Life's Universal Scaling Laws

Biological systems have evolved branching networks that transport a variety of resources. We argue that common properties of those networks allow for a quantitative theory of the structure, organization, and dynamics of living systems.

Geoffrey B. West and James H. Brown

Nearly 100 years ago, the eminent biologist D'Arcy Thompson began his wonderful book *On Growth and Form* (Cambridge U. Press, 1917) by quoting Immanuel Kant. The philosopher had observed that "chemistry . . . was a science but not Science . . . for that the criterion of true Science lay in its relation to mathematics." Thompson then declared that, since a "mathematical chemistry" now existed, chemistry was thereby elevated to Science; whereas biology had remained qualitative, without mathematical foundations or principles, and so it was not yet Science.

Although few today would articulate Thompson's position so provocatively, the spirit of his characterization remains to a large extent valid, despite the extraordinary progress during the intervening century. The basic question implicit in his discussion remains unanswered: Do biological phenomena obey underlying universal laws of life that can be mathematized so that biology can be formulated as a predictive, quantitative science? Most would regard it as unlikely that scientists will ever discover "Newton's laws of biology" that could lead to precise calculations of detailed biological phenomena. Indeed, one could convincingly argue that the extraordinary complexity of most biological systems precludes such a possibility.

Nevertheless, it is reasonable to conjecture that the coarse-grained behavior of living systems might obey quantifiable universal laws that capture the systems' essential features. This more modest view presumes that, at every organizational level, one can construct idealized biological systems whose average properties are calculable. Such ideal constructs would provide a zeroth-order point of departure for quantitatively understanding real biological systems, which can be viewed as manifesting "higher-order corrections" due to local environmental conditions or historical evolutionary divergence.

The search for universal quantitative laws of biology that supplement or complement the Mendelian laws of inheritance and the principle of natural selection might seem to be a daunting task. After all, life is the most complex and diverse physical system in the universe, and a systematic science of complexity has yet to be developed.

The life process covers more than 27 orders of magnitude in mass—from molecules of the genetic code and metabolic machinery to whales and sequoias—and the metabolic power required to support life across that range spans over 21 orders of magnitude.

Throughout those immense ranges, life uses basically the same chemical constituents and reactions to create an amazing variety of forms, processes, and dynamical behaviors. All life functions by transforming energy from physical or chemical sources into organic molecules that are metabolized to build, maintain, and reproduce complex, highly organized systems. Understanding the origins, structures, and dynamics of living systems from molecules to the biosphere is one of the grand challenges of modern science. Finding the universal principles that govern life's enormous diversity is central to understanding the nature of life and to managing biological systems in such diverse contexts as medicine, agriculture, and the environment.

Allometric scaling laws

In marked contrast to the amazing diversity and complexity of living organisms is the remarkable simplicity of the scaling behavior of key biological processes over a broad spectrum of phenomena and an immense range of energy and mass. Scaling as a manifestation of underlying dynamics and geometry is familiar throughout physics. It has been instrumental in helping scientists gain deeper insights into problems ranging across the entire spectrum of science and technology, because scaling laws typically reflect underlying generic features and physical principles that are independent of detailed dynamics or specific characteristics of particular models. Phase transitions, chaos, the unification of the fundamental forces of nature, and the discovery of quarks are a few of the more significant examples in which scaling has illuminated important universal principles or structure.

In biology, the observed scaling is typically a simple power law: $Y = Y_0 M^b$, where Y is some observable, Y_0 a constant, and M the mass of the organism.[1–3] Perhaps of even greater significance, the exponent b almost invariably approximates a simple multiple of $1/4$. Among the many fundamental variables that obey such scaling laws—termed "allometric" by Julian Huxley[4]—are metabolic rate, life span, growth rate, heart rate, DNA nucleotide substitution rate, lengths of aortas and genomes, tree height, mass of cerebral grey matter, density of mitochondria, and concentration of RNA.

The most studied of those variables is basal metabolic rate, first shown by Max Kleiber to scale as $M^{3/4}$ for mammals and birds.[5] Figure 1 illustrates Kleiber's now 70-year-old data, which extend over about four orders of magnitude in mass. Kleiber's work was generalized by subsequent researchers to ectotherms (organisms whose

Geoffrey West *is a senior fellow at the Los Alamos National Laboratory and a distinguished research professor at the Santa Fe Institute, both in New Mexico.* **Jim Brown** *is a distinguished professor of biology at the University of New Mexico in Albuquerque.*

© 2004 American Institute of Physics, S-0031-9228-0409-010-6

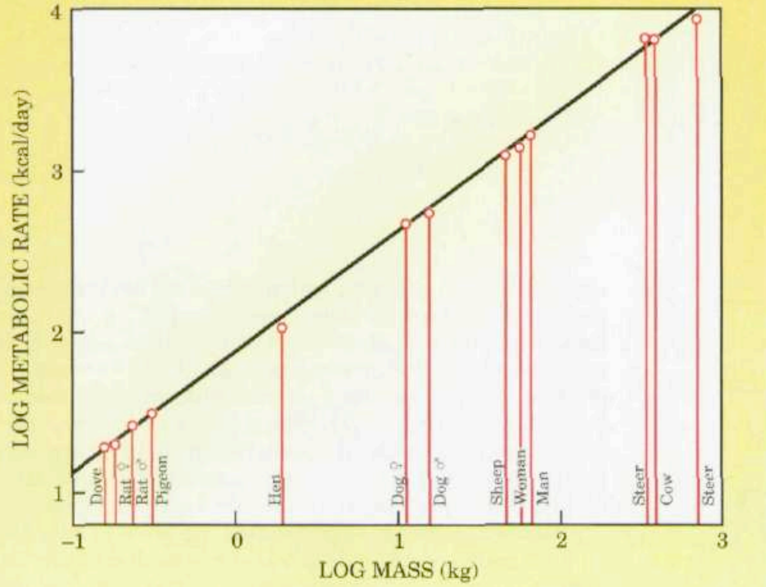


Figure 1. The basal metabolic rate of mammals and birds was originally plotted by Max Kleiber in 1932. In this reconstruction, the slope of the best straight-line fit is 0.74, illustrating the scaling of metabolic rate with the ¾ power of mass. The diameters of the circles represent estimated data errors of ±10%. Present-day plots based on many hundreds of data points support the ¾ exponent, although evidence exists of a deviation to a smaller value for the smallest mammals. (Adapted from ref. 5.)

