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Late Devonian Oceanic Anoxic Events and Biotic Crises: "Rooted" in the Evolution of Vascular Land Plants?

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ABSTRACT

Evolutionary developments among vascular land plants may have been the ultimate cause for oceanic anoxic events, biotic crises, global climate change, and geochemical and sedimentologic anomalies of Late Devonian age. The influence of vascular land plants on weathering processes and global geochemical cycles is likely to have increased substantially during the Late Devonian owing to large increases in root biomass associated with development of (1) arborescence (tree-sized stature), which increased root penetration depths, and (2) the seed habit, which allowed colonization of drier upland areas. We hypothesize that rapidly increasing root mass led to transient intensification of the rate of soil formation and to permanent gains in the thickness and areal extent of deeply weathered soil profiles. In the short term, greater pedogenesis caused increased sediment yields owing to episodic disturbance of developing soils and to increased nutrient fluxes to the oceans as a result of enhanced chemical weathering. Long-term effects included increased landscape stabilization, drawdown of atmospheric CO$_2$ through enhanced uptake in silicate weathering and burial of organic carbon, and global cooling. Coeval terrestrial paleobotanic developments and marine anoxic and extinction events are likely to have been linked causally through transient nutrient pulses that caused eutrophication of semirestricted epicontinental seaways, stimulating marine algal blooms. Correlativity of black shale horizons and episodes of extinction of tropical marine benthos implicates oceanic anoxia rather than global cooling as the proximate cause of the Late Devonian biotic crisis.

INTRODUCTION

The origin of the Late Devonian biotic crisis is a subject of continuing debate. Although various causes have been proposed, including bolide impacts, oceanic overturn, sea-level changes, and global climate change (Copper, 1986; Geldsetzer et al., 1987; McGhee, 1991; Claeys et al., 1992), none has gained general acceptance. Few, if any, of these theories have attempted to link Late Devonian extinctions to coeval paleobotanic events; however, the Givetian–Famennian epochs are characterized by important paleobotanic developments, including large increases in the maximum size of vascular land plants, in the biomass and complexity of floral communities, and in the geographic distribution of terrestrial vegetation (Fig. 1; Scheckler, 1986; Gensel and Andrews, 1987). In this paper, we propose that evolutionary innovations among vascular land plants were the ultimate cause of both the Late Devonian biotic crisis and a variety of coeval sedimentologic and geochemical anomalies. The main lines of evidence supporting this hypothesis are (1) close temporal relations between Late Devonian paleobotanic developments and major episodes of oceanic anoxia and mass extinction, and (2) a model that successfully links these paleobotanic developments to the Late Devonian biotic crisis and coeval sedimentologic and geochemical anomalies through changes in pedogenic rates and processes.

