

RESPONSE OF LATE CARBONIFEROUS AND EARLY PERMIAN PLANT COMMUNITIES TO CLIMATE CHANGE¹

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■ **Abstract** Late Carboniferous and Early Permian strata record the transition from a cold interval in Earth history, characterized by the repeated periods of glaciation and deglaciation of the southern pole, to a warm-climate interval. Consequently, this time period is the best available analogue to the Recent in which to study patterns of vegetational response, both to glacial-interglacial oscillation and to the appearance of warm climate. Carboniferous wetland ecosystems were dominated by spore-producing plants and early gymnospermous seed plants. Global climate changes, largely drying, forced vegetational changes, resulting in a change to a seed plant-dominated world, beginning first at high latitudes during the Carboniferous, reaching the tropics near the Permo-Carboniferous boundary. For most of this time plant assemblages were very conservative in their composition. Change in the dominant vegetation was generally a rapid process, which suggests that environmental thresholds were crossed, and involved little mixing of elements from the wet and dry floras.

INTRODUCTION

When the Carboniferous or “Coal Age” is popularly envisioned, steaming tropical jungles, giant insects, and bizarre plants take center stage. Although coal swamps were prominent in tropical lowland-wetland areas, distinct vegetation occupied tropical extrabasinal areas and the northern and southern temperate zones

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PERMIAN	UPPER	PERMIAN
	MIDDLE	
	LOWER	
UPPER CARBONIFEROUS	STEPHANIAN	Artinskian
		Sakmarian
		Asselian
		Stephanian C
	WESTPHALIAN	Stephanian B
		Barrulelian
		Cantabrian
		Westphalian D
	NAMURIAN	Bolshevik
		Duckmantian
		Langsettian
		Yeadonian (G1)
Marsdenian (R2)		
Kinderscoutian (R1)		
LOWER CARBONIFEROUS	VISEAN	Alportian (H2)
		Chokierian (H1)
		Arnsbergian (E2)
		Pendleian (E1)
TOURNAISIAN	MISSISSIPPIAN	

Figure 1 General stratigraphic nomenclature for the late Paleozoic.

(DiMichele & Aronson 1992, Chaloner & Lacey 1973, Chaloner & Meyen 1973, Meyen 1982, Cúneo 1996). The Late Carboniferous was a cold interval in geological history. The expansion and contraction of glaciers, primarily in the Southern Hemisphere (Martini 1997), affected global climate and vegetational patterns in ways similar to those of the Pleistocene. Consequently, the Late Carboniferous serves as an excellent model system and the only point of comparison from the deep past to the Recent from which to examine the response of vegetation to global warming and cooling (Gastaldo et al 1996).

In this review, we concentrate on vegetational patterns in the Late Carboniferous and Early Permian, particularly in the tropics, which have received the most intensive study. Figure 1 shows the relevant stratigraphic nomenclature.

CARBONIFEROUS AND PERMIAN VEGETATION

Carboniferous vegetation can be divided into three broad paleogeographic provinces (Chaloner & Lacey 1973): the tropical or Euramerican Province, the north-temperate or Angaran Province, and the south-temperate or Gondwanan Province.

These broad regions were characterized by distinctly different floras, and each contained multiple biomes reflective of climatic and edaphic differences within the province. Overlap among the provinces has been documented in several geographical areas (Broutin et al 1995, Chandra & Sun 1997). These provinces may have changed compositionally over time within the Carboniferous as indicated by mid-Carboniferous floras on Gondwana that were referred to as the Paracas flora (Alleman & Pfefferkorn 1988, Pfefferkorn & Alleman 1989, Iannuzzi et al 1998). The tropical coal belt appears to have developed during the Namurian A (Pendleian), during the late Early Carboniferous (Raymond 1996), probably in response to the onset of glaciation (Roberts et al 1995).

Raymond (1996) argued that glaciation increased global biogeographic differentiation by establishing and maintaining an ever-wet, ever-warm equatorial climate and by steepening the equator-to-pole temperature and rainfall gradient. This kind of climate persisted into the Permian, and an analysis of Permian vegetational zonation (Ziegler 1990) suggests strong parallels to that of the modern world (Walter 1985). Because of the similarity of climate in the Late Carboniferous and Early Permian, it is likely that Late Carboniferous vegetation was more complex in its biogeographic distribution than is currently understood.

Euramerica

The tropical Euramerican Province consisted of at least two major biomes: that of wetlands and that of seasonally dry environments (Cridland & Morris 1963; Havlena 1971, 1975; Broutin et al 1990; DiMichele & Aronson 1992; Falcon-Lang & Scott 2000). There is evidence of an even drier biome by the latest Early Permian and probably well before that time (DiMichele et al 2001). The ambiguity with which such vegetational zonation must be described reflects a significant taphonomic megabias (factors related to the formation and preservation of the fossil record that introduce large, systematic biases) in the terrestrial record (Gastaldo et al 1995, Behrensmeier et al 2000), namely that the biota of uplands or extrabasinal areas (Pfefferkorn 1980) was rarely preserved in the older fossil record. Consequently, our knowledge of it depends on (a) fortuitous preservation of specimens transported into the depositional lowlands or into the marine realm, (b) rare occurrences of marginal assemblages in basinal areas during brief periods when climate was conducive to growth of the flora there (Havlena 1961, 1982, Cunningham et al 1993), (c) the preservation of an extrabasinal flora at the base of a basin fill when sedimentation had started but conditions had not yet changed, or (d) the close juxtaposition of elevated limestone terrain and a karst valley (Leary & Pfefferkorn 1977; Leary 1975, 1981).

Wetlands The wetland biome is by far the best known and can be broadly subdivided into (a) the coal swamp flora of peat-forming mires and organic-rich swamps and (b) the flood basin flora of mineral or clastic substrate wetlands (Gastaldo

1987, Gastaldo et al 1996). These floras overlapped considerably in composition, although largely at the generic level, and there were intermediate environments such as clastic swamps.

