

REVIEW PAPER

Biophysical and size-dependent perspectives on plant evolution

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Abstract

Physical laws and processes have profoundly influenced plant evolution. Their effects are invariably size dependent and thus subject to scaling as well as biophysical analyses even though these effects differ depending upon the fluid (water or air) in which plants evolve. Although organisms cannot obviate the effects of physical laws and processes, the consequences of these effects can be altered by ontogenetic or phylogenetic alterations in geometry, shape, or orientation as well as in body size. These assertions are examined using theoretical insights and empirical data drawn from extant and fossil plants pertinent to four evolutionary transitions: (1) the evolution of multicellularity, (2) the transition from an aquatic to an aerial habitat, (3) the evolution of vascular tissues, and (4) the evolution of secondary growth by the independent acquisition of cambium. This examination shows how physical laws limit phenotypic expression, but how they also simultaneously provide alternative, potentially adaptive possibilities.

Key words: Algae, allometry, constraints, embryophytes, fossil record, scaling relationships.

Introduction

Understanding biophysics informs our understanding of plant ecology and evolution because (1) regardless of its habitat or phyletic history, every plant must exchange gases with the atmosphere, conduct fluids, intercept light, cope with mechanical forces, and reproduce; and (2) each of these functions is governed to some degree by the operation of physical laws and processes (Gates, 1980; Niklas, 1992; Nobel, 2005; Read and Stokes, 2006; Niklas and Spatz, 2012). For these reasons, it is possible to view organic evolution as an extended 'experiment' in how organisms respond to and cope with the laws governing chemical and physical phenomena. This assertion extends from the cellular mechanisms controlling the future planes of cell division to ecosystem function. It is tempered however with the recognition that evolution is as much the result of crisis-driven extinctions and historical accidents (Gould, 1989) as it is the result of unavoidable and persistent physical phenomena. The challenge is to separate the consequences of historical legacy from the effects of these phenomena.

Another assertion is that the effects of physical laws and processes are size dependent (Huxley, 1932; Niklas, 1994a, 2004) even at the level of individual cells (e.g. Sperry *et al.*, 2006). To paraphrase JHS Haldane's zoological metaphor, a poppy seed hitting a hard floor after falling a great height behaves differently from a coconut simply because of a difference in mass. It is critical, therefore, to consider evolution in terms of size-dependent (scaling) relationships, particularly since the fossil record reveals numerous changes in vegetative and reproductive size (e.g. Mosbrugger, 1990; Tiffney, 2004). The challenge here is to determine whether the scaling relationships observed for extant plants held true for fossil plants. For example, the leaf spectrum for functional traits indicates that extant plants with large leaves, on average, have thick twigs and that plants with thick twigs tend to branch more sparingly than plants with thin twigs that typically bear smaller leaves (Westoby and Wright, 2003; Olson *et al.*, 2009). If these 'rules' (known as Corner's rules) describe something essential about all plants, they will also hold for Phanerozoic

floras. If not, they reflect something about modern plants, not something universally true. The key to resolving this issue is to understand *mechanistically* how and why organisms converge on certain proportionalities.

A third assertion is that evolution occurs in two very different fluids, water and air, which has important consequences because the effects of physical laws differs in these two fluids. Fortunately, dimensionless numbers such as the Reynolds number (Table 1) and dimensional analyses can be used to address how physical phenomena operate in different fluids. Thus, plants should be defined broadly as eukaryotic photoautotrophs to encompass the rhodophytes and stramenopiles as well as the chlorobionta (which includes the embryophytes and the charophycean algae). The breadth of this definition is necessary because the ability to photosynthesize, synthesize cell walls, and evolve multicellular body plans has occurred independently at least six times and with varying degrees of success (Niklas and Newman, 2013). For example, consider the diversity of materials used to construct plant cell walls (Niklas, 2004), such as silica in diatom frustules and cellulose in land plant cells (with Young's elastic moduli in the range of 0.35–2.77 GPa and 110–220 GPa, respectively). Is it possible that the mechanical and chemical architecture of cellulosic cell walls was one key to the success of the land plants?

Table 1. Representative physical relationships, their quantitative expressions, and parameters that cannot be changed biologically. $\partial C_i/\partial x$ = concentration gradient of substance i ; $-\partial P/\partial l$ = negative hydrostatic pressure gradient; $A = \pi r^2$; A_p = projected area; C = taper-dependent proportionality factor (e.g. $C = 1.96$ for a cone); C_D = drag coefficient; d = reference dimension; D_f = drag force; D_i = diffusivity of substance i ; E = Young's modulus; g = acceleration due to gravity; H_{crit} = critical buckling height; J_i = flux rate of substance i ; r = radius; U = flow speed; ΔC_i = change in concentration of substance i ; $\Delta V/\Delta t$ = volumetric flow rate; δ = boundary layer thickness; μ = dynamic viscosity; ρ = bulk tissue density (or fluid density in drag force equation); ν = kinematic viscosity. For more information on the quantitative expressions, see Niklas and Spatz (2012).

