

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erage, scale as the $-1/4$ power of body mass, i.e., $(1/M) (dM/dt) \propto M^{-1/4}$ (Fig. 1).

However, based on an extensive data set gathered in part from published work, Marbà *et al.* (3) have now demonstrated that plant mortality and birth rates scale as the $-1/4$ power of body mass, whereas lifespans scale as the $1/4$ power of mass across virtually every major functional species group, including macroalgae, mosses, ferns, shrubs, lianas, seagrasses, and terrestrial succulents as well as mangroves and other tree species. Marbà *et al.* also have demonstrated that, across most of these species groups, population growth rates, $r = B/D$, are independent of body size (i.e., $r \propto M^0$). The one exception to this size “insensitivity” appears to be unicellular algae for which birth rates may exceed death rates, although, as the authors note, this may be because death rates are underestimated for small planktonic forms of life. If true, then most of the plant populations examined in this study were in demographic equilibrium ($r = 1.0$), suggesting that evolutionary constraints have optimized the tradeoff between life and death.

These analyses are significant and therefore exciting for at least two reasons. First, they are the first of their kind to provide a truly broad perspective on plant birth and death rates over the full range of plant life, and, second, the scaling relationships reported by Marbà *et al.* (3) appear to support the predictions of the metabolic optimality theory, which has been the center of recent controversy (e.g., refs. 14 and 15). Nevertheless, a number of caveats are worth considering. First, Marbà *et al.* calculated lifespans as the reciprocal of death rates, i.e., $E = \ln(2)/D$. Therefore, the relationship $E \propto M^{1/4}$ emerges automatically from $D \propto M^{-1/4}$, and, as such, it cannot be taken as an “independent” line of evidence supporting the metabolic optimality theory. Second, the proportional relationship $r \propto M^0$ says nothing about the magnitude of r with-

out benefit of knowing the numerical values of the allometric constants for birth and death rates (denoted here by β_1 and β_2), which, in theory, are free to numerically vary across different species groups. Specifically, $r = B/D = \beta_1 M^{-1/4} / \beta_2 M^{-1/4} = \beta_1 / \beta_2$ such that $r > 1.0$ when $\beta_1 > \beta_2$ and $r < 1.0$ when $\beta_1 < \beta_2$. Therefore, even if $B \propto D$ holds true across most or all species groups, it does

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not necessarily follow that population growth rates are equivalent or invariant across species groups (or that the same species group will manifest the same population growth rates when it occupies different habitats). Indeed, Marbà *et al.* fully acknowledge that the various functional species groups do not obey the same scaling rules, at least not exactly. For example, their statistical comparisons show that mortality rates decline more sharply with increasing body size across land plants (embryophytes) than across aquatic plants. These rates also decline more sharply across vascular plants as opposed to nonvascular plants, suggesting that increased size may confer benefits to terrestrial plants, particularly if they are vascular.

Third, as noted earlier, phrases like “birth rate” and “lifespan” have different meanings for different functional species groups. Consider unicellular algae that can asexually reproduce by simple cell division. For these species, each cell division cycle simultaneously represents a birth and a lifespan; it also can be viewed as the “pseudoextinction” or death of the parent cell. In contrast, the

birth rate and lifespan of a tree equate to seed set and germination and the time interval between germination and death, respectively. Perhaps a more serious concern is that tree birth rates are often calculated based on biomass-doubling times or, even more problematically, on annual biomass growth rates, which obtain very different results when compared with seed production and germination rates. Fourth and lastly, recent explications of the metabolic optimality theory predict that metabolic rates (and thus, presumably, birth and growth rates) should be temperature-dependent (16, 17), whereas Marbà *et al.* (3) find no evidence that mortality or birth rates scale with respect to body mass in a temperature-dependent manner. This may be the result of either statistical “noise” in their data set or the fact that the data for mortality rates were gathered from populations growing in a narrow band of temperature, but it does represent an inconsistency begging to be explored with additional data.

None of these caveats diminishes in any way the overall value of the analyses or conclusions of Marbà *et al.* (3). Many plant life history traits are still poorly understood despite the fact that they dictate much of the dynamics of Earth’s major ecosystems. The work of Marbà *et al.* has shed light on how some of the most important variables dictating population growth and stability vary as functions of body mass (which is itself a variable of no little importance to understanding plant ecology and evolution). Likewise, none of these concerns cast doubt *a priori* on the metabolic optimality theory, which has inspired a recent renaissance in the field of biological allometry. It is nevertheless evident that much future work is required to fully explore the implications of this theory and to test it rigorously to the point that a consensus can be reached regarding its success or failure. What can be said without hesitation is that, fortunately, we have a theory to test, and that is progress.

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