THE FOSSIL RECORD OF PLANT PHYSIOLOGY AND DEVELOPMENT—WHAT LEAVES CAN TELL US

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Abstract—Plants provide unmatched opportunities to evaluate long debated evolutionary patterns in terms of the detailed biology of the fossil organisms. Leaves serve here as an example of how those advantages can be exploited. Over the history of vascular plants, three important transitions in leaf evolution—the origin of laminate leaves, the progressive loss of seed plant morphological diversity, and the evolution of more angiosperm-like leaves—also represent major shifts in leaf development and physiology. These transitions often occurred in parallel in different lineages, such as the evolution of marginal growth in each of at least four independent origins of laminate leaves during the Devonian and Carboniferous. Each also entailed dramatic reorganizations of leaf hydraulics. For example, the length of the finest distributary vein order varies from up to tens of centimeters down to hundreds of microns in successive groups of dominant seed plants. Angiosperms impose an additional trend upon these patterns with the evolution of their uniquely high vein densities. Vein density strongly influences and can provide a proxy for other physiological characteristics, such as assimilation and transpiration rates. The large increase in transpiration capacity accompanying the evolution of angiosperm leaf traits may even play an important role in feeding precipitation and thereby altering local climate.

INTRODUCTION

A fossil resembling a fern frond could be of any age up to about 350 million years, but a best guess would be that it is from the Paleozoic. Similarly, best guesses for a fossil resembling a cycad would be Mesozoic and for one resembling an angiosperm would be Cenozoic. That these trends cut across lineages has long been known—by the early 1900s it was recognized that most of the Carboniferous "fern" foliage lacked abaxial sori and were likely to be seed plant-derived (Scott, 1909)—although only recently with the phylogenetic framework to understand that not just direct evolutionary transitions are involved, such as frondose ferns giving rise to frondose seed plants, but rather many independent convergences. As will be developed here, these convergent morphological trends represent broad shifts in developmental biology and hydraulic physiology, subjects far a field of most lines of paleontological inquiry that reflect the unique possibilities offered by plants and their fossils.

Because the preservation of terrestrial fossils is patchy in both space and time, marine invertebrates are the best suited for many analyses of macroevolution and most paleobotanical advancement has been focused either upon paleoecology—where bedding plane snapshots of ecology can be characterized even if their temporal distribution is sporadic—or upon systematics and whole plant reconstruction—where investigation is typically specific to localities or individual beds, so patchiness is not an issue. Plants will never be the best group in which to dissect diversity dynamics through time (although these preservational constraints led to a sample standardized diversity curve being produced for vascular plants (Knoll et al., 1979; Niklas et al., 1980) long before becoming a goal for invertebrate paleontologists). However, macroevolutionary questions can be addressed, albeit differently, with the paleobotanical record by making use of the unique preservational advantages plant fossils offer. The cell walls of plants ensure the frequent preservation of physiologically informative anatomy.

Cell walls also constrain development by prohibiting cell movement, thereby a more direct record of ontogeny is present in adult morphology. Finally, the relatively uniform functional requirements of plants have resulted in repeated evolution of morphologically and functionally similar structures, like leaves, roots, and wood.

Together, these advantages allow unparalleled opportunities to investigate the role of development and physiology in shaping morphological evolution. A strong foundation of such paleobotanical work has included investigation of the aerodynamics of wind pollination in seed and cone morphology (Niklas 1983, 1985), ontogeny of primary (Eggert, 1961) and secondary growth (Cichan, 1985), hormonal gradients in shaping primary (Stein, 1993) and secondary (Rothwell and Lev-Yadun, 2005) xylem anatomy, and the biomechanics of whole plant architecture (Niklas, 1992) and stem structure (Speck and Rowe, 2001).

Increasingly, this bridging of the evolutionary history of plant morphology and anatomy with its physiological and developmental implications has involved tools and theoretical frameworks more familiar to other paleontologists, inclu ding a functional design space of vascular anatomy (Wilson and Knoll, 2006), principal coordinates analysis of pollen anatomy evaluated in terms of reproductive syndrome (Leslie, in press), and simulations of evolution across a theoretical morphospace of shoot branching architecture selecting for biomechanical stability, light interception, and propagule dispersal capability (Niklas, 1994, 1997). Such opportunities exist throughout the organographic and ecological diversity of fossils plants. Here, developmental constraint and physiological function are explored through the example of morphological evolution in laminate leaves.

HORMONES AND TELOMES IN PLANT DEVELOPMENT

Cell migration and cell fate induction in response to shifting cell contacts is an integral part of animal development that is untraceable in the fossil record. In plants, cell walls prohibit cell movement and each cell's environment of cell-to-cell contacts is invariant once cell divisions are complete. The adult morphology of a plant organ is a direct summation of its on-

togeny without the palimpsest of tissue reworking that is typical of animals. Even in the few exceptions of vascular and fiber cells that possess a period early in ontogeny of invasive cell-tip extension between other cells, that history of shifting cell contacts is readily discernible in the final anatomy (Cichan, 1985).

