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Dynamic Carboniferous tropical forests: new views of plant function and potential for physiological forcing of climate

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Summary

The Carboniferous, the time of Earth's penultimate icehouse and widespread coal formation, was dominated by extinct lineages of early-diverging vascular plants. Studies of nearest living relatives of key Carboniferous plants suggest that their physiologies and growth forms differed substantially from most types of modern vegetation, particularly forests. It remains a matter of debate precisely how differently and to what degree these long-extinct plants influenced the environment. Integrating biophysical analysis of stomatal and vascular conductivity with geochemical analysis of fossilized tissues and process-based ecosystem-scale modeling yields a dynamic and unique perspective on these paleoforests. This integrated approach indicates that key Carboniferous plants were capable of growth and transpiration rates that approach values found in extant crown-group angiosperms, differing greatly from comparatively modest rates found in their closest living relatives. Ecosystem modeling suggests that divergent stomatal conductance, leaf sizes and stem life span between dominant clades would have shifted the balance of soil–atmosphere water fluxes, and thus surface runoff flux, during repeated, climate-driven, vegetation turnovers. This synthesis highlights the importance of 'whole plant' physiological reconstruction of extinct plants and the potential of vascular plants to have influenced the Earth system hundreds of millions of years ago through vegetation–climate feedbacks.

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I. Introduction

From the perspective of global climate and elemental cycles, the Pennsylvanian Subperiod of the Carboniferous (the ‘Coal Age’; 323–299 million yr ago (Ma)) is a distant mirror to global environments of the last several million years. Icehouse climates prevailed during the Late Paleozoic Ice Age (LPIA; 340–290 Ma), as they do today, characterized by orbital forcing of glacial–interglacial climate and sea-level cycles (Montañez & Poulsen, 2013) under systematically varying but overall low atmospheric $p\text{CO}_2$ (Montañez *et al.*, 2016). Both the LPIA and the most recent glacial state (during the Pleistocene Epoch of the past 2.6 Ma), in which humans evolved, feature a vegetated Earth with diverse and distinct biomes of pteridophytes (spore-bearing plants) and seed plants (DiMichele, 2014). However, the Pennsylvanian Earth had a few key differences: Carboniferous continents were aggregated into a global supercontinent, Pangaea, leaving much of the globe covered by an extensive ocean, Panthalassa; vast areas of the Pangaeon continent were of low elevation and very flat, leading to periodic extensive flooding by marine waters; the major glaciations that defined the rhythms of the LPIA were mainly or entirely confined to the southern hemisphere; although atmospheric $p\text{CO}_2$ was overall low (< 1000 ppm), proxy-based and geochemical mass balance modeling estimates of $p\text{O}_2$ range between 26% and 33% (Bergman *et al.*, 2004; Berner, 2009; Glasspool & Scott, 2010); and the flora and fauna of Pennsylvanian ecosystems were considerably different from those of the recent past and present with the notable absence of angiosperms, the most diverse and ecologically dominant modern plant group.

Substantial scientific efforts to understand the LPIA climate system have recently included complex models that account for the atmosphere, land surface, marine systems, and biosphere interactions (Poulsen *et al.*, 2007; Horton & Poulsen, 2009; Horton *et al.*, 2010; Heavens *et al.*, 2012, 2015). This work suggests that abiotic climate processes alone cannot account for the large-magnitude environmental and $p\text{CO}_2$ changes inferred from the geological record – and that the terrestrial and marine biospheres must have played a significant role in hydrological and elemental cycling and influencing the global climate system.

These findings raise a number of apparent contradictions. First, the Carboniferous Period was the time of peak peat accumulation and coal formation for the past half-billion years, by a wide margin (Glasspool & Scott, 2010; Nelsen *et al.*, 2016). Paradoxically, the tropical terrestrial ecosystems were dominated by now-extinct relatives of early-diverging vascular plants, pteridophytes, and seed plants (Fig. 1) – including lycophytes, sphenopsids, ferns, and pteridosperms (‘seed ferns’) – whose extant distant relatives exhibit low photosynthetic rates (Brodribb *et al.*, 2007; Brodribb & McAdam, 2011; McAdam & Brodribb, 2012). The inference of generally low photosynthetic rates is based on analyses of leaf anatomical properties, primarily stomatal density and size, leading to the hypothesis that stomatal conductance was low in early vascular plants (Franks & Beerling, 2009a,b). Furthermore, it has been assumed that high photosynthetic rates could not have evolved until maximum leaf diffusive capacity increased with the evolution of higher vein densities of angiosperms (*c.* 120 Ma) in the

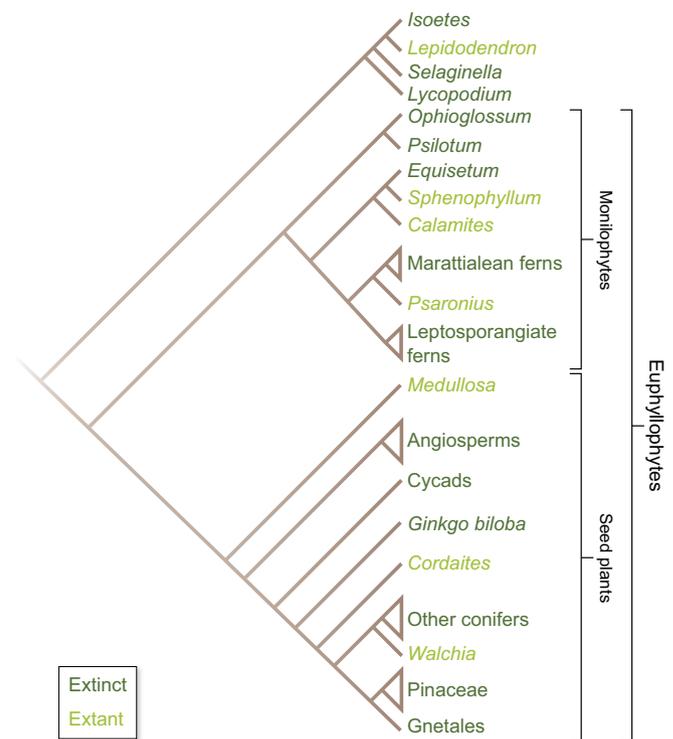


Fig. 1 A tree of key Pennsylvanian plants, their living relatives, and their evolutionary context. Triangles represent extant lineages with substantial biodiversity. The arborescent lycophytes are nested within two extant herbaceous lycophyte genera, *Selaginella* and *Isoetes*. Sphenopsids, including the extinct taxa *Sphenophyllum* and *Calamites*, are nested within the extant ferns (‘monilophytes’). Genetic analyses suggest that extant ferns form a monophyletic group (e.g. Pryer *et al.*, 2004), that extant gymnosperms (nonangiosperm seed plants) form a second monophyletic group with the gnetales as sister to the Pinaceae or extant conifers (e.g. Qiu *et al.*, 1999), and that angiosperms are a sister group to the gymnosperms (e.g. Burleigh & Mathews, 2004; Doyle, 2006, 2008, 2012), implying that angiosperms diverged from a lineage of seed plants that themselves diverged from extant gymnosperms before their last common ancestor. *Medullosa* represents the pteridosperms, an informal name for early-diverging seed plants that bore seeds on fern-like leaves.

Cretaceous period (Boyce *et al.*, 2009, 2010; Feild *et al.*, 2011; Boyce & Zwieniecki, 2012). Our integrated study of paleobotanical records, fossil cuticle morphology, anatomy, and isotopic composition, and process-based ecosystem modeling indicates a far larger range of possible assimilation rates (3–16 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the Carboniferous vascular plants, including certain groups with rates comparable to some modern angiosperms (Section IV).

Second, our understanding of the ecophysiology of keystone plants of Carboniferous tropical wetland ecosystems is extremely limited. Direct comparison of the ecologically dominant spore-bearing Carboniferous taxa with modern nearest living relatives (NLRs) would imply that they had physiologies that may have had limited instantaneous response capacities to environmental change (Franks & Beerling, 2009a,b; Brodribb & McAdam, 2011; McAdam & Brodribb, 2012; Franks *et al.*, 2014). This characterization of Carboniferous tropical vegetation is based on the finding that the majority of modern vascular spore-bearing plants

(lycophytes and ferns) are passive stomatal responders to abiotic stimuli, only capable of closing stomata passively as a result of dehydration (McAdam & Brodribb, 2012). However, no simple NLR comparison is available for the seed-bearing dominant taxa, which are all extinct. The observation that most of the seed plant dominants of the Carboniferous have low leaf vein density relative to modern extant angiosperms led to the assumption that they, too, probably had limited transpiration capacity (Boyce *et al.*, 2009, 2010). Thus, Carboniferous vegetation as a whole is typically considered to have had limited potential feedback on the Earth system in terms of biospheric water and carbon dioxide exchange. This inference, however, stands at odds with evidence of these plants' environmental specificity, changing distributions that track environmental conditions, and dispersal capacities across broad swaths of landscape while remaining faithful to habitat conditions (e.g. DiMichele & Phillips, 1996; Hilton & Cleal, 2007; Cleal, 2008a,b; DiMichele *et al.*, 2008; DiMichele *et al.*, 2009; Bashforth *et al.*, 2016b).

A notable feature of Pennsylvanian terrestrial ecosystems is that they were repeatedly and dynamically restructured over a hierarchy of timescales (10^5 – 10^7 yr), and in step with climate change. At the eccentricity scale (400 kyr) glacial-interglacial cycles, the tropical wetland (glacial maximums) and dryland (early glacial and interglacials) biomes were intercalated, dominating different parts of each successive cycle (Falcon-Lang, 2004; Falcon-Lang *et al.*, 2009; DiMichele, 2014; Bashforth *et al.*, 2016a). At million-year timescales, there are several points in the Carboniferous, characterized by major climate and atmospheric $p\text{CO}_2$ change, where both the wetland and dryland biomes were broadly restructured over short (meter- to 10 s of meter-scale) stratigraphic intervals (Phillips *et al.*, 1974; Pfefferkorn & Thomson, 1982; DiMichele *et al.*, 2009; Tabor *et al.*, 2013; Montañez *et al.*, 2016) (see section 'Dynamic aspects of Pennsylvanian vegetation' for further discussion). Moreover, many of these plants had large biogeographic ranges across major latitudinal regions and paleoclimate zones within those regions, probably related to their wind- and water-dispersal and pollination mechanisms (e.g. Wagner & Lyons, 1997; Tidwell & Ash, 2004; Moore *et al.*, 2014; Bashforth *et al.*, 2016a,b). Exceptions reside mainly in the pteridosperms, where large pollen and seed sizes suggest animal mediation, resulting in somewhat more restricted geographic ranges and shorter temporal ranges/higher species turnover (Raymond & Costanza, 2007).

Evidence of broad environmental distributions in some late Paleozoic plants and conservatism of composition and dominance-diversity structure within many plant assemblages over millions of years, despite repeated restructuring of vegetation and major climate changes throughout the Carboniferous and early Permian (e.g. DiMichele *et al.*, 2002, 2009, 2010; Tabor *et al.*, 2013; DiMichele, 2014), suggests, among other possible factors (e.g. differences in resource use and competition), a more dynamic range of physiological capabilities than studies of nearest living (phylogenetic) relatives might indicate. Additionally, close relationships exist in the modern world between different vegetation types and their climate associations (Köppen, 1936; Walter, 1985), including strong feedbacks between vegetation types and their local

environment. Thus, it is no surprise that the plants of the past also had such relationships, even if their magnitude was not identical to those seen today (e.g. Wnuk, 1996). Nonetheless, questions have been raised about the existence of these feedbacks in the geological past and whether Carboniferous plants had sufficient water-transport and carbon-fixation capabilities to have had a major impact on climate and biogeochemical cycles (Boyce *et al.*, 2009, 2010, 2017; Feild *et al.*, 2011).

