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Effects of the Middle to Late Devonian Spread of Vascular Land Plants on Weathering Regimes, Marine Biotas, and Global Climate

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The Middle to Late Devonian was an interval of major changes in both the terrestrial and marine biospheres. In the terrestrial realm, evolutionary innovations among early vascular land plants resulted in a far-reaching transformation of the structure and composition of terrestrial floras, heralded by the appearance of the first trees and forests and the spread of plants into harsher upland habitats. Increases in the size and geographic distribution of land plants at this time led to transient elevation of chemical and physical weathering rates, rapid increases in soil volume, and long-term changes in the hydrologic cycle, sediment fluxes, and landform stabilization. In the marine realm, a major biotic crisis (sometimes termed the Frasnian–Famennian mass extinction in reference to its stratigraphic peak, but consisting of eight to ten separate events) resulted in the extermination of about 70 to 80 percent of shallow-marine species and to the disappearance of the Middle Paleozoic reef-building community of stromatoporoids and tabulate corals. In the aftermath of extinction peaks, opportunistic taxa experienced short-lived acmes, and cold-water-adapted taxa radiated into vacated warm-water niches. Many of the extinction peaks were correlative with deposition of extensive organic-rich shale horizons in marine environments, reflecting widespread

development of anoxic bottomwater conditions in epicontinental seas, and elevated rates of organic carbon burial. These conditions (in addition to the intensified pedogenic weathering of silicates) led to rapid drawdown of atmospheric CO_2 levels, global climatic cooling, and the onset of continental glaciation toward the end of the Devonian period.

A variety of causal mechanisms have been postulated for these Middle and Late Devonian global events, including sea-level changes (Johnson 1974), oceanic overturn (Wilde and Berry 1984), tectonoclimatic factors (Copper 1986), bolide impacts (McLaren 1982), and environmental disturbances associated with the spread of vascular land plants (Algeo et al. 1995; Algeo and Scheckler 1998). All of these hypotheses account for the mass extinction event and for aspects of climate change linked to the global carbon cycle, but few of them satisfactorily explain unusual features of the biotic crisis (e.g., its duration and episodicity) or address the question of potential links with coeval developments in the terrestrial realm. In this regard, the "Devonian plant hypothesis" of Algeo et al. (1995) and Algeo and Scheckler (1998) is a holistic model that links coeval developments in the terrestrial and marine realms by focusing on the critical role of

to attain larger sizes (arborescence) (figure 12.1B; Banks 1980; Niklas 1985; Thomas and Spicer 1987; Beerbower et al. 1992). Finally, reproductive innovations led to the appearance of seeds in the Famennian, freeing plants from dependence on moist lowland habitats and permitting colonization of drier, harsher inland areas (figure 12.1C; Chaloner and Sheerin 1979).

The role of land plants in soil development and landscape stabilization increased in direct relation to their size and geographic distribution. Early land plants had relatively little effect on their physical environment because of their small size, shallow root systems, and ecological restriction to lowland habitats. The significance of the appearance of secondary supporting tissues and the seed habit was that these innovations permitted substantial increases in the size and geographic coverage of land plants. This increased plant biomass resulted in increases in soil volume and soil production rates. For this reason, the discussion of evolutionary innovations among early vascular land plants will focus on the development of arborescence, root systems, and the seed habit.

Arborescence

The maximum size of vascular land plants increased greatly during the Pragian to Givetian (late Early to late Middle Devonian) (figures 12.1, 12.2; Chaloner and Sheerin 1979; Edwards and Berry 1991; Beerbower et al. 1992; Algeo et al. 1995). By the late Givetian, woody shrubs and medium-sized trees had appeared independently in several clades—for example, cladoxylopsid ferns such as *Pseudosporochnus*, lepidosigillarioid lycopsids such as *Eospermatopteris*, aneurophyte progymnosperms such as *Rellimia* and *Tetraxylopteris*, and archaeopterid progymnosperms such as *Svalbardia* (Banks 1980; Gensel and Andrews 1984; Mosbrugger 1990). Among the early arborescent plants, archaeopterids established dominance during the Late Devonian (figure 12.1; Beck 1981; Scheckler 1986a,c; Edwards and Berry 1991). Some late Devonian archaeopterids were large having trunks thicker than 1.5 m in diameter and maximum heights in excess of 30 m (figure 12.2; Thomas and Spicer 1987; Snigirevskaya 1988, 1995; Trivett 1993; Meyer-

Berthaud et al. 1999, 2000). Further, archaeopterids (especially *Archaeopteris*) were among the most diverse and abundant arborescent plants of that age, ranging from tropical to boreal paleolatitudes (Petrosyan 1968; Beck 1981; Cross 1983; Gensel and Andrews 1984). High concentrations of archaeopterid remains are known from many Late Devonian (especially middle to late Frasnian) terrestrial and marginal marine successions, and monospecific archaeopterid forests may have been common in floodplain habitats at that time (Beck 1964, 1981; Stubblefield et al. 1985; Fairon-Demaret 1986; Scheckler 1986c; Thomas and Spicer 1987). After peaking in abundance between the mid Frasnian and mid Famennian, *Archaeopteris* declined precipitously during the mid to late Famennian, although still locally abundant [e.g., Bear Island (Nathorst 1902)], and disappeared by the early Tournaisian (figure 12.2; Beck 1981; Scheckler 1986a,c; Beerbower et al. 1992).

The reasons for the success of archaeopterid progymnosperms are not known for certain but may have been linked to their ability to produce multiple new crown branches (Meyer-Berthaud et al. 1999, 2000) and to create and maintain favorable microenvironments. Mass shedding of their leafy lateral branches (Beck 1964; Scheckler 1978; Meyer-Berthaud et al. 1999, 2000) would have created a deep mat of litter that not only would have affected soil moisture, pH, and humic content, but also might have favored their own free-sporing, heterosporous reproduction to the potential detriment of other plants, such as aneurophyte progymnosperms, which did not shed branch parts. Aneurophyte reproduction was probably homosporous (e.g., Taylor and Scheckler 1996), and, since the progymnosperm sporophytes show no evidence for clonal growth, it is very likely that aneurophyte gametophytes grew in the same well-lit, open habitats favored by sporophytes. Archaeopterids produced shaded, litter-strewn forests, and the vulnerability of aneurophytes to shading may have contributed to their rapid decline in diversity and abundance as archaeopterids spread during the early to mid Frasnian (Scheckler and Banks 1971a,b; Scheckler 1986a,c; Beerbower et al. 1992; Hill et al. 1997). The reason for the precipitous decline of *Archaeopteris* in the mid to late Famennian is

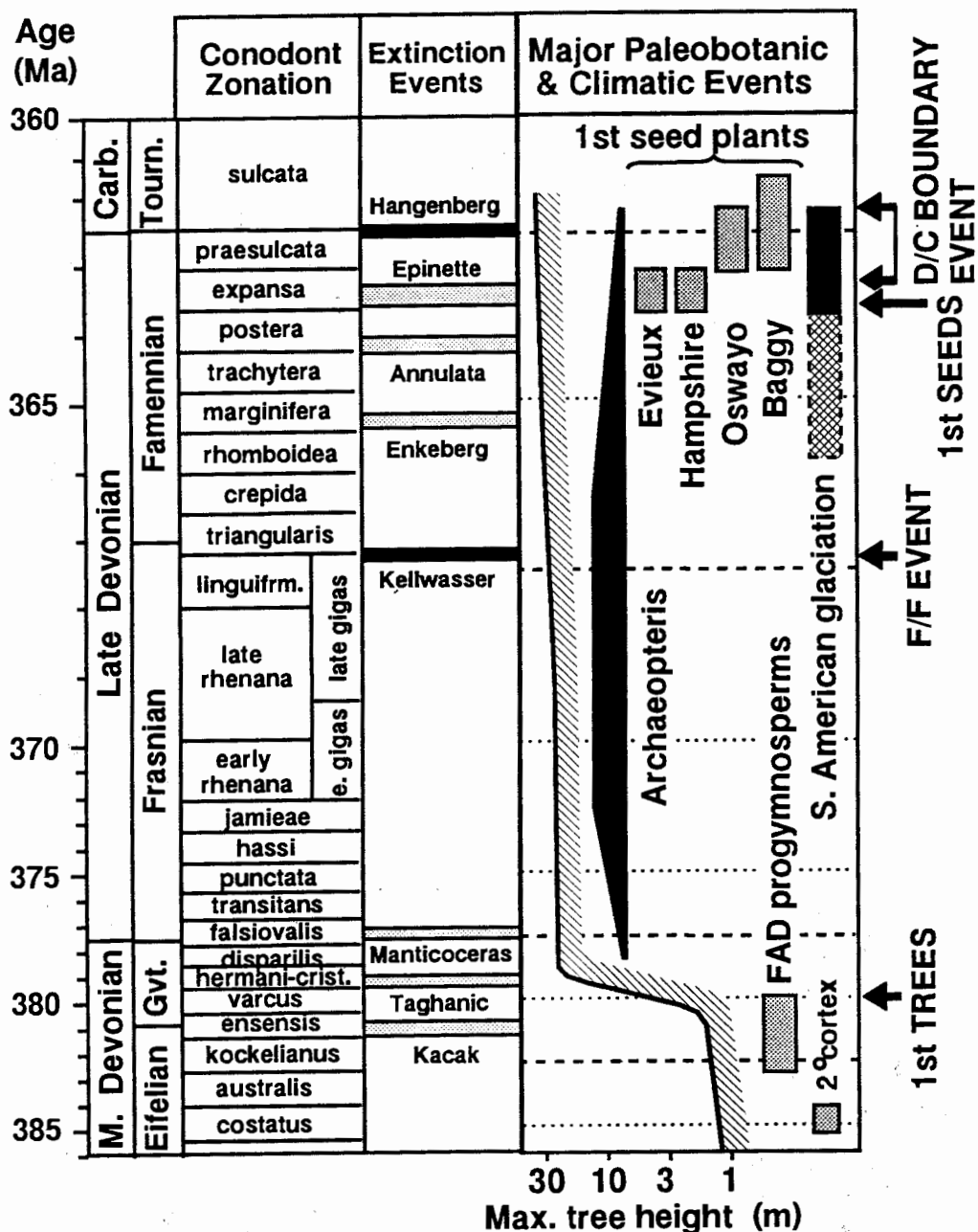# MIDDLE - LATE DEVONIAN PALEOBOTANICAL EVENTS