Plant growth is also spatially and temporally discrete. Primary growth typically occurs only in distal zones, called meristems. The secondary growth of wood and bark production found in some plants is similarly localized to discrete bands of dividing cells. Except for the possibility of wounding responses or for the eventual release from dormancy of buds set aside for later growth, no further cell division or expansion occurs once a tissue has been produced and left behind by the continuing growth of the distal meristems—a process that can be related to the discretely localized production of corallites or bryozoan zooids within a colony.

Cell type distributions in differentiating tissue are patterned along hormone gradients. Within the shoot system, auxin is produced in distal growing areas and then actively transported proximally (Gälweiler et al., 1998; Poli et al., 2003). Exposure to auxin leads to increased transport capacity, leading to the canalization of this auxin transport into discrete files of cells to the exclusion of surrounding cells, and, thus, to contiguous vascular strands made up of successive individual cells (Figure 1.1) (Sachs, 1975, 1991; Berleth et al., 2000). The vasculature reflects hormonal gradients resulting from meristematic growth, hence, the adult vascular pattern of a living or fossil plant provides an indirect, but permanent record of developmental process.

This logic can be applied to evolutionary investigation of all plant organs. For example, exclusively equal dichotomous branching was the ancestral condition for vascular plant axes, but increasingly unequal branching became common over the Devonian, culminating in some lineages with the evolution of small determinate lateral primordia production on the apex of a monopodial stem (with important developmental implications for the lateral organs: Sanders et al., 2007). Across the same period, axis vascular architectures also diversified. By modeling the likely hormonal distributions beneath meristem configurations suggested by Devonian branching patterns, Stein (1993) demonstrated that these well-known radiations
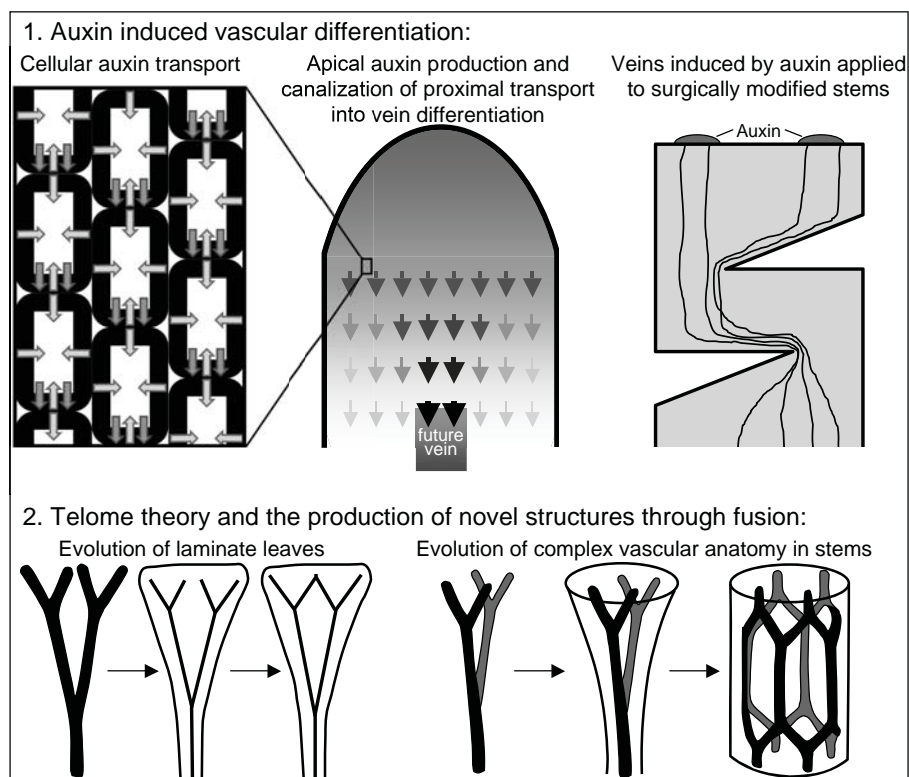
Figure 1—Alternative explanations for the patterning of vascular tissue. *1*, Differentiation of vasculature along auxin gradients. Left diagram: although auxin is actively imported into cells on all sides (white arrows), net flow is accomplished by auxin exporters (grey arrows) localized to the proximal end of each cell (after Berleth et al., 2000). Central diagram: exposure to auxin transport leads to the cellular differentiation of increased capacity to transport auxin, which results in increased transport capacity being canalized into contiguous cell files that differentiate as vascular strands while the auxin exposure of surrounding tissue is reduced. Right diagram: the differentiation of vasculature along auxin gradients can be reproduced in surgically excised stem segments by applying auxin to the cut distal end (after Sachs, 1991). *2*, Evolution of novel structures through the fusion of simple axes as according to the Telome Theory. Successive diagrams represent successive evolutionary—not ontogenetic—stages within each transformation series (after Zimmerman, 1952).

