

# GSA TODAY

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## Out of the Icehouse into the Greenhouse: A Late Paleozoic Analog for Modern Global Vegetational Change

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### ABSTRACT

A change to global greenhouse conditions following deglaciation occurred during the late Paleozoic. The deep-past data set preserved in the stratigraphic record can serve as a model system to understand vegetational responses during this kind of climatic change, especially in the tropics. No other time in Earth history so mimics the late Cenozoic or provides the long-term data set from which generalizations can be deduced. Two long-term glacial cycles have been identified in Permian-Carboniferous time. The waxing and waning of glaciers during the height of either ice age resulted mainly in spatial displacement of vegetation, and also in minor variations in tropical climate. Brief intervals of rapid deglaciation at the end of the Middle Pennsylvanian (Westphalian) and mid-Early Permian (Sakmarian) were accompanied by major changes in plant assemblages, including extinctions, changes in the

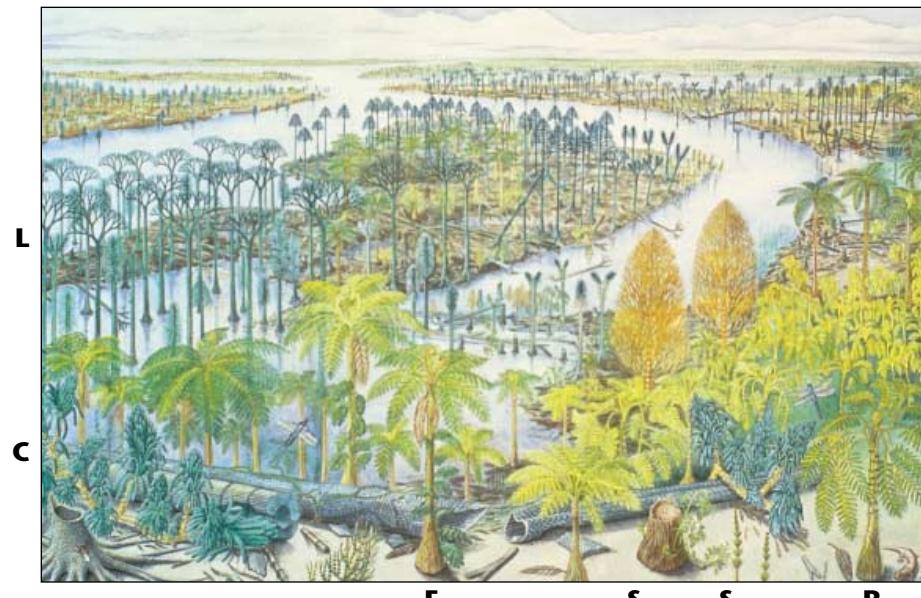


Figure 1. Reconstruction of middle late Carboniferous tropical coal swamp showing different plant communities made up of tree lycopods (L, tree club mosses), tree sphenopsids (two brushlike trees above letter S in center and tree scouring rushes), tree ferns (F), pteridosperms (P, seed plants with fernlike leaves; extinct group), and cordaites (C, seed plants with strap-shaped leaves; extinct group). From a painting by Alice Prickett, published in black and white in Phillips and Cross (1991, pl. 4).

spatial distribution of plants in the tropics and temperate zones, and nearly synchronous changes in the structure of vegetation throughout the globe. Although the plants of the late Paleozoic and the geography of that time differed entirely from those of today,

the rates, geographic distribution, and nature of vegetational changes can serve as portents of similar patterns in the transition to a modern greenhouse world.