Age (Ma)	Conodont Zonation	Extinction Events	Major Paleobotanic & Climatic Events

1st seed plants

Carb. / Tourn. — sulcata — Hangenberg

Famennian: praesulcata (Epinette), expansa, postera, trachytera (Annulata), marginifera, rhomboidea (Enkeberg), crepida, triangularis

Frasnian: linguifrm. / late gigas (Kellwasser), late rhenana, e. gigas, early rhenana, jamieae, hassi, punctata, transitans, falsiovalis

M. Devonian — Gvt.: disparilis (Manticoceras), hermani-crist., varcus (Taghanic), ensensis

Eifelian: kockelianus (Kacak), australis, costatus

Archaeopteris — FAD progymnosperms — S. American glaciation

Evieux, Hampshire, Oswayo, Baggy

2° cortex

D/C BOUNDARY — 1st SEEDS EVENT — F/F EVENT — 1st TREES

Max. tree height (m): 30 10 3 1

Figure 12.2.
Middle and Late Devonian botanical, marine, and climatic events. **A:** Trees and roots: first appearances for secondary cortex (periderm) and progymnosperms (Scheckler and Banks 1974; Chaloner and Sheerin 1979; Banks 1980; Gensel and Andrews 1984; Thomas and Spicer 1987; Stewart and Rothwell 1993; Taylor and Taylor 1993), maximum tree heights (Chaloner and Sheerin 1979; Gensel and Andrews 1984; Mosbrugger 1990), and peak abundance of *Archaeopteris* (Beck 1964; Scheckler 1986a,b; Beerbower et al. 1992). **B:** Seed plants: first seeds in Evieux, Hampshire, Oswayo, and Baggy formations (Fairon-Demaret 1986; Rothwell and Scheckler 1988); also shown is late Famennian continental glaciation in South America (Caputo 1985; Caputo and Crowell 1985), which is age constrained by miospore data (Streel 1986, 1992). Conodont zonation scheme from Ziegler and Sandberg (1984, 1990); extinction events are shown for comparison. Timescale is from Harland et al. (1990), although recent radiometric age studies (e.g., Claoué-Long et al. 1992) cast

unknown. Because of differences in habitat and reproductive strategy, direct competition with early seed plants is not likely a factor in its demise (Scheckler 1986a,b; Rothwell and Scheckler 1988).

Root Systems

Increases in the size of vascular land plants during the Middle and Late Devonian were undoubtedly accompanied by increases in the size of root systems. Among modern higher plants, a strong positive correlation exists between shoot mass and root mass, with roots accounting for 15 to 30 percent of total floral biomass in conifer forests and up to 75 percent in grasslands (Russell 1977). With regard to primary productivity, root growth is even more important, accounting for 40 to 85 percent of annual biomass turnover in modern forest, shrub, and grassland ecosystems (Fogel 1985; Comeau and Kimmins 1989). Furthermore, in harsh environments an even larger proportion of total net production is put into rootlets (e.g., Keyes and Grier 1981), suggesting that as early land plants began to colonize marginal new habitats, an important physiological adaptation may have been larger root systems.

Increases in the biomass and penetration depth of root systems coincident with the spread of arborescent vegetation during the Middle and Late Devonian are evidenced by root traces and by permineralized and compressed fossil roots in contemporaneous paleosols (e.g., see figure 12.4; Driese et al. 1997). The earliest root traces associated with vascular plants appeared in the late Pragian (mid-Early Devonian) in the form of short (centimeter-long), forked roots produced by herbaceous lycopods (e.g., *Asteroxylon, Drepanophycus*) and trimerophytes (e.g., *Psilophyton*). The appearance of deeply penetrating root systems coincided with the development of arborescent vegetation in the late Middle and Late Devonian (figure 12.3; Beerbower et al. 1992). In the Eifelian and Givetian, the root systems of archaeopterid and aneurophyte progymnosperms were generally shallow (<20 cm) (Scheckler 1986a, and unpubl. data; Beerbower et al. 1992), but by the Frasnian and Famennian, dominant genera such as *Archaeopteris* had massive root systems with penetration depths in excess of 100 cm (figures 12.3, 12.4; e.g., Beck 1953, 1967; Walker and Harms 1971; Snigirevskaya 1984a,b, 1988, 1995; Retallack 1985; LeJeune 1986; Driese et al. 1997; Scheckler, unpubl. data). Later gymnosperms possessed much the same type of root system as these progymnosperms and were probably equally effective with regard to pedoturbation (Scheckler 1995). Some nonprogymnosperms also developed extensive root systems during the Late Devonian (e.g., the tree lycopods *Cyclostigma* and *Lepidodendropsis/Protostigmaria*, the cladoxylalean fern *Pseudosporochnus*, and the zygopterid fern *Rhacophyton*, but these taxa were commonly restricted to wetland habitats and their root systems were generally shallower and unbranched or much less branched than those of contemporaneous progymnosperms (figure 12.3; Leclercq and Banks 1962; Schweitzer 1969; Scheckler 1974, 1986a,b; Jennings et al. 1983). The greater pedoturbational effectiveness of progymnosperms and gymnosperms relative to other clades was a result of differences in root structure: (1) the presence in both groups of a vascular cambium that allowed continuous, perennial growth with storage potential (i.e., wood and ray parenchyma), and (2) internal (i.e., endogenous and adventitious) production of lateral rootlets that could repeatedly arise and repenetrate a given volume of soil (figure 12.4; Scheckler, in press).

Seed Habit

Innovations in reproductive systems played a major role in the greening of land masses. The earliest land plants had a pteridophytic

Figure 12.2. (*continued*)
some aspects of this timescale in doubt. Famennian epoch is also supported by a recent radiometric study that yielded a date for the Devonian–Carboniferous boundary some 8 m.y. younger than that of the Harland et al. timescale (354.2±4.0 Ma vs. 362.4 Ma). Hence, substantial revision of the Devonian timescale is likely in the future.
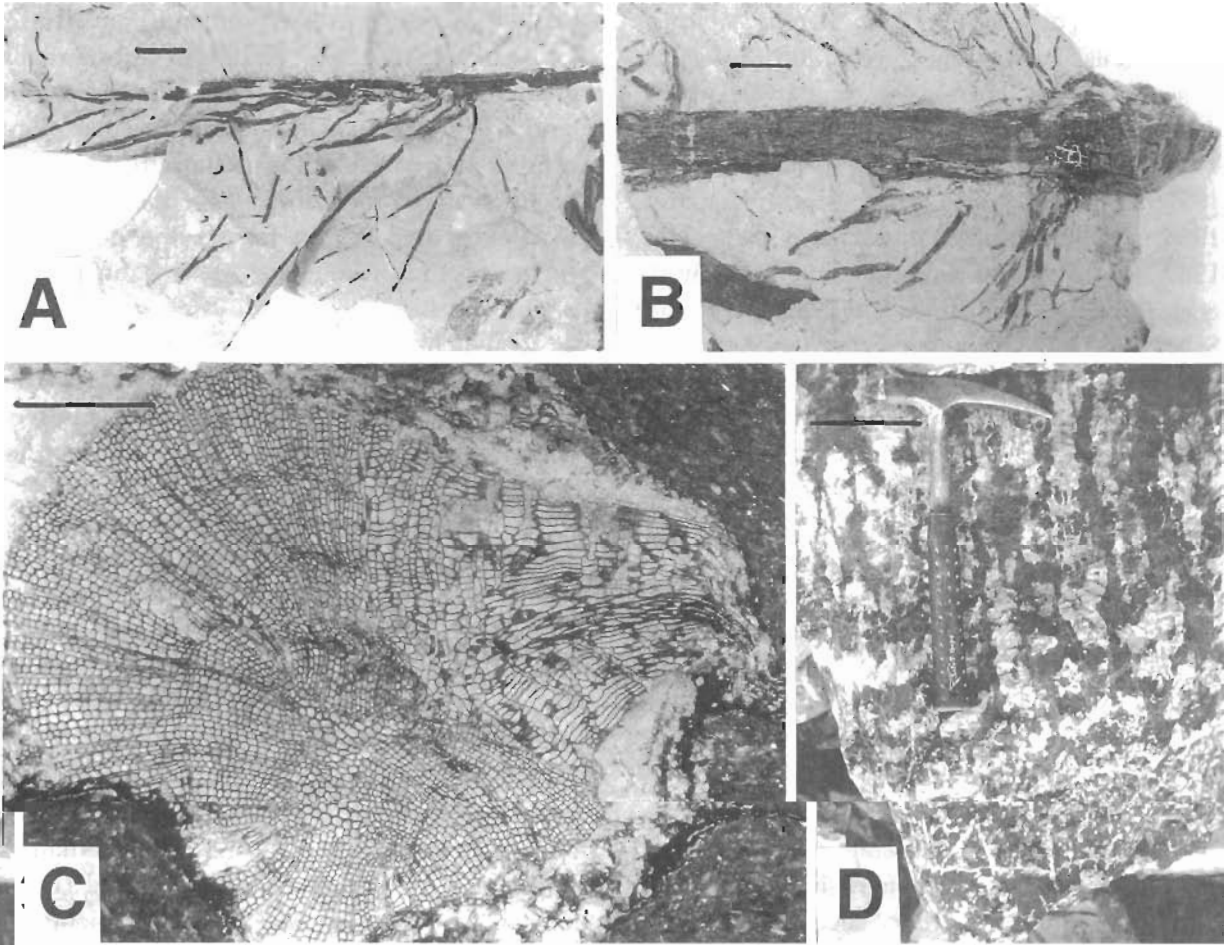
Figure 12.4.