Physical relationship	Quantitative expression	Invariant parameters
Reynolds number	$Re = \frac{dU}{\nu}$	ν
Fick's second law	$J_i = -D_i \frac{\partial C_i}{\partial x} = -D_i \frac{\Delta C_i}{\delta}$	D_i
Hagen–Poiseuille equation	$\frac{\Delta V}{\Delta t} = -\frac{\partial P}{\partial l} \left(\frac{\pi r^4}{8\mu} \right)$	μ
Greenhill–Euler equation	$H_{crit} = C \left(\frac{E}{\rho g} \right)^{1/3} r^{2/3} = C \left(\frac{EA}{\pi \rho g} \right)^{1/3} g$	g
Drag force	$D_f = 0.5\rho A_p U^2 C_D$	ρ

A fourth and final assertion deals with the equations describing the operation of physical laws and processes (Table 1). Inspection of these expressions reveals two types of parameters – those that cannot be changed by biological modifications and those that can be changed either ontogenetically or phylogenetically. Consider, for example, passive diffusion. The diffusivity of a substance cannot be altered by an organism, whereas the concentration gradient of a substance can be changed biologically by altering its consumption or production or by changing the distance between its source and sink (Gates, 1980; Nobel, 2005) – a feature that helps to explain why most algae have thin body plans with large surface areas. The existence of these two types of parameters is important because it shows that evolution is constrained by physical laws, but that the effects of these laws can be modified by biological innovation.

Given the huge scope of the topic at hand, the following sections can only illustrate broadly how a biophysical and size-dependent perspective informs our understanding of evolution. These sections are devoted to four important evolutionary transitions: (1) the transition from a unicellular to multicellular body plans, which involved micromechanical adjustments to the planes of cell division; (2) the transition from an aquatic to an aerial existence, which involved adjustments of pre-existing charophycean-like morphological and chemical characteristics; (3) the evolution of the vascular plants, which involved additional adjustments to symplastic and apoplastic transport systems, programmed cell death, and cell-wall patterning; and (4) the transition from primary to secondary growth, which involved convergent solutions to coping with drag forces and increasingly larger bending moments. An important feature appearing in each of these transitions is the role of tradeoffs resulting from the simultaneous performance of biological functions with conflicting physical requirements. These tradeoffs confined phenotypic expressions to specific morphological domains, but they also produced opportunities to expand or create new ones – a feature discussed in the concluding section.

The unicellular to multicellular transition

Fick's second law of diffusion reveals the advantages of being a small unicellular organism with a large surface area with respect to volume (Nobel, 2005), since this condition expedites the exchange of mass and energy between a cell and water (Table 1). Nevertheless, multicellularity has evolved at least twice in the rhodophytes, in the stramenopiles, and in the chlorobionta (Niklas and Newman, 2013). This convergence gives the impression that multicellularity conveys adaptive benefits. However, it is not always true that every evolutionary change requires a substantive or even measurable selective advantage (Grosberg and Strathmann, 2007; Lynch, 2012). Nor is it true that phenotypic responses to selection invariably conform to the direction of an adaptive advantage (Bonduriansky and Day, 2009). Thus, a theoretical model for filamentous bacteria shows that strains with the same fitness can produce genotypes differing in cell number

as a result of differences in cell division and death rates, or as a result of changes in the environmental carrying capacity (Rossetti *et al.*, 2011). This model, which has empirical support, also shows that differences in fitness attributable to morphology are not required *a priori* for the evolution of life cycles with multicellular entities (Rossetti *et al.*, 2011), although advantages may arise subsequently (Koschwanec *et al.*, 2011). The retention of multicellularity in some lineages therefore may reflect a largely random tend to increase in body size (Gould, 1989). Indeed, although examples are known of unicellular species arising from multicellular ancestors (Velicer *et al.*, 1998; Schirmermeister *et al.*, 2011), once an organism achieves multicellularity its capacity for contingent evolutionary reversion to the unicellular condition is reduced for reasons that have little or nothing to do with selection on fitness.

Regardless of whether multicellularity reflects the direct consequence of natural selection, cladistic analyses reveal that its acquisition releases organisms from functioning as gametes (which is the fate of most unicellular eukaryotes), lengthens the diploid phase in haploid–diploid life cycles (thereby expanding the genetic repertoire of gametes), and permits organisms to evolve a broader scope of phenotypic innovation as gene regulatory pathways increase in number or complexity (Bonner, 2004; Lane and Martin, 2010). However, the evolution of multicellular plants passed along a critical biophysical constraint: a relatively rigid cell wall (Niklas, 2004; Graham *et al.*, 2009). Consequently, cell division and morphogenesis occur in the absence of cell migration, a limitation that has been resolved by programmed cell death, differential asymmetric cell division, and anisotropic expansion (e.g. Geisler *et al.*, 2000; De Smet and Beeckman, 2011), all of which take on particular importance in plant development (Kim and Zambryski, 2005; Torii, 2012).

