

Climate change, plant extinctions and vegetational recovery during the Middle–Late Pennsylvanian Transition: the Case of tropical peat-forming environments in North America

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Abstract: A major extinction of terrestrial plants occurred at the end of the Westphalian (Middle Pennsylvanian) in the lowland tropics of North America. Approximately 67% of the species in peat-forming mires, and at least half the species in clastic wetlands were eliminated by changing climatic conditions, probably protracted moisture deficits or exaggeration of seasonal dryness. Independent studies suggest that the end of the Westphalian was marked by deglaciation in Gondwana and increase in global temperature.

In peat-forming habitats major floristic changes followed the extinction. Earliest Stephanian (Late Pennsylvanian) dominance-diversity patterns were highly variable temporally; several different plant groups that were of minor importance in Westphalian mires became major framework dominants, with high coal to coal variability. Ultimately opportunistic tree ferns, previously subdominant, became the dominant elements. Westphalian tree ferns were mostly small, cheaply constructed colonists with massive reproductive outputs and broad ecological amplitudes. Stephanian tree ferns were much larger and appear to have occupied sites for extended periods; they retained the cheap construction of earlier forms but added massive root mantles, which permitted greater height and girth. The ‘marsh’-forming lycopsid *Chaloneria* also became common in Stephanian mires. These elements formed mire landscapes that had few analogues in the older Westphalian mire forests, dominated by tree lycopsids. Generic dominance patterns in the Stephanian became fairly consistent after the initial period of irregularity; however, the species composition of Stephanian mires was highly variable within generic themes.

Ecological assemblages were persistent during most of the Westphalian and Stephanian. Patterns at the end-Westphalian suggest that high levels of species extinction disrupt self-regulatory properties of groups of species and create intervals of lottery-like ecological dynamics. Opportunists may have an advantage during these periods, but ultimately they must give rise to species capable of site occupation. Thus the size of the extinction, and the proximity of existing species that can recolonize vacated resource space, will dictate whether speciation or colonization will rebuild the new landscapes.

A major consequence of mass extinction is the vast change in ecological conditions. Disappearances of species or extreme reduction in their numbers or areal extent release previously sequestered resources, change the ecomorphic character of multispecies assemblages, and alter the numbers, kinds and strengths of interspecific interactions (Pimm 1991). The result is alteration of the ecological background through which evolutionary changes are filtered. Evidence from both the marine (Boucot 1983; Brett *et al.* 1990; Miller, 1993; Brett & Baird 1995) and terrestrial (Wing 1984; DiMichele & Phillips 1995) fossil records indicates that ecological assemblages may be long-lived with persistent (millions of years) dominance-diversity structure and resis-

tence to invasion, as long as extinction levels are low. Such patterns suggest that ecosystems can evolve properties of self-regulation and hierarchical structure (Miller 1990; Allen & Hoekstra 1992), which may have been important modes of organization on land and sea during much of the Phanerozoic. Separating periods of persistent dynamics are briefer intervals with elevated extinction levels and somewhat more chaotic dynamics. It is within these time periods that major evolutionary changes may be concentrated (Vermeij 1987; Brett & Baird 1995).

Plant communities in the Pennsylvanian-age lowland tropics were characterized by long periods of vegetational persistence. Assemblages with similar species composition and quantita-

tive dominance-diversity structure characterized particular habitats for intervals of millions of years before shifting abruptly to new equilibria. In both peat-forming mires (Phillips *et al.* 1985; DiMichele & Phillips 1995) and mineral-soil wetlands (Pfefferkorn & Thomson 1982) elevated levels of extinction and or origination accompanied major vegetational change. Regional climatic changes, particularly in rainfall, are the most likely factors causing vegetational change (Phillips & Peppers 1984; Cecil 1990; Winston 1990); like the Recent, the Pennsylvanian was a time of major polar glaciations (Frakes *et al.* 1992), and experienced extensive climatic and sea-level fluctuations (Ross & Ross 1987, 1988; Heckel, 1986, 1989; Cecil 1990).

The most profound vegetational change of the Pennsylvanian occurred during the Middle to Late Pennsylvanian (Westphalian–Stephanian) transition. At that time peat-forming mires were transformed from lycopsid dominance, which had persisted for more than nine million years, to tree-fern dominance. In addition, the hierarchical organization that characterized Westphalian mire landscapes (DiMichele & Phillips 1995) was replaced by vegetation with less spatio-temporal complexity (Willard & Phillips 1993). Westphalian landscapes had stereotypic patterns of resource partitioning largely defined by the tree lycopsids (Scott 1978; Collinson & Scott 1987*a, b*; DiMichele & Phillips 1985, 1994). This partitioning created a fabric that endowed ecosystems with a substantial degree of self-regulation of species turnover dynamics over geologically significant spans of time (DiMichele & Phillips 1994*b*). In contrast, the Early Stephanian wet tropics were dominated by opportunist tree-fern lineages or by seed plants that had survived the end-Westphalian extinctions (Pfefferkorn & Thomson 1982; Phillips *et al.* 1985). These extinctions, which affected both mires and clastic wetlands (Phillips *et al.* 1974; Gillespie & Pfefferkorn 1985; Peppers 1985), were at the root of the ecological differences. Such an extensive and temporally abrupt reorganization of plant communities suggests a threshold-like response of the system to extinction of the component species. As a consequence, the vegetation of the wet lowlands was taxonomically and structurally simplified, and the marked taxonomic differences between mires and clastic wetlands, which had characterized the Westphalian, were muted (DiMichele & Aronson 1992).

The study system: peat-forming mires

Peat formation was a major distinguishing

feature of the Pennsylvanian tropics. Vast tracts of swampy lowlands were covered with mires, a landscape indicative of high rainfall and high groundwater tables distributed throughout most of the year (Clymo 1987). Mire floras were quantitatively and, to a large extent qualitatively distinct from those of surrounding clastic wetlands during the Westphalian (Middle Pennsylvanian). Lycopsids dominated peat substrates, on average, for the entire Westphalian with subdominant cordaitan gymnosperms from the Westphalian B through early D. In contrast, floodplains, levees, and other clastic lowland environments were dominated by pteridosperms, sphenopsids, and tree ferns (compare Phillips *et al.* 1985 and Pfefferkorn & Thomson 1982; Peppers & Pfefferkorn 1970). This distinction was dramatically reduced in the Late Pennsylvanian when tree ferns and pteridosperms became dominant elements in all lowland-wetland habitats (Pfefferkorn & Thomson 1982; Phillips *et al.* 1985; DiMichele & Aronson 1992), although species differences may have remained.

Peat substrates present major physiological challenges to plants (Schlesinger 1978). Generally low pH, flooding during substantial parts of the year, chelation of mineral nutrients, and, especially in the case of domed peats, highly oligotrophic nutrient status, strongly select against most species. As such, mires can be visualized as semi-closed, edaphic islands. During the Pennsylvanian certain evolutionary lineages, most notably stigmarian lycopsids, were ecologically and evolutionarily centred in swamps and mires and had strongly partitioned these environments (Phillips & Peppers 1984; DiMichele & Phillips 1985, 1994*a*). Most groups, and the pteridosperms can serve as the best understood example, were centred in the broader lowland wetlands but had few or no species that grew uniquely or predominantly on peat substrates; generally only a small subset of species from these lineages could grow on peats (DiMichele *et al.* 1985; Beeler 1983; Schabillion & Reihman 1985). Sphenopsids, marattialean ferns, and cordaites had patterns similar to pteridosperms, although the cordaites, and to a lesser extent the marattialean ferns, may have evolved some mire-centered lineages (Costanza 1985; Trivett & Rothwell 1985; Lesnikowska 1989; Trivett 1992).

Sources of data

Data on mire vegetation come from two principal sources, coal-ball macrofossils and pollen-spore microfossils. Coal balls are carbonate concretions that contain structurally pre-

microfossils can be linked to parent plants (e.g. Mahaffy 1985; Willard 1993).

Most of our analysis and inference is based on coal-ball data of two types, profile and random sample. Profiles of coal balls are collected *in situ*; relative position of coal-ball layers within the coal bed is noted, which permits recovery of the original zonation of the plant litter (Fig. 1). Random samples of coal balls are collected from one locality without respect to the position of coal balls in the coal bed. Consequently, they represent the average composition of the permineralized peat at the collection site. A coal-bed summary can be obtained from a profile by averaging the composition of individual coal-ball zones. Palynological and compression fossil data are presented and discussed where appropriate, and in order to amplify coal-ball patterns. There are critical gaps in the coal-ball record, particularly in the early Stephanian, immediately following the extinctions at the end of the Westphalian, and palynological data are of particular importance in this interval. The coal-ball data base used in this analysis is described in Phillips *et al.* (1985), with some additions of coals from the Westphalian A and B of the United States (Winston & Phillips 1991; unpublished). Palynological data are mostly from Peppers (1985). Compression-impression species ranges are from Gillespie & Pfefferkorn (1979).

