Body size, geometry, longevity and metabolism: do plant leaves behave like animal bodies?

Peter B. Reich

Given their differing geometry, evolutionary history and hierarchical position, plant leaves and animal bodies provide a useful comparison in evaluating the roles of size and geometry in the scaling of biological form and function. Metabolism and longevity scale similarly with specific surface area (surface area per unit mass) for both plant leaves and animal organs and bodies, indicating a fundamental allometry between geometry, area- and mass-based gas exchange and biochemical processes. By contrast, metabolism and longevity scale with size (mass) in animals but not in leaves. These findings provide evidence for the general phenomenon of geometrically based, but not size-based, scaling relationships in nature.

The idea of spatial, temporal and hierarchical scaling (Box 1) has received substantial attention in the past decade across a range of biological sciences because it might help us to better understand and characterize overarching patterns and constraints and because it offers the hope of developing general models (conceptual, theoretical and predictive). One such area of interest is the scaling of size, metabolism, longevity, chemistry and structure in animals and plants, at both the whole-organism and tissue scales[1–10]. Given the complexity of biology, it would be useful if apparently dissimilar phenomena could be accounted for by comparatively few underlying principles[3,10].

It is an appropriate time to visit such issues because a variety of new perspectives, theories and databases have emerged recently[6–22]. Here, I explore some similarities and differences observed between animals and plants, focusing on plant leaves and animal organs and bodies, and the questions that arise out of such patterns.

Body size is recognized as an important factor in animal biology and has often been given central position in scaling studies[1–4]. Size-related scaling occurs for many variables, including membrane functioning, basal respiration, longevity and population dynamics[1–5]. Such relationships[1–3] are well described by power functions of the form, $Y = aW^b$. Proposed explanations for the similarity of body size-dependent patterns and the exponents of the power function equations have included size-related shifts in the surface area (SA):mass (M) and the SA:volume relationships[2,3]; density, compositional and/or membrane permeability changes with body size[2,3]; BIOMECHANICAL STRUCTURAL PRINCIPLES (see Glossary)[2,3] and, more recently, FRACTAL and nonfractal efficient transportation network theories[6–9]. Certain aspects of whole-organism ALLOMETRY have also received recent attention in plant ecology[7,8,10–12,22], but less so *vis-à-vis* issues related to metabolism and longevity of higher plants. The metabolism, longevity and chemistry of whole plants or plant parts, however, have been shown to scale with tissue SA/M (Refs 13–17,21).

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Why compare scaling relations in plants and animals?

Any convergence in the scaling of the biological traits of plants and animals would be evidence for adaptive evolution, given that these groups diverged early in evolutionary time[10]. Although the comparison of leaves with whole animals might sound intuitively strange, there is method to such potential madness. There is a rich history in scaling biology to assert that the more (evolutionarily, hierarchically, structurally and functionally) divergent the entities in question are, but the more similar they are in terms of allometric, STOICHIOMETRIC, size–metabolism, physiological–morphological, fractal or other scaling relations, the more robust is the conclusion that a general force or set of forces is structuring processes across a vast diversity of scales, and the more vivid the indication that every level of biological organization is responsive to the same forces[3,10]. Such forces could represent both physico–chemical and natural selection pressures and constraints[3,10,14] and should not be viewed from purely engineering or evolutionary perspectives. The existence of similar scaling relations among divergent and evolutionarily unrelated objects (e.g. cells, tissues, organs and organisms) is unlikely to occur by chance alone and therefore provides evidence for CONVERGENT EVOLUTION[3,6,10,11,14].

