

Sizing Up the Shape of Life

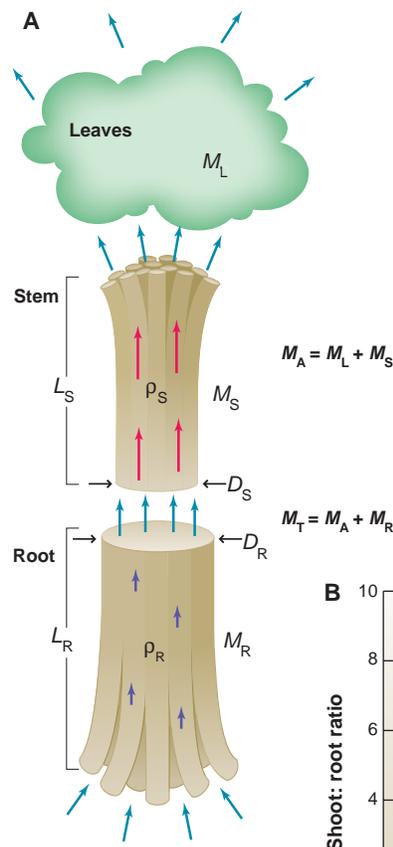
M. Scot Zens and Campbell O. Webb

As children, we are fascinated by the shapes and sizes of living things. As scientists, we try to explain them in terms of underlying biological, chemical, and physical processes. In a series of recent papers, an interdisciplinary group of researchers has set out to expose underlying patterns in the shapes and sizes of plants and animals, in their most simple and elegant forms. These investigators have developed biophysical models based on the mechanics of fluids and support systems. Confirmed by available data, these models are helping to unravel the biological and engineering limits that constrain the evolution of multicellular forms. This is the first truly synthetic treatment of allometric relationships (the scaling of organism size) in the history of biology.

In the latest paper in the series published on page 1517 of this issue, Enquist and Niklas (1) extend earlier work on plants (2–4) by investigating the allocation of biomass between body parts below ground (roots) and above ground (stem and leaves). The authors thus are able to make predictions about the large proportion of Earth's biomass that is tied up in the most cryptic plant tissue of all, the roots. Furthermore, they investigate the morphological implications of the hydraulic connection between root and stem tissues (see the figure). To conserve the flow of fluids through a plant, the length (L), cross-sectional area (D^2), and porosity (and therefore density, ρ) should each be proportional between stem and roots. Under this constraint, root (M_R) and stem mass (M_S) should also scale proportionally ($M_R \propto M_S$). Together with other plant allometric relations developed in earlier papers (2–4), this constraint leads to predictions about how the three basic plant body parts—roots, stems, and leaves—should scale in relation to one another. Leaf mass (M_L) should increase with stem mass (M_S), and with root mass (M_R), but not proportionally, because as the plant grows larger, there needs to be a greater allocation of biomass to the stem. Thus, $M_L \propto M_S^{3/4} \propto M_R^{3/4}$. By combining these relationships, the above-ground biomass ($M_A = M_S + M_L$) can be related to the below-ground biomass ($M_B =$

$M_R + M_R^{3/4}$). In the smallest plants, the above-ground biomass is relatively high because of the major contribution from leaves. But in larger plants, leaves contribute a smaller fraction of above-ground biomass so that $M_A \approx M_R$. Thus, as plant size increases, the ratio of above- to below-ground biomass (the shoot:root ratio $M_A:M_R$) declines steeply for small plants and then approaches an asymptote (see the figure) (5). The derivation by Enquist and Niklas of a size-specific prediction for this widely used ratio will be greatly appreciated by researchers comparing shoot:root ratios among plants of different total mass.