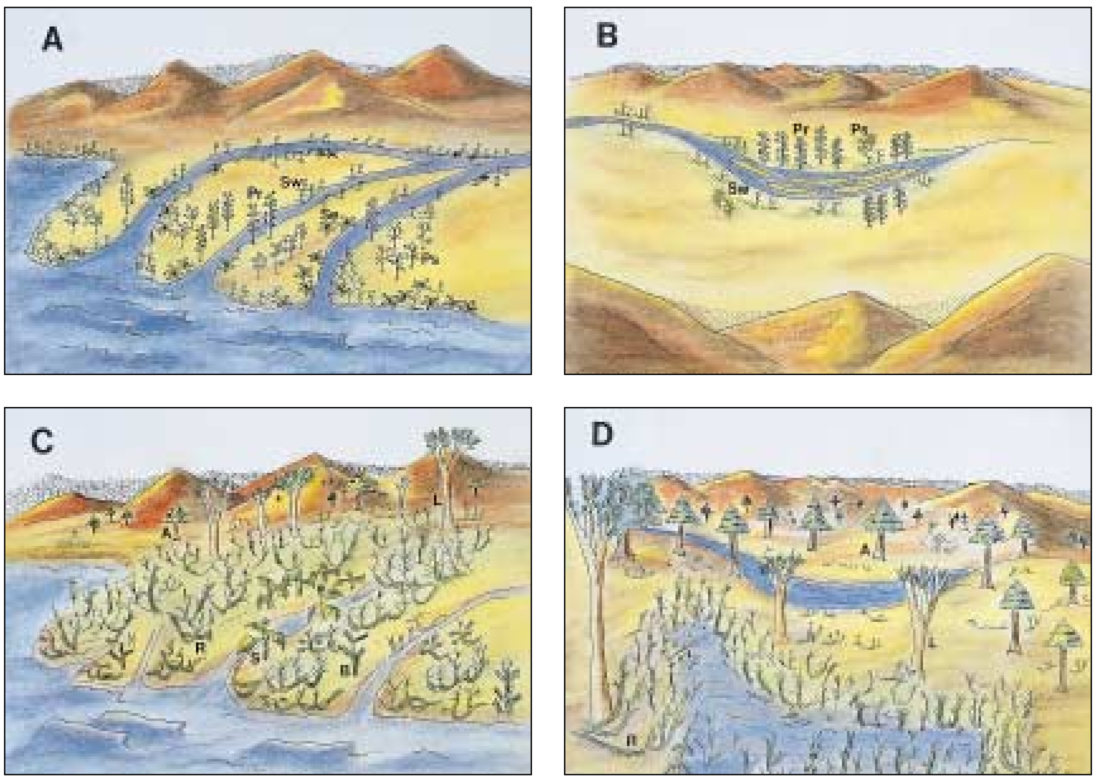

Figure 1. Paleobotanic reconstructions of (A) an Early Devonian coastal delta, (B) an Early Devonian upland flood plain, (C) a Late Devonian coastal delta, and (D) a Late Devonian upland flood plain. Early Devonian plants: Pr = *Pertica*, Ps = *Psilophyton*, Sc = *Sciadophyton*, and Sw = *Sawdonia*; Late Devonian plants: A = *Archaeopteris*, B = *Barinophyton*, L = tree lycopod, R = *Rhacophyton*, and S = seed plant. Data from Scheckler (1986), Gensel and Andrews (1984, 1987), and P. G. Gensel (personal commun.).

LATE DEVONIAN BIOTIC CRISIS AND ANOMALIES

During the Late Devonian biotic crisis (Frasnian-Famennian extinction), about 21% of families and 50% of genera among marine organisms disappeared (Sepkoski, 1986). This event was unusual in three respects (1) duration, ~20 m.y. (beginning in the Givetian, or late Middle Devonian); (2) episodicity, comprising at least eight separate episodes of extinction (House, 1985); and (3) selectivity, disproportionately eliminating tropical marine benthos (Bambach, 1985; Sepkoski, 1986). Extinctions were particularly severe among the middle Paleozoic reef community, dominated by stromatoporoids and corals (Fig. 2A; James, 1983), whereas high-latitude and cold-water species were less affected (Copper, 1986). The two extinction maxima of widest taxonomic impact occurred at or near the Frasnian-Famennian (F-F) and Devonian-Carboniferous (D-C) boundaries and are known as the Kellwasser and Hangenberg events, respectively (Fig. 3A; Talent et al., 1993).

The origin of the Late Devonian biotic crisis has been the subject of considerable debate. Much recent research has sought evidence of a bolide impact, an idea stimulated by proposals for such a catastrophic mechanism at the Cretaceous-Tertiary (K-T) boundary (Alvarez et al., 1980). Although minor iridium anomalies (Geldsetzer et al., 1987; Wang et al., 1993) and small concentrations of microspherules (Wang, 1992; Claeys et al., 1992) have been identified close to the F-F and D-C boundaries at several locales, siderophile element ratios are incompatible with those of meteorites, and these anomalies have been interpreted as resulting from concentration of metals by cyanobacteria or changes in redox conditions (Playford et al., 1984; Wang et al., 1993). Other causes proposed for the Late Devonian biotic crisis include climate change associated with global tectonics (Copper, 1986), oceanic overturn (Geldsetzer et al., 1987), and sea-level elevation changes (McGhee, 1991), but none of these fully accounts for the duration, episodicity, and selectivity of the crisis.

The Late Devonian is also characterized by an unusual combination of major excursions or permanent shifts in a variety of sedimentologic and geochemical records. Laminated black shales indicate episodic development of widespread oceanic anoxia in many cratonic sequences during this interval (Fig. 3, B–D). Deposition of organic-rich shales and coals during the Devonian-Carboniferous transition sequestered large quantities of isotopically light carbon in the sedimentary reservoir, causing an enrichment of marine carbonate δ^{13}C values of about 4‰ (Fig. 2B; Lohmann, 1988; Berner, 1989). A combination of increased burial of organic carbon and enhanced silicate weathering by vascular plants drew down atmospheric CO$_2$ levels from ~12–16 present atmospheric level (PAL) in the early–middle Paleozoic to ~1 PAL in the Carboniferous and Permian (Fig. 2C; Berner, 1994). Evidence of lowered atmospheric CO$_2$ is provided by changes in soil carbonate δ^{13}C (Mora et al., 1991) and by a marked decline in dolomite abundance across the D-C boundary (Fig. 2D). Marine evaporites of this age exhibit a +8‰ to +10‰ δ^{34}S excursion as a consequence of large-scale bacterial reduction of dissolved sulfate in association with burial of organic carbon (Fig. 2E; Holser et al., 1989). Drawdown of atmospheric CO$_2$ initiated global cooling, recorded as a about +3‰ enrichment of abiotic marine carbonate δ^{18}O values across the D-C boundary (Fig. 2F; Lohmann, 1988), and resulted in continental glaciation by the late Famennian (Fig. 3E; Caputo, 1985).