The biophysics influencing the orientation and location of the future cell wall during cell division may be the most critical developmental feature in all of plant evolution, since it influences the complexity of the plant body plan (Niklas, 2000). Among the charophycean algae and the embryophytes, the location of the future cell wall is prefigured by the appearance of the preprophase band and the phragmoplast (Graham *et al.*, 2009). The mechanisms underlying the orientation and location of these cytological features are not well understood. Early work showed that the application of pressure to a dividing cell forced the mitotic figure into the position in which the longitudinal axis is oriented at right angles to the applied pressure such that the future cell wall is oriented parallel to this direction (Kny, 1902; Lynch and Lintilhac, 1997) and that the planes of successive division tend to be at right angles to one another such that regular patterns of two, four, eight, etc. form in one plane when cell divisions are simultaneous (Geitler, 1951), a geometric analogue of Errera's rule.

More recent research using empirical data and computer simulations of cell division patterns indicates that multiple competing division planes exist, but that 'smaller area' configurations are, on average, achieved if significant differences exist in the surface areas of competing division planes (Besson and Dumais, 2011). Conversely, when small differences exist

among competing planes of division, the probability of achieving the one with the minimal area is inversely proportional to the difference in length of the division plane: in cells differing significantly in length, the shortest transverse division planes are achieved, whereas competing planes of cell division with similar surface areas are achieved with near equal probability in polygonal cells.

Besson and Dumais (2011) further speculate that a microtubule (MT) force-sensing system permits the MT cytoskeleton to mechanically move the nucleus into an equilibrium position. If a nucleus is positioned off centre during interphase, the MTs tethering it to the plasma membrane will bring the nucleus to an equilibrium position based on differences in the tensile forces generated among MTs differing in length. Shorter rather than longer MTs would be favoured collectively to achieve an equilibrium configuration, which automatically coincides with the minimal area plane that concurrently prefigures the formation of the pre-prophase band.

It is entirely reasonable to suggest that mechanically induced stresses are also involved in cell-wall orientation among embryophytes (Mirabet *et al.*, 2011). The simplest embryophyte cells are parenchyma cells with thin primary walls inflated by more or less uniformly distributed turgor (hydrostatic) pressure. However, at the vertices of adjoining cells, opposing tensile stresses are resolved into additional stresses acting in the radial direction on the angle of each vertex according to its size. In theory, the tensile stresses in walls at 180° should be equal and opposite and thus this angle experiences no additional radial stress from the resolution of the opposing tensile stresses in the two intersecting walls. However, these tensile stresses are resolved into progressively larger radial stresses as the angle of a vertex decreases, reaching their maxima as the angle approaches 0°. Because these additional radial stresses are correlated directly to the size of the angle, stresses are correlated to angle size such that a cell reaches mechanical equilibrium at equiangular vertices. Consequently, the observation that the vertices in the region of isodiametrical expansion can act as 'pivots' for wall rotation between successive divisions (so as to coincide with cellular mechanical equilibria) provides some evidence for the mechanical regulation of cell shape.

However, most scenarios cannot explain the mechanics of *elongating* cells, wherein existing walls rotate around their vertices to align either perpendicular or parallel to the longitudinal axis and future cell walls are generally oriented perpendicular to the growth axis. Here, the principal stress trajectories likely resolve the global stress patterns into orthogonal components and are thus likely to be oriented parallel and perpendicular to the growth axis. In this condition, cell walls may be oriented so as to minimize shear stresses, although it is becoming increasingly clear that different mechanisms affecting cell-wall growth have evolved (see Campàs *et al.*, 2012).

None of the preceding explains whether cell walls transduce radial stresses directly into specific cell shapes or whether mechano-sensitive elements in the cell membrane or cytoskeleton take on or augment this function (Schopfer, 2006). What can be said is that the biophysical mechanism(s) regulating

the locations of new cell walls is (are) ancient and that they involve mechanical cues resulting from stresses induced by hydrostatic pressure acting on pre-existing cell walls (Mirabet *et al.*, 2011).

The water to air transition

Chemical constraints as well as those imposed by physics played an important role in plant evolution, particularly in the transition from living in water to living in air. Small unicellular aquatic organisms have the advantages conveyed by Fick's second law for passive diffusion (Table 1). However, terrestrial plants, which inhabit the air, have at least two advantages over their aquatic counterparts because even pure water absorbs all wavelengths of visible light and because even a thin layer of water can pose a significant barrier to the passive diffusion of CO₂ and O₂ (Gates, 1980; Nobel, 2005). It is therefore not surprising that most aquatic plants live close to the air–water interface, possess active CO₂-uptake mechanisms (Raven, 1991), and manifest an interspecific surface area to volume scaling relationship with a 3/4 (rather than a Euclidean 2/3) scaling exponent, which maximizes surface area with respect to volume as cell sizes increase (Fig. 1). Nor is it surprising that unicellular plants lacking carbonate pumps have repeatedly colonized the soil wherein the air–water interface is on a scale approximated by the dimensions of algal cells. This feature is particularly true of the green algae (Lewis and McCourt, 2004; Lewis and Lewis, 2005), perhaps because of their tolerance of a wide soil pH range.