Peat swamps have been botanically analyzed for more than 150 years because of the preservation of plants as permineralizations, which are generally composed of calcium carbonate and known as coal balls (Phillips et al 1976). Vegetational studies based on coal balls (Phillips et al 1985) complement extensive studies of coal-forming vegetation based on palynology (Smith 1962, Hacquebard et al 1965, Kosanke 1988, Eble & Grady 1990). The dominant plants of peat-forming swamps and mires were the arborescent lycopsids, or giant club mosses, particularly during the Namurian and Westphalian, or in American terminology, the Early and Middle Pennsylvanian. Lycopsid trees were differentiated ecologically within swamps and mires (Phillips & Peppers 1984, DiMichele & Phillips 1985), although all appear to have been short-lived, rapidly growing, and physiologically distinct from other trees (Phillips & DiMichele 1992). Their bark accounts for the vast bulk of tissue in coals of Westphalian age (Phillips et al 1985).

During the Stephanian, roughly the Late Pennsylvanian, marattialean tree ferns dominated peat-forming habitats except in China, where lycopsid dominance continued in wetlands (Guo 1990). Tree ferns were largely opportunistic weeds in the Westphalian and large trees in the Stephanian, cheaply constructed with massive reproductive output (Lesnikowska 1989). Both lycopsids and ferns reproduced strictly by spores freely released into the ambient environment. Other important tree groups were the seed-producing cordaites, which were close relatives of the conifers, and which dominated in some mid-Westphalian swamps (Costanza 1985, Rothwell & Warner 1984), and medullosan pteridosperms or seed ferns, and the spore-producing calamites, close relatives of modern horsetails and scouring rushes and the only clonal trees in the wetland biome (Gastaldo 1992).

Flood basin habitats were far more environmentally heterogeneous than peat swamps (Gastaldo et al 1995). The same basic plant groups characterized clastic and peat soils; the relative dominance-diversity patterns, however, were distinct. Flood basin floras, except for swamps, were dominated by pteridosperms, ferns, and calamites in proportions depending on the time and environment under consideration (Scott 1977, 1978; Pfefferkorn & Thomson 1982; Gastaldo 1987). Clastic swamps were dominated by lycopsids and pteridosperms in the Westphalian and by ferns and pteridosperms in the Stephanian, with some lycopsid dominance remaining.

Seasonally Dry Environments Evidence for a seasonally dry biome in the Carboniferous tropics appears in rocks of Westphalian age near the beginning of the Middle Pennsylvanian (Scott 1984) with the advent of conifer remains. Throughout the Westphalian, conifers occurred as fusain, or fossil charcoal, in areas adjacent to contemporaneously rising uplands (Lyons & Darrah 1989). Such floras did not make their full appearance, however, until the Stephanian, in which they occurred as well-developed, strongly seed-plant-dominated assemblages

(Cridland & Morris 1963, McComas 1988, Winston 1983, DiMichele & Aronson 1992) containing many genera and species unknown in typical wetland habitats. Groups such as conifers, peltasperms, ginkgophytes, pteridosperms, and cordaites were complemented by minor amounts of ferns and sphenopsids and virtually no club moss trees. In general, the plants of this flora were more advanced evolutionarily than those of the wetland biome, reflecting an evolutionary bias, namely that of new body plans surviving preferentially in marginal areas under reduced competition for resources.

Angara

Meyen (1982) provided the only English synopsis of the north-temperate Angara flora, the study of which has focused mainly on biogeographic and stratigraphic patterns in the distribution of species rather than on the paleoecological structure of the plant assemblages. Studies by Oshurkova (1985, 1996), however, addressed paleoecological patterns.

Early Carboniferous vegetation was dominated by a variety of lycopsids mostly of a subtree stature. Four stratigraphically successive phases have been recognized, each of low diversity with various pteridosperms and sphenopsids complementing the dominant lycopsid taxa.

The lycopsid flora was rapidly replaced throughout Angaraland by a pteridosperm-dominated assemblage beginning in the late Early Carboniferous or the earliest Late Carboniferous. Pteridosperm dominance was relatively short-lived, but it signified major, widespread environmental changes, probably climatic cooling and a decrease in the seasonality of rainfall. Recently, Falcon-Lang (1999a) inferred such a climatic shift in the Early Carboniferous of Great Britain on the basis of growth ring patterns. With the appearance of the pteridosperm flora, the first traces of coal appeared in the Angaran Province. The accumulation of peat in the Late Carboniferous at these high latitudes indicates likely floristic segregation along environmental lines within the Angaran region beginning at this time, paralleling that development in Euramerica.

Pteridosperm dominance was followed by three successive floras characterized by cordaitan gymnosperms. Although related to the cordaites of the Euramerican Province, Angaran cordaites belonged to distinct families and are described collectively as Rufflorians. Ruffloria floras 1 and 2, the latter of which is the most diverse Angaran flora recorded, characterized the Late Carboniferous. These floras, despite their diversity of approximately 120 species, were almost entirely distinct taxonomically from the tropical Euramerican flora. Overlap occurred at the generic level only in common genera such as *Sphenophyllum*, *Annularia*, *Neuropteris*, and *Pecopteris*, in addition to some less common genera such as *Dicranophyllum*. Actual diversity in these assemblages may have been higher than presently believed and may require considerable taxonomic revision in light of recent investigations of the Carboniferous form genera to which these latter taxa belong. Cuticular analyses of pteridosperms (Zodrow & Cleal 1993, Krings & Kerp 1997) and

cordaites (Zodrow et al 2000) demonstrate much higher diversity than is recognizable by gross morphology alone. These floras showed some regional variation in taxonomic composition but represented common species pools throughout Angaraland. Dominant elements in most collections were mainly cordaites and the pteridosperms, especially *Angaropteridium*, and in places, sphenopsids.

