

INSIDE

- First International Secretary Named, p. 22
- 1996 Honorary Fellows, p. 23
- Call for Award Nominations, p. 26
- Southeastern Section 1997 Meeting, p. 32

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

Robert A. Gastaldo, Department of Geology, Auburn University, AL 36849-5305,

William A. DiMichele, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20506,

Hermann W. Pfefferkorn, Department of Geology, University of Pennsylvania, Philadelphia, PA 19104-6316

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

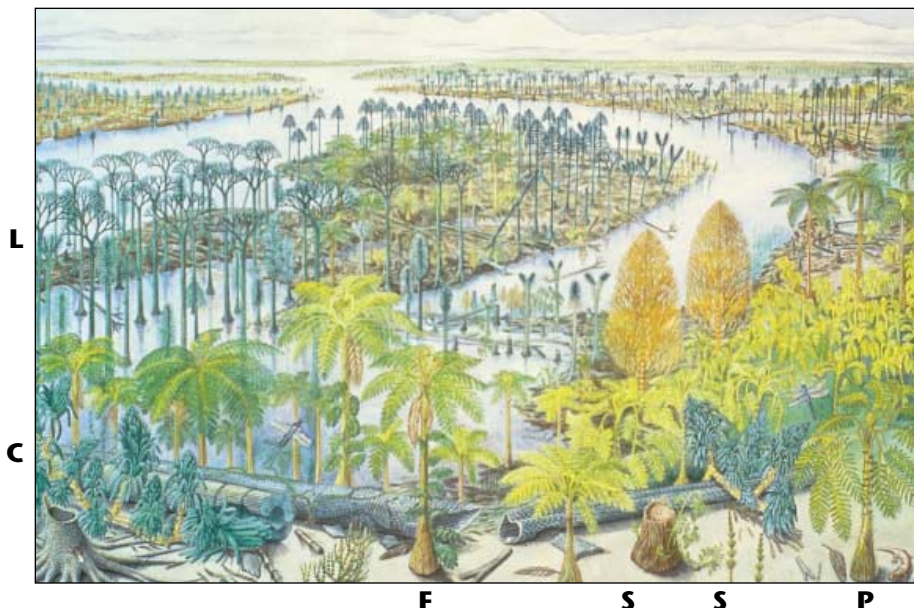


Figure 1. Reconstruction of middle late Carboniferous tropical coal swamp showing different plant communities made up of tree lycopods (L, tree club mosses), tree sphenopsids (two brushlike trees above letter S in center and tree scouring rushes), tree ferns (F), pteridosperms (P, seed plants with fernlike 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

SECOND CENTURY FUND

EARTH ♦ EDUCATION ♦ ENVIRONMENT

HAVE YOU MADE YOUR PLEDGE YET? MEMBERSHIP GOAL: \$1.5 MILLION

SECTION GOALS

CORDILLERAN	ROCKY MOUNTAIN	NORTH-CENTRAL	SOUTH-CENTRAL	NORTHEASTERN	SOUTHEASTERN
\$465,000	\$225,000	\$170,000	\$165,000	\$265,000	\$210,000

5-year pledges totaling \$250 or more will be eligible for a special drawing to be held at the 1996 Annual Meeting in Denver.

GSA TODAY (ISSN 1052-5173) is published monthly by The Geological Society of America, Inc., with offices at 3300 Penrose Place, Boulder, Colorado. Mailing address: P.O. Box 9140, Boulder, CO 80301-9140, U.S.A. Periodicals class postage paid at Boulder, Colorado, and at additional mailing offices. **Postmaster:** Send address changes to *GSA Today*, Membership Services, P.O. Box 9140, Boulder, CO 80301-9140.