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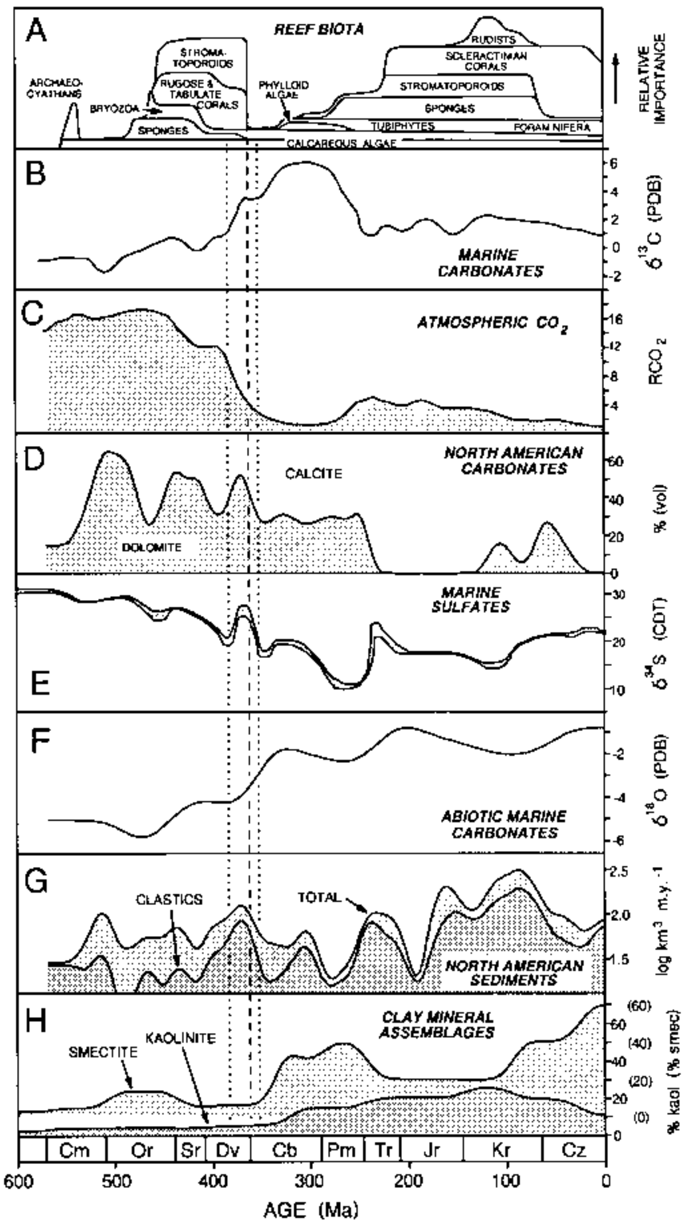

Figure 2. Phanerozoic records exhibiting Late Devonian anomalies: (A) dominant Phanerozoic reef-building groups (James, 1983); (B) marine carbonate $\delta^{13}C$ (Berner, 1989); (C) atmospheric CO_2 (RCO_2 is the ratio of CO_2 at a given time in the past to that at present; Berner, 1994); (D) North American dolomite abundance (as volume percent of total carbonate; this paper); (E) marine sulfate $\delta^{34}S$ (Holser et al., 1989); (F) abiotic marine carbonate $\delta^{18}O$ (Lohmann, 1988); (G) North American sediment survival rates (this paper); and (H) mineralogy of clay mineral assemblages (Weaver, 1967). PDB is Peedee belemnite

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VASCULAR LAND PLANT EVOLUTION