Scaling in whole plants and whole animals

Comparisons of plants with animals have been made, particularly by Niklas[10,11], who has characterized the relations between size and form, metabolism and reproductive effort, and examined their potential causes. He showed that, similar to animals, plants demonstrate substantial size-correlated scaling, some of which is consistent with animal scaling. Several important recent papers have highlighted general theoretical approaches to such scaling issues[6–9]. These papers, plus several new experimental and observational studies[18,22,23], suggest collectively that geometry, more particularly transportation networks[6–9,23], play a key role in structuring allometric scaling relations in plants and animals. In particular, one theory[7] suggests that a 3/4 power law scaling of metabolic rate versus organism size occurs because these are the maximal values for the effective surface area and linear dimensions for a volume-filling fractal-like network, which is required to

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Box 1. Scaling

The use of the word 'scaling' for certain biological phenomena probably derives in part from one of many uses of the word 'scale'. Scale is the key property of the process of making exactly proportional dimensions for the components of two entities of contrasting sizes, such as maps versus regions, or engineering drawings, such as blueprints versus entire buildings. In this context, scale is a human construct and is used as a tool. By contrast, scaling in nature is not typically assumed to be absolutely proportional, but instead to be approximately proportional, and to be a product of natural laws.

In its biological use, scaling tends to indicate a relatively systematic variation in a metric (e.g. of dimension, mass, volume, population, rate, etc.) of an entity or process, or its parts or components, in relation to other relevant processes, entities or components. Among the most well-known scaling phenomena are the relationships between animal body size and a host of physiological, life-history and ecological variables, including between body size and growth rate, metabolism, longevity, range size, diversity and population. It is generally thought that such scaling would be highly unlikely to occur by random chance. Hence, the discovery of the causes of such scaling should uncover new information about the structure of nature.

Scaling exists across gradients (e.g. of size, chemical concentration, geometry, or hierarchical complexity) because combinations of physico–chemical laws and natural selection constrain the combination of traits possessed by organisms and their tissues. A surprising number of (not necessarily mutually exclusive) factors can act as drivers of scaling (e.g. stoichiometry, allometry, life-history tradeoffs and structural engineering principles) because they either place immutable barriers to certain kinds of organismal organization or function, or they place selection advantages on certain combinations of characteristics, but not on others. Many potential explanations for the existence of scaling phenomena have been proposed (see main text). Given that many of these potential explanations operate at different hierarchical levels, it is plausible that several factors often act together to result in any given scaling relation.

transport materials to the sites of metabolism. Argument for the generality of a model is strengthened when the model appears to fit both animals and plants. Although several studies suggest[6,7] that many scaling processes operate similarly in all plants and all animals, others disagree[24,25], and such claims are difficult to assess thoroughly, in part given the inadequacy of the whole-organism empirical database, particularly that for larger, higher plants.

Multi-species data available for large plants (e.g. >10 cm height) typically involve dimensions or reproduction[10] and, almost universally, only for aboveground parts. Some recent studies have made advances in examining water flux–tree size scaling via comparison of sap flow, sapwood area and tree size[18]. However, interspecific data for longevity, SA/M, or metabolism of whole plants in the field are exceedingly rare. Most data involving whole-plant metabolic processes are derived from unicellular algae[10,17] and as far as I know, insufficient whole-plant SA data exist for higher plants that could be used for interspecific comparison. If such data do not include roots, they provide an incomplete view of whole plant allometry that makes conclusions circumspect. Root system longevity might be many times greater than for aboveground shoots, as is commonly the case for species that sprout following aboveground disturbance. Total root lengths or SA for higher plants in the field are virtually unknown. Thus, although higher animal bodies (e.g. mammal) are clearly not simple shapes, their SA can be approximated[1–3] much more easily than for entire higher plants, with their branching architecture, fibrous roots and numerous leaves. Although it is plausible, perhaps probable, that the metabolism and longevity of entire higher plants follows similar scaling allometry as in animals[6–8,22], it is not yet sufficiently evaluated empirically for us to be able to draw firm conclusions.

Scaling in plant leaves and animal bodies

By contrast, leaves have been better quantified than have whole plants. In previous studies, the longevity, SA/M, metabolism, morphology and chemistry of leaves of numerous species growing naturally in the field have been made[14,15,20,26]. Thus, leaves provide a complementary, and in some ways more reliable, source of data for evaluating scaling issues involving longevity and metabolism than do whole plants.

