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Pennsylvanian tropical floras from the United States as a record of changing climate

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ABSTRACT

Late Carboniferous (Pennsylvanian) fossil floras from the United States are well studied as adpression, permineralization, and palynomorph assemblages throughout the stratigraphic column. These data represent an intrabiomic record that can serve as a proxy for climate change in the Carboniferous tropics. The short-term climatic changes that accompanied the alternations between glacial and interglacial intervals did not alter the persistence of the ecological structure of the landscape. Even after floras had been extirpated over large parts of the North American continent in response to marine transgressions, the same plants and plant communities repeatedly returned when the sea receded. However, at the Westphalian-Stephanian boundary (approximately Desmoinesian-Missourian; Moscovian-Kasimovian boundary), major vegetational changes occurred that suggest a significant environmental threshold had been exceeded. Entire clades (most tree lycopsids and medullosans with very large seeds) became extinct, and tree ferns became dominant, changing the aspect of the ecological landscape. This change reflects the overall warming of Earth's climate, greater seasonality, and shorter periods of wet conditions in the tropics of the late Pennsylvanian.

Keywords: climate change, tropical, Pennsylvanian, United States, fossil floras.

INTRODUCTION

Plants reflect the climatic conditions under which they live through their ecology, morphology, and architecture. This paper synthesizes the dynamics of equatorial wetland vegetation near the mid-to-late Pennsylvanian transition (Westphalian-Stephanian,

Moscovian-Kasimovian boundary) in the eastern and central United States, which are interpreted here as a response to climate change that was driven by glacial pulses in Gondwana. The data sets represent floras preserved under isotaphonomic conditions throughout the Pennsylvanian. Two different but parallel data sets exist from two different soil types; these are histosols, originally

peat and now coal, and soils formed on clastic sediments, which are found today as mudstone and shale. The plants preserved in histosols are either in coal balls (i.e., early diagenetic concretions formed during the peat stage), or are found as spores and pollen macerated from the coal. In clastic rocks, plants occur mostly as adpressions (i.e., compressions and impressions). All these plants grew in a single biome, namely, the wet tropics, and, therefore, they represent a coherent picture of comparable data. The data from two types of substrate represented by three types of preservation allow us to analyze and understand the timing and turnover of vegetation in the tropics. Inasmuch as species composition is a reflection of physical habitat conditions, partially controlled by climate, changes in taxonomic composition through time also reflect changes in climate. Such changes in fossil floras through time have been recorded in various basins (Fig. 1) and represent a detailed proxy of climate changes in the wet tropics.

Carboniferous Tropical Lowland Floras, Plant Ecology, and Climate

Carboniferous tropical lowland floras were dominated by five major groups, lycopsids (club-mosses), sphenopsids (horse-tails), filicopsids (ferns), pteridosperms (seed ferns), and cordaites (a group of early coniferophytes). Lycopsids, sphenopsids, and ferns propagated with spores, whereas the last two (pteridosperms and cordaites) were gymnosperms and reproduced via seeds. Other groups of vascular plants (Noeggerathiales, early conifers) were rare or restricted to specific environments and are not considered

in this analysis. The five major groups were represented by trees that were constructed anatomically quite differently (Fig. 2). These anatomical differences resulted in different growth and reproductive strategies and often different ecological requirements. The tree forms of these five groups were the major producers of peat, but smaller forms (shrubs, dwarf shrubs, or herbs) existed in all five groups, too, and could dominate the flora locally.

The ecological requirements of these five groups differed with regard to permanent or semipermanent flooding, tolerance of sedimentation, and length of dry season. Shifts in substrate conditions are reflected in the changes in dominance of the groups over space or time (Gastaldo et al., 2004a; DiMichele et al., 2007) or in the changes in diversity if these changes reflected long-term trends (Peppers and Pfefferkorn, 1972; Pfefferkorn and Thomson, 1982). In the Pennsylvanian, high-level evolutionary lineages (roughly Linnean classes) were largely ecologically homogeneous, as shown by niche conservatism (DiMichele et al., 2001). Therefore, we can use taxonomic lists and dominance-diversity patterns in space and over time to interpret changes in ecological conditions. Plants reflect the climatic condition of the area in which they live. This fact led to the concept of biomes (Walter, 1985), which are climatic-ecophysiological-morphologic zones. Each of the Walter's 10 biomes is a climatic zone that can be recognized based on the

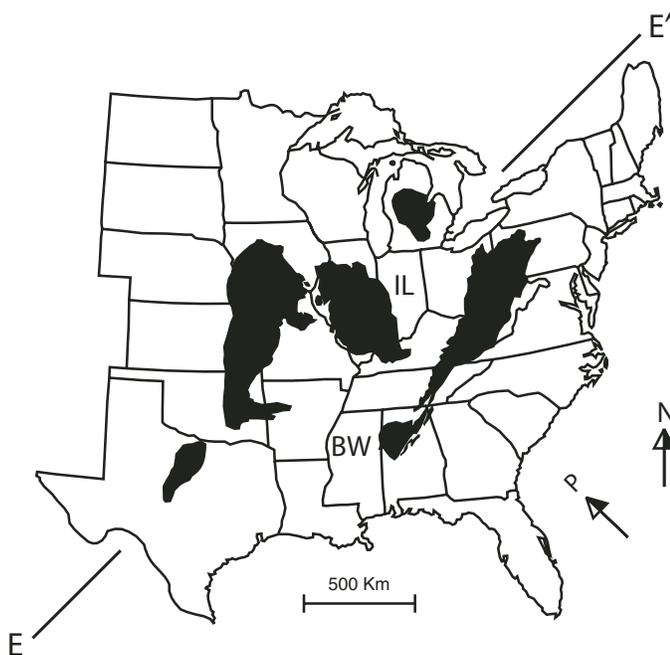


Figure 1. Late Carboniferous coal basins in North America. IL—Illinois Basin; BW—Black Warrior Basin. N—present north; P—paleo-north; E—E'—position of paleo-equator in Late Carboniferous time.