body temperature is determined by their surroundings), unicellular organisms, and even plants. It was then further extended to intracellular levels, terminating at the mitochondrial oxidase molecules (the respiratory machinery of aerobic metabolism). The metabolic exponent $b \approx 3/4$ is found over 27 orders of magnitude;[6] figure 2 shows data spanning most of that range. Other examples of allometric scaling include heart rate ($b \approx -1/4$, figure 3a), life span ($b \approx 1/4$), the radii of aortas and tree trunks ($b \approx 3/8$), unicellular genome lengths ($b \approx 1/4$, figure 3b), and RNA concentration ($b \approx -1/4$).

An intriguing consequence of these "quarter-power" scaling laws is the emergence of invariant quantities,[7] which physicists recognize as usually reflecting fundamental underlying constraints. For example, mammalian life span increases as approximately $M^{1/4}$, whereas heart rate decreases as $M^{-1/4}$, so the number of heartbeats per lifetime is approximately invariant (about 1.5×10^9), independent of size. Hearts are not fundamental, but the molecular machinery of aerobic metabolism is, and it has an analogous invariant: the number of ATP (adenosine triphosphate) molecules synthesized in a lifetime (of order 10^{16}). Another example arises in forest communities where population density decreases with individual body size as $M^{-3/4}$, whereas individual power use increases as $M^{3/4}$; thus the power used by all individuals in any size class is invariant.[8]

The enormous amount of allometric scaling data accumulated by the early 1980s was synthesized in four books that convincingly showed the predominance of quarter powers across all scales and life forms.[1,2] Although several mechanistic models were proposed, they focused mostly on very specific features of a particular taxonomic group. For example, in his explanation of mammalian metabolic rates, Thomas McMahon assumed the elastic similarity of limbs and the invariance of muscle speed,[1] whereas Mark Patterson addressed aquatic organisms based on the diffusion of respiratory gases.[9] The broader challenge is to understand the ubiquity of quarter powers and to explain them in terms of unifying principles that determine how life is organized and the constraints under which it has evolved.

Origins of scaling

A general theory should provide a scheme for making quantitative dynamical calculations in addition to explaining the predominance of quarter powers. The kinds of problems that a theory might address include, How many oxidase molecules and mitochondria are there in a cell? Why do we live approximately 100 years, not a million years or a few weeks, and how is life span related to molecular scales? What are the flow rate, pulse rate, pressure, and

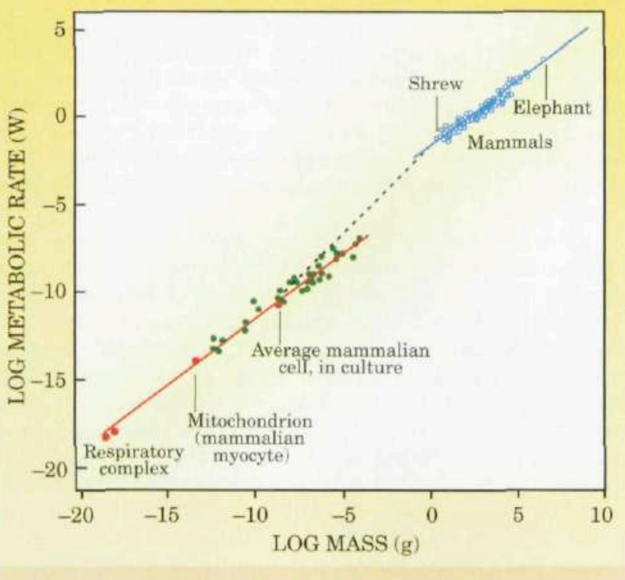


Figure 2. The ¾-power law for the metabolic rate as a function of mass is observed over 27 orders of magnitude. The masses covered in this plot range from those of individual mammals (blue), to unicellular organisms (green), to uncoupled mammalian cells, mitochondria, and terminal oxidase molecules of the respiratory complex (red). The blue and red lines indicate ¾-power scaling. The dashed line is a linear extrapolation that extends to masses below that of the shrew, the lightest mammal. In reference 6, it was predicted that the extrapolation would intersect the datum for an isolated cell in vitro, where the ¾-power reemerges and extends to the cellular and intracellular levels. (Adapted from ref. 6.)