Like animals, leaves of most species are discrete units with measurable SA and M, and with biophysical problems related to gas fluxes and energy balance. Leaves have evolved as plant parts rather than as independent entities, yet they are clearly subject to selection pressures. Moreover, if PHYSICO–CHEMICAL CONSTRAINTS impose SCALING LAWS on the behavior of biological entities, leaves must obey such laws. Hence, I compare scaling relationships in plant leaves and animals to address two questions. First, is there similarity in scaling for these two groups in spite of different evolutionary histories and hierarchical positions? Second, what does this comparison imply about the generality of body size and SA/M scaling relationships in nature? Because SA scales nonisometrically and proportionally with M in animals (Box 2), it is unclear whether such scaling relationships are associated with body size *per se* or only with factors that co-vary with size, such as specific surface area (SA/M), a metric describing the fundamental geometry (plus density) of objects, or other traits, such as transport networks that might also vary with SA/M (Refs 6–9). To make these comparisons, established scaling relationships between the size, morphology, metabolism and

Box 2. Relationships of surface area and mass in mammals and plant leaves

The relationships between surface area (SA) and mass (M) of animal bodies of various sizes have been explored by various researchers. Until recently, these relationships have not been widely examined in plant or plant parts, nor directly contrasted between animals and plants. Surface area/mass (SA/M) relationships in plant leaves and animal bodies are shown in Fig. Ia and Ib respectively. For mammals, SA is either for external surface (i.e. skin) or for internal surface (i.e. lungs). For leaves, SA is either for needle-leafed and broad-leafed species shown separately (if different) or pooled (if similar). The regression equations for significant relationships are given in Table I. Figure Ia details the relationship between SA and dry mass of mammals and of leaves (all species pooled). Figure Ib details the relationship between specific surface area (surface are per unit dry mass, SA/M) and M of mammal skin and lungs and of broad leaves and needle leaves. In some cases, regression was calculated from data provided in the source reference.

Table I. Regression equations for significant relationships shown in Fig. I

Line in Fig.	Regression equation[a]	r^2	P	Refs
I (a): skin	$\log SA = 0.52 + 0.70*\log M$	0.98	<0.001	a
I (a): lungs	$\log SA = 0.28 + 0.79*\log M$	0.94	<0.001	b
I (a): leaves	$\log SA = 1.74 + 1.11*\log M$	0.92	<0.001	c
I (b): skin	$\log SA/M = 0.52 - 0.30*\log M$	NA	NA	a
I (b): lungs	$\log SA/M = 0.28 - 0.21*\log M$	0.52	<0.001	b

[a] Abbreviations: M, mass; SA, surface area.

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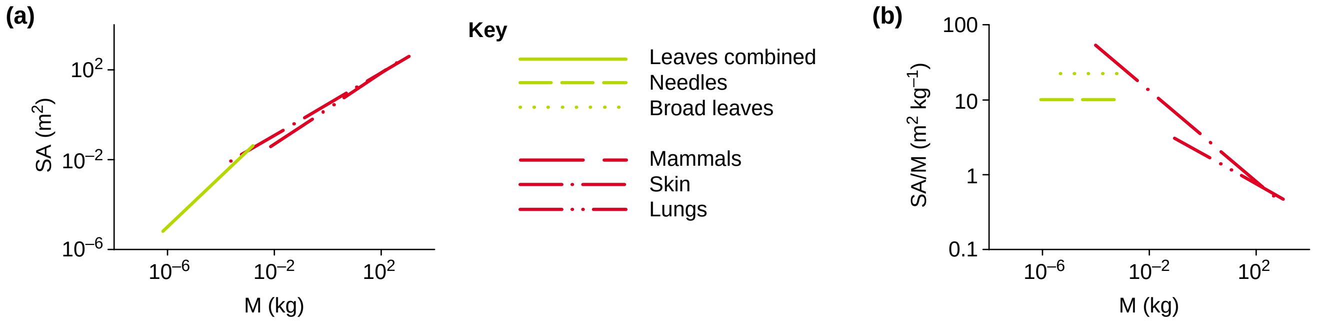

Fig. I

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longevity of field-grown plant leaves[14,15,26] are compared with established body-size relations in animals[1–6,27].