Copyright © 1996, The Geological Society of America, Inc. (GSA). All rights reserved. Copyright not claimed on content prepared wholly by U.S. Government employees within the scope of their employment. Permission is granted to individuals to photocopy freely all items other than the science articles to further science and education. Individual scientists are hereby granted permission, without royalties or further requests, to make unlimited photocopies of the science articles for use in classrooms to further education and science, and to make up to five copies for distribution to associates in the furtherance of science; permission is granted to make more than five photocopies for other noncommercial, nonprofit purposes furthering science and education upon payment of the appropriate fee (\$0.25 per page) directly to the Copyright Clearance Center, 27 Congress Street, Salem, Massachusetts 01970, phone (508) 744-3350 (include title and ISSN when paying). Written permission is required from GSA for all other forms of capture, reproduction, and/or distribution of any item in this journal by any means. GSA provides this and other forums for the presentation of diverse opinions and positions by scientists worldwide, regardless of their race, citizenship, gender, religion, or political viewpoint. Opinions presented in this publication do not reflect official positions of the Society.

SUBSCRIPTIONS for 1996 calendar year: **Society Members:** *GSA Today* is provided as part of membership dues. Contact Membership Services at (800) 472-1988 or (303) 447-2020 for membership information. **Nonmembers & Institutions:** Free with paid subscription to both *GSA Bulletin* and *Geology*, otherwise \$45 for U.S., Canada, and Mexico; \$55 elsewhere. Contact Subscription Services. **Single copies** may be ordered from Publication Sales. **Claims:** For nonreceipt or for damaged copies, members contact Membership Services; all others contact Subscription Services. Claims are honored for one year; please allow sufficient delivery time for overseas copies.

STAFF: Prepared from contributions from the GSA staff and membership.

Executive Director: Donald M. Davidson, Jr.

Science Editor: Suzanne M. Kay
Department of Geological Sciences, Cornell University,
Ithaca, NY 14853

Forum Editor: Bruce F. Molnia
U.S. Geological Survey, MS 917, National Center,
Reston, VA 22092

Managing Editor: Faith Rogers

Production & Marketing Manager: James R. Clark

Production Editor and Coordinator: Joan E. Manly

Graphics Production: Joan E. Manly, Adam S. McNally

ADVERTISING

Classifieds and display: contact Ann Crawford
(303) 447-2020; fax 303-447-1133

Issues of this publication are available electronically, in full color, from GSA as Acrobat "Portable Document Format" (PDF) files. These can be viewed and printed on personal computers using MSDOS or MSWindows, on Macintoshes, or on Unix machines. You must use the appropriate Adobe Acrobat Reader, available for free download from GSA and other online services. The more powerful Adobe Exchange program, available from commercial software suppliers, may also be used. Download the issues of *GSA Today* and/or the appropriate Readers using the Uniform Resource Locator (URL): <http://www.geosociety.org>. Issues of *GSA Today* are posted about the first of the month of publication.

This publication is included on GSA's annual CD-ROM *GSA Journals on Compact Disc*. Call GSA Publication Sales for details.

Printed with pure soy inks on recyclable paper in the U.S.A.

IN THIS ISSUE

Out of the Icehouse into the Greenhouse: A Late Paleozoic Analog for Modern Global Vegetational Change 1

In Memoriam 2

GSA on the Web 3

Washington Report 9

Environment Matters 10

GSAF Update 12

50-Year Fellows 13

Abstracts for Denver Set Record 14

Letters to the Editor 17

New Congressional Science Fellow 19

Comment and Reply 21

Dalziel Named International Secretary ... 22

Division News 22

1996 Honorary Fellows 23

Division and Section Grants for 1996 24

Call for Nominations—

Frye Award for Environmental Geology ... 11

Mentors in Applied Geology 23

Penrose, Day, Honorary Fellows 26

Young Scientist Award (Donath Medal) .. 28

Distinguished Service Award 30

National Awards 30

Southeastern Section 1997 Meeting 32

Bulletin and *Geology* Contents 36

Calendar 37

GSA Meetings 37

Classifieds 38

Each month, *GSA Today* features a short science article on current topics of general interest. For guidelines on submitting an article, contact *GSA Today* Science Editor S. M. Kay, Cornell University, (607)255-4701, fax 607-254-4780, E-mail: kay@geology.cornell.edu.

