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INSIDE

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

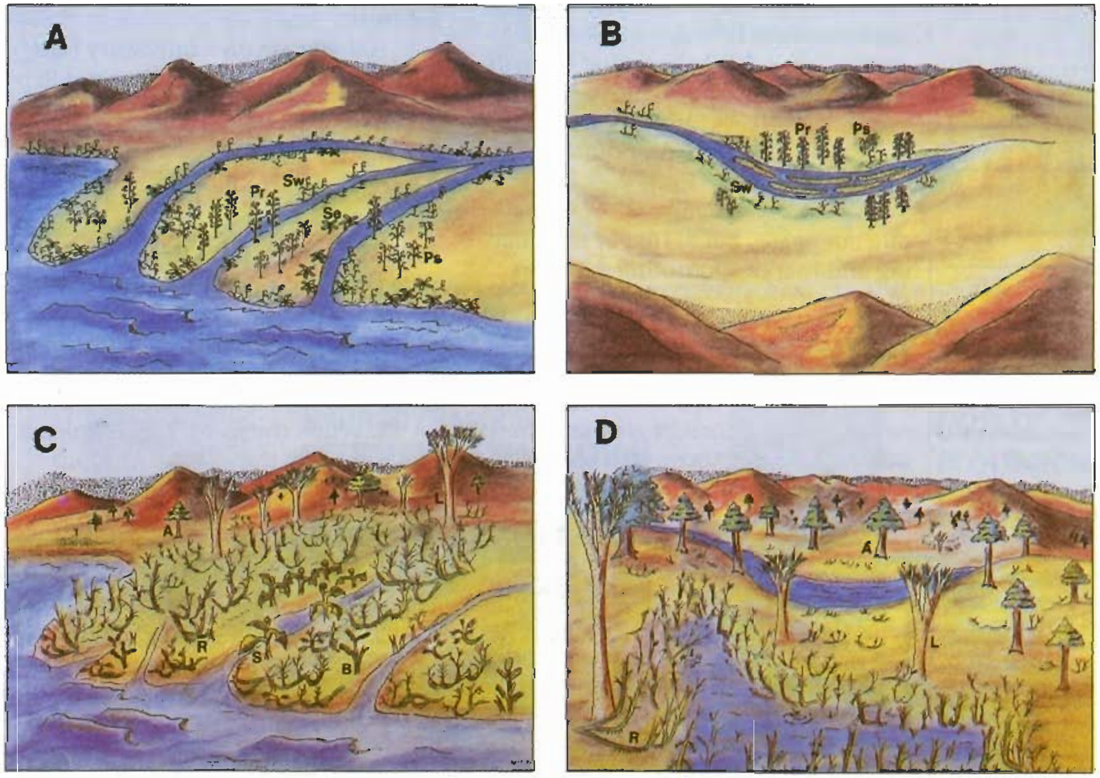

Figure 1. Paleobotanic reconstructions of (A) an Early Devonian coastal delta, (B) an Early Devonian upland flood plain, (C) a Late Devonian coastal delta, and (D) a Late Devonian upland flood plain. Early Devonian plants: Pr = *Pertica*, Ps = *Psilophyton*, Sc = *Sciadophyton*, and Sw = *Sawdonia*; 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.).

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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.

S = seed plant. Data from Scheckler (1986), Gensel and Andrews (1984, 1987), and P. G. Gensel (personal commun.).

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.