The pre-extinction system: late Westphalian mire landscapes

The late Westphalian was the zenith of coal-age tropical plant diversity and landscape complexity. The primordial Westphalian forests were a complex mixture of habitats each with distinct types of vegetation. Landscapes were strongly partitioned along taxonomic lines; each of several major clades had diversity and dominance peaks in particular types of physical settings (DiMichele & Phillips 1994).

A vegetational change occurred during the Westphalian-Stephanian transition that entailed not only extinction, but a fundamental alteration in the dynamics of wetland ecosystems. The Stephanian was a period of much greater vegetational uniformity among habitats. It is possible that the spectrum of environments colonized by plants was smaller than in the Westphalian, and that, overall, wetland vegetation encompassed significantly shorter physical gradients in substrate wetness, nutrient availability, and, perhaps, levels of physical disturbance.

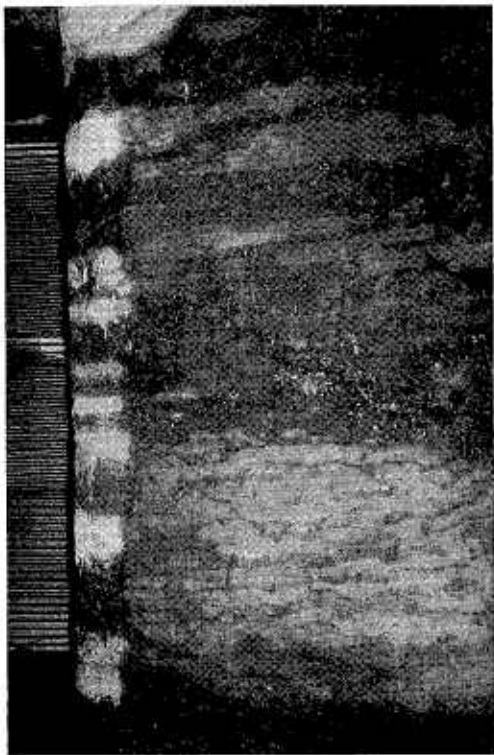


Fig. 1. Coal-balls *in situ*; Herrin No. 6 Coal Member, Carbondale Formation, late Westphalian D age; Old Ben Coal Company, No. 24 Mine, near Benton, Illinois. Coal balls are light-coloured material within the darker coal. Coal ball layers are extracted and analysed quantitatively, providing a partial record of vegetational change on the site through the time of peat accumulation.

served peat stages of the coal and that occur within coal seams (Phillips *et al.* 1976; DeMaris *et al.* 1983; Scott & Rex 1985). Coal balls preserve part of the original litter of the mire forest, often in exceptional anatomical detail. They occur in layers or aggregates (Fig. 1) and can replace much of the thickness of a coal seam, providing the basis for quantitative analysis of vegetational change during the history of peat accumulation (Phillips *et al.* 1977). Coals usually contain abundant pollen and spore microfossils, produced by plants of the mire vegetation. Incremental sampling of a coal seam can reveal fine-scale details of the history of peat accumulation, particularly when the more abundant

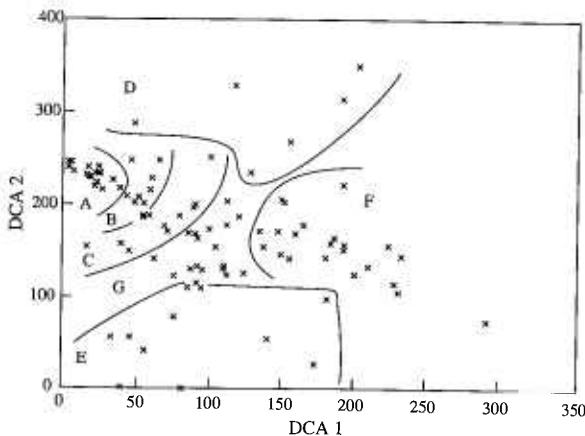


Fig. 2. Detrended correspondence analysis of coal-ball zones from late Westphalian D Herrin, Springfield, and Iron Post coals. Lines delimit groups of coal-ball zones with similar dominance patterns; letters refer to groups in Table 1 where dominance and life-history patterns are summarized.

Species assemblages in late Westphalian D mires

Peat-forming mires of the Westphalian D typically were composed of 40 to 50 species. Of the 50 species in our sample 31 were trees or subtrees, 19 were ground cover. As expected, this diversity was not randomly distributed among physical habitats, and several subenvironments can be recognized, each with a characteristic species assemblage (community-type) and dominance-diversity structure. The basic pattern is summarized in Fig. 2, an ordination of 96 zones from 7 profiles from three late Westphalian D coals, the Iron Post coal of Oklahoma, the Springfield coal of Indiana, and the Herrin coal of Illinois. This type of multi-community landscape is typical of all late Westphalian D coals we have studied; more detailed analyses of the Springfield and Herrin coals are published (Phillips & DiMichele 1981; Eggert *et al.* 1983; DiMichele & Phillips 1988; Willard 1993).

The zones (vegetational stands) in Fig. 2 form three major groups: assemblages dominated by the monocarpic lycopsid tree *Lepidophloios hallii*, assemblages dominated by the polycarpic lycopsids *Diaphorodendron scleroticum* or *Sigillaria* sp., and assemblages dominated by *Medullosa* spp. and the polycarpic lycopsid *Paralycopodites brevifolius*. Average species richness among these assemblage-types ranges from 7.2–8.2; major differences reside in the kinds of life histories that dominate, the average percentages of ground cover, and the amounts of

associated fusain and mineral matter. *Psaronius* tree ferns are components (5–15% biomass) of nearly all assemblages except those dominated by *Lepidophloios hallii* lycopsids. Calamites are minor elements and occur in greatest abundance in association with *Medullosa-Paralycopodites* and to a lesser extent with *Diaphorodendron* and *Sigillaria*.

Lepidophloios-dominated assemblages appear to have been best developed in habitats with extended periods of standing water. Species richness averages 7.2 in the 19 zones of the ordination, and includes low biomass and diversity of ground cover, vines, and understory trees and shrubs (Table 1). Quantitatively, lower vascular plants, particularly *Psaronius* tree ferns, are minor components and drop sharply in abundance as *Lepidophloios* proportions exceed 70% (DiMichele & Phillips 1988; Eble & Grady 1993). Ground cover and homosporous lower vascular plants both require exposed substrates, and their low abundances support the inference of flooded peat surfaces. In addition, the dominant *Lepidophloios* species produced seed-like 'aquacarp' (Phillips & DiMichele 1992), which had physical properties consistent with water dispersal (Phillips 1979).

Assemblages dominated by the polycarpic lycopsids, *Diaphorodendron* and/or *Sigillaria*, have variable composition. Species richness in these assemblages averages 7.7. Ground cover and vine richness averages 1.8 species per zone. However, quantitatively, ground cover and understory trees and shrubs were significant vegetational components, even if richness was low (Table 1). Levels of mineral matter and

Table 1. Dominance and average abundance of ground cover and life history groups in ordinations of late Westphalian D coals and early Stephanian Calhoun coal.