**Greenhouse** continued on p. 2

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**Greenhouse** *continued from p. 1*

## INTRODUCTION

Current debate over global warming has not resolved whether empirical observations reflect short-term excursions within longer term cyclical oscillations of climate or if they reflect a unidirectional long-term trend (Graham, 1995; Thompson, 1995; Webb, 1995). Regardless, a global greenhouse stands in marked contrast to the past 20 m.y. of glaciation and icehouse climate (Fischer, 1982). Consequently, the most recent icehouse period may be a poor model from which to deduce the likely dynamics of vegetational change under continuously directional warming. Other periods of pronounced

greenhouse climate, such as the Late Cretaceous and late Eocene, do not reflect the icehouse-greenhouse climate transition. Rather, these intervals of time represent high points or thermal maxima within long-persistent greenhouse intervals (Ziegler et al., 1987), rendering them unsuitable as analogs for the present or the near future (Sellwood et al., 1994). The only time in Earth history when the mosaic of a complex terrestrial vegetation (Fig. 1) was subjected to a transition from icehouse to greenhouse conditions, similar to the one we may now be experiencing, was during the late Paleozoic (Frakes et al., 1992; Crowley, 1994). Comparison of the present and this deep-past record can lead us to a more realistic framework from which to attempt a prediction concerning the dynamics of vegetational change during a period of icehouse to greenhouse climatic change.

In any period of rapid environmental modification it will be crucial to understand the fundamental principles that underlie vegetational change and recovery from disturbance. Such principles can be deduced from an understanding of late Paleozoic vegetational responses because of several parameters. The biota of the late Paleozoic was entirely distinct from that of today, providing an independent data set from which we can deduce general plant responses to changing extrinsic conditions. This is due, in large part, to the presence of similar environmental stresses that resulted in plant responses producing plant structure and architecture (*sensu* Halle, et al., 1978), life history spectra, and reproductive strategies similar to those of vegetation of the present. The floristic biogeography and zonation of the late Paleozoic parallel those of today (Ziegler, 1990). Overall, then, the systematic differences can be viewed as a means of strengthening the possibilities of recognizing fundamen-

## In Memoriam

### J. Wyatt Durham

Kensington, California  
July 10, 1996

### William H. Easton

Westlake Village, California  
July 7, 1996

### S. Warren Hobbs

Fort Collins, Colorado  
May 1996

### Ronald E. McAdams

Englewood, Colorado  
May 6, 1996

### Carl H. Savit

Houston, Texas

### Curt Teichert

Arlington, Virginia  
May 10, 1996

### Harry Tourtelot

Rolla, Missouri  
July 17, 1996

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## **Greenhouse** continued from p. 2

tal processes and permitting generalizations to be made about how vegetation responds to changing climate. The late Paleozoic plant record consists of assemblages that are preserved with high resolution and fidelity (Behrensmeyer and Hook, 1992; Burnham, 1993) in sedimentary environments representing fluvial, lacustrine, coastal plain, and deltaic settings. Plants colonized a wide variety of substrates, and communities are known from peat and clastic alluvial sediments. These assemblages provide snapshots in time of vegetational patterns during both glacial and interglacial cycles over the entire icehouse-greenhouse interval. Finally, late Paleozoic tropical plants and plant ecosystems are as well known as and possibly better known than their Holocene counterparts, in terms of their long-term response to abiotic stresses (sea level and climate fluctuations). From the late Paleozoic record, we conclude that many effects of an icehouse-greenhouse transition will probably be expressed dramatically in the tropics.

The late Paleozoic encompasses the decline of Earth's primeval forests and their replacement by seed-plant-dominated vegetation more typical of the Mesozoic. Increases in greenhouse gasses during the late Paleozoic occurred over millions of years (Berner, 1990, 1991; Graham et al., 1995). In contrast, similar accumulations may occur within markedly shorter intervals of time today (Francey et al., 1995). However, the time required for changes in plant life might not be significantly different. While late Paleozoic stages, as defined by plant fossils, lasted from 1 to 2 m.y., the change from one flora to another (widespread extinction, radiation, and propagation) marks the boundary between stages. We cannot yet put numerical values on the length of

time over which these turnovers occurred. However, the resolution of time within stratigraphic sections is increasing. In specific cases it is possible to constrain time either in the range of orbital cycles or even months for tidal sediments. In the near future we can expect to find stratigraphic sections that will allow us to put numerical values both on the duration of changeovers and on intervals of stasis. We expect change-overs to be in the range of 1–10 ka.