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 $\delta^{13}C$ 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 $\delta^{13}C$ (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‰ $\delta^{34}S$ 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 $\delta^{18}O$ 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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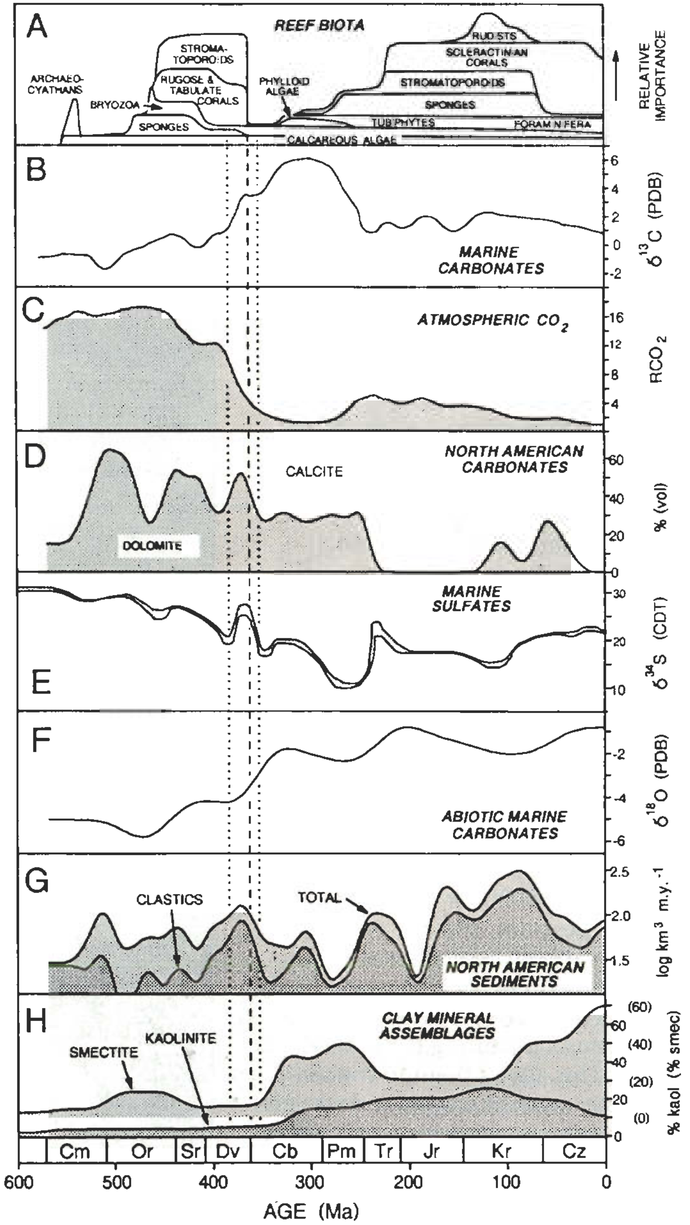

Figure 2. Phanerozoic records exhibiting Late Devonian anomalies: (A) dominant Phanerozoic reef-building groups (James, 1983); (B) marine carbonate δ^{13}C (Berner, 1989); (C) atmospheric CO$_2$ (RCO$_2$ is the ratio of CO$_2$ at a given time in the past to that at present; Berner, 1994); (D) North American dolomite abundance (as volume percent of total carbonate; this paper); (E) marine sulfate δ^{34}S (Holser et al., 1989); (F) abiotic marine carbonate δ^{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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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).

