

BOOK REVIEWS

Botanical Scaling

Plant Allometry. The Scaling of Form and Process. KARL J. NIKLAS. University of Chicago Press, Chicago, 1994. xvi, 395 pp., illus. \$62.50 or £49.95; paper, \$24.95 or £19.95.

Allometry—the change in shape, metabolism, or behavior with body size among related organisms—is surely one of the most fascinating phenomena in biology. As first recognized by Julian Huxley in the 1930s, allometry is a pervasive pattern in the fabric of life. Among animals, increases in body size bring fairly regular shifts in the relative size of brains, antlers, guts, and limb-bone diameters, in basal metabolisms, pulse rates, stride frequencies, and running speeds, and in food preferences, territory sizes, species numbers, and extinction rates. Interest in these zoological patterns and their causes has given rise to a spate of publications including two fine books (by Calder and Peters) in recent years. But until now no one has attempted to summarize and analyze the parallel patterns seen among plants.

Niklas makes the first such attempt in this wide-ranging book. Plants span a huge size range (from picoplankton to sequoias) and encompass a multiplicity of functions (mechanical support, photosynthesis, nutrient and water absorption) whose magnitude and integration must shift with size. Niklas begins by presenting 39 allometric relationships, or scaling laws, shown by plants or plant organs that vary in size and then discusses the possible significance and biological basis of each through the rest of the book. The patterns cover a wide sweep of botanical phenomena, and several are novel (but identified on the basis of limited data). Among unicellular algae, growth rate and chlorophyll concentration scale as roughly the 0.75 power of cell volume, while surface area scales as the 0.68 power. Leaf area is proportional to roughly the square of twig diameter. Stem diameter scales approximately as the 1.5 power of height in trees, but as the 0.75 power of height across mosses, herbaceous plants, and palms. The relative investment in stamens and in pistils and ovules increases with flower size; total seed mass increases proportionally to fruit mass in bird-dispersed angiosperms, but as the 1.67 power of cone mass in wind-dispersed conifers; and total reproductive mass scales as roughly the cube of stem diameter.

Two qualitatively different kinds of explanations for such patterns have historically been sought, focusing either on *how* an allometry is generated by a shared developmental pathway across related organisms or on *why* natural selection favors such an allometry (and associated developmental pathways) based on size-dependent changes in the fitness of different phenotypes. Niklas pursues both kinds of explanations, arguing by turns that “engineering constraints” (as detailed in numerous equations and calculations) or “developmental constraints” underlie particular scaling laws.

Parts of Niklas’s presentation are a tour de force, imaginative studies of the determinants of plant architecture that bridge elements of mathematics, biomechanics, physiology, ecology, systematics, and paleontology. I was particularly struck by his analysis showing (i) that nonwoody plants depart dramatically from the 1.5 power law relating stem diameter to height demonstrated in trees (and predicted by Greenhill in 1881); and (ii) that this departure is due to a shift in the material properties of stem tissue with plant height, reflecting a shift from dependence on parenchyma and collenchyma to sclerenchyma and wood fibers with increasing plant height. Niklas suggests that mosses, herbs, and palm trees pursue a “Young’s modulus” strategy, increasing the density, strength, and elasticity of their support tissue with increasing height, until further increases in stature can be achieved only by greater stem diameter, not density. Niklas’s work on the scaling of colony size, shape, and motility in the Volvocales is original and stimulating. So are his reviews of wind dispersal in plumose and in winged seeds (based on exciting work by Augsburger and Matlack), the scaling of seed relative to fruit mass, and the role of developmental allometry in floral evolution. Many readers will also appreciate the strong paleobotanical perspective that Niklas brings to bear on several issues.

In spite of these strengths, Niklas’s book has several flaws, stylistic and substantive. The writing is often ponderous and overly philosophical; many of the general issues raised have been discussed, more thoroughly and clearly, by others. The text is too cluttered with equations and calculations to appeal to beginners, yet much of the exposition (as well as the statistical appendix) is

too elementary for specialists. Some advanced topics (cladistics, for example) appear without preparation, yet some central concepts (the three basic kinds of allometric comparisons) are not introduced until near the book’s end. The graphic material is poorly lettered and designed.