## **LATE PALEOZOIC GLACIATION**

Polar glaciation began in the latest early Carboniferous (Visean-Namurian) and fluctuated in magnitude throughout the Permian-Carboniferous (Fig. 2). During these 75+ m.y., two ice ages peaked, one during the late Middle Pennsylvanian (late Westphalian) and the other in the Early Permian (Sakmarian). Orbital-driven glacial and interglacial oscillations were superimposed on these long-term trends (Frakes et al., 1992). The maximum extent of ice caps expanded gradually over the continents, taking an estimated 20 m.y. to reach their greatest coverage. Increasing evidence indicates that each ice age terminated abruptly over 1–10 ka.

The extent of polar glaciations (coverage and ice mass) during Milankovitch cycles has a direct effect on the distribution of rainfall in the tropics by affecting the pattern of atmospheric circulation and the latitudinal range and width of the intertropical convergence zone (Ziegler et al., 1987; Pfefferkorn, 1995). During glacial maxima, the intertropical convergence zone contracts toward the equator and migrates over a narrower latitude, resulting in ever-wet conditions within its area of influence. In contrast, during interglacial intervals, the intertropical convergence zone expands latitudinally and migrates during the yearly cycle over a wider latitudinal belt, resulting in a

change of climatic patterns and greater oscillations in seasonal moisture availability in the tropics. Specifically, there are much larger areas that experience strong wet-dry seasonality.

During the Middle Pennsylvanian (Westphalian) ice age, the waxing and waning of polar ice caps and glaciers were represented in the Euramerican tropics by cyclical sedimentary patterns. During Middle Pennsylvanian (Westphalian) glacial maxima, extensive peat-accumulating swamps developed under an ever-wet climate. Marine sediments reflecting a wide variance in climate were deposited during interglacial periods (glacial minima). Such sea-level changes are evidenced by paralic sequences bounded by transgressive erosional surfaces (Gastaldo et al., 1993) and may be covariant with changes from ever-wet to seasonally dry climates (Cecil, 1990). During the Early Permian glaciations, in contrast to the Westphalian, peat accumulation was far more limited and localized in areas of wettest tropical climates. Interglacials of that time period also were more intensely seasonal than comparable intervals in the Westphalian, on the basis of vegetational and paleosol patterns (Broutin et al., 1990).

During the Late Pennsylvanian (Stephanian), which falls between the two ice ages, Earth may have been warmer (Dorofyeva et al., 1982). Evidence from coal-resource distributional patterns (Phillips and Peppers, 1984) and from biofacies analysis (DiMichele and Aronson, 1992) indicates a generally drier or more seasonal Late Pennsylvanian (Stephanian) interval with pulselike oscillations between overall wetter and drier periods. These oscillations continued into the Permian, with an increasing prominence of drier climates in tropical lowland and intermontane areas. Drying continued

## **Greenhouse** continued on p. 4



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throughout the Permian, and ice caps and peat-accumulating systems were lost (Retallack, 1995). By latest Permian time, compressional tectonics, the oxidation of peat resources, and volcanic processes may have introduced vast quantities of CO<sub>2</sub> into the atmosphere, driving global temperatures toward their maximum (Erwin, 1996).

### LATE PALEOZOIC VEGETATION

The beginning of the Carboniferous is marked by a radiation of vascular plants that established five major groups. During the late Paleozoic, ecological dominance was strongly partitioned by the different higher taxonomic groups (see Fig. 1): tree club mosses (rhizomorphic lycopods) in swampy wetlands; tree scouring rushes (sphenopsids) in aggradational environments; ferns, including tree ferns, as weeds in a variety of disturbed settings; and seed plants (seed ferns or pteridosperms and cordaites) in better drained habitats. However, temporal and spatial exceptions are known to have existed—as, for example, peat-forming cordaites and pteridosperms. The dominance of each group of plants in a particular environment distinguishes the Carboniferous from later time periods. By the end of the Paleozoic, these patterns and groups had yielded, through a series of steps, to seed plants, which began to dominate in most habitats throughout the world (Niklas et al., 1983).

