Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations

William A. DiMichele [a,*], Hermann W. Pfefferkorn [b], Tom L. Phillips [c]

[a] Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC 20560, USA
[b] Department of Geology, University of Pennsylvania, Philadelphia, PA 19104, USA
[c] Department of Plant Biology, University of Illinois, Urbana, IL 61801, USA

Abstract

The Late Carboniferous glaciation reached its peak during the latter part of the Westphalian (late Desmoinesian). In the tropical Illinois basin this was the time of deposition of the Carbondale and lower Modesto Formations, characterized by the cyclic repetition of major coal deposits, black shales, limestones, gray shales and sandstones. These lithological changes evidence repeated major fluctuations in climate and sealevel. Fossil floras from the tropical ever-wet to seasonally wet terrestrial lithofacies, coals and shales above coals, remain compositionally similar throughout the 1–1.5 m.y. time interval.

Floras from coals, known from coal balls and palynology, characteristically were composed of three major plant communities: the wettest sites were dominated by monocarpic lycopsids, intermediate sites were dominated by polycarpic lycopsids, and areas subject to fires and intermittent flooding were dominated by medullosans and the small lycopsid *Paralycopodites*. Clastic-substrate environments were dominated by ferns and pteridosperms and conform to a single biozone, indicating their compositional unity and distinctness from earlier and later assemblages. The composition of lowland floras is poorly known from times between the deposition of coals and associated terrestrial rocks, intervals during which most of the lowlands were flooded and marine rocks were being deposited. Consequently, the temporally intermittent recurrence of lowland floras despite repeated, widespread environmental disruption may be explained either by vegetational persistence and migration of floras, or repeated disruption and reassembly. Several lines of evidence suggest persistence as a likely explanation.

1. Introduction

The Late Carboniferous is one of two great glacial ages that have occurred since colonization of the land by vascular plants (Frakes et al., 1992). The other of course is the Recent, where the effects of glacial waxing and waning have left a marked imprint on the faunas and floras of the globe. The

Carboniferous, therefore, may help us greatly in understanding the ways in which biota respond to widespread, repetitive environmental disruptions. As a point of comparison, the Late Carboniferous differs from the Recent in several major ways: species composition is entirely distinct; landscapes were codominated by several major lineages of plants (lycopsids, ferns, sphenopsids, seed plants) rather than seed plants alone; and levels of insect and tetrapod herbivory were significantly lower

* Corresponding author.

Shale - gray, sandy at top; contains marine fossils and sideritic concretions, particularly in the lower part

Marine Limestone

Marine Shale - black, hard, fissile; contains large spherodial concretions

Marine Limestone

Shale - gray, silty, pyritic and sideritic concretions and plant fossils common at base; marine fossils rare

Coal - locally contains claystone or shale partings

Underclay - gray, darker at top, calcareous in lower part

Shale - gray, sandy

Sandstone - fine grained, micaceous, occurs as nonchannel rippled-bedded facies gradational at base, or as channel facies with erosional base
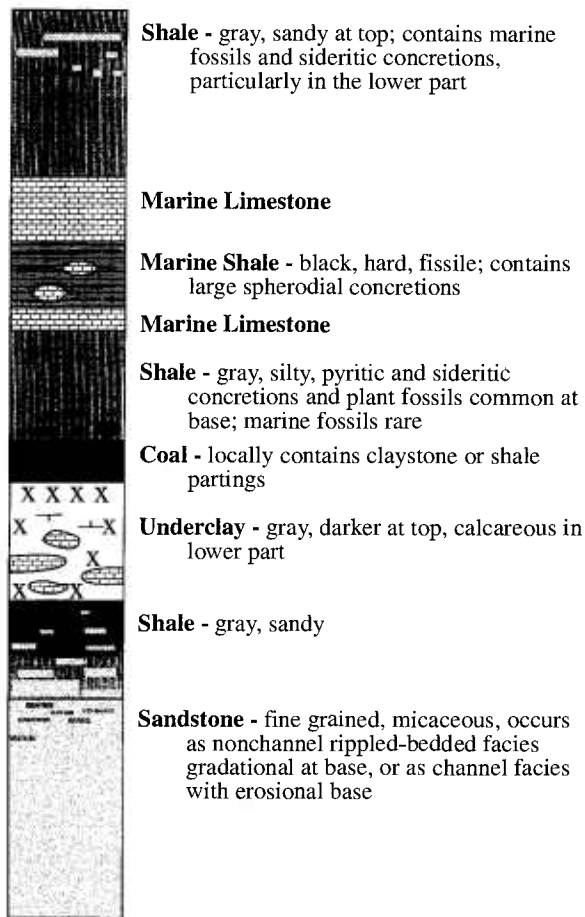
Fig. 1. Idealized Illinois-type cyclothem characteristic of the rock sequence associated with the major economic coals of the Carbondale Formation.

than at any later time (DiMichele and Hook, 1992). Consequently, comparison of Late Carboniferous and Recent vegetational responses to environmental change may help reveal ecological generalities about vegetational dynamics.
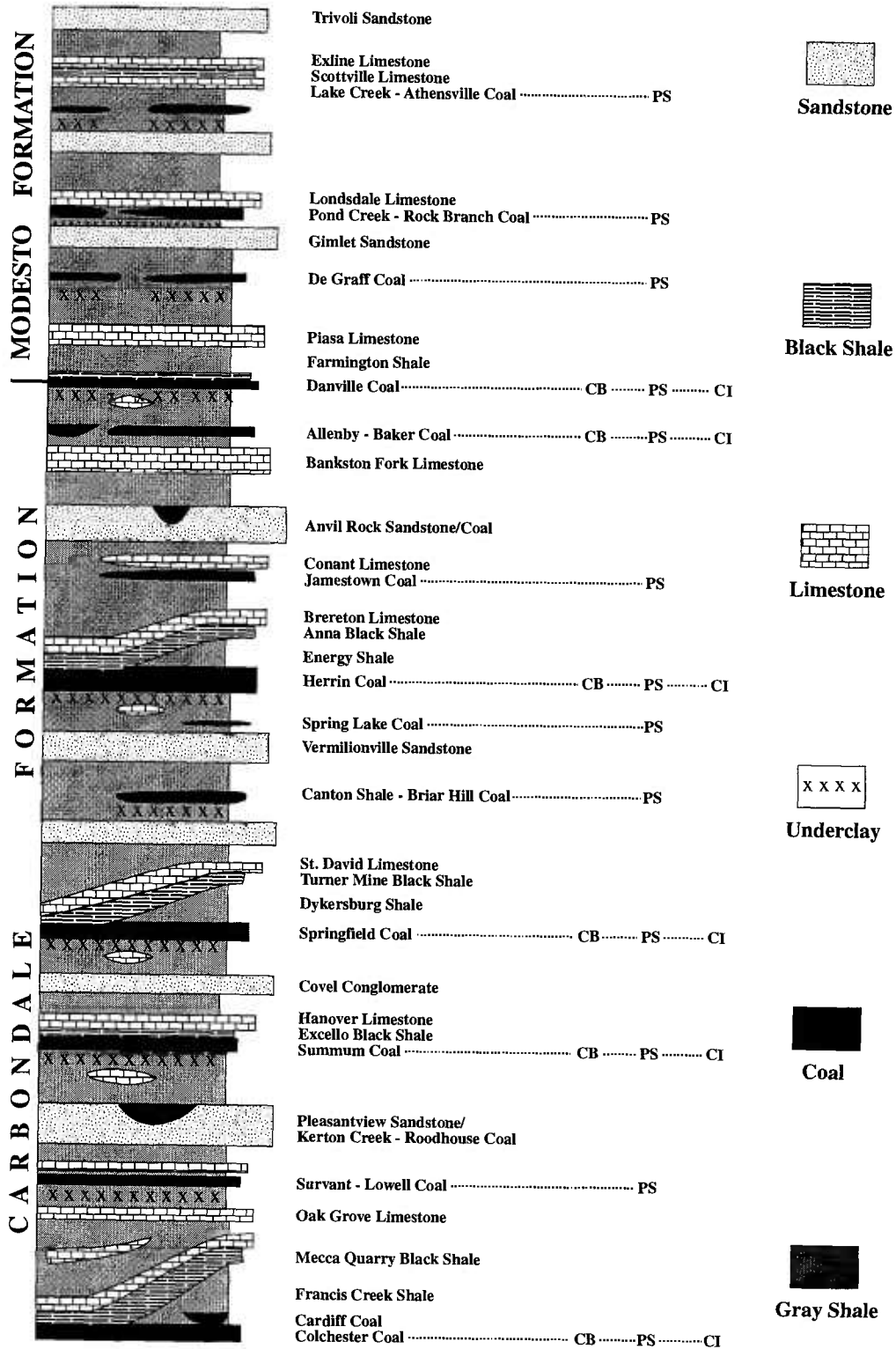
Late Carboniferous glaciations were centered in Gondwana, however, the effects of those glaciations were certainly seen and felt in the tropics, manifested as eustatic sealevel fluctuations and repetitive climatic changes (Heckel, 1989; Cecil, 1990). The location of Euramerica in the Late Carboniferous tropical rainy belt led to the formation of vast lowland peat-forming mires, the source of much of the modern coal deposits in eastern North American and western Europe. Partly as a result of coal exploitation and the exposure of large numbers of plant fossils, the vegetational record of the Late Carboniferous tropics is extensive. In fact, there may be more data on the floras and vegetational fluctuations of the Late Carboniferous tropics than on the modern tropics during glacial–interglacial cycles of the Recent. Both petrified and compressed macroplant remains and pollen-spore microfossils in a wide range of depositional settings reveal a complex vegetation and permit it to be tracked through a period of over 15 m.y. duration (Klein, 1990).

One of the most conspicuous attributes of Late Carboniferous floras is their persistence for extended periods of time. Persistent species associations have made floral biostratigraphy important in many Carboniferous terrestrial sequences (Read and Mamay, 1964; Wagner, 1984; Gillespie and Pfefferkorn, 1979), and permitted the coals from different parts of the section to be characterized both with pollen and spores and with macrofloral assemblages (Peppers, 1985; Phillips et al., 1985). These floristic patterns have been translated into community paleoecological analyses through temporally significant intervals of the Late Carboniferous (Phillips et al., 1974; Pfefferkorn and Thompson, 1982; DiMichele and Phillips, 1995). Most long-term ecological studies have focused on changing vegetational patterns. Vegetational persistence, like evolutionary stasis, is worthy of note and study in its own right, particularly when it occurs during a time period of known global environmental change.

The Late Desmoinesian (late Westphalian D; late Middle Pennsylvanian) was a time during which classic "cyclothems" developed in the midcontinent United States (Fig. 1). In the Illinois Basin there were repeated episodes of peat formation, represented today as coals, followed by inundation and deposition of freshwater and marine

Fig. 2. Lithologic composition of the Carbondale and lower Modesto Formations of the Illinois Basin. Collections noted by letter designations: CB = coal balls, PS = pollen and spores, CI = compression and impression assemblages.

Trivoli Sandstone

Exline Limestone
Scottville Limestone
Lake Creek - Athensville Coal ·································· PS

Sandstone

Londsdale Limestone
Pond Creek - Rock Branch Coal ····························· PS
Gimlet Sandstone

De Graff Coal ·· PS

Piasa Limestone
Farmington Shale
Danville Coal ································· CB ········ PS ········ CI

Black Shale

Allenby - Baker Coal ······················· CB ·······PS ··········· CI
Bankston Fork Limestone

Anvil Rock Sandstone/Coal

Conant Limestone
Jamestown Coal ··· PS

Limestone

Brereton Limestone
Anna Black Shale
Energy Shale
Herrin Coal ····························· CB ········ PS ········· CI

Spring Lake Coal ····························PS
Vermilionville Sandstone

Canton Shale - Briar Hill Coal ····················PS

| x x x x |

Underclay

St. David Limestone
Turner Mine Black Shale
Dykersburg Shale
Springfield Coal ························· CB ········· PS ·········· CI

Covel Conglomerate

Hanover Limestone
Excello Black Shale
Summum Coal ···················· CB ········ PS ·········· CI

Coal

Pleasantview Sandstone/
Kerton Creek - Roodhouse Coal

Survant - Lowell Coal ····························· PS

Oak Grove Limestone

Mecca Quarry Black Shale

Francis Creek Shale

Cardiff Coal
Colchester Coal ····························· CB ········PS ··········CI

Gray Shale

clastics, and marine limestones. Here we focus on the floras from coals and terrestrial shales and examine their patterns of persistence during this time period.