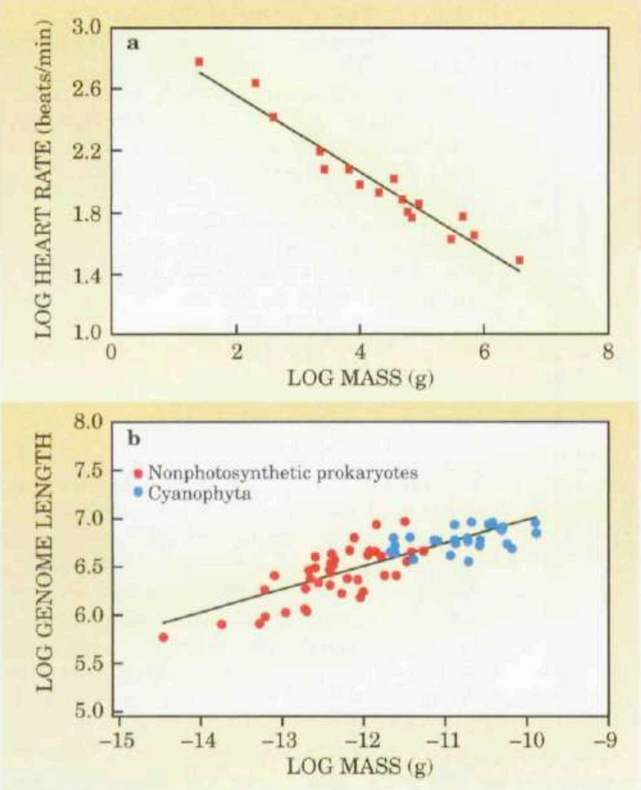


Figure 3. Simple scaling laws are not limited to metabolic rates. **(a)** A log–log plot of heart rate as a function of body mass for a variety of mammals. The best straight-line fit has a slope very close to −¼. (Adapted from ref. 14.) **(b)** A log–log plot of genome length (number of base pairs) as a function of cell mass for a variety of unicellular organisms. The best straight-line fit has a slope very close to ¼.

dimensions in any vessel of any circulatory system? How many trees of a given size are in a forest, how far apart are they, and how much energy flows in each branch? Why does an elephant sleep only 3 hours and a mouse 18?

Beginning in the late 1990s, we attempted to address such questions, first with Brian Enquist and later with others.[6,10,11] The starting point was to recognize that highly complex, self-sustaining, reproducing, living structures require close integration of enormous numbers of localized microscopic units that need to be serviced in an approximately "democratic" and efficient fashion. To solve that challenge, natural selection evolved hierarchical fractal-like branching networks that distribute energy, metabolites, and information from macroscopic reservoirs to microscopic sites. Examples include animal circulatory systems, plant vascular systems, and ecosystem and intracellular networks. We proposed that scaling laws and the generic coarse-grained dynamical behavior of biological systems reflect the constraints inherent in universal properties of such networks. These constraints were postulated as follows:

- Networks service all local biologically active regions in both mature and growing biological systems. Such networks are called space-filling.
- The networks' terminal units are invariant within a class or taxon.
- Organisms evolve toward an optimal state in which the energy required for resource distribution is minimized.

These properties, which characterize an idealized biological organism, are presumed to be consequences of natural selection. Thus, terminal units—the basic building blocks of the network in which energy and resources are exchanged—are not reconfigured as individuals grow from newborn to adult nor reinvented as new species evolve. Examples of such units include capillaries, mitochondria, leaves, and chloroplasts. Analogous architectural terminal units, such as electrical outlets or water faucets, are also approximate invariants, independent of building size or location. The third postulate assumes that the continuous feedback and fine-tuning implicit in natural selection lead to near-optimized systems. For example, of the infinitude of space-filling circulatory systems with invariant terminal units that could have evolved, the ones that did evolve minimize cardiac output. Minimization principles are potentially very powerful because they can be expressed mathematically as equations that describe network dynamics.

Guided by the three postulates, we and our colleagues built on earlier work to derive analytic models of the mammalian circulatory and respiratory systems and of plant vascular systems. The theory enables one to address the types of questions we raised at the beginning of this section and predicts quarter-power scaling of diverse biological phenomena even though the networks and associated pumps are very different. It allowed us to derive many scaling laws not only between organisms of varying size but also within an individual organism—for example, laws that relate the aorta to capillaries and growth laws that connect, say, a seedling to a giant sequoia. Where data exist, one generally finds excellent agreement, and where they do not, the theory provides testable predictions.

Metabolic rate

Aerobic metabolism is fueled by oxygen, whose concentration in hemoglobin is fixed. Consequently, the rate at which blood flows through the cardiovascular system is a proxy for metabolic rate so that the properties of the circulatory network partially control metabolism. The requirement that the network be space-filling constrains the branch lengths l_k to scale as $l_{k+1}/l_k = n^{-1/3}$ within networks, where n is the branching ratio, k is the branching level, and the lowest-level branch is the aorta. The 3 in the branching-ratio exponent reflects the dimensionality of space.

In 1997, we and Enquist derived an analytic solution for the entire network from the hydrodynamic and elasticity equations for blood flow and vessel dynamics.[10] We assumed, for simplicity, that the network was symmetric and composed of cylindrical vessels and that the blood flow was not turbulent. We also imposed the requirements that the network be space-filling and that dissipated energy be minimized.

Two factors independently contribute to energy loss: viscous energy dissipation, which is only important in smaller vessels, and energy reflected at branch points, which is eliminated by impedance matching. In large vessels such as arteries, viscous forces are negligible and the resulting pulsatile flow suffers little attenuation or dissipation. In that case, impedance matching leads to area-preserving branching. That is, the cross-sectional area of the daughter branches equals that of the parent, so radii scale as $r_{k+1}/r_k = n^{-1/2}$ and blood velocity remains constant. In small vessels such as capillaries and arterioles, the pulse is strongly damped by viscous forces, so-called Poiseuille flow dominates, and significant energy is dissi-