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 utiliza-

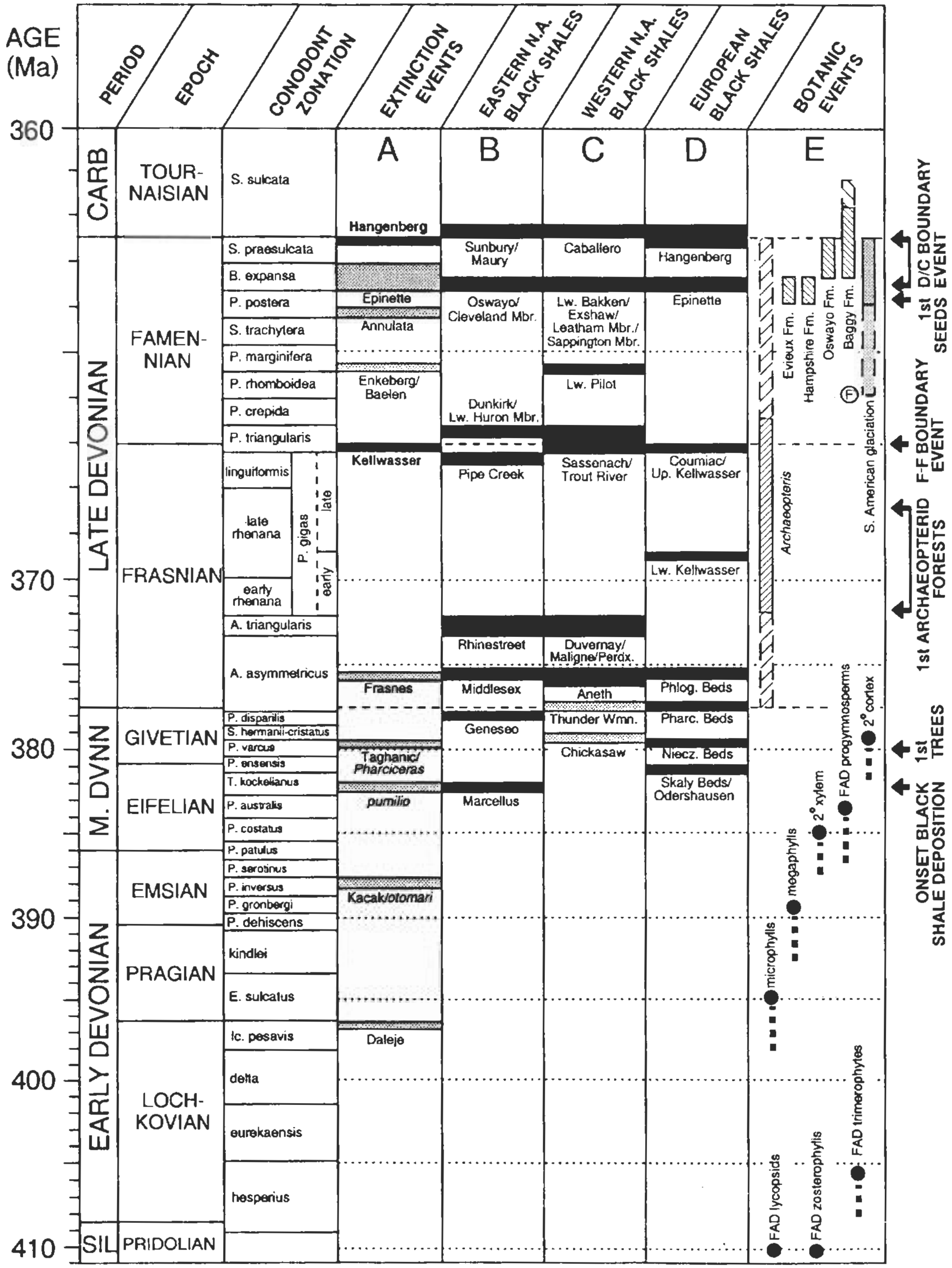
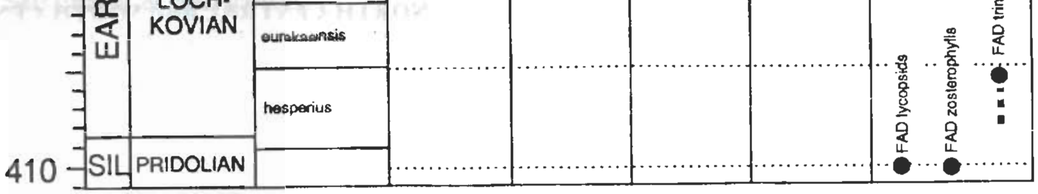


Figure 3. Correlation of Devonian events: (A) extinction events; black shales from (B) eastern North America, (C) central to western North America, and (D) Europe; and (E) paleobotanic events (data sources available upon request). For columns B–D, note that illustrated units represent anoxic maxima as 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).