For leaves, SA increases $\approx M^{>1.0}$, whereas the SA of mammals increases $\approx M^{3/4}$ (Box 2). SA of internal diffusing surfaces in animals, such as the alveolar SA and the pulmonary SA, also scale as the ≈1.0-power of external SA and $\approx M^{3/4}$ (Refs 27,28). Thus, in plant leaves, there is no tendency for SA/M to decrease with increasing M, whereas SA/M decreases with increasing M for both external and internal diffusive surfaces of animals (Box 2). Why does SA keep the same proportionality with M as M varies among leaves, but decrease proportionally as M increases among animals? The answer is simple and involves geometry: leaves can be approximated as linear (i.e. needles) or planar (i.e. broad leaves) surfaces (i.e. 1D or 2D), whereas most animals correspond to 3D shapes. As a needle increases in length or a planar leaf increases in width or length, SA/M changes modestly (assuming density remains constant) in contrast to the changing SA/M relationships of a rounder (e.g. animal) body as body diameter increases. As a result, by varying largely in 1D or 2D across a range of M, leaves retain relatively similar SA/M properties and functioning with respect to light interception and diffusive gas exchange with the atmosphere, which is not true for 3D bodies.

Standard metabolic rates (maintenance respiration in plants) scale to M as the ≈1.0-power in leaves and the ≈0.75-power in animals. Hence, mass-specific metabolic rates are unrelated to increasing M for either planar or needle-like leaves, but decrease markedly with M (–0.25-power) in animals (Box 3). By contrast, mass-specific respiration rates increase with a similar scaling exponent in relation to SA/M for plant leaves (0.92-power) and for animals (0.90–1.0-power). Net photosynthetic rates of leaves also show a similar scaling to SA/M to that shown by metabolic rate in animals (Box 3). Thus, in spite of contrary metabolism versus body size relationships among animals and leaves, they have similar scaling of metabolism to SA/M.

Animal longevity increases with increasing M and decreases with increasing SA/M (Box 3). By contrast, leaf longevity is unrelated to M but still decreases with increasing SA/M. Metabolic rates show similar scaling with longevity in animals and leaves (Box 3). Similar patterns exist for nutrients, such as nitrogen (N), in relation to SA/M in both leaves[14,17] and animals[3] (data not shown).

Thus, plant leaves and animals follow similar scaling relationships of metabolism, longevity and chemistry with respect to interspecific variation in their geometry (SA/M) but only animals do so in relation to body size (M). These results suggest that SA/M scaling relationships are a general phenomenon (that might have a variety of causes[1–11,14]), and that body-size scaling relationships involving these traits in animals (and plants) might be largely a consequence of SA/M scaling and related processes[1–10]. Moreover, any or all of the proposed explanations for body-size scaling[1–11] might be correct, even though size might not be essential to the scaling. What are the causes and implications of these similarities and differences in animal-body and plant-leaf scaling relationships?

Scaling, selection and biophysical constraints

For plant leaves, the most compelling explanations for SA/M-related scaling involve the combination of BIOPHYSICAL CONSTRAINTS on, and natural selection for, certain combinations of interrelated traits, including SA/M, leaf N, leaf longevity, net photosynthetic capacity and dark respiration rate[13–15,20,29]. These relationships probably reflect selection against short-lived leaves with low photosynthetic rates, owing to their low life-time productivity, together with the combination of developmental or physiological constraints that make it impossible to build a long-lived leaf with high or low SA/M, high N concentrations and high photosynthetic rates.

Leaves with high SA/M, low metabolic rates and short longevity do not exist[14,15]. This is probably a result of natural selection rather than of biophysical constraints[14]. Although it would be easy to build leaves with high SA/M, short leaf life span and low photosynthetic capacity, such flimsy, unproductive, short-lived leaves would ensure low total productivity over the leaf life span, making it difficult to pay back construction and maintenance costs[29]. Moreover, this is in general a strategy with no apparent advantages.