2. The Carbondale and lower Modesto Formations

The Carbondale Formation encompasses the principal mineable coal resources of the Illinois Basin. Rocks are of late Desmoinesian age, equivalent to the late Westphalian D or upper Moscovian in European Carboniferous terminology. The Desmoinesian–Missourian contact, which is approximately equivalent to the Westphalian–Stephanian contact (Peppers, 1985), is in the lower part of the Modesto Formation (Fig. 2). Where possible, we will consider vegetational patterns as they occur up to the end of the Desmoinesian, and hence into the lower Modesto Formation. Correlations within the Illinois Basin are presented in Nelson et al. (1991), and with other major Pennsylvanian-age basins in the United States and Europe by Peppers (1985).

2.1. Lithologic characteristics

The Carbondale Formation is dominated by the cyclic repetition of distinctive lithologies in characteristic patterns of superposition (Fig. 1). Many units are widely traceable, particularly the coals, black shales and limestones. The formation contains five major coals (Fig. 2), which in stratigraphic order are the Colchester coal at the base, the Summum coal (also called the Houchin Creek), the Springfield coal, the Herrin coal, and the Danville coal at the top (Willman et al., 1975). Most of the major coals are overlain by a similar sequence of lithologies: black, sheety marine shale, marine limestone, and marine gray shale. Locally, gray mudstone wedges of freshwater or brackish origin may lie between the top of the coal and the overlying marine unit. Such gray mustones apparently originated as overbank deposits from channels that were active contemporaneously with and immediately after coal deposition (Hopkins, 1958, 1968; Johnson, 1972; Eggert, 1982). Below each major coal is a well developed underclay.

A number of minor coals or coal horizons occur in the Carbondale. Named ones include the Cardiff coal, Survant-Lowell coal, Roodhouse-Kerton Creek coal, Briar Hill coal, Spring Lake coal, Jamestown coal, and Allenby-Baker coal; there are additional thin but laterally extensive coals throughout the section. Several small coals (correlations are uncertain) occur in the Desmoinesian portion of the lower Modesto Formation (Willman et al., 1975) and include the De Graff, Rock Branch-Lake Creek, and Pond Creek-Athensville coals. Several of the minor coals are overlain by black shale and-or limestone, repeating in miniature the patterns seen for the more widespread units. In other cases coals are very restricted and appear to represent localized channel fills (Willman and Payne, 1942; Wanless, 1957; DeMaris et al., 1983).

2.1.1. Depositional patterns in the late Desmoinesian

Much has been written about rocks of the Carbondale Formation, and considerable debate has ensued in an attempt to explain the much heralded and overstated regularity of lithologic reiteration, first recognized by Udden (1912). The debate on this subject has been polarized, focused more on the processes by which such repetitive patterns originated rather than on the repetition itself. A "cyclothem" school has focused on allogenic processes, principally eustatic sea-level fluctuations related to Gondwanan glaciations, which are argued to cause recurrent patterns of deposition on the low-gradient craton (Wanless and Shepard, 1936). The cyclothem model began to drift toward typology, leading to the concept of the "ideal" cycle and cyclothems as the basis of stratigraphic nomenclature (Kosanke et al., 1960). Recently, the concept has been rescued and retrieved, with more convincing focus on external forcing mechanisms and greater consideration of associated depositional environments (Wanless and Wright, 1978; Boardman et al., 1984; Heckel, 1989). The ideal cyclothem concept prompted a response from sedimentologists and a "delta" school developed, in which local, autogenic depositional processes related to delta-lobe progradation and abandonment were deemed wholly sufficient to explain

lithologic repetition (Elliot, 1968, 1969; Ferm, 1975; Horne et al., 1978). These deltaic models were developed almost entirely on the basis of coal-bearing sequences deposited in rapidly subsiding basins near rising source areas, such as the Appalachians. Many of the geologists working in the Illinois Basin understood the fluvial–deltaic genesis of clastic rocks there, but recognized that low gradients and restricted sediment input would permit the allogenic processes inherent in cyclothemic models to show through the local sedimentology (Hopkins, 1958, 1968; Zangerl and Richardson, 1963; Wanless et al., 1963, 1969, 1970; Johnson, 1972; Heckel, 1980; Eggert, 1982; Burk et al., 1987; and especially Wanless and Wright, 1978).

Rocks of the Carbondale and lower Modesto Formations were deposited on a low-gradient shelf or ramp with little relief (Nelson et al., 1991), distant from the sediment source areas in the tectonically active Appalachians and the Canadian Shield. Low sea-level at the end of the Mississippian (Hallam, 1992) resulted in deep erosion and development of an irregular surface throughout much of the Illinois Basin (Bristol and Howard, 1971, 1974; Howard, 1979), but by Desmoinesian time this topographic relief was mostly filled in. Tectonically active areas included the Du Quoin Monocline in southwestern Illinois and several positive areas, part of the LaSalle Anticlinorium, in east-central Illinois. Activity on these structures was minor during Desmoinesian time (Kolata and Nelson, 1991). The resultant low-gradient permitted sea-level changes to affect large areas of the craton; many lines of evidence indicate that widespread rock units were minimally time transgressive, probably deposited nearly synchronously throughout their extents (Nelson et al., 1991). In this physical setting sea-level fluctuations and climate, which are partially correlated, would be expected to have had major impact on sedimentary patterns. Coals are assumed to have formed at times of sea-level lowstand or during the initial phases of transgression (Heckel, 1980).

Recent studies have detected indications of tidal deposition in sandstones and mudstones associated with Carbondale coal seams (Burk et al., 1987;

Breyer, 1992). In combination with invertebrate and trace fossil evidence, tidal features indicate that terrestrial clastics, in particular gray roof shales associated with channels, may have formed on prograding coastlines subject to brackish influence. Such roof shales, and their enclosed plant and animal fossils, therefore, preserve near-shore environments rather than alluvial plains from continental interiors.

2.2. Allogenic controls on deposition

Evidence is now overwhelming that Gondwanan glacial dynamics and continental configurations interacted to control tropical sealevel and climatic fluctuations (Caputo and Crowell, 1985; Veevers and Powell, 1987; Crowley and Baum, 1991, 1992; Frakes et al., 1992). However, attempts to correlate individual eustatic events globally, or to deduce the extent and details of climatic change or fluctuations in atmospheric composition are problematic. A major complication may be local tectonics; Drummond and Wilkinson (1993) argue that within a single eustatic event local tectonic activity can cause the appearance of several apparent "cycles." Nonetheless, given the evidence of glaciation, it can be assumed safely that eustatic sea-level fluctuations are recorded in the rock record (Heckel, 1986, 1989; Ross and Ross, 1988). Their apparency is dependent on proximity to sediment source, gradient, and regional tectonic activity (Heckel, 1989; Ferm and Weisenfluh, 1989; Willard and Klein, 1990; Klein, 1992; Staub and Richards, 1993; Staub and Esterle, 1993). Climate also has been inferred to have had a major effect on lithologic patterns (Phillips and Peppers, 1984; Ziegler, 1989; Cecil, 1990; Winston, 1990; Suchy and West, 1991; Miller and West, 1993), again most recognizable in areas distant from orogenic belts (Klein, 1992; Cecil et al., 1993).

The Carboniferous glacial maximum occurred during the Westphalian with ice apparently in eastern Angara (Siberia), in the Northern Hemisphere, as well as Gondwana, in the Southern Hemisphere (Frakes et al., 1992). Thus, the Carbondale and lower Modesto Formations were deposited in the tropics during a period of extensive continental glaciation near the poles. It is likely

that glacial fluctuations during this time would have caused variations in global sea-level, estimated in the range of 50–150 m (Heckel, 1977; Gerhard, 1991; Crowley and Baum, 1991; Klein, 1992). Heckel (1989) has constructed a sea-level history for the North American Western Interior based on a detailed framework of correlation, with hypotheses of water depth tied directly to specific lithologies (Heckel, 1980). The pattern of fluctuations proposed by Heckel, and illustrated in his Fig. 2, provides the geographically closest estimate to the Illinois Basin. A plot of sea-level in the Illinois Basin using Heckel's criteria (Fig. 3) reveals a pattern similar to that inferred for the succession of rocks in the Western Interior.

According to Ziegler et al. (1987) icehouse intervals (times of low atmospheric CO_2 and global glaciation), such as the Westphalian, were times when the tropical rainy belt was strongly confined to the intertropical convergence by global atmospheric circulation patterns. Based on the distribution of coal resources, Phillips and Peppers (1984) drew a more detailed "wetness" curve and inferred that the late Westphalian was the time of "maximum wetness" in the Illinois Basin. Cecil (1990) has since proposed a yet more refined method for assessing regional climate. He argues that coals form during periods of perennially wet climates; carbonates and evaporites form in dry climates, with clastic deposition reaching its maximum during times of seasonal rainfall in warm climates. Using Cecil's criteria, much of the lithologic variation attributed to eustacy by Heckel (1989) could reflect climatic fluctuations (Fig. 4).

Clearly climate and eustacy should covary on some large spatial scale, given that both will be influenced by the waxing and waning of polar glaciers (Suchy and West, 1991). Tectonics also must be given due consideration, however. Even if tectonic activity were somehow responsive to distant glacial activity, the expected covariation with climate and eustacy should be minimal. Thus, tectonic factors remain wild cards, strongly affecting lithologic patterns but in ways dependent on the nature of sediment input, which will be linked to climate and eustacy. Many of the minor coals of the late Desmoinesian, for instance, could have formed during periods when tectonic activity

caused changes in local base level during otherwise stable times of climate or sea-level. In effect, apparently distinct coal seams would, in fact, be continuations of peat deposition interrupted by a momentary change in local base-level brought on by tectonic activity such as syndepositional growth faulting (Ferm and Weisenfluh, 1989).

3. Absolute time and duration

Estimation of absolute duration of the Carbondale and lower Modesto Formations is necessary to facilitate comparison with Recent analogues. Even though radiometric ages of Pennsylvanian beds are increasingly common, there are not yet enough dates to establish reasonably precise ages for all stage boundaries. Therefore, we have to use other considerations to establish the possible and probable lengths of the time interval under consideration.

The general length of the Late Carboniferous, combined with some other factors, can help bracket the time interval during which the Carbondale and lower Modesto Formations were deposited. If the overall length of the Carboniferous is taken to be 34 m.y. (19 m.y. after Klein, 1990), and it is divided by the number of recognized terrestrial stages (ten in the European chronostratigraphy; nine for the time interval considered by Klein, 1990), the mean duration is estimated to be 3.4 m.y. per stage (2.1 m.y. following Klein, 1990). The Carbondale and lower Modesto Formations represent the latter half of the Westphalian D Stage. Thus the time required to deposit this formation would be around 1.7 m.y. (850,000 yr following Klein, 1990). It is well known that stages or systems can be shorter or longer than the mean; however, this particular calculation is useful in evaluating the reasonableness of other estimates.