Finally, the Late Paleozoic Ice Age was the most extensive ice age in space and time since the Snowball Earth events of the Late Proterozoic Eon (750–580 Ma), potentially involving low-elevation (<1500 m) glaciers in the tropics (Soreghan *et al.*, 2014) and dynamic climate behavior (Montañez & Poulsen, 2013). Climate simulations of the LPIA that lack vegetation–climate–ice feedbacks fail to simulate large magnitude changes in continental ice and sea level inferred from geological archives (Horton & Poulsen, 2009; Montañez & Poulsen, 2013), implying an important role of the biosphere in influencing global water and carbon cycling.

The key to addressing these issues and paradoxes is to build an understanding of the 'whole-plant' physiologies of LPIA floral dominants. In this paper, we propose that such reconstructed physiologies should be based on the morphological features of the plants themselves, rather than solely on the limitations of modern phylogenetic relatives, and should incorporate the full suite of those morphological characteristics, from root-to-stem-to-leaf, both anatomical and external (e.g. Wilson *et al.*, 2015). Applying whole-plant understanding of extinct plants into process-based ecosystem and Earth system modeling is critical to refining our understanding of vegetation–climate feedbacks in deep time, including periods that may provide an insight into our climate future (Fig. 2).

II. Plants of the Pennsylvanian Tropical Realm

Keystone plants from Pennsylvanian ecosystems (323–299 Ma) are among the most completely studied plants of the fossil record (Fig. 3). An iconic group that dominated Middle Pennsylvanian (315–307 Ma) tropical wetland ecosystems was the arborescent lycophytes. This extinct lineage of tree-sized isoetalean lycophytes had very large (up to 2 m in diameter) trunks supported by bark rather than wood, limited vascular systems, in particular photosynthate transport tissue, and heterosporous reproduction (Fig. 3a; Phillips, 1979; Phillips & DiMichele, 1992). Also within the tropical wetlands, widespread and dominant in the better-drained habitats of flood plains, were the medullosan pteridosperms. This group of seed plants is notable for their complex vasculature with very hydraulically efficient tracheids (Cichan, 1986; Wilson *et al.*, 2008, 2015; Wilson, 2013), large leaf area arrayed in fern-like fronds of great size (Laveine, 1986), and large seeds and pollen grains, the latter suggesting animal pollination in some species (Fig. 3b; Andrews, 1945; Delevoryas, 1955; Laveine, 1986; Pfefferkorn & Thomson, 1982; DiMichele *et al.*, 2006; Cleal, 2008a,b; Wilson & Knoll, 2010; Wilson *et al.*, 2008). Medullosan plants have been interpreted to occupy a wide range of whole-plant architectures, from scandent and vine-like plants with small stems

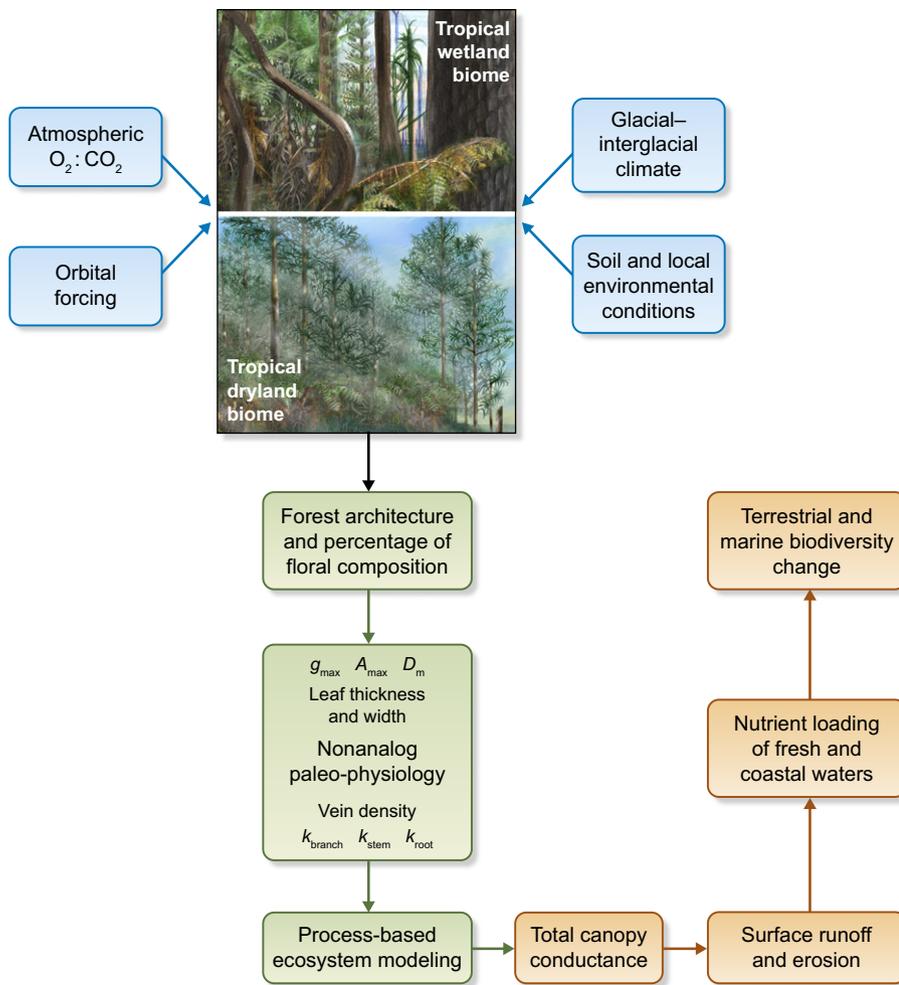


Fig. 2 Flow chart delineating connections and process-based linkages between many of the components of paleoecophysiology reconstruction. Blue boxes are solar system- to local-scale physical forcings acting on Carboniferous biomes. Green boxes are the empirically based or inferred plant to forest characteristics applied to the process-based ecosystem modeling, BIOME GGC v.4.2. Orange boxes are modeled output processes (total canopy conductance, surface runoff) and possible environmental and biological consequences.

containing large tracheids, to lax-stemmed or fully arborescent trees (Pfefferkorn *et al.*, 1984; Wilson & Fischer, 2011; Wilson *et al.*, 2015).

The wetlands harbored other important groups as well. Among these was the stem group marattialean tree fern *Psaronius* (Fig. 3d; Rößler, 2000; D’Rozario *et al.*, 2011), a small tree with substantial colonizing ability, found in swamps and moist-soil habits, even within otherwise strongly seasonally dry landscapes. Another group was the calamitalean sphenopsids, which had a clonal habit and occupied swamps, riverine corridors and lake margins, and disturbed wetland settings harbored both the clonal calamitalean sphenopsids (Gastaldo, 1992; Thomas, 2014; Falcon-Lang, 2015) and the thicket-forming to climbing sphenopsid *Sphenophyllum* (Batenburg, 1981; Cichan, 1985; Bashforth & Zodrow, 2007). The cordaitaleans, a representative of the stem group coniferophytes, are another group found within the swamps but were also dominant in seasonally dry settings. These plants varied in habit from large, woody trees, particularly in ‘upland’ environments (Fig. 3c; Falcon-Lang & Bashforth, 2005), to small trees and scrambling forms, in swampy settings (Rothwell & Warner, 1984; Falcon-Lang, 2004, 2005; Raymond *et al.*, 2010); all had strap-shaped, parallel-veined leaves. The great geographic and ecological extent of the cordaitaleans is indicated by the genus *Ruffloria*, which

was the dominant element of northern temperate forests during the Pennsylvanian (Chaloner & Meyen, 1973; Meyen, 1982, 1997).

Disarticulation of plant organs upon death has led to the use of form genera for isolated organs of many Pennsylvanian plants (Table 1), including stem taxa (e.g. *Medullosa*), leaf taxa (e.g. *Neuropteris ovata*), and reproductive structures (e.g. the seed/ovule *Pachytesta*) that otherwise were produced by the same plant (or by a group of closely related species). Reassembling whole plants from isolated organs bearing different names remains a challenge, but fossils found attached, in close and repeated taphonomic association, and with anatomical similarities have proven to be guides to the morphology of the living plant (Bateman & Hilton, 2009). It should be noted that the morphological and, consequently, ecological diversity and disparity found within a fossil genus is likely to vary considerably depending on how well characterized that group may be – not all species are preserved and interspecific incompatibilities that are easily observed among living plants (e.g. pollen incompatibility) may not be observable in the fossil record.

1. Dynamic aspects of Pennsylvanian vegetation

Pennsylvanian tropical regions of Euramerica were characterized by temporal shifts between wetland and seasonally dry plant

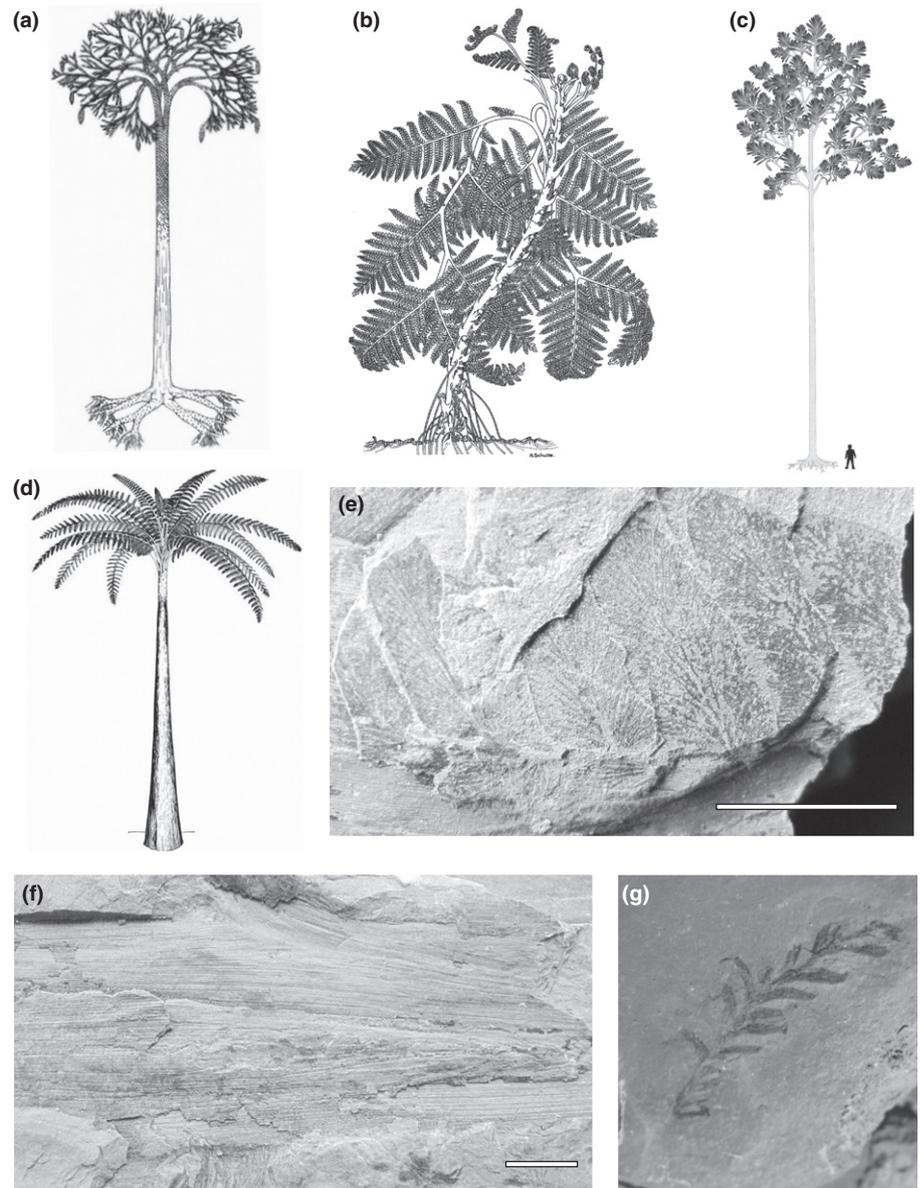


Fig. 3 Reconstructions of key Pennsylvanian plants and representative fossils.