Group Dominant	n	GC	LVP	SP	HP	AQ
Late Westphalian D						
A <i>Lepidophloios</i> > 70%	7.2	1.7	2.7	1.7	0.3	2.5
B <i>Lepidophloios</i> > 50%	8.7	2.3	3.3	2.1	0.2	3.1
C <i>Lepidophloios</i> > 40%	7.1	1.7	3.2	1.6	0.1	2.2
D <i>Lepidodendron</i> > 40%	9.3	1.5	2.8	1.5	0.2	5.0
E <i>Diaphorodendron</i> / <i>Sigillaria</i> > 40%	7.7	1.8	2.6	1.9	0.8	2.5
F <i>Medullosa</i> / <i>Paralycopodites</i> / <i>Psaronius</i>	8.2	2.2	3.0	2.0	0.7	2.2
G Mixed Dominance	9.9	3.4	4.2	2.6	0.6	2.6
Average	8.3	2.1	3.1	1.9	0.5	2.8
Calhoun Coal—Early Stephanian						
A <i>Psaronius</i> / <i>Medullosa</i> / <i>Sigillaria</i>	8.0	3.5	3.5	2.5	2.0	000
B <i>Medullosa</i> / <i>Psaronius</i> / <i>Sigillaria</i>	10.0	5.5	5.5	3.2	1.0	000
C <i>Medullosa</i> / <i>Psaronius</i>	10.7	7.0	7.0	2.3	1.3	000
D <i>Psaronius</i>	10.0	7.0	7.5	2.5	000	000
Average	9.7	5.8	5.9	2.6	1.1	000

Group letters refer to coal-ball zones within areas marked by the same letters on the respective ordination (Figs 2 & 3). Numbers refer to average number of species within each category. n, species richness; GC, ground cover; LVP, homosporous lower vascular plants; SP, seed plants; HP, free-sporing heterosporous plants; AQ, aquacarpic plants (*sensu* Phillips and DiMichele 1992). Ground cover will also be listed in one of the other categories.

charcoal are not notably elevated in these assemblages. We suggest that they were characteristic of wet peats with occasional flooding and minor levels of physical disturbance.

Assemblages enriched in or dominated by medullosan pteridosperms and *Paralycopodites brevifolius* are associated with elevated levels of mineral matter and charcoal (Calder 1993; DiMichele & Phillips 1988; Johnson 1979). Average species richness is 8.2, with 2.2 species of ground cover or vines (Table 1). Subdominant species include a variety of life histories and growth forms, many of which are preferentially associated with mineral matter in coal (see literature summary in DiMichele & Phillips 1994) or that also occur in clastic swamp deposits. This vegetation can be characterized broadly as ecotonal, flourishing in habitats disturbed by flooding and possibly fire in areas often near the margins of peat bodies (Eble 1990; Eble *et al.* 1994).

Temporal patterns and hierarchical organization in the Westphalian

The type of landscape organization described above persisted within mires of western Euramerica for approximately two to three million years, based on the timescale of Hess & Lippolt (1986; Klein 1990). Landscapes partitioned among lycopsids, tree-ferns, and medullosans

have been identified in all Late Westphalian D coals from which coal balls have been recovered: the Secor coal of Oklahoma (DiMichele *et al.* 1992), the Iron Post coal of Oklahoma (Phillips *et al.* 1985), the Springfield coal of Indiana (Eggert *et al.* 1983; Mahaffy 1988; Willard 1993), the Middle Kittaning coal of Pennsylvania (Feng 1989), the Herrin coal of Illinois (Phillips & DiMichele 1981; Mahaffy 1985; DiMichele & Phillips 1988), the Upper Freeport coal of Ohio (Phillips *et al.* 1985), the Baker coal of Kentucky (Phillips *et al.* 1985), and the Danville coal of Indiana. Palynological studies of other coals within this stratigraphic interval confirm a unity of composition and ecological structure (Peppers 1985; Kosanke 1988; Pierce *et al.* 1991; Eble *et al.* 1994).

When examined through the entire Westphalian, mire landscapes appear to be hierarchically organized.

1. Several levels of spatial organization can be identified, and each has certain temporal dynamics that operate only at that scale. In particular we recognize ecomorphs (guilds) within species assemblages (communities), and species assemblages within landscapes (DiMichele 1994).

2. The basic species assemblages (communities) identified in late Westphalian D mires occurred throughout the entire Westphalian. Distinct dominance-diversity structure, dominant species groups, and associated physical

attributes were conserved for > 9 Ma (DiMichele & Phillips 1995). Late Westphalian D mires were only one of several mire landscape types that existed sequentially during the Westphalian (Phillips & Peppers 1984; Phillips *et al.* 1985). The average species composition of earlier landscapes varied according to the proportions of the major species assemblages each contained. But the biotic characteristics of any particular species assemblage and the physical conditions with which it was associated remained distinct throughout the Westphalian. Thus, changes in the relative abundances of dominant species on a coal-bed average, and thus in the landscape composition of mires, was due mostly to changes in the proportions of different physical habitats.

3. Although there was substantial species turnover during the Westphalian, this turnover was largely on ecomorphic themes within habitats; species generally replaced others of the same clade, with similar growth architecture and life history, and remained within the habitat limits typical of those clades. Thus, in the broadest sense of ecomorphic patterns, intrahabitat organization persisted despite species turnover. Within habitat species turnover suggests an element of biotic control on species replacement, an emergent assemblage property beyond a strictly individualistic organization. We have attempted to document and detail these patterns elsewhere (DiMichele & Phillips 1994a).

Westphalian marattialean ferns

The marattialean ferns are a single, and most noteworthy, exception to the general pattern of Westphalian habitat restriction. Although broadly present in mires beginning in the Westphalian C (Peppers 1985), the first real abundances recorded by coal-ball macrofossils are not until near the Westphalian C–D transition in Iowa (Phillips *et al.* 1985). Marattialean ferns do not become generally abundant until the middle of the Westphalian D, and do so in both mires (Phillips & Peppers 1984) and clastic wetlands (Pfefferkorn & Thomson 1982).

Most *Psaronius* (*Pecopteris* in compression) species in the Westphalian were small trees, possibly a few were sprawling ground cover (Lesnikowska 1989). Large *Psaronius* trees began to appear in compression preservation during the Westphalian D (Pfefferkorn 1976), but truly large trees are not known from mires until the Stephanian. Unlike most other groups *Psaronius* species appear to have had very broad ecological amplitudes, permitting them to become interstitial opportunists within a variety

of other vegetation types. Their free-sporing life histories apparently limited the colonizing ability of *Psaronius* species to environments with exposed substrates.

Extinction patterns and the Westphalian–Stephanian transition

The transition from the Westphalian (Middle Pennsylvanian) to the Stephanian (Late Pennsylvanian) was marked by a major extinction of tropical lowland plants, particularly in North America (western Euramerica). White & Thiesen (1913) first recognized the major floristic change, based on compression foliage. Later Kosanke (1947) detected the change in Illinois Basin coals using palynology. Recognition that this was a major extinction of lycopsid genera and included a major vegetational change became evident when coal-ball and palynological data were combined (Phillips *et al.* 1974). Monographic revisions of plant groups preserved in coal balls indicate a much broader extinction that includes most of the species of Westphalian tree ferns (Lesnikowska 1989) and pteridosperms (Taylor 1965). Palynological work in the U.S. (Peppers 1985; Kosanke 1988), and Europe (Stechesgolev 1975) demonstrates that the extinction was time transgressive from west to east across the Euramerican tropics, occurring in western Russia in the early part of the Stephanian. *Lycospora*-bearing lycopsids persisted in Europe during the Stephanian but at markedly reduced abundance (see Lorenzo 1979; Phillips *et al.* 1985). Stephanian lowland, wetland habitats were both more uniform and lower in species richness than those of the Westphalian, except perhaps in Cathaysia where floras typical of Euramerican wetlands persisted into the Late Permian (Phillips *et al.* 1985; Ziegler 1990; Guo 1992). Parts of the Cathaysian tropics apparently remained continuously wet throughout the Carboniferous, providing a refugium for the most moisture-sensitive floras.

Causation

Extinctions during the Westphalian–Stephanian transition appear to have been caused by changing climatic conditions in the tropics. Reduction in the amount of rainfall and increased seasonality in its distribution are the most likely factors to have affected the wetland biome. Peat-forming environments would have been the most sensitive landscapes within that biome. Because mires contained many edaphic-

specialist taxa, climatic changes could have greatly affected migration routes between refugial safe sites. Lower levels of extinction are expected for clastic compression floras, which represent wetland plants with broader edaphic tolerances and thus access to a greater variety of migration routes.

Several studies have inferred regional drying in western Euramerica during the Westphalian–Stephanian transition. Phillips & Peppers (1984) used coal resource abundances from the Appalachians and Midcontinent coal basins as indicators of general environmental moisture availability. Their data suggest a marked period of drying coinciding with the transition and extinction. Cecil (1990) and Cecil *et al.* (1985) drew similar conclusions from the analysis of coal geochemistry, coal-body geometry, and analysis of clastic rocks associated with coals. Winston (1986, 1989) identified plant tissues in polished blocks of coal, and, based on current ecological understanding of the plants, inferred a climate signature like that of the other studies.