Another way to approach the age, duration, and rate questions is to look at a single "cyclothem." As throughout the geological record, time will be represented mostly by gaps. However, some parts of this "cyclothem" represent continuous deposition and can be used to make an estimate of minimum duration. We will consider the "ideal
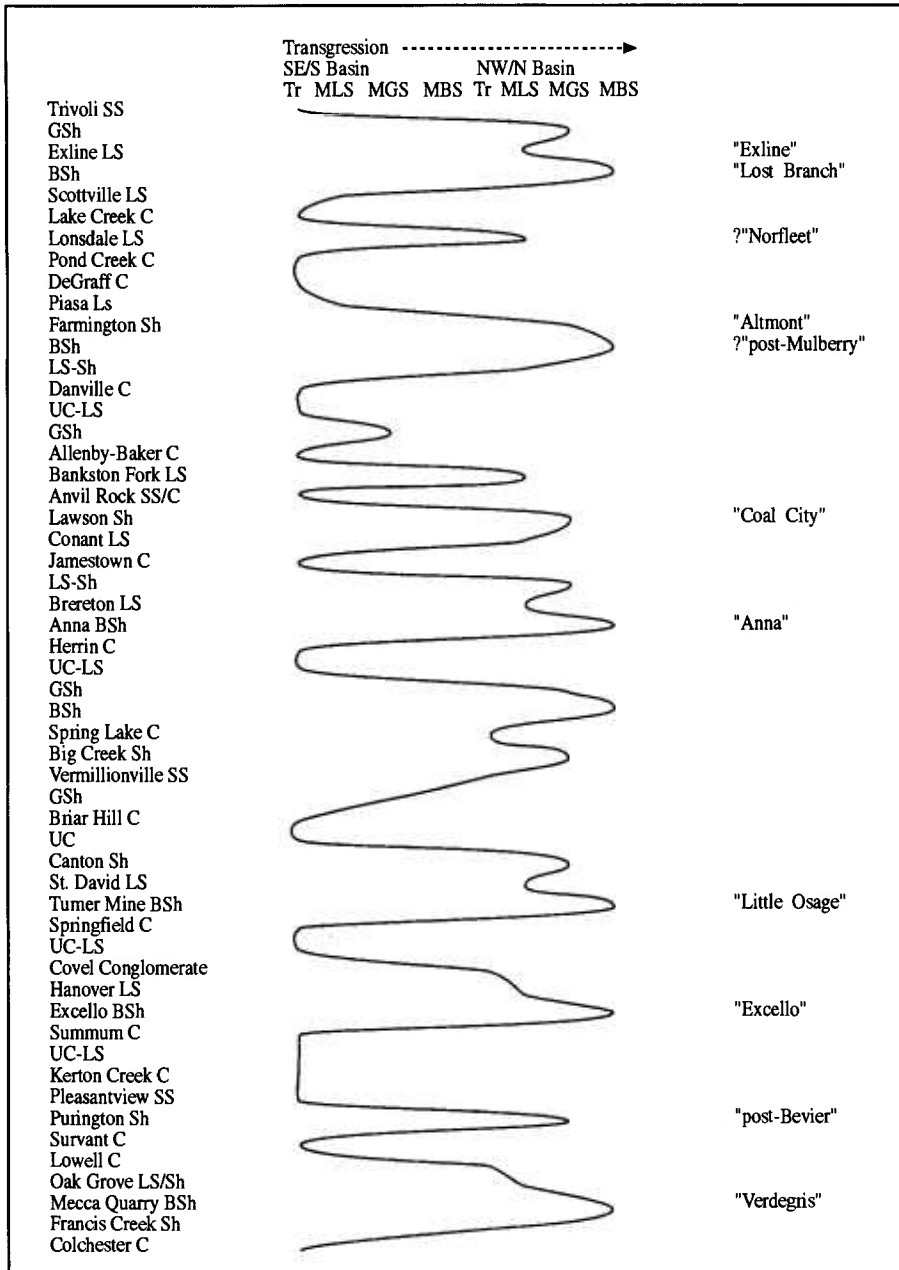
Fig. 3. Inferred sealevel fluctuations during the late Desmoinesian, using the criteria of Heckel (1989). Direction and extent of transgression are generalized from the southeast/southern part of the basin to the northwest/northern part of the basin. Suggested correlations with the inferred midcontinent highstands of Heckel (1989) shown on right. $Tr =$ terrestrial coals and mudstones; $MLS =$ marine limestones; $MGS =$ marine gray shales; $MBS =$ marine black shales. In stratigraphic column, $SS =$ sandstone, $Gsh =$ gray shale, $Bsh =$ black shale, $Sh =$ shale, $LS =$ limestone, $C =$ coal, $UC =$ underclay.
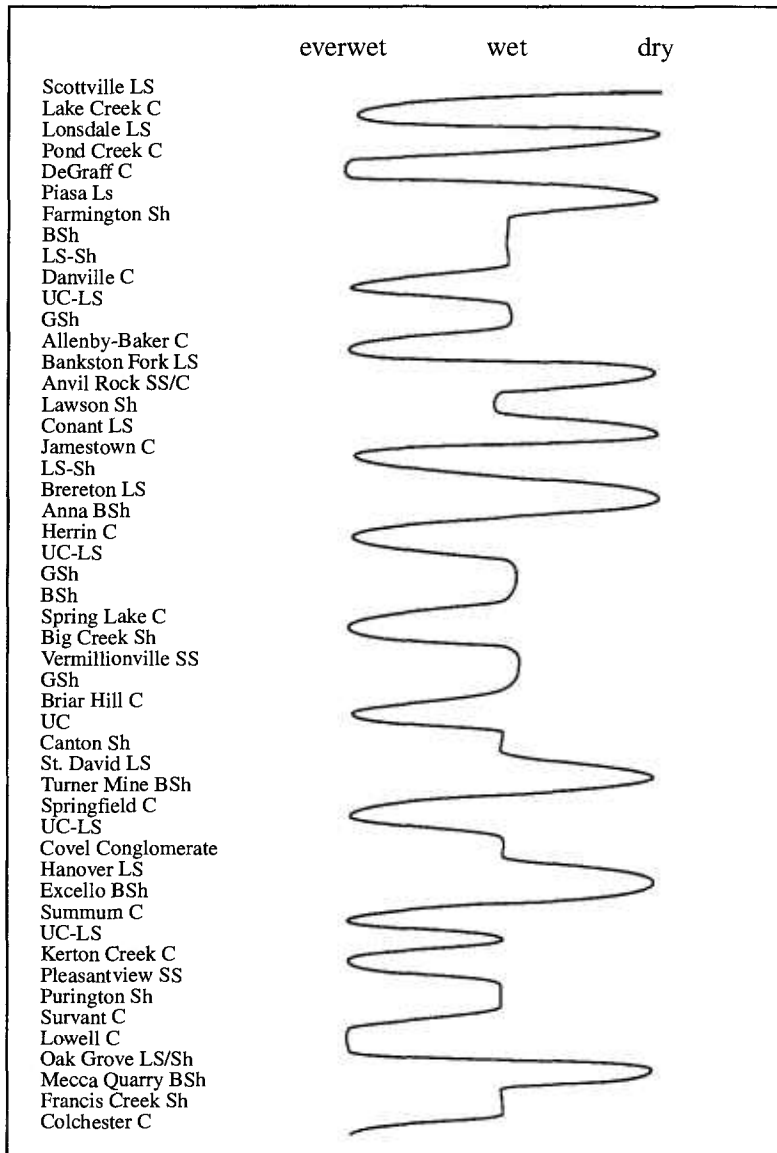
Fig. 4. Inferred climatic fluctuations during the late Desmoinesian, using the criteria of Cecil (1990). In stratigraphic column, SS = sandstone, Gsh = gray shale, Bsh = black shale, Sh = shale, LS = limestone, C = coal, UC = underclay.

Illinois Cyclothem" (Fig. 1). Clastic sediments underlying the coal bed include sandstone, gray mudstone with freshwater limestone nodules in its upper part, and underclay. Channel sands and gray mudstones appear to have formed in a single avulsion event and, therefore, may have formed in as little as one to two thousand years. Gray

mudstone with limestone nodules immediately below the coal may have formed in freshwater lakes and could represent as much as an additional few thousand years. The coal bed, on the other hand, may have taken 10–20 thousand years to form. This figure is derived by noting that 12 m thick peats have accumulated in Indonesia over

the last 8000 yr, and that peats of 20–30 m thickness formed in some of the lowland wetlands of the Late Carboniferous, computed by assuming an average rate of compaction of 10:1 between fresh peat and bituminous coal. Black shales above coal beds represent marine incursions that may have been stable for long time intervals, perhaps of a few hundreds to thousands of years; they could also represent a period of reduced sediment influx into the basin, resulting in a highly condensed section of several thousand years duration. Overlying gray shales may be tidally influenced, and could have formed over very short periods of time (Burk et al., 1987). In the case of the Francis Creek Shale, source of the famous Mazon Creek flora and fauna, sedimentation has been shown to have been very rapid; nodules formed rapidly, contemporaneously with mudstone deposition, and were sometimes eroded and redeposited within the shale. So, in general, the rocks themselves indicate rapid deposition.

Using the numbers discussed above, a single cyclothemic rock package could have formed in as little as 24,000 yr if very few gaps in sedimentation are assumed. If larger gaps existed, upper limits of 65,000–129,000 have been suggested (Klein, 1990). Nine major "cyclothems" have been described from the Carbondale Formation, with perhaps three additional in the lower Modesto Formation in the Illinois Basin (Willman et al., 1975), which does not account for minor lenticular coals found between most of the major beds. This is broadly in agreement with the sea-level curve of Heckel (1989) for the midcontinent. Thus, the length of time represented by the Carbondale and lower Modesto Formations could be as short as 290,000 yr or as long as 1.5 m.y. If the 15 limestone-black shale cycles of Heckel (1989) are combined with the cycle periodicities of Klein (1990), minimum and maximum estimates are 360,000 and 1.9 m.y. duration, respectively.

The considerable differences between maximum and minimum estimates of duration allow us only to state that the processes we are describing took place over a time interval of between 300,000 yr and 2 m.y.; 1.0–1.5 m.y. seems to be a reasonable compromise value, considering the likelihood that sedimentation gaps were considerable.

4. Plant fossils of late Desmoinesian age

4.1. Types of plant fossils

Fossil plants from the Carbondale Formation have been studied intensively for many decades. The Mazon Creek flora from the Francis Creek Shale above the Colchester coal, for example, is one of the best known Carboniferous-age plant-bearing deposits (Pfefferkorn, 1979). Fossils are of three types: pollen and spore microfossils mostly from coals, compression–impression macrofossils from mudstones and sandstones, and petrified peat-stages of coals, called coal balls (Phillips et al., 1976), that preserve the fabric of the original peat and the anatomy of the original plant parts.

Microfossil palynomorphs can be liberated from most Pennsylvanian coals and many clastic sediments by a variety of preparation techniques. Small coal samples provide a large number of specimens, which, due to the small size and dispersibility of microfossils, broadly represent the composition of the local vegetation. Consequently, coal can be sampled from most exposures or cores. There are two major limitations to palynological analyses in paleoecological research, preparation bias against large spores (particularly pollen and prepollen of medullosans) and differential spore production by parent plants. Standard preparation techniques limit palynological preparations to spores and pollen less than 200 µm in diameter, which biases against pollen grains of medullosan pteridosperms in particular, most species of which exceed the 200 µm upper size limit. Quantitative analyses of Westphalian D macrofossil assemblages show medullosans to be third in abundance behind lycopsids and tree ferns in Westphalian D coals (Phillips et al., 1985), and a dominant element of clastic compression floras (Pfefferkorn and Thomson, 1982). So the absence of these forms from palynological studies is noteworthy. Of greater concern for quantitative studies is differential production of spores by parent plants (Mahaffy, 1985; Willard, 1993; DiMichele and Phillips, 1994); comparison of coal-ball and palynological patterns indicates that many lycopsids and tree ferns in particular tend to be overrepresented in pollen and spore counts from coals.

Rank order abundances of spores, however, still conform reasonably well with patterns deduced from studies of coal-ball macrofossils.

Coal balls are the principal source of information on the peat-substrate, "coal" floras used in this paper. Coal balls are calcium carbonate (sometimes silicate) concretions that form during the earliest diagenetic stages within the original parent peat body of a coal bed (DeMaris et al., 1983; Phillips et al., 1976; Scott and Rex, 1985). Entombed within the mineral matrix is the original plant litter that made up the peat fabric, although the cell walls of the plants have been coalified to the same rank as the surrounding coal (Lyons et al., 1985). Coal balls occur as layered to aggregate masses within many coal beds, sometimes replacing the entire bed thickness. Means for extracting profiles of coal balls and for subsequent quantitative analysis are described by Phillips et al. (1977). The data used in this paper is presented in Phillips et al. (1985), and DiMichele and Phillips (1995) discuss multivariate techniques of data analysis. Although in situ, coal-ball occurrences are localized within a coal bed and occur most abundantly in the Upper Carboniferous/ Pennsylvanian. They are particularly abundant in the Carbondale Formation, with the most massive occurrences from the Springfield and Herrin coals; however, they are absent from many coal beds. Differential organ production and tissue decay also affect the reliability of coal-ball data in reconstructing parental vegetation.

Compression and impression fossils come principally from roof shales of coal seams. Roof shales represent a variety of depositional environments (Gastaldo et al. (1995), and for the most part preserve floras from clastic flood basins in the fluvial–deltaic wetlands. Such deposits may have been associated with rising sea level (Heckel, 1989). Deposition of deltaic muds above coal seams appears to have occurred in localized regions of shore-line progradation, and accounts for many of the areally restricted fresh to brackish water, plant-bearing, gray roof shales that locally overlie coal bodies in the Carbondale Formation (Shabica, 1979; Eggert, 1982; Treworgy and Jacobson, 1979; Demaris et al., 1983; Hopkins, 1958; Nelson et al., 1991). Compression–impression floras are rarely

in place, but frequently occur in environments that indicate only limited, local transport. This inference is borne out by studies of plant incorporation into modern depositional environments (Scheihing and Pfefferkorn, 1984; Burnham, 1989; Gastaldo and Huc, 1992). Autochthonous and parautochthonous compression–impression floras can be analyzed quantitatively to provide a rank-order picture of dominance in the source vegetation; the quadrat method of Pfefferkorn et al. (1975) was employed in these analyses.

Coal floras (palynological or coal-ball) and superjacent roof-shale compression floras differ significantly in quantitative and taxonomic composition (Peppers and Pfefferkorn, 1970; Scott, 1978; DiMichele et al., 1985, 1991; Mapes and Gastaldo, 1986), which reflects the considerable edaphic differences between peat and clastic subtrates. Taken together, however, compressions and coal-floras provide a broad picture of the lowland wetlands during the wettest climatic intervals. It is possible that they reflect the transition from glacial maxima to waning polar glaciation. In the tropics this would translate into a change from wettest tropical climates, with the lowest volumes of clastic transport, to the early phases of more seasonal climates, with increasing transport of siliciclastics (Cecil, 1990).