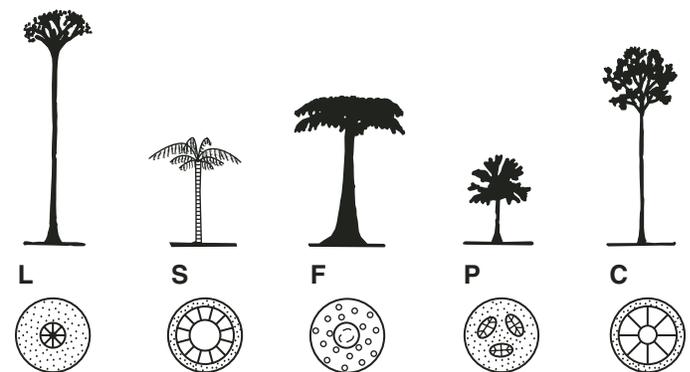


Figure 2. Reconstruction of typical representatives of the five dominant tree groups of Late Carboniferous plants and schematic cross sections of their differently constructed stems: L—lycopsid (*Lepidodendron*) reconstruction after DiMichele (1979); stem consists mostly of secondary bark (periderm and cortex, dotted pattern) with a small-diameter cylinder of secondary wood (xylem, radial lines). S—sphenopsid (*Calamites*) reconstruction after Remy and Remy (1978); stem has a thin cortex, a thick cylinder of secondary xylem (wood), and a large pith cavity (without pattern); this reconstruction is quite different from the classical ones of this group but represents the largest trees within this group. F—tree-fern (*Psaronius*) reconstruction after Morgan (1959); stem consists mostly of root mantle (pattern of circles) and a basally small stem that expands upward with primary ribbon-shaped vascular bundles. P—pteridosperm (*Medullosa*) reconstruction after Pfefferkorn et al. (1984); stem consists of vascularized cortex in which several bundles of secondary xylem (wood) are embedded. C—early coniferophyte (*Cordaites*) reconstruction after Grand'Eury (1877); stem consists of a woody cylinder with a modest-sized pith cavity and a thin bark.

morphology of the plants growing therein, regardless of systematic affinity. This taxon-free approach was extended to the late Paleozoic by Ziegler (1990). In the present study, only one biome is considered, the tropical biome, and differences within it with respect to wetness can be discerned. In other words, it is possible to evaluate the degree of Pennsylvanian seasonality, which, in the tropics, is expressed as the number of dry months and, to some degree, whether there are one or two dry seasons.

EARLY PENNSYLVANIAN (LANGSETTIAN) FLORAL PERSISTENCE

The Black Warrior Basin (Fig. 1, BW) is a foreland basin, triangular in shape, that is bounded on the southwest by the Ouachita orogen, on the southeast by the Appalachian orogen, and on the north by the Nashville dome (Thomas, 1995). The siliciclastic succession of the Lower Pennsylvanian, the Pottsville Formation, reflects rapid tectonic subsidence of the basin and eustatic influences (Thomas, 1988; Pashin, 1994), and its thickness, up to 2.5 km, contains the economic coal resources in the basin. Both autochthonous and parautochthonous macrofloras are well preserved throughout the coal-bearing rocks (e.g., Gastaldo et al., 2004a, 2004b).

The Pottsville Formation in the Black Warrior coalfield is characterized by numerous marine-nonmarine depositional cycles (Pashin, 2004). Each cycle begins with a ravinement surface that is overlain by a <1 m interval that preserves a marine-fossil assemblage within a condensed section (maximum flooding surface; Liu and Gastaldo, 1992; Gastaldo et al., 1993; Pashin, 1998). Above the condensed section, there is a thick (10–100 m) gray mudstone interval that coarsens upward into sandstone and conglomerate. Sandstones, in turn, are overlain by a heterogeneous coal zone that forms the top of each cycle and consists of mudstone, sandstone, conglomerate, underclay, and coal. The boundaries of cycles are identified easily in outcrop and core, and they can be approximated in geophysical well logs as occurring just beneath the maximum gamma count (Pashin, 2004). Hence, these boundaries effectively serve as time lines across the basin. Thirteen depositional cycles have been identified from the base of the Pottsville Formation (Lower Boyles cycle) to the Brookwood cycle, and their depocenters are spatially distributed according to changes in southern Appalachian tectonism (Pashin, 1994, 2004). Palynomorphs and marine invertebrates indicate that strata from the Black Creek through Brookwood coal zones are of Langsettian (Westphalian A) age (Eble and Gillespie, 1989); a single macrofloral element in the Brookwood zone has been used as the basis to assign a Duckmantian (Westphalian B) age to the coal zone (Lyons et al., 1985). However, the presence of a pteridospermous vine—*Lyginopteris hoeninghausii*—in the Brookwood supports the placement of the flora in the Langsettian (Pfefferkorn et al., 2000). Langsettian plant-fossil assemblages of the Warrior Basin are dominated by lycopsid, sphenopsid, and cordaitalean canopy trees, filicopsid and pteridosperm understory, and leaves assignable to sphenophyllalean, filicopsid,

and pteridosperm (lyginopterids, medullosans, and ?callistophytaleans) ground cover and/or vines. The spatial distribution of early Pennsylvanian taxa at any point in time across the landscape is a complex mosaic (Gastaldo et al., 2004a).

The flora of the Mary Lee coal zone, in particular, has been examined at high resolution in both spatial and temporal scales and can serve as a model for early Pennsylvanian vegetation. Erect, in situ forests are preserved above each of the four coals in the coal zone (Gastaldo et al., 1990) as the result of coseismic base-level changes (Gastaldo et al., 2004b). Forty-seven form taxa have been identified within the autochthonous Blue Creek coal peat-mire forest, which Gastaldo et al. (2004a, 2004b) assigned to 32 biological taxa. Within an area of ~0.5 km², the proportion of biomass contributed from canopy trees varied anywhere from 36% to 66%, understory plants contributed from 13% to 52%, and ground cover and vines made up the remainder of the forest. The most systematically diverse assemblages were dominated by a mix of lepidodendrids, *Lepidophloios*, sigillarians, and abundant calamiteans where the canopy biomass dominated the assemblage.