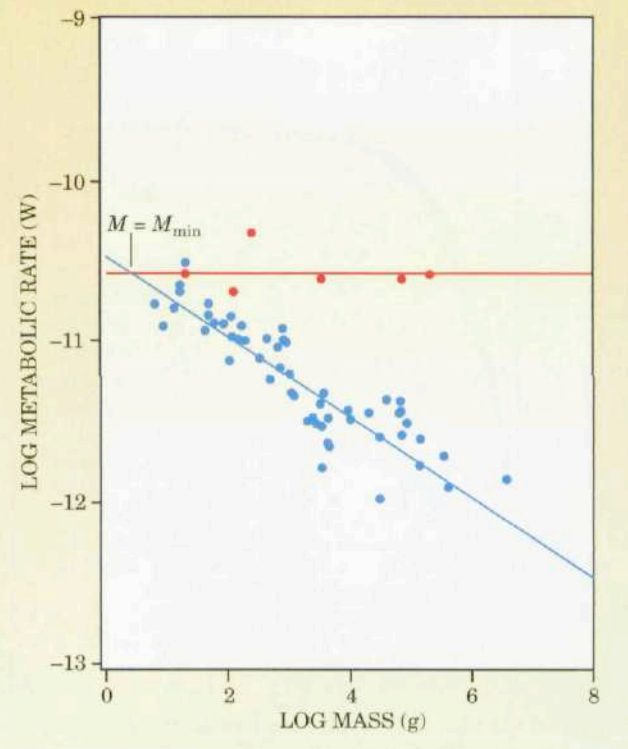


Figure 4. Cells in living organisms and cells cultured in vitro have different metabolic rates. The plot shows the metabolic rates of mammalian cells in vivo (blue) and in vitro (red) as a function of organism mass M. While still in the body and constrained by vascular supply networks, cellular metabolic rates scale as $M^{-1/4}$ (blue line). Cells removed from the body and cultured in vitro generally take on a constant metabolic rate (red line) predicted by theory. Consistent with theory, the in vivo and in vitro lines meet at the mass M_{min} of a theoretical smallest mammal, which is close to that of a shrew. (Adapted from ref. 6.)

pated. For such flow, minimization of dissipated energy leads to area-increasing branching with $r_{k+1}/r_k = n^{-1/3}$, so blood slows down and almost ceases to flow in the capillaries. Because r_{k+1}/r_k changes continuously from $n^{-1/2}$ to $n^{-1/3}$ as branching increases, the network is not strictly self-similar. Nevertheless, the length ratio l_{k+1}/l_k does remain constant throughout the network and the network has some fractal-like properties.

Allometric relations follow from the invariance of capillaries and the prediction from energy optimization that the total blood volume is proportional to the body mass, as observations confirm. We derived the scaling of radii, lengths, and many other physiological characteristics and showed them to have quarter-power exponents. Quantitative predictions for those and other characteristics of the cardiovascular system, such as the flow, pulse, and dimensions in any branch of a mammal, are in good agreement with data.

The dominance of pulsatile flow, and consequently of area-preserving branching, is crucial for deriving quarter powers and, in particular, the $^3/_4$ power describing metabolic rate B. However, as body size decreases, tubes narrow and viscosity plays an increasing role. Eventually, even major arteries become too constricted to support wave propagation, and steady Poiseuille flow dominates. As a result, branching becomes predominantly area increasing and metabolic rate becomes proportional to M, rather than $M^{3/4}$. Networks with constricted arteries are highly inefficient because energy is dissipated in all branches; a limiting-case animal whose network supported only steady flow would have a beating heart but no pulse and would not have evolved. The limiting-case idea allows one to estimate, in terms of fundamental parameters, the size of the smallest animal. For mammals, theory predicts M_{min} of about 1 g. That's close to the mass of a shrew, which is indeed the smallest mammal. Although no mammals exist with masses smaller than the shrew, a linear extrapolation of B to lower masses is meaningful: As figure 2 shows, the extrapolation intersects metabolic-power data at the location of an isolated mammalian cell, a tiny "mammal without a network."

Because of the changing roles of pulsatile and Poiseuille flow with body size, as mass decreases, the exponent for B should depend weakly on M, exhibiting calculable deviations from 3/4 as observed.

From molecules to forests

Metabolism is organized at a number of levels, and at each level new structures emerge. The result is a hierarchy of networks, each with different physical characteristics and effective degrees of freedom. Yet metabolic rate continues to obey $^3/_4$-power scaling. That invariance is in contrast to the analogous situation in physics. Scaling, as manifested in structure functions or phase transitions, for example, persists from quarks through hadrons, atoms, and ultimately to matter. Yet no continuous universal behavior emerges: Each level manifests different scaling laws.

Metabolic energy is conserved as it flows through the hierarchy of sequential networks, each presumed to satisfy the same general principles and, therefore, the same quarter-power scaling. The continuity of flow imposes boundary conditions between adjacent levels. Those conditions, in turn, lead to constraints on densities of the invariant terminal units, such as mitochondria and respiratory molecules, that interact between levels. So, for example, the total mitochondrial mass relative to body mass is correctly predicted to be $(M_{\text{min}} m_{\text{m}}/m_{\text{c}} M)^{1/4} \approx 0.06\, M^{-1/4}$, where m_{m} is the mitochondrial mass, m_{c} is the average cell mass, and M is in grams.

The control exercised by networks is further exemplified by culturing cells in vitro and so liberating them from network hegemony. Cells in vivo adjust their number of mitochondria appropriately to the size of the host mammal as dictated by the resource supply networks. In vivo cellular metabolic rate thereby scales as $M^{-1/4}$, as seen in figure 4. In vitro cultured cells from different mammals, however, are predicted to develop the same metabolic rate, about 3×10^{-11} watts. The figure shows that the in vivo and in vitro values coincide at M_{min}, so cells in shrews work at almost maximal output. No wonder shrews live short lives!