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-

Greenhouse continued on p. 3

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

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 (Behrensmeier 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*



GSA ON THE WEB

GSA's presence on the World Wide Web is growing. New, useful material is being added regularly. Visit us soon. Our Web address is: <http://www.geosociety.org>. That will take you to our home page, and from there you can link to many informational resources. Here are some highlights:

View the **Meetings** page for complete information on the 1996 GSA Annual Meeting in Denver. Use the live links to expand on the information that appeared in the June issue of *GSA Today*. Now all abstracts submitted electronically for Denver '96 are available, linked to the program.

Go to our **Membership** section to learn about the GSA Employment Service. You'll also find out how to become a GSA Campus Representative, or how to get Member or Student forms to join GSA. You'll also find information here on how to nominate a GSA member to **Fellowship** standing.

In our **Publications** section, read the tables of contents and abstracts of journal articles each month for *GSA Bulletin* and *Geology*. You'll also find information for authors on preparation of articles for submission to GSA publications. Specific

guidelines for submissions to *Geology* are a recent addition. There are 12 months of complete issues of *GSA Today*, in living color, that you can read or download. In our **Web Catalog of GSA Publications**, search all GSA's nonperiodical titles in print, read descriptions and tables of contents (for books), or copy from the catalog. Entries from the GSA Data Repository starting in 1992 are now on the Web, in Adobe Acrobat format for FTP download.

In the **Education** section, read about GSA's educational programs, including PEP (Partners for Education), and Project Earth S.E.E.D. What is IEE? Find out in the **Institute for Environmental Education** section.

See our **Administration** section for information on GSA Medals and Awards, and other general information about GSA.

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 CO₂ 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 lycopsids) 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 (Archangel'sky, 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.

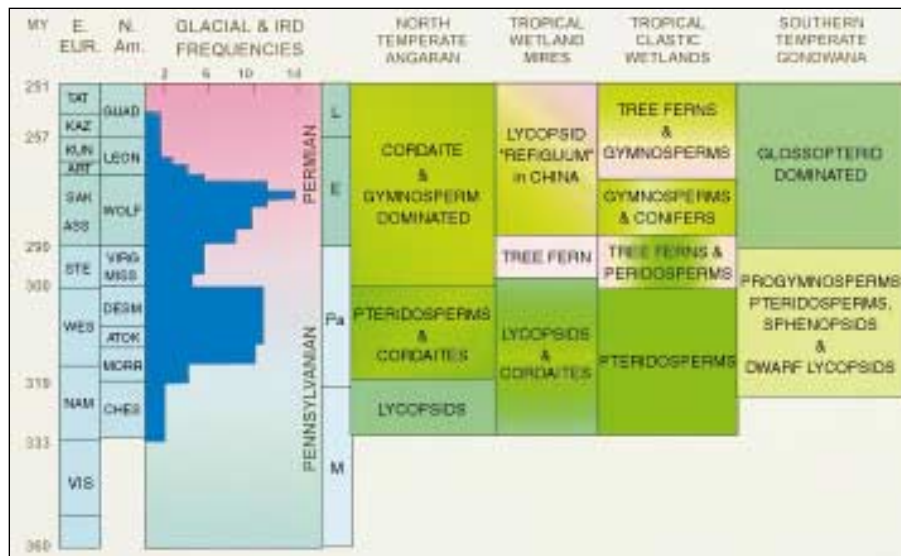
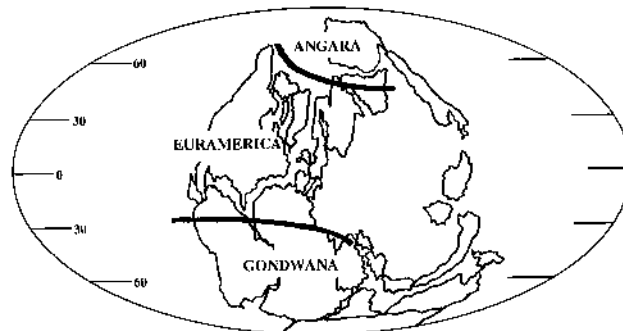