Recently Frakes *et al.* (1992) have re-evaluated the evidence for late Palaeozoic glaciations. They find that the Westphalian was a time of glacial maximum. This maximum ended abruptly at the Westphalian–Stephanian boundary, and the early Stephanian saw greatly diminished glaciation and possibly an increase in global temperature. Changes in the extent of polar glaciations directly affect the width and position of the intertropical convergence zone (see Parrish 1982; Ziegler *et al.* 1987), which in turn affect the amount and periodicity of annual rainfall. This joins with the other lines of evidence to suggest a global, allogenic cause for plant extinctions in the Westphalian tropical wetlands.

Turnover

Species origination and extinction were calculated on the basis of stratigraphic range data. Two types of calculation were performed using coal-ball data. The first considered the actual origination and extinction between coals through the later Westphalian D and early Stephanian. This method does not account for the Signor–Lipps effect, in which an extinction is ‘smeared’ backwards stratigraphically due to sampling effects. To account for this we also examined summary turnover between the latest Westphalian mires, a group uniformly dominated by lycopsids, tree ferns and pteridosperms, and early Stephanian mires, dominated by tree ferns and pteridosperms. In effect the comparison is restricted to two different types of

ecosystem, each internally uniform. The summary turnover also was broken down into two ecomorphic groups, trees and ground cover/vines/shrubs. Summary extinction and origination were calculated for compression–impression data reported by Gillespie & Pfefferkorn (1985), and for coal palynological data reported by Peppers (1985).

Table 2. *Species diversity, origination, and extinction during the late Westphalian and early Stephanian based on coal-ball data*

Coal	First occurrences	Last occurrences	Species richness
Stephanian			
Calhoun	3	—	31
Duquesne	5	7	36
Friendsville	5	0	30
Bristol Hill	5	2	27
Westphalian			
Baker	0	17	39
Lower Freeport	0	7	46
Herrin	7	2	48
Middle Kittaning	0	2	43
Springfield	3	4	47

Table 3. *Extinction, survivorship and origination based on spore-pollen data (from Peppers 1985)*

43 total species in late Westphalian
19 species terminate in late Westphalian D (44.2% extinction)
24 species range through W/S boundary (55.8% persistence)
26 total species in early Stephanian
2 species originate in early Stephanian (7.7% origination)

Species richness, origination, and extinction patterns are presented in Table 2 for nine stratigraphically successive coals from the late Westphalian and early Stephanian. A ‘species’ in this compilation is either a reconstructed whole plant for which isolated organs have been reassembled, or it is a diagnostic organ or group of organs. Seeds of pteridosperms, for example, are used as proxy for parental plant species, even though they may underrepresent true species diversity; at present there are too few reconstructions of most pteridosperm groups to use whole-plant data. *Psaronius* species are mostly presented as whole plants, based on the work of Lesnikowska (1989); reproductive organs were used as proxy for whole plants where their

Table 4. Extinction, survivorship and origination based on clastic compression data (from Gillespie & Pfefferkorn 1979)

18 total species in late Westphalian

9 species extinct in late Westphalian (50% extinction)

Lepidodendron aculeatum, *Asolanus camptotaenia*, *Neuropteris heterophylla*, *N. rarinervis*,*Mariopteris nervosa*, *Alethopteris serlii*, *Annularia radiata*, *Annularia sphenophylloides*, *Sphenophyllum majus*

9 species range through W/S boundary (50% persistence)

Neuropteris scheuchzeri, *N. ovata*, *Pecopteris miltonii*, *P. unita*, *P. hemitelioides*, *Asterophyllites equisetiformis*,*Annularia mucronata*, *A. stellata*, *Sphenophyllum emarginatum*

10 total species in early Stephanian

1 species originates in early Stephanian (10% origination)

*Pseudomariopteris ribeyronii***Table 5.** Stratigraphic ranges of coal-ball plants in the late Westphalian and early Stephanian

	Stephanian				Westphalian					
	Ca	Du	Fr	Br	Da	Ba	LF	He	Ki	Sp
Bot. pseudoantiqua	x	=	=	=	=	=	=	x	=	x
B. forensis	x	x	x	x	x	x	=	x	=	x
B. cratis								x	=	x
Anachoropteris involuta (lateral)	x	x	x	x						
A. clavata	x	=	x							
A. gillotii	x	=	=	=	=	=	=	x	=	=
A. involuta (adaxial)					x	x	x	x	x	x
A. sp.								x		
Apotropteris minuta	x									
Sermaya biseriata	x	x	=	=	=	=	=	x	=	=
Z. berryvillensis (Biscalitheca)	x	x	x	x						
Z. illinoiensis (Corynepteris)	x	x	=	=	x	x	=	x	=	=
Rhabdoxylon americanum	x									
Ankyropteris brongniartii	x	x	=	=	=	=	=	x	=	x
Ankyropteris n. sp.	x	x	x	x						
Phillipopteris globoformis		x								
Doneggia compleura		x								
Calamite (Pendulostachys)	x									
Arthropitys (Calamocarpon)	x	x	x	=	x	x	=	x	=	x
Arthropitys (Calamostachys a.)	x	=	x							
Arthropitys (Palaeostachya d.)										
Calamodendron						x	=	=	=	x
Sphenophyllum (Bowmanites sp.)					x	=	=	x	=	x
Sphenophyllum (Peltastrobis r.)					x	=	=	x	=	x
Callistophyton poroxyloides	x	x	x	x						
Callistophyton boysetii					x	x	x	x	x	x
Schopfiastrum decussatum	x	=	=	=	=	x	=	x	=	=
Heterangium (Conostoma quadrat.)	x	x	x							
Heterangium (C. villosum)	x	x								
Heterangium (C. platyspermum)	x	x	=	=	=	=	x	x	x	x
Heterangium (C. kestospermum)				x	=	=	=	x	=	x
Physostoma calcaratum							x	=	=	=
Cyathotheca ventilaria		x								
Stellastelara parvula		x	=	=	=	=	=	=	x	x
S. baxteri										x
Cordaixylon (Cardiocarpus ovi.)	x	x	x	=	x	x	=	x	=	x
Mesoxylon priapi (Mitro. vinc.)	x	x								
Psaronius (Scoleopteris majopsis)									x	
Psaronius (S. parkerensis)				x						
Psaronius (Ariangium pygmaem)	x									
Psaronius (S. calicifolia)										x
Psaronius (S. valumii)						x	=	x	=	x
Psaronius (S. mamayi)						x	=	x	=	x
Psaronius (S. gnoma)					x	x	=	=	=	x

Psaronius (<i>S. latifolia</i> A)						X	X	=	X	X	X
Psaronius (<i>S. minor</i>)						X	=	=	X	=	X
Psaronius (<i>S. altissima</i>)							X	X	=	=	X
<i>P. chasci</i> (<i>S. illinoensis</i>)	X	X	X	X							
<i>P. blicklei</i> (<i>S. monothrix</i>)	X	=	X								
<i>P. magnificus</i> (<i>S. latifolia</i> B)	X	X	X	X							
Medullosa (<i>Pachytesta hexang.</i>)	X	X	X								
Medullosa (<i>P. berryvillensis</i>)	X	X	X								
Medullosa (<i>P. incrassata</i>)	X										
Medullosa (<i>P. illinoense</i>)	X	=	X	=	=	=	=	=	X	=	X
Medullosa (<i>P. composita</i>)											X
Medullosa (<i>P. stewartii</i>)		X?						X	=	=	X
Medullosa (<i>P. saharasperma</i>)							X	=	X	=	X
Medullosa (<i>P. noci</i>)											X
Medullosa (<i>P. gigantea</i>)				X	=	=	X	X			
Medullosa (<i>P. vera</i>)									X	=	=
Medullosa (<i>P. hoskinsii</i>)									X	=	=
Medullosa (<i>Stephanospermum</i> cl.)	X	=	=	=	=	=	=	=	X	=	=
Medullosa (<i>Stephanospermum</i> sp.)			X	=	=	=	=	X			
Medullosa (<i>Hexapterospermum</i> sp.)		X									
Medullosa (<i>H. delevoryii</i>)									X		
Medullosa (<i>Albertlongia incostata</i>)									X	=	X
Medullosa endocentrica	X	X	=	=	=	=	=	=	=	=	=
<i>Sutcliffia insignis</i>							X	=	X	X	X
<i>Coronostoma quadrivasatum</i>	X										
<i>Lepidodendron hickii</i>							X	X	X	X	X
<i>Lepidophloios hallii</i>							X	X	X	=	X
<i>Lepidophloios johnsonii</i>							X	=	X	=	X
<i>Paralycopodites brevif.</i>								X	X	X	X
<i>Hizemodendron serratum</i>								X	=	=	X
<i>Diaphorodendron scleroticum</i>						X	X	X	X	X	X
<i>Synchysidendron resinolum</i>						X	X	X	X	X	X
<i>Sublepidophloios</i> sp.										X	X
<i>Chaloneria periodica</i>						X	X	=	X	=	X
<i>Chaloneria cormosa</i>	X	X	X								
<i>Sigillaria</i> sp.						X	X	=	X	=	X
<i>S. approximata</i> (<i>Mazocarpon oed.</i>)	X	=	X	X							
<i>Sigillaria</i> (<i>M. villosum</i>)		X									
<i>Sigillaria</i> (<i>M. bensonii</i>)	X										
<i>Paurodendron fraipontii</i>	X	X	X	=	=	X	=	X	=	X	

x, present in a coal; =, presence in a coal inferred by occurrences in earlier and later coals. Ca, Calhoun coal (IL); Du, Duquesne coal (OH); Fr, Friendsville coal (IL); Br, Bristol Hill coal (IL); Da, Danville coal (IN); Ba, Baker coal (KY); LF, Lower Freeport coal (OH); He, Herrin coal (IL); Ki, Middle Kittanning coal (PA); Sp, Springfield coal (IL).