The calculations that yield quarter-power scaling depend only on generic network properties. The observation of such scaling at intracellular levels therefore suggests that subcellular structure and dynamics are constrained by optimized space-filling, hierarchical networks. A major challenge, both theoretically and experimentally, is to understand quantitatively the nature and structure of intracellular pathways, about which surprisingly little is known.

Energy transported through the network fuels the metabolic machinery that maintains biological systems.

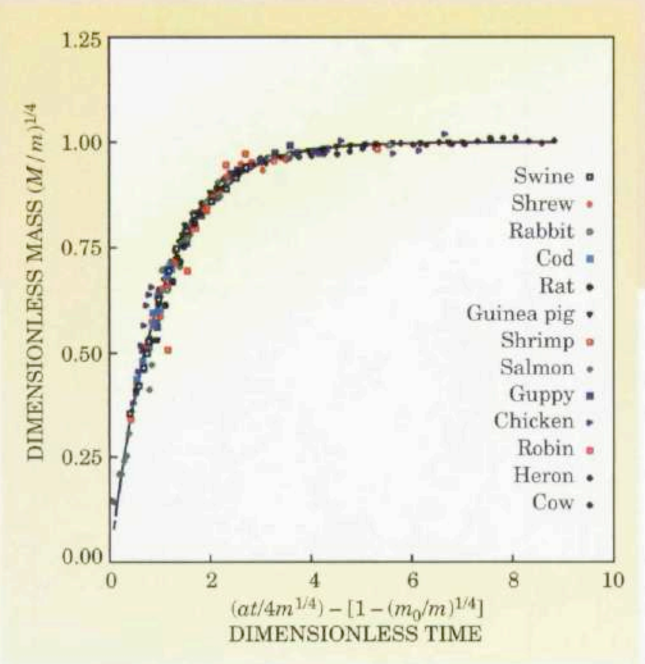


Figure 5. The universality of growth is illustrated by plotting a dimensionless mass variable against a dimensionless time variable. Data for mammals, birds, fish, and crustacea all lie on a single universal curve. The quantity M is the mass of the organism at age t, m_0 its birth mass, m its mature mass, and a is a parameter determined by theory in terms of basic cellular properties that can be measured independently of growth data. (Adapted from ref. 11.)

In addition, that energy is used to grow new cells for added tissue. Thus metabolic rate has two components, maintenance and growth, and can be expressed as $B = N_c B_c + E_c \mathrm{d}N_c/\mathrm{d}t$, where N_c is the number of cells, B_c is the metabolic rate per cell in mature individuals, E_c is the energy required to grow a cell, and t is time. The equation gives a natural explanation for why we all stop growing: The number of cells to be supported ($N_c \propto M$) increases faster than the rate at which they are supplied with energy ($B \propto M^{3/4} \propto N_c^{3/4}$), which allows a determination of the mass at maturity. Moreover, the parameters in the growth equation are determined by fundamental properties of cells. As a consequence, one can derive a universal scaling curve valid for the growth of any organism. As figure 5 shows, the curve fits the data well for a variety of organisms, including mammals, birds, fish, and crustacea. The idea behind the universal growth curve has recently been extended by Caterina Guiot and colleagues to parameterize tumor growth.[12] Thus, growth and life-history events are, in general, universal phenomena governed primarily by basic cellular properties and quarter-power scaling.

Temperature has a powerful effect on those basic properties—indeed, on all of life—because of its exponential effect on biochemical reaction rates. The Boltzmann factor $e^{-E/kT}$, where E is an activation energy, k is Boltzmann's constant, and T is the temperature, describes the effect quantitatively. Combined with network constraints, the Boltzmann factor predicts a joint universal mass and temperature scaling law for times and rates connected with metabolism, including longevity and rates of growth, embryonic development, and DNA nucleotide substitution in genomes. All times associated with metabolism should scale as $M^{1/4} e^{E/kT}$ and all rates as $M^{-1/4} e^{-E/kT}$, with approximately the same value for E. Data covering fish, amphibians, aquatic insects, and zooplankton confirm the prediction. The best-fit value for E, about 0.65 eV, may be interpreted as an average activation energy for the rate-limiting biochemical reactions.

Size and temperature considerations suggest a general definition of biological time determined by just two universal numbers, the scaling exponent ¼ and the energy E. When adjusted for size and temperature, all organisms, to a good approximation, run by the same universal clock with similar metabolic, growth, and even evolutionary rates.

The basic principles that yield allometric scaling in animals may also be applied to plants, whose vascular systems are effectively bundles of long microcapillary tubes driven by a nonpulsatile pump. One can derive many scaling relationships within and between plants, including those for conductivity, fluid velocity, and, as first observed by Leonardo da Vinci, area-preserving branching. Metabolic rate scales as $M^{3/4}$ and trunk diameter (like aorta diameter) scales as $M^{3/8}$. Thus B scales as the square of trunk diameter.

Steady-state forest ecosystems, too, can be treated as integrated networks satisfying appropriate constraints. The network elements are not connected physically, but rather by the resources they use. Scaling in the forest as a whole mimics that in individual trees. So, for example, the number of trees as a function of trunk diameter scales just like the number of branches in an individual tree as a function of branch diameter. As figure 6 shows, both scalings are described by predicted inverse-square laws.

Criticisms and controversies

The theoretical framework reviewed here has now been published for long enough to have attracted a number of critical responses. Broadly speaking, they fall into three categories: data, technical issues, and conceptual questions.