Figure 2. Relation between global glaciation and vegetative change during the late Paleozoic in different tropical environments and the north and south temperate belts. Glacial ice extent, from Frakes et al. (1992), is based upon tillites (glacial) and ice-rafted deposits (IRD). Vegetation distributional 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 (flood-plain) 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 lycopsids 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),

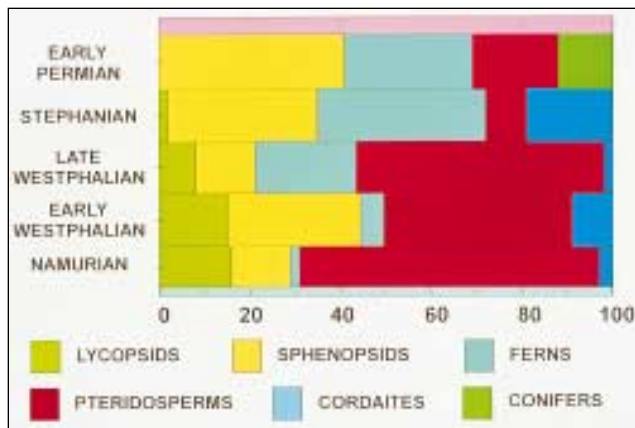


Figure 4. Changes in dominance patterns of major plant groups in the clastic swamp environment of the tropics throughout the Pennsylvanian (late Carboniferous) and earliest Permian. Data from North America and Europe (Pfefferkorn and Thomson, 1982).

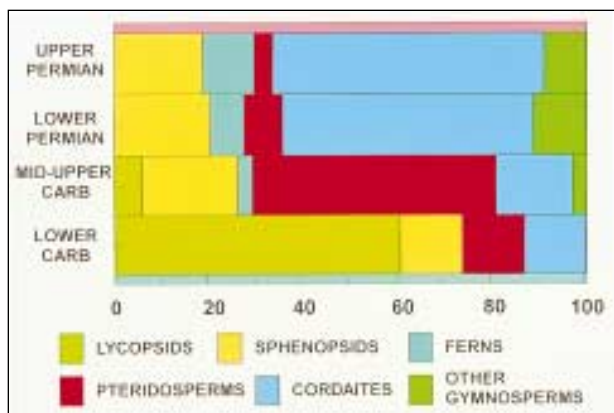


Figure 5. Changes in dominance patterns of major plant groups in the clastic swamp environment of the northern temperate realm throughout the Pennsylvanian (late Carboniferous) and Permian. Data from Kazakhstan (Meyen, 1982).

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, pulslike 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 biomic 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 lycopsid-rich flora prior to the onset of polar glaciations (Fig. 5). At or near the middle to late Namurian boundary, the lycopsid flora was replaced by a low-diversity but widespread flora dominated by seed ferns and cordaites (Rufliorians) 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 cordaite-dominated assemblages (Rufliorian 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, cordaite-rich floras (Rufliorian 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 on p. 6

(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 (Archangel'sky, 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 Archangel'sky, 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; Archangel'sky, 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 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.

ACKNOWLEDGMENTS

William L. Crepet, Louis Derry, Robert W. Kay, and two anonymous reviewers offered helpful discussions and

review of the manuscript. We thank T. L. Phillips for granting permission to use the reconstruction of a Pennsylvanian peat swamp. This research has been supported by various funding agencies, including the National Science Foundation to Gastaldo, the American Chemical Society, the Deutsches Forschungsgemeinschaft, the Research Foundation of the University of Pennsylvania, and the Smithsonian Institution. Evolution of Terrestrial Ecosystem Program contribution #30.