One of these green plant invasions was particularly important. Current phylogenies show that the charophycean algae are most closely related to the embryophytes (Graham, 1993; Lewis and McCourt, 2004; Archibald, 2009). The earliest charophycean colonists may have been unicellular soil dwellers (Stebbins and Hill, 1980) or organisms participating in symbiotic relationships with fungi (Niklas and Kutschera, 2010). However, based on the attributes of extant charophytes most closely related to the embryophytes, the last common ancestor probably had plasmodesmata (Cook *et al.*, 1998), a filamentous body construction, and a physiological

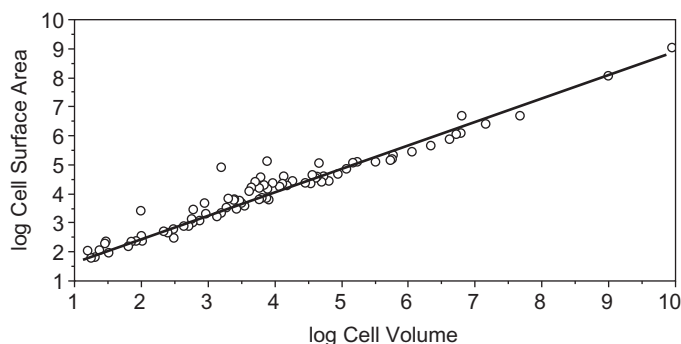


Fig. 1. Log₁₀-transformed data for cell surface area plotted against transformed data for cell volume (original units in μm). The solid line is a reduced major axis regression curve with a slope of 0.76. Data from Niklas (1994).

repertoire capable of polar auxin transport (Boot *et al.*, 2012) and the ability to synthesize sporopollenin and lignin or similar polymers (Sørensen *et al.*, 2011). It also likely lacked a contiguous cuticular membrane. Plasmodesmata provide avenues for the passive and active transport of nutrients and phytohormones; a filamentous tissue construction maximizes surface area with respect to body volume and facilitates gas and water passive diffusion (Niklas, 2000); and the ability to synthesize desiccation- and degradation-resistant polymers provides advantages to a semi-terrestrial organism (Kroken *et al.*, 1996; Graham *et al.*, 2009).

These attributes nevertheless limit the ability of any plant to cope vegetatively with desiccation, thereby probably restricting growth and reproduction to habitats with free-standing water. The sexual life cycle of this ancestor probably involved the retention of egg cells within a multicellular structure that provided protection and nutrients before and perhaps after fertilization. The presence of degradation-resistant cell-wall layers, similar to sporopollenin, in the zygotes of green algae closely related to the embryophytes (Kroken *et al.*, 1996; Graham *et al.*, 2009) may have provided a 'seed bank' mechanism permitting the ancestral species to persist in habitats subjected to periods of drying sufficient to kill adult plants, an attribute that would have provided a competitive advantage over other terrestrial colonists incapable of forming cyst-like zygotes. Finally, it is likely that the last common ancestor of the charophycean algae and the embryophytes had a haplobiontic–haploid life cycle (Graham, 1993; Niklas and Kutschera, 2010). Thus, the dominance of a multicellular diploid generation among extant vascular plants necessitated delayed zygotic meiosis and a transfer of function of the degradation-resistant polymers protecting zygotes to those protecting spores.

The nonvascular to vascular transition

Considerable importance is often attached to the evolution of stomata and the cuticle when reviewing how plants adapted to life on land (or, more accurately, adapted to life in the air). However, extant liverworts lack stomata, while the presence of stomata on the sporangia of poikilohydric mosses and hornworts may signify that these structures performed different functionalities than those observed for extant homeohydric taxa: for example, stomata may have functioned to promote tissue dehydration for spore release as *Sphagnum* pseudostomata do today (Duckett *et al.*, 2005). Likewise, although the function of the cuticle is typically discussed in terms of water conservation and UV protection, tensile mechanical tests show that the cuticle is also remarkably strong and optimally placed to cope with the hydrostatic stresses generated by turgid ground tissues (Matas *et al.*, 2004). The cuticle is also important during early development because it prevents the fusion of the neighbouring cell walls of closely packed organs. The evolution of a contiguous cuticle may have driven the evolution of water-conducting tissues as a result of precluding ecotohydric water transport and absorption.

Whether the first hydraulic tissues transported water apoplastically like xylem or symplastically like phloem remains

conjectural as well, since the function of such a delicate tissue would not be easily deduced from fossils. However, it is noteworthy that phloem, and not xylem, is the principal venue for water transport in developing leaves and transports significant quantities of water as a result of phloem loading in mature organs (Ayer *et al.*, 2003; Turgeon, 2006)

(Fig. 2A). It is conceivable, therefore, that the first specialized tissues for transport in the earliest land plants conveyed water and photosynthates symplastically (Fig. 2B), just as it is possible that the phloem-like leptom of some extant mosses transports water as an indirect consequence of the basipetal transport of photosynthates in the xylem-like