of branching and vascular architectures were largely different manifestations of a single underlying pattern of meristematic diversification. The general lack of anatomical diversification in roots can be similarly explained; the simplicity and uniformity of root anatomy relative to that of shoots has been related to the stability and uniformity of their soil environment (Esau, 1953), but may be more directly attributable to the limited range of hormonal environments possible in roots as constrained by their endogenous branching and distal transport of auxin toward (rather than proximally away from, as in shoots) the unmodified root apex (Boyce, 2005a).

Importantly, the above is at odds with "Telome Theory" (Zimmermann, 1952; Wilson, 1953, Stewart, 1964; Kenrick 2002), the dominant framework for interpreting plant evolution for more than half a century and one exhumed with increasing frequency with modern evolution of development studies (Sussex and Kerk, 2001; Harrison et al., 2002; Langdale et al., 2002; Beerling and Fleming, 2007). In Telome Theory, a simple axis—dubbed a telome—with a single, central vascular strand is taken as the basis of all elaborations of plant form. Any more complex structure, such as a stem or leaf with multiple vascular strands, is taken as the evolutionary fusion of an-

cestrally separate telomes, a concept that is typically reduced to simple, evocative cartoon transformation series (Fig. 1.2) that have been widely reproduced. By this approach, the veins of complex structures are homologized to the remnants of formerly distinct axes, but this does not take into account the mechanisms of vascular induction in plant development. If multiple distinct telomes (each with their own apical meristem) are homologized to multiple veins in a single, more complex organ (formed by a single apical meristem) that would require that vascular differentiation is independent of meristem structure and somehow basally induced through connection with older vasculature rather than apically induced through meristem produced hormonal gradients. That requirement directly violates what we know of plant development and, indeed, violated what was known of plant development at the time telomes were first popularized: surgical manipulations of stem apices clearly indicate that vascular differentiation is not basally, but apically induced by the meristem (Wardlaw, 1950) and that the surficial application of synthetic auxins to the apex can substitute for excised primordia in inducing stem vascular patterning (Ma and Steeves, 1992) (Figure 1.1). In addition to previous criticisms of the hypothetical nature of many intermediate steps envisaged in Telome Theory (Kaplan, 2001), its merely descriptive nature without the positive benefits of predictive utility (Niklas, 2004), and general lack of testability (Stein and Boyer, 2006), Telome Theory has had a directly negative impact in obscuring understanding of the evolution of morphological complexity and novel structures by emphasizing the accretion of dubiously homologous structures rather than the elaboration of meristematic growth types.

FOSSIL HISTORY OF LEAF MORPHOLOGY AND DEVELOPMENT

A pattern common to many evolutionary radiations is an early rise in morphological disparity while diversity is still low followed by a saturation of morphological potential without further increase in disparity as diversity continues to increase (Foote, 1995, 1997; Miller and Foote, 1996; Wagner, 1997; Lupia, 1999). The Paleozoic innovation of laminate leaves among vascular plants shares this well-known pattern,

but allows for its dissection in terms of leaf development and further provides at least four independent repetitions of laminate leaf evolution for comparative study (Boyce & Knoll, 2002).

Paleozoic Leaf Origins and Development

Laminate leaves with multiple veins are found among ferns and seed plants as well as the extinct Sphenophyllales sphenopsids and archaeopterid progymnosperms. A simple morphological and functional approximation of a leaf in the form of determinate lateral branch systems cannot be ruled out for the common ancestor of some of these lineages because the phylogenetic placement of important vascular plant fossils is poorly constrained. However, since the earliest representatives of these four groups each possessed only finely dissected terminal photosynthetic units, laminate leaves represent a later evolutionary innovation independently derived in each lineage. Indeed, the number of laminate leaf evolutions may be significantly higher: leaf laminae may be independently derived in each of Filicales, Marattiales, Ophioglossales, and Zygopteridales depending upon the true relationships among "ferns" (Rothwell, 1999; Pryer et al., 2001; Rothwell and Nixon, 2006). The affinities of the laminate Noeggerathiales are similarly ambiguous.

