

COMPUTER MODELS OF EARLY LAND PLANT EVOLUTION

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■ **Abstract** Computer models are used to mimic the early evolution of ancient vascular plants (tracheophytes). These models have three components: (a) an N -dimensional domain of all mathematically conceivable ancient morphologies (a morphospace); (b) a numerical assessment of the ability (fitness) of each morphology to intercept light, maintain mechanical stability, conserve water, and produce and disperse spores; and (c) an algorithm that searches the morphospace for successively more fit variants (an adaptive walk). Beginning with the most ancient known plant form, evolution is simulated by locating neighboring morphologies that progressively perform one or more tasks more efficiently. The resulting simulated adaptive walks indicate that early tracheophyte evolution involved optimizing the performance of many tasks simultaneously rather than maximizing the performance of one or only a few tasks individually, and that the requirement for optimization accelerated the tempo of morphological evolution in the Silurian and Devonian.

INTRODUCTION

The evolutionary appearance of vascular plants (tracheophytes) altered Earth's environment by paving the way for animal life onto land and by irrevocably altering Earth's atmosphere and terrestrial depositional regimes (Willis & McElwain 2002, Berner et al. 2003). Their appearance also sparked one of the most dramatic bursts of diversifying evolution in the history of life (Gensel & Andrews 1984, Niklas et al. 1984, Knoll et al. 1984). For example, the oldest vascular plant fossils from Late Silurian rocks were small and structurally very simple organisms (Chaloner & Sheerin 1979; Raven 1984, 1985; Taylor & Taylor 1993; Stewart & Rothwell 1993; Niklas 1997a). Yet, by the end of the Devonian, approximately 46 million years later, plants diversified phylogenetically and structurally to encompass all of the major land plant lineages and the full spectrum of organizational grades represented in present-day floras, with the exception of flowering plants (Figure 1).

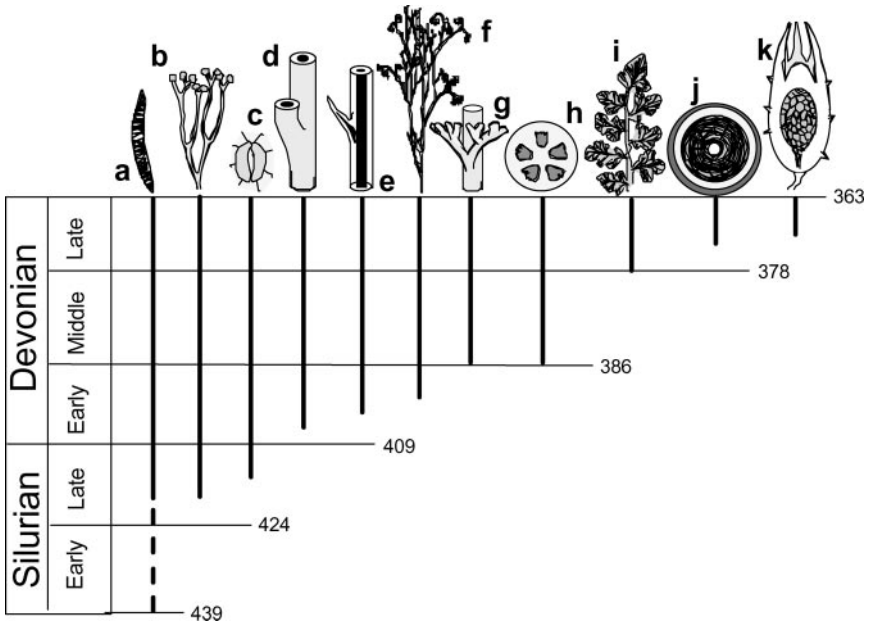


Figure 1 Timeline for some major Silurian-Devonian phenotypic innovations. Vertical bars denote first appearance and range of figured features in the fossil record: (a) tracheids, (b) isobifurcate branching with terminal sporangia, (c) stomata with guard cells, (d) unequal branching of vascular axes, (e) vascularized leaf-like enations, (f) overtopping (the unequal elevation of a dichotomously branched system with lateral branches), (g) planated lateral branches, (h) dissected primary vasculature, (i) fern-like leaves (megaphylls), (j) stems with periderm and wood, and (k) seeds.

Why plant evolution was so rapid during the Late Silurian-Devonian time interval remains problematic. Lessons drawn from evolutionary theory provide limited insights. For example, the first tracheophytes were by definition the first metaphtes to gain access to geographically expansive and environmentally heterogeneous habitats that were biologically unpopulated by modern standards. Founder populations and low intra- and interspecific competition, such as those characterizing the early terrestrial landscape, are likely to foster rapid genomic evolution and morphological diversification (Lande 1985). Small organisms also tend to have higher mutation rates and shorter reproductive cycles than larger organisms—two features that in theory can accelerate the tempo of evolution (Niklas 1997a). Selection was also probably intense during the colonization of land, especially in terms of coping with a demanding physical environment that differed significantly from the ancestral aquatic habitats from which the first land plants undoubtedly emerged (Raven 1984, 1985; Graham 1993).

However, evolutionists continue to argue over the genomic mechanisms and types of environments that evoke adaptation. In this context, one of the most provocative metaphors for evolution was proposed by Sewall Wright (1931, 1932),

who conceived of adaptation as the result of a series of walks over fitness landscapes with adaptive hills and maladaptive valleys. This image draws sharp attention to the relationship between the number, location, and height of fitness peaks and values, and the genomic or phenotypic transformations among neighboring variants that attend an increase in relative fitness. This heuristic device has been profitably explored in terms of animal morphology and evolution (e.g., Raup 1961, 1962; Raup & Michelson 1965; Thomas & Reif 1993; McGhee 1999). Likewise, it provides a vehicle with which to explore plant evolution.

As noted, the most ancient vascular land plants were remarkably morphologically simple, and their phenotypes can be easily mimicked with the aid of computers. Likewise, the fundamental biological tasks that all plants must accomplish to grow, survive, and reproduce are well known (Gates 1965, Nobel 1983, Niklas 1992, Taiz & Zeigler 2002). Therefore, it is not exceptionally difficult to quantify the relative fitness of theoretical phenotypes in terms of the performance of one or more of these tasks (Niklas 1994; 1997b,c).