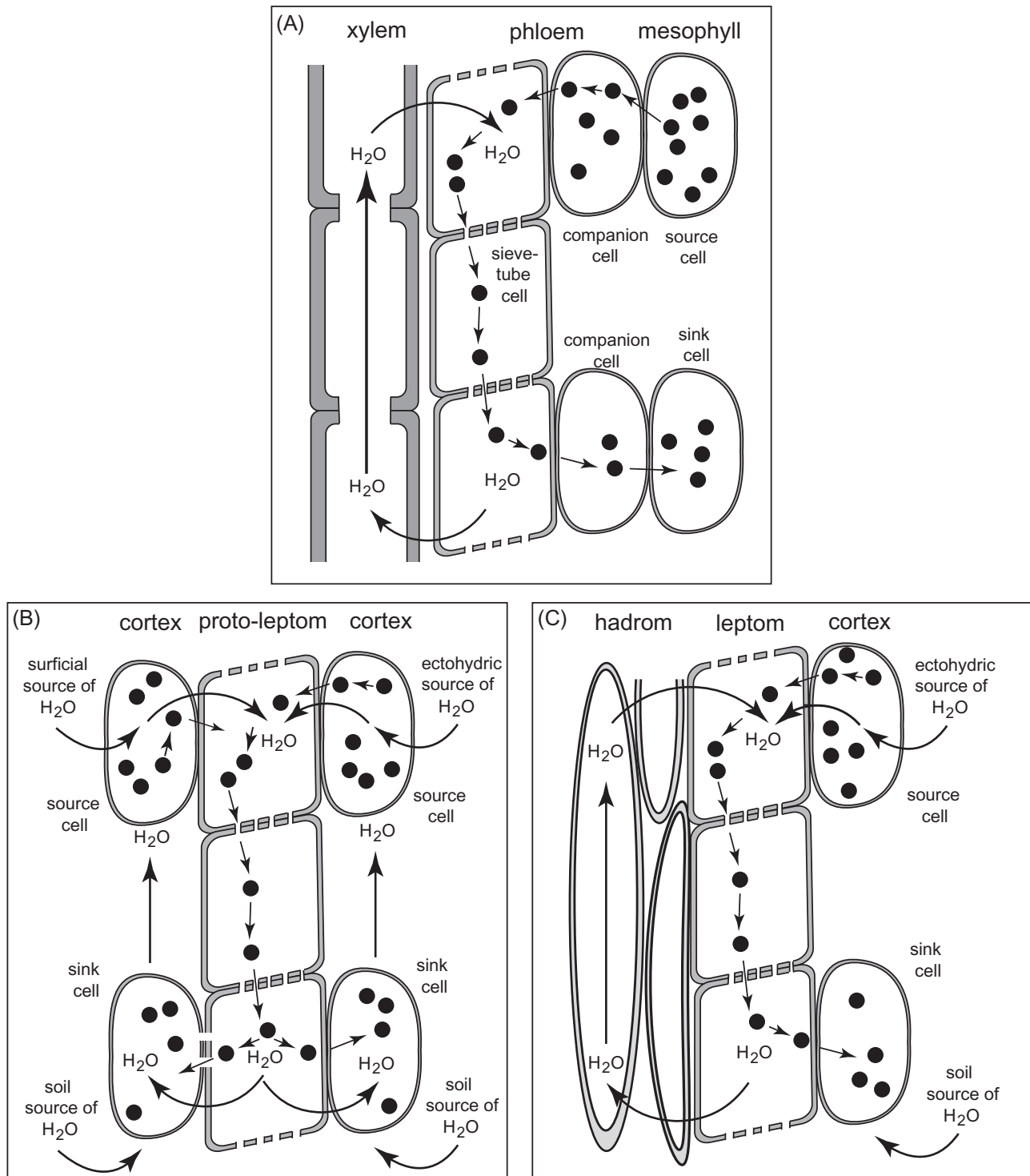


Fig. 2. Diagram of phloem loading in an extant angiosperm, for example in *Salix* (A), a hypothetical symplastic water transport system driven by external water sources and a solute concentration gradient (B), and a hypothetical hadrom-leptom system with a phloem-like loading component (C). Solutes denoted by black dots; concentrations gradients indicated by numbers of black dots.

hadrom (Fig. 2C). If so, a plausible scenario is that, because of their small size, the most ancient land plants could rely on passive diffusion for the acropetal symplastic transport of water using basipetally decreasing solute concentrations in a leptom. Plant stature could have increased with the evolution of a xylem-like hadrom tissue capable of apoplastically transporting water (supplied in part by the ectohydric wicking of water) driven by a simple hadrom solute-loading system. The transition from this condition to a true vascular system with xylem and phloem loading required the evolution of cell-wall patterning and differential thickening (Oda and Fukuda, 2012) and programmed cell death, both of which are prefigured in nonvascular plants. The differential thickening and lignification of xylem cells empowered tracheids and vessel members to resist implosion by virtue of the mechanical reinforcement of cell walls and by virtue of lignin's hydrophobic ability to prevent the hydration of cellulose, which is weaker when wet than when dry (Schuetz *et al.*, 2012).

Another important component to understanding the evolution of the earliest vascular plants is the hydraulic consequences of altering the morphology of the stele from a simple centrally located haplostele to steles in which xylem is located closer to the stem periphery (e.g. actinosteles and siphonosteles). The work of Roth and Mosbrugger indicates that the optimization of water transport depends on the location of conducting cells as well as on cell number (Roth *et al.*, 1994; Roth and Mosbrugger, 1996). Their work also shows that protosteles contribute little or nothing to mechanical stability because they occupy a mechanical 'safe site' in which bending and twisting stresses have negligible magnitudes, whereas actinosteles and siphonosteles progressively contribute to mechanical stability by deploying comparatively stiff cells in locations that experience larger stresses.