4.2. Sources of data

Fig. 2 shows the stratigraphic distribution of Carbondale Formation and basal Modesto Formation plant fossils used in this study, by fossil type (coal ball, spore–pollen, compression–impression).

Coal balls have been found in the Colchester, Summum, Springfield, Herrin, Baker (Allenby), and Danville coals in the Illinois Basin. Basic vegetational patterns and details of collecting localities are reported by Phillips et al. (1985). No systematic collections have been made in the Colchester coal; all observations are based on small field samples made by geologists of the Illinois State Geological Survey and staff of the paleobotany laboratory of the University of Illinois. Systematic profile and random samples of coal balls were collected from the Summum

(Houchin Creek) coal in the Peabody Coal Company Northern Illinois Mine, east of the LaSalle Anticlinorium in the northeastern part of the Illinois Basin. The quantitative makeup of the coal-ball samples broadly agrees with the palynological composition of the coal in the area, but differs significantly from Summum coal microfloras from the rest of the basin (Peppers, 1970). The Springfield coal has been a major source of coal balls, particularly in Indiana on the eastern margin of the outcrop. The samples used in this study come from the Lemon Brothers Kennedy Pit, the AMAX Wabash Mine, and the Eby Pit of the Peabody Coal Company Lynnville Mine, all in western Indiana. Coal ball samples from the Springfield coal compare reasonably well with palynological samples from the coal, when biases of over- and under-production of palynomorphs are accounted for (Willard, 1993; Mahaffy, 1985). The Herrin coal of southern Illinois and western Kentucky has been a major source of coal balls for paleobotanical floristic studies. Profile and random samples have been collected from numerous mines; those used in this study come from the Sahara Coal Company Mine No. 6 (Phillips and DiMichele, 1981), and the Old Ben Coal Company Mine No. 24 (DiMichele and Phillips, 1988). As with the Springfield coal, the agreement between coal ball and palynological patterns is good if differential palynomorph-production biases are considered (Mahaffy, 1988; Phillips et al., 1985). Several random samples of coal balls from the Baker (Allenby) coal have been collected from spoils of the abandoned Hart and Hart Mine in western Kentucky; again, coal-ball and palynological samples are in broad agreement (Peppers, 1985; Phillips et al., 1985). A small random collection of coal balls was made from the Danville coal in western Indiana; coal balls were encountered more widely in this coal earlier in the century when mining activity was greater. The sample available to us is small (54 coal balls) but does provide insight into local composition of the bed. All collections are housed in the Paleobotanical Research Center, University of Illinois, Urbana, Illinois.

Pollen and spore quantitative data were taken from the report of Peppers (1985), which summa-rizes his stratigraphic analyses of Illinois Basin coals. Peppers' data were reported categorically (present, common, abundant, very abundant) with rough percentage values attached to each category. We have converted these to 1%, 5%, 10%, and 20%.

Compression–impression floras are known from many levels in the Carbondale and Modesto Formations. Floras from six levels are considered in this analysis, and compared with floras from the top of the Tradewater Formation, immediately below the Carbondale, and earliest Missourian portion of the Modesto Formation. Collections are presently housed in a number of institutions: the Illinois State Geological Survey (Champaign, IL), the Paleobotanical Research Center of the University of Illinois (Urbana, IL), the Field Museum of Natural History (Chicago, IL), the National Museum of Natural History (Washington, DC), the Department of Geology of Knox College (Galesburg, IL), the Department of Geology of Augustana College (Rock Island, IL), the Davenport Public Museum (Davenport, IA), the Florida State Museum (Gainesville, FL— collections formerly at Indiana University), the Paleobotanical Laboratories of Harvard University (Cambridge, MA), and the Geologische Bureau voor het Mijngebied van de Rijks Geologische Dienst (Heerlen, The Netherlands). Collections were made in both active mines and from natural exposures. Quantitative counts of fossils were made only from collections from shales above the Colchester and Danville coals according to the methods of Pfefferkorn et al. (1975). Quantitative calculations were made at the generic level.

The Mazon Creek flora from the Francis Creek Shale (Pfefferkorn, 1979), above the Colchester coal, is well represented by collections in numerous institutions. The flora or elements of it have been described in many publications, some of which give overviews and taxonomic counts, so a solid base for further comparison is available. Some of these data are reviewed in Pfefferkorn et al. (1975). Collections from shales above the Summum, Springfield, and Herrin coals are also well known, and represent "typical" late Westphalian D floras. The Carterville flora, preserved in siderite nodules, has been reported by Gastaldo (1977) from shales above the Herrin coal. Floras from gray shale

Table 1
Range through stratigraphic distribution of coal-ball plants in the Carbondale Formation

	Dn	Ba	He	Sp	Su		Dn	Ba	He	Sp	Su
Botryopteris "pseudoantiqua"	−	−	x	x	x	*Psaronius (S. latifolia)*	x	x	x	x	
B. forensis	x	x	x	x	x	*Psaronius (S. minor)*	x	−	x	x	−
B. cratis			x	x	x	*Psaronius (S. altissima)*		x	−	x	−
Anachoropteris gillotii	−	−	x	−	x	*Medullosa (Pachytesta illinoense)*	−	−	x	x	−
A. involuta (adaxial shoots)	x	x	x	x	x	*Medullosa (Stephano. elongatum)*	−	−	x	−	−
A. cadyi			x			*Medullosa (Stephanospermum sp.)*			x		
Sermaya biseriata	−	−	x	−	−	*Medullosa (Hexaptero. delevoryii)*			x		
Zygopteris illinoiensis	x	x	x	−	x	*Medullosa (Albertlongia incostata)*			x	x	−
Ankyropteris brongniartii	−	−	x	x	−	*Medullosa (Pachytesta composita)*				x	x
Arthropitys (Calmocarpon)	x	x	x	x	x	*Medullosa (Pachytesta stewartii)*	−	−	−	x	−
Arthropitys (Palaeost. decacnema)		x	−	−	−	*Medullosa (Pachytesta saharasperma)*		x	x	x	
Calamodendron sp.		x	−	x	−	*Medullosa (Pachytesta noei)*				x	
Sphenophyllum (Bowmanites sp.)	x	−	x	x	−	*Medullosa (Pachytesta gigantea)*	−	−	x		
Sphenophyllum (Pelta. reedae)	x	−	x	x	x	*Medullosa (Pachytesta vera)*			x	−	−
Callistophyton boysetii	x	x	x	x	x	*Medullosa (Pachytesta hoskinsii)*			x	−	−
Schopfiastrum decussatum	−	x	x	−	−	*Sutcliffia insignis*		x	x	x	
Microspermopteris aphylla					x	*Lepidodendron hickii*		x	x	x	x
Heterangium (Conost. platyspermum)	−	−	x	x	−	*Lepidophloios hallii*	x	x	x	x	−
Heterangium (Conost. kestospermum)	−	−	x	x	−	*Lepidophloios johnsonii*		x	x	x	−
Stellastellara parvula	−	−	−	x	−	*Paralycopodites brevifolius*			x	x	−
S. baxteri				x		*Hizemodendron serratum*		x	−	x	−
Pennsylvanioxylon (C. oviformis)	x	x	x	x	x	*Diaphorodendron phillipsii*					x
Psaronius (Scolecopteris majopsis)			x			*D. scleroticum*	x	x	x	x	−
Psaronius (S. calicifolia)				x	−	*Synchysidendron resinosum*	x	x	x	x	−
Psaronius (S. valumii)		x	x	x		*Sublepidophloios sp.*			x		−
Psaronius (S. mamayi)		x	x	x		*Chaloneria periodica*	x	x	x	x	x
Psaronius melanedrus					x	*Sigillaria sp.*	x	x	x	x	−
Psaronius (S. gnoma)	x	x	−	x	−	*Paurodendron fraipontii*	−	x	x	x	x

x = identified occurrence; − = presence inferred by earlier or later identified occurrence (not all coals are included, permitting a species range to terminate without a later identified occurrence in the data set). Dn = Danville coal; Ba = Baker coal; He = Herrin coal; Sp = Springfield coal; Su = Summum coal. Danville coal (Dn) at top of section.

occur within the Bankston "cyclothem" and from above the Danville coal; siderite nodules have been collected above the Danville coal near Terre Haute, Indiana.

4.3. Patterns in peat-forming vegetation

The Carbondale Formation contains approximately 15 discrete coal beds, depending on how correlations are drawn among some of the areally restricted, smaller coal bodies (Willman et al., 1975). Pollen and spores have been recovered from most of these (Peppers, 1985); coal balls are known mainly from the major, widely mined coals (Phillips et al., 1985). Based on coal balls, we have identified 56 plant species in the interval (Table 1).

The data in Table 1 are drawn from the literature and our own samples. Species counts are based on "whole plants" (in which individually named organ taxa from one parent plant have been assembled into an aggregate species), or on "proxy" organs, such as seeds, which are more diagnostic of species-level diversity than vegetative organs in some lineages of plants (for example, medullosan pteridosperms). Peppers (1985) lists 52 species of "the most diagnostic" spores and pollen in the same interval, suggesting rough parity with macrofossil taxa.

4.3.1. Stratigraphic patterns

The Westphalian D was an interval of high taxonomic richness but also high extinction affect-

ing many taxa that had originated earlier in the Pennsylvanian. The result was a major vegetational change at the transition between the Middle and Late Pennsylvanian (Westphalian–Stephanian; Desmoinesian–Missourian), both in peat forming environments (Phillips et al., 1974; Phillips and Peppers, 1984) and in the surrounding wetlands (Pfefferkorn and Thomson, 1982). Of the 56 total coal-ball species in the Carbondale Formation, 16 spanned the Desmoinesian, originating before and occurring afterward, 27 originated earlier and terminated during the late Desmoinesian, 12 were unique to the interval, and one originated within and carried on into the Late Pennsylvanian. Omitting questionable Late Pennsylvanian identifications of otherwise Desmoinesian species reduces the number that span the late Desmoinesian to 14, and raises the number of terminations to 29. Palynological patterns are similar (Peppers, 1985): of 52 species that occurred within the Desmoinesian, 19 spanned the interval, 31 originated earlier and terminated within, and two originated within and continued into the Late Pennsylvanian.

Species turnover was low in the Desmoinesian through the Herrin Coal. Patterns of species loss above that level, up to the Middle–Late Pennsylvanian boundary, may reflect sampling biases and the backward smearing of apparent extinctions known as the Signor-Lipps effect. However, the apparent loss of one common lycopsid, *Paralycopodites* (a small tree), at the level of the Herrin coal suggests that extinctions were accelerating during the later part of the interval. A similar pattern is displayed by the palynological data, where, of the 39 species that terminated within the late Desmoinesian, 21 disappeared above the Herrin coal, but only seven extended to the Desmoinesian–Missourian boundary.

4.3.2. Quantitative data and vegetational patterns

Eleven profile or random samples of coal balls were analyzed quantitatively; coal-bed summaries from each collecting site are presented in Table 2. Detrended correspondence analysis (DCA) ordination was performed on the seam summary data. Results (Fig. 5) show that samples from the Summum coal and the Eby pit of the Springfield

coal lie well outside a cluster formed by the other samples. All but those from the Summum, Eby Pit, and Danville sites are dominated by the lycopsid *Lepidophloios hallii*, with significant amounts of *Psaronius* tree ferns, *Medullosa* pteridosperms, and the lycopsid trees *Diaphorodendron scleroticum* and *Synchysidendron resinosum*.

The Summum sample is the most divergent; it is dominated by the lycopsid *Diaphorodendron phillipsii*, with subdominant cordaitean gymnosperms. The Summum sample may be typical only of the northeastern part of the coal body. Palynological samples, drawn from a broader area than the coal balls (Peppers, 1970), reveal dominance by *Lycospora granulata*, the spore of *Lepidophloios hallii*, throughout most of the extent of the coal. Abundance of small *Diaphorodenron* species (*D. phillipsii* and *D. vasculare*) is typical of older coals in the Desmoinesian, including the Colchester, an unnamed coal above the Murphysboro equivalent, the Murphysboro equivalent and the Buffaloville (Phillips et al., 1985). Thus, there appears to be a vegetational break between the Summum and the rest of the coals in the Carbondale Formation.

The remaining coal-bed summaries cluster most closely with other samples from the same coal. The outlying sample from the Eby Pit comes from a high ash upper bench ("split") of the Springfield coal in an area proximal to channel activity. *Medullosa* dominance and abundant *Paralycopodites* are typical of ecotonal environments transitional between organic substrates and clastic swamps throughout the late Desmoinesian. Some zones within profiles from the Herrin and Springfield coals have composition similar to the Eby summary (DiMichele and Phillips, 1988; Old Ben VS 3–5, zones 1–5), indicating that the Eby data represent one of several typical elements of a late Desmoinesian mire landscape. The data are divergent only when considered at the level of coal-bed summary.