(a) Reconstruction of an arborescent lycophyte, from Taylor *et al.* (2009). (b) Reconstruction of an arborescent but lax-stemmed medullosan pteridosperm, from Andrews (1945) with permission from Missouri Botanical Garden Press, St Louis, USA. Note that the large, compound frond systems are drawn as if the plant were wilting in order to fit the plant within a single illustration. Additional perspectives on medullosan growth and form can be found in Pfefferkorn *et al.* (1984), Wilson & Fischer (2011), and Wilson *et al.* (2015). (c) Reconstruction of an extrabasinal, or 'upland' giant cordaitalean tree, from Falcon-Lang & Bashforth (2005), with permission. It is likely that these trees were abundant in environments that are represented at low frequencies in the fossil record. (d) Reconstruction of *Psaronius*, from Taylor *et al.* (2009). Note that the majority of the volume of the stem is made up of root mantle, rather than leaf and stem tissue. (e) Medullosan (*Neuropteris*) leaf from Indiana, USNM Locality 38327. Bar, 1 cm. (f) *Cordaites* leaf from Indiana, USNM Locality 38327. Bar, 1 cm. (g) Walchian conifer leaf impression from New Mexico.

communities, tracking linked changes in low-latitude climate, high-latitude continental ice extent, and atmospheric $p\text{CO}_2$ (Fig. 4; DiMichele *et al.*, 2009, 2010; DiMichele, 2014; Montañez, 2016; Montañez *et al.*, 2016). At the 10^5 yr timescale, there is an oscillatory pattern throughout the Pennsylvanian of relatively wetter flora characteristics of swamp habitats and those floras of seasonally dry habitats, rich with woody cordaitaleans and a variety of other taxa. This oscillation is most easily observed in coal-bearing deposits throughout North American and European basins (Falcon-Lang, 2004; Plotnick *et al.*, 2009; Falcon-Lang & DiMichele, 2010; DiMichele, 2014; Bashforth *et al.*, 2016b). In these settings and at this timescale, sea level minima (suggesting maximum accumulation of high-latitude ice sheets) coincide with expanded tropical everwet floras near the equator, whereas maximum flooding intervals (times of maximum deglaciation) and subsequent falling stages of sea level (early glacials) are notable for the expansion of summer-wet or seasonally dry forests

(DiMichele *et al.*, 2010; Horton *et al.*, 2012; Cecil *et al.*, 2014). This oscillation, mechanically linked to eccentricity-scale (10^5 yr) glacial–interglacial cycles, persists throughout the 24 Myr period of the Pennsylvanian and into the earliest Permian.

A second, longer-term (10^6 – 10^7 yr) trend on which the eccentricity scale variability is superimposed, marks a secular change in Pennsylvanian forests, particularly tropical forests. A series of turnovers in composition, but, more significantly, in the relative proportions of the major groups (lycophytes, pteridosperms, marattialean tree ferns, sphenopsids, cordaitaleans, and conifers) occurs at several intervals during the Pennsylvanian and near the Carboniferous–Permian boundary (Pfefferkorn & Thomson, 1982; Phillips & Peppers, 1984; Phillips *et al.*, 1985; Cleal & Thomas, 2005; Cleal *et al.*, 2012; van Hoof *et al.*, 2013; Tabor *et al.*, 2013). Notably, these restructuring events coincide with periods of major change in tropical climate and, in most cases, atmospheric CO_2 concentrations.

Table 1 Key organ or form genera for Pennsylvanian plants and their associated whole-plant concept

	Common Carboniferous form genera		
	Leaves	Stems	Other
Arborescent lycophytes	<i>Lepidophylloides</i>	<i>Diaphorodendron</i> <i>Lepidodendron</i> <i>Lepidophloios</i> <i>Sigillaria</i> <i>Synchysidendron</i>	<i>Stigmara</i> (rhizomorph)
Medullosans	<i>Neuropteris</i> <i>Macroneuropteris</i> <i>Alethopteris</i>	<i>Medullosa</i>	<i>Pachytesta</i> (seeds) <i>Myeloxylon</i> (petioles)
Cordaites	<i>Cordaites</i>	<i>Cordaixylon</i> <i>Pennsylvanioxylon</i> <i>Cordaites</i> <i>Mesoxylon</i>	<i>Amyelon</i> (roots)
Psaronius	<i>Pecopteris</i>	<i>Psaronius</i>	<i>Psaronius</i> (roots)

2. Pennsylvanian-early Permian biomes

Montañez (2016) characterized these million-yr scale changes in quantitative dominant elements of the vegetation and associated change in architecture and/or structure as a series of biomes (Fig. 4). A shift in the tropical wetland forests from lycophyte dominance (wetland biome (WB) 1) in the early Pennsylvanian (~317–318 Ma) to woody cordaitalean–lycophyte forests (WB 2) overlaps with initiation of the main phase of Pennsylvanian glaciation (Fielding *et al.*, 2008). Additional quantitative changes in abundance and new floral dominants occurred at the onset (*c.* 311 Ma) of long-term waning of Gondwanan ice sheets, elevated atmospheric $p\text{CO}_2$ (Montañez *et al.*, 2016), and increased seasonality (DiMichele *et al.*, 2009). Two subsequent turnovers appear to be contemporaneous with the return of short-lived but intense glaciations and associated climate deterioration in the paleotropics. The first shift between WB 2 and 3 (*c.* 308 Ma) involved marked loss of cordaitaleans and a distinct rise in tree fern abundance (Pfefferkorn & Thomson, 1982). The second and best characterized of the Pennsylvanian turnover events (WB 3–4) occurred at the Middle to Late Pennsylvanian Boundary (MLPB, 306 Ma; Desmoinesian-Missourian boundary in the American stratigraphic system), where a major turnover occurred in glacial-phase wetland forests, from dominance by arborescent lycophytes to dominance by *Psaronius* tree ferns and medullosan pteridosperms (Phillips *et al.*, 1974; Phillips & Peppers, 1984; DiMichele *et al.*, 2002, 2006; Cleal, 2007; Falcon-Lang *et al.*, 2011a).

This ecological threshold event at the MLPB was coincident with a decrease in $p\text{CO}_2$ to below 300 ppm and the lowest glacial phase CO_2 concentrations (< 200 ppm) of the reconstructed Pennsylvanian record (Montañez *et al.*, 2016). Following this turnover, lycophytes were greatly reduced in abundance and diversity in Late Pennsylvanian tropical wetlands of Euramerica, but remained significant in wetland ecosystems of eastern Pangaea (i.e. north China) well into the Permian Period (e.g. Hilton & Cleal, 2007;

Zhou *et al.*, 2008; Wang *et al.*, 2012). The remainder of the Late Pennsylvanian witnessed the dominance of water stress-tolerant marattialean tree ferns (WB 3) and their stepped emergence as swamp-community dominants (WB 4) in environments which also contained abundant pteridosperms (Pfefferkorn & Thomson, 1982; DiMichele *et al.*, 2009). Notably, the transition from lycophyte-dominated to fern- and pteridosperm-dominated tropical wetland forests is a major biotic transition in the Paleozoic Era and one that probably exerted significant change on the global carbon and hydrologic cycles. The final turnover was a permanent replacement of the wetland biome by seasonally dry woodland flora (cordaitaleans and conifers; dryland biome (DB 2)) that occurred across the Carboniferous–Permian boundary (299 Ma) coincident with widespread aridification (DiMichele *et al.*, 2009; Tabor *et al.*, 2013; Opluštil *et al.*, 2013), a drop in $p\text{CO}_2$ to sub-300 ppm concentrations (Montañez *et al.*, 2016), and probably peak O_2 : CO_2 values (Glasspool & Scott, 2010). Wetland plants at this time became restricted to spatially discontinuous habitats in large parts of Euramerica.

In addition to the glacial–interglacial floral cyclicality and the longer-term intervals of floral restructuring in the lowland tropical forests, several other distinct biomes can be defined that were distributed spatially throughout Pangaea and persistent throughout the Pennsylvanian (Fig. 5). The distinct tropical, seasonally dry biome maintained permanent populations in western equatorial Pangaea (New Mexico, Arizona, Utah, and Colorado, extending to western Kansas, Oklahoma, and Texas during drier times) and perhaps in the mountainous regions of central Pangaea (e.g. Atlantic Canada and European basins) throughout the Pennsylvanian (Broutin *et al.*, 1990; DiMichele *et al.*, 2011; Bashforth *et al.*, 2014; Thomas & Cleal, 2017) and probably consisted of several distinct ecozones. Initially dominated by cordaitaleans this assemblage became richer in conifers, including the stem group conifer *Walchia* (Fig. 3g), toward the close of the Pennsylvanian and during the early Permian (Rothwell *et al.*, 1997; Falcon-Lang *et al.*, 2011b; Hernandez-Castillo *et al.*, 2009). At this time, northern hemisphere temperate regions of Angaraland were covered by forests dominated by cordaitalean *Ruffloria* trees (Meyen, 1982). The southern hemisphere warm temperate forests were codominated by medullosans, *Psaronius*, and calamitaleans and various kinds of lycophyte. Many of the extratropical biomes maintained similar compositions throughout the Pennsylvanian, with the largest and most significant change being the aforementioned replacement of lycophyte-dominated, tropical wetland biomes with tree fern- and seed fern-dominated floras. The high-latitude tundra biome may have been much richer in bryophytes than present-day analogous settings and probably included seed ferns and small isoetalean lycophytes (LePage *et al.*, 2003; Ricardi-Branco *et al.*, 2013).