Late Devonian root systems. **A:** Compressed young root system (*Callixylon petryi*) of progymnosperm tree *Archaeopteris* that shows numerous lateral rootlets. Parts of this specimen (UAPC S4630) are also petrified and demonstrate that the lateral rootlets were endogenous. **B:** Compressed older root system of *Archaeopteris* to show clusters of adventitious lateral rootlets (specimen UAPC S4631b). Specimens in (A) and (B) are from the lower Frasnian Yahatinda Formation of Alberta, Canada. Scale bars in (A) and (B) = 1 cm. **C:** Cross-section of a petrified aneurophyte progymnosperm root that shows the secondary xylem and secondary phloem produced by its perennial bifacial vascular cambium (n.b., asymmetry is common in roots that press against objects in the soil). Also visible on the right is a longitudinal section of an endogenous lateral rootlet; note cell arrangement at its point of attachment to the tetrarch main root. This specimen (CUPC 1990.4-9R) is from the lower Frasnian Oneonta Formation of New York. Scale bar = 1 mm. **D:** Vertical profile of a paleosol horizon (vertisol) showing in its upper part wedge-shaped peds and large calcrete tubes typical of those formed around major roots of *Archaeopteris* in semiarid environments, and in its lower part small root traces typical of the much-branched root systems of either young progymnosperms (e.g., *Archaeopteris*) or early gymnosperms (e.g., *Moresnetia* or *Dorinnotheca*), all of which are present in this flora. The paleosol is from the mid Famennian Evieux Formation of Belgium. Scale bar = 10 cm.

Scheckler 1987; Rothwell and Scheckler 1988; Rothwell et al. 1989; Beerbower et al. 1992; Hilton and Edwards 1996).

The appearance of seeds can be dated rather precisely to the mid to late Famennian (figure 12.2). The earliest known seeds are *Moresnetia zalesskyi* and *Dorinnotheca streelii* (Evieux Formation, Belgium) and *Elkinsia polymorpha* (Hamp-

shire Formation, West Virginia), which date to the lower VCo spore zone (Famennian 2c). These were followed by the slightly younger seeds *Archaeosperma arnoldii* (Oswayo Formation, Pennsylvania), *Aglosperma quadripartita* [Quartz Conglomerate Group (below the Tongwynlais Formation) of the Upper Old Red Sandstone at Taffs Well, Wales], *Spermolithus devonicus*

(Kiltorcan Formation, Eire), *Kerryia mattenii* (Coomhola Formation, Eire), and *Xenotheca devonica* (Baggy Formation, England), which date to the LV-LN spore zones (Fa2d-basal Tn1b) of the latest Devonian (Chaloner et al. 1977; Gillespie et al. 1981, Fairon-Demaret 1986, 1996; Fairon-Demaret and Scheckler 1987; Rothwell and Scheckler 1988; Rothwell et al. 1989; Rothwell and Wight 1989; Streel and Scheckler 1990; Hilton and Edwards 1996). The Fa2c and Fa2d (lower VCo-LV) spore zones correlate with the upper *postera*–lower *expansa* and upper *expansa–praesulcata* conodont zones, respectively (Richardson and Ahmed 1988). Seed plants were not common, however, until after the latest Devonian collapse of the progymnosperm *Archaeopteris* forests, when gymnosperms diversified and filled ecological niches in Early Carboniferous floodplain and upland forest environments (Scheckler 1986a; Rothwell and Scheckler 1988; Beerbower et al. 1992). Moreover, competition with seed plants does not seem to have been a major factor in the demise of *Archaeopteris*, since they occupied different floodplain habitats and exploited different features of successful reproductive biologies (Scheckler 1986a,b; Rothwell and Scheckler 1988; Beerbower et al. 1992).

EFFECTS OF EARLY VASCULAR LAND PLANTS ON WEATHERING PROCESSES, PEDOGENESIS, AND THE HYDROLOGIC CYCLE

Weathering Processes

The spread of forests and associated, deeply rooted soils during the late Middle and Late Devonian is likely to have caused major changes in weathering processes and pedogenesis (soil formation). With regard to chemical weathering in the soil environment, higher land plants play a major role in the production of (1) organic acids, which are released through root mycorrhizae, (2) humic and fulvic acids, which are produced through bacterial decay of complex organic compounds, and (3) carbonic acid, which is generated through oxidation of

organic matter in soils (Knoll and James 1987; Johnsson 1993; Drever 1994). Substantially greater quantities of acid are produced per unit land area in vascular than in nonvascular plant ecosystems because of the greater gross primary productivity of the former—for example, 600 to 6,000 g m^{-2} yr^{-1} in forests and grasslands versus less than 1,000 g m^{-2} yr^{-1} in nonvascular bryophytic and less than 100 g m^{-2} yr^{-1} in algal–lichen ecosystems (Fogel 1985; Longton 1988; Comeau and Kimmins 1989). This accounts for observations of higher rates of chemical weathering in vascular plant ecosystems (e.g., Cawley et al. 1969; Berner 1994), which are estimated to exceed those of nonvascular ecosystems by a factor of about seven on the basis of rock-weathering studies (Cochran and Berner 1993; Moulton and Berner 1998) and soil and groundwater analyses (Drever and Zobrist 1992; Cochran and Berner 1996). In addition to acid production, the greater weathering effectiveness of higher plants is also caused by the three-dimensional (i.e., volumetric) contact area of their rootlets and roothairs compared to the largely two-dimensional (i.e., surficial) contact area of algae and lichens with weathering substrates (e.g., Russell 1977; Viles and Pentecost 1994). These observations cast doubt on proposals that pre-Silurian microfloras consisting of bacteria, algae, and lichens could have brought about an intensity of chemical weathering *per unit land area* comparable to that of higher land plants (e.g., Schwartzman and Volk 1989; Keller and Wood 1993; Horodyski and Knauth 1994).