Ruffloria flora 3 was characteristic of the Early Permian and continued to be dominated by Rufflorian cordaites, the pteridosperm *Angaropteridium*, and sphenopsids. Coexisting with Ruffloria 3 was a flora that Meyen (1982) characterized as the first of four Ruffloria-Cordaite floras. Such floras were dominated by Rufflorians, more typically Euramerican cordaites, sphenopsids, and minor amounts of ferns. As with the Carboniferous floras, there were regional differences in dominance and diversity patterns that reflected variation of a common species pool.

Ruffloria-Cordaite floras 3 and 4 were typical of the Late Permian. These floras included a number of genera that appeared earlier during the Early Permian in the Euramerican Province, such as the genera *Comia* and *Compsopteris* and the callipterids. Also in this species pool were Euramerican genera such as *Neuropteris*, *Annularia*, and *Pecopteris*. In Euramerica, floras with these taxa represented the later development of the seasonally dry tropical flora.

Gondwana

Late Paleozoic floras of Gondwanaland were sharply divided into two types: those of Late Carboniferous character and those of Permian character. These floras were strikingly different. The Late Carboniferous flora was described by Archangelsky (1986, 1990) as being of low diversity but uniformly developed across the Gondwanan continent between 30°S and 60°S. The flora consisted of the likely pteridosperms *Nothorhacopteris*, *Botrychiopsis*, and *Triphyllopteris*, among others (Vega & Archangelsky 1997), and the lycopsids *Bumbudendron*, *Malanzania*, and *Lepidodendropsis*. Other leaves were assigned to *Cordaites*, although they were not clearly aligned to the Euramerican species of that form genus, and the ginkgophytes (Archangelsky & Cuneo 1990).

Permian floras of Gondwanaland were significantly more diversified biogeographically than those of the Late Carboniferous (Cúneo 1996), and the floristic provinciality changed during the course of the Permian. The characteristic plant of this flora was *Glossopteris*, a genus with many species, probably highly differentiated ecologically. Conifers and ferns were also important and dominated vegetation in some regions. Sphenopsids and lycopsids remained important components locally. In general, however, the Permian flora was nearly entirely distinct from that of the Late Carboniferous, suggesting a major environmental shift between these two periods.

Gondwanan climate was cool-temperate to periglacial as well as monsoonal over long time intervals throughout the Late Carboniferous and Early Permian (Parrish 1990). This view is certainly suggested by the plants (Archangelsky 1983, Retallack 1980) and sedimentological features (Krull 1999). Retallack (1980)

presented a detailed picture of the vegetation throughout this interval in the Sydney Basin of Australia, where the Late Carboniferous flora grew in floodplain settings and was dominated by several different pteridosperms. Isoetoid lycopsids may have been mangroves in protected coastal areas, paralleling other cormose lycopsids in Euramerica (Blanton-Hooks & Gastaldo 1997). With the onset of glaciation in the Permian (López-Gamundí 1997), the flora changed dramatically with the appearance of *Glossopteris* and the disappearance of most of the Late Carboniferous elements. The Permian flora appears to have been differentiated environmentally, although any given environment supported vegetation of low diversity. For the Early Permian, Retallack (1980) identified tundra vegetation dominated by the pteridosperm *Botrychiopsis* (Retallack 1999), taiga vegetation dominated by the glossopterid *Gangamopteris*, which marked the tree line, and swamp forests rich in *Glossopteris* species, many accumulating peat (which later became coal).

The first of these coals was thin and accumulated in narrow mires with characteristic features of permafrost, including a *Gangamopteris*-dominated flora. Later coals were thicker, apparently accumulating under more cold-temperate conditions, and were dominated by *Glossopteris* (Krull 1999). The petrography of such coals was described by Diessel (1986, 1992), who developed a method of inferring vegetational structure and composition from the petrographic character of the coal. Bustin (1997) summarized these studies and compared Gondwanan Permian coal formation to that of modern cold-temperate environments. For the Late Permian, Retallack (1980) described the appearance of new kinds of vegetation in alluvial plain environments associated with local uplift and tectonically induced drying of the Sydney Basin. This vegetation included a wider variety of conifers (Archangelsky & Cúneo 1987, Stockey 1990) in families that appeared to be restricted regionally.

In Antarctica, at least three phases of vegetational change have been reported, primarily on the basis of the palynological record (Playford 1990). Certain early palynological reports have come under suspicion of contamination during processing (Schopf 1983), resulting in discounting of reports of Euramerican taxa in otherwise regionally distinct Gondwanan assemblages. The microfloral zones recognized by Kyle & Schopf (1982) encompassed the latest Carboniferous and Early Permian in which there was an interpreted increase in the abundance of cordaitan and pteridosperm taxa (Schopf & Askin 1980). The *Parasaccites* Zone, which may cross the systemic boundary, was interpreted to preserve not only cordaites and pteridosperms but also early glossopterids, cycadophytes, and ginkgophytes. Still greater palynological diversity was reported from the *Prothaloaxpinus* Zone, in which there was an increase in presumably glossopterid disaccate pollen. At least in the Weller coal measures there was an expansion of pteridophyte spores, which has been attributed to a warming trend in the region (Playford 1990). Kyle & Schopf (1982) correlated the palynoflora in the Weller coal as Artinskian or "Aktastinian-Baigendzhinian" (Early Permian) in age. Fluvial and paludal environments in the Amery Group of the Prince Charles Mountains yielded a palynoflora that was somewhat younger, although the exact stratigraphic

position is debatable. The *Praecolpaites* Zone originated from a reasonably diverse flora that was dominated by glossopterids but comprised a variety of other groups.