Table 6. Tree extinction, survivorship and origination based on coal-ball data. Psaronius taxonomy from Lesnikowska (1989). Taxa of medullosans based on ovules, of Arthropitys on cones

- 30 total species of trees in late Westphalian
 26 species extinct in late Westphalian (86.7% extinction)
Calamodendron sp., *Palaeostachya decacnema*, *Lepidodendron hickii*, *Lepidophloios hallii*, *L. johnsonii*, *Diaphorodendron scleroticum*, *Synchysidendron resinolum*, *Hizemodendron serratum*, *Paralycopodites brevifolius*, *Sigillaria* sp., *Psaronius (Scoleopteris) majopsis*, *P. calcifolia*, *P. valumii*, *P. manayi*, *P. gnoma*, *P. latifolia* (type A of Lesnikowska, 1979), *P. minor*, *P. altissima*, *Hexapterospermum delevoryii*, *Albertlongia incostata*, *Pachytesta composita*, *P. stewartii*, *P. saharasperma*, *P. noi*, *P. vera*, *P. hoskinsii*
 4 species range through W/S boundary (13.3% persistence)
Stephanospermum elongatum, *Pachytesta illinoense*, *Pachytesta gigantea*, *Calamocarpon insignis*
 17 total species of trees in early Stephanian
 13 species originate in early Stephanian (76.5% origination)
Psaronius chasci, *P. blicklei*, *P. magnificus*, *P. parkerensis*, *P. (Araiangium) pygmaem*, *Hexapterospermum* sp., *Pachytesta hexangulata*, *P. berryvillensis*, *P. incrassata*, *Sigillaria approximata*, *Sigillaria (Mazocarpon villosa)*, *Sigillaria (Mazocarpon bensonii)*, *Pendylostachys cingulatum*

Table 7. Ground cover, vine and shrub extinction based on coal-ball data. Reproductive organs used as proxy for natural species where whole-plant reconstructions have not been completed

18 total species of ground cover, vines and shrubs in late Westphalian
 6 species extinct in late Westphalian (33.3% extinction)
Physostoma calcaratum, *Callistophyton boysetii*, *Chaloneria periodica*, *Botryopteris cratis*,
Anachoropteris involuta (adaxial shoots), *A. cadyii*

12 species range through W/S boundary (66.6% persistence)
Conostoma kestospermum, *C. platyspermum*, *Schopfiastrum decussatum*, *Botryopteris 'pseudoantiqua'*,
B. forensis, *Anachoropteris gillotii*, *Sermaya biseriata*, *Zygopteris illinoiensis*, *Ankyropteris brongniartii*,
Medullosa endocentrica, *Cordaixylon dumusum*, *Paurodendron fraipontii*

25 total species of ground cover, vines and shrubs in early Stephanian
 13 species originate in early Stephanian (52.0% origination)
Callistophyton poroxyloides, *Conostoma quadrivasatum*, *C. quadratum*, *Coronostoma villosum*,
Anachoropteris involuta (lateral shoots), *A. clavata*, *Zygopteris berryvillensis*, *Rhabdoxylon americanum*,
Apotropteris minuta, *Ankyropteris n. sp.*, *Phillipopteris globoformis*, *Norwoodia angustum*,
Chaloneria cormosa

Table 8. Summary extinction and origination patterns at Westphalian–Stephanian boundary based on coal-ball data

	Extinctions	Originations
Trees	86.7%	76.5%
Ground cover	33.3%	52.0%
Total	66.7%	61.9%

associations with stems and leaves are unknown. Range-through data were used. This means that a species was assumed to be present in a given coal if it was found in both younger and older coals; range-through data compensate for differences in sampling intensities among coals. Coal balls have not been found in the last few coals of the Westphalian. However, palynological data indicate persistence of the same basic flora up to the end of the Middle Pennsylvanian (Peppers 1985; Kosanke 1988; Kosanke & Cecil 1989).

Tables 3 to 8 summarize the species extinction and origination patterns between the late Westphalian and early Stephanian; data in each table are from the same stratigraphic interval. Our ecological analyses indicate that late Westphalian and early Stephanian coals represent two distinct types of ecosystems, with ecological homogeneity characteristic of each interval.

Coal palynological data (Table 3, from Peppers 1985) sample mire ecosystems, the same environments as coal balls. Pollen and spore extinctions although elevated at the Westphalian–Stephanian boundary are lower than those found using coal balls. Many pollen and spore 'species' have been documented to come from more than one whole-plant species (e.g. Good 1975; Lesnikowska 1989; Willard 1989; DiMichele & Bateman 1992) and thus may

represent multi-species clades, which would reduce apparent extinction levels.

Table 4 summarizes turnover in compression–impression species listed in Gillespie & Pfefferkorn (1979); they used only species that occurred widely and abundantly in Euramerica, so the sample is not comprehensive. Summary extinction levels are near 50% for this sample and indicate that losses of dominant species were not simply confined to mires, but affected the entire tropical lowlands.

Ecomorphic extinction bias

Origination and extinction patterns for coal-ball plants were calculated from data in Table 5. Coal-ball data are divided into ecomorphic groups (Tables 6 and 7) and demonstrate that trees suffered proportionately nearly three times greater extinction than shrubs, ground cover, and vines. Despite such higher losses, tree origination in Stephanian mires was only 25% greater than that for the other groups. Thus the extinction was composed selectively of trees in all major phylogenetic groups. Nearly all the compression–impression taxa reported were trees. Coal-ball data are summarized in Table 8.

The post-extinction system: early Stephanian mire communities

Stephanian mires typically were composed of 25–35 species. Proportionally more of these species were ground-cover and vines than in Westphalian assemblages; 25 of 42 species in our Stephanian samples compared with 19 of 50 species in our Westphalian samples (Table 1). Trees continued to be the major biomass components of the mires, although tree dom-

inance-diversity patterns were distinct from those of the Westphalian. In general, early Stephanian mires had stereotypic quantitative composition at the generic level; the most abundant peat producers were *Psaronius* tree ferns, medullosan pteridosperms, and sigillarian lycopsids. Data from both macrofossils (Lesnikowska 1989; Willard & Phillips 1993) and microfossils (Peppers 1985; Helfrich & Hower 1989; Willard & Phillips 1993) suggest, however, that species dominance patterns varied quite significantly through time from one coal seam to the next, but not in any directional fashion (Peppers 1985) or in association with clearly identifiable changes in the physical environment of the tropics.

Ordination of 11 zones from two coal-ball profiles from the Calhoun coal of Illinois summarizes a pattern typical of early Stephanian (Missourian) mires (Fig. 3). Coal-ball and palynological analyses have revealed similar patterns in the Friendsville and Bristol Hill coals of Illinois (Willard & Phillips 1993), the Otter Creek coals of Kentucky (Helfrich & Hower 1989), the Redstone coal of West Virginia (Grady & Eble 1990), and the Duquesne coal of Ohio (Pryor 1993). Overall, these analyses reveal significantly less taxonomic and dominance-diversity distinction among assemblages, and less clear ties to recurrent habitat factors than found in Westphalian mires. In a broad sense, Stephanian mire communities seem to be divisible into three or four principal assemblages. Most are heavily dominated by or enriched in tree-ferns. Of secondary importance are medullosans, and less commonly still are sigillarians, with variable amounts of tree ferns in either of these assemblages. *Sigillaria brardii* was a polycarpic lycopsid that typically occurred in clastic substrate habitats; in Stephanian mires sigillarian stands were most common during early phases of peat accumulation and thus enrich lower zones of some coal-ball and palynological profiles (Grady & Eble 1990; Grady *et al.* 1992; Willard & Phillips 1993; Helfrich & Hower 1989) in closest association with the clastic seat earth. Calamites can occur in association with any of the other assemblages, although they tend to be most abundant in the lower parts of the coal beds or in association with clastic partings (Grady & Eble 1990; Pryor 1993), a distribution similar to that found in the Westphalian.