Although land plants appeared in the Late Ordovician or Early Silurian and vascular plants diversified in the Late Silurian and Early Devonian (Edwards and Berry, 1991), full colonization of land surfaces is likely to have been a protracted process that continued throughout the Devonian and later. Initially, the impact of land plants on their physical environment was negligible owing to small size, limited biomass, shallow rooting, and restriction to moist lowland habitats. As land plants increased in size and became more abundant and geographically widespread, they exerted a progressively stronger influence on their physical substrate. Two evolutionary innovations are of major significance in this regard: (1) arborescence, or tree-sized stature, and (2) the seed habit. With the advent of supporting tissues (2° xylem, 2° cortex) in the Middle Devonian (Fig. 3E), several groups of vascular plants (lycopods, cladoxylaleans, progymnosperms) exhibited increases in stature (Fig. 4; Chaloner and Sheerin, 1979; Mosbrugger, 1990). However, Middle Devonian trees mostly occupied riparian habitats, and flood-plain forests probably developed in the Frasnian with the appearance of the progymnosperm *Archaeopteris*. This genus, which grew ~30 m high, became the dominant element of terrestrial floras between the mid-Frasnian and mid-Famennian, but declined rapidly with the appearance of seed plants (Fig. 3E; Beck, 1981; Gensel and Andrews, 1984; Scheckler, 1986). Seed plants spread rapidly during the latest Famennian owing to the advantages conferred by seeds, including ability to adapt to diverse ecological conditions and to occupy drier upland habitats (Fig. 3E; Gillespie et al., 1981; Rothwell et al., 1989).

Close temporal relations exist between Late Devonian anoxic and extinction events and these paleobotanic developments. First, the onset of a protracted late Middle–Late Devonian interval of widespread oceanic anoxia (Fig. 3, B–D) followed closely the advent of secondary vascular supporting tissues (Fig. 3E) and coincided broadly with rapid increases in the maximum size of vascular land plants in the Middle Devonian (Fig. 4). Second, the F-F boundary Kellwasser event occurred within the mid-Frasnian to mid-Famennian interval of archaeopterid dominance and might represent the rapid spread of this genus (Fig. 3E). Third, the D-C boundary Hangenberg event is preceded by the appearance of the earliest known seeds by one conodont zone, or about 0.5 m.y. (Fig. 3E; Gillespie et al., 1981; Rothwell et al., 1989). In each case, an important paleobotanic development that probably led to a large increase in root biomass preceded major paleontologic, sedimentologic, and geochemical events by no more than a few million years. In this regard, first appearances are less

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information about the key themes and key points presented at the forum.

In the 1970s and 1980s, the extractive-industries (petroleum and minerals)–oriented companies hired more graduating earth science students than any other category of employer, formerly providing employment to about two-thirds of all graduates. Employment and employment opportunities in these industries have declined sharply over the past decade. Domestic growth is expected to be flat. Contributing to the continuing low level of employment is the fact that extractive companies are increasingly moving their operations overseas, where they are hiring foreign nationals.

Employment opportunities in environmentally oriented companies are the brightest of those in any geoindustry. However, the evolution and maturation of the industry and its technologies has reduced employment opportunities when compared to the recent past. Competitive pressures have prompted personnel restructuring, including layoffs in some areas and the replacement of higher paid managers with lower paid, entry-level staff. Slow to moderate growth in employment is anticipated and should provide the greatest opportunities to students with B.S. and M.S. degrees. Continuation of the federal government's domination of environmental regulations will probably favor large, multidisciplinary firms.

Shrinking budgets have been and will continue to be responsible for decreasing employment of earth scientists by state and federal government agencies. The number of state-funded positions for professional staff in state geological surveys has declined about 8% in the past four years, while the number of contract employees has increased. Positions in the USGS have also declined over the past decade. These trends are likely to continue. Even larger reductions have occurred in the U.S. Bureau of Mines.

In academia, the number of faculty positions is expected to remain constant over the next 5–10 years. Faculty positions supported by external funds probably will decrease, because many of these positions do not provide revenue to the universities. Some universities are using postdoctoral fellows in place of teaching assistants. This creates more temporary slots for scientists seeking permanent positions.

Earth science job opportunities in the coming decade likely will be in positions that address important societal problems, such as natural hazards, health, infrastructure, energy and resource needs, and environmental protection and remediation. Employers will be seeking geoscientists who have knowledge of aqueous geochemistry, earth surface processes, and the youngest part of the geological time scale. Particularly attractive will be graduates with a solid foundation in fundamental science (biology, chemistry, engineering, geology, physics), mathematics, and computer science and with skills in foreign language and oral and written communication. Forum participants expressed the sense that the generally prevailing college and university earth science curriculum, which has changed little over the past 50 years, must be redesigned to provide a multidisciplinary base that integrates scientific knowledge and basic scientific skills that would allow students to adapt to changing societal priorities. Although the forum did not provide a specific plan for revision, participants agreed that earth science societies and colleges and universities should encourage reform in several ways, including:

- Bringing together the academic community, professional societies, government, and industry to coordinate curricular reform.
- Developing benchmarks for the content of courses.
- Providing recognition and awards for innovative courses, curricula, and teaching excellence.