With regard to physical weathering processes, the spread of higher land plants may have changed the residence time of material in the soil environment and the texture and mineralogy of pedogenic weathering products (figure 5; Drever 1994). Vegetation retards the transport of sediment from hillslopes, leading to a transport-limited as opposed to a weathering-limited soil regime (Stallard 1985; Johnsson 1993). In the absence of a densely interwoven mat of plant roots, weathering products are rapidly swept from hillslopes, accumulating as immature sediments in alluvial fans and

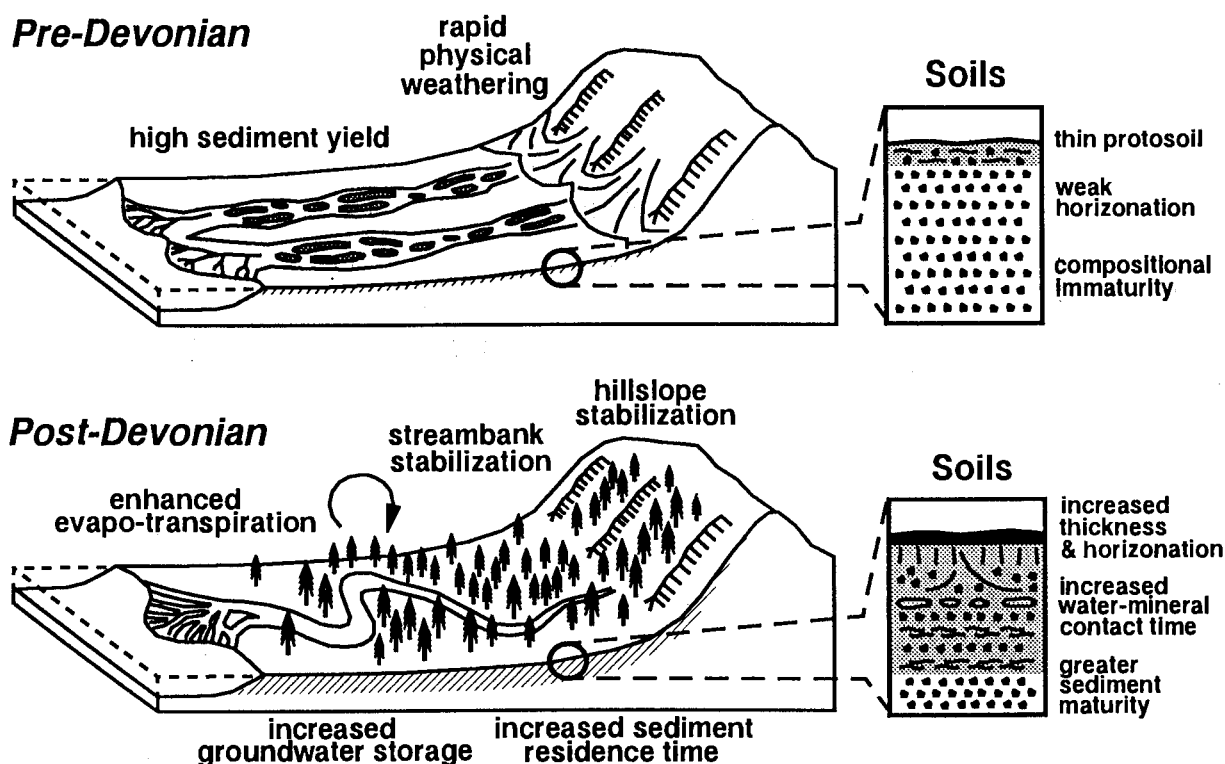# HYDROLOGIC CYCLE & PEDOGENIC WEATHERING

Figure 12.5.
Changes in the hydrologic cycle and pedogenic weathering processes as a consequence of the Middle-to-Late Devonian spread of vascular land plants (see text for discussion).

braided streams. Thus, development of a higher land-plant cover may have stabilized land surfaces, allowing more time for weathering of surface rocks to a finer-grained, compositionally more mature product (Schumm 1968; Johnsson 1993; Drever 1994). This process may account for apparent secular changes in sediment maturity, such as an increase in the clay content and compositional maturity of Silurian fluvial clastics relative to equivalent Cambro-Ordovician facies (Cotter 1978; Feakes and Retallack 1988; Retallack 1985, 1990). Secular changes in compositional maturity also may have come about through selective weathering of minerals containing nutrients essential for plant growth. For example, pre-Silurian sandstones are richer in chemically labile K-feldspars, and lower Paleozoic clastic sediments contain higher K_2O/Na_2O ratios than equivalent Mesozoic–Cenozoic facies, suggesting more complete decomposition of K-bearing minerals

from the mid Paleozoic onward because of the potassium demand of higher land plants (Basu 1981; Maynard et al. 1982; Holland 1984; Nesbitt et al. 1996).

With regard to rates of chemical and physical weathering, it is important to note that changes in these parameters associated with the spread of vascular land plants in the Middle and Late Devonian were transient rather than permanent (figure 12.6). This transience is dictated by the fact that, at geologic timescales (e.g., $> 10^7$ yr), fluctuations in chemical weathering rates are dampened by negative feedbacks involving (1) longer time constants for the sources of atmospheric CO_2 (i.e., volcanic and metamorphic degassing) than for its sinks (i.e., silicate weathering and organic carbon fixation), and (2) temperature dependence of chemical weathering rates [i.e., cooling as a consequence of atmospheric CO_2 drawdown would reduce the rate of CO_2 utilization via silicate weathering

ATMOSPHERIC CO$_2$ DRAWDOWN

A) Pre-Devonian

B) Late Devonian
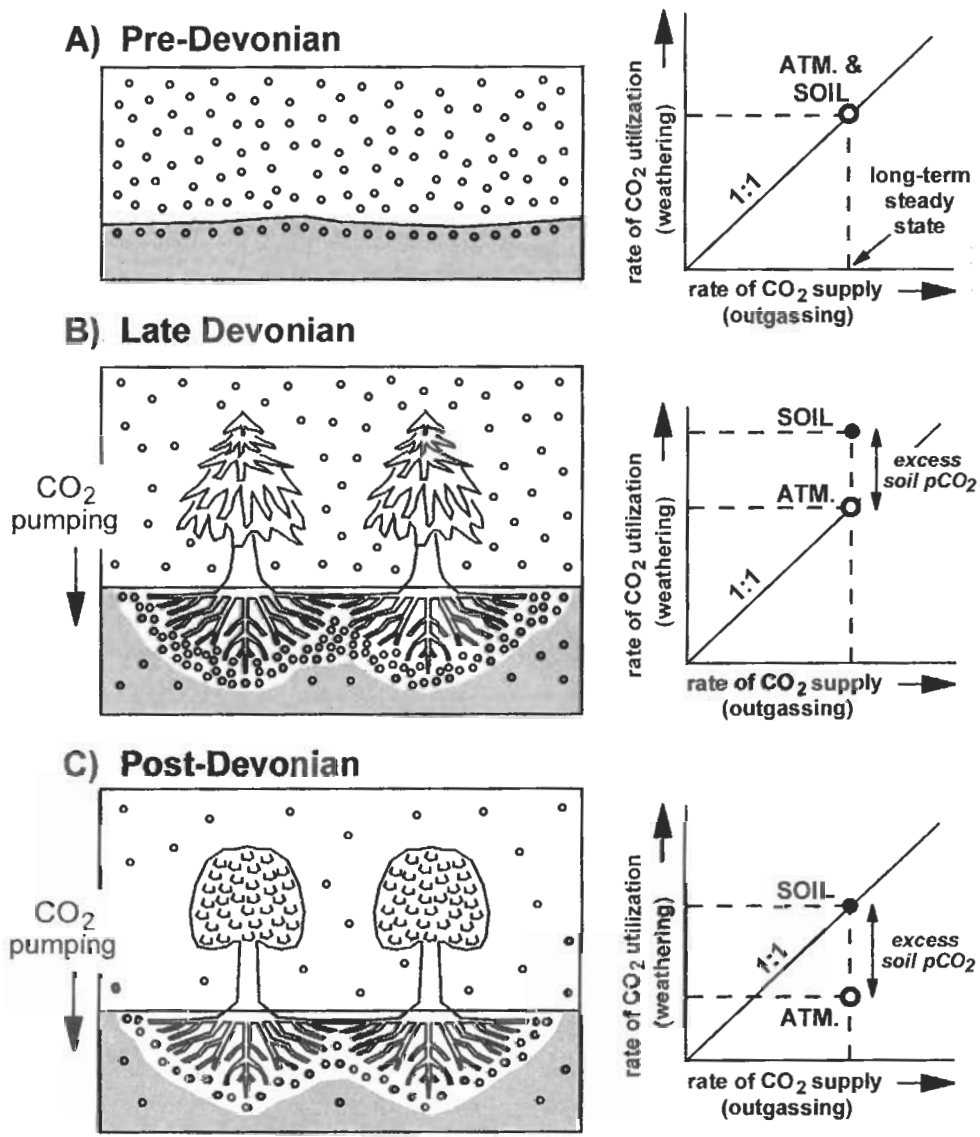

C) Post-Devonian

Figure 12.6.
Changes in atmospheric and soil CO_2 levels as a consequence of the Middle-to-Late Devonian spread of vascular land plants. **A:** In the largely unvegetated pre-Devonian world, atmosphere and soil CO_2 levels were similar. **B:** During the Middle and Late Devonian, active pumping of carbon into soils by land plants initiated atmospheric pCO_2 drawdown. **C:** in the post-Devonian, terrestrial floras maintain artificially low atmospheric CO_2 and high soil CO_2 levels via intensive carbon pumping. Because of a long-term steady state in CO_2 supply via volcanic and metamorphic degassing and the requirement that geochemical sources and sinks balance, CO_2 levels in the soil environment (where silicate mineral weathering takes place) must have been similar both before and after the spread of land plants. However, during the transient interval in which CO_2 uptake by terrestrial floras first intensified but atmospheric CO_2 levels remained high, soil CO_2 levels are likely to have been much higher than at present, resulting in enhanced pedogenic weathering.