Microfloral analyses of coal seams have found floras of similar diversity to those recognized in autochthonous macrofloral assemblages (Woerner, 1981). Eble et al. (1994) assessed both vertical and lateral palynological trends in the Mary Lee coal seam and found, overall, that the peat was dominated by the arborescent lycopsids *Lepidodendron* and *Lepidophloios* (*Lycospora* dispersed microspore), and spores of other lycopsid genera occurred less frequently (*Crassispora*—sigillarian; *Densosporites*—small lycopsids). Changes in diversity and systematic proportions were found both vertically and spatially within the coal—higher diversities occurred near the peat-mire margin, where ash (clastic overbank sedimentation) and sulfur (sulfur-reducing bacterial activity) content are highest (Eble et al., 1994).

The diversity pattern, systematic composition, and facies-dependent taxonomic/taphonomic associations persist throughout all 13 coal cycles in the basin. Such persistence was recognized early (Gillespie and Rheams, 1985), and nearly all taxa preserved within the lowest coal-bearing cycle (Black Creek cycle; Pryor and Gastaldo, 2000) also are found in the Brookwood cycle (Lyons et al., 1985). Similarly, attempts to biostratigraphically divide the early Pennsylvanian within the basin using palynology have not met with success (Eble and Gillespie, 1989); no cycle can be differentiated from any other cycle on the basis of the microflora.

VEGETATIONAL STABILITY DURING THE ASTURIAN (WESTPHALIAN D) OF THE ILLINOIS BASIN

The Illinois Basin (Fig. 1, IL), which covers much of Illinois, southwestern Indiana, and western Kentucky, underwent episodic subsidence through the Paleozoic (Kolata and Nelson, 1990), and deep erosion occurred in association with a rapid

withdrawal of the sea in the late Mississippian. This resulted in a system of incised valleys up to 140 m deep. The basin was distant from sediment sources in more tectonically active areas, such as the Appalachians or the Canadian Shield (Nelson et al., 1990), and filling of this high-relief surface during the Pennsylvanian was gradual. By the later middle Pennsylvanian (Desmoinesian), however, a low-gradient shelf or ramp had developed (Nelson and Lumm, 1984).

It was during late middle Pennsylvanian time (Asturian–Westphalian D–Desmoinesian) that the principal, widespread, and mineable coal beds of the Illinois Basin accumulated. These coal beds are exceptionally continuous and widespread, and they formed in what may have been the largest tropical mires in Earth history (Greb et al., 2003). They occur in the Carbondale Formation, which is characterized by the repetition of marine and terrestrial lithologies in a characteristic superposition sequence described as “cyclothem” (Weller, 1930; Langenheim and Nelson, 1992). These have been attributed genetically to variations in sea level driven by glacial-interglacial cycles reflective of south polar ice volume (Wanless and Weller, 1932; Wanless and Shepard, 1936; Heckel, 1989). The Illinois Basin had low topographic relief but underwent significant subsidence during the deposition of the Carbondale Formation. This combination resulted in widespread expression of the lithologic units of individual cyclothem (Kolata and Nelson, 1990). Such patterns continued into the superjacent Modesto Formation, which contains the boundary between the Desmoinesian and Missourian (the middle and late Pennsylvanian; approximately equivalent to the Westphalian-Stephanian and Moscovian-Kasimovian boundary).

Typically, the terrestrial rocks of a Midcontinent cyclothem consist of channel-form sandstones overlain by floodplain shales overprinted by pedogenesis. Based on personal observations of the authors from both outcrop and core, the paleosols are typically vertic in character, often with calcareous nodules, indicative of formation under conditions of seasonal dryness on well-drained landscapes. The paleosols are gleyed at the top, indicative of overprinting by increasing moisture, and they are overlain by a coal bed (histosol) of variable thickness. The formation contains five major coal beds (Colchester [No. 2], Houchin Creek [No. 4], Springfield [No. 5], Herrin [No. 6], Danville [No. 7]) and several minor mineable coals that are somewhat more areally restricted in distribution or only reach mineable thickness locally (Willman et al., 1975). Late Asturian (Westphalian D–Desmoinesian) floras from the Midcontinent are known both from clastic rocks, as adpressions, and from coal, preserved as coal balls (permineralized peat) and as pollen and spores. In all assemblages, regardless of preservation, the basic temporal patterns are similar: landscape habitat patterns of dominance-diversity structure reappear with the advent of each new coal bed–roof shale couplet. The patterns found in coal-ball floras of the Desmoinesian have been summarized in a number of papers. At the most detailed level, Phillips et al. (1977), Phillips and DiMichele (1981, 1998), DiMichele and Phillips (1988, 1996a), and Willard (1993) examined detailed patterns of statistically recurrent plant assemblages

within the Springfield and Herrin coals. Such statistical analyses were extended to four coals, the Springfield, Herrin, Baker, and Danville, from the same area of the southeastern Illinois Basin (DiMichele et al., 2002). These analyses found three major end-point assemblages, with overlaps among them. The most common assemblages, dominated by the lycopsid tree *Lepidophloios hallii*, are of low diversity and contain few species of ground cover, understory, or vines, suggesting saturated substrate conditions. This interpretation is consistent both with the reproductive biology of the dominant plant (Phillips, 1979) and the lack of ground cover or free-sporing plants that would have needed exposed substrates to complete their life cycles. The second assemblage was dominated or enriched in the lepidodendrid genera *Diaphorodendron* and *Synchysidendron*, with abundant marattialean tree ferns, pteridosperms, and small ground cover. Low fusain levels and a nonsignificant association with clastic matter in the coal beds lead to the conclusion that these plants may have occupied habitats of wet, but periodically exposed substrates. The final common assemblage was dominated by medullosan pteridosperms of various taxa and the lycopsid tree *Paralycopodites*. Such assemblages were differentially associated with clastic partings in the coal beds or with heavily degraded peat, suggesting nutrient enhancement and possible ecotonal, transitional status between peat and mineral substrate communities.