Mixed Gondwanan-Euramerican floras have been reported in many areas along the border of the two regions. Wagner (1962) documented a mixed Cathaysian-Gondwanan flora from Turkey, and El-Khayal & Wagner (1985) reported a mixed flora of Late Permian age from Saudi Arabia. The overlap of floral provinces is manifested by Zechstein-type conifers (e.g. *Pseudovoltzia*, *Ullmannia*) and Cathaysian plants (e.g. gigantopterids, *Lobatannularia*). In addition, El-Khayal & Wagner (1985) reported several species that are identical to those found in Turkey, including a *Glossopteris* (Archangelsky & Wagner 1983), which unites these assemblages on a climatic basis.

LATE CARBONIFEROUS CLIMATE

The Late Carboniferous was a globally cold interval, in the sense of Fischer (1982). Glaciation in the Southern Hemisphere may have involved large continental ice sheets (Visser 1993, 1997), although smaller glaciers in dispersed centers may have been more common than ice sheets, both near the pole and in high-altitude parts of the temperate zone (Dickens 1996). During this time, atmospheric CO₂ levels appear to have been low, contributing to the cold conditions (Berner 1998), and oxygen levels may have been high (Berner et al 2000). Glaciation began in the Early Carboniferous, possibly as early as the Tournaisian (Roberts et al 1995, Saltzman et al 2000), albeit long-term glacial-interglacial oscillations apparently did not develop fully until near the end of the Early Carboniferous (Frakes et al 1992, López-Gamundí 1997, Smith & Read 2000). Glacial-interglacial oscillations likely had major effects on patterns of atmospheric circulation affecting the tropics by causing changes in the width and degree of oscillation of the Intertropical Convergence Zone.

Once entrained, the pattern of deposition on the cratonic margins suggests repeated rises and falls of sea level (Ross & Ross 1988), probably paralleling those seen in the current ice age that result from the expansion and contraction of large facies (DiMichele et al 1996). Such changes in sea level were likely major contributors to perceived periodicity of depositional cycles in Late Carboniferous rocks, particularly on the craton. "Cyclothems" (Heckel 1986) record the repetition of marine and terrestrial environments and likely represent the compound effects of eustasy, tectonics, and climate (Klein & Willard 1989, Cecil 1990, Gastaldo et al 1991, Demko & Gastaldo 1996, Greb & Chesnut 1996). It is most likely that changes in the base level (in most cases, sea level), especially when caused in significant part by glacial-interglacial oscillations, were strongly correlated with climatic changes in the tropics. Such changes were recorded in terrestrial rocks, which vary from coals, indicative of high levels of available moisture, to paleosols with features indicative of seasonality in moisture delivery (Cecil 1990).

Models of Late Carboniferous climate (Crowley & Baum 1992, Crowley et al 1996) suggest cool climates in the tropics during intervals of peat formation. Climates also may have changed from one state to another over periods shorter than 100,000 years (Crowley & North 1988). Such geologically rapid changes are indicated in the geological record (Frakes et al 1992) by equally rapid changes in floras (Phillips & Peppers 1984).

The continents of this period were beginning to coalesce into Pangaea, creating a large land mass on the equator (Scotese et al 1999). Consequently, strongly monsoonal patterns of atmospheric circulation posited for the tropics would have strongly affected patterns of rainfall and vegetational development across the tropical regions (Parrish 1982).

Studies of coal quality and paleobotanical patterns suggest a directional trend from tropical rainfall toward more seasonal and perhaps generally drier conditions throughout the Pennsylvanian, a trend that became particularly prominent at the Westphalian-Stephanian boundary. Climates appear to have become markedly more seasonal in the Stephanian (Phillips & Peppers 1984, Schutter & Heckel 1985, Cecil 1990, Winston 1990, Donaldson & Eble 1991). Strong evidence suggests that in the early and middle Westphalian time domed mires were the source of major coal beds, whereas evidence from coal palynology and petrography suggests that planar peats predominated during the late Westphalian (Cecil et al 1985, Winston & Stanton 1989, Cecil 1990). In climate-sensitive characteristics of fossil floras, changes similarly reflect changing climatic conditions in the late Westphalian (Pfefferkorn & Thomson 1982). For the Stephanian, the evidence from paleofloras suggests distinct oscillations in wetter and drier climatic intervals (DiMichele & Aronson 1992).

VEGETATIONAL RESPONSE TO CHANGING CLIMATE

Climatic changes affect vegetation on many spatial and temporal scales. Paleontology traditionally has been assigned analysis of those dynamics that leave their imprint on scales of hundreds of thousands to millions of years when, in fact, much shorter-term responses can be resolved. One of the major challenges faced by ecologists and paleoecologists alike is understanding how processes operating on different spatiotemporal scales affect patterns and constrain or enhance processes on larger or smaller scales. At this time, such understanding is elusive, even though patterns on different scales can be described.

Short-Term Responses

Vegetational responses to disturbances such as fires, floods, river avulsions, and changes in canopy structure can be considered short term. It is clear that climatic change may bring about directional changes in the frequencies and magnitudes of such events, so that such effects may be manifested on longer time scales.