There are additional elements of many Stephanian mires not found in the Calhoun coal samples from Berryville. Most importantly are assemblages enriched in the lycopsid *Chaloneria*, the source of *Endosporites* microspores. *Chal-*

neria was abundant in many coals, beginning in the earliest Stephanian, immediately after the extinctions of the latest Westphalian (Phillips *et al.* 1974; Peppers 1985). Megafossils or spores of *Chaloneria* are most common in the lower parts of coal beds or in association with clastic partings (Helfrich & Hower 1989; Grady & Eble 1990; Willard & Phillips 1993; Pryor 1993). Vegetation dominated by *Chaloneria* probably was physiognomically distinctive; the plant appears to have been short, maybe a metre or so in height, with a pole-like habit (Pigg & Rothwell 1983) and formed the Carboniferous equivalent of 'marshes' (DiMichele *et al.* 1979). Cordaites also have been found to be important components of some Stephanian mires (e.g., the Duquesne coal of Ohio, Rothwell 1988; Pryor 1993; the Friendsville coal of Illinois, Willard & Phillips 1993), where they occur most commonly in lower zones, or in proximity to clastic partings (Trivett & Rothwell 1985; Pryor 1993).

Using the Duquesne coal as an example, Pryor (1993) described recurrent assemblages as a series of 'successional' stages, beginning with cordaites and sigillarians, proceeding through marsh-like assemblages dominated by *Chaloneria*, and ending with progressively greater dominance of medullosans and ultimately *Psaronius* tree ferns. The progression appears to have been driven largely by temporal changes in edaphic conditions as an increasingly thick, nutrient-poor peat substrate developed. Similar 'successional' patterns have been described by Grady & Eble (1990) from palynological studies of the Redstone coal, where they correlate with directional changes in ash and inertinite content of the coal. The successional patterns retain the characteristic Stephanian pattern of generic rather than specific identity. The intermediate and ultimate tree-fern and medullosan species composition seems to be relatively unpredictable.

Short gradient lengths are typical of most Stephanian mires. The abundance of tree ferns imparts a similar ecomorphic aspect to most of the assemblages, and the generally uniformly high biomass of ground cover and vines suggests that substrates remained exposed for extended periods of time. The vagaries of density independent disturbance and subsequent colonization patterns appear to be major controls on local taxonomic composition.

When compared at the generic level, Stephanian coal-ball floras are similar to contemporaneous compression-impression floras from clastic, floodbasin habitats (compare data in Pfefferkorn & Thomson 1982; Phillips *et al.* 1985; DiMichele & Aronson 1992). This presents

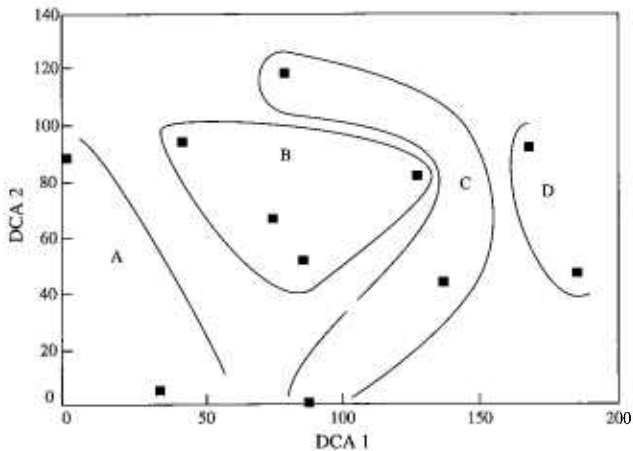


Fig. 3. Detrended correspondence analysis of coal-ball zones from Berryville VS 1 and VS 2, early Stephanian Calhoun coal. Lines delimit groups of coal-ball zones with similar dominance patterns; letters refer to groups in Table 1 where dominance and life-history patterns are summarized.

a sharp contrast to Westphalian patterns, and is indicative of a general homogenization of the tropical wetland vegetation in the early Stephanian.

Comparison of pre-extinction and postextinction landscapes

Life histories

The patterns of Westphalian and Stephanian mire communities cannot be compared in a one to one manner. Foremost, the biologies and life histories of the respective dominant taxa, lycopsids and tree ferns, were markedly different. The lycopsids were structurally diverse and had ecological strategies spanning the spectrum from weedy opportunists to site-occupying K-strategists (DiMichele & Phillips 1985; Phillips & DiMichele 1992), although direct comparisons to any extant forms are difficult. Tree ferns as a group, on the other hand, had broad ecological amplitudes, reflecting their massive reproduction and cheap construction; trees were non-woody, and were supported by adventitious root mantles composed mostly of air spaces (Ehret & Phillips 1977; Lesnikowska 1989). There is no evidence that any species of *Psaronius* were primary colonizers of the deep, standing-water habitats occupied by some species of Westphalian lycopsids. Palynological patterns from Westphalian coals indicate differential distributions of tree-fern species relative to contemporaneous channels, although the factors controlling these distributions are open to speculation at

present (Willard 1993; Mahaffy 1988).

Tree ferns of Stephanian mires retained mass reproduction of small, highly dispersible spores, reflecting the opportunistic life histories of their ancestors. However, they also attained large sizes, estimated from organ diameters (stems, roots, petioles) and *in situ* trunk diameters of > 1 m; maximum organ dimensions are larger than any reported from Westphalian mires (Lesnikowska 1989). Clastic deposits of the late Westphalian do preserve large tree fern trunks (Pfefferkorn 1976; Lesnikowska 1989) suggesting that many Stephanian mire species may have descended from Westphalian clastic-swamp taxa. The dominance of tree ferns in mires mirrored their dominance in the clastic wetlands of the Stephanian, reducing the dominance-diversity disparity between mires and clastic wetlands that typified the Westphalian. Willard and Phillips (1993) report large *Psaronius* trunks that apparently persisted through most of the time of accumulation of a Stephanian coal-ball mass over 0.6 m thick that had replaced nearly the entire seam thickness. Mickle (1984) reports large diameter trunks in which the stem had rotted out at the base, implying that the stem could die back at the base as it grew from the top, supplied with water and nutrients by the living root mantle. These observations imply that large, site occupying *Psaronius* trees were components of Stephanian mires. Size and evidence of site occupation suggest that the more r-selected, opportunistic species of the Westphalian had been replaced by, or given rise to, more typically K-selected, site occupying forms.

Table 9. Richness and abundance patterns of ground cover and vines by coal-ball zone in profiles of Westphalian Herrin coal and Stephanian Calhoun coal

Coal	Age	Coal-ball Profiles	n/P	S/Z	%B/Z
Calhoun	Stephanian	Berryville VS 1 & 2	10	5.3	4.2
Herrin	Westphalian	Old Ben 3 & 5	9	1.8	3.0
Herrin	Westphalian	Sahara 4 & 5	13	3.3	4.3

n/P = total species richness of profiles, S/Z = average species richness per profile zone, %B/Z = average percent of total biomass per zone Ground cover and vines only.

Ecological gradients

Stephanian mires had markedly shorter ecological gradients than late Westphalian peat-forming ecosystems (Fig. 4). This is suggested by detrended correspondence analyses (Fig. 3) in which axis length reflects directly the extent of species turnover, four units representing approximately complete turnover between end-points (Gauch 1982). Short Stephanian gradients are in part an artifact of lower species-level taxonomic resolution of tree fern and pteridosperm litter, a problem with coal-ball samples throughout the Pennsylvanian. This is mitigated, however, by the generally low species diversity of the dominant tree ferns and pteridosperms in any one deposit, determined by the relative abundances of diagnostic organs such as *Scolecoperis*, *Psaronius* stems, or pteridosperm ovules. Overall, the Stephanian gradient, the life histories of the plants (many requiring exposed substrates for life-cycle completion), and dominance-diversity patterns suggest that many of the physical habitats colonized and stabilized by Westphalian plants, particularly lycopsids, either did not occur or were unoccupied in Stephanian mires.