Does the real world fit these astonishingly simple predictions? The fit to data spanning the entire size range of seed plants is

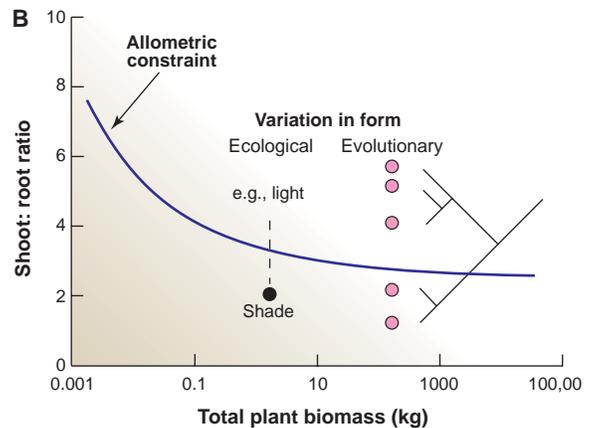


A matter of size. (A) A plant, as modeled by Enquist and Niklas (1). Water flow is conserved through roots, stem, and leaves, by constraining the length (L), cross-sectional area (D^2), and porosity (ρ) of roots and stem so that these parameters scale isometrically. (B) The ratio of above-ground (shoot) to below-ground (root) biomass predicted by Enquist and Niklas, using parameters derived from their table 1 (1): $M_A/M_R = [2.59M_R + (M_R/1.95)^{0.75}]/M_R$. The curve represents the predicted allometric constraint. Observed variations around this curve are caused by ecological and evolutionary effects.

impressive. The trends, described by simple power functions, seem to apply universally, across major phylogenetic divisions and across diverse ecological conditions.

Some of the trends explain over 80% of variation in the logarithmically scaled sizes of plant body parts. Does this then mean that allometry reduces the diversity of life forms to a few equations? Far from it. A careful inspection of the figures in the Enquist and Niklas paper reveals the enormous diversity of forms that remain in the residuals (the deviations of the data from the model). For example, for a given value of stem biomass, leaf biomass varies up to 100-fold among different plant species. What appears as mere scatter from the distant perspective of allometric scaling laws represents huge differences in plant form and function (consider the mass ratio of trunk:leaves for a baobab tree compared with a slender palm). With the universal trends as a baseline, we can now concentrate our attention on how variation around those predictions is associated with the diverse ecological conditions that plants experience, and with the variations among species that result from divergent evolutionary histories (see the figure).

The authors provide one striking example by comparing leaf-to-stem scaling in angiosperms and conifers. The conifers (in these data sets) averaged 2.6 times the leaf biomass of the angiosperms, after stem biomass was accounted for in the framework of the allometric theory. It is important to recognize that allometric theory was necessary for this dramatic comparison, because, in simple ratio data, the relation is confounded by the size of the plants. General allometric theory thus provides the framework to investigate a great variety of form and growth-rate phenomena that have hitherto defied effective analysis. One might even consider that the division of diversity in biological form into variable and allometrically constrained (“variant” and “invari-



M. S. Zens is in the Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, USA. E-mail: scot.zens@dartmouth.edu C. O. Webb is in the Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA. E-mail: campbell.webb@yale.edu

ant") components is akin to the recognition that variation in biological form results from both indeterministic and deterministic components ("chance and necessity") (6).

Given its significance, this research program should be generating far more interest in the ecology and evolution fields than we see at present. So far, the trends have been evaluated mainly across diverse species, but have yet to be shown across individuals within a species, or within individuals as they grow. By placing individuals in ecological conditions where they are likely to confront allometric constraints, experiments have the potential to verify the existence of the constraints where they act (that is, at the level of the individual plant). In addition, key assumptions of this theory remain to be confirmed. For example, does wood density really remain constant during the ontogeny of the plant? As such data become available, we will be able to subject allometric models to the scrutiny they deserve.

If the new theory proves robust, the implications are both practical and profound. Given the great difficulty in measuring

roots, sound theoretical predictions of below-ground biomass will be of great practical value. One timely application will be in large-scale biomass models that predict how much carbon plants sequester from the atmosphere (7, 8). In these cases, scaling rules can provide functional forms and boundary predictions of total biomass for seed plants in virtually every type of terrestrial ecosystem. Allometric theory also provides a foundation for appropriate measures of growth, to compare ecological performance among plants of different sizes. These measures could replace the standard "relative growth rate" (RGR), which implicitly ignores non-photosynthetic tissue in the underlying assumption of exponential individual growth.