(Berner and Rye 1992; Caldeira 1992; Berner 1994)]. However, significant short-term perturbations in global weathering rates (figure 12.6B) are possible because the rate of supply of

CO_2 via degassing is effectively constant at the timescales associated with pedogenic weathering processes (e.g., $< <10^7$ yr). Thus, a transient increase in weathering intensity at these

timescales (e.g., driven by land-plant evolution) would have to be counteracted by (1) a decrease in atmospheric pCO_2, (2) a decrease in global temperature, or (3) both. Eventually, this would yield a new equilibrium state (figure 12.6C) in which global weathering intensity is comparable to that prior to the transient disturbance (figure 12.6A), and in which atmospheric pCO_2, global temperature, or both, remain permanently at levels lower than those prior to the disturbance. Because of the stronger dependence of silicate weathering rates on temperature than on soil pCO_2 (Velbel 1993; Gwiazda and Broecker 1994), the dominant factor in producing a negative feedback on transient increases in weathering intensity is likely to be global cooling rather than atmospheric CO_2 drawdown. These considerations suggest that any increases in chemical and physical weathering rates associated with the spread of vascular land plants would have been a transient phenomenon, which is consistent with a transient sedimentation rate anomaly reported for the Middle and Late Devonian (Dineley 1984; Gregor 1985; Algeo et al. 1995; Retallack 1997; Algeo and Scheckler 1998).

Pedogenesis

The spread of vascular land plants resulted in profound changes in soil types, the thickness and geographic extent of soils, and rates of pedogenesis on a global scale (Retallack 1990, 1997; Algeo et al. 1995). Prior to the advent of vascular plants, land surfaces may have consisted largely of barren rock and thin microbial protosoils (Retallack 1985, 1986, 1990, 1992; Beerbower et al. 1992), similar to modern "desert crusts" formed of cyanobacterial mats (Campbell 1979; Whitford and Freckman 1988; Watson 1992). The advent of vascular land plants appears to have been closely linked to global changes in soil types, as most of the major types of the modern world first appeared during the Devono-Carboniferous (figure 12.7). For example, the oldest known histosol is the Rhynie Chert from the Early Devonian, and the earliest probable alfisols, ulti-

sols, and spodosols are all of Late Devonian or Early Carboniferous age (Retallack 1986; Mack and James 1992) (but note that classification of paleosols using modern soil nomenclature is tentative because of the lack of information on pH and base status). These soil types, which form today mainly beneath temperate-zone forests, probably reflect contemporaneous afforestation of land surfaces. Vertisols, although present in pre-Devonian successions, became increasingly common during the Devonian (e.g., Allen 1986; Driese and Mora 1993) and, especially, during the Carboniferous (e.g., Goldhammer and Elmore 1984; Wright 1987; Wright and Robinson 1988; Ettensohn, Dever, and Grow 1988; Goldstein 1991; Vanstone 1991; Muchez et al. 1993; Driese et al. 1994; Retallack and Germán-Heins 1994; Gill and Yemane 1996). Vertisols (see figure 12.4D) are characterized by wedge-shaped peds bounded by slickensided surfaces that result from high concentrations of swelling clays (e.g., smectite), and such clays are generated in large quantities in the type of seasonally wet climate that is associated with temperate-zone vegetation (Wilding and Tessier 1988; Mack and James 1992).

A fundamental change in soil weathering processes may be indicated also by a major shift in the clay-mineral composition of shales during the Devono-Carboniferous from illite- and chlorite-dominated assemblages to smectite- (or mixed-layer illite/smectite-) and kaolinite-dominated assemblages (Weaver 1967, 1989; Algeo et al. 1995). Smectite and kaolinite are produced in large amounts in the soil environment, principally through alteration of biotite and plagioclase feldspar precursors. Production of these minerals is closely associated with soil leaching: smectites and related expandable clay minerals are the major weathering products of many parent rock types subject to moderate leaching in temperate to semiarid climates, whereas kaolinite is favored under conditions of strong leaching in humid tropical climates (Velde 1985; Singer and Munns 1991). Although smectite-rich paleosols are known to have developed in warm, seasonally wet paleoclimates in the absence

zone forest soils today, is first encountered in wet lowland soils of the early Frasnian and in dry upland soils of the Early Carboniferous (Retallack 1985). The timing of these pedogenic changes is consistent with the timing of important terrestrial floral developments likely to have influenced soil development—for example, widespread afforestation of lowlands in the Frasnian and the spread of gymnosperms into upland areas in the Early Carboniferous.

Rates of pedogenesis are likely to have varied considerably in association with the changes in soil types and thicknesses documented here. Rapid increases in soil thickness during the Middle and Late Devonian are *prima facie* evidence for a (transient) elevation of chemical weathering rates, because modern soils exhibit a strong positive correlation between rates of breakdown of soil mineral constituents and the density and rate of growth of roots and rootlets [which are linked to rates of production of soil acids (Newman and Andrews 1973; Russell 1977)]. This inferred acceleration of soil formation rates, although primarily due to increases in terrestrial floral biomass, also may have been promoted by positive feedbacks between (1) evolving root systems and soil development, via a shift from a weakly rooted rhizomatous mode to a deeply rooted free-standing mode (figures 12.3, 12.4) as soils increased in thickness and compositional maturity (Banks 1985), and (2) accumulating soil humus and floral biomass, via enhanced rates of recycling of organic detritus by soil fungi and bacteria, permitting greater standing floral crops (Thomas and Spicer 1987; Klepper 1987; Retallack 1990). Whereas any increase in soil formation rates during the Middle and Late Devonian would have been transient, changes in soil depth (and structure and type) (figure 12.5) were permanent, reflecting a new equilibrium maintained dynamically by the continuous presence of a large terrestrial floral biomass since the Late Devonian.

Increases of organic carbon burial occurred not only in marine black shales of this time, but also in coeval terrestrial coal beds. Partly this was the result of the huge expansion of terrestrial primary productivity. But the evolution of large, wetland-tolerant plants (tree lycopsids and

some zygopterid ferns) formed increasingly common and thicker coal beds throughout the Givetian, Frasnian, and Famennian (figure 12.1; Schweitzer 1969; Goodarzi et al. 1989, 1994; Goodarzi and Goodbody 1990; Scheckler 1986a,b,c; Beerbower at al. 1992). By the latest Devonian to Early Carboniferous, arborescent lycopsids (e.g., *Cyclostigma, Protolepidodendropsis, Lepidodendropsis, Sublepidodendron*) were fully wetland tolerant and formed extensive coal swamps (Scheckler 1986a; Beerbower et al. 1992), a clade-dependent ecosystem that would continue through most of the Carboniferous (DiMichele and Phillips 1996).

The Hydrologic Cycle

The spread of terrestrial vegetation is likely to have altered the global hydrologic cycle (figure 12.5). With regard to recirculation of atmospheric water, forests promote evapotranspiration and increase precipitation through changes in land surface albedo and atmospheric turbulence (Shukla and Mintz 1982; Sud et al. 1993). With regard to surface runoff, a dense vegetative cover reduces runoff, total discharge, and peak discharge during floods *for a given level of precipitation* (Schumm 1968, 1977; Faulkner 1990). Even though the rate of evapotranspirative recirculation (and, hence, precipitation) would have increased in a vegetated world over that of an earlier nonvegetated world, surface runoff nonetheless would have been reduced in the former as a result of the greater storage capacity of the thick soils developed in association with vegetation.

The reduction in runoff associated with vegetation also would have led to lower landscape erosion rates and sediment yields. Sediment yields in the modern world peak in semiarid environments with an annual precipitation of about 250 to 350 mm yr^{-1} (figure 12.8A,B; Summerfield 1991), but in the absence of a higher plant cover, sediment yields may have covaried positively with increases in precipitation to much higher precipitation rates (figure 12.8C,D; Schumm 1968, 1977). The reduction in modern sediment yields at precipitation rates greater than 250 to 350 mm yr^{-1}

floodplains by the earliest vascular land plants (Thorne 1990; Beerbower et al. 1992) and points out the potential for diachronous effects as a consequence of the progressive spread of land plants from the Ordovician to the Carboniferous.

MIDDLE AND LATE DEVONIAN MARINE EVENTS AND GLOBAL CLIMATE CHANGE

The Middle and Late Devonian is characterized by important events not only in the terrestrial but also in the marine realm. In the latter, a protracted biotic crisis eliminated the Middle Paleozoic reef community and resulted in a far-reaching turnover among tropical-marine benthic groups. The biotic crisis was probably related in some manner to contemporaneous development of widespread anoxia in shallow epicontinental seas, and bottomwater anoxia contributed to high rates of organic carbon burial and to C- and S-isotopic anomalies in marine sediments of this age. Changes in the global carbon cycle associated with massive burial of organic carbon (as well as with enhanced pedogenic weathering of silicates) were the primary factor leading to coeval changes in global climate, such as rapid drawdown of atmospheric CO_2, climatic cooling, and the onset of continental glaciation. Whether events in the marine realm and changes in global climate during the Middle and Late Devonian were precipitated by or otherwise linked to the evolutionary development of vascular land plants (discussed previously) is open to question, although a strong circumstantial case can be made in favor of such a scenario.