Alternatively, there are no long-lived leaves with low SA/M that have high mass-based metabolic rates[14], probably because of biophysical constraints. It might be impossible to build a leaf with very high nutrient concentrations and photosynthetic rates that is also physically robust, durable and resistant to herbivory[14,20,30]. Building N-rich leaves can enable a species to have the potential for high rates of carbon gain[14]. Several constraints, however, limit this potential from being achieved as SA/M decreases[14,31–33]: (1) the opportunity to intercept light or to exchange CO_2 diffusely with the atmosphere (per unit M) declines, because both processes are directly related to SA; (2) there is greater internal shading and potential diffusional limitations and therefore less light and CO_2 reach the site of photosynthesis; and (3) a lesser fraction of the N allocated to a leaf is available for use in photosynthetic compounds. Moreover, many plant species succeed by maximizing survival rather than growth rate and in such cases, extended leaf longevity and low metabolic rates would be selected when SA/M is low[13].

Similar lines of reasoning have been used to explain why large animals (i.e. low SA/M) have long life spans, slow growth rates and low metabolism[1–5]. The relationships between SA/M and mass-specific metabolic rates[3,27,28], where SA represents either internal diffusive (e.g. lungs) or external animal surfaces, show similar scaling and are mechanistically analogous to SA/M versus metabolic relations in leaves. These explanations are consistent with some elements of structural engineering, compositional, transport network and surface law arguments raised to explain the animal and plant body size or SA/M scaling phenomenon[1–5,10]. Whether leaf or animal, high SA/M of an important diffusive surface enables high mass-specific rates of gas flux that are required for high mass-specific rates of biochemical reactions and that, in turn, require high concentrations of key nutrients, which need to be efficiently transported to the sites of gas flux. Possessing such combinations of traits is advantageous under certain ecological situations, but not others.

It is self-evident that natural selection operates within the boundaries placed by physico–chemical constraints, and probable that both operate together to lead to the strong scaling relationships observed in nature[7,10,14]. For instance, the upper boundary of scaling relationships between metabolism and leaf longevity appears to have strong physico–chemical constraints and the lower boundary has no physico–chemical constraints[20]. If only physico–chemical constraints controlled scaling, we would expect to find a triangular scatter with an upper boundary and no lower boundary. However, the lower boundary of this scaling relationship is as sharp as the upper boundary (i.e. there is no more variance on the lower than on the upper side of the scaling line)[14]. Although the lower boundary has no physico–chemical constraint, there are some obvious evolutionary constraints, as described above (e.g. no advantages to unproductive, short-lived leaves). Whether the same contrasting processes (physical constraint versus selection) explain the upper versus lower bounds of scaling relationships (such as metabolism–longevity) in animals as in plant leaves is not known. Although this argument has been made in a general sense, the available data are not definitive.

Why do leaves not follow size-based scaling as in animals? External (e.g. SA/M) and internal (e.g. EFFICIENT DISTRIBUTION NETWORKS) drivers of geometric scaling and their consequences should still apply, with modification, to functionally 1D or 2D organisms[7]. Therefore, assuming that these factors contribute to the existence of body-size laws[6–9], it would be reasonable to conclude that similar body-size laws of 3D entities should apply for functionally 1D or 2D organisms or parts of organisms, such as leaves, regardless of the shape, except for extremely nondimensional organisms, such as filamentous

Box 3. Metabolic rate, longevity, surface area and mass relationships between mammals and plants

The relationships between metabolic rate, longevity, surface area (SA) and mass (M) for animals or for plant leaves have been considered as being of fundamental importance by some researchers. However, the implications of the similarities or dissimilarities in these relationships for leaves versus animals have not been considered. In Fig. I, data are shown for the relationships between surface area/mass (SA/M) , metabolic rate and longevity in plant leaves and animal bodies. For mammals, SA is either for external surface (i.e. skin) or for internal surface (i.e. lungs). For leaves, SA is either for needle-leafed and broad-leafed species shown separately (if different) or pooled (if similar). Metabolic rate is standard metabolic rate for mammals and dark respiration rate for leaves. Photosynthetic rates are also shown for leaves where labeled. The regression equations for significant relationships are given in Table I. Figure Ia details the relationship between metabolic rates and M for mammals and leaves. There was no significant relationship between photosynthetic capacity and M or between dark respiration and M. Figures Ib and Ic detail relationships between metabolic rates and SA/M or longevity for mammals and leaves. Figures Id and Ie detail relationships between longevity and M or SA/M.