In addition to these end-point assemblages, each coal has unique or uncommon vegetation types. For example, the Danville coal is enriched in *Sigillaria*, a lycopsid often found in association with conditions indicative of moisture stress. The Baker coal is enriched in assemblages dominated by the small lycopsid *Chaloneria*, often in association with the groundcover sphenopsid *Sphenophyllum*, suggestive of marsh-like conditions (DiMichele et al., 1979). Finally, the Springfield coal has rare assemblages dominated by or with abundant lycopsids of unusual affinity, such as *Sublepidophloios*, *Lepidodendron*, and some undescribed forms. Tree ferns also are particularly abundant in the Springfield coal, and different species occur closer to or farther from active drainage channels in the peat mire. The patterns of tree-fern distribution are revealed most fully by palynology (Mahaffy, 1988; Willard, 1993). When examined over longer time scales using coal-ball data (Phillips et al., 1985; DiMichele and Phillips, 1996b; DiMichele et al., 1996, 2002) or pollen and spores (Peppers, 1985, 1996; Eble et al., 2001), it was found that these same assemblages reappeared in each succeeding coal bed in which adequate spatial sampling was possible. What appeared to be major differences in generic and species composition of different coal beds was discovered to be, rather, either differences in the proportion of the samples dominated by the different vegetation types, or by differences in the relative degree of overlaps among these vegetation types by coal bed. Thus, apparent “average” differences among the dominance-diversity patterns between coals reflect differences in the degree to which the landscape was apportioned among the major vegetation types at any given time. The adpression (clastic compression and impression) record from the Carbondale Formation is similar to that of coal balls

and coal palynology because it also demonstrates little species turnover and persistent dominance-diversity structure. Minimal floristic turnover occurs between the Colchester (Mazon Creek flora) and the Danville coals (Pfefferkorn, 1970, 1979). As such, the entire formation belongs to the *vestita* biozone of Wagner (1984). Floras, of course, reflect habitat differences encountered in the clastic-enriched environments of flood basins of the time. In some cases, for example, adpression floras represent the final forests of the peat-forming vegetation, buried in place by transgressive clastics (e.g., Gastaldo et al., 1995), whereas in most cases, they represent floras that grew on mineral soils in clastic wetland habitats (e.g., Willard et al., 1995). The majority of floras are dominated by either pteridosperms or marattialean tree ferns (Pfefferkorn and Thomson, 1982).

THRESHOLD-LIKE FLORISTIC RESPONSE TO CLIMATIC AND ENVIRONMENTAL CHANGE

The transition from the middle to the late Pennsylvanian witnessed a major floristic change within the wetland biome as recorded in the central and western regions of equatorial Pangea (Fig. 3). This involved a wholesale change from wetlands dominated by lepidodendrid lycopsids to dominance by marattialean tree ferns (Phillips et al., 1974; Kosanke and Cecil, 1996; DiMichele and Phillips, 1996b). These patterns appear to be a response to a strong pulse of global warming at or near the Westphalian-Stephanian boundary (Frakes et al., 1992; Cleal and Thomas, 2005). Possibly, warming was caused by an increase in atmospheric CO₂ (Cleal et al., 1999), followed by a generally warmer, though not ice-free, world through most of the Stephanian.

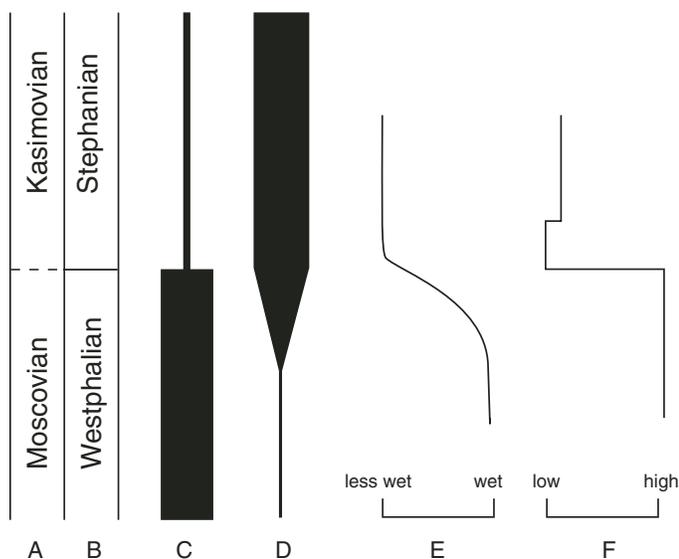


Figure 3. Changes across the Westphalian-Stephanian (Moscovian-Kasimovian) boundary (columns A and B) in frequency of tree lycopsids (column C), tree ferns (column D), wetness (column E) in the Illinois Basin, and ice volume on Gondwana (column F; after Frakes et al., 1992).

The details of this change are well documented in the literature and occur in both the floras of peat-forming environments and in that of mineral soil/clastic wetlands. Tree ferns increased in species diversity, in coverage on the wetland landscape, and in relative abundance, within floras beginning in the middle of the Westphalian D–Asturian. Sampling across the boundary between the Westphalian and Stephanian (Desmoinesian-Missourian) is hampered by some taphonomic factors that tend to enhance the apparent differences between the two floras. Specifically, in central Europe, there is a widespread hiatus at the boundary marked, for instance, by the Holz Conglomerate in the Saar-Lorraine Basin. This hiatus may be present in the Appalachian Basin of the United States extending to the Canadian Maritimes (Wagner and Lyons, 1997), where thick, well-developed paleosols occur at the stratigraphic position of the floristic change (Gillespie and Pfefferkorn, 1979). In the Midcontinent Illinois Basin, however, there appears to be a conformable transition between rocks of the Desmoinesian and Missourian, from which palynological samples have been obtained (Peppers, 1996). In this section, as elsewhere, the same abrupt disappearance of the lepidodendrid lycopsids is seen.