In terms of specifics, the perennial life form of most tracheophytes is the spore-producing (sporophyte) generation. The sporophytes of ancient vascular plants were leafless and made up of branched cylindrical (stem-like) axes (Chaloner & Sheerin 1979, Stewart & Rothwell 1993, Taylor & Taylor 1993). The branching architectures of these ancient sporophytes varied, often significantly, across contemporary species. However, in very general terms, all of the possible architectural variants can be mathematically simulated with the aid of relatively few parameters, i.e., axial length, diameter, the probability of branching, the angle of branching, and the rotation angle of axes with respect to ground level. The reproductive organs of these ancient sporophytes were also simple in appearance and in their pattern of attachment to branches (see Gensel & Andrews 1984). Most sporangia were spheroidal or fusiform, and all were attached either to the sides of branches or at the tips of main or smaller lateral ones, e.g., *Zosterophyllum* and *Cooksonia*, respectively. Some ancient plants bore clusters of tightly aggregated or fused sporangia, e.g., *Yarravia oblonga*. However, regardless of sporangial position and degree of clustering or fusion, most ancient sporophytes freely shed their spores and relied exclusively or largely on wind for spore dispersal. Thus, to model reproductive efficacy, only a few variables need to be considered, i.e., sporangial elevation above ground and spore number and size.

In terms of the basic requirements for growth and survival, the most ancient land plants differed little or not at all from modern day plants, which manufacture their living substance using light energy to rearrange raw materials gathered directly from their immediate physical environment (atmospheric gases, water, and minerals). Therefore, at the level of the individual organism, all plants other than those that have acquired secondarily a parasitic lifestyle, must perform four very basic functions to grow and survive. They must (a) intercept sunlight; (b) exchange atmospheric gases with the fluid that surrounds them (air or water); (c) acquire, transport, and conserve water; and (d) cope with externally applied mechanical forces. Additionally, evolution requires genomic changes, which are typically achieved by sexual recombination and, over longer time periods, mutation.

Importantly, the performance of each of these fundamental biological obligations can be evaluated quantitatively by means of comparatively simple physical or chemical laws and processes (Gates 1965, Nobel 1983, Niklas 1992). Light interception can be qualified in terms of the surface area the plant body projects toward the sun and how this projected surface area varies as a function of time of day, latitude, or season (Niklas & Kerschner 1984). The exchange of atmospheric gases between the plant body and its external environment, as well as the ability to acquire and transport water, can be quantified in terms of the relationship between body surface area and volume and some well-known, comparatively simple equations from fluid mechanics (Nobel 1983, Niklas 1992). Likewise, the capacity of a plant to deal with bending and twisting mechanical forces can be quantified rigorously with the aid of engineering theory (Niklas 1992). Finally, it cannot escape attention that many aspects of plant reproduction, such as spore dispersal, can be modeled using simple aerodynamic principles (Okubo & Levin 1989).

The real challenge in terms of modeling plant evolution is to assess the simultaneous performance of all of these basic biological obligations, because many of the tasks essential to growth and survival have antagonistic design requirements. For example, the capacity to intercept sunlight and to exchange carbon dioxide or oxygen between the plant body and its surrounding fluid increases as a function of surface area, whereas the ability to conserve water decreases (Gates 1965, Nobel 1983). Likewise, simple computations indicate that a cantilevered beam (a horizontal stem) is the best orientation for light interception but the worst orientation in terms of mechanical stresses (Niklas 1992). Indeed, when viewed with a biophysical or engineering perspective, none of the basic biological tasks plants perform can be maximized without decreasing or imperiling the performance of another necessary task. In this sense, the relationships among organic form-function generally involve optimization rather than maximization. But differently, single-task devices can perform their ascribed functions perfectly, at least in theory. In contrast, multitasked devices, whether organic or inorganic, invariably involve compromises and tradeoffs—they perform all of their ascribed tasks reasonably well, but no task perfectly (see Horn 1979, Kauffman & Levin 1987).

THE MORPHOSPACE, RELATIVE FITNESS, AND ADAPTIVE WALKS

The Morphospace

The procedure used to construct a multidimensional domain containing all mathematically conceivable early vascular land plant morphologies (the morphospace) has been described in detail elsewhere (Niklas & Kerchner 1984; Niklas 1994, 1997a,b,c). Briefly, each morphological variant is assembled from cylindrical axes (branch-like elements) with uniform girth and tissue density. The orientation of each axis with respect to the vertical and horizontal planes of reference is specified by a bifurcation angle ϕ and a rotation angle γ (each ranging between 1° and 180°). The number of axes for a particular morphology is determined by assigning

a probability value for apical bifurcation p , where $p = 0$ indicates no branching and $p = 1$ indicates branching (Figure 2). Each morphology is restricted to ten levels of branching N ; the maximum number of axial elements for each morphology is thus 2047. Mathematically, $p = 8 p_{n-(k+1)} / (N+k)$, where $p_{n-(k+1)}$ is the probability of terminating branching at the next generated (higher) level of branching and $N+k$ designates the previously generated level of branching. The length of each axis L is stipulated to be directly proportional to the probability of branching, i.e., axial length is a linear function of p such that the basal-most axial element is always as long as or longer than any more distal (higher level) axial element.

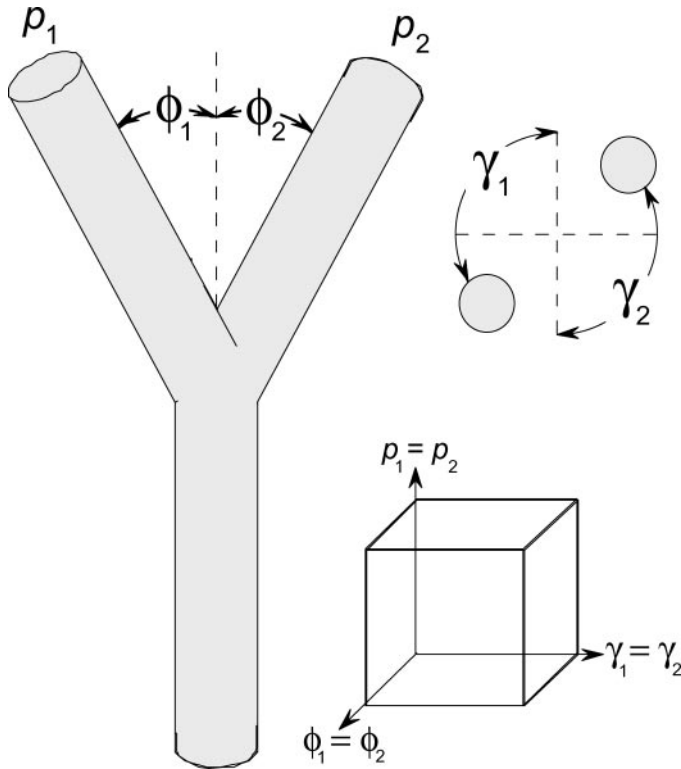


Figure 2 Mathematical variables used to construct the morphospace of ancient vascular plants. The orientation of each set of companion axes subtended by a single axis is specified by a branching angle ϕ and a rotation angle γ . The probability of an axis branching subsequent to its appearance is designated as p . Morphologies in the isobifurcate subdomain of the morphospace for early vascular plants have axes with equal branching angles ($\phi_1 = \phi_2$) and rotation angles ($\gamma_1 = \gamma_2$) and probabilities of branching ($p_1 = p_2$) such that these morphologies can be located in a simple Cartesian coordinate system (see *lower right cube*). Morphologies in the anisobifurcate subdomain have unequal angles and probabilities of branching (not shown).