Marine Biotic Crisis

The Middle and Late Devonian biotic crisis, one of the "Big Five" mass extinctions of the Phanerozoic (Sepkoski 1986; Raup and Boyajian 1988; McGhee 1996), resulted in the disappearance of about 20 to 25 percent of families, 45 to 60 percent of genera, and 70 to 82 percent of species of marine biota (Sepkoski 1986, 1996; Jablonski 1991). This biotic crisis differed from other well-studied mass extinctions in three important respects: (1) duration, spanning an interval of about 20 to 25 million years (Sepkoski 1996; McGhee 1996), (2) episodicity, comprising at least eight to ten separate events (House 1985; Bayer and McGhee 1986; Scrutton 1988; Becker 1993), and (3) selectivity, being largely restricted to tropical marine biota (Bambach 1985; Sepkoski 1986; Scheckler 1986a).

With regard to episodicity, this crisis was characterized by fluctuations in extinction rates producing a "stepwise" extinction pattern with peak intensities at intervals of a few million years (Walliser 1996a,b). Many biotic groups exhibit this stepwise extinction, including rugose corals, brachiopods, ammonoids, and benthic foraminifera (House 1985; Copper 1986; Bayer and McGhee 1986; Kalvoda 1986, 1990; Scrutton 1988; Boucot 1990; Simakov 1993; Schindler 1993; Becker 1993; Talent et al. 1993; McGhee 1996). The most profound extinctions were associated with (1) the Frasnian–Famennian (F/F) boundary (or Upper Kellwasser horizon), and (2) the Devonian–Carboniferous (D/C) boundary [or Hangenberg horizon (Sepkoski 1986, 1996)]. The duration of these extinction peaks is uncertain, but estimates based on conodont zones suggest events of less than 20 ky duration (Sandberg, Ziegler, et al. 1988).

With regard to selectivity, the Middle and Late Devonian biotic crisis was particularly severe for tropical marine organisms, especially benthic groups. The Middle Paleozoic reef community, dominated by stromatoporoids and tabulate corals, was under stress as early as the Eifelian, although massive reefs continued to be constructed into the late Givetian and early Frasnian (Burchette 1981; Sepkoski 1986; James 1983; Bambach 1985). These large reefs declined rapidly during the mid to late Frasnian and disappeared at the F/F boundary, to be replaced during the Famennian by small stromatolitic structures built by cyanobacteria (Krebs 1974; Playford et al. 1976, 1984). A few marine biotic groups thrived during the biotic crisis, especially high-latitude and cold-water taxa [e.g., siliceous

+0.5‰ PDB in the Middle Devonian to +4.5‰ PDB in the Late Carboniferous (Veizer et al. 1986; Popp et al. 1986; Lohmann and Walker 1989; Berner 1989). This shift in $\delta^{13}C$ appears to have occurred in a stepwise manner—for example, with abrupt increases (+2‰ to +3‰) associated with individual episodes of widespread organic carbon burial and followed by decreases of somewhat lesser magnitude. For those C-isotopic excursions that have been well studied (e.g., the F/F boundary Upper Kellwasser horizon; Playford et al. 1984; McGhee et al. 1986; Buggisch 1991; Halas et al. 1992; Joachimski and Buggisch 1993; Joachimski et al. 1994; Wang et al. 1996), the shifts appear to have been synchronous and of uniform magnitude on a global scale. The synchroneity, uniformity, and facies-independence of these C-isotopic excursions are strong evidence that they represent global shifts in $\delta^{13}C$ of the oceanic surface ΣCO_2 reservoir (Joachimski and Buggisch 1993). Reports of negative carbonate $\delta^{13}C$ excursions at major boundaries (e.g., F/F) (Xu et al. 1986; Wang et al. 1991; Geldsetzer et al. 1993; Yan et al. 1993; Wang et al. 1996) are likely to represent either geochemical changes in water masses isolated from the global ocean or contamination of carbonates by ^{13}C-depleted organic matter (e.g., Wang et al. 1996).

In marine environments, high rates of organic carbon burial are generally associated with increased production and burial of reduced sulfur, mainly as iron sulfides (Berner 1978; Berner and Raiswell 1983; Berner and Canfield 1989). Coburial of reduced (organic) C and reduced (sulfide) S during the Late Devonian is evidenced locally by (1) positive covariance of total organic carbon and total sulfur (a proxy for reduced S) in black shales of that age (e.g., Leventhal 1987), and (2) association of positive sulfide S-isotopic anomalies with organic-rich horizons (e.g., Geldsetzer et al. 1987; Wang et al. 1996), and globally by (3) positive covariance of marine carbonate $\delta^{13}C$ and marine evaporite $\delta^{34}S$ values (Holser et al. 1989). A major excursion in marine evaporite $\delta^{34}S$ values (+8‰ to +10‰) between the Middle Devonian and mid Mississippian is likewise

attributable to enhanced burial of ^{34}S-depleted reduced S (Holser et al. 1989). Coburial of large quantities of reduced C and S during the Late Devonian would have released large quantities of molecular oxygen (O_2) to the atmosphere (Kump and Garrels 1986; Berner and Canfield 1989), which is evidenced by coeval increases in the abundance of fossil charcoal, reflecting a greater frequency of forest fires in an oxygen-rich atmosphere (Chaloner 1989; Jones and Chaloner 1991), and by gigantism of terrestrial invertebrates, reflecting an enhanced ability to take up oxygen in tissues through diffusion (Graham et al. 1995).

Global Climate Change

Atmospheric CO_2 levels dropped precipitously during the Devono-Carboniferous as a consequence of elevated silicate weathering rates and enhanced burial of organic carbon (Berner 1992, 1997, and pers. comm., 1995). Atmospheric pCO_2 estimates based on global carbon cycle models suggest a decrease from pre-Devonian concentrations of 4 to 20 PAL (present atmospheric level, generally taken as a preindustrial value of 270 ppmV) to mid-Carboniferous concentrations of about 1 PAL (Berner 1991, 1993, 1994). Imprecision in these estimates is largely the result of uncertainty regarding relative rates of chemical weathering by nonvascular algal-lichen floras versus higher land plants (Berner 1994), and recent studies supporting low weathering efficiency ratios (about 0.15) (e.g., Drever and Zobrist 1992; Cochran and Berner 1996; Moulton and Berner 1998) would favor higher atmospheric pCO_2 estimates for the pre-Devonian (about 12 to 20 PAL). The latter values are independently supported by C-isotopic analysis of soil carbonates (Mora et al. 1991, 1996; Yapp and Poths 1992, 1996) and by analysis of stomatal densities in contemporaneous terrestrial plants (McElwain and Chaloner 1995).

Rapid drawdown of atmospheric CO_2 levels is likely to have been the main cause of coeval climatic cooling, culminating in a brief episode of continental glaciation in the latest Devonian.

Evidence for climatic cooling during the Devono-Carboniferous is provided by a net +4‰ shift in the marine carbonate $\delta^{18}O$ record—that is, from –5‰ PDB (or less) to –1‰ PDB (Lohmann and Walker 1989), most of which occurred within a time interval of about 7 to 15 m.y., spanning the Devono-Carboniferous boundary (Popp et al. 1986; Dunn 1988; Brand 1989). The rapid, ubiquitous nature of this O-isotopic shift argues against both a diagenetic mechanism (e.g., Degens and Epstein 1962) and a secular change in the $\delta^{18}O$ composition of seawater (e.g., Holland 1984). Rather, the shift is likely to reflect a significant cooling of tropical sea surface temperatures (SSTs) (i.e., by about 16°) (cf. Craig 1965), or, if coeval growth of Gondwanan icesheets caused a +0.5‰ ^{18}O enrichment of seawater (Crowley and Baum 1991), by about 14°C. Thus, assuming no other changes in the $\delta^{18}O$ composition of seawater, tropical SSTs may have cooled from about 40°C in the Devonian to near-modern temperatures of about 24° to 26°C in the Carboniferous (Veizer et al. 1986). Although these estimated temperature changes are large, they may not be unrealistic in view of recent studies demonstrating temperature changes of 3° to 8°C in tropical SSTs at glacial timescales (i.e., <<1 m.y.) during the Pleistocene (Emiliani and Ericson 1991; Rostek et al. 1993; Anderson and Webb 1994). The strongest argument in favor of temperature control of Devono-Carboniferous marine carbonate $\delta^{18}O$ values is the link it provides to coeval changes in organic carbon burial rates, atmospheric CO_2 levels, and global climate.

Rapid global cooling is likely to have been responsible for a brief episode of continental glaciation during the latest Devonian. Glacigenic deposits of probable Famennian age, including diamictites with striated and polished pebbles, rhythmites with dropstones, erratic boulders, and striated pavements, are widespread in northern Brazil, and potentially correlative deposits are present in North Africa and Argentina, implying glaciation over an area more than 3,500 km long (Caputo 1985; Caputo and Crowell 1985; Frakes et al. 1992). Caputo (1985) assigned this event a "mid-Famennian"

age, but Streel (1986, 1992) redated it as latest Famennian ("Strunian" = middle *praesulcata* conodont zone). The latter age is more consistent with Late Devonian eustatic trends—a late Famennian sea-level fall (Johnson et al. 1985) may be the eustatic signature of continental icesheet growth.