Intellectually, Niklas’s treatment has a number of weaknesses. First, in attempting to cover the wide range of phenomena inherent in plant allometry Niklas often depends too heavily on his own work and overlooks major contributions by others. He cites not one of the key publications by Cowan, Farquhar, Field, Gates, Givnish, Gutschick, Mooney, or Parkhurst on stomatal conductance and related topics in physiological ecology; does not cite seminal work by Lieth or Rosenzweig on the relation between plant productivity and precipitation; does not cite important research by Tilman and his colleagues on optimal cell size in planktonic algae; and does not cite central findings by Fisher, Givnish, Honda, King, Menges, Tilman, and Waller on biomechanical adaptations for energy capture, optimal plant height, optimal branching patterns, and the self-thinning law. As a consequence, his arguments suffer and are sometimes simplistic, poorly grounded, and at least to this reviewer, unconvincing.

Second, in many figures and tables the precise sources of data (or the data themselves) are not given; often it is not clear whether Niklas or the original investigator is responsible for determining the allometric relationship presented. Niklas professes great concern for the importance of “phylogenetic effects,” of the idiosyncratic scaling laws shown by one lineage and not others and their possible influence on the overall trends seen across a broader taxonomic sample. Yet how are we to assess the importance of such effects if the taxa for a given analysis are not even listed? A key instance of this problem is table 5.1, which Niklas uses to conclude (i) that during the early evolution of land plants the proportion of morphological variation within plant families declined relative to that between families; and (ii) that a substantial portion of the early morphological evolution of land plants may have been nonadaptive.

Finally, Niklas’s overall conceptual framework for analyzing the basis for allometry—development or selection—seems somewhat deficient. The author states his great admiration for D’Arcy Thompson, who sought explanations for differences in shape among organisms in terms of the constraints that physical and chemical laws place on their development, avoiding any invocation of natural selection. Niklas claims to depart from Thompson in the latter respect, and indeed to be an adaptationist, but it seems clear (p. 317) that he



Vignettes: Academic Admirers

The romantic age of the 19th century glamorized the fallow, wan physical appearance typical of patients with tuberculosis. Thus, when Daniel Chester French began his work on the statue of John Harvard that remains a notable feature of the Harvard Yard, he seized upon the fact that John Harvard was known to have had tuberculosis to model a face "delicate . . . and sensitive in expression."

—Thomas M. Daniel, Joseph H. Bates, and Katharine A. Downes, in *Tuberculosis: Pathogenesis, Protection, and Control* (Barry R. Bloom, Ed.; ASM Press)

In good part through their successes, the unbuttoned [Richard] Feynmans and Jim Watsons have become the reigning model of the brilliant scientist. It is a modern type whose credo is that talent is all, rank is little; you can never believe the experts, but you can and must work it out yourself; you say whatever is on your mind if you are really good enough; and you can follow your drives and instincts without shame. We recognize here a kin of Jean Jacques Rousseau's child of nature, his gifts unspoiled and uninhibited by what Feynman calls the "baloney" that pompous fools like to pass off as high civilization.

—Gerald Holton, in *Einstein, History, and Other Passions* (American Institute of Physics)

views a major role of natural selection to be the preservation of developmental and morphological stasis within lineages. Even Niklas's frequent invocation of "engineering constraints" as possible explanations for allometric laws—for example, elastic toppling as a constraint on the height-diameter relationship—does not represent a clear argument based on natural selection. Such engineering constraints alone can never account for a tight fit of species to an allometric curve, only for their restriction below some critical threshold (for example, the critical toppling height at a given diameter). Only if selection and energetic constraints are also considered can engineering analyses provide a biological explanation of an allometric pattern (for example, plants should not only lie below the toppling threshold, they should be as slender as possible at a given height to minimize the cost of further increments in height, thus maximizing the rate of upward growth and competitive ability). Nowhere does Niklas incorporate such considerations into models for evolutionarily favored strategies, and nowhere does he explicitly recognize that adaptations are context-dependent and not imposed mainly by invariant physical and chemical laws. Future work on allometry and its implications for the ecology and evolution of plants must take both of these central points into account.