The morphospace has two subdomains, one containing all equally branched (isobifurcate) morphologies and another containing all unequally branched (anisobifurcate) morphologies. The isobifurcate subdomain contains all morphologies for which $\phi_1 = \phi_2$, $\gamma_1 = \gamma_2$, and $p_1 = p_2$. The anisobifurcate subdomain contains all morphologies for which $\phi_1 \neq \phi_2$, $\gamma_1 \neq \gamma_2$, and $p_1 \neq p_2$ (Figure 2). Because L is a function of p , it also follows that $L_1 \neq L_2$ for this subdomain.

The entire morphospace is constructed by independently varying each of the variables used to construct the morphologies in each of the two subdomains. The spatial ordering of morphological variants is predetermined by assigning ascending numerical values to each of the variables, e.g., the bifurcation angle varies in 1° increments, the probability of branching varies in 0.01 increments. In the isobifurcate subdomain, ϕ , γ , and p were plotted orthogonally, i.e., the location of any variant in the subdomain is specified by a unique set of Cartesian coordinates. The anisobifurcate subdomain is spatially far more complex, i.e., it is a six-dimensional space with ϕ_1 , ϕ_2 , γ_1 , γ_2 , p_1 , and p_2 axes.

Fitness Landscapes

The relative fitness of each hypothetical morphology can be evaluated using basic physics or engineering principles that describe quantitatively the performance of each task designated to influence growth, survival, and reproductive ability. The ability of each morphological variant to perform one or more of these tasks can then be divided by the maximum performance level in a particular landscape. To compute the relative fitness of morphologies performing two or more tasks simultaneously, H , it is assumed that each task contributes equally and independently to overall fitness such that the fitness of a particular variant h is given by the formula $h = \varphi^{1/N}$, where φ is the product of the performance levels of the number the tasks performed N . For example, if the numerical performance of two tasks is designated by the quantities A and B , the relative fitness of a particular variant morphology is given by $H = (A_{max}B_{max}/AB)^{1/2}$, where A_{max} and B_{max} are the performance levels of the most efficient variant in the particular landscape.

As noted, all of the fitness landscapes are predicated on the performance of one or more of four tasks assumed to dictate survival and reproduction: light interception, maintaining mechanical stability, dispersing spores, and conserving water. These tasks can be considered in isolation or in sets of two or more tasks performed simultaneously. Thus, there are four 1-task landscapes, six 2-task landscapes, four 3-task landscapes, and one 4-task landscape. The methods for quantifying the performance of these tasks are provided in detail elsewhere (Niklas & Kerchner 1984; Niklas 1994, 1997b,c). However, each is reviewed briefly here.

Light interception is quantified for each morphological variant in the entire domain by integrating the area under the curve generated by plotting the projected surface S_p divided by the total surface area S of the variant as a function of the solar angle θ for the values $1^\circ \leq \theta \leq 180^\circ$ using an algorithm that accounts for the self-shading of branch-like axes (see Niklas & Kerchner 1984). Mechanical stability is calculated by computing the total bending moment on the single basal

vertical axis of each morphological variant. Noting that a bending moment M is the product of a bending force (weight W) and the length of a lever arm ℓ , the bending moment of each distal axis in a branching architecture m_i is a function of $W = \pi \rho D^2 L / 4$, where D is diameter and ρ is the bulk tissue density (assumed to equal 1000 kg/m^3 for all axes) and its specified bifurcation and rotation angles (which specify the orientation of an axis and thus its lever arm length). The total bending moment at the base of any variant is a complex quantity to compute because it is the sum of all the bending moment of all axes and because these axes are joined together and oriented differently as a function of the level of branching. It is computed numerically. Nevertheless, the maximum bending moment can be computed with the aid of a computer (see Niklas 1997a,b,c).

The ability of each variant to conserve water is gauged to be a simple linear function of total plant surface area, i.e., it is assumed that all surface areas have equivalent rates of evapotranspiration. Finally, spore dispersal is assumed to rely exclusively on wind. Therefore, a simple ballistic model can be used if it is assumed that all sporangia are at the tips of all distal axes and that all sporangia are equivalent in size and thus spore number per sporangium. This ballistic model is given by the formula $x = HU/T$, where x is maximum distance of spore dispersal, H is plant height, U is ambient wind speed, and T is the spore terminal settling velocity (see Okubo & Levin 1989). Plant height is a function of the number, length, and orientation of all axes composing a particular morphology, the ambient wind speed depends on plant height (because wind speeds typically decrease exponentially toward ground level), and the terminal settling velocity is taken as 0.15 m/s (the average velocity of *Lycopodium* spores). These assumptions and specifications obtain the scaling relationship $x \propto H^2$ across all morphologies, which indicates that the spore-dispersal range is, on average, proportional to the square of plant height.

Adaptive Walks: The Search Algorithm

The purpose of these walks is to identify the sequence of morphological variants with progressively higher relative fitness as defined by performing one or more designated tasks. Each walk begins at the same location in the morphospace, which corresponds to the morphology of the most ancient vascular plants, such as *Cooksonia* and *Steganotheca*, i.e., an isobifurcate variant consisting of one or two levels of branching in which all terminal axes bear sporangia (see Figure 9A). From this location, a search algorithm evaluates the relative fitness of all neighboring variants using a specified fitness criterion (e.g., light interception, light interception and mechanical stability, or light interception and mechanical stability and conservation of water). If one or more neighboring variants have an equivalent or higher relative fitness, the walk proceeds to their locations in the morphospace. This process continues until the relative fitness of the morphologies in the last iteration of a search is higher than that of all surrounding variants in the terminal steps. By definition, these morphologies occupy adaptive peaks on the landscape.

Fitness landscapes can be stable or unstable. That is, an adaptive walk can proceed through the morphospace such that the criterion defining relative fitness

remains constant to obtain a stable fitness landscape. Alternatively, the criterion used to define relative fitness can be changed arbitrarily at any time during a walk to mimic a change in selection pressure or an unstable fitness landscape.

ADAPTIVE PEAKS AND THEIR PHENOTYPIC OCCUPANTS

On Stable Landscapes

Using the aforementioned protocols, computer simulations of early vascular plant evolution indicate that comparatively few hypothetical morphologies are capable of maximizing the performance of any one of the four single tasks. In contrast, the number of morphologies capable of optimizing the performance of two or more tasks simultaneously increases as the number of tasks increases. However, the overall (global) relative fitness of these multitask morphologies decreases significantly (Table 1). These simulations indicate that adaptive evolution may be more rapid and easier when selection acts on the ability to perform multiple rather than single tasks.