Ground cover and vines

Comparisons of ground cover and vine abundances are summarized in Table 9 for four coal-ball profiles from the Westphalian D Herrin coal and two profiles from the Stephanian Calhoun coal. Average biomass of ground cover is not significantly different between the Westphalian and Stephanian samples, nor is the total number of ground-cover species found within any of the profiles. However, the average number of species per coal-ball zone was markedly higher in the Stephanian samples. This difference reflects greater variability among Westphalian assemblages, where ground cover is lacking in many cases. This is consistent with longer ecological gradients in the Westphalian, and is reflected in greater spread of the data in ordinations of coal-

ball profile zones. During the Stephanian the same species recur from one zone to the next in profiles, leading to a more uniform taxonomic signature in the groundcover across assemblages.

Disturbance

Disturbance levels within Pennsylvanian mires are difficult to quantify. There appear to have been several major disturbance agents: fire, indicated by fusain (mineral charcoal), severe floods, indicated by clastic partings or elevated levels of mineral matter in the coal, generally unfavorable climatic conditions, indicated indirectly by plant size, average thickness of coal seams. Disturbance levels may have differed between late Westphalian and early Stephanian mires, although evidence is indirect. Fusain (mineral charcoal) abundances are lower in the Stephanian based on coal-ball analyses (Phillips *et al.* 1985). Tree sizes are generally larger in the Stephanian, determined from maximum dimensions of isolated organs. 'Marshes' composed of small stature vegetation, such as *Chaloneria*, are proportionally more abundant in the Stephanian. Finally, Stephanian coals generally are considerably thinner than those of the late Westphalian. These factors present an ambiguous picture of disturbance. In general, however, they suggest that individual Stephanian mires may have had lower levels of serious disturbance than prevailed during the Westphalian, permitting the development of larger plants in virtually all lineages. However, the general thinness of coal seams, and the frequent occurrence of marsh-like vegetation suggests that climates and depositional settings conducive to peat-formation were shorter lived during the Stephanian

Stephanian gigantism

Plants of thick peat substrates, particularly those minimally influenced by the influx of clastics,

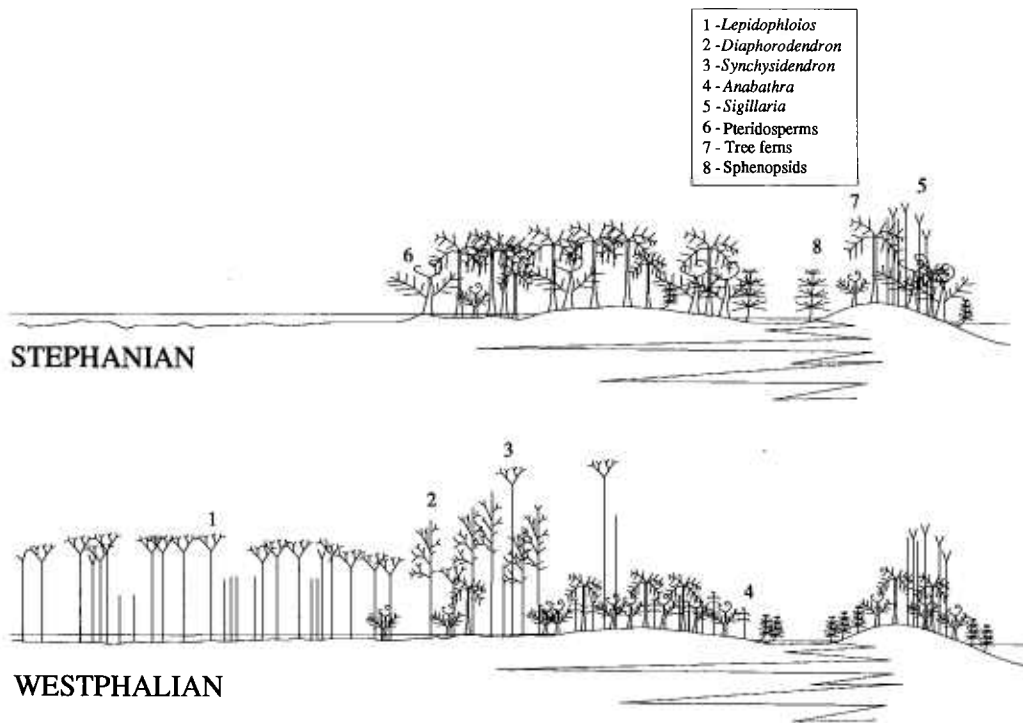


Fig. 4. Hypothetical intramire gradients in Westphalian and Stephanian. Wettest, standing water environments on left, intermittently flooded peat substrates in centre, clastic-peat transitional environments grade to 'levee' environments on right. Plants from similar lineages are shown to be larger in the Stephanian.

appear to have been smaller than their relatives on mineral substrates (Pfefferkorn 1976; DiMichele & DeMaris 1987; Gastaldo 1986), which is consistent with patterns in modern tropical mires (Anderson 1964, 1983). In the Westphalian, stem diameters of the dominant lycopsids recorded from coal balls are estimated to be 25–35 cm in *Diaphorodendron* and *Lepidophloios* respectively (DiMichele 1979, 1981), whereas trunks > 1 m diameter are encountered commonly in shales above or associated with coals. The only other Westphalian plants with moderate to large stem diameters were cordaites (*Pennsylvanioxylon* and *Mesoxylon*, up to 20 cm diameter) and calamites (*Arthropitys*, up to 12 cm diameter) from Westphalian B coals of the Appalachians. During the Westphalian, therefore, lycopsids may have been the only tall trees in what appear to have been stunted mire forests. Excluding the Westphalian B exceptions, maximum organ diameters (stems, roots, petioles) of subdominant taxa in mires were less than 10 cm, mostly less than 5 cm (e.g. Andrews & Agashe 1965; Costanza 1985; Lesnikowska 1989).

Stephanian coal balls reveal increases in the maximum sizes of tree ferns, pteridosperms, and sphenopsids, based on measurements of isolated organs. Large plant stature in Stephanian mires has been alluded to (Andrews & Agashe 1965; Galtier & Phillips 1985) but has not been examined systematically. Large size also has been documented for some Stephanian clastic compression taxa, such as *Calamites gigas* (Barthel & Kerp 1992).

Size increases within broad clades cannot be constrained more narrowly by phylogenetic analysis at the present time due to the incomparability of anatomically preserved and compression-impression based species. Lacking this framework, we suggest several possible causative mechanisms, perhaps interrelated. The simplest explanation is that trees of larger stature migrated into and occupied mire habitats following the extinction event, in the absence of competitors. Large size has been documented in several Westphalian groups dominant in clastic substrate habitats, including tree ferns (Pfefferkorn 1976) and pteridosperms (Wnuk & Pfefferkorn 1984; Pfefferkorn *et al.* 1984). In this

case large stature would be a happenstance of the ancestry of the colonizing species. Suggestions that Stephanian mires were largely topogeneous (Grady & Eble 1990; Donaldson & Eble 1991) may have permitted the survival of species from, or derived from ancestors in, clastic substrate areas. Harvey & Dillon (1985) found higher levels of inertinites in Stephanian coals, suggesting higher nutrient levels either permitting attainment of larger size or the migration into mires of species requiring higher levels.

Because of the edaphic qualities of peat substrates, and the resultant 'island' nature of mires within the greater lowland wetlands, simple migration of species from clastic to peat substrates may have been inhibited by physical factors alone. In such a landscape mires may have presented opportunities much like modern islands, on which small to medium stature plants often undergo phyletic size increases. Lineages of ancestrally small plants show consistent trends to larger size in island environments where competition for resources is reduced (Carlquist 1974). In a highly disrupted post-extinction tropics, the edaphic-island nature of mires, in combination with greatly reduced species diversities, may have permitted the rapid evolution of larger size in many surviving clades. Given the extensive extinction of trees, the opportunity for island-type, low-competition, opportunistic dynamics should have been enhanced in the post-extinction period.

A final consideration is a general reduction in the amount of severe, intramire disturbance during the Stephanian. Under such conditions natural selection may have permitted trees to achieve larger sizes, ultimately driven by intrinsic developmental factors and evolutionary size increase.