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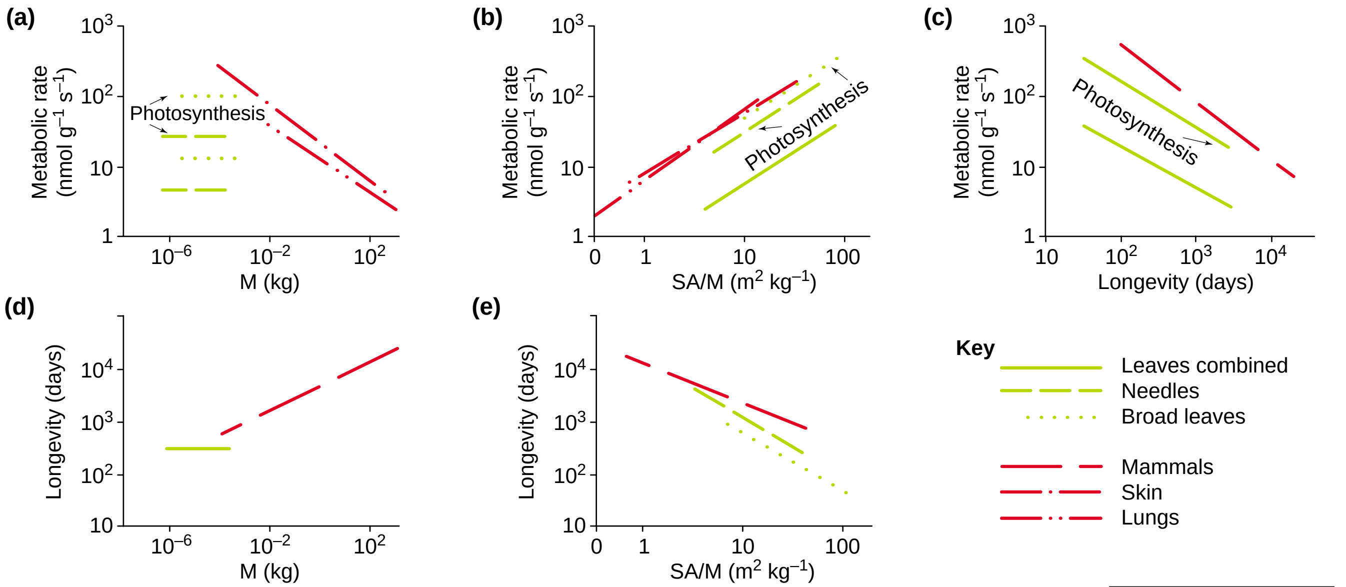

Fig. I

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Table I. Regression equations for significant relationships shown in Fig. I[a]