Finally, it should be noted that the ability to sense gravity is required regardless of whether a plant lives in water or on land and that this ability involves compressive forces exerted on cell membranes, which stimulates the reorientation of cells or organs (Mouliat and Fournier, 2009; Blancaflor, 2013). For example, when a root is placed askew, amyloplast resedimentation and subsequent cytoplasmic alkalization in the cells of the columella are rapidly followed by the relocalization of auxin efflux carriers that changes the flow of auxin through the root and generates a lateral auxin gradient across the root cap. The extension of this gradient to cells in the elongation zone results in 'top-to-bottom' differential cell elongation, which subsequently reorients the root (Baldwin *et al.*, 2013).

The primary to secondary growth transition

The evolution of tall plants need not have been limited by the mechanical properties of primary tissues, since some can be as stiff as wood. Bending tests indicate that the hypodermal tissue of the giant moss *Dendrolignotrichum dendroides* has an average Young's modulus of 4.55 GPa (Frenzke *et al.*, 2011), which exceeds the Young's modulus reported for the sclerenchyma isolated from *Aristolochia macrrophylla* (3.08

GPa; Köhler *et al.*, 2000) and is roughly 60% the value of the average Young's modulus reported for green conifer wood (7.33 GPa; Niklas and Spatz, 2010). Indeed, the material properties of primary tissues can exceed that of some species of wood (e.g. the Young's modulus of coconut palm stems is on the order of 30 GPa) (Gibson, 2012).

The evolution of plant height was just as likely constrained by two other important factors: limitations on the vertical transport of water and limitations on the cross-sectional area of stems. The limits on the former are revealed by the well-known Hagen–Poiseuille equation (Table 1), which shows that any increase in the vertical pathway of water flux increases the resistance to flow as a result of a negative hydrostatic pressure gradient (Zimmermann, 1983; Niklas and Spatz, 2004, 2012; Niklas, 2007; Woodruff and Meinzer, 2011). The solution to this limitation is to increase either the radii or the numbers of water-conducting cells. Inspection of the fossil record during the early phase of vascular plant evolution reveals that both of these hydraulic 'stratagems' were employed and that plant height increased accordingly (Fig. 3). The limitation placed on stem height by cross-sectional area is revealed by the equally well-known Greenhill–Euler formula for critical buckling height (McMahon, 1976), which shows that, for any construction material or combination of materials (i.e. $E/\rho g = \text{constant}$), height increases as the 1/3 power of stem area (Table 1). An alternative solution is to employ stiffer materials (i.e. increase E), which can dramatically increase height with respect to stem radius (Fig. 4). Another solution is to deploy the stiffest materials at or near the perimeter, which experiences the maximum stresses: an insight into the evolution of plant anatomy (Speck and Vogellehner, 1988, 1994; Speck, 1994; Speck and Rowe, 2003).

In light of the Hagen–Poiseuille and the Greenhill–Euler equations, perhaps one of the most 'elegant' events in plant evolution was the evolution of lateral cambia (the phellogen and convergent forms of a vascular cambium documented in the fossil record), which simultaneously increase the number of water-conducting cells and the cross-sectional area of stems and roots: excellent reviews of the hydraulic and structural advantages of a bifacial vascular cambium are provided by Rowe and Speck (2004), Woodruff and Meinzer (2011), and Carlquist (2012); the mechanical contributions of the outer bark (phellem) are discussed by Xu *et al.* (1997) and Niklas (1999a). Importantly, this 'event' occurred in very different plant lineages, for example the lycopods, horsetails, progymnosperms, and the seed plants (Mosbrugger, 1990). For three of these lineages, the capacity to form secondary xylem may have been prefigured by the ability to form wound tissue, since trimerophytes (which are believed to be the last common ancestors to the arborescent horsetails, progymnosperms, and seed plants) had the ability to produce localized periderm in response to damage induced by fungi or animals (Banks and Colthart, 1993).

Regardless of the anatomical or geometrical innovations that resulted in taller plants, gaining height imposed a considerable physical constraint: that is, the effects of wind-induced drag (Vogel, 1994; Ennos, 1997; Anten and Sterck, 2012) and the dynamical harmonics that can ensue among