Disturbance Late Carboniferous and Permian terrestrial ecosystems were subject to the same kinds of disturbances as modern systems. Consequently, it can be assumed that the relative importance and magnitude of disturbance agents varied both geographically and temporally. Fire is perhaps the best documented through the preservation of fusain and its petrographic equivalent, fusinite (Scott 1989, Teichmüller 1989, Scott & Jones 1994). In coal swamps, certain vegetation types have been found to be preferentially associated with charcoal and mineral matter, especially those enriched in medullosan pteridosperms and the lycopsid *Paralycopodites* (DiMichele & Phillips 1988, 1994), transitional between peat and clastic substrates (Pryor & Gastaldo 2000). The consequences of fires in peat swamps were highly variable, including termination of peat accumulation, changes in dominance patterns, or no detectable effects on vegetational composition (Scott & Jones 1994). Fires also have been documented in better-drained environments including floodplains (Scott 1978, Falcon-Lang 1999b) and possibly uplands (Falcon-Lang & Scott 2000). Models of the oxygen content of the Late Carboniferous atmosphere suggest very high levels (Berner et al 2000), possibly causing higher fire frequencies than those of today (Beerling et al 1998). This conclusion has been disputed (Falcon-Lang & Scott 2000) on the basis of analysis of fossil wood in upland ecosystems. The effects of canopy disturbance, such as that caused by wind, can be seen only under peculiar preservational circumstances, although they may be inferred from spatial variation in assemblages representing rapid burial of a single forest. Such uprooting of trees (blowdown) was described by Wnuk & Pfefferkorn (1987) in organic shales preserved beneath a late Middle Pennsylvanian coal seam. In this deposit, whole trees, both canopy and understory, were preserved and demonstrated preferential directions of fall. Unfortunately, a deposit of this type does not record the nature of ecological recovery after such a catastrophic, short-term event.

When contemporaneous vegetation can be evaluated over a wide geographic area, it may be possible to determine which associations of plants represent opportunists specialized to disturbed environments. In a single Early Carboniferous autochthonous forest, Ware & Gastaldo (2000) identified discrete associations of canopy, subcanopy, and groundcover taxa in varying ratios. These data demonstrate variation in the pteridosperm biomass that accumulated on the forest floor in proportion to the amount of canopy biomass. These studies were supported by others that found differences in the cuticular thickness of pteridosperm leaves, reflecting growth in sun versus shade (Schabillion & Reihman 1985, Arens 1997). Determination of the light regimes under which plants grew permits separation of taxa that preferred open growth habitats, possibly resulting from canopy disturbances, from those that preferred closed canopies.

The consequences of flooding for vegetation must be inferred indirectly. Studies of coal swamp assemblages preserved in coal balls (Phillips & DiMichele 1981, DiMichele & Phillips, 1988, DiMichele & Phillips, 1996a) suggest the existence of specialized, low-diversity assemblages lacking ground cover and adapted to standing-water conditions. Such assemblages were dominated by the lycopsid tree

Lepidophloios and have been found in clastic swamps as well (Gastaldo 1987). On the basis of reproductive morphology and patterns of occurrence, few Late Carboniferous plants, other than arborescent lycopsids and calamites, appear to have been tolerant of long-duration flooding or partial burial by sediment (Gastaldo 1992), a disturbance mode that would have dramatically altered local landscapes.

Succession Succession has been documented in tropical coal swamps, both with megafossils and microfossils. Analysis of this process examined dynamics similar to those studied by both neocologists and paleoecologists evaluating Quaternary vegetation. A Late Carboniferous peat-forming mire may have taken up to 10,000 or more years to accumulate (White et al 1995, DiMichele et al 1996). Over such a long period, successional patterns may be seen both as repeated transitions between one vegetation type and another or as a directional pattern of vegetational change through the period of accumulation of the peat body (DiMichele & Phillips 1994). In the latter case, vegetational change was likely driven by changes in climate during peat accumulation or by changes in edaphic conditions brought on by thickening of the peat substrate.

Transition frequency analysis of data from coal-ball macrofossils, especially data on patterns of root penetration, have revealed patterns of succession in peat-forming mires. Raymond (1988) identified three plant communities in a Middle Pennsylvanian coal from Iowa: those dominated by cordaitan gymnosperms, those dominated by medullosan pteridosperms and marattialean tree ferns, and those dominated by arborescent lycopsids, in that order of temporal succession. Studies of peat preservation suggest that the three assemblages grew under different environmental conditions and followed one another as peat accumulated, showing only minor intercalations. The pattern suggests a strong environmental control on vegetational change during peat accumulation.

Pryor (1993) similarly found a directional trend in dominance patterns in a Late Pennsylvanian coal bed in Ohio. In this instance, subtree lycopsids were succeeded by pteridosperm and marattialean tree fern vegetation with extensive shrubs and a fern ground cover, which were then succeeded by a canopy of marattialean tree ferns. Although there were minor reversals of this pattern during peat accumulation, there was a clear overall temporal trend in patterns of dominance.

DiMichele & Phillips (1988) did not find such patterns of successional change in a profile analysis of a thick, late Middle Pennsylvanian coal seam from Illinois. Rather, they recorded a shifting pattern of recurrence among three major plant assemblages representing a very wet to less wet gradient. The different kinds of successional patterns in peat-forming environments depend on the particular geographic site sampled within the ancient swamp. Spatial variability in edaphic conditions, including proximity to clastic influx, variations in nutrient availability, and variation in topography exerted by subsurface geology, would have played a major role in vegetational recurrence patterns.

Palynological studies, combined with analyses of coal petrography and sedimentology, provide a powerful means of analyzing vegetational changes in

peat-forming mires and of correlating such changes with environmental controls. Such combined analyses were pioneered by Eble and colleagues and focused mainly on coal beds of the Appalachian Basin of the eastern United States (e.g. Eble & Grady 1993, Eble & Greb 1997, Eble et al 1999, Greb et al 1999b). Two broad patterns in peat accumulation, relative to environmental controls, were detected from these analyses. Many peat bodies appear to have accumulated under planar, or rheotrophic (nutrients come from groundwater sources), conditions in which water chemistry and depth were the major controlling factors on plant distribution (Cecil et al 1985). In such environments, vegetation was heterogeneous, and distinct patterns of vertical succession are not detectable. Vegetational dynamics in planar mires were described palynologically for numerous coals in tropical Euramerica (Mahaffy 1985, 1988; Bartram 1987; Grady & Eble 1990; Eble & Grady 1993; Willard 1993; Eble et al 1994; Hower et al 1994; Eble & Greb 1997, Eble et al 1999; Greb et al 1999b). Other peats showed patterns of vertical succession attributable to progressive doming of peats, in which hydrology was controlled almost entirely by rainfall. Such mires are described as ombrotrophic and find analogues among modern peats in the Indonesian archipelago (Anderson 1964).