Two primary modes of leaf growth have been documented among living plants: the discrete marginal growth documented in some ferns (Pray, 1960, 1962; Zurakowski and Gifford, 1988) and the diffuse intercalary growth not confined to the margin documented in some angiosperms (Pray, 1955a, b; Poethig and Sussex, 1985a, b; Dolan and Poethig, 1998). Associated with these alternative modes of growth are venation patterns that are consistent with developmental expectations. Marginally growing leaves have veins oriented towards and ending exclusively along the portion of the margin along which growth occurred (Figure 2.1), consistent with vein differentiation along a gradient derived from the proximal transport of auxin produced in the distal marginal meristem. Diffusely growing leaves have many hierarchical veins orders including internally directed veins and vein endings throughout the leaf (Figure 2.2), consistent with vein differentiation in response to more complex patterns of auxin production and transport (Aloni et al., 2003; Scarpella et al., 2006) associated with the more complex patterns of growth (e.g. Foster, 1952).
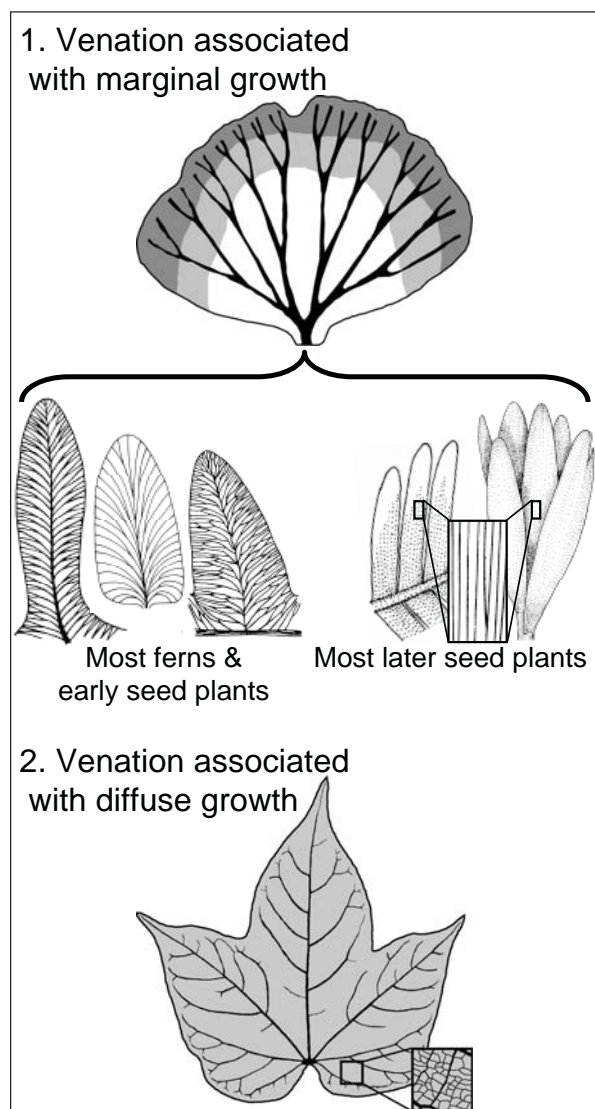
Figure 2—Association of leaf venation and growth patterns. *1*, Marginal growth results in marginally directed open or reticulate veins that end at the margin along which growth occurred (modified from Boyce, 2007). Within marginally growing leaves, different morphologies and venation patterns are associated with most earlier seed plants and ferns (left images: modified from Boureau and Doubinger, 1975) versus most Mesozoic seed plants (right images: modified from Stewart and Rothwell, 1993). *2*, Diffuse intercalary growth throughout the leaf, as in most angiosperms, results in much more complex vascular patterns that typically involve many hierarchical levels of reticulating veins which include internally directed veins that do not end at the margins (modified from Boyce, 2007).

Making use of this relationship between morphology and development, patterns of morphological evolution preserved in fossils can provide an indirect record of developmental evolution: fossils with strictly marginal vein endings indicate marginal growth while the presence of internally directed vein endings indicate alternatives to marginal growth (Fig. 2).

From the Devonian first appearance of laminate leaves until the Permian appearance of the gigantoperids, all leaves only have veins that run to the margin, suggesting each independent evolution of a laminate leaf involved the evolution of marginal laminar growth (Boyce and Knoll, 2002). Furthermore, each lineage replicates an evolutionary succession of morphologies, in which the earliest laminate forms possess simple, equally branching veins fanning out to the distal margin whereas later forms include vein curvature, unequal branching, and other characteristics that suggest modified marginal growth whereby growth rates vary along the marginal meristem. The maximum disparity of this system is rapidly achieved by the mid-Carboniferous, well before taxonomic diversity plateaus, and is then maintained through later time (Boyce and Knoll, 2002; Boyce, 2005b), a pattern often repeated among invertebrates (Erwin, 2007) that in this case can be explained as a reflection of developmental constraint: the limited possible modifications of marginal growth were explored by each of several plant lineages long before maximum taxonomic diversity was achieved and further increases in morphological disparity were not possible until the evolution of complete departures from marginal growth in more angiosperm-like leaves (Boyce & Knoll, 2002).