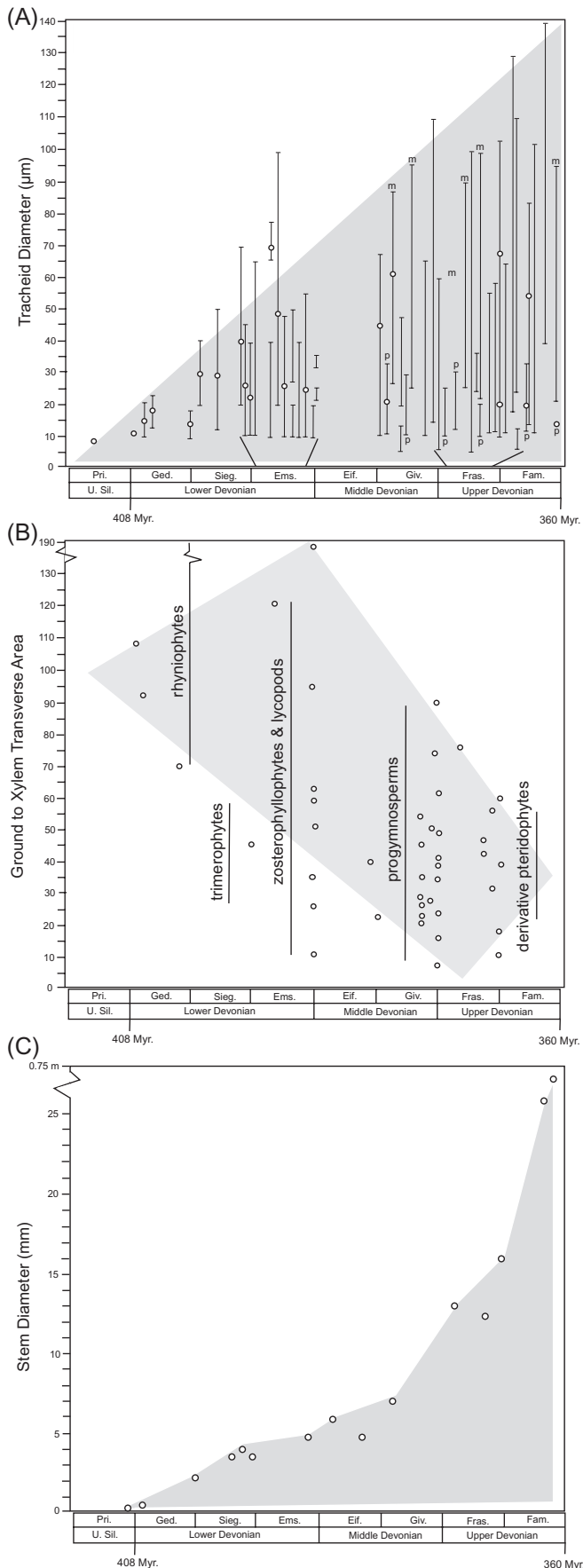


Fig. 3. Early Phanerozoic trends in tracheid diameter ranges and means (A; m = metaxylem; p = protoxylem), the quotient of

branches (James *et al.*, 2006; Spatz *et al.*, 2007; de Langre, 2012). Inspection of the pertinent formula (Table 1) reveals that a reduction in the projected area reduces drag forces linearly. For many aquatic plants, this is accomplished by means of highly flexible tissues (Koehl, 1979; Harder *et al.*, 2006). For terrestrial plants with more rigid tissues, drag can be reduced by the downwind flexure of stems and the curling of leaf laminae that can also reduce the drag coefficient, which further reduces drag forces (Vogel, 1989). These phenomena reflect the fact that the shear modulus of most plant tissues is significantly lower than the elastic modulus (Niklas, 1992). An alternative and more dramatic solution is to shed redundant organs. Analyses of the working and breaking stresses within the canopies of large trees indicate that terminal twigs have small factors of safety compared to older branches and are thus the most likely portions of canopies to break under high wind speeds (Niklas and Spatz, 2000). The fossil record indicates that the factors of safety calculated for arborescent lycopods and other tree species changed as a function of plant height, the degree of branching, and leaf size and shape (Niklas and Speck, 2001).

Finally, the evolution of thigmomorphogenesis was essential for survival both in water and on land, since it permits plants to adaptively modify the material properties of tissues as well as the morphology of organs in response to the magnitudes and directions of externally applied mechanical forces (Koehl, 1979; Telewski, 2006; Moulia *et al.*, 2011). Since wind-induced drag forces exert bending moments at the base of plants that require equal counter moments to maintain mechanical stability (Ennos, 1993, 2000), the evolution of thigmomorphogenetic responses was necessary for root systems capable of adjusting to the locations and magnitudes of mechanical strains and stresses (Fig. 5).

Concluding remarks and future directions

The use of physical laws to understand the evolutionary transitions discussed in this review shows that plants perform numerous tasks simultaneously and that the performance of these tasks involves tradeoffs that can confine the domain of phenotypic expression because of the necessity for trait covariation. However, the physical laws influencing evolutionary transitions also reveal that tradeoffs necessitate (and thus potentially drive) subcellular, cellular, or organographic modifications that can expand or even create new domains of phenotypic expression. Indeed, each of the four evolutionary transitions is prefigured in one or more ways by the ancestral functional traits of the previous plant grade or clade. This aspect of evolution is evident empirically: variation among critical plant functional traits can exceed one order of magnitude for species occupying the same site (e.g. Westoby *et al.*,

the areas of stem ground tissue and xylem (vertical lines denote ranges for each of the five plant groups) (B), and maximum stem diameter (C). Data from Niklas (1985).