lating marine algal blooms (Fig. 5). Such blooms may have been the source

ent fluxes have caused eutrophication and transient expansion of oxygen-

finer grained, compositionally more mature product was promoted by sion 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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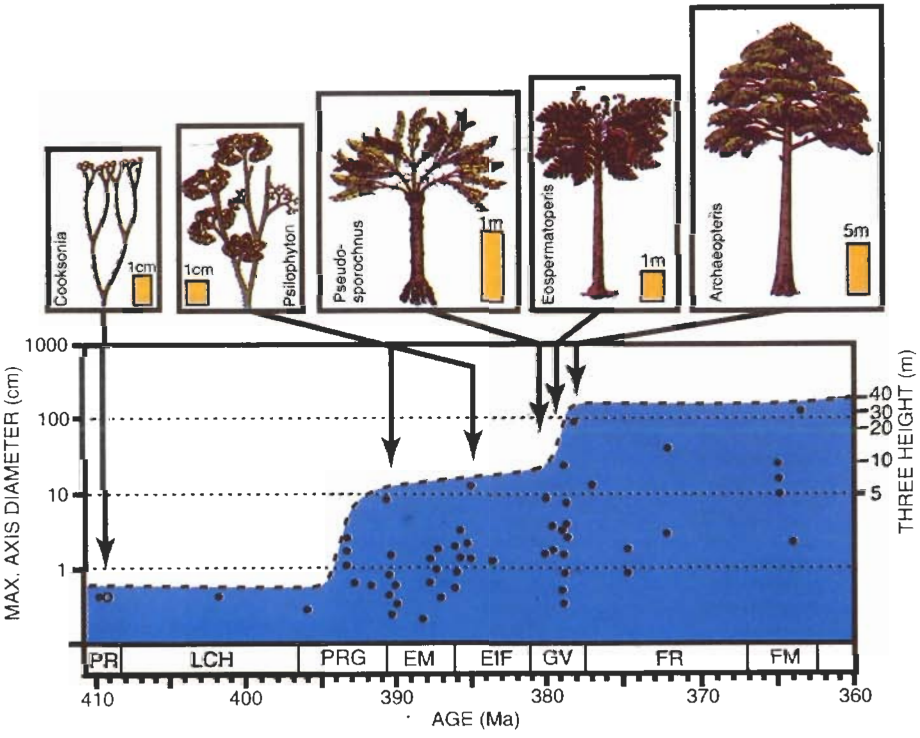

Figure 4. Maximum size of vascular land plants during the Devonian; note the rapid increase associated with appearance of trees in the Givetian. Maximum diameters of plant axes, estimated tree heights, and representative fossil genera from Chaloner and Sheerin (1979), Gensel and Andrews (1984), and Mosbrugger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

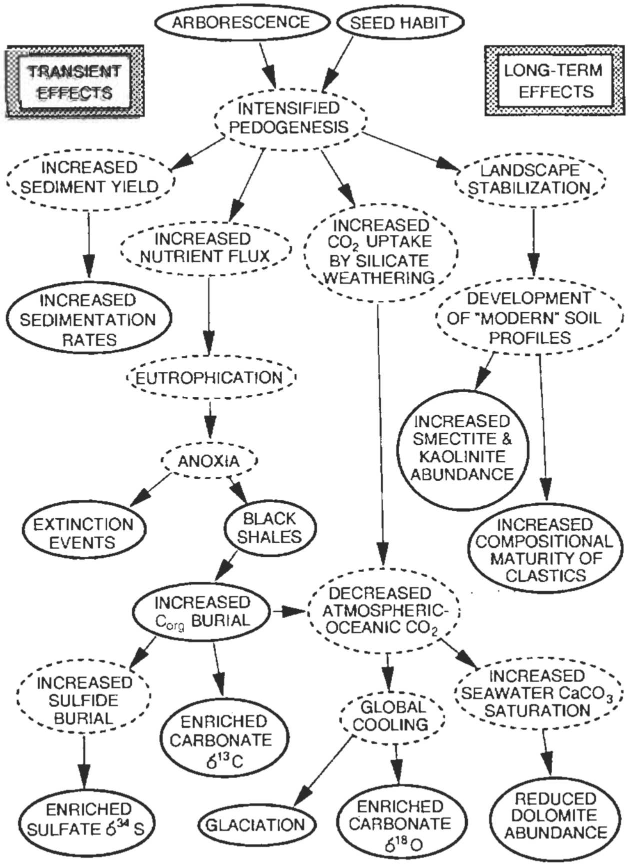

Figure 5. Model linking Late Devonian geochemical, sedimentologic, and climatic anomalies to the development of arborescence and the seed habit among vascular land plants. Features are arrayed by relative duration, transient effects on the left and long-term effects on the right. Solid outlines indicate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

ACKNOWLEDGMENTS

North American sediment mass-age distributions were compiled from

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CORDILLERAN SECTION

and global climate change during the Late Devonian.

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