There was a consensus that earth science societies need to become more proactive in promoting the earth sciences to policy makers and the public at large in order to ensure the continued viability of the profession. The societies could promote earth sciences in several ways:

- Encouraging colleges and universities to provide integrative earth science courses and experiences for nonmajors, particularly for preservice and in-service K–12 teachers.
- Working with colleges and universities to inject earth science perspectives into allied professions, such as engineering, and to prepare earth science students for nontraditional careers in areas such as law, business, and politics.
- Working with academia and industry to provide access to lifelong, high-quality learning for practicing earth scientists.
- Encouraging and, where appropriate, coordinating the participation of earth scientists in local, state, and federal policy debates and decisions.

The key word at the forum was change. Employment opportunities for earth scientists have decreased significantly over the past decade, and this pace is likely to continue into the future. In the face of this rapid change, colleges and universities need to be constantly assessing their curricula. Geoscientists must work together to ensure a well-educated and skilled earth science workforce that will be able to meet the future needs of society, such as preserving the environment and providing an adequate supply of natural resources for a growing population. Perhaps the most important role for earth science societies in managing this change is the collection and dissemination of human resource data that can serve as the basis for wise decision making on employment and education issues. ■

Southeastern Section Meeting to Include Symposium on Energy and the Environment

A symposium, "Energy and the Environment in the Next Century," at the GSA Southeastern Section meeting in April will feature speakers from both the private and public sectors. The objective of the symposium, sponsored by GSA's Institute for Environmental Education, is to look at the many facets of the issue of energy use and its effects on the environment, according to organizer Otto Kopp (University of Tennessee).

Some of the subjects will be: acceptable levels of toxicity, fossil fuels and CO_2, the economics of nuclear power, and techniques for monitoring the environmental impact of energy production. The symposium will be open to all attendees at the GSA Southeastern Section meeting in Knoxville, Tennessee, April 6–7, 1995.

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important than increases in abundance and biomass, which are harder to quantify but significantly more important in terms of geochemical consequences.

DEVELOPMENT OF THE RHIZOSPHERE AND SOILS

Soils are the geochemical interface between the lithosphere and the atmosphere-hydrosphere, and their importance in global geochemical cycles has been largely underappreciated. Although thick Precambrian soil profiles are known, generally high rates of physical weathering in the pre-Devonian probably yielded widespread barren rock surfaces and thin microbial protosoils similar to modern desert crusts (Campbell, 1979). Increases in the size and geographic distribution of large vascular plants and in root biomass probably resulted in substantial increases in the depth and volume of soils during the Late Devonian (Retallack, 1986).