The preceding paragraphs summarize much of our present understanding of the vegetation during the main phase of the LPIA. Long-term studies of the biotic communities from this period have produced an excellent understanding of their taxonomic diversity, form and architecture, and paleoecology. Several decades of geological investigations, in particular in the paleotropics, have produced a detailed stratigraphy, physical and biological, an

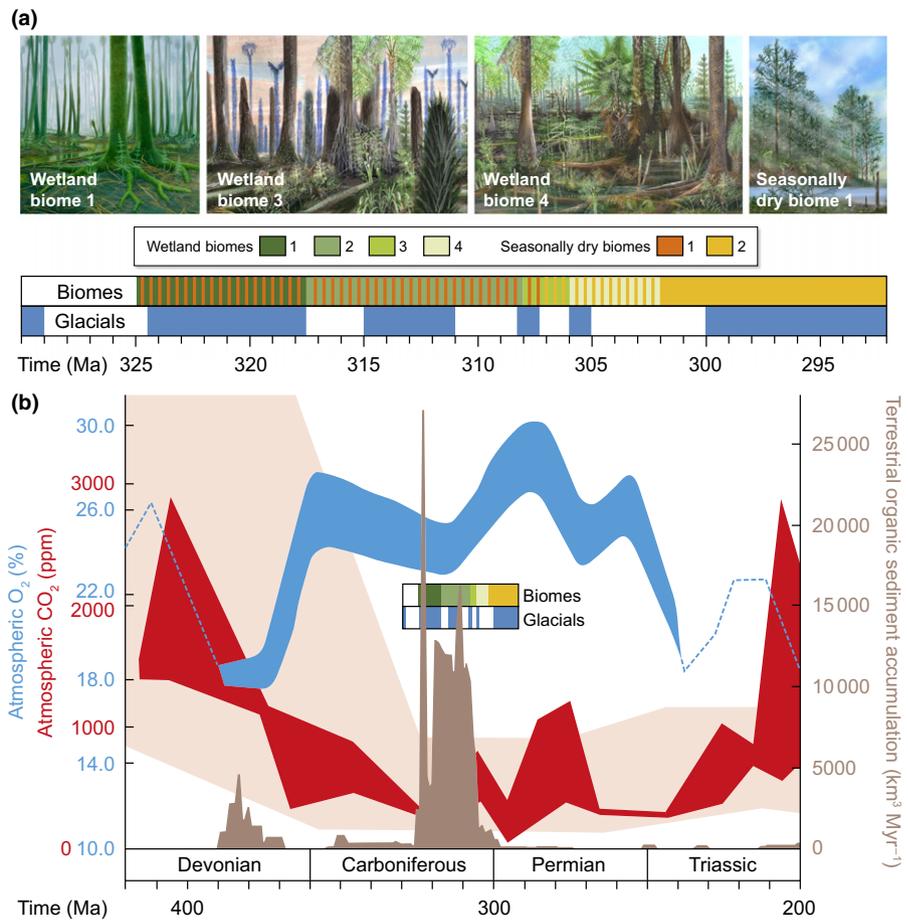


Fig. 4 Temporal distribution of tropical Pennsylvanian and early Permian biomes, paleoatmospheric $p\text{CO}_2$ and $p\text{O}_2$, and glaciation history adapted from Montañez (2016). Panel (a) is a detailed inset of the biome-glaciation history shown in (b). Wetland biome 1 (WB 1) owned, commissioned by and courtesy of the City and County of Denver, K. Johnson, and J. Vriesen. WB 3 and 4, and seasonally dry biome 1, courtesy of Mary Parrish (National Museum of Natural History, Smithsonian Institution). See text for detail of biome distributions. Pink shading around the CO_2 curve represents the 16 and 84 percentile-uncertainty around the estimates.

understanding of the paleogeography and tectonic regimes, and characterization of the paleoclimate and its dynamics. These studies have revealed initial insights into biogeographic patterns and biodiversity, and their dynamics in time and space. There remains, however, much to be learned with regard to translating diversity of species and forms to function – a research area that is ripe for investigation but has hardly been explored.

Given the clear distinction between the plant species of the past and those of the present, we suggest that a step forward in understanding paleo-plant physiology is through the development of a ‘whole plant’ conceptual model approach. This approach is based on the understanding that the physiology of plants is governed by the principles of biophysics and is influenced by the anatomical and architectural aspects of plants. It further considers phylogenetically shared attributes of physiology determined from modern plants, while undertaking explicit analysis of the anatomical and architectural aspects of the extinct plants themselves, based on material found in the fossil record. The wealth of paleobotanical material offers the opportunity to compare and contrast potential physiological function of Pennsylvanian taxa within and between phylogenetic clades, and can then be extended to ecophysiological characterization of the larger plant assemblages and paleobiomes. Understanding functional diversity is probably the only approach to delineating the limits of terrestrial plants to cycle

carbon and water (Cadotte *et al.*, 2009), particularly in paleoenvironments characterized by atmospheric compositions and environmental conditions different from the modern world (Feng *et al.*, 2014). Importantly, this approach is based on observations and inferences from the biome community members themselves, thus vastly improving confidence in the results.

III. Conceptual insights into paleoecophysiology

The quantitative ecology and ecophysiology of extinct plants have received much attention in the 20th and 21st centuries. Many approaches have focused on analysis of the NLRs of plants found in the fossil record. To date, most methods have managed the challenge of reassembling whole plants from isolated organs by focusing on isolated organs: individual stems or leaves. After Woodward’s (1987) pioneering work employing stomatal analyses to reconstruct atmospheric CO_2 concentration, dozens of publications have explored leaf-level gas exchange through analysis of fossilized stomata (e.g. McElwain & Chaloner, 1995; Edwards *et al.*, 1998; McElwain, 1998; Beerling & Royer, 2002; Konrad *et al.*, 2008; Franks & Beerling, 2009a,b; McElwain *et al.*, 2016a; Montañez *et al.*, 2016). Other work on leaves has explored changes in vein length per area (Boyce & Knoll, 2002; Boyce *et al.*, 2009) or stable isotopic (O, H, C) signatures of transpiration found in fossil leaves (e.g. Diefendorf

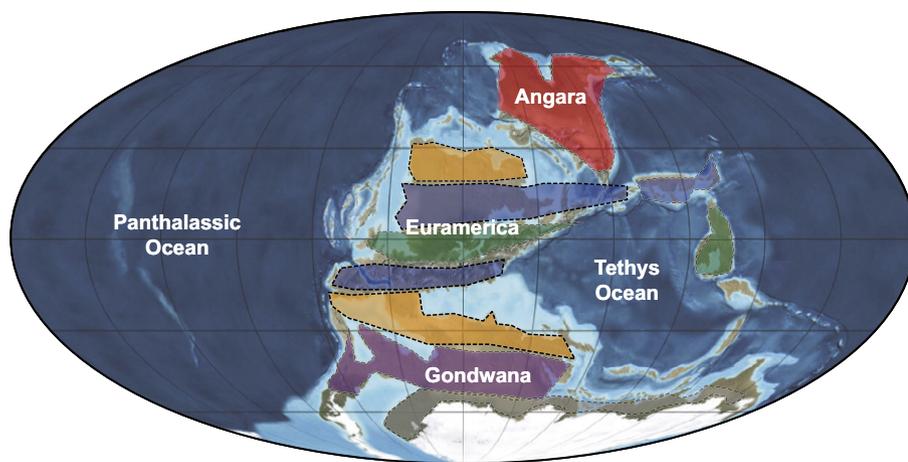


Fig. 5 Generalized diagram of Middle and Late Pennsylvanian biomes during a glacial phase. Green, tropical everwet forests; blue, subtropical forests, sometimes seasonally dry; orange, deserts; red, Angaran northern temperate forests dominated by *Ruffloria*; purple, southern hemisphere temperate forests; gray, tundra. Local vegetational dynamics were likely to be strongly influenced by topography and climate, including oceanographic influences. Paleogeographic map base from Blakey (<http://jan.ucc.nau.edu/rcb77/nam.html>).

et al., 2010; Hren *et al.*, 2010; Sachse *et al.*, 2012). Quantitative analyses of extinct plants have focused on their biomechanical properties (e.g. Rowe *et al.*, 1993; Rowe & Speck, 1998; Spatz *et al.*, 1998; Masselter *et al.*, 2007; Wilson & Fischer, 2011). Using biomechanical and biophysical principles, recent investigations of late Paleozoic plants have included analysis of extinct plant hydraulics (Cichan, 1986; Wilson *et al.*, 2008; Wilson & Knoll, 2010; Wilson & Fischer, 2011; Wilson, 2013; Strullu-Derrien *et al.*, 2014). Despite these efforts, there has been little to no whole-plant physiological work attempted, particularly for deep time, because there are significant obstacles to assembling the disparate parts of a plant (Wilson *et al.*, 2015). The following subsections review recent advances and attempts to integrate different organs into a ‘whole-plant model’ that can be employed for ecosystem modeling and ultimately integrated into Earth system models.

1. No single anatomical variable captures plant physiology

Generalizing expected physiological response to the environment, whether past, present, or future, based on individual anatomical features is important as a first step in developing a conceptual modeling of a complex system. In assessing the past, this may be out of necessity – simply because fossils have limited preserved physical and chemical information from which to adequately assess physiological processes. However, plants function as an integrated system of organs and physiological processes in a dynamic environmental context. This presents a singular problem for paleobotanical attempts to reconstruct physiology. As a complex system that is frequently preserved in the form of isolated organs, the whole-plant anatomy of fossil plants is rarely understood, even among extinct angiosperms with similar-looking extant relatives, despite remarkable fossil discoveries (e.g. Chloranthaceae reproductive structures; Friis *et al.*, 2015). One approach to resolving this taphonomic problem has been to identify an anatomical feature that can function as a proxy for the entire plant’s physiology (e.g. stomatal density, vein length per area). Although these traits record important aspects of plant physiology, it is

important to recognize that they are merely parts of an integrated physiological system that includes root, stem, and leaf tissues and their individual and collective functions. A full accounting of the physiology of an extinct plant ideally includes the whole plant or as much of the whole plant as can be accounted for (Fig. 6).

2. Whole-plant physiology – the ‘Mr Potato Head’ approach

The fossil record of extinct plants contains combinations of organs and physiological properties that have no modern extant analogs particularly among floras from the distant past. For example, medullosan stems had xylem composed of tracheids with resistance to water flow comparable to that of vessel-bearing secondary xylem (Cichan, 1986; Wilson *et al.*, 2008), but which also bore leaves with only modest vein lengths per area (Boyce & Zwieniecki, 2012; Raymond *et al.*, 2014) but highly conductive and abundant stomata (Montañez *et al.*, 2016). Reconciling these novel combinations of ecophysiological features can be done by applying a method that is similar to the children’s puzzle toy ‘Mr Potato Head’ (© Hasbro); in this model, parameters such as root area, stem xylem, branch architecture, vein length per area, stomatal frequency, and other factors are considered as components of an integrated system in which different values can be substituted. For example, in a medullosan ‘Mr Potato Head’ model, the root, stem, branch, and stomatal properties approach those of angiosperms, whereas the vein length per area is equivalent to that of extant gymnosperms – much like a toy with an ear substituted for a nose (Table 2). Using this method, unfamiliar combinations of anatomical structures can be understood individually and in their whole-plant context. An alternative conceptual model for nonanalog whole-plant physiologies is the nonanalog biomes of the Quaternary, where pollen analyses demonstrate unique species combinations which are not found anywhere in existence in the modern world (Williams & Jackson, 2007). The complete absence of a modern analog makes for a complex interpretation of their functioning and interaction/adaptation to the prevailing climate.