Turning to specifics, the few hypothetical morphologies capable of maximizing the performance of any one of the four biological tasks used to quantify relative fitness are, for the most part, comparatively simple in general appearance (Figure 3). The simplest of these are those that maximize the capacity to conserve water as gauged by minimizing their total surface area (Figure 3A). These hypothetical phenotypic variants are Y-shaped and similar in general appearance to the most ancient vascular plants, such as *Cooksonia*. Thus, water conservation may have been achieved early on in the evolutionary history of land colonization. However, from a mathematical perspective, these Y-shaped morphologies are trivial because they are those used to initiate each adaptive walk, whether on single- or multiple-task landscapes.

In contrast, the most complex single-task morphologies are those that possess lateral branching systems confined in part or entirely to the horizontal plane and elevated on a single vertical main axis (Figure 3C). Some of these morphologies are located in the isobifurcate subdomain, whereas others are found in the

TABLE 1 Relationships among the number of tasks used to qualify relative fitness, the number of morphologies identified as either maximizing or optimizing these tasks, and the relative fitness of these morphologies. (n = number of fitness landscape permutations)

Number of tasks defining fitness	Number of morphologies (mean \pm SE)	Relative fitness (mean \pm SE)
1 ($n = 4$)	2.50 \pm 1.0	35.3 \pm 1.80
2 ($n = 6$)	3.33 \pm 1.6	11.6 \pm 0.68
3 ($n = 4$)	6.25 \pm 0.5	7.5 \pm 0.14
4 ($n = 1$)	20	2.4

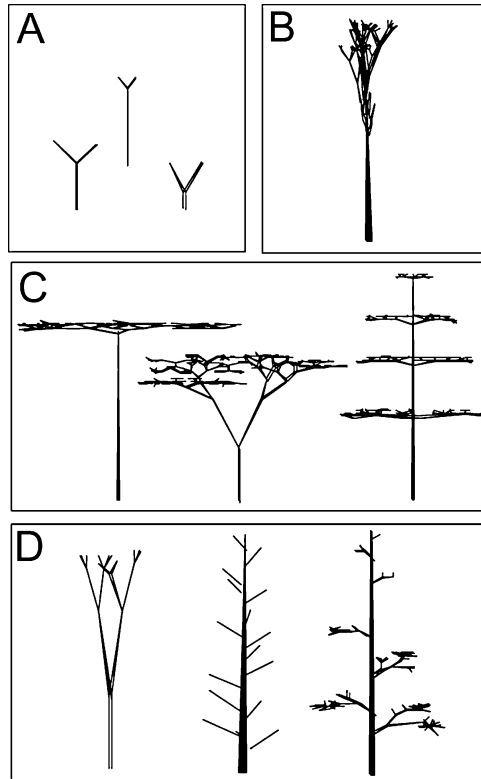


Figure 3 Phenotypes identified by adaptive walks on single-task landscapes capable of maximizing water conservation (A), spore dispersal (B), light interception (C), and mechanical stability (D).

anisobifurcate subdomain of the morphospace for ancient tracheophytes. Because the latter are reached only by an extensive series of hypothetical morphological transformations, the adaptive walks reaching these morphologies are generally highly branched.

The morphologies capable of optimizing the performance of two or more tasks are typically far more diverse in general appearance than those maximizing the performance of a single task (Figures 4–6). Some of these variants are simple Y-shaped *Cooksonia*-like morphologies (Figure 4A,B), whereas others are strikingly reminiscent of the fossil remains of some zosterophyllophytes, such as *Zosterophyllum*, an ancient group of vascular plants (Figure 5D). As noted, the number of morphologies identified as equally efficient at performing two or more tasks simultaneously increases as the number of tasks increases (Table 1). For example, on average, 3.3 morphological variants are reached by adaptive walks on the six 2-task landscapes (Figure 4), whereas 6.5 variants are reached by walks on the four 3-task landscapes (Figure 5). When all four tasks are considered

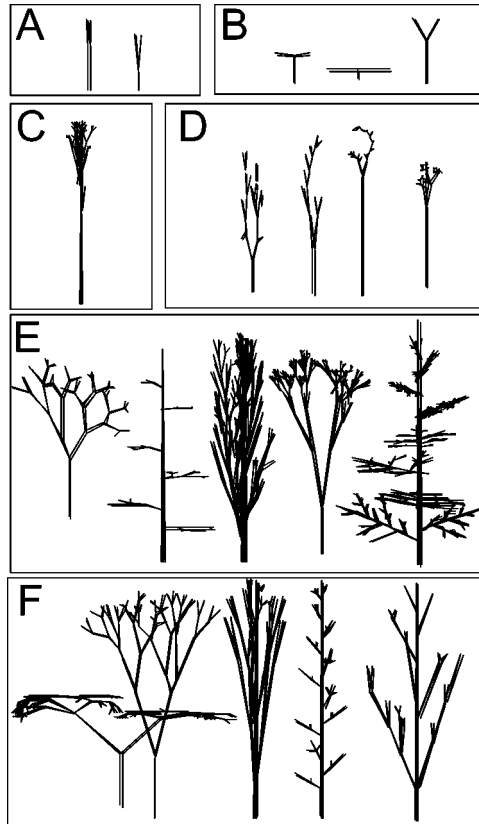


Figure 4 Phenotypes identified by adaptive walks on 2-task landscapes capable of optimizing mechanical stability and water conservation (A), light interception and water conservation (B), mechanical stability and spore dispersal (C), spore dispersal and water conservation (D), light interception and mechanical stability (E), and light interception and spore dispersal (F).

simultaneously, a total of 20 equally efficient morphologies is reached by an adaptive walk (Figure 6).

Although the number of morphologies reached by adaptive walks increases as the complexity of landscapes increases, the relative fitness of functionally optimal morphologies, on average, decreases (Table 1). It must be noted that the currency by which fitness is measured differs across the various fitness landscapes, e.g., amount of light harvested, spore number and dispersal range, and bending moment at the base of each morphology. However, comparisons of relative fitness across the different fitness landscapes are possible provided that the fitness of the ancestral *Cooksonia*-like morphology that initiates each adaptive walk on any landscape is used to normalize the fitness of all other morphological variants for each landscape. With this protocol, the average relative fitness of morphologies

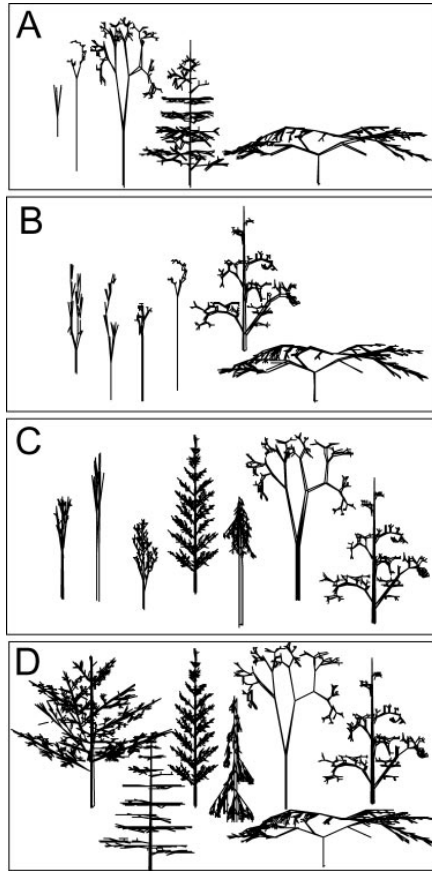


Figure 5 Phenotypes identified by adaptive walks on 3-task landscapes capable of optimizing light interception, mechanical stability, and water conservation (A); light interception, spore dispersal, and water conservation (B); mechanical stability, spore dispersal, and water conservation (C); light interception, mechanical stability, and spore dispersal (D).