Developmental hypotheses are based upon the correlation of characteristics of leaf shape and venation present in fossils with those of the few living lineages in which development has been studied. Although consistent with known developmental mechanisms, however, the extremely limited sampling of a small number of angiosperms and filicalean ferns raises concern that correlations might represent phylogenetic coincidence rather than causal requirements of different laminar growth types. The diversity of unstudied living groups provides the opportunity to test developmental predictions based upon leaf morphology and venation and thereby determine whether developmental interpretation of fossils is reasonable. As predicted, flower petals and cycad leaflets with strictly

marginal vein endings have been shown to have marginal growth similar to what has been demonstrated in ferns, despite the common ancestor of ferns and seed plants not having laminate leaves at all (Boyce, 2007). Frequent, extreme convergence of leaf morphology does reflect evolutionary convergence of leaf development.

Later Transitions Associated with Marginal Leaf Growth

Ferns and seed plants initially shared the full range of morphologies derived from marginal growth, but the seed plants progressively lost most of that disparity and became limited to a narrow subset of such morphologies (Boyce, 2005b). Elongate laminae with a single vein order leading straight courses exclusively to the distal margin (Fig. 2.1)—a form rarely exhibited by ferns—first appear in the mid-Carboniferous Cordaitales and becomes progressively more common among seed plants thereafter.

This trend in leaf morphologies broadly corresponds to the replacement over the Permian and Triassic of the wetland seed plant taxa important in the Paleozoic record with those that will dominate the Mesozoic. The origination of taxa in drier environments and their radiation with the contraction of Carboniferous and Early Permian tropical wetlands represents a great increase in the reproductive disparity used to define higher taxa (DiMichele and Aronson, 1992), however leaf patterns indicate a loss in vegetative disparity. These patterns may well be linked: unlike later taxa, the earlier seed plants tend to have frond-borne reproductive structures like the ferns with which they share a diverse array of leaf morphologies (Boyce, 2005b). Since fulfillment of multiple functions typically results in multiple suboptimal forms (Niklas, 1997), dual roles in both photosynthesis and reproduction likely fostered morphological diversity in the leaves of ferns and Paleozoic seed plants. Organ segregation in later seed plants may have been important in drier environments in order to avoid direct competition for water and nutrients between photosynthetic and reproductive organs and because the optimum times for their production were likely distinct in seasonally variable environments, however this important evolutionary innovation enabled a morphological contraction and specialization upon a more restricted range of vegetatively efficacious leaf morphologies (Boyce, 2005b).

Innovations and constraints are often evoked with regard to morphological radiations and their limitation, but here the constraints may be upon the morphologically diverse ferns, where leaf-borne reproductive organs have remained the rule with few exceptions, while an important evolutionary innovation of reproductive segregation from leaves meant the seed plants were free to specialize on a narrow range of leaf morphologies. Although that statement is somewhat misleading—later seed plants likely would encompass greater overall disparity if whole plant morphology were considered instead of just leaf morphology—it is nonetheless important because such contrarian patterns are always a risk given the partial datasets with which paleontologists must necessarily always work.

Evolution of Angiosperm-Like Leaves

More complex, angiosperm-like venation patterns, hypothesized to indicate the evolution of non-marginal forms of leaf growth, have evolved independently at least ten times among fern and seed plant lineages over the last 250 million years (Boyce, 2005b). Among the seed plants, there are the Gnetales, Permian gigantopterids, and some Triassic leaves attributed to the peltasperms. Among ferns, there are *Ophioglossum* of the Ophioglossales, *Christensenia* of the Marattiales, and a number of lineages among the Filicales starting with the Dipteridaceae in the Triassic and continuing with a variety of Polypodiaceae, Blechnaceae, Dryopteridaceae, and other derived families radiating in the Cenozoic.

These leaf characteristics have been used in the past to argue for the complete reinvention of a laminate leaf after passing through a leafless bottleneck that was perhaps aquatic or desert adapted in the case of angiosperms themselves (Doyle and Hickey, 1976) or to argue for angiosperm affinity for a variety of seed plants (Melville, 1969; Asama, 1985; Cornet, 1986), however the frequent evolution of these characteristics among ferns suggests such interpretations are unnecessary. Instead, the repeated evolution of these characteristics among herbaceous to understory plants in warm, wet environments, may well be an indication of the original ecological setting of angiosperm evolution (Boyce, 2005b) as is consistent with ecophysi-

ological studies of basal living angiosperm taxa (Feild et al., 2004).