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Other Books of Interest

The Molecular Basis of Cancer. JOHN MENDELSON, PETER M. HOWLEY, MARK A. ISRAEL, and LANCE A. LIOTTA [Eds.]. Saunders, Philadelphia, 1994. xviii, 574 pp., illus. \$130 or £100.

The editors of this textbook begin their preface by noting that molecular biology has revolutionized our understanding of malignant transformation and that the study of malignancy has had a comparable effect with respect to understanding of the molecular and genetic bases of normal cell growth and proliferation. Their exposition of cancer and related processes is accordingly intended to "explain, rather than to merely recount," what is now known about "a disease which until recently was thought about in purely descriptive terms." Although clinicians are among the intended audience for the book, its focus is not on clinical manifestations or treatment *per se* but on "scientific underpinnings." In all the book consists of 23 chapters by a total of 45 authors. Section 1, covering malignant transformation, contains accounts of cell cycle regulation, oncogenes, and neoplastic drugs (Murakami *et al.*), the molecular and cytogenetics of hematopoietic malignancies (Gauwerky and Croce), viral carcinogenesis (Howley), mutagenesis and multistage carcinogenesis (Weinstein *et al.*), tumor suppressor genes (Levine), oncogenes (Rosen), and growth factors and signal transduction (Tronick and Aaronson). Section 2

is devoted to the growth and spread of cancer, beginning with a discussion of the cytogenetics of neoplasia (Gilewski and Norton) and including chapters on cellular adhesion mechanisms involved in metastasis (Buck), tumor angiogenesis (Folkman), and molecular mechanisms of metastasis (Stracke and Liotta). Section 3 consists of chapters on specific malignancies—lymphoid and hematopoietic neoplasms (Gaidano and Dalla-Favera, Khouri *et al.*), childhood neoplasms (Israel), and lung, colon and rectal, and breast cancer (Johnson, Fearon, Dickson and Lippman). The final section is devoted to the molecular basis of cancer therapy, with papers on various types of therapy—chemotherapy (Scotto and Bertino), radiation therapy (Fuks and Weichselbaum), monoclonal antibody therapy (Maloney *et al.*), and gene therapy (Tolstoshev and Anderson)—as well as on growth factors (Mendelsohn and Gabrilove) and cellular immunity (Herberman). Each chapter in the book has its own reference list, consisting heavily of references to the primary literature, and there is a subject index for the volume as a whole. The book is printed on glossy paper and is illustrated largely with (sometimes rather blurry) line drawings.

Katherine Livingston

Cell Physiology Source Book. NICHOLAS SPERELAKIS, Ed. Academic Press, New York, 1995. xvi, 738 pp., illus. \$99 or £76.

This work is conceived as a successor to Hugh Davson's "classic" and "monumental" *Textbook of General Physiology*, which was first published in 1951 and appeared in its fourth and final edition in 1970. Davson notes in a foreword that the expansion of the field would today make preparation of such a work an impossible task for a single author. Sperelakis has enlisted in the enterprise 48 other contributors to produce a total of 50 chapters (not reprints from the literature as the book's title might suggest) written at a level intended to be suitable for an audience ranging from advanced undergraduates to researchers in other fields. He asked the contributors to consider comparative physiology, developmental changes, pathophysiology, membrane diseases, and molecular biology as related to their particular topics and to provide treatments that would be "comprehensive, but didactic, . . . beginning in an elementary fashion and ending in a sophisticated and quantitative treatise." The opening section of the book, Biophysical Chemistry, Electrochemistry, Metabolism, Second Messengers, and Ultrastructure, comprises 10 chapters, beginning with accounts of the biophysical chemistry of cellular electrolytes by Freedman and of the physiological struc-