Profiles of coal balls have been collected only from the Summum, Springfield, and Herrin coals in the late Desmoinesian. Figs. 6–8 are ordinations based on the major profiles from each coal, plotted on the same scale; each point is a layer, or zone, of coal balls from a multilayered profile. The Summum coal clearly differs in composition from

Table 2
Relative abundances (percentages) of species in coal-ball samples from Carbondale coals. Counts made using the techniques of Phillips et al. (1976). Coal designations as in Fig. 5. Danville (Dan) coal at top of section

	Dan	Bak	Ky	OB3	OB4	SA5	SA4	Eby	Lem	Wab	Sum
Lepidophloios hallii	2.1	21.6	11.7	50.9	29.0	29.0	43.7	3.7	37.6	24.2	0.0
Lepidophloios johnsonii	0.0	5.0	3.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidophloios sp.	0.0	13.0	18.0	0.0	0.0	0.0	0.0	0.0	6.6	0.0	0.0
Sublepidophloios sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	22.7	0.0	0.0
Lepidodendron hickii	0.0	2.0	4.4	0.1	0.0	0.1	0.0	0.0	6.3	0.2	0.1
Diaphoro. scleroticum	5.7	2.4	4.8	5.2	9.2	11.4	4.0	0.0	0.1	20.2	0.0
Diaphoro. phillipsii	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	69.2
Synchysi. resinosum	6.9	14.0	11.0	5.9	7.6	6.2	5.2	0.1	1.0	12.3	0.0
Diahorodendraceae	11.1	5.0	3.8	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
Hizemodendron serratum	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.1	0.2	0.0
Paralyco. brevifolius	0.0	0.0	0.0	7.9	0.0	2.9	0.0	19.5	0.0	0.6	0.0
Sigillaria sp.	20.2	1.3	2.1	1.4	1.1	0.3	2.2	0.0	0.0	20.2	0.0
Chaloneria periodica	0.7	0.7	2.8	0.0	0.0	0.0	0.0	0.0	0.1	0.3	0.1
Paurodendron fraipontii	0.0	0.0	0.2	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.1
Lycopsids spp.	13.4	3.0	3.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Psaronius spp.	30.1	10.9	10.5	12.3	12.4	17.7	16.1	14.9	7.0	9.5	15.6
Medullosa spp.	7.0	11.7	13.5	10.4	27.3	18.6	20.4	56.4	13.8	12.1	1.2
Sutcliffia insignis	0.0	0.3	0.3	0.1	0.1	0.0	0.1	0.0	0.0	0.3	0.0
Callistophyton boysetii	0.4	0.0	0.2	1.7	0.9	3.7	1.2	0.1	0.1	0.2	0.1
Heterangium spp.	0.0	0.1	0.0	0.1	0.0	0.3	0.2	0.1	0.1	0.2	0.0
Schopf. decussatum	0.0	0.1	0.2	0.0	0.0	0.1	0.1	0.0	0.0	0.1	0.0
Arthropitys spp.	0.4	1.0	0.8	2.1	4.6	1.7	1.7	0.2	0.1	0.2	0.6
Calamodendron sp.	0.0	1.0	0.0	0.0	0.0	0.0	0.0	1.7	1.5	0.0	0.0
Sphenophyllum spp.	1.5	5.8	6.9	1.0	0.4	2.0	1.3	1.6	2.1	1.3	2.2
Botryopteris forensis	0.1	0.1	0.0	0.1	0.1	0.2	0.0	0.0	0.0	0.0	0.1
Botryopteris 3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Botryopteris 4	0.1	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Botryopteris 5	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.1	0.0
Botryopteris sp.	0.1	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0
Anachorop. involuta	0.0	0.1	0.4	0.1	0.1	1.0	0.1	0.0	0.1	0.0	0.3
Anachoropteris sp.	0.2	0.3	0.3	0.0	0.1	0.1	0.1	0.0	0.0	0.1	0.0
Ankyropteris glabra	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.1	0.0
Zygop. illinoiensis	0.4	0.1	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.1	0.0
Un ferns	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Pennsylvanioxylon sp.	0.2	0.1	0.6	0.3	1.0	0.7	0.1	0.1	0.0	0.0	10.5
Stelastellara parvula	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Stelastellara baxteri	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.0

the others and shares no common species assemblages, determined by dominance-diversity patterns. The Herrin and Springfield have essentially the same landscape structure, with three species assemblages (communities) recurring within each coal (Phillips and DiMichele, 1981; DiMichele and Phillips, 1988). These three are: (1) assemblages dominated by monocarpic lycopsids, primarily *Lepidophloios hallii*, with low species richness and low percentages of ground cover and free sporing

plants, which we infer to represent areas with the longest periods of standing water; (2) assemblages dominated by the polycarpic lycopsid *Diaphorodendron scleroticum* with various subdominants comprising a complex of pteridosperms, lycopsids, tree ferns, and ground cover, which we interpret as wet, but irregularly flooded habitats; (3) assemblages dominated by a variety of *Medullosa* pteridosperm species and/or the small lycopsid *Paralycopodites brevifolius* including

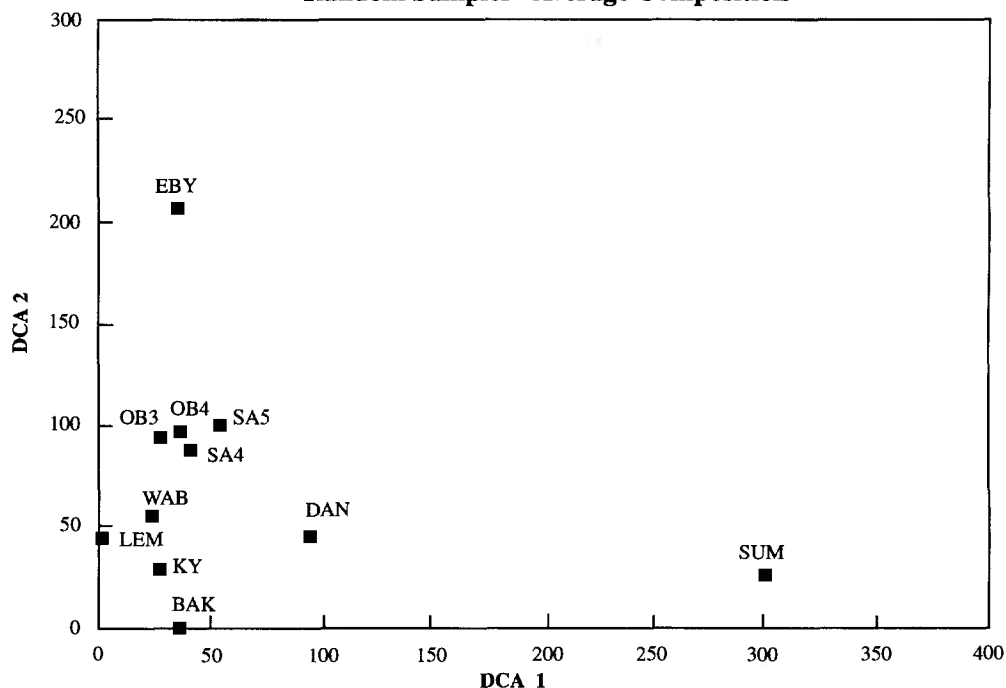## DCA CARBONDALE COALS
Random Samples - Average Composition

Fig. 5. Detrended correspondence analysis ordination of Carbondale coals based on coal-ball, seam average composition. $SUM=$ Summum coal; $LEM=$ Springfield coal, Lemon Brothers 2 1/2 Pit; $WAB=$ Springfield coal, AMAX Wabash Mine; $EBY=$ Springfield coal, Peabody Coal Company Eby Pit; $OB3=$ Herrin coal, Old Ben Coal Company No. 24 Mine, VS 3-5; $OB4=$ Herrin coal, Old Ben Coal Company No. 24 Mine, VS 4; $SA4=$ Herrin coal, Sahara Coal Company Mine No. 6, VS 4; $SA5=$ Sahara Coal Company Mine No. 6, VS 5; $BAK=$ Baker coal, Hart and Hart Mine, RS 1; $KY=$ Baker coal, Hart and Hart Mine, RS 2; $DAN=$ Danville coal, western Indiana. Ordination based on data in Table 2.

abundant ground cover, tree ferns, and calamites, and enriched in clastics and fusain (mineralized charcoal), which appear to be ecotonal between clastic and peat swamps. Other assemblages occur rarely, and two are of particular note. Assemblages dominated by *Sigillaria* sp. we interpret to be periodically dry peat surfaces based on several attributes of sigillarian morphology and distribution: the reinforced structure of rootlets (Eggert, 1972), evidence of rhythmic stem growth (Wnuk, 1985), and the principal occurrence of the genus in intermittently flooded clastic-substrate habitats. Assemblages dominated by or enriched in *Chaloneria* and *Sphenophyllum* form a low canopied vegetation with low species richness, analogous to a modern-day marsh (DiMichele et al., 1979; Pryor, 1993).

Random samples of coal balls from the Baker (Allenby) and Danville coals reveal similar patterns. The Baker is rich in *Lepidophloios hallii*, and contains a notable subset of specimens with the distinctive *Chaloneria–Sphenophyllum* assemblage. Although not quantitatively abundant in the coalbed averaged summary, this assemblage occurs more commonly than in other late Desmoinesian coals and presages the abundance of *Chaloneria* that appears in coals immediately following the major extinctions at the end of the Desmoinesian (Peppers, 1985). The Danville coal sample is quite distinctive in its abundance of *Psaronius* tree ferns and *Sigillaria* lycopsids, a pattern typical of Late Pennsylvanian coals, which otherwise lack many of the species and species assemblages the Danville shares with other Desmonesian coals.
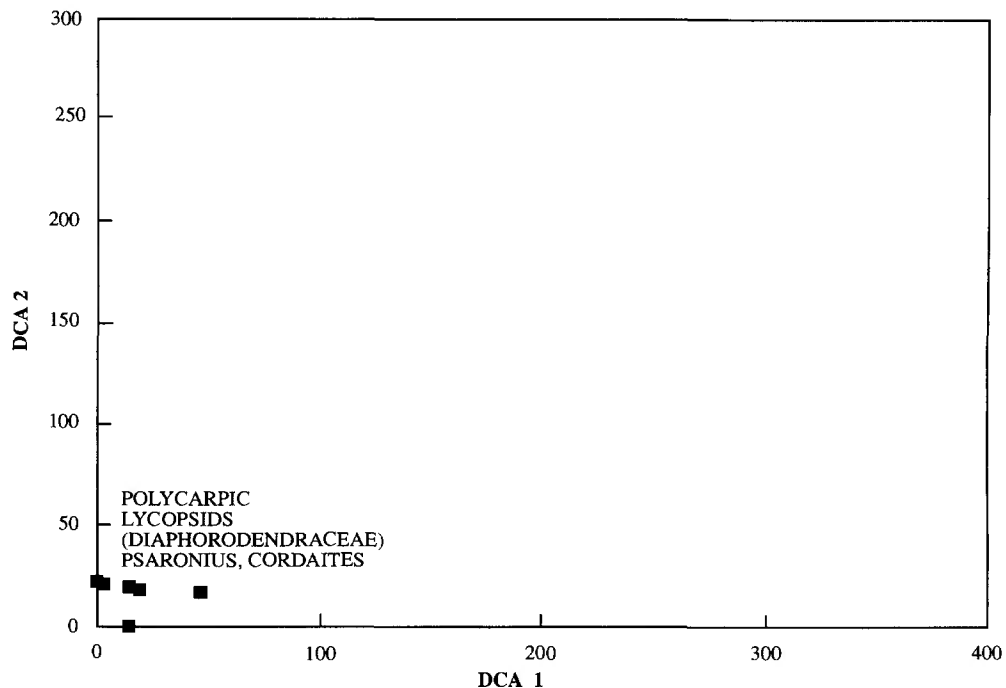
DCA SUMMUM COAL

Fig. 6. Detrended correspondence analysis ordination of Summum coal coal-ball Vertical Section 1. Each point represents one zone of coal balls. Very little differentiation is evidenced among assemblages, all dominated by *Diaphorodenron phillipsii*, *Psaronius* spp. , and cordaites producing *Cardiocarpus oviformis* ovules.