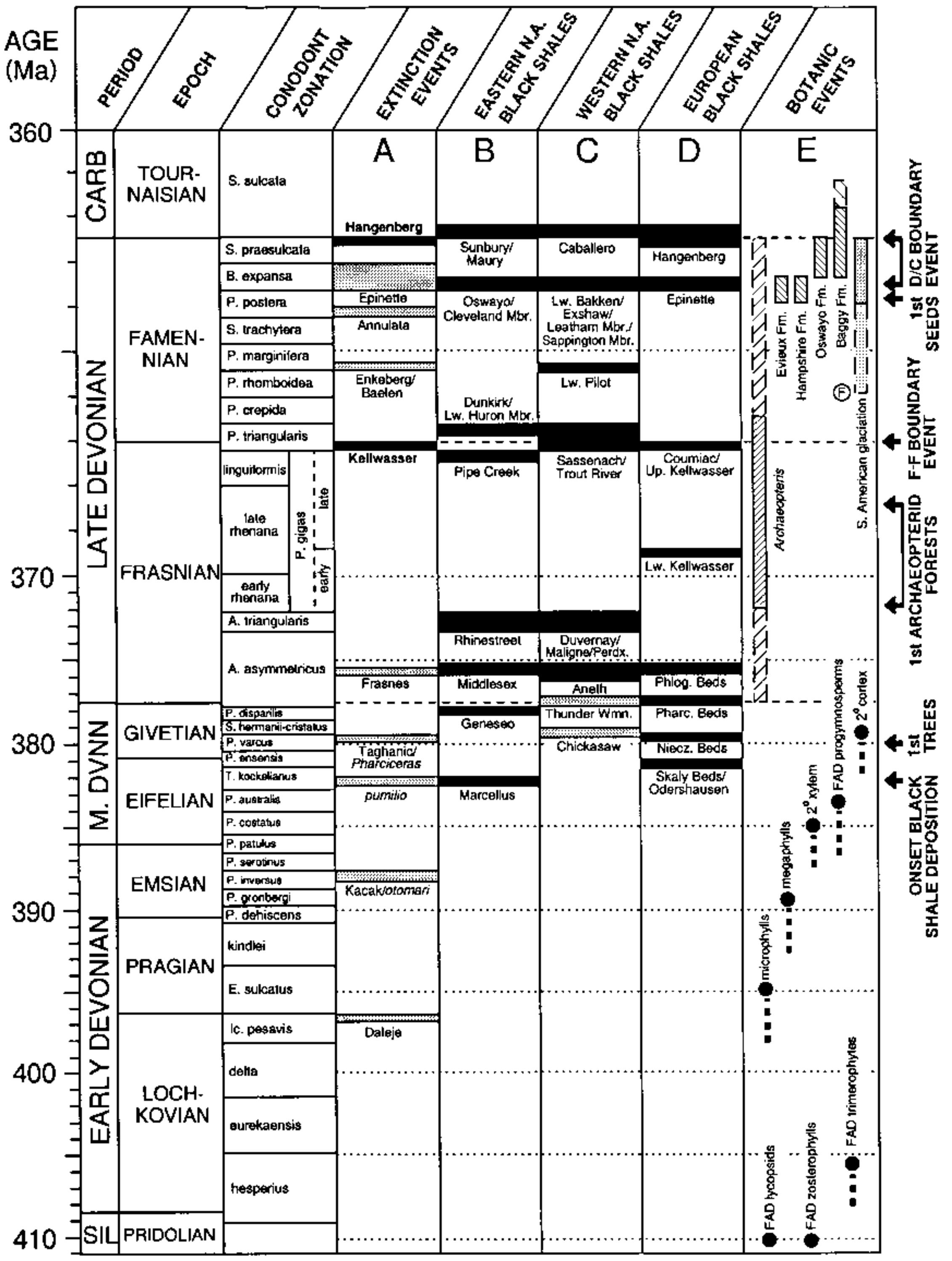

Figure 3. Correlation of Devonian events: (A) extinction events; black shales from (B) eastern North America, (C) central to western North America, and (D) Europe; and (E) paleobotanic events (data sources available upon request). For columns B–D, note that illustrated units represent anoxic maxima as determined by total organic carbon content; black shales were deposited through much of the late Middle and Late Devonian in some areas. In column E, FAD = first appearance datum; the range and peak abundance of *Archaeopteris* are shown by dashed and solid lines, respectively; and the age of South American glaciation is restricted by occurrence of *Foerstia* (F; dashed; Caputo, 1985) and miospores (solid; Streel, 1986). Conodont zonation from Ziegler and Sandberg (1990), and time scale from Harland et al. (1990).

Development of the rhizosphere had important short- and long-term effects on sedimentologic and geochemical processes associated with weathering (Fig. 5). In the short term, global weathering rates increased as relatively fresh substrates were physically and chemically attacked by rapidly spreading root systems. Enhanced physical weathering may have accompanied the transition from largely unvegetated to vegetated uplands, during which increases in root density would have accelerated mechanical breakup of rock but exerted only a weak stabilizing influence against erosion by episodic droughts, landslides, and wildfires (Stallard, 1985), yielding transient increases in regional or global particulate fluxes (Fig. 2G). Elevated chemical weathering rates resulted from "pumping" of atmospheric CO_2 into the soil during rhizosphere expansion. Rapid drawdown of atmospheric CO_2 led to a negative feedback on weathering rates, reestablishing a long-term balance in the rate of CO_2 utilization through weathering and the rate of CO_2 supply through volcanic outgassing (Berner, 1992, 1994). The transient increase in chemical weathering rates associated with rhizosphere expansion is likely to have caused a pulse in nutrient flux to the oceans, resulting in eutrophication of semirestricted epicontinental seas and stimulating marine algal blooms (Fig. 5). Such blooms may have been the source of high concentrations of marine algal matter in Upper Devonian black shales (Maynard, 1981) and of enigmatic fossils of wide geographic but restricted stratigraphic occurrence such as *Protosalvinia* (*Foerstia*; Schopf and Schwietering, 1970). Analogous relations have been documented from the modern Black and Baltic Seas, in which anthropogenic and natural increases in nutrient fluxes have caused eutrophication and transient expansion of oxygen-depleted bottom waters (Kuparinen and Heinänen, 1993; Lyons et al., 1993).