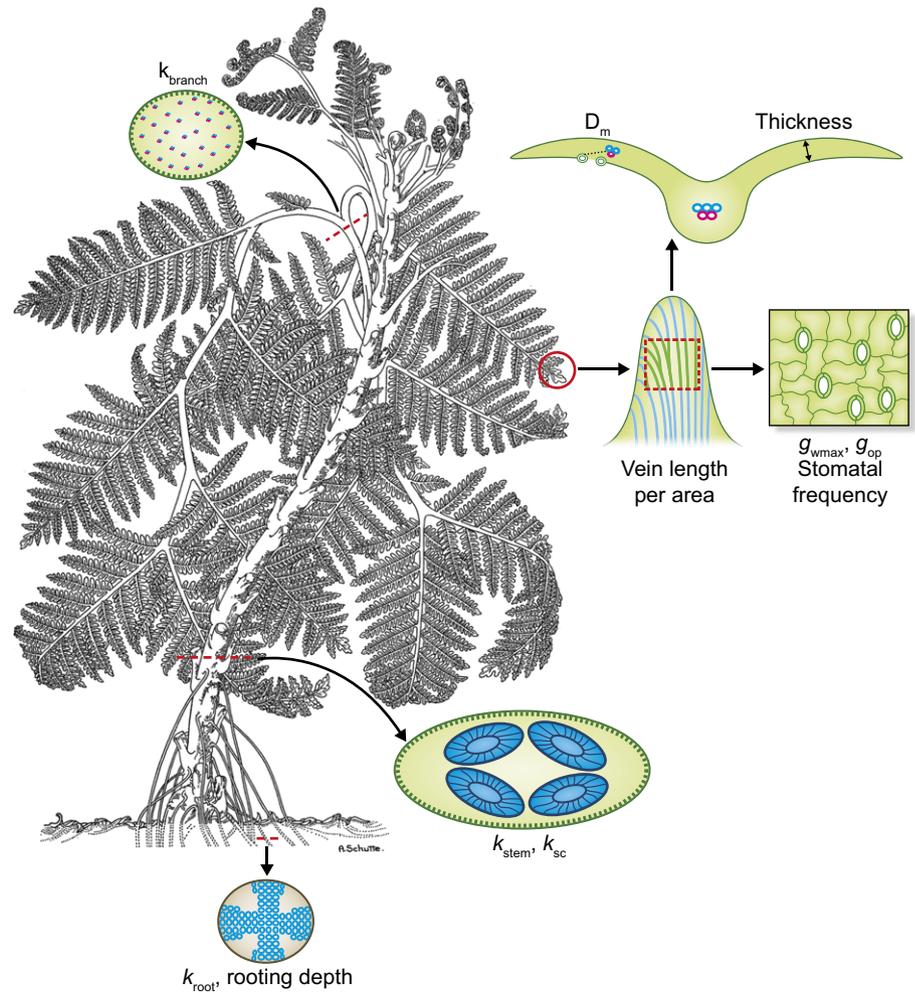


Fig. 6 Key plant parameters for reconstructing 'whole plant' water transport physiology against the backdrop of *Medullosa thompsonii* from Andrews (1945) with permission from Missouri Botanical Garden Press, St Louis, USA. From root to leaf: root anatomy can be used to determine rooting depth, and root xylem can be used to determine the hydraulic conductivity of roots (k_{root}). Stem anatomy and xylem anatomy, in particular, can be used to determine the hydraulic conductivity of individual tracheids (k_{sc}) and whole stems (k_{stem}). At the branch scale, the number of conduits and their individual hydraulic conductivity can be used to quantify the conductivity of a single branch (k_{branch}). Within leaves, the total vein length per unit leaf area is a component of the hydraulic constraints within a leaf, along with the stomatal density/index (stomatal frequency), maximum water vapor exchange of an individual stomatal complex (g_{wmax}) and its operational maximum (g_{op}), the mesophyll path length (D_m) and leaf thickness.

Table 2 Stem and leaf parameters for medullosans, *Cordaites*, and two gymnosperms: *Dioon edule* and *Ginkgo biloba*

	Tracheid diameter (μm)	D_v (mm vein mm^{-2} leaf area)	Stomatal aperture (μm)	Stomatal density (No. mm^{-2})
Medullosans	<i>Medullosa noei</i> root: 193 ± 51	<i>Neuropteris ovata</i> : 2.3 ± 0.36	<i>Neuropteris ovata</i> : 21–36	<i>Neuropteris ovata</i> : 184–277
	<i>Medullosa noei</i> stem: 142 ± 42	<i>Macroneuropteris scheuchzeri</i> : 1.87 ± 0.28	<i>Macroneuropteris scheuchzeri</i> : 19–31.5	<i>Macroneuropteris scheuchzeri</i> : 181–299
<i>Cordaites</i> sp.	25 ± 8.7	1.4–4.0	50	35
<i>Dioon edule</i>	45–50	2.2	22	90–100
<i>Ginkgo biloba</i>	40	1.2–1.6	11	170

Vein length per unit area (D_v) values for *Dioon edule* and *Ginkgo biloba* are from Boyce *et al.* (2009). Stomatal values for *G. biloba* are preindustrial values from Barclay & Wing (2016). *Medullosa noei* root tracheid diameters are from Steidtmann (1944), and other measurements are from Greguss (1968), Wilson *et al.* (2008), Wilson & Knoll (2010), and J. P. Wilson (unpublished).

3. Quantitative approaches to leaf water movement

Leaves are among the most abundant macrofossils and, consequently, have received the majority of attention from previous research focused upon extinct plant physiology. Review studies of modern and extinct plants and comparative methods have existed for some time (Beerling & Royer, 2002; Sack & Holbrook, 2006; Boyce *et al.*, 2009; Feild *et al.*, 2011; Willis & McElwain, 2016). With fossil leaf cuticles being relatively

abundant and well preserved as far back as hundreds of millions of years, maximum stomatal conductance has been frequently determined microscopically using measures of stomatal density, guard cell size, and aperture morphology and inferred pore depth (Fig. 6). However, this yields only an anatomically maximum conductance value that, operationally, must be constrained by environmental limits affecting opening and closing of the stomata if the actual gas exchange of the plant is to be estimated.

Recent work on early-diverging vascular plants has indicated an important role for stomatal behavior, in addition to stomatal size and frequency, in regulating overall leaf response to environmental stress. Particular emphasis has been placed on the differential response rate of lycophyte and fern stomata relative to the faster, active responses observed in angiosperm leaves. It has been suggested that lycophyte and pteridophyte guard cells are insensitive to ABA, with turgor pressure regulated solely by water loss (Brodribb & McAdam, 2011), which, in turn, is hypothesized to slow the leaf response rate to drought stress. If ABA insensitivity and slow leaf responses to drought stress are found throughout lycophytes and ferns, and are ancestral within the seed plants – including, perhaps, medullosans and cordaitaleans – then the ecologically dominant Pennsylvanian plants may have responded slowly to environmental stress as well. However, interpreting stomatal behavior from Pennsylvanian plants is challenging for two reasons: first, there is no leaf anatomical feature that is diagnostic for ABA insensitivity with preservation potential in the geological record, and second, many Pennsylvanian plants have a contrasting mixture of organ-level traits. For example, the Pennsylvanian giant arborescent lycophyte, *Lepidodendron*, and its closest living relative, the modern herbaceous *Isoetes*, and possibly *Selaginella* – frequently used in experimental studies for understanding *Lepidodendron* – are quite distinct from one another in size, morphology, and anatomy. *Lepidodendron* leaves bear numerous, conductive stomata but only a single leaf vein (e.g. Beerling, 2002) whereas medullosans combine high stem conductivity, high stomatal conductivity, and low vein length per area. Determining the stomatal behavior of extinct plants in the context of nonanalog plant anatomy and morphology remains a challenge.

Two methods could shed light on this question: viewing stomatal control in the context of cavitation vulnerability and observations from molecular biology. Plants that are predicted to have high vulnerability of xylem to cavitation based on abundant pits and tracheid diameters may have required active control over stomatal closure in order to coordinate leaf and stem resistance to drought stress, as theorized by Sperry *et al.* (2002). Molecular biological insights may provide additional lines of evidence. Key intermediate proteins responsible for binding and response to ABA in guard cells have been found to exist – and retain functionality – in bryophytes, leading to some speculation that dynamic stomatal control may have evolved and existed earlier than previously thought (Chater *et al.*, 2011). However, more recent molecular studies suggest that the original function of ABA response genes may have been for sex determination within the gametophyte of ferns, perhaps becoming coopted later within the guard cells of seed plants as part of the dynamic stomatal control response system (McAdam *et al.*, 2016). Environmentally restricted stomatal conductance in modern plants because of light, CO₂, and drought conditions (Hetherington & Woodward, 2003) may be considered potentially more physiologically similar to extinct plants where sufficient genetic evidence exists (e.g. Doi *et al.*, 2015). Combining biophysical evidence, geochemical analysis, and insights from molecular biology may clarify the history of fast vs slow stomata in extinct land plants.

Recognition of the importance of mesophyll conductance (g_m) in many living plants (Raven, 1998; Niinemets, 1999; Flexas *et al.*, 2012; Tosens *et al.*, 2016) presents an additional challenge because mesophyll is infrequently preserved in fossil leaves. Recent work has looked toward the application of finite element modeling or diffusion equations to quantify paleo-gas exchange using anatomical parameters derived from fossilized stomata (Konrad *et al.*, 2008; Franks *et al.*, 2014; McElwain *et al.*, 2016b; Veromann-Jürgenson *et al.*, 2017). This involves modeling stomatal conductance to water vapor and CO₂ with mesophyll resistance ($1/g_m$) as an assumed conservative fraction of stomatal conductance (McElwain *et al.*, 2016a). Although the value of g_m is often experimentally derived, it is also related to cellular morphology such as cell wall thickness (Tomás *et al.*, 2013; Tosens *et al.*, 2016) as a function of diffusional distance of CO₂ within and between cells (Tholen & Zhu, 2011). Given that extant spore-bearing and gymnosperm species show thicker cellular features, tightly packed mesophyll (Veromann-Jürgenson *et al.*, 2017), and smaller substomatal air-filled spaces (Brodribb *et al.*, 2010), defining g_m through fossil anatomical features is important, particularly for the Paleozoic, as an evolving constraint on leaf gas exchange.

Additional studies of leaves have explored the role of vein length per area and leaf architecture on the evolution of plant physiology (Fig. 6). The high vein length per area values seen among some angiosperm lineages has led to the hypothesis that diffuse leaf development among angiosperms minimized the distance between veins and substomatal chambers, thus increasing short-term replacement of transpired water from leaves (Boyce *et al.*, 2009; Boyce & Lee, 2010; Brodribb & Feild, 2010; Feild *et al.*, 2011). These reports are grounded within comparative study of leaf hydraulics through analysis of microfluidic devices, which demonstrate that close proximity between hydraulic conduits and sites of evaporation increases simulated leaf hydraulic capacity (Noblin *et al.*, 2008). However, vascularization of leaves is only one part of leaf hydraulics; at the cellular scale, symplastic and apoplastic water movement is regulated by aquaporin type and density in plasma membranes (Morillon & Chrispeels, 2001; Prado & Maurel, 2013). Key aquaporins in the model bryophyte, *Physcomitrella patens*, have been shown to be very diverse when compared with shared protein families in *Arabidopsis thaliana* and *Zea mays* (Danielson & Johanson, 2008). These results indicate derived extravascular water regulation in plants that diverged early in land plant evolution.

In light of these previous studies, the hypothesized morphological simplicity (e.g. low leaf vein density) and simple developmental capacity of early vascular plants' leaves, when compared with the leaves of extant tropical angiosperms (high vein length per unit area, D_v), have led to the conclusion by some (Boyce *et al.*, 2010, 2017) that no extinct plants were capable of functioning at the 'modern' amounts of transpiration and assimilation found within extant angiosperms that dominate the planet today. If the hypothesis that leaf morphological simplicity must translate into whole-plant physiological simplicity is true – that is, if *Lepidodendron* functioned as a 30-m-tall *Isoetes* based on low vein length per area – then Paleozoic plants did not possess a high capacity to influence their local to global environment through photosynthesis or

transpiration at a value equivalent to modern angiosperm tropical forests.

Leaves, however, are not the only organs in land plants. A more comprehensive model of the gas-exchange and photosynthetic capacity of extinct plants must account for the whole-plant physiology. The fossil record contains abundant anatomical and morphological complexity through the 100 million yr that separate the earliest vascular plants from *Medullosa*, strongly implying that the ecological and evolutionary pace of Paleozoic terrestrial ecosystems was not static, and this complexity can be measured and assessed in a quantitative way.