Potonié & Koorders (1909), Leclercq (1926), and Teichmüller (1955) suggested that modern tropical peat accumulations could serve as models for Carboniferous coals. Smith (1962, 1964), however, was among the first to argue on the basis of palynological and petrographic profiles for domed mires during the Late Carboniferous. Patterns of directional, if sometimes oscillating, succession have been described that generally record a trend from lycopsid trees and pteridosperms to tree ferns and small lycopsids in upper layers of the peat (Eble & Grady 1990, Pierce et al 1991, Pierce et al 1993, Greb et al 1999a). As with coal ball macrofossil analyses, distinct assemblages have been recognized in association with the base of the coal, with mineral partings, and with different degrees of peat decay, suggesting relationships with nutrient availability, standing water, and even seasonality of rainfall.

In summary, vegetational analyses of tropical coal beds record the effects of climate during the period of peat accumulation. Both palynological and macrofossil analyses indicate that some peats accumulated under strong influences of ground water, masking the effects of directional climatic trends as long as water levels were sufficiently consistently high to support swamp vegetation. In such environments, sedimentological analysis may reveal climatic changes that separated benches of coal, recording an end to peat accumulation followed by reinitiation; such changes were often rapid and repeated. Other peats appear to have accumulated under conditions of consistently high rainfall and recorded directional successional trends related largely to the self-regulatory process of peat doming and progressive restriction of available nutrients.

Such fine resolution of long-term vegetational trends is not possible in most clastic depositional systems because of the considerable hiatuses in sediment accumulation and the taphonomic consequences of very short-term accumulation of plant debris (Gastaldo et al 1995, Wing & DiMichele 1995) in most floodplain

settings. It is possible, however, to evaluate these assemblages over longer time scales when the same (isotaphonomic) depositional settings have been preserved within fifth- and fourth-order cycles, particularly in coastal-deltaic regimes. Scott (1978) and Pryor & Gastaldo (2000), using finely split, layer-by-layer analysis, quantitatively examined patterns of vegetational change on floodplains and in clastic swamp habitats. They generally found compositional stability within a given setting, representing periods of accumulation of tens to hundreds of years, suggesting long-lived mature forests as the source vegetation.

Patterns of Persistence and Change During Glacial-Interglacial Fluctuations

The environmental signature of the Late Carboniferous and Early Permian, like that of the Holocene, was one of change. Glacial-interglacial fluctuations and their attendant climatic and sea level fluctuations were superimposed on yet longer-term climatic trends, reflecting patterns of atmospheric circulation, the slow movement of continental regions into different climatic zones, or transitions from globally cold to warm conditions. Consequently, from first principles, vegetation might be expected to respond by ever changing. This expectation has been confronted squarely by Quaternary paleoecology. In the temperate zones, particularly of the Northern Hemisphere, there is good evidence that plant species track climate individually, reflecting their individually evolved tolerances, rather than as part of integrated vegetational units (Webb 1988, Overpeck et al 1992). The pattern of environmental tracking is not so clear in the modern tropics, however. The study of long cores from Amazonia suggests some vertical movements of plants superimposed on a pattern of lowland vegetational persistence (Collinvaux et al 2000). The alternative hypothesis suggests that tropical vegetation broke up into a large number of refugia from which forests reexpanded (Burnham & Graham 1999).

As viewed from the Paleozoic, a major concern for all such analyses is what constitutes sameness in vegetational composition from temporal point to point. If temporally successive assemblages appear to be drawn from the same species pool or biome but in different proportions, do they constitute nonanalogue assemblages? What is the standard? How different must two assemblages be to be considered "different"? Studies of ancient marine communities attempted to answer some of these questions (Bennington & Bambach 1996, Bennington & Rutherford, 1999), but a solution remains elusive (Ivany 1999).

In Late Carboniferous terrestrial systems, the concept of sameness was partly or perhaps largely defined by contrasts between very different vegetation types that succeeded each other temporally. Changes from one vegetation type to the other occurred relatively rapidly on all scales of spatiotemporal resolution in all paleogeographic provinces, although they were resolved at different levels in each province on the basis of the degree of study and the nature of available fossils. In the Euramerican tropics, such changes have been identified on several spatial

scales: within the lowland-wetland species pool or biome at the Westphalian-Stephanian boundary (Pfefferkorn & Thomson 1982, Phillips & Peppers 1984), between the wetland biome and the seasonally dry biome during the Early Permian (Fredericksen 1972, Broutin et al 1990, DiMichele & Aronson 1992), and between the seasonally dry and seasonally wet biomes during the late Early Permian (Ziegler 1990, DiMichele et al 2001). In the Angaran Province, significant vegetational change has been recognized mainly at the biome level during the transition from the Early to the Late Carboniferous (Meyen 1982). In Gondwanaland, such changes have been described mainly at the level of biomes, particularly at the transition from the Carboniferous to the Permian (Retallack 1980, Archangelsky 1990, Cúneo 1996), although smaller-scale patterns within species pools have been discussed (Archangelsky 1990). Alleman et al (1995) described seven different plant communities from strata in a single section that nevertheless represent a single ecological landscape that did not change while these beds were deposited.

Stability and Instability Within a Biome The concept of changing vegetation in the face of glacial-interglacial oscillation is most firmly established for the late Pleistocene and Holocene temperate zone. Thus, the place to look for such patterns in the Late Carboniferous and Permian is in the temperate regions. Archangelsky (1990) stated the following: “In Gondwana, Carboniferous and Early Permian strata show drastic changes of floral assemblages through successive plant horizons. This pattern defines Gondwana as a Late Paleozoic floristic unit characterized by continuous migrational flows...” He attributed this finding to continental mobility and associated paleoclimatic changes. This comment suggests a temperate-zone vegetational response not unlike that recorded in the Holocene.