Long-term effects of rhizosphere development on weathering processes included increased landscape stabilization and a shift from weathering-limited to transport-limited weathering regimes (Fig. 5; Stallard, 1985; Johnsson, 1993). Weathering of rocks to a finer grained, compositionally more mature product was promoted by (1) production of organic and carbonic acids by roots, (2) trapping of moisture in soils, and (3) increased water-rock contact time as a result of soil stabilization and enhanced evapotranspirational recirculation (Berner, 1992). These developments are consistent with an Early Carboniferous shift from

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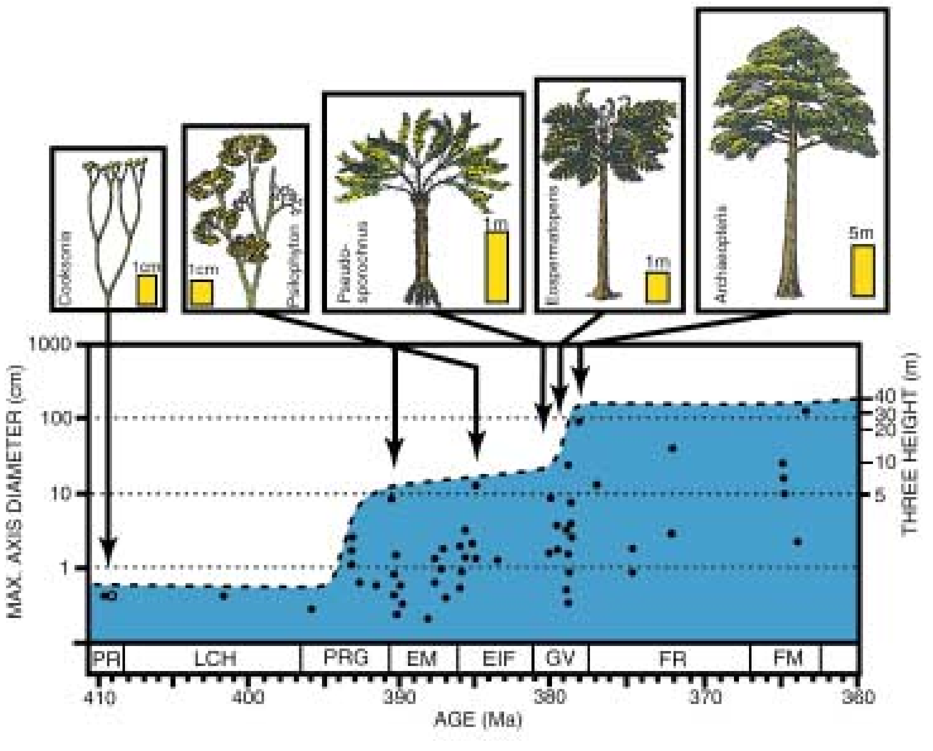

Figure 4. Maximum size of vascular land plants during the Devonian; note the rapid increase associated with appearance of trees in the Givetian. Maximum diameters of plant axes, estimated tree heights, and representative fossil genera from Chaloner and Sheerin (1979), Gensel and Andrews (1984), and Mosbrugger (1990).