Permian-Carboniferous terrestrial vegetation can be divided into three broad biogeographic realms (Fig. 3): (1) the pantropical Euramerican (or Amerosinian) floral realm (Wagner, 1993), the best known and most intensively studied, (2) the north-temperate Angaran floral realm (Meyen, 1982), and (3) the south-temperate Gondwanan floral realm (Archangelsky, 1990). These three biogeographic realms were occupied by different plants, but the vegetational turnover occurred in all three at about the same time (Wagner, 1993). However, there might be differences in the timing of turnover of as much as one stage between different climatic belts, owing to the buffering of environmental change by local or regional physiographic differences and the resulting lag time in vegetational turnover. These major vegetational turnovers appear to be in part the result of geologically rapid (1–10 ka) migrations of groups of plants from one climatic belt to another. In contrast, slow migration of genera or species over millions of years has been documented by Laveine (1993). These two processes are different in nature and should not be confused. Knowledge of the slow migration can improve our understanding of biogeographic barriers during times of evolutionary stasis.

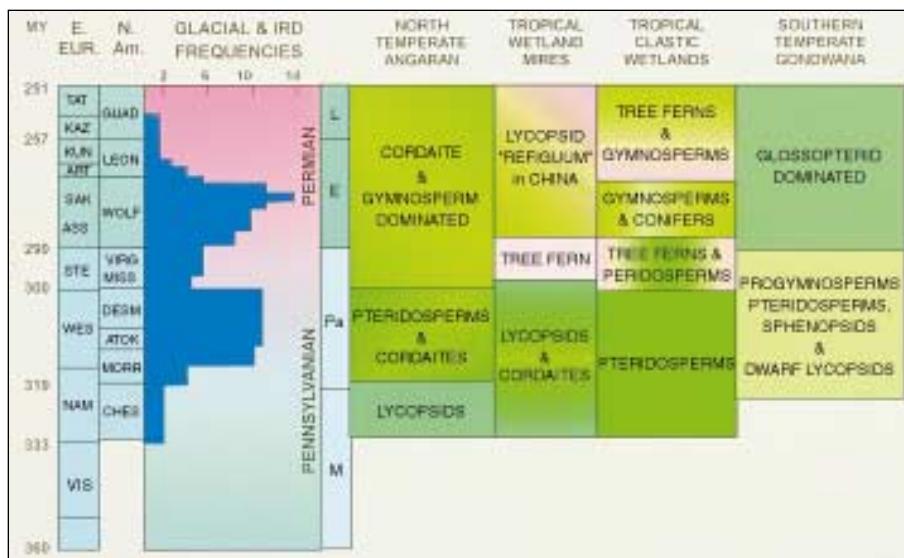
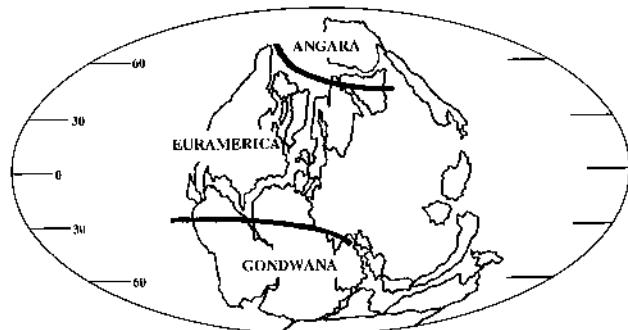


Figure 2. Relation between global glaciation and vegetative change during the late Paleozoic in different tropical environments and the north and south temperate belts. Glacial ice extent, from Frakes et al. (1992), is based upon tillites (glacial) and ice-rafterd deposits (IRD). Vegetation distributional patterns are derived from sources cited in the text. M = Mississippian; Pa = Pennsylvanian; E = Early; L = Late; VIS = Visean; NAM = Namurian; WES = Westphalian; STE = Stephanian; ASS = Asselian; SAK = Sakmarian; ART = Artinskian; KUN = Kungurian; KAZ = Kazanian; TAT = Tatarian; CHES = Chesterian; MORR = Morrowan; ATOK = Atokan; DESM = Desmoinesian; MISS = Missourian; VIRG = Virgilian; WOLF = Wolfcampian; LEON = Leonardian; GUAD = Guadalupian.