4. Quantitative approaches to stem water movement

Although much attention has been focused on the terminal portion of the water transport pathway (i.e. the leaves), the role played by stems in facilitating water transport from roots is a relatively understudied area – in living and fossil plants – and may explain differences in species adaptive characteristics growing under similar water stress conditions (Johnson *et al.*, 2011). Structural characteristics of stem-conducting tissue reflect the biophysical compromises between the opposing functions of the xylem: the need to supply water at the same rate of loss from transpiration without loss of function through vessel cavitation (Manzoni *et al.*, 2013). Stem hydraulics directly affect daily canopy conductance, generally reducing midday stomatal conductance (Zhang *et al.*, 2013). Thus, at the level of an individual plant, stem tissue conductance is a central constraint limiting maximum conductance of a canopy, based on leaves and stomatal features. It is a well-documented feature of trees that stem storage of soil water is an essential intermediate pool for use by canopy leaves to replace water lost daily through transpiration (Tyree & Ewers, 1991; Holbrook, 1995), yet this is rarely discussed as a limiting factor in leaf-focused studies. Notably, the fossil record of stem anatomy is rich, permitting quantification of plants' stem properties which, in turn, shed light on the functional morphology and architectural tradeoffs among extinct plants.

The first major quantitative advance to the study of water transport, with particular emphasis on stems, was articulated in 1948: that water transport, being driven by the evaporative gradient between leaf tissue and the atmosphere and passing through empty cells, should function in a fashion analogous to Ohm's law (van den Honert, 1948). These observations were elaborated upon in the 1970s and 1980s (Zimmermann, 1983) and the predicted inverse relationship between hydraulic efficiency and cavitation resistance was validated using the centrifuge method on excised segments of living plants (Tyree & Sperry, 1989; Tyree & Ewers, 1991; Comstock & Sperry, 2000). Modeling advances in the last two decades, coupled with refined parameters from experimental analyses, significantly expanded the methods available to account for variation in longitudinal morphology, conduit wall thickness, pit structure, and connectivity (Lancashire & Ennos, 2002; Choat *et al.*, 2004, 2006, 2008, 2011; Hacke *et al.*, 2004; McCulloh *et al.*, 2004; Sperry & Hacke, 2004; Jansen *et al.*, 2007, 2009; Choat & Pittermann, 2009; Pittermann *et al.*, 2010; Brodersen *et al.*, 2014).

Recent work has focused on the hydraulic conductivity of early vascular plants such as the paleobotanical icons *Medullosa* and *Cordaites* (Wilson *et al.*, 2008, 2015; Wilson & Knoll, 2010; Wilson & Fischer, 2011; Wilson, 2013). These analyses employ tracheid morphology parameters, including diameter and length, in addition to information about pit type, frequency, and porosity, thereby accurately reflecting the key hydraulic constraints in xylem cells (Fig. 6). These studies have demonstrated that xylem cells conferring high stem hydraulic capacity – comparable to the conductivity of angiosperm vessels – evolved independently in several Paleozoic lineages, including the medullosans and calamitaleans in the Pennsylvanian tropical wetlands (Wilson *et al.*, 2008; Wilson & Knoll, 2010; Wilson, 2013, 2016). They further document that, at the same time, extinct coniferophytes from both wet and seasonally dry ecosystems with dense, pycnoxylic (low amounts of parenchyma) xylem, such as cordaitaleans, occupied what, in the modern world, is the conifer portion of the hydraulic ecospace. Therefore, at the origin of the coniferophyte clade, early-diverging coniferophytes already occupied that portion of the hydraulic landscape occupied by modern members of the same lineage.

5. Quantitative approaches to root water movement

Root fossils are commonly found in the fossil record, especially in paleosols. Fossil roots provide yet another part of the plant hydraulic system that can be characterized in considerations of physiological constraints on gas exchange (Fig. 6). Vascular plant root systems, including those assignable to lycophytes, are known from the Early Devonian, and those roots have been considered to be derived through division of the shoot apical meristem, followed by gravitropic growth, but recent fossil discoveries have demonstrated complex patterns of lateral branching and interaction with soil environments (Matsunaga & Tomescu, 2016; Xue *et al.*, 2016; Hetherington & Dolan, 2017). Well-preserved fossils suggest that the earliest vascular plants may have borne two types of roots: root axes that are homologous to stem axes, and small, laterally branched, nongravitropic organs specialized for absorption and stabilization like extant root systems (Matsunaga & Tomescu, 2016). Euphyllophytes are thought to have evolved roots independently, and recent fossil discoveries have demonstrated that several taxa developed extensive root systems from root thickenings ('rootballs') (Soria & Meyer-Berthaud, 2004; Giesen & Berry, 2013). Three-dimensional complexity of root systems diversified dramatically among plant taxa during the Devonian with a well-developed rhizosphere emerging soon after terrestrialization (Willis & McElwain, 2016). Branching in roots of early land plants increased access to water and nutrients (e.g. calcium, phosphorus) which, in turn, increased growth rates by permitting higher atmospheric CO₂ assimilation (Morris *et al.*, 2015). By the Pennsylvanian Subperiod, arborescent plants, such as cordaitaleans and arborescent lycophytes, had extensive root systems, with interpreted tap root systems reaching depths of up to 1 m in soils (Davies & Gibling, 2011; Hetherington *et al.*, 2016), extensive root systems further attested to by the abundance of roots that are anatomically preserved in coal ball material. Pennsylvanian plants

with other novel anatomical features feature roots that are more familiar in organization, development, and anatomy; medullosan pteridosperms, for example, feature roots with a eustele and wide tracheids (Steidtmann, 1944).

Homology between Paleozoic Era plant root systems and stem systems permits the quantification of root hydraulic transport rates, even if the organs themselves are derived from unfamiliar developmental mechanisms. Although not yet utilized, dimensions from these fossil roots can provide the basis for estimating limits to water use by plants based on the established relationship between root area and water flux (q , kg s^{-1}) where:

$$q = \frac{4Lv\pi r}{r(1-n)} \left[\ln \left(\frac{2Lv\pi r^2}{2v} \right) \right]^{-1} kd\Psi$$

in which L is the mean root length (m), v is the rooting depth (m), r is the mean root radius, n is a factor associated with soil type, k is the soil and root surface hydraulic conductivity ($\text{kg s}^{-1} \text{m}^{-3}$), and $d\Psi$ is the difference in the soil and root surface water potentials (Pa) (Campbell, 1991; Ogle *et al.*, 2004). Ignoring $kd\Psi$ in this equation, the remainder becomes a scalar to evaluate the separate and combined effects of root size and soil density on potential water absorption and transpiration. Employing quantitative, physical models such as these in studies where stem and root fossils are found intact and in place provides a new and intriguing means for assessing the evolution of root constraints on plant water availability (cf. Holmes & Galtier, 1976; Hueber & Galtier, 2002; Soria & Meyer-Berthaud, 2004; Hao *et al.*, 2010).

Using models and methods similar to those employed for stems, the preserved vascular tissue from roots permits reconstruction of conduit-specific hydraulic conductivity values (J. P. Wilson, unpublished). Generally, roots are much more conductive to water than stems. In comparison to stems, there is evidence that vessel cellular properties in roots, including cell wall thickness and lumen diameter – commonly used to determine probability of cavitation – are better correlated with overall stem vessel conductivity (Pratt *et al.*, 2007) than relationships derived from stems. The forest- and regional-scale effects of roots on soil hydraulic properties are profound: in addition to water movement within plants, roots redistribute water within soil profiles, which for large forested regions can have profound effects on atmospheric hydrologic cycling (Lee *et al.*, 2005).

IV. High-productivity Carboniferous plants

Several independent lines of analysis point toward the capacity for high hydraulic supply to leaves and high photosynthetic rate among lineages of Pennsylvanian plants. Process-based ecosystem modeling of canopy average and maximum sunlit assimilation suggest photosynthetic rates of a medullosan forest stand between 9 and 16 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ using fossil-derived stomatal conductance under a range of late Paleozoic $\text{O}_2 : \text{CO}_2$ values (Fig. 8; Montañez *et al.*, 2016). Independent analysis of hydraulic path length and leaf hydraulic capacity (K_{leaf}) in anatomically preserved medullosan leaves further suggests high maximum photosynthetic rates (11–16 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Medullosans have single-tracheid

conductivity values that approach those observed in some tropical angiosperms reflecting their large tracheid diameters (up to 250 μm) and abundant pits. Large (e.g. 37 \times 20 μm per guard cell) and relatively abundant (stomatal index between 10 and 25) stomata on medullosan foliage support a modeled high stomatal conductance based on scaling relationships between g_{max} and assimilation rate for a range of species of varying vein density (A to g_{max} in Fig. 5; McElwain *et al.*, 2016b). In sum, a paleoecophysiology characterized by high photosynthetic rates is supported by medullosan stem hydraulics, leaf and frond architecture, hydraulic path length, and stomatal conductance (Figs 5, 7, 8). Conversely, low conductance and low photosynthetic rates are inferred when focused only on vein length per area.

The broadleaved coniferophyte *Cordaites*, now extinct, also functioned with a physiology that is distinct from its NLRs *Ginkgo biloba*, the gnetales and crown-group conifers. Hydraulic conductivity of cordaitalean tracheids is comparable to the conductivity observed in extant conifers despite the presence of torus-margo pits among modern representatives. *Cordaites* achieved an equal conductivity through the presence of multiple circular-bordered pits on the radial walls, which lowered the resistance of its wood at the cost of decreased safety from air-seeding. Broad cordaitalean leaves with multiple parallel veins in close proximity to stomata suggest a maximum photosynthetic rate of nearly 11 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, although lower values were probably more

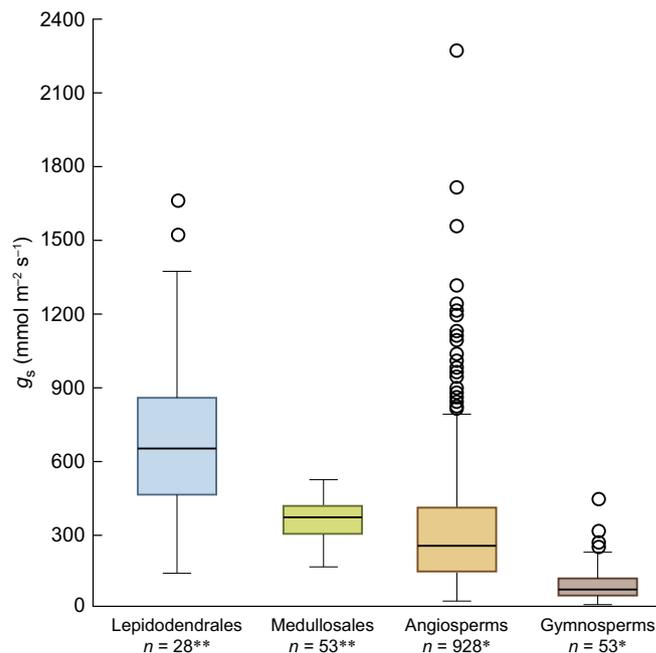


Fig. 7 A comparison of measured stomatal conductance (g_s) from a global survey of vegetation from Maire *et al.* (2015) (*) with estimated operational g_s (** this study) for keystone taxa of the Carboniferous tropical wetland forests. g_s was estimated from measured g_{max} values from Montañez *et al.* (2016) by assuming that $g_s = 0.25 (g_{\text{max}})$ following the observation of McElwain *et al.* (2016b) and Franks *et al.* (2014). Box lower bound, horizontal line, and upper bound define the 25th, median, and 75th percentile of data, respectively; whiskers define c. 1st and c. 99th percentiles of data; circles are outliers. Medullosan stomatal conductance and lycophyte stomatal conductance are high because of high stomatal frequency and/or large stomata.