REFERENCES CITED

- Archangelsky, S., 1990, Plant distribution in Gondwana during the late Paleozoic, *in* Taylor, E. L. and Taylor, T. N., eds., *Antarctic paleobiology*: New York, Springer-Verlag, p. 102–117.
- Behrensmeyer, A. K., and Hook, R. W., editors, 1992, Paleoenvironmental contexts and taphonomic modes in the terrestrial fossil record, *in* Behrensmeyer, A., et al., *Terrestrial ecosystems through time*: Chicago, University of Chicago Press, p. 15–138.
- Berner, R. A., 1990, Atmospheric carbon dioxide levels over Phanerozoic time: *Science*, v. 249, p. 1382–1386.
- Berner, R. A., 1991, A model of atmospheric CO₂ over Phanerozoic time: *American Journal of Science*, v. 291, p. 339–376.
- BROUTIN, J., and eight others, 1990, Le renouvellement des flores au passage Carbonifère Permien: Approches stratigraphique, biologique, sédimentologique: *Académie des Sciences Comptes Rendus*, ser. II, v. 311, p. 1563–1569.
- Burnham, R. J., 1993, Time resolution in terrestrial macrofloras: Guidelines from modern accumulations, *in* Kidwell, S. M., and Behrensmeyer, A. K., eds., *Taphonomic approaches to time resolution in fossil assemblages: Short Courses in Paleontology*, v. 6, p. 57–78.
- Cecil, C. B., 1990, Paleoclimate controls on stratigraphic repetition of chemical and clastic rocks: *Geology*, v. 18, p. 533–536.
- Crowley, T. J., 1994, Pangean climates, *in* Klein, G. D., ed., *Pangea: Paleoclimate, tectonics, and sedimentation during accretion, zenith, and breakup of a supercontinent*: Geological Society of America Special Paper 288, p. 25–39.
- Cuneo, N. R., 1987, Sobre la presencia de probables Ginkgoales en el Permico inferior de Chubut, Argentina: *Simposio Argentino de Paleobotanica y Palinologica*, Actas VII, p. 47–49.
- Cuneo, N. R., 1996a, The Carboniferous-Permian vegetational transition in the Southern Hemisphere: An appraisal: *International Organization of Paleobotany Conference*, 5th, Santa Barbara, California, Abstracts, p. 21.
- Cuneo, N. R. 1996b, Permian phytogeography in Gondwana: *Palaeogeography, Palaeoclimatology, Palaeoecology* (in press).
- DiMichele, W. A., and Aronson, R. B., 1992, The Pennsylvanian-Permian vegetational transition: A terrestrial analog to the onshore-offshore hypothesis: *Evolution*, v. 46, p. 807–824.
- DiMichele, W. A., and Phillips, T. L., 1995, The response of hierarchically structured ecosystems to long-term climate change: A case study using tropical peat swamps of Pennsylvanian age, *in* Stanley, S. M., et al., eds., *Effects of past global change on life*: Washington, D.C., National Academy Press, p. 134–155.
- DiMichele, W. A., and Phillips, T. L., 1996, Climate change, plant extinctions and vegetational recovery during the Middle-Late Pennsylvanian transition: The case of tropical peat-forming environments in North America, *in* Hart, M. B., ed., *Biotic recovery from mass extinctions*: Geological Society of London Special Publication 102, p. 201–221.
- DiMichele, W. A., Pfefferkorn, H. W., and Phillips, T. L., 1996, Persistence of Late Carboniferous tropical vegetation during glacially-driven climatic and sea-level fluctuations: *Palaeogeography, Palaeoclimatology, Palaeoecology* (in press).