Figure 3. Distribution of floral realms in latest Pennsylvanian time (290 Ma). Northern temperate (Angara), tropical (Euramerica), and southern temperate (Gondwana) realms can be distinguished. Continental position redrawn from Denham and Scotese's 1988 computer program, Terra Mobilis.



Major vegetational changes have been noted at the base of the Late Carboniferous, within the Early Pennsylvanian (Namurian), near the Middle-Upper Pennsylvanian (Westphalian-Stephanian) boundary, during the transition from the Carboniferous to the Permian, and near the Sakmarian-Artinskian boundary. Each changeover corresponds to significant increases or decreases in polar ice volumes and global temperature (Fig. 2). In all these cases and in all parts of the world, the patterns of vegetational organization yield to increased dominance by opportunistic weedy taxa or, ultimately, to the extinction-resistant life histories of seed plants.

### TROPICAL PATTERNS

Each of the floral realms can be subdivided into “biomes” characteristic of particular climatic and ecological conditions, and each is further subdivisible into landscape units. The Euramerican realm

includes a “wet” biome, characterized by mire (peat-forming) and clastic (floodplain) wetland vegetation. These are the plants typically reconstructed in most Carboniferous “coal swamp” dioramas. Less well known, but present throughout most of the Late Carboniferous, was a tropical “dry” biome with a flora rich in gymnosperms and which included conifers (Lyons and Darrah, 1989). This flora entered the tropical lowlands only during short periods of regional dryness (probably the result of increased seasonality; Elias, 1936; DiMichele and Aronson, 1992).

Mires within the “wet” biome were dominated by lycopods and cordaites throughout the Middle Pennsylvanian (Westphalian); tree ferns appeared in mires of the latest Middle Pennsylvanian (mid-Westphalian D). Following major extinctions at the Middle-Late Pennsylvanian (Westphalian-Stephanian) boundary that reached nearly 70% of the known species (DiMichele and Phillips, 1996),

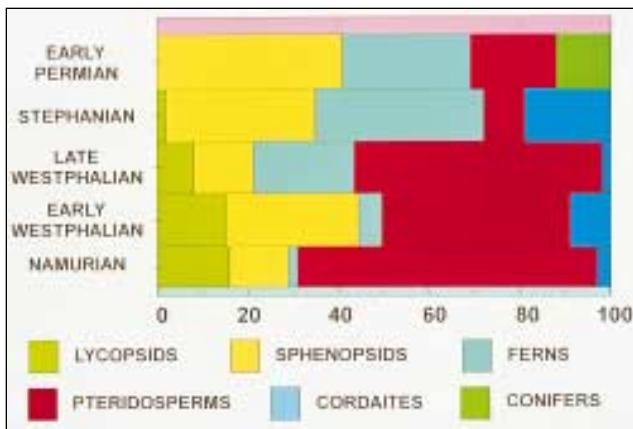


Figure 4. Changes in dominance patterns of major plant groups in the clastic swamp environment of the tropics throughout the Pennsylvanian (late Carboniferous) and earliest Permian. Data from North America and Europe (Pfefferkorn and Thomson, 1982).