identified as optimizing two or four tasks is 11.6 and 2.4, respectively (Table 1). In contrast, the average relative fitness of those morphologies capable of maximizing the performance of one task is 35.3. Therefore, as the number of tasks used to define relative fitness increases, the capacity to perform these tasks decreases.

On Unstable Landscapes

Environments can change, often dramatically, even over ecological timescales (10^2 to 10^4 years). It is therefore naïve to believe that selection persistently acts on the performance of one task or any particular combination of tasks, especially over timescales relevant to evolutionary or geological history (10^5 to 10^6 years).

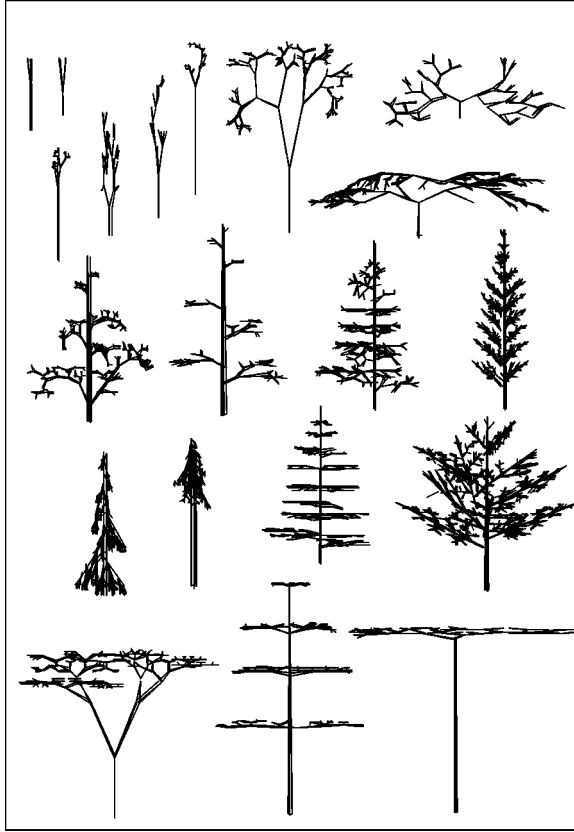


Figure 6 Phenotypes identified by adaptive walks on the 4-task landscape capable of optimizing mechanical stability, water conservation, light interception, and spore dispersal.

As noted, the consequences of shifting selection can be modeled by initiating an adaptive walk on one landscape and subsequently changing the landscape one or more times. In this way, the criteria used to quantify relative fitness change as a walk proceeds through a morphospace. Unfortunately, there are no a priori rules for how or when a particular landscape changes. Therefore, the number of permutations of shifting landscapes is literally astronomically large.

Nevertheless, the fossil record and the preceding simulations provide some guidance. As noted, the oldest known vascular land plant fossils are *Cooksonia*-like in their general appearance. Computer simulations also indicate that these morphologies were capable of maximizing water conservation (see Figure 3A). To explore the consequences of shifting selection, it is therefore reasonable to initiate an adaptive walk on a fitness landscape defined by conserving water and to subsequently shift this landscape into one or more of any of the 11 multitask landscapes as the walk proceeds through the morphospace.

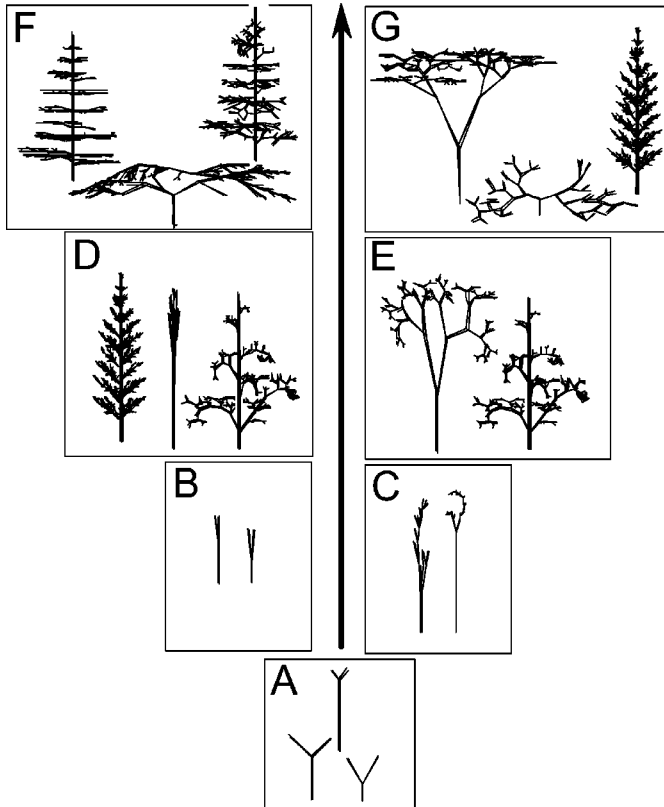


Figure 7 Phenotypes identified by two different adaptive walks on shifting fitness landscapes. Following the vertical arrow, the two walks begin with the phenotypes identified as maximizing water conservation (A), bifurcate into two different 2-task landscapes [water conservation and mechanical stability (B); water conservation and spore dispersal (C)]; enter the same 3-task landscape [mechanical stability, spore dispersal, and water conservation (D,E)]; and come to closure by reaching accessible morphological optima on the 4-task landscape (F,G).

Two such simulations are shown in Figure 7. Each simulation begins on the same landscape, then enters two different 2-task landscapes, after which each enters the same 3-task landscape. Both walks come to an end in the single 4-task landscape. These two simulations illustrate an important feature, which resurfaces in all similar walks through unstable landscapes. Even though adaptive walks enter the same fitness landscape, they locate different morphological optima depending on how relative fitness was defined in previous portions of walks. For example, among the five optimal morphologies reached by the two adaptive walks entering the two 3-task landscapes, only one is the same, whereas none of the morphological optima reached by the two walks on the 4-task landscape is the same (Figure 7).