LEAF VASCULAR PHYSIOLOGY

Of a plant's entire water transport pathway from soil uptake, transport through root and shoot, and ultimate transpirational loss through the stomata, at least a third of the total resistance is concentrated in the last few centimeters represented by the leaf (Sack and Holbrook, 2006). Hence, the large shifts in fossil leaf venation patterns—treated above only as indications of developmental processes—also have important repercussions for hydraulic physiology. As tantalizing as that may be, understanding of the underlying mechanisms and importance of these physiological transitions is not quite available. The ecological diversity and economic importance of flowering plants—and simply their overwhelming abundance—has made them the natural focus of most plant physiological research. However angiosperms represent a dramatic departure with regard to many aspects of plant form and, presumably, function. The poor analogy they present for other vascular plant groups results in both a lack of clear physiological expectations for paleontologically important morphologies and difficulty in appreciating what exactly might be unique about the angiosperms themselves. Nonetheless, progress is being made on both fronts and important traits can at least be suggested, if not always fully understood.

General leaf physiology has been reviewed elsewhere (Sack and Holbrook, 2006), as have the specific advantages likely to have been imparted by the network architecture of angiosperm venation, such as increasing biomechanical support (Givnish 1979) and providing hydraulic redundancy that may both maximize the exploitation of transient light flecks in shaded plants (Boyce, 2005b; Feild and Balun, 2008) and minimize the disruptiveness of insect herbivory and other damage (Roth-Nebelsick et al., 2001; Sack et al., 2003). The emphasis here is upon distinct, but related solutions to a shared challenge—equitable water distribution across a leaf—that will be important for evaluating the physiological implications of evolutionary transitions in leaf morphology.

For any leaf, angiosperm or otherwise, a strong gradient in water potential might naturally be expect-ed whereby more water is available to the proximal tissues closest to the stem water source while most of the water has been lost to surrounding tissue and ultimately transpiration before the distal reaches of the leaf are supplied. This expectation has been borne out in a functional design space involving the simplest venation architecture, a single unbranched vein, in which the maximum lamina that can be hydraulically supported is evaluated across four variables: axial resistance along the vein, radial resistance out of the vein, resistance to transport through the mesophyll, and cuticular/stomatal resistance to water loss to the atmosphere (Zwieniecki et al., 2004). All the basic single-vein leaf morphologies seen in real plants—including needle, scale, and awl shapes—could be reproduced with this model, but long, narrow needles were difficult to achieve because too much water is lost proximally in the leaf unless extreme resistance combinations are imposed that limit photosynthesis. The fine veins of leaves are leaky pipes that must both transport water along the pipe and distribute water out to surrounding tissue; extreme morphologies like long needles highlight that the properties that promote efficacy at one of these two functions will undermine the other.

In contrast with the above expectation, leaves generally show a relatively even distribution of water across the laminar surface. The key point to understanding this phenomenon is that vascular anatomy is not static, but rather proximal to distal gradients in anatomically controlled hydraulic resistance properties counteract and mute the anticipated gradients in water potential. In the leaf veins of extant *Pinus*, the number and diameter of conduits varies so that axial resistance is lowest proximally and radial resistance decreases distally (Zwieniecki et al., 2005). A distinct, but related strategy is found among angiosperms. Equitable water distribution is achieved by the presence of low resistance vessels in the larger veins, but only higher resistance tracheids in the smaller veins, with the resulting pressure differential ensuring that all of the smaller distributary veins are equally served (Zwieniecki et al., 2002).

Thus, although vascular anatomy is typically presented in terms of the characteristics of static cross-sections, as is suitable for taxonomic descriptions of living and fossil plants, what may ultimately matter for the plant are the gradients in how that anatomy

changes. Thus, although new fossil discoveries are often the key to paleontological advancement, understanding the physiology of fossil plants will require the revisiting of existing paleobotanical collections for traits that have not been recognized previously as important. The *Pinus* results should, in theory, be widely applicable to the open, dichotomous veins of most marginally growing laminate leaves whether those veins are the only vein order or are fed by a larger midvein. However, whether similar anatomical gradients have been converged upon with each evolution of marginal growth is unknown. Similarly, the independent evolutions of vessels that are dispersed across the vascular plants (Carlquist and Schneider, 2001) include at least two other evolutions of angiosperm-like leaves with the gigantopterid (Li and Taylor, 1999) and gnetalean (Carlquist, 1996; Feild and Balun, 2008) seed plants, but vessels are typically reported from stem or root and it is not clear whether a differential distribution of vessels between vein orders is involved in the hydraulics of convergent examples of angiosperm-like leaves.

EVOLUTION OF LEAF HYDRAULIC ARCHITECURES

Length of Finest Veins

The independent evolution of marginal growth in multiple Paleozoic lineages, the later loss in seed plants of morphological disparity maintained by the ferns, and the evolution of angiosperms and other taxa with departures from marginal growth (Figure 3.1): the transitions between each of these states also represent large transitions in the length of the ultimate leaf vein order that delivers water to the photosynthetic tissue (Figure 3.2).