- Dorofeyeva, L. A., Davydov, V. I., and Kashlik, D. S., 1982, Mode of temperature variation in the late Paleozoic of the southwest Darvaz: *Akademiya Nauk SSSR Doklady*, Earth Science Section, v. 263, p. 81–89.
- Elias, M. K., 1936, Late Paleozoic plants of the Midcontinent region as indicators of time and of environment: *International Geological Congress*, 16th, Comptes Rendus, v. 1, p. 691–700.
- Erwin, D. H., 1996, The mother of mass extinctions: *Scientific American*, v. 275, p. 72–78.
- Fischer, A. G., 1982, Long-term climatic oscillations recorded in stratigraphy, *in* Berger, W. H. and Crowell, J. C., eds., *Climate in Earth history*: Washington, D.C.: National Academy Press, p. 97–104.
- Frakes, L. A., Francis, J. E., and Syktus, J. I., 1992, Climate modes of the Phanerozoic: Cambridge, UK, Cambridge University Press, 274 p.
- Francey, R. J., Tans, P. P., Allison, C. E., Enting, I. G., White, J. W. C., and Troller, M., 1995, Changes in oceanic and terrestrial carbon uptake since 1982: *Nature*, v. 373, p. 326–329.
- Galtier, Jean, 1996, The Lower Carboniferous Rhaconopteris is not a fern nor a progymnosperm: *International Organization of Paleobotany Conference*, 5th, Santa Barbara, California, Abstracts, p. 32.
- Gastaldo, R. A., 1987, Confirmation of Carboniferous clastic swamp communities: *Nature*, v. 326, p. 869–871.
- Gastaldo, R. A., Demko, T. M., and Liu, Y., 1993, The application of sequence and genetic stratigraphic concepts to Carboniferous coal-bearing strata: An example from the Black Warrior basin, US: *Geologische Rundschau*, v. 82, p. 212–226.
- Graham, J. B., Dudley, R., Aguilar, N. M., and Gans, C., 1995, Implications of the late Palaeozoic oxygen pulse for physiology and evolution: *Nature*, v. 375, p. 117–120.
- Graham, N. E., 1995, Simulation of recent global temperature trends: *Science*, v. 267, p. 666–671.
- Guo, Yingting, 1990, Paleoeology of flora from coal measures of Upper Permian in western Guizhou: *China Geological Society Journal*, v. 15, p. 48–54.
- Halle, Francis, Oldeman, R. A. A., and Tomlinson, P. B., 1978, *Tropical trees and forests*: Berlin, Heidelberg, New York, Springer-Verlag, 441 p.
- Kareiva, P., and Wennergren, U., 1995, Connecting landscape patterns to ecosystems and population processes: *Nature*, v. 373, p. 299–302.
- Laveine, J. P., 1993, The distribution of Eurasiatic late Paleozoic floras: A main tool for paleogeographic relationships: *Biostratigraphy of Mainland Southeast Asia: Facies & Paleontology*, v. 2, p. 347–359.
- Leary, R. L., 1980, Reclassification of *Megalopteris* sp.? Arber (1904) from the Culm Measures of northwest Devon as *Lesleya* sp.: *Review of Palaeobotany and Palynology*, v. 30, p. 27–32.
- Lyons, P. C., and Darrah, W. C., 1989, Earliest conifers in North America: Upland and/or paleoclimatic indicators?: *Palaios*, v. 4, p. 480–486.
- Meyen, S. V., 1982, The Carboniferous and Permian floras of Angaraland (a synthesis): *Biological Memoirs*, v. 7, 109 p.
- Nichols, D. J., Jarzen, D. M., Orth, C. J., and Oliver, P. Q., 1986, Palynology and iridium anomalies at Cretaceous-Tertiary boundary, south-central Saskatchewan: *Science*, v. 231, p. 714–717.
- Niklas, K. J., Tiffney, B. H., and Knoll, A., 1983, Patterns in vascular land plant diversification: *Nature*, v. 303, p. 614–616.
- Pfefferkorn, H. W., 1995, We are temperate climate chauvinists: *Palaios*, v. 10, p. 389–391.