Taken at face value, simulations such as these indicate that the morphologies with the highest relative fitness at any stage in the adaptive evolution of a lineage depend in part on prior selection regimes because these regimes define the range of phenotypes that are available for the next round of selection, i.e., morphological optimization is historically contingent. If there is a lesson to be learned, it is that we should not expect the mechanisms of adaptive evolution to achieve the best conceivable morphologies but rather only those that are the best relative to what is available based on past history.

DEVELOPMENTAL CONSTRAINTS

Thus far, it has been assumed that all adaptive walks are developmentally unfettered, i.e., morphological transformations in one parameter are assumed to be independent of transformations in other parameters. Likewise, all transformations are assumed to be equiprobable. But it is clear that development is a highly coordinated process such that transformations in one morphological feature are dependent on changes in other features. Additionally, all transformations are not equally possible because all possible genomic variants are not achieved by even very large populations of sexually reproducing organisms. Even though plants may be more phenotypically plastic compared to animals (see Sultan 1987, 1992; Sharloo 1991), the importance of developmental constraints in understanding adaptation cannot be neglected (Gould 1980, Thomas & Reif 1993).

The role played by developmental constraints in plant evolution is far too complex to address here. But it can be evaluated, albeit crudely, by restricting adaptive walks from entering designated portions of the morphospace for early vascular plants. Indeed, the simplest mathematical way to model this is to limit walks to phenotypes that only have equal branching ($p_1 = p_2$), nonovertopped branches ($\phi_1 = \phi_2$), or planated branches ($\gamma_1 = \gamma_2$) such that phenotypes with $p_1 \neq p_2$, $\phi_1 \neq \phi_2$, and $\gamma_1 \neq \gamma_2$ are developmentally impossible. At issue is whether walks that are thus restricted reach more, fewer, or equal numbers of phenotypes capable of maximizing the performance of one task or optimizing the performance of two

TABLE 2 Comparisons of mean number (\pm SE) of maximal (single-task) or optimal (multi-task) phenotypes reached by unrestricted adaptive walks (see Table 1) and those restricted to morphologies with equal branching ($p_1 = p_2$), nonovertopped branches ($\phi_1 = \phi_2$), or nonplanted branches ($\gamma_1 = \gamma_2$) (see Figure 1). Numbers in bold indicate restricted walks reach more maximal or optimal phenotypes than unrestricted walks

Number of tasks	Unrestricted walks	Restricted walks		
		($p_1 = p_2$)	($\phi_1 = \phi_2$)	($\gamma_1 = \gamma_2$)
1	2.50 \pm 1.0	2.25 \pm 1.0	2.25 \pm 1.5	2.75 \pm 2.1
2	3.33 \pm 1.6	2.50 \pm 0.8	3.83 \pm 0.4	2.83 \pm 1.2
3	6.25 \pm 0.5	6.25 \pm 0.5	8.25 \pm 1.0	8.25 \pm 1.0
4	20	18	18	19

or more tasks, i.e., the number of phenotypes reached by unfettered walks serves as a null hypothesis.

The results of this approach are summarized in Table 2. With the exception of the adaptive walks on the 4-task landscape, developmentally fettered walks reach an equal or a larger number of phenotypes than do unrestricted walks. For example, walks on the four single-task landscapes confined to only those morphologies with $\gamma_1 = \gamma_2$ reach, on average, 2.75 phenotypes per landscape, whereas developmentally unfettered walks on the same landscapes achieve, on average, 2.50 phenotypes. Similar comparisons show that restricting the access of adaptive walks by imposing developmental constraints has little or no effect on the number of phenotypic variants occupying adaptive peaks.

However, the relative fitness of the phenotypes reached by constrained walks is significantly less than that of the phenotypes reached by unconfined walks. For example, the mean relative fitness of the variants reached by unfettered walks on single-task landscapes is 35.3 (see Table 1), whereas the mean relative fitness of the variants reached by walks on the same landscapes but confined to morphologies with planated lateral branches (i.e., $\gamma_1 = \gamma_2$) is 1.61. Simulations such as these indicate that the imposition of a developmental constraint does not necessarily reduce the number of phenotypes that can be reached by adaptive walks, but it can significantly reduce the repertoire of these morphologies and thus the relative fitness of morphologies occupying adaptive peaks.

ADAPTIVE TRENDS AND THE TELOME THEORY

All of the computer simulations presented so far bear on one of the most pervasive and far-reaching theories to explain early land plant morphological evolution. First proposed by Zimmerman (1930, 1953, 1965) and later expounded with vigor by others (see Stewart & Rothwell 1993), this theory, called the telome theory, argues that the most ancient tracheophytes consisted of simple paired distal axes (called telomes) subtended by unbranched axes (called mesomes). These telomes and mesomes are envisioned to have been subsequently modified by one or more developmental processes—planation, overtopping, reduction, recurvature, and webbing—to obtain all known extant or extinct plant morphologies.

Each of these processes is easily envisioned, although the developmental mechanisms by which they are achieved are as undoubtedly complex as they are currently unknown. Planation occurs when neighboring axes become oriented in a single plane with respect to the horizontal; overtopping results from the differential growth in the lengths of interconnected axes such that some become longer or shorter than their companions; reduction in the size of some telomes can aggregate or positionally subordinate some axes with respect to others; recurvature requires the differential expansion of one side of an axis with respect to the opposing side; and, finally, webbing is the developmental introduction of tissues between adjoining (and presumably planated) axes.

As noted, Zimmerman argued that all of the morphological transformations attending early land plant evolution can be explained by the operation of two or

more of these five processes. For example, fern and seed plant leaves (traditionally called megaphylls) are believed to have evolved by reduction and overtopping (to yield plant architectures with main vertical stems bearing lateral branching systems) and by planation and webbing of lateral branches (to give rise to megaphylls). Likewise, the intricate reproductive organs of modern-day horsetails are postulated to have evolved by means of reduction, recurvature, and some degree of fusion or webbing.

The telome theory has been criticized, and rightly so, for a variety of reasons (Niklas 2000, Kaplan 2001). One obvious problem with the theory is its vagueness regarding the developmental mechanisms responsible for overtopping, planation, etc. Indeed, these terms are descriptive rather than explicative in nature. Another criticism is that the telome theory never explains why certain morphological transformations occur as opposed to others, nor does it stipulate the sequence of processes foreshadowing the appearance of a particular morphology. Why should planated and webbed lateral branch systems evolve? Are the leaves of ferns or seed plants functionally adaptive in terms of light interception or some other biological requirement? Did these megaphylls evolve as the result of the simultaneous operation of reduction, overtopping, planation, and webbing, or did planation and webbing occur after reduction and overtopping? Questions such as these can be answered retrospectively (and only in small part) by examining the fossil record, but the telome theory sheds little light on them.