CAUSES OF MIDDLE AND LATE DEVONIAN MARINE EVENTS AND GLOBAL CLIMATE CHANGE

There is, at present, no consensus regarding the causes of Middle and Late Devonian marine anoxic and extinction events and coeval changes in global climate. A variety of mechanisms have been postulated, including plate tectonics, eustasy, oceanic overturn, and bolide impacts, all of which contain plausible elements. In discussing causality, however, one should bear in mind that most events in Earth history are a response not to a single factor but to complex interactions among a set of factors, and that it is necessary to distinguish between proximate and ultimate causes for a given event. Furthermore, to achieve robustness, a model for global events of a given age must account for *all* coeval phenomena through a set of interrelated causal factors (i.e., an appeal to separate mechanisms for different phenomena would represent special pleading for temporal coincidences). With regard to the Middle and Late Devonian, valid hypotheses must account for unique aspects of the marine biotic crisis (i.e., its duration, episodicity, and selectivity) and its relationship to geochemical anomalies in coeval marine strata. Existing models for Middle and Late Devonian global events will be evaluated here and compared with the model of Algeo et al. (1995), which focuses on the potential role of vascular land plant evolution.

Existing Models for Marine Events and Global Climate Change

Tectonism and climate change can have far-reaching consequences on the evolution and

extinction of contemporaneous biotas. The Middle-to-Late Devonian biotic crisis has been attributed to cooling of tropical seasurface waters as a consequence of changes in ocean circulation or plate geometry (e.g., closure of a warm paleo-Tethyan Ocean and deflection of cold high-latitude currents into equatorial areas) (Copper 1986; Stanley 1988; Schindler 1990, 1993). If climatic cooling did play a direct role in the biotic crisis, then it must have occurred episodically and in concert with marine anoxic events, bcause of the correlativity of such events with extinction horizons (Algeo et al. 1995). Although multiple factors may have contributed to climate change at a range of timescales, stresses on marine biotas are more likely to have been caused by short-term cooling associated with episodes of increased organic carbon burial rather than to long-term effects associated with changes in ocean circulation. Global warming has also been proposed as a mechanism for the Devonian biotic crisis (Thompson and Newton 1988; Brand 1989), but this hypothesis is difficult to reconcile with evidence of contemporaneous continental glaciation (Caputo 1985; Caputo and Crowell 1985), drawdown of atmospheric pCO_2 (Berner 1991, 1994), and disproportionate destruction of tropical rather than boreal fauna (McGhee 1996).

Tectonic factors may have been important in either triggering or enhancing individual episodes of marine anoxia and organic carbon burial (e.g., through thrust loading of foreland basins and areal expansion of mid-depth oxygen-minimum zones) (Ettensohn, Miller, et al. 1988). In support of this idea are (1) early initiation of anoxia in areas proximal to active orogens, as evidenced, for example, by black shales of Pragian age in the northern Appalachian Basin, adjacent to the Acadian Orogen (Woodrow et al. 1988), and (2) migration of anoxic areas cratonward in response to foreland basin thrust loading, as in the Late Devonian central Appalachian Basin (Ettensohn, Miller, et al. 1988). Although tectonic factors were important at a minimum in enhancing marine anoxia in periorogenic areas, their significance for widespread deposition of organic-rich facies

in tectonically stable epicratonic regions is unclear.

Global sea-level changes (eustasy) have been widely cited as a possible mechanism for both marine anoxic and extinction events. The Middle and Late Devonian biotic crisis has been attributed both to sea-level rises (transgressions), which would promote bottomwater anoxia through increased water depths and enhanced water-column stratification (Berry and Wilde 1978; Johnson et al. 1985), and to sea-level falls (regressions), which would cause habitat loss within epicontinental seas (Johnson 1974; Sandberg, Poole, and Johnson 1988). Although most black shale horizons of that age are thought to be correlative with eustatic transgressions (e.g., Sandberg, Poole, and Johnson 1988; Sandberg, Ziegler, et al. 1988), a role for sea-level rises in precipitating episodes of extinction is doubtful because eustatic cycles of this age are similar in frequency and amplitude to others throughout the Phanerozoic, few of which are associated with mass mortality (Johnson et al. 1985; Haq et al. 1987). Further, although eustatic rises during the Middle and Late Devonian may have predisposed epicontinental seas to low-oxygen conditions, additional factors must have been operative at this time to have produced intense anoxia on an intercontinental scale. On the other hand, models invoking marine regressions are fundamentally improbable because (1) Middle and Late Devonian sea-level elevations were generally high and stable or rising (e.g., Johnson et al. 1985), and (2) much larger regressions in association with Pleistocene continental icesheet growth have had little effect on marine biotas.

Overturn of sulfidic open-ocean bottomwaters, as a consequence either of long-term surfacewater cooling and thermocline breakdown (Wilde and Berry 1984) or of a bolide impact (Geldsetzer et al. 1987), has been proposed to account for both the marine biotic crisis and widespread anoxia in epicontinental seas during the Middle and Late Devonian. A fundamental prediction of this model is a catastrophic decline in marine primary productivity following overturn (i.e., a Strangelove Ocean) (Hsü

and McKenzie 1985; Kump 1991), resulting in (1) a reduced flux of labile organic matter from marine phytoplankton to the seafloor, (2) lower bacterial sulfate reduction rates (because of the paucity of labile organic matter) and, hence, lower marine sulfide $\delta^{34}S$ values, and (3) lower marine carbonate $\delta^{13}C$ values as a consequence of a reduction in the C-isotopic fractionation between shallow- and deep-water masses that is dynamically maintained by phytoplankton. However, existing petrographic and isotopic data are inconsistent with this model: (1) organic matter in Middle–Upper Devonian black shales is overwhelmingly of marine algal origin (Maynard 1981; Jaminski et al. 1998), (2) early diagenetic sulfides in black shales exhibit significant ^{34}S enrichments (Maynard 1980; Goodfellow and Jonasson 1984; Geldsetzer et al. 1987; Halas et al. 1992), suggesting elevated rates of bacterial sulfate reduction owing to the greater availability of labile marine organic matter, and (3) marine anoxic event horizons correlate with positive carbonate $\delta^{13}C$ excursions, suggesting *enhanced* rather than diminished photosynthetic fixation and burial of ^{13}C-depleted organic matter (Joachimski and Buggisch 1993).

A bolide impact was postulated as a mechanism for the Frasnian–Famennian mass extinction and associated marine anoxic event (McLaren 1982), and intensive research has generated some evidence for one or more bolide impacts at or stratigraphically close to the F/F boundary, including (1) iridium anomalies in Australia, China, and Canada (Playford et al. 1984; Hurley and Van der Voo 1990; Geldsetzer et al. 1987; Wallace et al. 1991; Wang et al. 1991, 1993, 1994), (2) microtektites in China and Belgium (Wang 1992; Wang and Chatterton 1993; Claeys et al. 1992; Claeys and Casier 1994), and (3) a probable impact site in Sweden, the 55-km-diameter Siljan Ring structure (368 ± 1 Ma) (Hodge 1994; McGhee 1996). However, the strength of the geochemical evidence for an impact is questionable, because (1) concentrations of iridium and other platinum group elements are generally low compared to those at the Creta-

ceous–Tertiary boundary, (2) some elemental ratios are not compatible with a meteoritic origin, and (3) enrichment of platinum group metals in some sections is probably the result of other factors, such as slow sedimentation rates, changes in redox conditions, or cyanobacterial concentration (Playford et al. 1984; Geldsetzer et al. 1987; Dyer et al. 1989; Orth et al. 1990; Wang et al. 1993). Furthermore, not all of the reported iridium anomalies and microtektite horizons coincide stratigraphically with the F/F boundary, and a number of boundary sections proximal to the presumed impact site lack physical or geochemical evidence of such an event (McGhee et al. 1986; Hurley and Van der Voo 1990; Claeys et al. 1992; Nicoll and Playford 1993; Wang et al. 1994; McGhee 1996).

Important issues need to be addressed with regard both to the evidence for a Late Devonian bolide impact and to the significance of such an event for contemporaneous shallow-marine ecosystems. The intense search for physical and chemical evidence within a narrow stratigraphic window centered on the F/F boundary raises the possibility of sampling bias and suggests the need for a control test—a search for evidence of extraterrestrial inputs in "background" strata that are not proximal to the F/F boundary. Also unresolved is whether impact layers are more prevalent than average within Upper Devonian strata because of a preservation bias associated with anoxic marine environments (e.g., exclusion of burrowing benthos would preclude disruption of thin impact ejecta blankets that would otherwise be bioturbated out of existence). Such a preservation bias might account for the fact that evidence of bolides has been found at several horizons within the Upper Devonian, some of which are not correlated with extinction episodes. Finally, even if one or more impacts did indeed occur during the Late Devonian, it would be necessary to consider (1) whether these played any significant role in the Middle and Late Devonian biotic crisis, and (2) if so, whether that role was amplified relative to the size of the impactor because of preexisting destabilizing stresses within Late Devonian

shallow-marine ecosystems. Thus, the most important questions turn not on the existence of an impact but on its consequences.