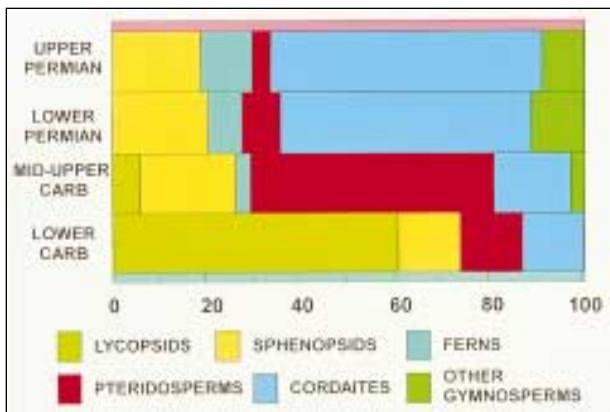


Figure 5. Changes in dominance patterns of major plant groups in the clastic swamp environment of the northern temperate realm throughout the Pennsylvanian (late Carboniferous) and Permian. Data from Kazakhstan (Meyen, 1982).

tree ferns dominated Late Pennsylvanian mires.

Clastic wetland habitats were largely pteridosperm dominated throughout the Middle Pennsylvanian (Gastaldo, 1987). Beginning in the latest Middle Pennsylvanian, tree ferns rapidly established themselves as codominants and continued as dominant to codominant taxa throughout the Late Pennsylvanian (Pfefferkorn and Thomson, 1982). The predominance of tree ferns during the Late Pennsylvanian followed extinctions in the clastic wetlands that, although less severe, paralleled those of the mires. The extinctions within the pteridosperm groups were accompanied by speciation that vastly increased the number of tree fern taxa of the later Paleozoic (Fig. 4).

The extinction events at the Middle Pennsylvanian–Late Pennsylvanian (Westphalian-Stephanian) boundary induced a thresholdlike internal reorganization of the wetlands (DiMichele and Phillips, 1995). The tree ferns that became dominant descended from opportunistic weedy forms in the older Westphalian landscapes. These plants were well suited to compete for space and resources in disrupted, postextinction landscapes, owing to their reproductive strategy of producing massive quantities of highly dispersible spores, a “cheaply” constructed body (one consisting largely of simple parenchyma cells), and an ability to tolerate low nutri-

ent conditions. This signaled the beginning of the breakdown of the landscape between groups of plants. The high taxonomic level at which the data are summarized in Figures 2, 4, and 5 masks certain patterns at lower levels of ecological organization, particularly the persistence of dominance-diversity patterns within habitats and the replacement of species on ecomorphic themes through time (DiMichele et al., 1996). The major patterns revealed by these data are persistence of communities and landscapes over millions of years, disrupted only by major extinction events that lead to relatively rapid reorganization and establishment of new persistent patterns.

In spite of renewed polar glaciation, pulselike climatic drying continued throughout the tropics into the Early Permian. Continued drying, in part the result of Pangean assembly, progressively eliminated tracts of continuous wetland habitat crucial to the survival of the wet biome. The exception occurs in south China, where a Westphalian-type flora persisted in mires until the Late Permian (Guo, 1990). Seed plants, which were resistant to increasingly dry conditions by virtue of both reproductive and vegetative adaptations, became the dominant elements in most tropical habitats, even in geographically isolated patches of wetlands. The Chinese “refugium” never served as a source for repopulation of the wetlands

elsewhere in the world during the Permian. The transition from the wet to the dry biome was not accompanied by extensive mixing of the component species. Rather, each retained its distinctive taxonomic and ecomorphic characteristics. At this temporal scale, replacement rather than a competitive displacement is strongly indicated. Additionally, it appears that higher levels of ecological organization may have spatial-temporal unity and take part in dynamics not predictable from the study of lower level population or community dynamics. The biotic transition appears to have been independent of internal vegetational dynamics that occurred within each biome.

The dry biome became increasingly dominated by conifers in parts of Euramerica throughout the Asselian (Broutin et al., 1990). It was not until the Sakmarian-Artinskian deglaciation that tree ferns re-emerged as dominant elements within a vegetation that was characterized by a diversity of seed plants (Read and Mamay, 1964). Their re-emergence indicates a change to increased moisture availability within the tropics.