Line in Fig. I	Regression equation[b]	r^2	P	Refs
I (a): skin	log standard metabolic rate = 1.35 – 0.27*logM	0.89	<0.001	a
I (a): lungs	log standard metabolic rate = 1.11 – 0.23*logM	0.79	<0.05	b
I (b): skin	log standard metabolic rate = 0.88 + 0.90*logM	NA	NA	a
I (b): lungs	log standard metabolic rate = 0.82 + 1.0*logM	NA	NA	b
I (b): leaves (pooled)	log respiration = –0.15 + 0.92*logSA/M	0.58	<0.0001	c,d
I (b): broad leaves (photosynthesis)	log photosynthetic capacity = 0.69 + 0.97*logSA/M	0.61	<0.0001	c,e
I (b): needle leaves (photosynthesis)	log photosynthetic capacity = 0.40 + 1.01*logSA/M	0.67	<0.0001	c,e
I (c): mammals	log standard metabolic rate = 4.38 – 0.82*log longevity (days)	0.65	<0.001	a
I (c): leaves (pooled)	log photosynthetic capacity = 3.54 – 0.66*log longevity (days)	0.78	<0.0001	c,e
I (d): mammals	log longevity = 3.69 + 0.23*logM	0.62	<0.001	a
I (e): mammals	log longevity = 4.09 – 0.77*log SA/M	NA	NA	a
I (e): broad leaves	log longevity = 3.85 – 1.10*log SA/M	0.38	<0.0001	c,e
I (e): needle leaves	log longevity = 4.18 – 1.13*log SA/M	0.54	0.0001	c,e

[a] Where available from other sources, the slope relationships involving animals tend to be close to those shown here.

[b] Abbreviations: M, Mass; SA, surface area.

algae and fungi, which have been selected to maximize linear dimensions to occupy sparsely a maximal volume[7]. Although it is thus unclear why plant leaves follow SA/M scaling, but not body-size scaling, perhaps it is related to their unique functions (and relatively small range of size).

The most important functions of leaves involve light harvesting and gaseous diffusion with the atmosphere, both of which are SA-based processes. A key tradeoff[13,14,20,34] is between maximizing instantaneously these SA-based yields with efficient (i.e. minimal) investment of carbon and nutrients versus maximizing the conservation of carbon and nutrients over time, thus increasing long-term efficiency, which requires minimizing SA and nutrient investment per unit mass of carbon. This tradeoff exists because the maximum short-term efficiency strategy has many ecological disadvantages associated with fragility, high susceptibility to herbivory and high energy costs. Inasmuch as most environments are suboptimal rather than optimal, these disadvantages collectively make this strategy no more evolutionarily sound than the opposite or intermediate strategies. Given the 1D and 2D geometry of leaves, perhaps this leaf syndrome tradeoff has strong enough consequences for leaf form and function that the biophysical pressures for size-related scaling (in relation to these traits) have minimal impact across the relatively small size range of leaves. In essence, although leaves vary in size across three orders of magnitude, perhaps this is sufficient for (size-related) structural engineering or optimal transport network principles[6–10] to come only weakly into play. Moreover, a recent study suggests that leaf size might be evolutionarily related to twig size, inflorescence size and plant hydraulics, but not to SA/M and the associated suite of traits, and that these represent two independent axes of evolutionary diversification (D.D. Ackerly *et al.*, unpublished). Improved understanding of these issues and their connections represents an important future research opportunity.

Do scaling relations hold at every sub-scale?

It is possible that important scaling phenomena place constraints on biological form and function across very large gradients, yet play little role in structuring trait combinations and biological form and function at segments of the total gradient. The broad scaling phenomena might place outer bounds on the combination of values of any set of variables in question, yet might exert minimal control and yield little understanding of their relationship across narrower parts of the range, where other factors might be of pre-eminent importance[30]. As the range of a given parameter (size, length, %N and SA) narrows (e.g. comparing lizards or alpine grasses rather than all animals or plants), other factors and sources of variation become increasingly important in determining other traits. Examples include the relationships of leaf longevity and other leaf traits in grasses or trees with highly constrained leaf phenology[30], or relations between body size and other metrics for animals of similar size but different natural histories[24,25]. By contrast, allometric scaling relationships help explain enormous differences among organisms that do vary dramatically in size (and hence in geometry).