In the first morphologies exhibited by marginally growing leaves, small fan-shaped forms and those with a midvein and secondaries, typically the fine veins are approximately on the order of a centimeter long. Most later ferns have maintained that overall architecture, however later seed plants tend to have only a single order of veins despite large laminar surfaces, resulting in veins that can be tens of centimeters long (Boyce, 2005b). For example, an *Alethopteris* pinnule borne by a Carboniferous medullosan seed plant and a *Pseu-*

doctenis pinnule borne by a Jurassic cycadalean seed plant were each derived from marginal growth and may each be 2 cm wide by 10 cm long and have identical vein densities, but the *Alethopteris* distributary fine veins branch off a midvein and will only traverse the 1 cm of half the pinnule width while the cycad has only a single vein order and each fine vein must span the entire 10 cm length—and such leaves with a single vein order running the entire leaf length were already up to a meter long in the first Carboniferous seed plant with this morphology, *Cordaites* (Taylor and Taylor, 1993). [The single veins of Paleozoic arborescent lycopsid leaves must also span the entire distance of a leaf that can be up to a meter long (Andrews and Murdy, 1958; Kosanke, 1979), however these leaves may well have represented a succulent strategy of high water use efficiency and low assimilation rates that would not be strictly comparable to the hydraulic issues faced by these seed plants.] The transition from distributary leaf veins of about a centimeter length as in basal seed plants (as well as ferns and other independent evolutions of laminate leaves) to tens of centimeters length as in more derived seed plants presents distinct challenges for equitable hydraulic support.

Distribution of water equally along the leaky pipe of such lengthy leaf veins is overcome in conifers by systematically altering resistance properties along the vein, as discussed above. Conifer leaf veins consist of multiple files of developmentally related tracheids. Distally along the vein, there are fewer tracheid-producing cell divisions and axial resistance increases and radial resistance decreases with this tapering (Zwieniecki et al., 2005). *Ginkgo* leaf veins possess a similar architecture (Esau, 1960) and capacity for creating gradients in vein properties, but other taxa with exceedingly long veins, such as cycads (Bierhorst, 1971) and *Cordaites* (Harms and Leisman, 1961), have anatomies, distinct from that of conifers that do not seem to lend themselves to the conifer strategy. How hydraulic demands are met in these taxa is unclear and will require anatomical investigation involving serial sectioning along the entire length of the leaf in coal balls or other appropriately preserved fossils (e.g. Chaney et al., 2006).

The above issues are largely bypassed by the angiosperms and other groups with angiosperm-like venation. Because of their hierarchical vein network, the
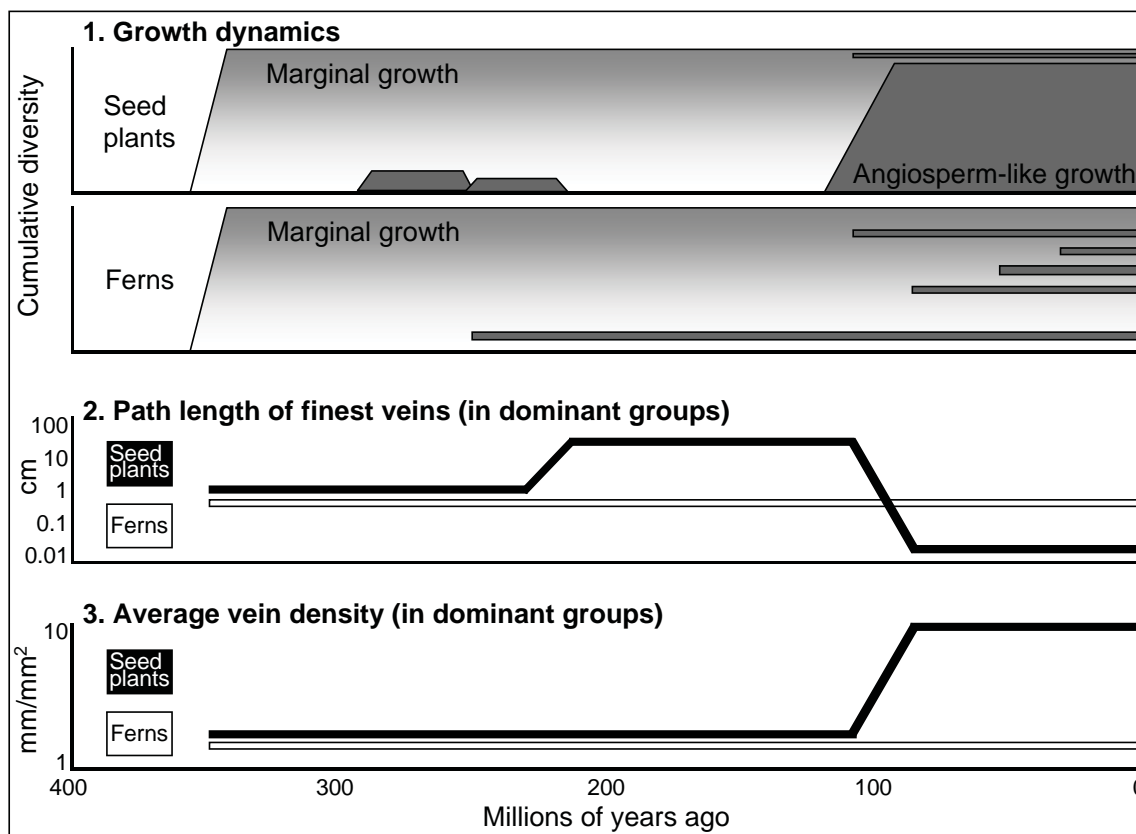
Figure 3—Qualitative summary of leaf developmental and hydraulic evolutionary patterns. 1. Relative prevalence of marginal versus angiosperm-like diffuse intercalary leaf growth in seed plants and ferns. 2. Average path length of the finest vein order remains stably near 1 cm through time in ferns, but varies from 1 cm up to more than 10 cm then down to a fraction of 1 mm in seed plants. 3. Vein density averages about 2 mm per mm^2 of leaf surface for all plants through time, with the exception of angiosperms for which density values can be dramatically higher.