## NORTH-TEMPERATE PATTERNS

The Angara floral realm was dominated by a lycopid-rich flora prior to the onset of polar glaciations (Fig. 5). At or near the middle to late Namurian boundary, the lycopid flora was replaced by a low-diversity but widespread flora dominated by seed ferns and cordaites (Rufolian) that were persistent throughout the Middle Pennsylvanian wetlands. Near the Middle Pennsylvanian–Late Pennsylvanian boundary a further floristic change ensued, resulting in the rise of high-diversity cordait-dominated assemblages (Rufolian 2 assemblage) (Meyen, 1982); Wagner (1993) suggested that this floral change may be coeval with time-equivalent tropical vegetational changes. The pteridospermalean (seed fern) component of the Angaran Middle Pennsylvanian flora is the major casualty following vegetational reorganization. The subsequently dominant, cordait-rich floras (Rufolian 3) have been suggested to be tolerant of freezing conditions. As in the tropical zone, the floras of Angara become progressively more enriched in and dominated by other seed plants (gymnosperms) as major climatic changes caused extinctions in, and reorganizations of, the regional ecological structure (Fig. 5).

## SOUTH-TEMPERATE PATTERNS

As in the tropical and north temperate zones, the Gondwana zone had several distinct vegetational regions in the late Paleozoic (Cuneo, 1996b). The northernmost parts of the Gondwana continent

## Greenhouse continued from p. 5

(northern South America and North Africa) were in the tropics, and fossil assemblages from these areas are distinctly Euramerican. All other parts of the continent were in the south temperate Gondwana biogeographic zone. Major floral changes occurred on the Gondwana continent in the Southern Hemisphere at or near the mid-Carboniferous and Carboniferous-Permian boundaries. Prior to the mid-Carboniferous and the inception of glaciation, biomes were characterized by progymnosperms and pteridosperms. There is still debate as to the exact timing of floral change, because the onset of glaciation may have affected the plant biogeography in continental interiors earlier (Archangelsky, 1990).

Floristic turnover at the mid-Carboniferous boundary is characterized by a flora that was made up of taxa like *Nothorhacopteris*, which appear to be similar in aspect to forms dominating early Carboniferous floras in the tropics. Several of the dominant taxa were considered to be progymnosperms. However, recent work has shown that some of them were pteridosperms (Vega and Archangelsky, 1996; Galtier, 1996). Scouring rushes (sphenopsids) and club mosses (lycopsids) also were present, but they were small in the cooler areas; they grew to tree size only in the warmer areas (Peru, Niger). Ferns were rare or absent. The highest diversity floras occupied the lower latitudes, whereas the low-diversity floras are known from more poleward regions.

At or near the Carboniferous-Permian boundary, this late Carboniferous flora was replaced by one dominated by seed-bearing glossopterids, large trees with deciduous leaves (Cuneo, 1996a). Early glossopterids appeared suddenly, accompanied by the extinction of many of the Carboniferous elements. The simple venation of these early forms cannot be distinguished from the genus *Lesleya* that occurred in seasonally dry areas of the tropics as early as earliest Pennsylvanian (Namurian) time in Illinois (Leary, 1980). If actually related to glossopterids, *Lesleya* would have been at least partly preadapted to a seasonally cold climate of the Southern Hemisphere (Leary, 1980; Archangelsky, 1990) by virtue of its origin in seasonally dry parts of the tropics.

The *Glossopteris*-dominated flora persisted throughout the Permian and diversified in complexity of leaf venation and reproductive structures. In addition, tropical plants appeared in the temperate areas in response to higher rainfall and due to the drying of most of the tropical areas. The temperate areas of Gondwana were clearly not very cold (Cuneo, 1987), certainly much warmer than hypothesized by climate models (Yemane, 1993). This is reflected in the successful colonization by

conifers, sphenopsids, ferns, pteridosperms, ginkgophytes, and cordaites. One aspect that has been neglected in most previous discussions is the fact that there must have been glacial and interglacial intervals and that the interglacial periods could have been very warm, providing for part of the vegetational record.