4.4. Patterns in vegetation on clastic substrates

The best known compression–impression floras come from shales above the major mined coals in the Illinois Basin: the Colchester, Summum, Springfield, Herrin, and Danville coal beds. Small floras have been collected from shales above several other coals in the Carbondale Formation. Floras were sampled originally to solve stratigraphic problems (Pfefferkorn, 1970, 1974, 1975). Species counts for the Colchester coal interval (Mazon Creek flora) were based on "whole" plants, in which the most diverse kind of organ belonging to a particular clade of plants (for example: medullosan foliage, as opposed to seeds or stems), was used as proxy for diversity (Pfefferkorn, 1979). Ninety-six plant species are present in the Mazon Creek flora, which is an allochthonous flora drawn from several habitats in the lowland landscape (Pfefferkorn, 1979). This

number is nearly twice as large as species richness estimates from Carbondale coal balls (Phillips and DiMichele, 1981), a not surprising result given the greater nutrient levels and microhabitat heterogeneity thought to characterize clastic landscapes in comparison to peat mires. The Mazon Creek flora is a good proxy for the maximum expected richness of a coal roof-shale flora in the Carbondale Formation because of the uniformity among the numerous collections and collecting sites in the Francis Creek shale (source of the Mazon Creek flora), and the great intensity of collecting that has occurred over the past 100 years.

4.4.1. Stratigraphic patterns

The late Desmoinesian has yielded some of the best known and richest floras in North America. The late Desmoinesian (Carbondale and lower Modesto Formations) can be distinguished clearly from the early Desmoinesian (upper Tradewater
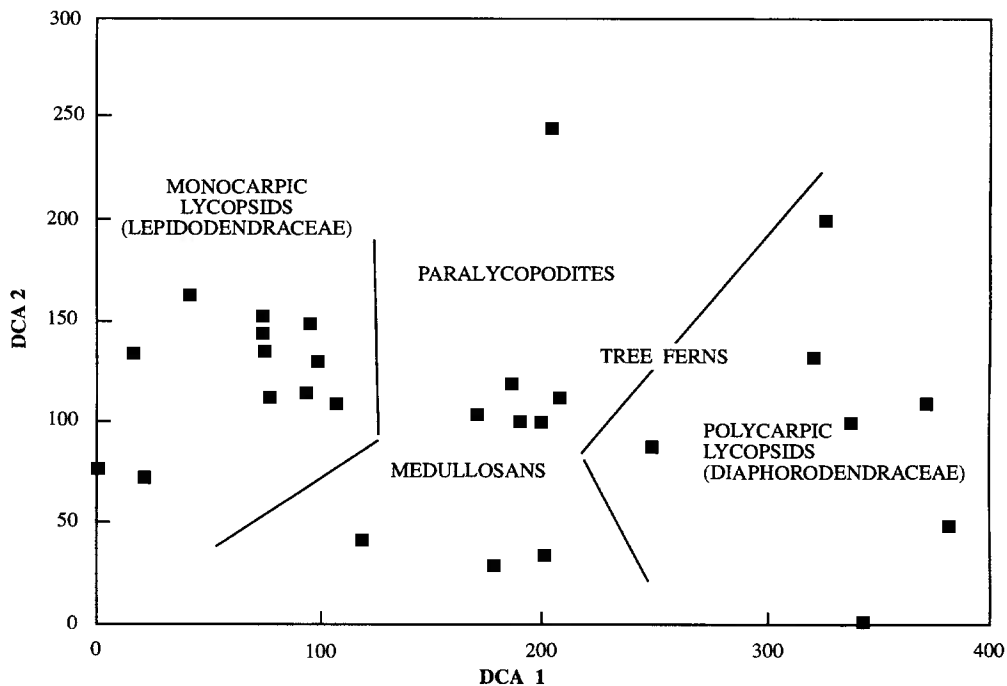
DCA SPRINGFIELD COAL

Fig. 7. Detrended correspondence analysis ordination of Springfield coal coal-ball profiles from the AMAX Wabash Mine, Lemon Brothers 2 1/2 Pit, and Peabody Coal Company EBY Pit. Each point represents one zone of coal balls. Three basic assemblages are recognizable within a gradient: standing water sites dominated by monocarpic lycopsids of the Lepidodendraceae (*Lepidophloios*, *Sublepidophloios*, and *Lepidodendron*); wet, periodically exposed peats dominated by lycopsids of the Diaphorodendraceae, *Diaphorodenron scleroticum* and *Synchysidendron resinosum*; "ecotonal" habitats enriched in mineral matter and charcoal dominated by medullosan pteridosperms and the lycopsid *Paralycopodites*. Tree ferns occur widely with highest abundances in the ecotonal and periodically exposed habitats.

Formation) by the appearance of species such as *Pseudomariopteris riberonii*, *Pecopteris unita*, *Lobatopteris vestita*, and *Odontopteris schlotheimii* (Table 3). It is an interval in which the number of *Pecopteris* species increases to 11 from five in the underlying beds of the upper Tradewater Formation (Pfefferkorn, 1979). Throughout this interval there is no change in species composition. The flora of the Danville coal bed contains the same species as the Mazon Creek flora. These floras are dominated by *Neuropteris ovata*, *N. scheuchzeri* and several *Pecopteris* species. The entire Carbondale Formation belongs to the *vestita* Biozone of Wagner (1984).

At the present time there is no information on compression–impression floras from the lower Modesto Formation. The flora from the next high-

est coal, above the Chapel coal bed is typically Missourian (Stephanian), including *Odontopteris brardii*. *Sigillaria brardii* occurs slightly higher in the section. Other floras from the upper Modesto formation, although containing typically Stephanian elements, retain patterns of *N. ovata*, *N. scheuchzeri*, and *Pecopteris* dominance.

4.4.2. Quantitative data and vegetational patterns

Floras large enough for quantitative sampling were counted and are presented in Table 4. Three counts are from the base of the Carbondale Formation and one from just above the top of the Carbondale Formation (the top of the Danville coal bed marks the top of the Carbondale Formation, Wilman et al., 1975). Most floras growing on clastic substrates during this strati-
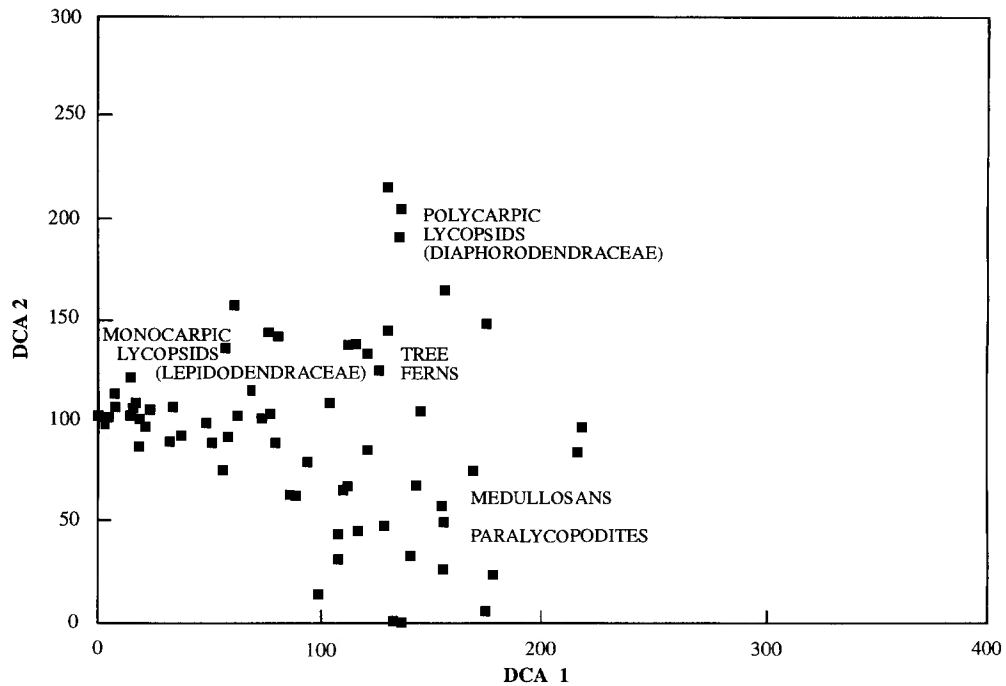
DCA HERRIN COAL

Fig. 8. Detrended correspondence analysis ordination of Herrin coal coal-ball profiles from the Old Ben No. 24 Mine and the Sahara Coal Company No. 6 Mine. Each point represents one zone of coal balls. The gradient and recurrent assemblages are the same as those found in the Springfield coal (Fig. 7).

graphic interval were dominated by either pterido-sperms (here called Type I floras: mostly medullosan pteridosperms represented by *Neuropteris* dominance) or by ferns (here called Type II floras: mostly marattialean tree ferns of the genus *Pecopteris*). The other three plant groups are less common and do not change significantly in the data set available. As Pfefferkorn and Thomson (1982) point out, pteridosperm-domi-nated floras are typical for earlier parts of the Pennsylvanian, but tree fern-dominated floras do not occur before the late Desmoinesian, that is, the Carbondale Formation. The dominance pat-terns in floras from clastic substrates does not change throughout the Carbondale Formation and is quite distinct from the dominance pattern observed in the peat-forming environments of the late Desmoinesian, where lycopsids were the princi-pal dominants. Note, however, that tree fern abun-dances increased in peat forming habitats, based

on coal-ball samples, at approximately the same time as tree ferns rose to dominance in clastic habitats.

5. Discussion

Vegetation of the tropical lowlands during the late Desmoinesian shows clear patterns of persis-tent landscape gradients, dominance-diversity architecture and species composition for a period of between 1.0–1.5 m.y. The same pattern is found for peat substrates and clastic flood basins. This was a time of maximum southern and northern hemisphere glaciation (Frakes et al., 1992), proba-bly accompanied by extensive eustatic sealevel fluctuations (Heckel, 1980, 1989), and repetitive climatic changes (Phillips and Peppers, 1984; Cecil, 1990) in response to changes in the extent of ice cover. If climatic changes were general, or at least

Table 3
Ranges of selected plant fossils from clastic environments preserved as compressions and impressions. Only the most common taxa are listed

Stratigraphy	MO (top)	Da	Ba	He	Sp	Su	MC	SF (bottom)
Neuropteris scheuchzeri	r	x	x	x	x	x	x	x
Neuropteris ovata	r	x	–	x	x	–	x	x
Pecopteris sp.	c	c	c	c	c	c	c	r
Pecopteris unita	–	x	–	x	–	–	x	
Lobatopteris vestita	–	x	–	x	x	–	x	
Odontopteris sp.	r	x	–	x	–	–	x	
Odontopteris brardii	c							
Sigillaria brardii	x							

c = common, x = present in most collections, r = present but not in every collection, – = expected to be found. SF = Spoon Formation (below Carbondale Formation, early Desmoinesian), MC = Mazon Creek, above Colchester Coal, Su = shales above Summum coal, Sp = shales above Springfield coal, He = shales above Herrin coal, Ba = shales associated with coal above Bankston Fork limestone (probably Allenby-Baker), Da = shales above Danville coal, MO = Upper Modesto Formation, above Chapel coal (post-Desmoinesian; earliest Missourian).

Table 4
Quantitative counts (percent abundance) of compression–impression floras from the Carbondale Formation (from Pfefferkorn et al., 1975). Species are combined into major groups to show overall pattern

Shale above:	Colchester coal		Colchester coal	Danville coal
Locality:	Mazon Creek, IL		Galesburg, IL	Terre Haute, IN
	Type I	Type II	Type I	Type II
Lycopsids	10	6	2	11
Sphenopsids	18	14	12	21
Ferns	25	50	17	51
Pteridosperms	44	30	64	16
Cordaites	1	0	4	1
Sample size	803	3808	1634	301

regionally extensive throughout the tropics, why or how did landscape gradients and species assemblages persist in the face of environmental change?

From the perspective of vegetational ecology, the issue of persistence is an enigma that has not been resolved within our limits of observation. Recurrent plant assemblages have been identified on all scales of observation, from the average landscape composition represented by coal-ball random samples, whole-seam palynological samples, or averaged "roof-shale" assemblages, to specific gradients and "communities", such as those identifiable in late Desmoinesian coals or in site specific roof-shale floras. Successive coal seams or roof-shale floras appear to be separated by time intervals on the order of 100,000 yr or more, at least within the Illinois Basin. Where are the species, and the assemblages they create in the interim?

Perhaps the simplest explanation is to presume that floras survived intact in areas beyond the limits of our sampling during periods when conditions were unfavorable for coal formation within the Illinois Basin. In such a scenario late Carboniferous vegetational assemblages would parallel the Tertiary "geofloras" of Chaney (1947). This scenario is consistent with the retention of ecomorphic vegetational structure for millions of years; despite species turnover during the Westphalian (Morrowan, Atokan and Desmoinesian), replacement taxa tended to be close relatives of the extinct forms, with similar architectures and habitat preferences (DiMichele and Phillips, in press). Only when the dominant trees suffered extinctions exceeding 70% did new patterns of organization emerge (DiMichele and Phillips, in press). These patterns suggest that species interactions helped to channel turnover dynamics and patterns of species replacement, as long as the fabric of dominant species remained largely intact at both the community and landscape levels. It argues for emergent properties at the level of species assemblages; similar patterns have been described from the Paleozoic marine realm (Brett et al., 1990; Aberhan, 1994)

Alternatively, widespread climatic change could have produced species assemblages throughout the tropics quite different from those prevailing during or immediately after the major periods of peat formation, as has been argued to have happened to temperate vegetation during the Pleistocene

(Cole, 1985; Overpeck et al., 1992). This explanation is more in keeping with the expectations of modern ecology, where species are thought to respond individually to changing environmental conditions, and where there are supposedly no real emergent, assemblage-level properties. The repeated reassembly of the same taxonomic associations during successive times in the late Desmoinesian would then reflect little more than individual species recolonizing the physical habitats most suitable for completion of their life histories, within the limits set by the broader climatic context. Unfortunately, no evidence has yet been adduced from Late Carboniferous drier periods to suggest quantitatively different vegetation types composed mostly of the same species that predominated during the intervals of wettest climate.