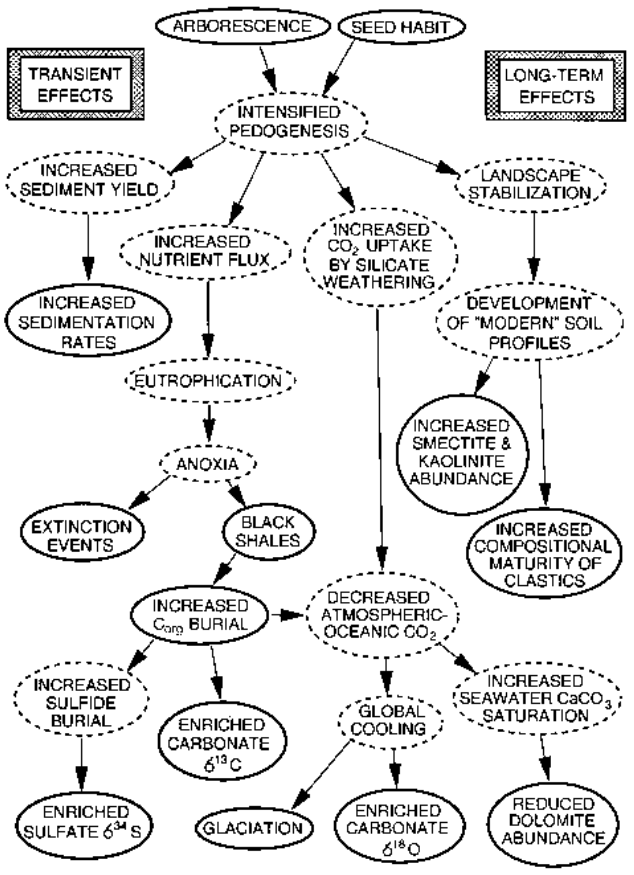

Figure 5. Model linking Late Devonian geochemical, sedimentologic, and climatic anomalies to the development of arborescence and the seed habit among vascular land plants. Features are arrayed by relative duration, transient effects on the left and long-term effects on the right. Solid outlines indicate documented geologic records; dashed outlines indicate processes linking records. See text for discussion.

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illite-chlorite– to smectite-kaolinite–dominated clay mineral assemblages (Fig. 2H; Weaver, 1967). At present, formation of smectite and kaolinite is closely associated with moderate to strong pedogenic weathering in temperate to semiarid and in humid tropical climate zones, respectively (Singer and Munns, 1991).

CONCLUSIONS

The influence of vascular land plants on weathering processes and global geochemical cycles is likely to have increased substantially during the Late Devonian owing to development of arborescence and the seed habit. These paleobotanic innovations led to rapid expansion of the global rhizosphere, resulting in a transient intensification of the rate of soil formation and in a permanent increase in the thickness and areal extent of deeply weathered soils. Intensified chemical weathering may have caused a transient increase in riverine nutrient fluxes, resulting in eutrophication of semirestricted epicontinental seaways and stimulating marine algal blooms and widespread deposition of black shales. Correlativity of black shale horizons with episodes of extinction of tropical marine benthos implicates oceanic anoxia rather than global cooling as the proximate cause of the Late Devonian biotic crisis. Drawdown of atmospheric CO_2 and global cooling were secondary effects of enhanced silicate weathering and rapid organic carbon burial. Thus, evolutionary developments among vascular land plants are likely to have been the ultimate cause of oceanic anoxic events, biotic crises, and global climate change during the Late Devonian.

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■ 1995

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New Orleans, Louisiana
November 6–9
Ernest N. Morial
Convention Center,
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General Chair: *William R. Craig, University of New Orleans*
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GSA SECTION MEETINGS

NORTHEASTERN SECTION

Radisson Hotel and Conference Center in Cromwell, Hartford, Connecticut, March 20–22, 1995. Information: Gregory McHone, Graduate Liberal Studies Program, Wesleyan University, 255 High St., Middletown, CT 06457, (203) 344-7930, fax 203-344-7957.

SOUTHEASTERN SECTION

Knoxville Hilton Hotel, Knoxville, Tennessee, April 6–7, 1995. Information: Robert D. Hatcher, Jr., Dept. of Geological Sciences, University of Tennessee, Knoxville, TN 37996-1410, (615) 974-2368, fax 615-974-2368, E-mail: bobmap@utkvx.utk.edu.

NORTH-CENTRAL and SOUTH-CENTRAL SECTIONS

University of Nebraska, Lincoln, Nebraska, April 27–28, 1995. Information: Robert F. Diffendal, Jr., 113 Nebraska Hall, University of Nebraska–Lincoln, Lincoln, NE 68588-0517, (402) 472-2410, fax 402-472-2410, E-mail: rfd@unlinfo.unl.edu.

ROCKY MOUNTAIN SECTION

Montana State University, Bozeman, Montana, May 18–19, 1995. Information: Stephan G. Custer, Department of Earth Sciences, Montana State University, Bozeman, MT 59717-0348, (406) 994-6906, fax 406-994-6923, E-mail: uessc@msu.oscs.montana.edu.

CORDILLERAN SECTION

University of Alaska, Fairbanks, Alaska, May 24–26, 1995. Information: David B. Stone, Geophysical Institute, University of Alaska, Fairbanks, AK 99775-0800, (907) 474-7622, fax 907-474-7290, E-mail: ffdbs@aurora.alaska.edu.

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