In the Illinois Basin section (Fig. 4), the palynological record (Phillips et al., 1974; Peppers, 1985, 1996) reveals an abrupt disappearance of those lycopsids that produced *Lycospora*-type (*Lepidophloios*, *Lepidodendron*, *Paralycopodites*, *Hizemodendron*) and *Granasporites*-type microspores (*Diaphorodendron*, *Synchysidendron*). These were the major lepidodendrids of peat and mineral substrate wetlands during the Westphalian (Scott, 1978; Gillespie and Pfefferkorn, 1979; Pfefferkorn and Thomson, 1982; DiMichele and Phillips, 1996b; Gastaldo et al., 2004a). The coal-ball macrofossil record (DiMichele and Phillips, 1996b) demonstrates an overall species extinction of nearly 67%, including 87% of the tree species and 33% of the ground cover and vines. Of 48 whole-plant species identified in the several coals just prior to the extinction boundary, 32 terminate their ranges and 16 extend into the late Pennsylvanian. Thus, there is a major disruption of the vegetational structure, and there is a release of vast amounts of resource space.

The flora of the immediate postextinction peat-forming landscapes is known in the Illinois Basin solely from palynology. Many genera that had been minor components through the later Westphalian rose to dominance for short periods of time, often only in a single coal bed (Fig. 4). For example, major short-term abundance increases are recorded for the marattialean tree-fern spore *Cyclogranisporites*, for *Endosporites*, the spore of the small lycopsid *Chaloneria*, for the sigillarian lycopsid spore *Crassispora*, and for smaller-sized pteridosperm pollen. Each of these palynomorphs shows a spike in abundance in a different coal bed, and all such coal bed-to-coal bed changes within this narrow stratigraphic interval occur before tree-fern spores, in general, undergo sustained increases in abundance. This suggests a lottery-like dynamic. Between each successive coal bed the dominance-diversity patterns change until tree ferns become the dominant element. Marattialean tree ferns were “cheaply”