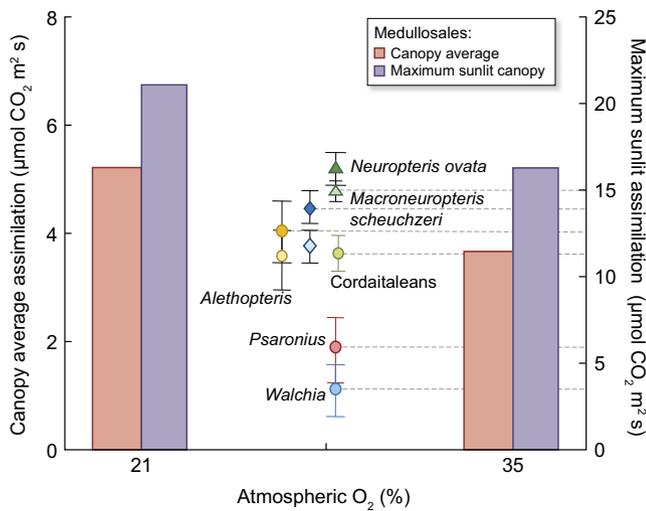


Fig. 8 Modeled and empirically inferred carbon dioxide assimilation for major Carboniferous plant groups. Simulated values using BIOME BGC v.4.2 are shown as maximum sunlit canopy (purple bars) and net canopy average values (red bars) and were modeled for 400 ppm CO₂ and range of hypothesized atmospheric pO₂. Empirically derived photosynthetic assimilation rates are shown as average values (colored outline symbols ± 2 SE) and were made using the scaling relationship between g_{max} and assimilation rate (solid color symbols; McElwain *et al.*, 2016b) and vein-to-stomata distance and its empirically determined relationship K_{leaf} and A_{max} (Brodrribb *et al.*, 2007).

Table 3 Maximum stomatal conductance (g_{max}) values for various extinct Carboniferous–Permian taxa

Representative taxa	Average g _{max} (mol m ⁻² s ⁻¹)	± 1σ (mol m ⁻² s ⁻¹)
Medullosales (medullosans)	3.7	3.5
<i>Sphenophyllum</i>	0.4	0.2
Lepidodendrales (lycopsids)	4	1.8
Cordaitales (cordaitaleans)	2.4	3.1
Ferns (mostly marattialean tree ferns)	0.3	0.3

representative of dryland specimens (Fig. 8). These results approximate maximum photosynthetic rates found within the broadleaved gymnosperm *G. biloba* (9 µmol CO₂ m⁻² s⁻¹), which is noteworthy as one of the few living gymnosperms with pycnoxylic wood, broad leaves and parallel, but dichotomous, venation – similar to features found in *Cordaites*. Root xylem of wetland *Cordaites* were highly conductive, with secondary xylem containing multiseriate circular-bordered pits along the radial walls (J. P. Wilson, unpublished). Taken together, the cordaitalean whole-plant physiology (roots, stems, and stomata) supports a model that is distinct from their distant, living relatives *G. biloba*, the gnetales, and crown-group conifers and closer to early-diverging angiosperms.

The extinct arborescent lycophytes remain a physiological enigma. The abundance of lycophyte reproductive and vegetative structures throughout the first two-thirds of the Pennsylvanian SubPeriod and lack of juvenile specimens have been interpreted as supporting rapid growth rates and, presumably, high

photosynthetic rates (Cleal & Thomas, 2005), but alternate interpretations are possible (Boyce & DiMichele, 2016). However, some lycophytes contain high frequencies of stomata on their leaves (e.g. 450 stomata mm⁻² in *Lepidodendron dichotomum*), despite a relatively small stomatal index, because of below-average epidermal cell size, resulting in estimated g_{max} values of 2.7–8.3 mol m⁻² s⁻¹ (Fig. 7; Tables 2, 3; Montañez *et al.*, 2016). Furthermore, the small amount of secondary xylem found in lycophyte stems is more conductive than would be expected, with tracheids larger than typical seed plants and occasionally exceeding 80 µm in diameter (Cichan, 1986; J. P. Wilson, unpublished). Further tests of these hypotheses at the whole-plant scale are necessary to determine the physiology of lycophytes, but a photosynthetic rate exceeding that of the lycophytes that are frequently subject to experimental and physiological analysis (i.e. *Selaginella* and its close relatives; *Selaginella longipinnae* (A_{max} = 6.15 µmol CO₂ m⁻² s⁻¹); *Selaginella pallescens* (A_{max} = 1.689 µmol CO₂ m⁻² s⁻¹); Brodrribb *et al.*, 2007) is likely.

Whole-plant analysis of these plants and other Pennsylvanian paleobotanical icons yields an insight into landscape-scale and physiological processes. When aspects of leaf and stem biology are integrated, plant stress resistances can be defined that elucidate ecological strategies. For example, high stomatal conductance in medullosans, combined with the limited ability of stem tracheids to resist cavitation and embolism, implies a physiology that was resistant to stress from low atmospheric pCO₂ characteristic of the deepest interglacial episodes (Montañez *et al.*, 2016). Avoiding low-pCO₂ stress was accomplished by moving large volumes of water to leaf surfaces, permitting stomata to remain open and, thus, allowing large volumes of gas exchange. However, the same features that permitted a high hydraulic supply to leaves and increased volumes of gas exchange simultaneously increased medullosans' vulnerability to drought stress (Fig. 9). Conversely, the mechanically reinforced tracheids of cordaitalean stems and limited stomatal conductance, relative to medullosans, imply that the cordaitaleans possessed substantial drought stress resistance at the cost of vulnerability to carbon dioxide limitation at low atmospheric CO₂ concentrations.

Under identical environmental conditions, water-use efficiency modeled using BIOME-BGC v.4.2 predicts major differences between the dominant Pennsylvanian plants (Fig. 10; Montañez *et al.*, 2016). *Medullosa* and *Psaronius* had four and six times the water-use efficiency of *Lepidodendron*, respectively; this difference reflects elevated photosynthetic rates in the medullosans and more conservative stomatal conductance in the tree ferns. Such distinct physiological capabilities between lycophytes and tree ferns result in significant effects on the landscape by producing major changes in transpiration and surface runoff as the tree ferns replace lycophytes at the MLPB. For example, for the MLPB ecological threshold, the replacement of lycophyte-dominated wetlands by tree fern-dominated wetlands resulted in a 50% decrease in evapotranspiration, from 7.57 × 10⁻⁹ to 3.88 × 10⁻⁸ m³ s⁻¹ (cms). A reduction in evapotranspiration of this magnitude would have resulted in a 50% increase in surface runoff, assuming no net change in precipitation, which probably affected physical and chemical weathering in Pennsylvanian landscapes, perhaps

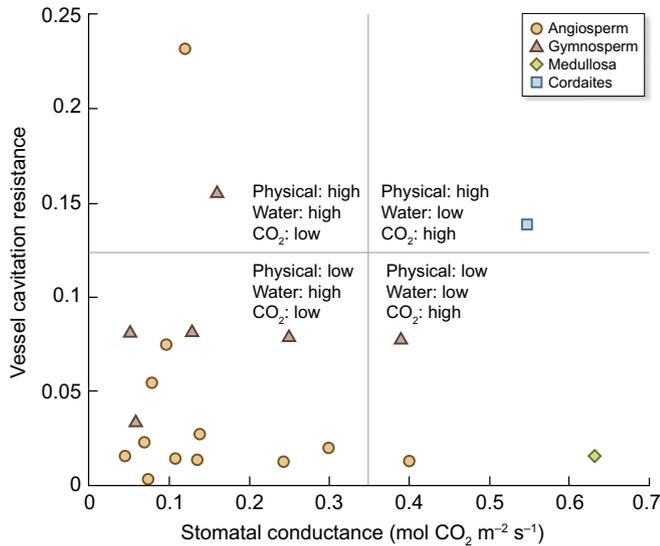


Fig. 9 Modeled leaf and stem hydraulic features of Pennsylvanian genera *Cordaites* and *Medullosa* in comparison to living gymnosperms and angiosperms. Stomatal conductance to CO_2 is on the x-axis (based on Day *et al.*, 1991; Loreto *et al.*, 1992, 2003; Picon *et al.*, 1996; Auge *et al.*, 2000; Day, 2000; DeLucia *et al.*, 2003; Dang & Cheng, 2004; Bota *et al.*, 2004; Herrick *et al.*, 2004; Ethier *et al.*, 2006; Zazzaro, 2006; Galmé *et al.*, 2007; Niinemets *et al.*, 2009; Montañez *et al.*, 2016), and the stem resistance to cavitation (defined as the square of thickness-to-span of xylem-conducting cells) is on the y-axis (stem vessel thickness based on Donaldson, 1983; Cato *et al.*, 2006; Rathgeber *et al.*, 2006; Sun *et al.*, 2006; Wilson *et al.*, 2008; Hacke & Jansen, 2009; Ramírez *et al.*, 2009; Domec *et al.*, 2010; De Micco *et al.*, 2008, 2016; Carvalho *et al.*, 2015). Labels in quadrants refer to qualitative stress tolerances of components, where 'physical' refers to structural stress based on wood strength, 'water' refers to drought, and 'CO₂' refers to atmospheric supply.

ultimately increasing nutrient concentrations in littoral environments (Figs 2, 10).

1. Nonuniformitarian combinations of organ-level anatomy and morphology

What anatomical features permit us to infer high photosynthetic and transpiration rates? In short, nonuniformitarian anatomy across the whole plant. Large tracheids are found within Pennsylvanian-age seed plants (particularly and notably medullosans) and spore-bearing plants, notably including *Sphenophyllum*, a sphenopsid. Some of the arborescent lycophytes may fall into this category as well. Leaves of many Carboniferous plants contain stomata at relatively high densities and with larger sizes, leading to higher g_{max} values than many of their NLRs (Tables 2, 3; Wilson *et al.*, 2015). Moreover, uncompressed fossil leaves preserved in coal balls tend to be quite thin from top to bottom, frequently < 2 mm thick, which places stomata in close proximity to vascular tissue even at low vein lengths per unit area. Finally, large leaf areas are notable for *Psaronius*, *Cordaites*, and *Medullosa* (e.g. Laveine, 1986), and, when combined with highly efficient xylem, result in Huber values (leaf area : sapwood area ratios) that are comparable with values found in extant tropical angiosperms.

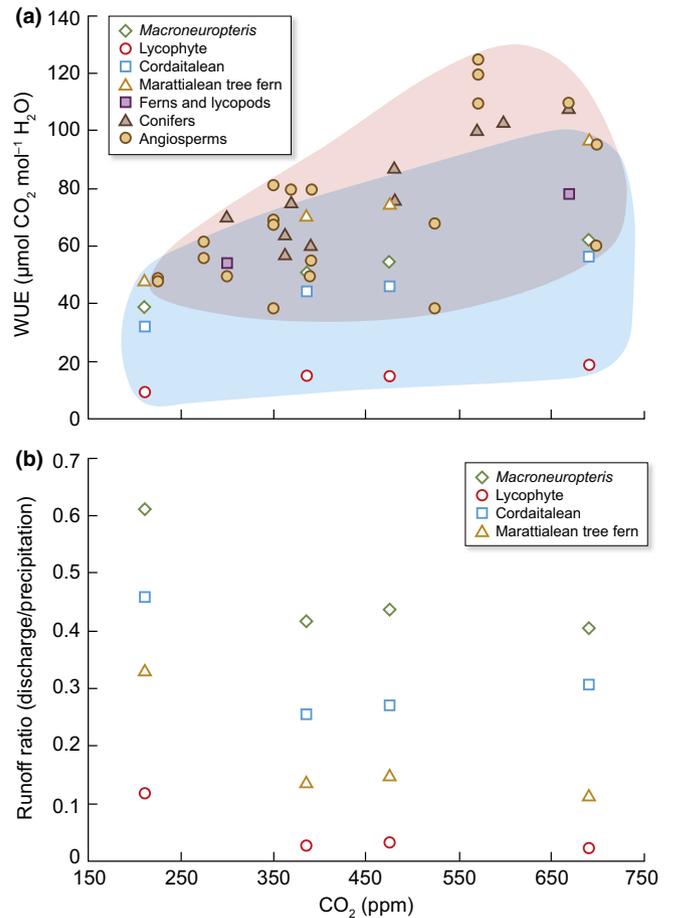


Fig. 10 Intrinsic water-use efficiency (WUE) for modern and Carboniferous plants and modeled surface runoff ratios for the Carboniferous. (a) Intrinsic WUE values for modern (closed symbols, delineated by pink shading) and dominant Carboniferous taxa (open symbols, delineated by blue shading) over a range of atmospheric $p\text{CO}_2$. Modern values are derived from various CO_2 enrichment studies; paleo-values are from BIOME-BGC v.4.2 simulations utilizing fossil leaf morphology and nitrogen composition. (b) Modeled runoff ratio, calculated from simulated discharge to input precipitation for Carboniferous taxa over the same range of atmospheric $p\text{CO}_2$ values.