In 1982, Alfred Heusner analyzed data on mammalian metabolic rates and concluded that the power-law exponent was ⅔ rather than ¾, indicative of a simple surface-to-volume rule. His suggestion met with strong opposition, and after the statistical debate subsided, the ubiquity of quarter powers was widely accepted.[2] Recently, however, the controversy was resurrected by Peter Dodds and coworkers and by Craig White and Roger Seymour, all of whom concluded that a reanalysis of data indeed supports the ⅔ exponent, especially for the smaller mammals with masses less than 10 kg that dominate the dataset.[13] More recently we, Van Savage, and others, assembled and analyzed the largest compilation of such data to date.[14] We gave equal weight to all sizes and found a best single-power fit of 0.74 (+0.02, −0.03), although we did confirm for small mammals a trend towards smaller exponents that is in qualitative agreement with earlier theoretical predictions.[10]

Although we authors disagree with critiques of the ¾-scaling exponents, we recognize that such criticisms have raised important empirical and statistical issues about data interpretation.

Dodds and colleagues also criticized our derivation of the ¾ exponent for mammals. In their reanalysis, they minimized the total impedance of the pulsatile circulatory network rather than the total energy loss, which is the sum of viscous energy dissipated (related to the real part of the

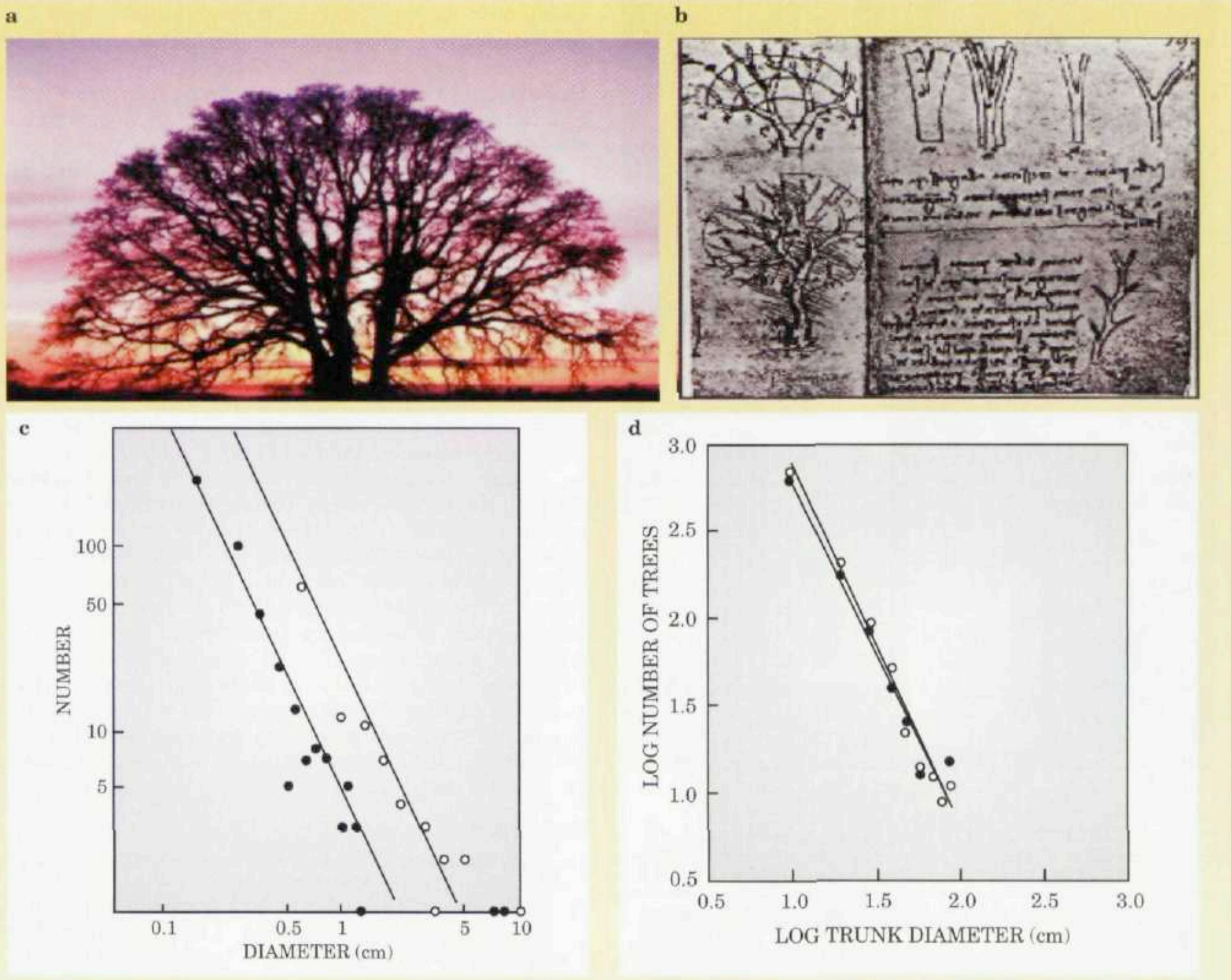
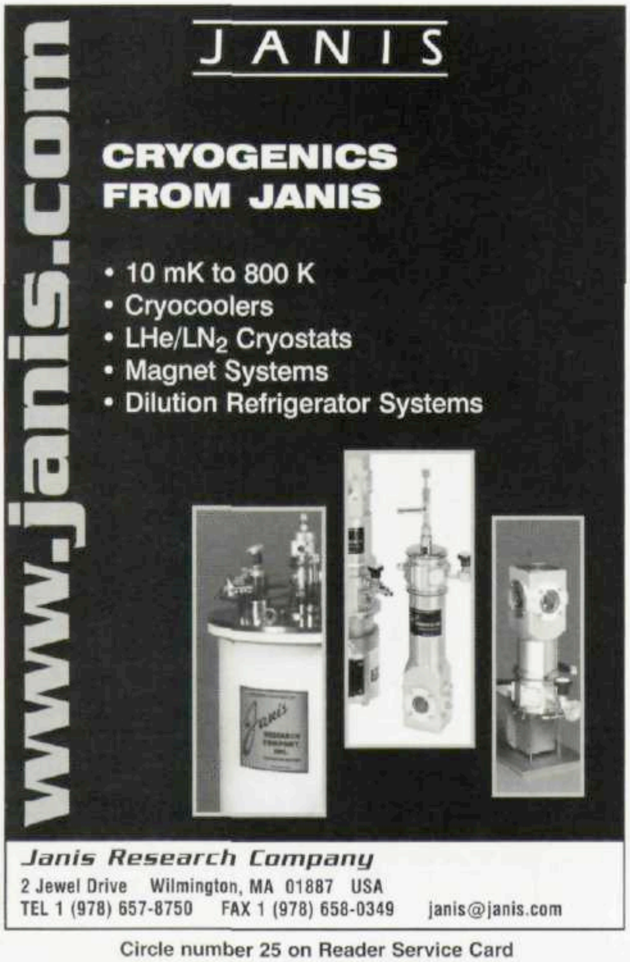