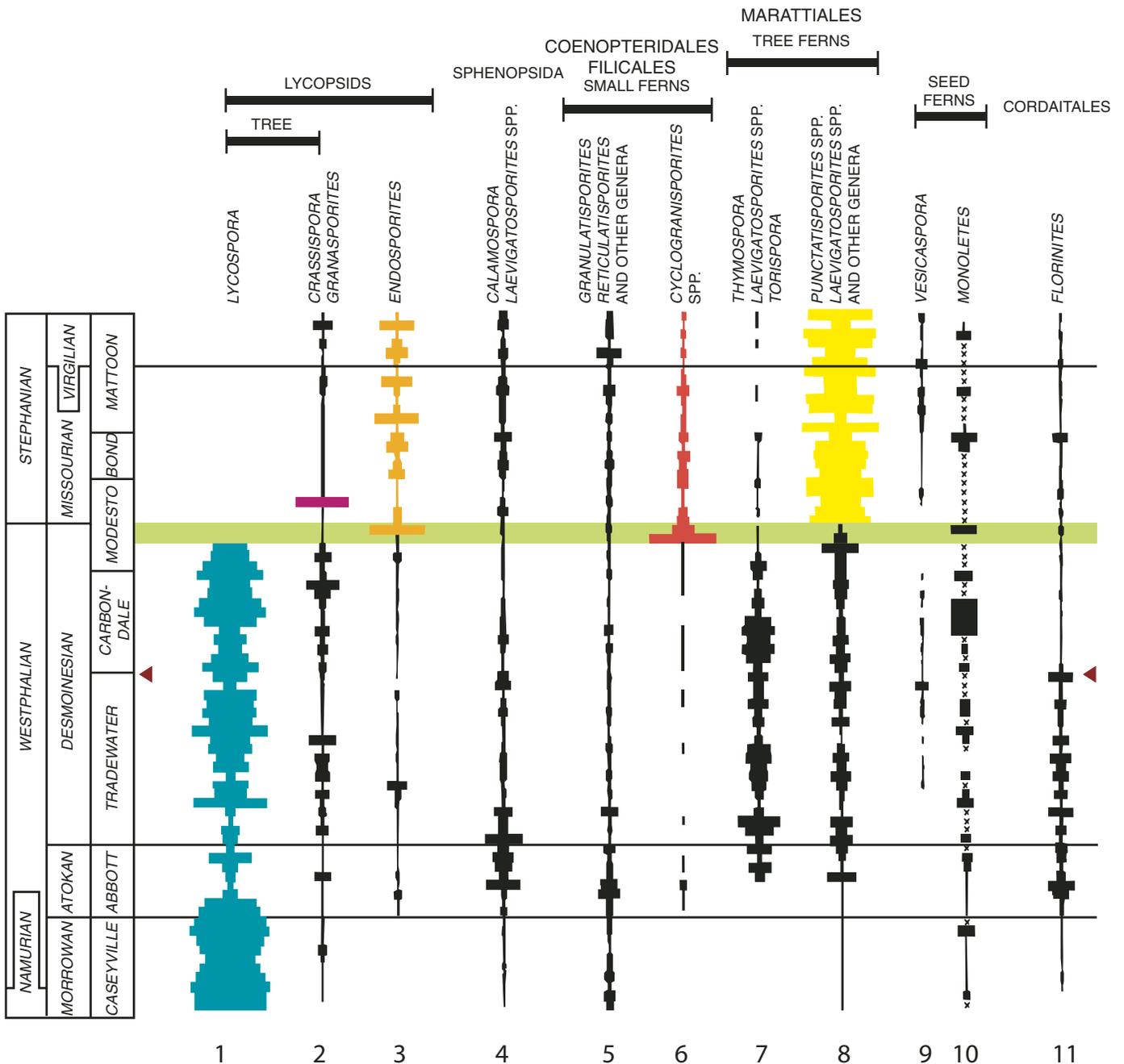


Figure 4. Distribution (in percentages) of spores and pollen from Pennsylvanian coals of the Illinois Basin showing the change around the Westphalian-Stephanian (Moscovian-Kasimovian) boundary (modified after Phillips et al. [1974], based on data by R.A. Peppers). The interval in which major changes occurred in the flora is shown in green, and groups that experienced major change are colored: *Lycospora*- and *Granaspores*-bearing lycospid trees (column 1 and part of 2) became extinct at the beginning of the critical interval; other tree lycospids show fluctuations (2—*Crassispora*, purple bar) or become significantly more common in certain beds (3—*Endosporites*); small ferns (6—*Cyclogranisporites* spp.) thrive during the period of disturbance; some tree-fern groups become rarer (7), while others become dominant in the flora (8) following the perturbation. An earlier time (marked by triangles) that saw changes in dominance-diversity pattern in clastic substrate floras saw only small changes in floras of peat mires. Plant groups designated by numbers 4, 5, 9-10 do not show any significant change at either threshold. Cordaitales (11 – *Florinites*) has the last more common appearance just below the first threshold but does not appear to be influenced by the second one.

constructed plants (DiMichele and Phillips, 1994) because they attained tree habit by virtue of a thick mantle of adventitious roots, consisting largely of air spaces (e.g., Ehret and Phillips, 1977). These trees produced high volumes of homosporous spores, greatly exceeding the numbers produced by other plants relative to the production of vegetative biomass. As free-sporing ferns, these spores not only had capacity for wide dispersal, but they could establish populations from one or a few individuals due to the potential for gametophytic self-fertilization. Cheap construction, likely rapid growth, massive production of disseminules, and capacity for wide, rapid dispersal qualify marattialean tree ferns as opportunistic, “weedy” taxa (ruderals). Their life-history biologies may have given them a great advantage across disrupted landscapes in which resources had been released by the extinction of previously incumbent, dominant forms. Coal-ball analyses indicate some level of recovery of diversity, but the number of species known from Stephanian coals of the Illinois Basin is somewhat less than that from the Westphalian, standing at 42. The ratio of trees to ground cover and vines was considerably different from the Westphalian to the Stephanian: 30/18 in the former and 18/25 in the latter. Krings et al. (2003) considered this ratio to reflect a decrease in the openness of the canopy as a consequence of the replacement of the pole-like lycopsids, which had late-developing crowns or tiny persistent crowns, by the tree ferns, which had lifelong relatively large crowns of lacy leaves. Such a change in forest architecture is considered to have favored the survival of vines, which Krings et al. (2003) have documented in great detail. It also might be considered that disturbance regimes occurred more frequently and to a greater extent in late Pennsylvanian landscapes, and these conditions favored the development of vines and ground cover. Evidence from a variety of physical environmental sources indicates a period of global warming at the Westphalian-Stephanian boundary (Frakes et al., 1992). Prior to this time interval, however, glacial-interglacial cycles were attended by associated climatic changes that led not only to changes in base level within the basinal lowlands, but to cyclic changes in the amount and annual distribution of rainfall. Coal beds are but one part of a glacial-interglacial cycle. The “seat earth” or “underclay” beneath these coal beds is a paleosol that supported vegetation different from that responsible for the formation of peat. This is suggested by deeply penetrating roots and paleosol morphologies indicative of deep water tables, well below those that would be reachable by the shallow roots of lycopsids, calamites, pteridosperms, or tree ferns. The likely sources of these deep roots are cordaitalean or conifer trees in the later Westphalian (e.g., Falcon-Lang and Bashfort, 2005). The authors’ observations of coal underclays beneath the Springfield (No. 5), Herrin (No. 6), and Danville (No. 7) coal beds show them to be Vertisols, indicative of seasonally dry climates, quite different from those under which the coals formed. Similar observations were made by Cecil et al. (2003), who traced the horizon below the Lower Kittanning coal bed (= Colchester [No. 2] coal bed of the Illinois Basin Carbondale

Formation) from the Appalachian Basin through the Midcontinent to the intermontane regions of the western United States. They followed this horizon not only in the equatorial belt, but as much as 1500 km to the north (paleo-orientation), thus crossing several climate zones. That study revealed increasing evidence of seasonal climate and even aridity from east to west (current continental orientation). Thus, clearly, climatic cyclicality in and of itself was not sufficient to cause major restructuring of wetland vegetation.

It is clear, however, that other aspects of climate may have been changing at or near the Westphalian-Stephanian boundary. We have already noted the rise in the species diversity, areal distribution, and quantitative abundance of tree ferns beginning in the middle Westphalian D–Asturian (Pfefferkorn and Thomson, 1982) (Fig. 4, at level of triangles, boundary between Tradewater and Carbondale Formations; Fig. 5, at earlier threshold). Cleal et al. (1999) reported a decrease in stomatal density in the pteridosperm *Neuropteris ovata* at this same time, prior to the disappearance of the lycopsid forests. Both of these biological changes presage the changes that took place near the stage boundary. Evidence from south polar sediments (Frakes et al., 1992) indicates a drop in the frequency of physical indicators of glacial activity, suggesting reduced ice volumes. In addition, the physical coverage of the tropical cratonic regions by peat-forming mires decreased significantly during the early Stephanian (Cleal and Thomas, 2005), and the general thickness of coal beds, even in the broad, flat areas of the American Midcontinent, was reduced significantly (Phillips and Peppers, 1984). This physical evidence suggests a decline in the extent and duration of climatic conditions suitable for wetland development and peat accumulation. It is of note that Cleal and Thomas (2005) and Kerp (1996) have suggested that tectonic activity was of greater importance than climate change in the demise of Westphalian wetland forests and the peat-forming environments of which these plants were a part. We disagree with aspects of this conclusion, recognizing that the argument implicating tectonics has multiple parts, summarized nicely by Cleal and Thomas (2005). Major tectonic activity in central Europe changed the character of coal basins from broad and paralic to narrow, isolated, and limnic. As Cleal and Thomas (2005, p. 21) noted, such activity would result in “parts of the wetlands to be drained, thereby destroying the edaphic conditions necessary for the growth of the wetland dominant plants.” However, they go on to argue that such tectonic activity disrupted wetland habitats, in general, and caused greater impact than could be expected from climatic changes.