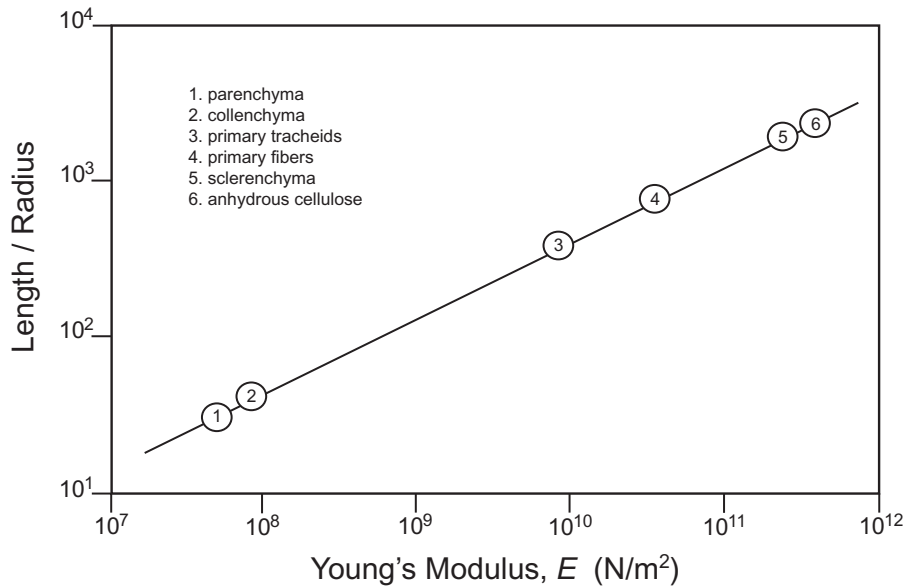


Fig. 4. The slenderness ratio (length divided by radius) of hypothetical stems composed exclusively of each of six different materials plotted as a function of Young's elastic moduli (E) of the materials (values taken from various sources; see Niklas and Spatz, 2012). Stem lengths calculated using the Greenhill–Euler formula (see Table 1).

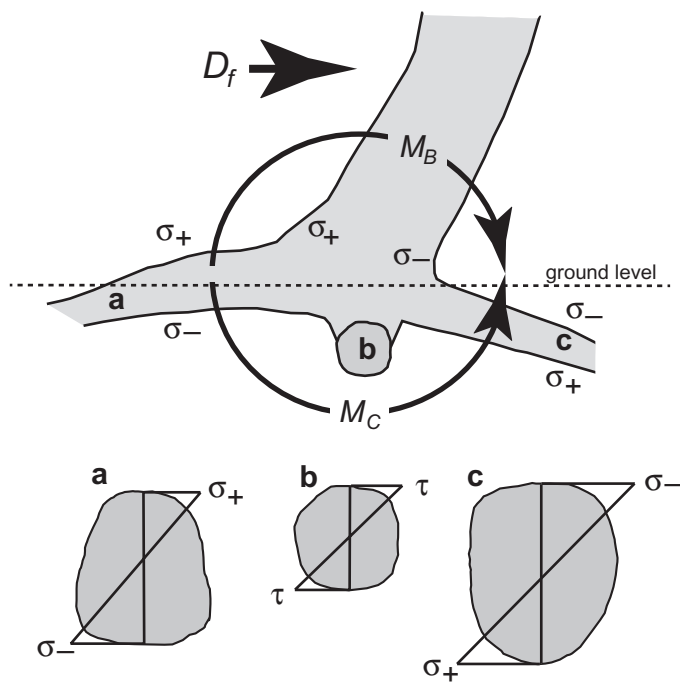


Fig. 5. Diagram of the bending moment (M_B) generated by a drag force (D_f), the counter moment (M_C) required to maintain mechanical stability, and the tensile, compressive, and shearing stresses (σ_+ , σ_- , and τ , respectively) produced in roots oriented directly upwind, orthogonal to the wind, and directly downwind (a, b, and c, respectively). Stress distributions in the three roots are illustrated for representative transverse sections (adapted from Niklas, 1999b).

2002; Westoby and Wright, 2003). It is also revealed theoretically with the aid of computer simulations, which show that the number of functionally equivalent plant phenotypes

increases as the number of functional tasks performed increases (Niklas, 1994b) and that a large number of possible trait combinations can confer equivalent fitness (Marks and Lechowicz, 2006).

Among the other lessons that can be drawn from considering the effects of physical laws and process on plant evolution is that phenotypes reflect biophysical compromises. Evolution can optimize but not maximize the performance of each of the functional obligations required for growth, survival, and reproductive success. Under some circumstances, a particular set of functional traits might become the object of intense natural selection, such as the suite of traits (e.g. cuticular thickness and composition, leaf size and shape, and vascular anatomy) permitting a plant to survive under xerophytic or hydrophytic conditions. However, over a lineage's long history, the focus of natural selection will likely shift many times such that phyletic inertia carries ancestral traits that may not be well equipped to deal with current conditions but may be useful at some future time.

These and other lessons can help to direct as well as inform future lines of research. Successful evolutionary experiments documented in the fossil record, particularly those that were convergent among different plant lineages, may highlight new biomimetic prospects. For example, the proportionalities of tubular leaves and septate stems may provide insights into the construction of light-weight yet optimally strong structures, and the chemical composition of degradation-resistant charophycean cell-wall polymers might assist in the identification of synthetic compounds that resist chemical erosion. These speculations may seem farfetched until one considers the commercial success of self-cleaning films patterned after the Lotus effect (Barthlott and Neinhuis, 1997) or the many engineered cellular materials patterned after plant cellular structures (Gibson *et al.*, 2010).

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