Zimmerman's ideas are nevertheless useful because they provide a lexicon of terms for the morphological transformations observed in the fossil record and for those identified by the computer simulations presented here. In turn, these simulations suggest the adaptive significance of the transformations envisioned by the telome theory. For example, adaptive walks on 1-task landscapes identify overtopped morphologies with planated lateral branching systems as those capable of maximizing spore dispersal, light interception, or mechanical stability (see Figure 3B–D). Similar morphologies are reached by the adaptive walks on multiple task landscapes (see Figures 4–6). This convergence indirectly supports the supposition that overtopping and planation, which have occurred independently in a number of plant lineages, may be functionally adaptive.

This supposition is reinforced when we examine the sequences of morphologies identified by different adaptive walks. For example, starting with a simple *Cooksonia*-like phenotype (left in Figure 8), the adaptive walk on the fitness landscape defined by light interception and mechanical stability identifies a larger more branched variant (Figure 8). As this particular walk progresses, it identifies larger and more overtopped phenotypes bearing lateral branching systems that become more planated. Although webbing is not within the repertoire of the morphospace used in this simulation, more complex computer simulations indicate that the capacity to intercept sunlight is dramatically improved if some or all of the distalmost axes (telomes) of phenotypes are interconnected by photosynthetic tissues. Finally, the sequence of morphologies shown in Figure 8 gives credence to the notion that overtopping likely preceded planation. In turn, planation likely preceded the appearance of webbed leaves during the evolution of vascular land plant lineages, i.e.,



Figure 8 Successive morphological transformations along one branch of an adaptive walk on the landscape for simultaneously optimizing light interception and mechanical stability (see Figure 4E). Successive transformations (arranged from *left to right*) involve overtopping and planation (as described by the telome theory).

computer simulations provide circumstantial evidence that overtopping, planation, and webbing are functionally adaptive.

CAVEATS AND DESIDERATA

Computer models such as the ones presented here are heuristic tools. They provide an opportunity to test assumptions about how a particular biological or physical system operates or behaves. Their validity can be evaluated by comparing predicted with observed behavior. When observation and prediction disagree, the assumptions upon which a model rests are either incorrect or incomplete. However, the obverse is not true. When predicted and observed behavior agrees, the assumptions upon which a model rests cannot be said to be sufficient and necessary. The reason is simple—a model can describe the behavior of a system for the wrong reasons. This caveat is important, because the only rigorous test of a computer model is to experimentally manipulate the system it purports to describe and to see if the model predicts the outcome for each manipulation.

Unfortunately, we cannot experiment with history. We can only observe it. For this reason, the most conservative interpretation of the simulations presented here is that six general properties emerge logically (mathematically) from the assumptions made about early vascular plant evolution. These properties are as follows: (a) the number of equally fit morphological variants is predicted to increase as the number of functional tasks subject to selection increases; (b) the relative fitness of these phenotypes decreases as the number of tasks increases; (c) therefore, morphological diversification is easier on complex as opposed to simple fitness landscapes; (d) constraints on how morphology can be developmentally altered do not a priori limit the number of equally fit variants that can be reached by adaptive walks; (e) however, the relative fitness of these variants is significantly lower than the phenotypic optima that can be reached by unfettered adaptive walks; and (f) adaptive walks on shifting fitness landscapes (used to mimic changes in the

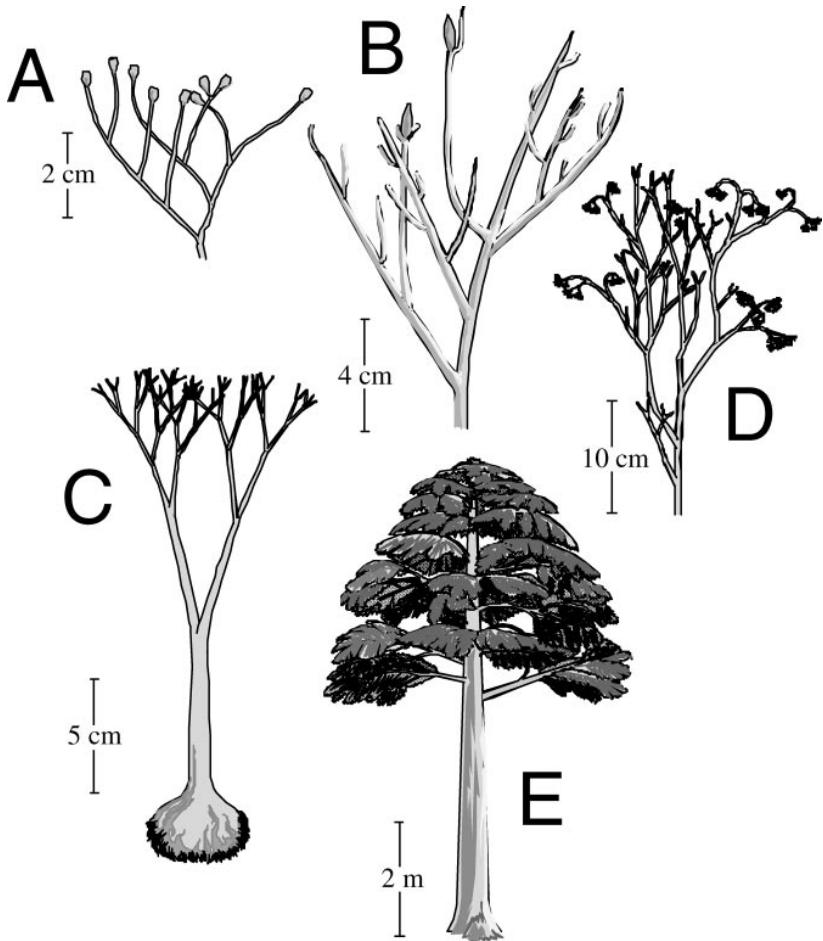


Figure 9 Reconstructions of representative fossil plants from the Late Silurian-Devonian time interval (A and B–E, respectively). (A) *Steganotheca*, (B) *Rhynia*, (C) *Horneophyton*, (D) *Psilophyton*, and (E) *Archaeopteris*.

focus of selection) identify morphological optima that often differ significantly from those on stable fitness landscapes (used to mimic constant selection).

Currently, the only criteria for evaluating whether these properties pertain to real land plant evolution is the extent to which the morphologies identified as occupying adaptive peaks coincide with those observed in the fossil record and the extent to which each of these six properties makes biological sense. In terms of the first criterion, the walks on the landscape for water conservation—a biological task undoubtedly required for surviving on land—identify phenotypes that are strikingly similar to those of the most ancient vascular land plants (e.g., *Cooksonia*, *Steganotheca*, *Rhynia*, and *Horneophyton*) (Figure 9A–C). As more tasks are added to construct more functionally demanding landscapes, other more complex

morphologies are identified as occupying adaptive peaks. Some of these variants are remarkably similar in general appearance to more evolutionarily derived vascular plant fossils (e.g., *Psilophyton* and *Archaeopteris*) (Figure 9D,E). Finally, the morphological transformations attending some walks coincide with those proposed by the telome theory, and many of these transformations reoccur in the fossil record of different land plant lineages, suggesting that they are functionally adaptive.