We would modify their conclusions by noting that there is clear evidence from the modern world that climate is the primary control on plant distribution (Walter, 1985); hence, there is a strong conformation of major biomes with climatic variables and not tectonic regimes. Secondly, in such areas as the American Midcontinent during the Westphalian-Stephanian transition, there was no significant tectonic disruption of basinal continuity, no nearby tectonic uplift, and peat beds (histosols) continued to accumulate throughout the area over

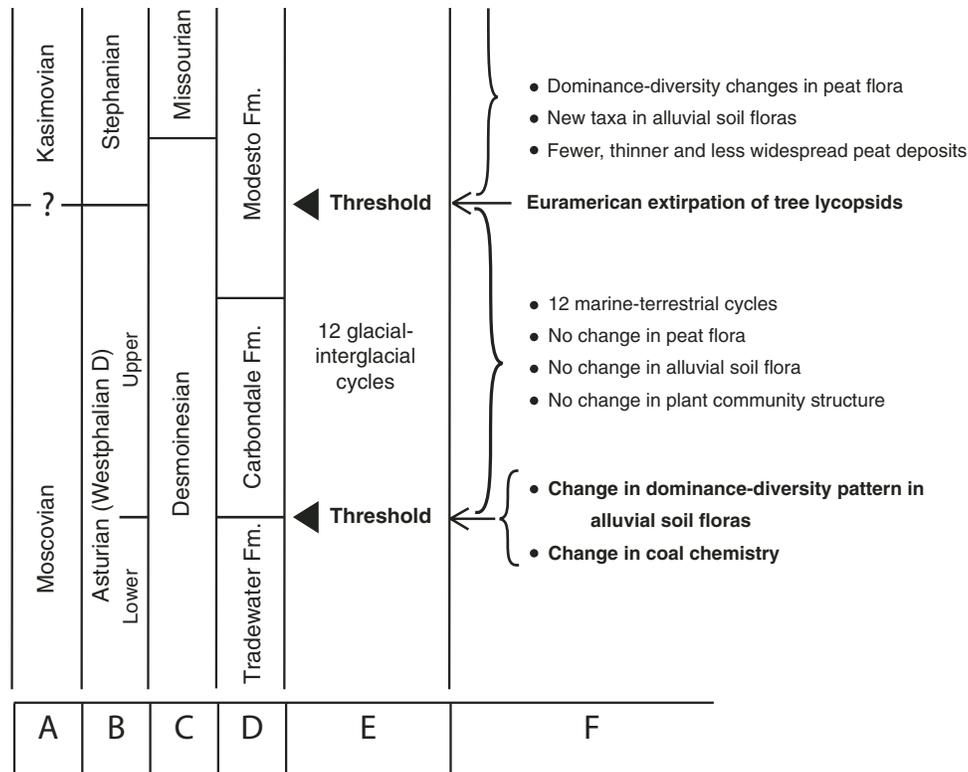


Figure 5. Changes of tropical floras on peat substrates (histosols) and clastic soils during part of the Pennsylvanian in Illinois during a drying trend in generally wet-tropical climatic conditions. Two threshold events can be distinguished that are quite different in their effects. The 12 marine-terrestrial (glacial-interglacial) cycles between these events show no significant change in the floras. Columns A–C—chronostratigraphies; column D—lithostratigraphy in Illinois Basin; column E—thresholds and cycles; column F—changes at, between, and after thresholds.

at least 1–2 m.y. Thus, sampling was isotaphonomic at the level of the basic physical environments in which the plants were preserved. Indications of increasing CO_2 (Clea et al., 1999), decreasing intervals of wet climate inferred from peat thickness (Phillips and Peppers, 1984), and paleosol evidence of strong seasonal oscillations in climate prior to the boundary event (e.g., Cecil et al., 2003), all support climate as the only variable of significance to change across this interval.

Finally, the rate of change of tectonics and rate of vegetation change at the Westphalian-Stephanian are simply not congruent. Tectonic uplift requires durations of time on the order of millions of years, although such uplift may occur locally on scales of kilometers in a million years (parts of the modern Andes). The floral change at the Westphalian-Stephanian boundary, which is documented in areas with and without significant diastems, is nearly instantaneous, implying a widespread and fast-acting causative agent. One might expect that tectonic uplift might affect air circulation patterns and, hence, rainfall and perhaps temperature patterns in a localized area. Tectonic uplift also may affect the availability of suitable habitat to permit plant dispersal and range changes, thus preventing such biological responses as the range expansion of lycopsids surviving in the eastern equa-

torial regions of Pangea back into the western regions. However, tectonic activity alone is an unlikely causative agent of plant extinctions and the elimination of wetlands over the broad expanse of western and central equatorial Pangea.