Discussion

Extinction thresholds and ecological disequilibrium

The major vegetational change following the end-Westphalian extinctions suggests that high levels of species extinction, especially when concentrated in framework trees, leads to loss of ecosystem self-regulatory properties. Examination of the persistence of the Westphalian indicates that persistence, both at the level of assemblages (communities) and multi-assemblage landscapes (DiMichele & Phillips 1995) was the dominant theme. Species turnover occurred between every coal bed, based on palynological (Peppers 1985) or coal-ball (Phil-

lips *et al.* 1985) data. Yet, the ecomorphic aspects of the major assemblages remained recognizably the same throughout the entire Westphalian. Species tended to be replaced ecologically by congeners with similar morphology and ecological preferences, although whether from migration into mires from an external source or by *in situ* speciation we cannot discern. These data indicate that as long as species turnover was low, the remaining species created a selective filter that only permitted certain forms to colonize vacated resource space. High levels of extinction, and associated major vegetational change suggest thresholds beyond which the remaining species cannot regulate subsequent colonization of available resources.

The largest extinction within the Westphalian is considerably smaller than that at the end. It occurred near the A-B boundary and is marked by the disappearance of *Lyginopteris* and *Neuraethopteris*, as well as other minor plants. However, the lycopsid trees, which were the major framework plants of mires, survived. Species turnover based on coal balls is approximately 30%; the coal-ball record of this interval is sparse, but there do appear to have been some changes in the vegetational organization of mires after the event. In particular, cordaites appeared as elements of 'ecotonal' assemblages, occupying heavily decayed peat surfaces, often in association with medullosans (e.g., Rock Springs coal of Tennessee, Phillips *et al.* 1985). Early cordaites may have extended the length of the Westphalian mire gradient by colonizing severely decayed peat surfaces, enlarging the scope of the 'ecotonal' parts of mires. Overall, though, the cordaites became a part of mires without disrupting the basic landscape structure. The Westphalian A-B extinction and its ecological consequences indicate that significant, but smaller extinctions, where the major tree forms survive, do not have the same catastrophic effect on ecosystem structure and composition as extinctions that remove the basic framework trees.

Coal-ball macrofossils do not occur in coals immediately above the Westphalian-Stephanian boundary. Consequently palynology provides the most complete record of the ecological events within mires that follow immediately after the major extinctions. With the loss of numerous species the environments of earliest Stephanian mires appear to have been open to colonization by new species or by expansion of surviving, previously subdominant lineages. Most notably, 'marshes' dominated by *Chaloneria* became major parts of some thin, boney coals. Through seven coals in the upper half of

the Modesto Formation of Illinois coal-to-coal variability in spore-species dominance is high; included as occasional dominants on a whole-seam basis are *Chaloneria*, *Sigillaria*, and tree ferns producing *Punctatisporites obliquus* and *P. minutus* spores. The dominance patterns stabilize in the overlying Bond Formation, where *Sigillaria*, several tree fern species, and calamites begin to occur with greater consistency (Peppers 1985). The coal-ball record of the later Stephanian A consistently records tree-fern dominance with subdominant pteridosperms (Phillips *et al.* 1985; Willard & Phillips 1993; Pryor 1993).

It would appear from the palynological patterns during the early post-extinction interval that either climate or mire edaphic conditions were highly variable, and generally not suitable for the development of major peat bodies. Each successive mire was dominated by a different suite of species, including many that were subtrees, such as *Chaloneria*, which formed marsh-like vegetation. The mutualistic relationships that characterized the Westphalian had evolved over millions of years, beginning in the latest Devonian, permitting persistent vegetational patterns to appear. Disruption of this system apparently eliminated these kinds of interactions, and thus long-persistent vegetational patterns. As a result of low species diversity and little ecological structure (particularly evidence of strong resource partitioning), early Stephanian mire assemblages were highly invulnerable by species that could tolerate the rigours of low-nutrient, physically stressful, peat substrates. They offered opportunities for newly evolved species to establish under reduced resource competition and exclusion.

Rise to dominance of opportunists

The ultimate dominance of marattialen tree ferns reflects the rise of cheaply constructed plants with massive reproductive output of highly dispersible isospores (capable of establishing a new population from one spore under some circumstances). Westphalian marattialeans had what can be described in general terms as an opportunistic, fugitive life history strategy. Trees were generally of small stature; tree habit was made possible by a mantle of adventitious roots composed mostly of aerenchyma. The foliage bore large numbers of sporangia, in which were produced collectively billions of spores.

Ferns also recovered and dominated many landscapes after the Cretaceous–Tertiary extinctions, the now-famous ‘fern-spike’ (Tsichudy *et al.* 1984). This brief period of dominance was not followed, however, by development of a

fern-dominated vegetation. The K–T pattern may differ from the Westphalian–Stephanian pattern for several reasons. First, it is likely that the palynological fern-spike was produced by small, ground cover ferns rather than tree ferns. The potential of these plants to give rise to trees was limited. Second, it is clear that many arboreal lineages of seed plants survived the extinction as local populations. These populations ultimately fuelled the re-establishment of vertically stratified woodlands and forests (Wing & Tiffney 1987; Wolfe & Upchurch 1986, 1987; Hickey 1984; Johnson 1992; Johnson & Hickey 1990). Thus, sources of seed were available from which new ecosystems could begin to develop.

In contrast, Stephanian lowlands appear to have been regionally devastated by climate changes that, even if brief geologically, would have been long-term on an ecological timescale. Additionally, whole Westphalian clades were very narrowly distributed ecologically, particularly those centered in the lowland wetlands (rhizomorphic lycopsids, medullosan pteridosperms, and calamites) restricting the ability of many to survive as isolated populations. The heterosporous reproductive adaptations of many of the more advanced lycopsids strongly limited them to aquatic and semi-aquatic habitats (Phillips 1979), which would have constrained their ability to recolonize patchy open habitat spaces not connected by continuous wetlands. Finally, marattialians were trees, even if relatively small trees, which gave them the ability to spawn forms capable of canopy formation, and dominance of a stratified ecosystem. As disaster forms, marattialian tree ferns were thus capable of locating available resources rapidly and then dominating local landscapes in the face of other tree taxa through rapid growth, tolerance of low nutrient conditions, and abundant reproduction on site.

Implications for ecosystem dynamics

Vegetational dynamics of the Pennsylvanian tropics, and, in fact, of most times in the Earth's history that have been studied in detail (e.g. the Tertiary, Wing 1982; Burnham 1983), demonstrate a greater degree of congruence with the predictions of ‘Clementsian’ ecosystem theories than with ‘Gleasonian’ (individualistic) models. As a generality, neo-plant ecologists have embraced Gleasonian principles and rejected Clementsian concepts, particularly as originally formulated (Clements 1916). Pointing to Pleistocene palynological data (e.g. Webb 1988; Delcourt & Delcourt 1987; Overpeck *et al.* 1992), the ‘fossil record’ has been found to be

in full support of the Gleasonian view. The differences between the Pleistocene patterns and those of deeper time do not reside in sampling scale; it is possible to resolve ecological time from palynological sampling nearly as finely in the Pennsylvanian as in the Pleistocene (e.g. Eble & Grady 1990; Willard 1993; Mahaffy 1985; Pierce *et al.* 1993). Such incompatibilities as exist may reflect real dynamical differences between the Pleistocene ice ages and the vast bulk of Earth history, differences between temperate and tropical dynamics, different scales of analysis, or different philosophies about what constitutes a vegetational unit of interest. Data from the pre-Pleistocene fossil record suggest a need for more serious consideration of modern attempts at Clementsian-type syntheses. The view of ecosystems as *systems*, with hierarchical organization and emergent properties above and beyond those of the component populations, has remained an integral part of ecology (Patton & Odom 1981; Salthe 1985; O'Neill 1989; O'Neill *et al.* 1986; Allen & Hoekstra 1992). However, due to the inherent complexity of ecosystems the theoretical elegance of Gleasonian individualism has yet to emerge. A complete theory of ecosystem organization must explain patterns on all scales of spatio-temporal observation; even if a general hierarchical model with the simplicity of the Gleasonian view has not come to fruition, the fossil record suggests a need for it, and for the rejection of individualistic models as all-powerful explanatory defaults.

The data from the Pennsylvanian represent an entirely different ecosystem from any that existed afterward. Dominance of substantial parts of the landscape by lower vascular plants, the development of ecological partitioning in concert with the modernization of the vascular plant flora, and the high degree to which the plants were structurally adapted to particular, narrow parts of the landscape, present ecologists with a natural test system for broader theories. To the degree that patterns of temporal behaviour in Pennsylvanian systems are congruent with those predicted for and documented in modern systems, our level of confidence in general principles is enlarged.

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