## DISCUSSION

The late Paleozoic offers the best pre-Pleistocene opportunity to observe the response of terrestrial vegetation to short-term and long-term fluctuations in glacial conditions, the ultimate end of an ice age, and change to a global greenhouse. In fact, the patterns of change in the tropics, in particular, appear to be better documented for the Permian-Carboniferous tropics than for those of today. Several conclusions and generalities can already be drawn from study of these long-extinct ecosystems.

Despite difficulties in correlation, a case can be made for approximate synchronicity of changes in plant communities throughout the world in response to severe global physical stresses. These consequences might be offset in time by as much as a stage because some climatic belts or environments are able to buffer consequences of changes until threshold levels are overcome. The "recovery" phases following periods of major glacial onset or retreat are complex and dependent on local factors, both biotic (for example, ability of species to extend their ranges into an area) and abiotic.

Ecosystems appear to be able to "absorb" regional to global species extinctions below some threshold level. Our data do not yet permit us to pinpoint this with great accuracy, but it appears to be less than 50% and probably more than 10% of common species of trees and shrubs. Such background turnover and replacement are visible at the species level in data derived from peat-forming mires and clastic wetlands. When this threshold extinction level is surpassed, reorganization takes place and results in a different dominance-diversity structure. Floras and vegetation in both the tropical and north-temperate regions persist for millions of years despite background extinction, only to change approximately simultaneously during a period of glacial onset or deglaciation and global warming.

When ecosystems are physically disrupted by short-term but severe and widespread perturbations, opportunists will have a distinct advantage in securing and maintaining dominance. The lowland-wetland, tropical Late Pennsylvanian (Stephanian) is, in some ways, analogous to an extended "fern spike" recognized as the initial recovery phase following the Cretaceous-Tertiary extinction event (Nichols et al., 1986).

The concept of refugium is elusive. An area of survival of archaic vegetation (relative to the rest of a floristic realm) does not constitute a refugium if the plants cannot migrate back to previously occupied areas when conditions return to those approximating the pre-extinction environment. Both abiotic factors, such as the lack of clear routes of dispersal, and biotic factors, such as incumbent advantage, can prevent an expansion of vegetation from a potentially refugial area.

Ultimately, species with life histories and structural adaptations that precondition them to survive under physically inhospitable conditions will survive to attain dominance. During the late Paleozoic these were almost exclusively groups of seed plants. The pattern has continued, with subsequent global and regional ecological perturbation resulting in dominance of the landscape by an ever narrowing phylogenetic spectrum of plants after the late Paleozoic. Within the seed plants, dominance has been narrowed largely to angiosperms. Within angiosperms, composites and grasses have become ever more dominant over wider areas of Earth's surface as a consequence of climatic changes.

Patterns in the late Paleozoic provide us with one certainty: global warming presents plants with conditions that are markedly different from those found during periods of icehouse climate. The waxing and waning of glaciers are, in and of themselves, a climate-mode to which vegetations become attuned. Global warming breaks the mold and encourages the establishment, quite rapidly (in geological terms at a stage boundary; probably on the order of 1–10 ka), of new kinds of vegetation, the origins of which are as much due to evolutionary innovation as to reorganization of species associations. Extinctions break the hold incumbent taxa have over the resources and favor or permit the establishment of new species, although apparently those descended from opportunistic and/or extinction-resistant ancestors. Past patterns, when coupled with recently developed ecological concepts such as the recognition of thresholdlike responses to perturbation (Kareiva and Wennergren, 1995), provide a basis to speculate on responses to change.

Although the interactions between vegetation and climate are complex, they do conform to some general and recurrent patterns that exist on different scales in space and time. Recognizing patterns and principles of change at the icehouse-greenhouse transitions of the late Paleozoic will enable us to use this understanding to make predictions about changes to come.

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