lengths of the fine veins of an angiosperm are likely to be hundreds of microns, not tens of centimeters. This is true even in cases of parallel venation among angiosperms, such as grasses and palms: corn leaves (*Zea*) may superficially resemble those of *Cordaites*, but the maize has a finer order of cross veins linking the parallel veins (in addition to possessing vessels and a higher overall vein density). Aside from the conifer-related Gnetales, the leaves of angiosperms simply are not hydraulically comparable to those of the seed plant contemporaries among which they evolved.

Leaf Vein Density
Although a number of independent groups have converged upon angiosperm venation patterns, one aspect

of angiosperm leaves is entirely unprecedented: their capacity for extremely high vein densities (Boyce et al., in review). Each of the Paleozoic origins of laminate leaves involved vein densities that averaged about 2 mm of vein length per mm^2 of lamina surface and rarely reached below 1 mm/mm^2 or above 4 mm/mm^2, a range that has been maintained through later history in most groups. Angiosperms, however, average 8 mm/mm^2 and can reach higher than 20 mm/mm^2 (at least in more derived angiosperms, the low densities seen in basal ANITA-grade taxa suggest high vein density was a later innovation). Encroachment of densities above 5 mm/mm^2 is present in angiosperm-like leaves of gigantopterid and gnetalean seed plants and dipterid ferns, however none have densities higher

than 7 mm/mm^2 and other convergences upon angiosperm venation patterns have densities as low as 1 mm/mm^2.

Because resistance is high to water transport through the photosynthetic mesophyll tissue (Cochard et al., 2004), gas exchange and carbon assimilation rates are tightly coupled to the distance through the mesophyll that water must traverse between vein and stomata (Brodribb et al., 2007) and, hence, to vein density. In that context, angiosperm leaves represent a substantial departure from the photosynthetic physiology of all other plant groups and suggest the substantially lower assimilation capacities seen in non-angiosperms relative to angiosperms in modern environments were the norm for pre-angiosperm environments, since vein density among non-angiosperms has been stable for 350 million years. Furthermore, given the importance of the vein-stomata distance, that stability of vein densities in non-angiosperms since the Late Devonian is all the more remarkable since stomatal densities have fluctuated by more than an order of magnitude with changing atmospheric CO_2 concentrations (McElwain and Chaloner, 1995; Beerling and Woodward, 1997).

As the primary focal point of plant/atmosphere interaction, the role local climate plays in determining viable leaf morphologies has made those morphologies useful climatic indicators (Wolfe, 1993; Wilf, 1997; Wilf et al., 1998), however those leaves may, in some cases, also play an important role in shaping local climate. The recycling of rainwater through evapotranspiration accounts for up to 50% of the rainfall in modern, lowland tropical rainforests and ensures precipitation evenness and reliability (Worden et al., 2007). Because transpiration capacity is closely correlated with vein density, transpiration levels could have been an order of magnitude lower before the advent of the uniquely high leaf vein densities of angiosperms. Thus, since precipitation is the single greatest predictor of diversity (Kreft and Jetz, 2007), tropical biodiversity would have been considerably lower before the advent of the angiosperm contribution to convective rainfall recycling that results from their unique leaf traits. Furthermore, this may explain important differences in forest structure through time: vines and lianas, which make use of ground water, have been important since the Carboniferous (Kerp and Krings, 1998), while true epiphytes, which have no connection to ground water and are dependent upon reliably frequent precipitation, are predominantly a Cenozoic phenomenon (Boyce et al., in review). The Intertropical Convergence Zone will always ensure a tropical belt of relatively high rainfall, but the character of that rainy belt may have been sizably affected by successive revolutions in leaf evolution.

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