In terms of the second criterion, each of the six properties makes biological sense. For example, the rapid rate of morphological diversification observed after land plants evolved mechanisms to cope with dehydration (see Niklas et al. 1984, Knoll et al. 1984) is consistent with the prediction that morphological diversification became easier on complex as opposed to simple fitness landscapes. Likewise, it is biologically reasonable to suppose that the morphological diversity manifested by extant species occupying similar or identical habitats vouchsafes that very different phenotypes can have equivalent capacities for growth, survival, or reproductive success.

Computer simulations of morphological evolution are still very much in their infancy, especially in terms of constructing morphospaces and understanding the developmental mechanisms that permit or confine phenotypic transformations in them (see Thomas & Reif 1993, McGhee 1999, Niklas 2003). However, as conceptual tools, they provide opportunities to explore the logical consequences of popular metaphors for evolution, such as Sewall Wright's adaptive walks on fitness landscapes, and by so doing, quantify the possible biological structure and dynamics of opportunistic historical events that distinguish some evolutionary episodes as more adaptive than others.

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LITERATURE CITED

- Berner RA, Beerling DJ, Dudley R, Robinson JM, Wildman RA Jr. 2003. Phanerozoic atmospheric oxygen. *Annu. Rev. Earth Planet. Sci.* 31:105–34
- Chaloner WG, Sheerin A. 1979. Devonian macrofloras. *Devonian Syst., Spec. Pap. Palaeontol.* 23:145–61
- Gates DM. 1965. Energy, plants, ecology. *Ecol.* 46:1–16
- Gensel PG, Andrews HN. 1984. *Plant Life in the Devonian*. New York: Praeger
- Gould SJ. 1980. The evolutionary biology of constraint. *Daedalus* 109:39–52
- Graham LE. 1993. *Origin of Land Plants*. New York: Wiley
- Horn HS. 1979. Adaptation from the perspective of optimality. In *Topics in Plant Population Biology*, ed. OT Solbrig, S Jain, GB Johnson, PH Raven, pp. 48–61. New York: Columbia Univ. Press
- Kaplan DR. 2001. The science of plant morphology: definition, history, role in modern biology. *Am. J. Bot.* 188:1711–41
- Kauffman SA, Levin SA. 1987. Towards a general theory of adaptive walks on rugged landscapes. *J. Theor. Biol.* 128:11–45
- Knoll AH, Niklas KJ, Gensel PG, Tiffney BH. 1984. Character diversification patterns of evolution in early vascular plants. *Paleobiology* 10:34–47
- Lande R. 1985. Expected time for random

- genetic drift of a population between stable phenotypic states. *Proc. Natl. Acad. Sci. USA* 82:7641–45
- McGhee GR Jr. 1999. *Theoretical Morphology: The Concept and Its Applications*. New York: Columbia Univ. Press
- Niklas KJ. 1992. *Plant Biomechanics: An Engineering Approach to Plant Form Function*. Chicago: Univ. Chicago Press
- Niklas KJ. 1994. Morphological evolution through complex domains of fitness. *Proc. Natl. Acad. Sci. USA* 91:6772–79
- Niklas KJ. 1997a. *The Evolutionary Biology of Plants*. Chicago: Univ. Chicago Press
- Niklas KJ. 1997b. Adaptive walks through fitness landscapes for early vascular land plants. *Am. J. Bot.* 84:16–25
- Niklas KJ. 1997c. Effects of hypothetical developmental barriers and abrupt environmental changes on adaptive walks in a computer-generated domain for early vascular land plants. *Paleobiology* 23:63–76
- Niklas KJ. 2000. The evolution of leaf form function. In *Leaf Development and Canopy Structure*, ed. B Marshall, JA Roberts, pp. 1–36. Sheffield: Sheffield Acad.
- Niklas KJ. 2003. The bio-logic machinery of plant morphogenesis. *Am. J. Bot.* 90:515–25
- Niklas KJ, Kerschner V. 1984. Mechanical photosynthetic constraints on the evolution of plant shape. *Paleobiology* 10:79–101
- Niklas KJ, Tiffney BH, Knoll AH. 1984. Apparent changes in the diversity of fossil plants: a preliminary assessment. In *Evolutionary Biology*, ed. M Hecht, W Steere, B Wallace, 12:1–89. New York: Plenum
- Nobel PS. 1983. *Biophysical Plant Physiology Ecology*. New York: Freeman
- Okubo A, Levin SA. 1989. A theoretical framework for data analysis of wind dispersal of seeds pollen. *Ecology* 70:329–38
- Raup DM. 1961. The geometry of coiling gastropods. *Proc. Natl. Acad. Sci. USA* 47:602–9
- Raup DM. 1962. Computer as aid in describing form in gastropod shells. *Science* 138:150–52
- Raup DM, Michelson A. 1965. Theoretical morphology of the coiled shell. *Science* 147:1294–95
- Raven JA. 1984. Physiological correlates of the morphology of early vascular plants. *Bot. J. Linn. Soc.* 88:105–26
- Raven JA. 1985. Comparative physiology of plant arthropod land adaptation. *Philos. Trans. R. Soc. London B* 309:272–388
- Sharloo W. 1991. Canalization, genetic developmental aspects. *Annu. Rev. Ecol. Syst.* 22:265–94
- Stewart WN, Rothwell GW. 1993. *Paleobotany the Evolution of Plants*. Cambridge: Cambridge Univ. Press
- Sultan SE. 1987. Evolutionary implications of phenotypic plasticity in plants. *Evol. Ecol.* 21:127–78
- Sultan SE. 1992. Phenotypic plasticity and the neo-Darwinian legacy. *Evol. Trends. Plants* 6:61–71
- Taiz L, Zeiger E. 2002. *Plant Physiology*. Sunderland, MA: Sinauer
- Taylor TN, Taylor EL. 1993. *The Biology Evolution of Fossil Plants*. Englewood Cliffs, NJ: Prentice-Hall
- Thomas RDK, Reif W-E. 1993. The skeleton space: a finite set of organic designs. *Evolution* 47:341–60
- Willis KJ, McElwain JC. 2002. *The Evolution of Plants*. New York: Oxford Univ. Press
- Wright S. 1931. Evolution in Mendelian populations. *Genetics* 16:97–159
- Wright S. 1932. The roles of mutation, inbreeding, crossbreeding selection in evolution. *Proc. 6th Int. Congr. Genet.* 1:356–66
- Zimmerman W. 1930. *Die Phylogenie der Pflanzen*. Jena, Ger.: Gustav Fischer
- Zimmerman W. 1953. *Evolution. Die Geschichte ihrer Probleme und Erkenntnisse*. Freiburg, Ger.: Karl Alber
- Zimmerman W. 1965. *Die Telomtherorie*. Stuttgart, Ger.: Gustav Fischer



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