At the very least, the theory of allometry has been rejuvenated and its horizons greatly expanded. More optimistically, we may begin to see at organismal scales some of the synthesis of the physical and biological sciences that has been so apparent and powerful at the molecular level. We can even envision mechanistic links

with macroecological and evolutionary models of community structure and abundance (9, 10). And when we next walk in the forest, we can see anew how the physical processes necessary for life explain the similarities (and differences) in form between a diminutive forest herb and the redwood tree that towers above it.

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PERSPECTIVES: COSMOLOGY

Tales of Singularities

G. W. Gibbons and E. P. S. Shellard

To celebrate Stephen Hawking's 60th birthday, a workshop and symposium were held in Cambridge from 7 to 11 January 2002 (1). The title of the meeting, "The Future of Theoretical Physics and Cosmology," was taken from Hawking's inaugural lecture in 1979 as Lucasian Professor (the chair of Isaac Newton and Paul Dirac). Colleagues, collaborators, and former students took stock of what has been achieved in fundamental physics since Hawking began his career and considered the future of the subject.

George Ellis (University of Cape Town) recalled that Hawking began working in cosmology just before the discovery in 1965 of the cosmic microwave background (CMB)—primordial light reaching us from all directions in the sky. The burning issue at that time was whether the universe had a beginning. Was it in a steady state of exponential expansion or did it originate in a Big Bang, a singular state where the known laws of physics break down and the curvature of space becomes very high or infinite?

The CMB data clearly favored the Big

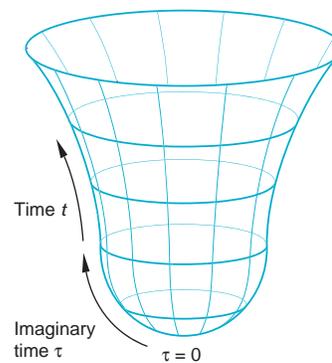
Bang, bearing evidence of a time when our universe was much hotter and denser than it is now. Using the singularity theorems of Roger Penrose, Robert Geroch, and Hawking, George Ellis and Hawking showed that the classical equations of general relativity require a singularity in our universe's past unless one invokes some unusual form of matter, which in effect antigravitates.

Current observations suggest that the situation is more complicated. There is strong evidence that during its first fraction of a second, the universe underwent a period of exponential expansion or inflation. And there is good (although not yet conclusive) evidence that today, the expansion of the universe is accelerated by antigravitating "dark energy" (also called quintessence). Does this mean that the singularity theorems may not apply and that the universe may not have had a beginning? Not according to Alan Guth (MIT) and Alex Vilenkin (Tufts University), who showed that even an everywhere ex-

panding universe filled with antigravitating material cannot be extended infinitely into the past.

Guth recalled another meeting in Cambridge some 20 years ago, when the quantum fluctuations produced during inflation were discussed and characterized. Hawking played a leading role in these discussions. The latest CMB observations are providing the first observational indications that inflationary fluctuations provided the primordial seeds around which galaxies and other structures in the universe formed. The NASA Microwave Anisotropy Probe (MAP) satellite is now scanning the cosmic microwave sky and many other experiments and surveys are under way. These studies will yield a wealth of observational data on the early universe, allowing a more detailed search for the theoretically predicted signatures of inflation.

Ambitious cosmological theories about the origin of the universe, such as Hartle and Hawking's no-boundary proposal (see the first figure), will increasingly run the gauntlet of these discriminating observational tests. Theoreticians must match the quality of the observations with the accuracy of their predictions. This process will require massive computational effort using,



Out of nothing. Hawking's no-boundary proposal links imaginary and real time in one extended spacetime called an instanton. In effect, the instanton describes the creation of the universe from nothing.

The authors are at the Department of Applied Mathematics and Theoretical Physics, University of Cambridge, Cambridge CB3 0WA, UK. E-mail: G.W.Gibbons@damtp.cam.ac.uk and E.P.S.Shellard@damtp.cam.ac.uk