Figure 6. Trees and forests exhibit similar scaling behavior. **(a)** A typical tree exhibits multiple branching levels. **(b)** A page from Leonardo da Vinci's notebooks illustrates his discovery of area-preserving branching. **(c)** The number of branches (closed circles) and roots (open circles) in a tree varies roughly as the predicted inverse square of the diameter, indicated by the straight lines. The data are from a Japanese forest. (Adapted from ref. 17.) **(d)** The number of trees of a given size as a function of trunk diameter also follows a predicted inverse-square law (to within the error of the best-fit lines). The data, from a forest in Malaysia, were collected in 1947 (open circles) and 1981 (filled circles) and illustrate the robustness of the result—the composition of the forest changed over the 34 years separating the data, but the inverse-square behavior persisted. (Adapted from ref. 18.)

impedance) and the loss due to reflections at branch points (related to the imaginary part). They did not, however, impose impedance matching, so their analysis allowed reflections at branch points and therefore did not minimize total energy loss. Consequently, they failed to obtain a $3/4$ exponent.

Space filling, invariant terminal units, area-preserving branching, and the linearity of network volume with M are sufficient to derive quarter powers. The last two properties follow from network dynamics by way of minimizing energy loss. Is there a more general argument, independent of dynamics and hierarchical branching, that determines the special number 4? Jayanth Banavar and coworkers assumed, like us, that allometric relations reflect network constraints.[15] But they proposed that quarter powers arise from a more general class of directed networks that need not have fractal-like hierarchical branching. They showed that if the flow is sequential between the invariant units being supplied—cells or leaves, for example—rather than hierarchically terminating on such units, then a scaling exponent of $3/4$ is obtained. Their result follows from minimizing flow rate rather than minimizing energy loss and assumes, in agreement with observation, that network volume scales linearly with body mass. A further consequence of their model (and also ours) is that in d dimensions, the metabolic exponent is $d/(d+1)$: The special number 4 thus reflects the three-dimensionality of space.

The cascade model of Charles-Antoine Darveau and colleagues provides another alternative.[16] In that model, the total metabolic rate is expressed as the sum of fundamental, mostly intracellular contributions, such as ATP synthesis. Darveau and coworkers assume each contribution B_i obeys a power law; conservation of energy requires the metabolic rate to be $B = \Sigma B_i$ with each B_i equal to a coefficient c_i multiplying the mass raised to a power α_i.



JANIS

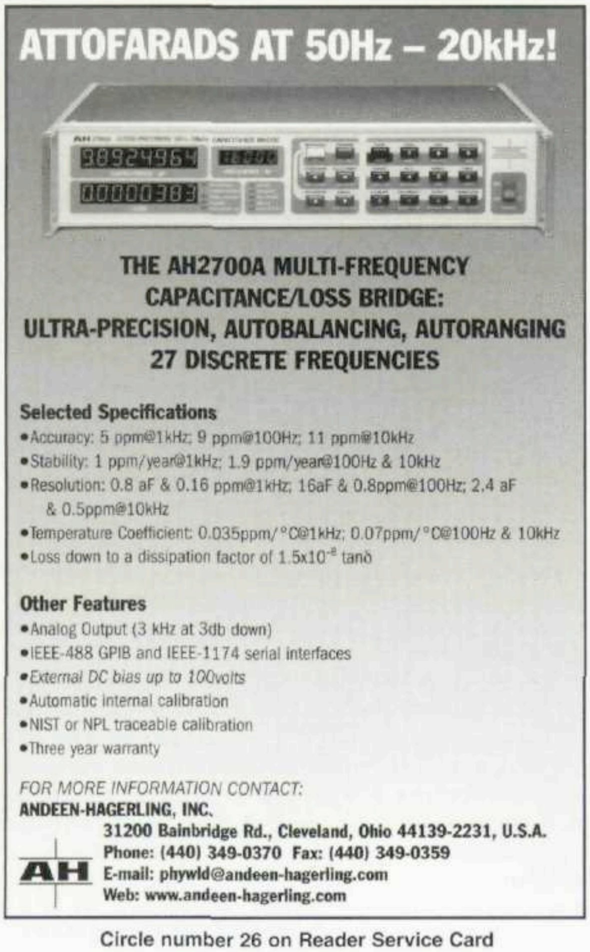
www.janis.com

CRYOGENICS FROM JANIS

- 10 mK to 800 K
- Cryocoolers
- LHe/LN$_2$ Cryostats
- Magnet Systems
- Dilution Refrigerator Systems

Janis Research Company
2 Jewel Drive Wilmington, MA 01887 USA
TEL 1 (978) 657-8750 FAX 1 (978) 658-0349 janis@janis.com

Circle number 25 on Reader Service Card



ATTOFARADS AT 50Hz – 20kHz!