A position intermediate between these two extremes calls for the regional extirpation of the flora as sea level rose or widespread climatic changes took place. When conditions within the basin returned to those favorable for coal formation or the development of extensive clastic wetlands, flora and vegetation similar to that present in the area thousands of years earlier also returned. Recolonization may have ensued from areas of survival, perhaps in the Appalachian Basin or further to the east; in this sense the mosaic of the tropical landscape would have included (potentially vast) areas sheltered from climatic changes from which species could respond to the return of suitable habitat space. In this scenario, coevolved species groups within the stable "species pool" (in the sense of Buzas and Culver, 1994) would continue to regulate turnover dynamics and vegetational architecture because they would be lost only regionally. The survival of Westphalian-type vegetation into the Late Permian of China (Guo, 1990) is direct evidence supporting the existence of such "refugia."

The issue of individualism versus group properties in the regulation of plant community dynamics is an old one that goes back to the early part of this century (Clements, 1916; Gleason, 1926). Neoecology, strongly supported by Pleistocene and Holocene palynological studies, particularly of the temperate zone, has championed reductionist approaches to ecosystem organization—all vegetational patterns can be understood by study of population dynamics. Studies of floral and faunal patterns on the spans of time encompassed by the geological record reveal patterns at odds with reductionist approaches. Reconciliation of these divergent patterns may lie mostly in the consideration of scale, both spatial and temporal. Pleistocene studies claiming non-analogous extinct vegetation types often fail to step back far enough spatially to find scales on which vegetational persistence can be recognized. How different must an assemblage be, either quantitatively or qualitatively, to be called a non-analogue? The answer seems to demand a regional view rather than one focused within a single biome. On the other hand, studies of ancient vegetation rarely focus on short-time dynamics of species groups, where individualistic patterns are most likely to be manifested. Quite fine resolution of the Carboniferous fossil record is possible, paticularly with palynological sampling, but patterns on such fine scales have not been integrated with the larger patterns. Only when observations from these different temporal and spatial scales are combined can a complete, predictive theory of community ecology be developed.

Acknowledgements

bution no. 23 from the Evolution of Terrestrial Ecosystems Program at the National Museum of Natural History, which also provided partial support for the research.

References

Aberhan, M., 1994. Guild structure and evolution of Mesozoic benthic shelf communities. Palaios, 9: 516–545.

Boardman, D.R., Mapes, R.H., Yancey, T.E. and Malinky, J.M., 1984. A new model for depth-related allogenic community succession within North American Pennsylvanian cyclothems and implications on the black shale problem. In: N.J. Hyne (Editor), Limestones of the Mid-Continent. Tulsa Geol. Soc. Spec. Publ., 2: 141–171.

Brett, C.E., Miller, K.B. and Baird, G.C., 1990. A temporal hierarchy of paleoecologic processes within a Middle Devonian epeiric sea. In: W. Miller III (Editor), Paleocommunity temporal dynamics: the long-term development of multispecies assemblages. Paleontol. Soc. Spec. Publ., 5: 178–209.

Breyer, J.A., 1992. Shale facies and mine roof stability: a case study from the Illinois basin. Geol. Soc. Am. Bull., 104: 1024–1030.

Bristol, H.M. and Howard, R.H., 1971. Paleogeographic map of the sub-Pennsylvanian Chesterian (Upper Mississippian) surface in the Illinois Basin. Ill. State Geol. Surv. Circ., 458, 16 pp.

Bristol, H. and Howard, R., 1974. Sub-Pennsylvanian valleys in the Chesterian surface of the Illinois basin and related Chesterian slump blocks. Geol. Soc. Am. Spec. Pap., 148: 315–334.

Burk, M.K., Deshowitz, M.P. and Utgard, J.E., 1987. Facies and depositional environments of the Energy Shale Member (Pennsylvanian) and their relationships to low-sulfur coal deposits in southern Illinois. J. Sediment. Petrol., 57: 1060–1067.

Burnham, R.J., 1989. Relationships between standing vegetation and leaf litter in a paratropical forest: implications for paleobotany. Rev. Palaeobot. Palynol., 58: 5–32.

Buzas, M.A. and Culver, S.J., 1994. Species pool and dynamics of marine paleocommunities. Science, 264: 1439–1441.

Caputo, M.V. and Crowell, J.C., 1985. Migration of geological centers across Gondwana during Palaeozoic Era. Geol. Soc. Am. Bull., 96: 1020–1036.

Cecil, C.B., 1990. Paleoclimate controls on stratigraphic repetition of chemical and clastic rocks. Geology, 18: 533–536.

Cecil, C.B., Dulong, F.T., Cobb, J.C. and Supardi, 1993. Allogenic and autogenic controls on sedimentation in the central Sumatra basin as an analogue for Pennsylvanian coal-bearing strata in the Appalachian basin. Geol. Soc. Am. Spec. Pap., 286: 3–22.

Chaney, R.W., 1947. Tertiary centres and migration routes. Ecol. Monogr., 17: 139–148.

Clements, F.E., 1916. Plant succession, an analysis of the development of vegetation. Carnegie Inst. Publ., 242.

Cole, K., 1985. Past rates of change, species richness, and a model of vegetational inertia in the Grand Canyon, Arizona. Am. Nat., 125: 289–303.

Crowley, T.J. and Baum, S.K., 1991. Estimating Carboniferous sea-level fluctuations from Gondwanan ice extent. Geology, 19: 975–977.

Crowley, T.J. and Baum, S.K., 1992. Modeling late Paleozoic glaciation. Geology, 20: 507–510.

DeMaris, P.J., Bauer, R.A., Cahill, R.A. and Damberger, H.H., 1983. Prediction of coal balls in the Herrin Coal. Ill. State Geol. Surv. Contract-Grant Rep., 1982-3, 69 pp.

DiMichele, W.A. and Hook, R.W. (Rapporteurs), 1992. Paleozoic terrestrial ecosystems. In: A.K. Behrensmeyer et al. (Editors), Terrestrial Ecosystems through Time. Univ. Chicago Press, pp. 205–325.

DiMichele, W.A. and Phillips, T.L., 1988. Paleoecology of the Middle Pennsylvanian-age Herrin coal swamp (Illinois) near a contemporaneous river system, the Walshville paleochannel. Rev. Palaeobot. Palynol., 56: 151–176.

DiMichele, W.A. and Phillips, T.L., 1994. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica. Palaeogeogr. Palaeoclimatol. Palaeoecol., 106: 39–90.

DiMichele, W.A. and Phillips, T.L., 1995. The response of hierarchically-stuctured ecosystems to long-term climate change: a case study using tropical peat swamps of Pennsylvanian age. Effects of Past Global Change on Life. Natl. Res. Counc. Geophys. Study Comm., Washington, DC, pp. 134–155.

DiMichele, W.A., Mahaffy, J.F. and Phillips, T.L., 1979. Lycopods of Pennsylvanian age coals: Polysporia. Can. J. Bot., 57: 1740–1753.

DiMichele, W.A., Phillips, T.L. and McBrinn, G.E., 1991. Quantitative analysis and paleoecology of the Secor coal and roof-shale floras (Middle Pennsylvanian, Oklahoma). Palaios, 6: 390–409.

DiMichele, W.A., Phillips, T.L. and Peppers, R.A., 1985. The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants. In: B.H. Tiffney (Editor), Geological Factors and the Evolution of Plants. Yale Univ. Press, New Haven, pp. 223–256.

Drummond, C.N. and Wilkinson, B.H., 1993. Carbonate cycle stacking patterns and hierarchies of orbitally forced eustatic sealevel change. J. Sediment. Petrol., 63: 369–377.

Eggert, D.A., 1972. Petrified Stigmaria of sigillarian origin from North America. Rev. Palaeobot. Palynol., 14: 85–99.

Eggert, D.L., 1982. A fluvial channel contemporaneous with deposition of the Springfield Coal Member (V), Petersburg Formation, northern Warrick County, Indiana. Ind. Geol. Surv. Spec. Rep., 28, 20 pp.

Elliot, R.E., 1968. Facies, sedimentation successions and cyclothems in productive coal measures in the East Midlands, Great Britain. Merc. Geol., 2: 331–372.

Elliot, R.E., 1969. Deltaic processes and episodes: the inter-

pretation of productive coal measures occurring in the East Midlands, Great Britain. Merc. Geol., 3: 111–135.

Ferm, J.C., 1975. Pennsylvanian cyclothems of the Appalachian Basin, a retrospective view. U.S. Geol. Surv. Prof. Pap., 853: 57–64.

Ferm, J.C. and Weisenfluh, G.A., 1989. Evolution of some depositional models in Late Carboniferous rocks of the Appalachian coal fields. Int. J. Coal Geol., 12: 259–292.

Frakes, L.E., Francis, J.E. and Syktus, J.I., 1992. Climate Modes of the Phanerozoic. Cambridge Univ. Press, Cambridge, 274 pp.

Gastaldo, R.A., 1977. A Middle Pennsylvanian nodule flora from Carterville, Illinois. In: R.C. Romans (Editor), Geobotany. Plenum, New York, pp. 133–155.

Gastaldo, R.A. and Huc, A.-Y., 1992. Sediment facies, depositional environments, and distribution of phytoclasts in the Recent Mahakam River delta, Kalimantan, Indonesia. Palaios, 7: 574–590.

Gastaldo, R.A., Pfefferkorn, H.W. and DiMichele, W.A., 1995. Taphonomic and sedimentologic characterization of "roof-shale" floras. Geol. Soc. Am. Mem., 185: 341–352.

Gerhard, L.C., 1991. Stratigraphy in the modern generation. Kans. Geol. Surv. Open-File Rep., 91-24, 13 pp.

Gillespie, W.M. and Pfefferkorn, H.W., 1979. Distribution of commonly occurring plant megafossils in the proposed Pennsylvanian System Stratotype. In: K.J. England et al. (Editors), Proposed Pennsylvanian System Stratotype, Virginia and West Virginia. 9th Int. Congr. Carbonif. Stratigr. Geol. Guidebook Field Trip, 1, pp. 87–96.

Gleason, H.A., 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club, 53: 7–26.

Guo, Yingting, 1990. Palaeoecology of flora from coal measures of Upper Permian in western Guizhou. J. China Coal Soc., 15: 48–54.

Hallam, A., 1992. Phanerozoic Sea-level Changes. Columbia Univ. Press, New York, 266 pp.

Heckel, P.H., 1977. Origin of phosphatic black shale facies in Pennsylvanian cyclothems of mid-continent North America. AAPG Bull., 61: 1045–1068.

Heckel, P.H., 1980. Paleogeography of eustatic model for deposition of midcontinent Upper Pennsylvanian cyclothems. In: T.D. Fouch and E.R. Magathan (Editors), Paleozoic Paleogeography of West-Central United States. SEPM Rocky Mt. Sect., Denver, CO, pp. 197–215.

Heckel, P.H., 1986. Sea-level curve for Pennsylvanian eustatic marine transgressive-regressive depositional cycles along midcontinent outcrop belt, North America. Geology, 14: 330–334.

Heckel, P.H., 1989. Updated Middle–Upper Pennsylvanian eustatic sea level curve for midcontinent North America and preliminary biostratigraphic characterization. In: C.R. 11th Int. Congr. Carbonif. Stratigr. Geol., 4: 160–185.

Hopkins, M.E., 1958. Geology and petrology of the Anvil Rock Sandstone of southern Illinois. Ill. State Geol. Surv. Circ., 256, 49 pp.

Hopkins, M.E., 1968. Harrisburg (No.5) Coal reserves of southeastern Illinois. Ill. State Geol. Surv. Circ., 431, 25 pp.

Horne, J.C., Ferm, J.C., Carruccio, F.T. and Baganz, B.P., 1978. Depositional models in coal exploration and mine planning in Appalachian Region. AAPG Bull., 62: 2379–2411.

Howard, R.H., 1979. The Mississippian–Pennsylvanian unconformity in the Illinois basin—old and new thinking. In: 9th Int. Congr. Carbonif. Stratigr. Geol. Field Trip 9, Part 2, Invited Pap. Ill. State Geol. Surv., pp. 34–42.