Another example bridges our consideration of leaves and whole plants. Across the vast spectrum of size, larger plants have slower growth rates than do smaller plants[10,22,35], and hence are more likely to have lower metabolic rates of key components, such as photosynthetic tissues[23]. However, within a part of the total size range of plants this might not always be true[19,36]. For sympatric species in a tropical rainforest, trees that are larger when mature have greater metabolic rates than do tree species that are typically smaller, probably because of selection pressures related to heterogeneity in canopy position and light availability, and hence in associated benefits and costs of specific metabolic traits[19]. Trees that are typically taller spend a greater fraction of their lives in sunlit environments, where high metabolic rates are advantageous, whereas individuals of shorter species spend more time in shaded habitats, where low metabolic rates are advantageous[19,38,39]. Metabolic rates might also hypothetically increase with plant height, owing to increasing costs of support structures[36,37], whereas other theoretical considerations, such as declining water transport efficiency, might act to decrease metabolic rates with increasing plant height[23]. These conflicting patterns, and their causes, demonstrate the need to identify both overarching scaling that confines the structure and function of organisms and organs within broad domains[6–9,14], and finer scale forces that further modulate the inter- and intraspecific traits of organisms and their tissues[20,34,38,39]. Physico–chemical drivers of scaling are likely to be systematically general and operate at the broadest scales, but provide little resolution at fine scales. Alternatively, selection-based drivers are likely to operate systematically less frequently across all life forms and scale, but are more likely to provide detailed answers to the persistent questions of life. Both are important, but they provide different kinds of answers to different kinds of questions.

Conclusions

The comparison between plant leaves and animals shows no evidence of common body-size scaling relations, but there is strong evidence that metabolism and longevity do scale convergently with SA/M in both kinds of entities. This evidence supports the idea that, associated with variation in SA/M and related variables[6–9,14], there are unavoidable biophysical constraints and related ecophysiological tradeoffs and selection advantages and/or disadvantages that collectively drive convergent scaling relationships in all organisms. Given that leaves and animals have similar geometrically based scaling, how do we interpret the lack of convergence of leaves and animals with respect to size-related scaling? If size-related scaling rules are physico–chemical in nature, they should apply to

Glossary

Allometry: relative mass, volume, dimension, or growth of a part or the whole of an organism in relation to a measure of another part or the whole of an organism.

Biomechanical structural principles: rules governing a specific kind of physical constraint involving the engineering mechanics of living organisms being considered as structural entities.

Biophysical or physico–chemical constraints: physical and/or chemical laws or features that place limits on the possible biological alternative traits or trait combinations. These limits can either be absolute (e.g. gravity) or work in conjunction with natural selection as part of tradeoff scenarios (e.g. tradeoff between rigid strength versus flexibility). These biophysical constraints can lead to scaling phenomena.

Convergent evolution: the process whereby similar forces lead to similar evolutionary outcomes in independent evolutionary events. Processes that lead to scaling have often been hypothesized to also lead to convergent evolution, and have been proposed as explanations for observed convergence.

Efficient distribution networks: living organisms are sustained by the transport of materials through linear networks that branch to supply all parts of the organism. Such networks are efficient when they minimize the scaling of transport distances and times. The geometry of such hierarchical networks tend to be fractal in nature.

Fractal: any of various and often extremely irregular curves or shapes for which any suitably chosen part is similar in shape to a given larger or smaller part when magnified or reduced to the same size.

Scaling laws: quantitative relationships, usually between pairs of variables, across various temporal, spatial, geometric or hierarchical scales, in which proportional change in one factor is highly correlated with proportional change in another factor (Box 1).

Stoichiometry: application of the laws of definite proportions and of the conservation of matter and energy to chemical reactions and processes; especially the quantitative relations of constituents in chemical entities.

discrete organs, such as leaves. This suggests that body-size relations of whole plants and animals are either important artifacts of geometric scaling (i.e. there is nothing about size *per se* that is important), are purely evolutionarily driven but for some unknown reason do not apply to leaves, or result from the interplay of both.

Complete answers to the questions and issues raised here do not exist. Characterizing, first, whether, how and why scaling rules that apply across broad gradients hold at narrower ecological scales; and second, identifying and separating the roles of selection and physico–chemical constraints in scaling, represent major voids in our understanding and hence important avenues for future research. Separating finer scale evolutionary from broader scale physico–chemical drivers of scaling relationships will not be easy, however, because, in some cases, the former might be highly influenced by the latter[1–15].

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