In contrast to this pattern, the tropics of Euramerica recorded patterns of long-persistent vegetational associations in peat-forming environments during the Westphalian and again in the Stephanian, but on a different compositional theme (Phillips et al 1985, DiMichele et al 1996). From one coal bed to the next, each separated by climatic and sea level changes (Cecil 1990), similar vegetational gradients and basic intramire community associations can be identified quantitatively. Such persistent associations were not compositionally identical but appear to have been drawn repeatedly from the same species pool in roughly the same proportions, with some notable comings and goings as a consequence of species turnover through background extinction. Gradients of taxa by environmental variables were conserved.

During such periods of vegetational stability, species turnover was strongly confined to ecomorphic themes, such that the loss of a lycopsid tree from low-diversity, flooded habitats resulted in replacement by a congener. Similarly, extinction of a medullosan pteridosperm or a cordaite species also resulted in replacement within the ecological fabric by an ecomorphic congener or close relative within the same phylogenetic lineage (DiMichele & Phillips 1996b). Coal ball studies suggest that

ecomorphic replacement and general preservation of ecological structure occur with background extinction levels of 10% or less (DiMichele & Phillips 1996b). Such low levels of background extinction may permit the fabric of species interactions to remain intact, thus exerting strong influence on species replacement dynamics.

Similar patterns were found in flood basin environments during this same period at the level of large-scale changes within the tropical wetland species pool (Pfefferkorn & Thomson 1982). Data from compression fossils recorded in cores through European coal basins revealed a pattern much like that of the coal beds themselves, of repeated similar vegetational associations through the early part of the Late Carboniferous (Purkynová 1977, Havlena 1982). Analysis of species turnover also revealed that vegetation can tolerate about 10% turnover and remain structurally intact (Gastaldo et al 1998).

What happened to vegetation between the coal-forming intervals? Did it migrate intact to other areas outside of the sampling window of the depositional realm? Did it break up into isolated refugia from which it emerged once regional climate became favorable again? Presently, such questions cannot be answered. A hint may be gained from deposits such as that of the Hamilton Quarry, a Late Pennsylvanian deposit from Kansas (Rothwell & Mapes 1988, Cunningham et al 1993). The Hamilton deposit appears to have formed during a time of regional seasonal dryness and lowstand, and it includes conifers and other elements of dry-habitat vegetation. It also includes typically Carboniferous wetland plants that may have been living along wet stream bottoms in refugia.

Rapid Changes in Vegetational State Within a Biome Near the boundary between the Middle and Upper Pennsylvanian, approximately the boundary between the Westphalian and Stephanian, the tropical lowlands experienced a major plant extinction and subsequent change in patterns of vegetational dominance and diversity. These changes appear to be a consequence of rapid changes in climate, probably caused by a pulse of global warming (Frakes et al 1992) associated with strong drying throughout much of the tropics (Phillips & Peppers 1984, Cecil 1990, Winston 1990). The changes that occurred, although major when examined quantitatively in terms of both species extinction and change in ecological structure and dynamics, were clearly confined to lowland-wetland vegetation and represent a reorganization of that particular species pool within its distinctive set of ecological and edaphic tolerances.

The pattern, first identified by Phillips et al (1974) on the basis of coal palynology, involves a major extinction of the dominant lycopsid trees and their replacement by marattialean tree ferns. A similar change has been documented in compression fossils of North America, although with taxonomic resolution somewhat lower than that from coal balls (Gillespie & Pfefferkorn 1979). In both compression and coal ball assemblages, tree ferns began to rise in quantitative importance before the extinction, but they did not reach dominant levels until afterward (Pfefferkorn & Thomson 1982, Phillips et al 1985, Willard & Phillips

1993, Pryor 1993). The dominance-diversity changes occurred in a rapid but time-transgressive manner from west to east across the Euramerican tropics (Phillips & Peppers 1984), but they never happened in parts of China, where Westphalian-type floras persisted into the Late Permian (Guo 1990, Chandra & Sun 1997). Macrofossil studies indicate a species loss in coal swamps through this transition of approximately 67% (DiMichele & Phillips 1996a), including 87% of the tree species.

Detailed study of the vegetational characteristics of the extinction, on a coal-by-coal basis, is limited to coal palynology. Through a sequence of seven coals (all lacking coal ball macrofossils), Peppers (1985) documented high variability among dominant elements. Dominants varied among the lycopsid tree *Sigillaria*, the marsh-forming lycopsid subtree *Chaloneria*, and several kinds of tree ferns, with locally abundant calamites and pteridosperms. Patterns stabilized later in the Stephanian with the rise of marattialean tree ferns of several species and subdominance of pteridosperms and calamites.

Several structural ecological changes were brought about by the extinction. These included shortening of the wet-dry gradient through extinction of the lycopsid tree *Lepidophloios*, which colonized standing-water habitats; homogenization of lowland landscapes to dominance by tree ferns and pteridosperms in most habitats in both flood basins and peat swamps; increased stem diameters and inferred tree sizes of pteridosperms, trees ferns, and sphenopsids relative to their Westphalian ancestors; and a decline of nearly 50% in species diversity in coal swamps (DiMichele & Phillips 1996a, 1996b).

Tree ferns of the Westphalian were largely opportunistic weeds, although larger, stand-forming species began appearing in the latest Westphalian (Pfefferkorn & Thomson 1982, Lesnikowska 1989). DiMichele & Phillips (1996b) suggested that the extinction removed patterns of incumbent advantage and permitted a lottery-like period of ecological and evolutionary escalation, much as Vermeij (1987) described for marine ecosystems after periods of major extinction. The resulting advantage went to opportunistic species capable of rapid exploitation of the disrupted landscapes and large pools of available nutrients. Marattialean tree ferns produced massive quantities of spores, were cheaply constructed, and as a group had wide ecological tolerances. Such taxa have the ability to colonize physical space and expropriate resources rapidly in ecological time, which may have given them an advantage in evolutionary time as well.