THE AH2700A MULTI-FREQUENCY CAPACITANCE/LOSS BRIDGE:
ULTRA-PRECISION, AUTOBALANCING, AUTORANGING
27 DISCRETE FREQUENCIES

Selected Specifications

- Accuracy: 5 ppm@1kHz; 9 ppm@100Hz; 11 ppm@10kHz
- Stability: 1 ppm/year@1kHz; 1.9 ppm/year@100Hz & 10kHz
- Resolution: 0.8 aF & 0.16 ppm@1kHz; 16aF & 0.8ppm@100Hz; 2.4 aF & 0.5ppm@10kHz
- Temperature Coefficient: 0.035ppm/°C@1kHz; 0.07ppm/°C@100Hz & 10kHz
- Loss down to a dissipation factor of 1.5x10^{-8} tanδ

Other Features

- Analog Output (3 kHz at 3db down)
- IEEE-488 GPIB and IEEE-1174 serial interfaces
- *External DC bias up to 100volts*
- Automatic internal calibration
- NIST or NPL traceable calibration
- Three year warranty

FOR MORE INFORMATION CONTACT:
ANDEEN-HAGERLING, INC.
31200 Bainbridge Rd., Cleveland, Ohio 44139-2231, U.S.A.
Phone: (440) 349-0370 Fax: (440) 349-0359
E-mail: phywld@andeen-hagerling.com
Web: www.andeen-hagerling.com

Circle number 26 on Reader Service Card

Using data for the c_i and α_i, they obtained a good fit for B, consistent with the $^3\!/\!_4$-power law, but rejected the idea that transport networks constrain cellular behavior. However, they did not offer any first-principles explanation for why the B_i scale or why most of the exponents α_i cluster around $^3\!/\!_4$.

The alternate models summarized in this article do not provide a general dynamical scheme or set of principles for calculating detailed properties of specific systems or phenomena, even at a coarse-grained level. They were designed almost exclusively to understand only the scaling of mammalian metabolic rates and do not address the extraordinarily diverse, interconnected, integrated body of scaling phenomena across different species and within individuals. They do, however, raise significant conceptual questions about universality classes of biological networks and the minimal set of assumptions needed to construct a general quantitative theory of biological phenomena.

Scaling is a potent tool for revealing universal behavior and its corresponding underlying principles in any physical system. Ubiquitous quarter-power scaling is surely telling us something fundamental about biological systems. Major technical and conceptual challenges remain, including extensions to neural systems, intracellular transport, evolutionary dynamics, and genomics. One of the big questions is, Why does the theory work so well? Does some fixed point or deep basin of attraction in the dynamics of natural selection ensure that all life is organized by a few fundamental principles and that energy is a prime determinant of biological structure and dynamics among all possible variables?

References

1. T. A. McMahon, J. T. Bonner, *On Size and Life*, Scientific American Library, New York (1983).
2. K. Schmidt-Nielsen, *Scaling: Why Is Animal Size So Important?*, Cambridge U. Press, New York (1984); R. H. Peters, *The Ecological Implications of Body Size*, Cambridge U. Press, New York (1983); W. A. Calder III, *Size, Function and Life History*, Harvard U. Press, Cambridge, MA (1984).
3. K. J. Niklas, *Plant Allometry: The Scaling of Form and Process*, U. of Chicago Press, Chicago (1994); J. H. Brown, G. B. West, eds., *Scaling in Biology*, Oxford U. Press, New York (2000).
4. J. S. Huxley, *Problems of Relative Growth*, Dial Press, New York (1932).
5. M. Kleiber, *The Fire of Life: An Introduction to Animal Energetics*, Robert E. Krieger, Huntington, NY (1975).
6. G. B. West, W. H. Woodruff, J. H. Brown, *Proc. Natl. Acad. Sci. USA* **99**, 2473 (2002).
7. E. L. Charnov, *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*, Oxford U. Press, New York (1993); M. Ya. Azbel, *Proc. Natl. Acad. Sci. USA* **91**, 12453 (1994).
8. B. J. Enquist, K. J. Niklas, *Nature* **410**, 655 (2001).
9. M. R. Patterson, *Science* **255**, 1421 (1992).
10. G. B. West, J. H. Brown, B. J. Enquist, *Science* **276**, 122 (1997); J. F. Gillooly et al., *Nature* **417**, 70 (2002). See also R. Lewin, *New Sci.* **162**, 34 (1999).
11. G. B. West, J. H. Brown, B. J. Enquist, *Nature* **413**, 628 (2001).
12. C. Guiot et al., *J. Theor. Biol.* **225**, 147 (2003).
13. P. S. Dodds, D. H. Rothman, J. S. Weitz, *J. Theor. Bio.* **209**, 9 (2001); C. R. White, R. S. Seymour, *Proc. Natl. Acad. Sci. USA* **100**, 4046 (2003).
14. V. M. Savage et al., *Funct. Ecol.* **18**, 257 (2004).
15. J. R. Banavar, A. Maritan, A. Rinaldo, *Nature* **399**, 130 (1999); J. R. Banavar et al., *Proc. Natl. Acad. Sci. USA* **99**, 10506 (2002).
16. C.-A. Darveau et al., *Nature* **417**, 166 (2002).
17. K. Shinozaki et al., *Jpn. J. Ecol.* **14**, 97 (1964).
18. N. Manokaran, K. M. Kochummen, *J. Trop. Ecol.* **3**, 315 (1987). ■

Copyright of Physics Today is the property of American Institute of Physics -- Physics Today and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.