DISCUSSION

The Northern Hemisphere vegetation patterns in the Pennsylvanian tropics exhibit two distinct patterns of response to changing climate during the icehouse. Cyclothem deposition is recognized as representing rapid and high-magnitude fluctuations in sea level, linked to global climate change (Heckel, 1986, 1995). The ultimate drivers of these changing climates, which appear to have been controlled by Milankovitch-scale orbital parameters, remain conjectural (Montañez and Soreghan, 2006). As demonstrated here, vegetation preserved both within Langsettian (= Westphalian A; early Pennsylvanian) and Asturian (= Westphalian D; latest middle Pennsylvanian) cyclothem shows persistent landscape structure over million-year intervals, regardless of preservational state (adpression vs. permineralization), plant proxy (macrofloral part vs. palynological disseminule), or facies association (mineral substrate vs.

peat-accumulating wetlands). Clade-level conservatism marks these floras, where the same cohort of taxa (with little alteration in assemblage composition) characterizes each stratigraphic stage. Although not presented in this contribution, the same patterns of persistence in the Carboniferous tropics have been identified in the Serpukhovian (= Namurian A; Gastaldo et al., 1995; Pfefferkorn et al., 2000; Gastaldo et al., 2006). Such patterns of persistent terrestrial vegetation have been recognized for nearly a century and are used to subdivide Pennsylvanian stratigraphy at the stage level (Wagner, 1984).

However, the patterns of species turnover between successive coal beds within any given regional stratigraphic sequence affect only ~5%–10% of the known diversity; this turnover tends to be elevated, including greater loss and addition of new taxa, across stage boundaries. When the growth habits of individual taxa occurring within pre- and postboundary floras are evaluated, it is clear that ecological roles are conserved within clades as taxonomic turnover takes place, e.g., lyginopterid (pteridosperm) vines in the Langsettian are replaced by callistophytalean vines (pteridosperm) in the Duckmantian. In reality, many taxa first found preserved after the Mississippian-Pennsylvanian boundary (global sea-level lowstand resulting from maximum glacial ice buildup in Gondwana) persist in large numbers until the late Westphalian on a continental scale. It is this incumbency exhibited by the dominant plants throughout the wetlands that may be the ecological reason for their success.

Vegetational persistence breaks down in the late Asturian, when a shift in dominance occurred from one clade (lycopsids) to another (tree ferns), and there was a continental extirpation of members of the formerly dominant clade (Fig. 5). The dynamic pattern of plant assemblage recurrence, first seen in the Langsettian and throughout the Westphalian, changed dramatically. The marked increase in tree-fern diversity and the earliest cases where floras are dominated by tree ferns occurred in clastic wetlands in the mid-Asturian (Pfefferkorn and Thomson, 1982; Pfefferkorn et al., 2000) (Fig. 5, at earlier threshold), although tree ferns also began to increase in mires at about the same time (Phillips et al., 1985). Lycopsids preferred habitats in which water tables were high, and only one group—sigillarians—possessed ecological tolerances that allowed them to colonize better-drained soils (DiMichele and Phillips, 1996b). It was the sigillarians that survived the climatic perturbation and continued into the Stephanian, where they co-occur with pteridosperms in mineral substrate settings.

There is not an immediate wholesale replacement of lycopsids by tree ferns in the tropical lowlands. Rather, immediately following extirpation of “lepidodendrids” at the Westphalian-Stephanian boundary and before tree-fern expansion to dominance in the earliest Stephanian, there is a short stratigraphic interval during which overall diversity increases and other taxa are found to codominate within the landscape (Fig. 4). These include pteridosperms (Medullosaceae—understory) and cormose lycopsids (Chaloneriaceae—ground cover; Phillips et al., 1974), as well as sphenopsids (Sphenophyllaceae—ground

cover) and cordaites (understory; DiMichele et al., 1985). The dominance by tree ferns in both peat and mineral substrate lowland settings, characteristic of the Stephanian, begins just after this interval of ecological reorganization. A threshold is passed when turnover exceeds 20% of diversity, and previous incumbents can be replaced by another clade (Pfefferkorn et al., 2000; Fig. 4). It must be noted that this landscape reorganization occurred within a single biome, the tropical lowlands, and it marks a distinctive shift in the vegetational mosaic to dominance by clades that were present previously but the role(s) of which were expanded when habitats opened. It is quite possible that other Carboniferous biomes underwent similar responses, but data from outside the tropical wetlands are scarce.

Biomes possess their own internal dynamics (DiMichele et al., 2005) and the intrabiomic vegetational change that exists between the Westphalian and Stephanian in Euramerica occurred in response to increased seasonality from a wet tropical climate, with no or a very short dry season, to a more pronounced seasonal tropical climate (Cecil et al., 1985). This shift is evidenced by the change in the proportion of gleyed to better-drained paleosols within the Asturian (= Westphalian D), particularly in strata close to the boundary, where more vertic and calcic soils are encountered (Cecil et al., 2003). Similarly, the reduction in thickness and extent of coals late in the Asturian and particularly in the Stephanian (Phillips et al., 1974), in combination with increasingly common Vertisols and Calcisols in the latter, indicate a shift in rainfall patterns (Cecil and Dulong, 2003). As the effects of seasonality became more pronounced, vegetation responded.

The end of arborescent lycopsid dominance in the late Asturian (= Westphalian D) occurred most likely in response to an increase in the duration of dry seasons. As the landscape experienced a decrease in areally extensive tracts of land in which high water tables existed, lycopsid populations also decreased because the reproductive biology of most of these particular taxa requires wind and water for dispersal and standing water for fertilization and germination (Phillips, 1979; Phillips and DiMichele, 1992). A reduction in spatial distribution of suitable habitats would constrain and isolate populations. It appears that lycopsids with large megaspores were not the only group impacted, so were sphenopsids (*Calamocarpon*) that had similarly large megaspores. Similarly, it also may have affected the medullosans that produced very large seeds (the extinction of large *Pachytesta* taxa). Tree ferns also reproduce by spores, but these are small and produced in large numbers. These spores require moist conditions for germination and sufficient rainfall during a season when gametes can be produced and fertilization occurs. Tree ferns do not require standing-water conditions for this to happen. Hence, the reproductive strategy of this group involving high fecundity and airborne distribution of spores allowed them to colonize soils developed under a climate characterized by more seasonal rainfall. Once the dominance of lycopsids was ended and their population numbers were reduced, tree ferns spread into the available space.

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