Johnson, D.O., 1972. Stratigraphic analysis of the interval between the Herrin (No. 6) Coal and the Piasa Limestone in southwestern Illinois. Thesis. Univ. Illinois, Urbana-Champaign, 105 pp.

Klein, G. de Vries, 1990. Pennsylvanian time scales and cycle periods. Geology, 18: 455–457.

Klein, G. de Vries, 1992. Climatic and tectonic sea-level gauge for midcontinent Pennsylvanian cyclothems. Geology, 20: 363–366.

Kosanke, R.M., Simon, J.A., Wanless, H.R. and Willman, H.B., 1960. Classification of the Pennsylvanian strata of Illinois. Ill. State Geol. Surv. Rep. Invest., 214, 84 pp.

Kolata, D.R. and Nelson, W.J., 1991. Tectonic history of the Illinois Basin. In: M.W. Leighton et al. (Editors), Interior Cratonic Basins. AAPG Mem., 51: 263–284.

Lyons, P.C., Hatcher, P.G., Brown, F.W., Thompson, C.L. and Millay, M.A., 1985. Coalification of organic matter in a coal ball from the Calhoun coal bed (Upper Pennsylvanian), Illinois Basin, United States of America. In: Proc. 10th Int. Congr. Carbonif. Stratigr. Geol., 1: 155–159.

Mahaffy, J.F., 1985. Profile patterns of coal and peat palynology in the Herrin (No. 6) Coal Member, Carbondale Formation, Middle Pennsylvanian of southern Illinois. In: Proc. 9th Int. Congr. Carbonif. Stratigr. Geol., 5: 155–159.

Mahaffy, J.F., 1988. Vegetational history of the Springfield coal (Middle Pennsylvanian of Illinois) and the distribution of the tree fern miospore, Thymospora pseudothiessenii, based on miospore profiles. Int. J. Coal Geol., 10: 239–260.

Mapes, G. and Gastaldo, R.A., 1986. Late Paleozoic non-peat accumulating floras. In: T. Broadhead (Editor), Land Plants, Notes for a Short Course. Univ. Tenn., Dep. Geol. Sci. Stud. Geol., 15: 115–127.

Miller, K.B. and West, R.R., 1993. Reevaluation of Wolfcampian cyclothems in northeastern Kansas: significance of subaerial exposure and flooding surfaces. Kans. Geol. Surv. Bull., 235: 26–52.

Nelson, W.J., Trask, C.B., Jacobson, R.J., Damberger, H.H., Williamson, A.D. and Williams, D.A., 1991. Absaroka Sequence. Pennsylvanian and Permian Systems. In: M.W. Leighton et al. (Editors), Interior Cratonic Basins. AAPG Mem., 51: 143–164.

Overpeck, J.T., Webb, R.S. and Webb III, T., 1992. Mapping eastern North American vegetation change of the past 18 ka: no analogues and the future. Geology, 20: 1071–1074.

Pfefferkorn, H.W., 1970. Use of plant megafossils in correlation of the Pennsylvanian of the Illinois Basin with the Upper Carboniferous of Europe. Geol. Soc. Am. Abstr. with Programs, 2: 652.

Pfefferkorn, H.W., 1974. The compression flora of the

McLeansboro Group (Upper Pennsylvanian) of Illinois. Geol. Soc. Am. Abstr. with Programs, 6: 1055.

Pfefferkorn, H.W., 1975. Biostratigraphy of the Pennsylvanian of the Illinois Basin (USA) based on plant megafossils. In: Abstr. 8th Int. Congr. Carbonif. Stratigr. Geol., Moscow, pp. 212–213.

Pfefferkorn, H.W., 1979. High diversity and stratigraphic age of the Mazon Creek Flora. In: M.H. Nitecki (Editor), Mazon Creek Fossils. Academic Press, New York, pp. 129–142.

Pfefferkorn, H.W. and Thomson, M.C., 1982. Changes in dominance patterns in Upper Carboniferous plant fossil assemblages. Geology, 10: 641–644.

Pfefferkorn, H.W., Mustafa, H. and Hass, H., 1975. Quantitative Charackterisierung oberkarboner Abdruckfloren. Neues Jahrb. Geol. Palaeontol. Abh., 150: 253–269.

Peppers, R.A., 1970. Correlation and palynology of coals in the Carbondale and Spoon Formations (Pennsylvanian) of the northeastern part of the Illinois Basin. Ill. State Geol. Surv. Bull., 93, 173 pp.

Peppers, R.A., 1985. Comparison of miospore assemblages in the Pennsylvanian System of the Illinois Basin with those in the Upper Carboniferous of Western Europe. In: C.R. 9th Int. Congr. Carbonif. Stratigr. Geol., 2:483–502.

Peppers, R.A. and Pfefferkorn, H.W., 1970. A comparison of the floras of the Colchester (No. 2) Coal and Francis Creek Shale. In: W.H. Smith et al. (Editors), Depositional Environments in Parts of the Carbondale Formation—Western and Northern Illinois. Ill. State Geol. Surv. Guidebook Ser., 8: 61–74.

Phillips, T.L. and DiMichele, W.A., 1981. Paleoecology of Middle Pennsylvanian age coal swamps in southern Illinois—Herrin Coal Member at Sahara Mine No. 6. In: K.J. Niklas (Editor), Paleobotany, Paleoecology, and Evolution. Praeger Press, New York, 1, pp. 231–284.

Phillips, T.L. and Peppers, R.A., 1984. Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrence. Int. J. Coal Geol., 3: 205–255.

Phillips, T.L., Avcin, M.J. and Berggren, D., 1976. Fossil peat of the Illinois Basin. Ill. State Geol. Surv. Educ. Ser., 11, 39 pp.

Phillips, T.L., Peppers, R.A. and DiMichele, W.A., 1985. Stratigraphic and interregional changes in Pennsylvanian coal-swamp vegetation: environmental inferences. Int. J. Coal Geol., 5: 43–109.

Phillips, T.L., Kunz, A.B. and Mickish, D.J., 1977. Paleobotany of permineralized peat (coal balls) from the Herrin (No.6) Coal Member of the Illinois Basin. In: P.N. Given and A.D. Cohen (Editors), Interdisciplinary Studies of Peat and Coal Origins. Geol. Soc. Am. Microform Publ., 7: 18–49.

Phillips, T.L., Peppers, R.A., Avcin, M.J. and Laughnan, P.F., 1974. Fossil plants and coal: patterns of change in Pennsylvanian coal swamps of the Illinois Basin. Science, 184: 1367–1369.

Pryor, J.S., 1993. Patterns of ecological succession within the

Upper Pennsylvanian Duquesne coal of Ohio (USA). Evolut. Trends Plants, 7: 57–66.

Read, C.B. and Mamay, S.H., 1964. Upper Paleozoic floral zones and floral provinces of the United States. U.S. Geol. Surv. Prof. Pap., 434-K: 1–35.

Ross, C.A. and Ross, J.R.P., 1988. Late Paleozoic transgressive–regressive deposition. SEPM Spec. Publ., 42: 227–247.

Shabica, C.W., 1979. Pennsylvanian sedimentation in northern Illinois: examination of delta models. In: M.H. Nitecki (Editor), Mazon Creek Fossils. Academic Press, New York, pp. 13–40.

Scheihing, M.H. and Pfefferkorn, H.W., 1984. The taphonomy of land plants in the Orinoco Delta: A model for the incorporation of plant parts in clastic sediments of Late Carboniferous of Euramerica. Rev. Palaeobot. Palynol., 41: 205–240.

Scott, A.C., 1978. Sedimentological and ecological control of Westphalian B plant assemblages from west Yorkshire. Proc. Yorks. Geol. Soc., 41: 461–508.

Scott, A.C. and Rex, G., 1985. The formation and significance of Carboniferous coal balls. Philos. Trans. R. Soc. London, 311B: 123–137.

Staub, J.R. and Esterle, J.S., 1993. Provenance and sediment dispersal in the Rajang River delta/coastal plain system, Sarawak, East Malaysia. Sediment. Geol., 85: 191–201.

Staub, J.R. and Richards, B.K., 1993. Development of low-ash, planar peat swamps in an alluvial-plain setting: the No. 5 Block Beds (Westphalian D) of southern West Virginia. J. Sediment. Petrol., 63: 714–726.

Suchy, D.R. and West, R.R., 1991. Genetic stratigraphy of the Fort Scott Limestone (Pennsylvanian, Desmoinesian), southeastern Kansas. Kans. Geol. Surv. Bull., 233: 195–206.

Treworgy, C.G. and Jacobson, R.J., 1979. Paleoenvironments and distribution of low-sulfur coal in Illinois. In: Proc. 9th Int. Congr. Carbonif. Stratigr. Geol., 4: 349–359.

Udden, J.A., 1912. Geology and mineral resources of the Peoria Quadrangle. U.S. Geol. Surv. Bull., 506, 103 pp.

Veevers, J.J. and Powell, C.M., 1987. Late Paleozoic glacial episodes in Gondwanaland reflected in transgressive–regressive depositional sequences in Euramerica. Geol. Soc. Am. Bull., 98: 475–487.

Wagner, R.H., 1984. Megafloral zones of the Carboniferous. In: C. R. 9th Int. Congr. Carbonif. Stratigr. Geol., 2: 109–134.

Wanless, H.R., 1957. Geology and mineral resources of the Beardstown, Glasford, Havana and Vermont Quadrangles. Ill. State Geol. Surv. Bull., 82, 233 pp.

Wanless, H.R. and Shepard, F.P., 1936. Sea level and climatic changes related to late Paleozoic cycles. Geol. Soc. Am. Bull., 47: 1177–1206.

Wanless, H.R. and Wright, C.R., 1978. Paleoenvironmental maps of Pennsylvanian rocks, Illinois Basin and northern midcontinent region. Geol. Soc. Am. Map and Chart Ser., 23, 32 pp.

Wanless, H.R., Tubb Jr., J.B., Gednetz, D.E. and Weiner, J.L., 1963. Mapping sedimentary environments of Pennsylvanian cycles. Geol. Soc. Am. Bull., 74: 437–486.

Wanless, H.R., Baroffio, J.R. and Trescott, P.C., 1969. Condi-

tions of deposition of Pennsylvanian coal beds. Geol. Soc. Am. Spec. Pap., 114: 105–142.

Wanless, H.R., Baroffio, J.R., Gamble, J.C., Horne, J.C., Orlopp, D.R., Rocha-Campos, A., Souter, J.E., Trescott, P.C., Vail, R.S. and Wright, C.R., 1970. Late Paleozoic deltas in the central and eastern United States. In: J.P. Morgan (Editor), Deltaic Sedimentation—Modern and Ancient. SEPM Spec. Publ., 15: 215–245.

Willard, D.A., 1993. Vegetational patterns in the Springfield coal (Middle Pennsylvanian, Illinois Basin): comparison of miospore and coal-ball records. Geol. Soc. Am. Spec. Pap., 286: 139–152.

Willard, D.A. and Klein, G. de Vries, 1990. Tectonic subsidence history of the central Appalachian Basin and its influence on Pennsylvanian coal deposition. Southeast. Geol., 30: 217–239.

Willman, H.B. and Payne, J.N., 1942. Geology and mineral resources of the Marseilles, Ottowa, and Streator quadrangles. Ill. State Geol. Surv. Bull., 66, 388 pp.

Willman, H.B., Atherton, E., Buschbach, T.C., Collinson, C., Frye, J.C., Hopkins, M.E., Lineback, J.A. and Simon, J.A., 1975. Handbook of Illinois Stratigraphy. Ill. State Geol. Surv. Bull., 95, 261 pp.

Winston, R.B., 1990. Implications of paleobotany of Pennsylvanian-age coal of the central Appalachian basin for climate and coal-bed development. Geol. Soc. Am. Bull., 102: 1720–1726.

Wnuk, C., 1985. The ontogeny and paleoecology of *Lepidodendron rimosum* and *Lepidodendron bretonense* trees from the Middle Pennsylvanian of the Bernice Basin (Sullivan County, Pennsylvania). Palaeontographica B, 195:153–181.

Zangerl, R. and Richardson, E.S., 1963. The paleoecological history of two Pennsylvanian black shales. Field Mus. Nat. Hist. Field. Geol. Mem., 4, 352 pp.

Ziegler, A.M., 1989. Phytogeographic patterns and continental configurations during the Permian Period. In: W.S. McKerrow and C.R. Scotese (Editors), Palaeozoic Palaeogeography and Biogeography. Geol. Soc. London Mem., 12: 363–379.

Ziegler, A.M., Raymond, A., Gierlowski, T.C., Horrell, M.A., Rowley, D.B. and Lottes, A.L., 1987. Coal, climate, and terrestrial productivity—the present and Early Cretaceous compared. In: A.C. Scott (Editor), Coal and Coal-Bearing Strata—Recent Advances. Geol. Soc. London Spec. Publ., 32: 25–49.