2. Using whole-plant modeling to develop and test 'paleo-plant' hypotheses

Whole-plant reconstructions play a key role in quantifying the evolutionary history of plant physiology by developing and testing hypotheses for extinct plants, based on data from those plants themselves, rather than on parameters inferred from NLRs. Such studies place quantitative constraints on the influence of terrestrial plants in shaping the Earth's climate history. If assimilation rates can be derived, then gas-exchange models can be used in an inverse method to quantify the ambient CO_2 concentrations and further refine leaves as paleo- $p\text{CO}_2$ proxies (Franks *et al.*, 2014; McElwain *et al.*, 2016a, 2017; Montañez *et al.*, 2016; Franks & Royer, 2017). Second, using fossil-derived parameters to derive key water-transport constraints from root-to-leaf-to-water permits paleobotanists to 'revive' extinct species. Process-based, mechanistic models that rely on biophysics provide a reality check on

predictions made by whole-plant reconstructions. Basic principles affecting heat, mass, and momentum transfer must also be considered given the dynamic range of Earth's atmospheric composition over the period that vascular plants have existed. Dynamic simulation modeling, in particular, is critical for understanding the coordination of processes, such as water transport by different parts of plants, under different climate and environmental conditions.

Ongoing work to understand the functional limits of extinct plants using process-based models is important for helping us to better understand physiological (plant) forcing of past climate through its influence on the water and carbon cycles. Using key parameters derived from fossil plants, basic aspects of physiology specific to particular Pennsylvanian plant taxa can be quantified, such as the effects on stem and root vascular tissue cavitation resulting from the evaporative demand placed on leaves (Fig. 9). This leads to understanding of ecological feedbacks, such as increased or decreased total leaf area affecting canopy evaporative demand, that are constrained by stem and root water supply. Because leaf area limits are confined within a climate-environmental envelope, air-seeding thresholds of the stem and root tissue may be determined, in turn helping to elucidate whether stomatal closure in Paleozoic plants was passive or active as a function of vascular safety margin in leaves. If the leaf safety margins are low, then 'fast' or 'sensitive' stomata are required to prevent lethal amounts of water loss. If the safety margins are high, slower or ABA-insensitive stomata are permitted.

V. Lessons learned

1. Whole-plant methods are critical

A paleoplant view should account for all of the anatomical features of a plant functioning in an integrated system. For example, stomatal conductance has to be scaled to both leaves and stems; these organs determine the functional limits of stomata. Leaf-specific parameters, including vein length per unit area, should be considered within their anatomical and organographic context, including but not limited to mesophyll path length, leaf thickness, and leaf area. To determine leaf area, leaves and branches have to be scaled to stems and roots. Finally, plants themselves must be situated within their own environment, including the climatic and atmospheric conditions of the time.

2. Long evolutionary branches

The evolutionary distance between Carboniferous plants and their NLRs is large. Over 300 million yr, these divergences between the lycophytes, sphenopsids and stem group marattiale ferns, pteridosperms, and stem group gymnosperms and conifers are nested deep within the vascular plant tree (Fig. 1). Employing the lycophyte (*Selaginella*), which is most frequently analyzed as an NLR, to compare with *Lepidodendron* is a suboptimal strategy. An improved method would begin by reconstructing the whole hydraulic pathway in a Carboniferous plant and then choosing an equivalent with similar physical and physiological characteristics,

rather than relying solely on an NLR or an ecological and/or ecophysiological equivalent that has no phylogenetic relatedness *sensu* McElwain & Chaloner's (1995) NLE approach.

Carboniferous plants have complex physiologies that bear little resemblance to their NLRs as a consequence of anatomical, morphological, and developmental differences. The large size of lycophyte stomata, despite the limited water-transport tissue found throughout the stem and leaves, results in a whole-plant physiology that is akin to a slow-growing seed plant, such as a cycad. However, even extant relict gymnosperms, such as cycads, contain taxa that exhibit fast-growing features: extant cycad stomata show closing behaviors more similar to modern grasses and crop than to their closest extant relatives, conifers and *G. biloba* (Elliott-Kingston *et al.*, 2016), and some cycads produce new leaves at a high rate (*Lepidozamia peroffskyana*). Cordaitaleans, sphenopsids, and medullosans have whole-plant physiologies that are comparable with mesic, shrubby dicot and monocot angiosperms, respectively. As a whole, we hypothesize that Carboniferous pteridophytic (spore-bearing) vascular plants are like extant gymnospermous seed plants, and Carboniferous seed plants compare with angiosperms, particularly basal angiosperms and monocots.

VI. The big picture: an active role for early forests in Late Paleozoic climate

Significant vegetative forcing of the hydrologic cycle is a novel implication of widespread Pennsylvanian tropical forests that included dominant tropical elements with assumed slow or passive stomatal control but with the capacity for high transpiration (e.g. lycophytes or *Psaronius*). Medullosans and *Psaronius*, for example, could have transpired large volumes of water but, if passive stomatal control is widespread among pteridosperms and pteridophytes, also could have been slower to respond to environmental changes than angiosperms with the same leaf area. Such an unusual (compared with today) coupling of physiological behavior could have dramatically altered climate and surface conditions on local, regional, and global scales during the repeated turnovers in vegetation, especially given the associated dynamic fluctuations in atmospheric CO₂ (Montañez *et al.*, 2007, 2016). Modeling studies of modern and future climate reveal that physiological responses of terrestrial vegetation to increasing CO₂ concentrations and/or water stress can feed back on regional surface temperatures, hydroclimate, and terrestrial C sequestration, which, in turn, can translate into much broader-scale changes in climate, continental runoff, and atmospheric greenhouse gas concentrations (Betts *et al.*, 2007; de Boer *et al.*, 2011; Gedney *et al.*, 2006; Nugent & Matthews, 2012; Skinner *et al.*, 2016; Swann *et al.*, 2012).

We hypothesize that if the aforementioned significant differences in leaf conductance and hydraulic capacity (Fig. 10a) existed among late Paleozoic plant groups then repeated turnovers in plant composition, architecture, and structure at the eccentricity to million-year scale (e.g. the biome shifts of Fig. 2) would have led to substantial change in the degree of physiological forcing of the hydrologic cycle and climate during key intervals of the LPIA. Paleobotanical observations and quantitative inferences coupled with process-based ecosystem modeling indicate that replacing

tropical wetland forests dominated by lycophytes, with high g_{\max} (average of $4.0 \pm 2.0 \text{ m m}^{-2} \text{ s}^{-1}$), with those dominated by marattialean tree ferns and cordaitaleans, with lower g_{\max} (average of $0.3 (\pm 0.3)$ and $2.3 (\pm 3.1) \text{ m m}^{-2} \text{ s}^{-1}$, respectively) would have caused a 200+% increase in surface runoff relative to received precipitation when holding climate constant (Fig. 10b). The consequent increased fluvial and groundwater discharge to coastlines would have perturbed nutrient supply and productivity, the efficiency of the marine biological pump, and ultimately carbon cycling between the Earth's surface C reservoirs (cf. Steinthorsdottir *et al.*, 2012; Fig. 2). Changes in the terrestrial component inevitably influence the marine realm as the components of the Earth system are fully interconnected.

Unique to Earth's penultimate icehouse, *c.* 300 Ma, anomalously high $\text{O}_2 : \text{CO}_2$ ratios and $p\text{O}_2$ concentrations (up to 26–30%) undoubtedly further influenced plant characteristics and gas exchange, and, in turn, surface environmental conditions (cf. Beerling & Berner, 2000; Poulsen *et al.*, 2015). Elementary analysis of gas exchange under atmospheric $p\text{O}_2$ of up to 25% leads to the expectation of higher photorespiration burdens on Carboniferous plants, perhaps even limiting terrestrial plant productivity (Beerling *et al.*, 2002). There is, however, no evidence to support such a hypothesis – Pennsylvanian plants survived and diversified without the evolution of carbon-concentrating mechanisms such as C_4 photosynthesis. The biological adaptations or environmental conditions that permitted plants to evade this biochemical constraint have been explored for some taxa such as lycophytes (Green, 2010) but await further investigation. Rather, we hypothesize that for specific intervals of the Carboniferous and early Permian, characterized by very low $p\text{CO}_2$ (< 300 ppm) and high $p\text{O}_2$, the unique atmospheric composition would have differentially affected the gas-exchange capacity, photosynthetic physiology, and water-use efficiency of plant groups and thus their ecological competitiveness (Montañez *et al.*, 2016). Therefore, ecophysiological reconstructions of these extinct plant communities and their potential to feed back on surface environmental conditions, atmospheric greenhouse gas composition, and climate must consider the full range of atmospheric composition.

Plant adaptation to environmental forcing and scaling to ecosystem and biome responses is complex, involving the interplay of many biological and environmental conditions that can be challenging to quantify. In this review, we highlight the multiple facets of physiological functioning of extinct plants that can be quantitatively constrained and argue the importance of integrating them into 'whole plant' physiology reconstructions. Ultimately, major progress in our understanding of climates and the biosphere of the deep past requires a systems-based approach in which plants are a focal point given their dynamic interface with surface environments. Such an integrated 'systems' perspective must be built on a foundation developed using process-based ecosystem modeling. Such modeling must be integrated with detailed anatomical and paleontological data and culminate with Earth system modeling that incorporates reconstructed physiologies, plant functional types, and biomes appropriate for the period of interest. This review has elucidated a much broader spectrum of physiological functioning in extinct Carboniferous plants than

previously understood and considered. Such considerations reveal the limitations of assuming that ancient plant functional traits and types can be equated with nearest living phylogenetic relatives, and provide a road map for identifying more appropriate nearest living equivalents for long-extinct plants that, themselves, can be amenable to experimental analysis. Identifying the physiological properties of extinct plants, assembling them into whole-plant models, and identifying NLEs from the whole-plant perspective will yield a more comprehensive and nuanced understanding of vegetation–climate feedbacks throughout the evolutionary history of plants.

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Author contributions

J.P.W. and I.P.M. planned and organized the review and collaborated with J.D.W., W.A.D. and J.C.M. to perform the analyses, the ecosystem modeling, and literature review. C.J.P. and J.D.W. oversaw the Earth system and ecosystem modeling and integration. M.T.H. and I.P.M. conducted the geochemical analyses. All authors contributed to the Carboniferous vegetation study and to various components of the manuscript preparation.

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