The increase in size among virtually all plant groups that survived the extinction is reminiscent of the size changes seen among plants that colonize islands (Carlquist 1974). It is possible that in a fragmented, postextinction landscape associated with considerable release from competitive, stabilizing selection, size increases were made possible by relaxation of long-standing constraints. Any explanation of this phenomenon must account for its occurrence across clade lines. It is possible that changing concentrations of atmospheric gases, particularly CO₂ (Berner 1998), resulted in higher growth rates and biomass production.

Cold Interval-Warm Interval Transition: Interactions Between Biomes

Beginning in the Stephanian, throughout the Euramerican tropics, floras appeared that were clearly distinct in taxonomic composition from those of the wetlands and were associated with indicators of seasonally dry climates (Mapes & Gastaldo 1987, Broutin et al 1990, DiMichele & Aronson 1992). These “extrabasinal” floras (see Pfefferkorn 1980) were initially few and were intercalated as distinct beds among typically Late Carboniferous floras. This pattern suggests that the climatic excursion at the Westphalian-Stephanian boundary was the first in a series of oscillations that began to dry and warm the tropics, whereby the pulses of warming and drying brought an upland, or extrabasinal, flora into the basins and thus into the depositional and preservational window (Cridland & Morris 1963). By the middle Early Permian, the trend toward drying and warming was clearly established and associated with a marked change in the flora throughout most of the tropics except in China (Fredericksen 1972, Knoll 1984).

The new flora was dominated by seed plants, including conifers, pteridosperms, ginkgophytes, and cycads. It was notably poor in ferns, lycopsids, and sphenop-sids, which were the framework plants of Late Carboniferous assemblages. The seasonally dry biome underwent significant changes through time (Read & Mamay 1964) due to gradual species turnover. Thus, this biome had internal dynamic properties not unlike those of the tropical wet biome and represented a distinct species pool, one having almost nothing in common with the ever-wet biome at the species level. The contrast between modern tropical wet and seasonally dry biomes is similarly sharp (Ziegler 1990).

The new flora made its earliest appearances in the early mid-Westphalian (Westphalian B or Duckmantian). Scott & Chaloner (1983) and Scott (1984) described fusinized remains of conifer foliage from a typical lowland-wetland assemblage. Lyons & Darrah (1989) tabulated the occurrences of all pre-Stephanian conifer fossils and found that all are preserved as charcoal and all occur in basins proximate to contemporaneously rising upland regions. This finding suggests that the charcoal was formed in fires in the highlands and transported into the adjacent basins. Conifer remains, because of their robust character and distinctive architecture, are more easily recognized than other elements of the flora that might be preserved as charcoal and serve as signature plants for this seasonally dry biome. The early conifer fossil record indicates that the two biomes existed side by side in the tropics much earlier than the first occurrences of well-preserved macrofloras would indicate.

As drying in the tropics continued, the seasonally dry biome was further replaced in the lowlands by a flora adapted to still drier but perhaps seasonally wet conditions. DiMichele et al (2001) described a flora from the latest Early Permian of Texas that preserved a number of taxa previously known only from the Mesozoic, including the conifer *Podozamites*, the cycad *Dioonitocarpidium*, and

Agathis-like conifer seeds. These were mixed with a number of taxa characteristic of the Late Permian Zechstein flora (Schweitzer 1986), including the conifers *Ullmannia* and *Pseudovoltzia*, and the possible cycad *Taeniopteris eckhardtii*. The Zechstein flora, known from the Late Permian of Germany and England, preserved other typically Mesozoic elements.

A significant aspect of this new flora is its implications regarding the Permian-Triassic extinction on land. Retallack (1995) presented evidence for major devastation of terrestrial environments at this time in Earth's history, and his findings from the Southern Hemisphere have been extended to Europe (Looy et al 1999). The occurrence of distinctly Mesozoic elements in the Early and Late Permian, however, indicates that many lineages survived this devastation, which may have had its strongest effect in the basinal lowlands and hence on those sites in which fossil assemblages are preserved most commonly (Gastaldo et al 1995). Colonization of the lowlands by conifers, cycadophytes, and pteridospermous seed plants in the later Triassic and Jurassic obviously did not occur by reevolution of these Paleozoic taxa; rather, migrations from extrabasinal refugia must have fueled the recovery.

FINAL COMMENTS

In a recent paper, Paine et al (1998) noted that multispecies assemblages have evolved in the presence of disturbance and could likely accommodate even very large, infrequent disturbances if they were within the typical range of disturbance intensity. These authors suggested that major changes in the fundamental state of an ecosystem would result from compound perturbations that prevent a system from recovering and permanently change its structure. The terrestrial fossil record supports their basic conclusions. As reviewed above, species pools, recognized largely as biomes, appear to be stable associations for long periods. Biomes replace each other in space as a consequence of major climatic changes. Within such species pools there are various degrees of assemblage stability in time and space. Changes from one state to another—changes in dominance-diversity pattern and taxonomic composition—within a biome appear to correlate with environmental changes of great magnitude that bring about extinction levels that exceed background levels.

The fossil record also sheds light on the debate regarding community stability, that is, the classic Clementsian-Gleasonian dichotomy: Do multispecies assemblages have emergent group properties, or are they happenstance associations? In the temperate zone, species individualism seems to be the rule on virtually all scales of time and space, as long as there is significant climatic fluctuation over time to act as a forcing mechanism. In the tropics, species assemblages appear to be more persistent and may have emergent properties, such as those seen in ecomorphic species replacement patterns brought about by incumbency and niche partitioning. Only by examining the compositional and quantitative patterns of assemblages over intervals of geological time can such patterns be glimpsed, even dimly.

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