- Pfefferkorn, H. W., and Thomson, M. C., 1982, Changes in dominance patterns in upper Carboniferous plant-fossil assemblages: *Geology*, v. 10, p. 641–644.
- Phillips, T. L., and Cross, A. T., 1991, Paleobotany and paleoecology of coal, *in* Gluskoter, H. J., et al., eds., *Economic Geology: U.S.: Boulder, Colorado, Geological Society of America, Geology of North America*, v. P-2, p. 483–502.
- Phillips, T. L., and Peppers, R. A., 1984, Changing patterns of Pennsylvanian coal-swamp vegetation and implications of climatic control on coal occurrences: *International Journal of Coal Geology*, v. 3, p. 205–255.
- Read, C. B., and Mamay, S. H., 1964, Upper Paleozoic floral zones and floral provinces of the United States: *U.S. Geological Survey Professional Paper* 454-K, 35 p.
- Retallack, G. J., 1995, Permian-Triassic life crisis on land: *Science*, v. 267, p. 77–80.
- Sellwood, B. W., Price, G. D., and Valdes, P. J., 1994, Cooler estimates of Cretaceous temperatures: *Nature*, v. 370, p. 453–455.
- Thompson, D. J., 1995, The seasons, global temperature, and precession: *Science*, v. 268, p. 59–68.
- Vega, J. C., and Archangelsky, Sergio, 1996, *Austrocalyx jejenensis* Vega and Archangelsky, gen. et sp. nov., a cupulate rhacopteroid pteridosperm from the Carboniferous of Argentina: *Review of Palaeobotany and Palynology*, v. 91, p. 107–119.
- Wagner, R. H., 1993, Climatic significance of the major chronostratigraphic units of the Upper Palaeozoic: *International Carboniferous-Permian Congress*, XIIth, *Comptes Rendus*, v. 1, p. 83–108.
- Webb, T., III, 1995, Clues to global change: Carbon exchange anomalies: *Geotimes*, v. 41, no. 8, p. 19–20.
- Yemane, K., 1993, Contribution of Late Permian palaeogeography in maintaining a temperate climate in Gondwana: *Nature*, v. 361, p. 51–54.
- Ziegler, A. M., 1990, Phytogeographic patterns and continental configurations during the Permian Period; *in* McKerrow, W. S., and Scotese, C. R., eds., *Palaeozoic palaeogeography and biogeography*: Geological Society of London Memoir 12, p. 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* Scott, A. C., ed., *Coal and coal-bearing strata—Recent advances*: Geological Society of London Special Publication 32, p. 25–49.

Manuscript received July 1, 1996; revision received August 7, 1996; accepted August 9, 1996. ■

PUBLICATIONS OF RELATED INTEREST FROM GSA

- Pangea: Paleoclimate, Tectonics, and Sedimentation during Accretion, Zenith, and Breakup of a Supercontinent (SPE288, \$72.50, Member price \$58.00)
- Economic Geology, U.S. (GNA-P2, \$80.00, Member price \$65.00)
- Gondwana Master Basin of Peninsular India between Tethys and the Interior of the Gondwanaland Province of Pangea (MWR187, \$42.00, Member price \$33.60)
- Historical Perspective of Early 20th Century Carboniferous Paleobotany in North America (MWR185, \$105.00, Member price \$84.00)
- Permian-Triassic Pangean Basins and Foldbelts along the Panthalassan Margin of Gondwanaland (MWR184, \$75.00, Member price \$60.00)
- Recent Advances in Coal Geochemistry (SPE248, \$11.00, Member price \$8.80)

FOR MORE INFORMATION OR TO PLACE AN ORDER CONTACT

GSA Publication Sales, P.O. Box 9140, Boulder, CO 80301

1-800-472-1988, fax 303-447-1133, E-mail: pubs@geosociety.org