The "Devonian Plant Hypothesis"

Whereas the models just discussed take little or no consideration of terrestrial developments, the "Devonian plant hypothesis" of Algeo et al. (1995) and Algeo and Scheckler (1998) focuses on potential links between coeval events in the terrestrial and marine realms. Critical in establishing such links is the role of soils as a geochemical interface between the atmosphere/hydrosphere and lithosphere, and the role of plants as a mediator of weathering intensities and geochemical fluxes (figure 12.9). Specifically, enhanced pedogenesis associated with the rapid spread of vascular land plants during the Middle and Late Devonian is likely to have resulted in elevated fluxes of soil solutes (especially biolimiting nutrients) as a consequence of (1) enhanced mineral leaching, (2) fixation of nitrogen by symbiotic root microbes, and (3) shedding of plant-derived detrital carbon compounds. The large flux of terrestrial plant litter is likely to have promoted development in riparian and paralic habitats of complex food webs of detritivores, bacteria, and fungi, which were capable of yielding soluble growth factors that enhanced the productivity of contemporaneous marine phytoplankton. Thus, elevated riverborne nutrient fluxes may have promoted eutrophication of semi-restricted epicontinental seas and stimulated algal blooms (figure 12.9). Circumstantial evidence for high marine primary productivity during the Middle and Late Devonian is (1) the large proportion of marine algal matter in coeval black shales (e.g., Maynard 1981; Jaminski et al. 1998), and (2) the wide geographic but restricted stratigraphic distribution of enigmatic fossils such as *Protosalvinia*, which may have been the product of such algal blooms (Schopf and Schwietering 1970). Analogous links are known from modern coastal waters and restricted marine basins, in which natural or anthropogenic nutrient loading has led to eutrophication and algal blooms

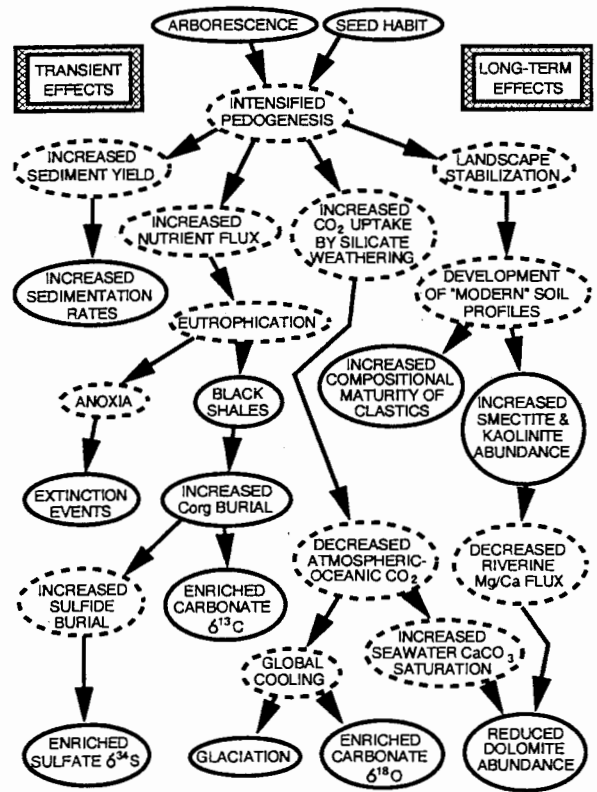## EFFECTS OF LAND PLANT EVOLUTION

Figure 12.9.
Flowchart model linking the development of arborescence and seeds among vascular land plants to Middle and Late Devonian marine biotic and global sedimentological, geochemical, and climatic events. Events are arrayed by relative duration with transient effects on the left and long-term effects on the right. *Solid outlines* indicate documented geologic records; *dashed outlines* indicate processes inferred to link records (see text for discussion).

(e.g., Fong et al. 1993; Lyons et al. 1993; Turner and Rabalais 1994). However, although the repeated temporal coincidence of marine extinction events and organic-rich horizons supports a link of both phenomena to episodic development of widespread bottomwater anoxia, it is uncertain whether oxygen deprivation itself or some related factor (e.g., climate cooling via enhanced organic carbon burial) was the principal agent of biotic destruction.

Support for this model may be provided by temporal relations between events in the terrestrial and marine realms during the Middle and Late Devonian (see figure 12.2). Potentially significant temporal coincidences include (1) a rapid increase in the size of vascular land plants

(see figures 12.1, 12.3) and the onset of marine anoxia in many areas during the Eifelian and Givetian, (2) diversification and spread of progymnosperms and an increase in the frequency and intensity of marine anoxic events in the late Givetian, (3) the mid to late Frasnian spread of *Archaeopteris* forests and the Frasnian–Famennian boundary event, and (4) the mid to late Famennian appearance of seed plants and the Devonian–Carboniferous boundary event. Of these temporal coincidences, only the last one is reasonably tightly constrained, i.e., the appearance of seed plants is known to predate the D/C boundary (Hangenberg) extinction event by about two conodont zones, probably representing no more than 1 m.y. (Sandberg, Ziegler, et al. 1988). This lag could be imputed to the temporally sigmoidal expansion characteristic of most biotic radiations (Sepkoski 1979), and, in this regard, it is important to bear in mind that the effects of plants on their physical environment depend less on first appearances than on actual increases in their abundance, biomass, and geographic distribution. In the case of seed plants, this expansion did not begin until just before and after the D/C boundary (Scheckler 1986a; Rothwell and Scheckler 1988; Beerbower et al. 1992).

Although the "Devonian plant hypothesis" is robust in accounting for most observed biotic and geochemical patterns associated with the Middle and Late Devonian, it is important to note that land plants were not evolving in a vacuum, and that the environmental effects associated with their evolution were mediated by coeval tectonic, eustatic, and atmospheric developments. Thus, any accurate representation of causation of these events must depend on a complex set of interactions among multiple factors (e.g., figure 12.9). In this regard, an important question is whether plant-induced changes in weathering processes represented merely a background factor predisposing epicontinental seas to low-oxygen conditions, in which case Middle and Late Devonian marine anoxic episodes must have been triggered by other factors (e.g., eustatic transgressions), or whether specific paleobotanical developments (e.g.,

rapid spread of a newly evolved taxon) could have precipitated episodes of marine anoxia and biotic extinction lasting no longer than 1 million years. The answer to this question has significant implications for rates and patterns of land plant evolution and terrestrial ecosystem development. A second question is whether changes in global climate and geochemical fluxes, related to the spread of land plants, produced stresses in marine ecosystems that increased their susceptibility to other agents of destruction. Specifically, if marine ecosystems were already under severe stress because of weathering-related changes in geochemical fluxes, then a relatively small bolide or drop in global seawater temperature might have been sufficient to cause widespread ecological disruption. Since the frequency of bolide impacts rises sharply with decreasing diameter (Shoemaker et al. 1990), temporal coincidence of Middle and Late Devonian marine anoxic events with bolide impacts might not have been statistically improbable under such conditions. Additionally, global temperature, including that of seawater, was declining at this time (Berner 1997, 1998) presumably as a result of atmospheric CO_2 depletion.

TESTING THE "DEVONIAN PLANT HYPOTHESIS"

Support for the "Devonian plant hypothesis" of Algeo et al. (1995) and Algeo and Scheckler (1998) rests primarily on two considerations: (1) temporal correlations between important developments in the terrestrial and marine realms during the Middle and Late Devonian, such as the appearance of arborescence and seeds and peak episodes of marine anoxia and biotic extinction (figure 12.2), and (2) a plausible mechanism to link these developments without appeal to temporal coincidences or multiple causalities (figure 12.9). Although coevality of events neither demonstrates causality nor reveals its directionality, a model that successfully links a wide range of coeval events to a single ultimate cause or conjunction of factors is

implicitly self-supporting. However, the critical test of any hypothesis is its ability to make testable predictions (cf. Alvarez et al. 1980), and, in this context, the "Devonian plant hypothesis" offers a variety of testable predictions that could be used to test its validity. Facets of the hypothesis that might serve as a focus for future research efforts include (1) relative timing of Middle and Late Devonian paleobotanical developments and marine anoxic and extinction events, (2) secular changes in the composition and structure of paleosols (e.g., depth of rooting and degree of textural and chemical horizonation), (3) secular changes in the bulk mineralogy, geochemistry, and texture of clastic sediments, (4) secular changes in the provenance and geochemistry of sedimentary organic matter, and (5) secular changes in the C-, S-, and O-isotopic composition of marine precipitates as a record of geochemical changes in the oceanic/atmospheric system. It should be noted that strong spatial heterogeneity in most of the relevant paleobotanical, sedimentological, and geochemical parameters is likely to make assessment of the "Devonian plant hypothesis" inherently more difficult than the search for physical and chemical evidence of bolides, and, hence, a far larger database will be needed to provide a fair test of the hypothesis. Furthermore, no single dataset is likely to resolve the issue, and acceptance or rejection of the hypothesis ultimately will depend on a better understanding of interrelations among diverse phenomena.

CONCLUSIONS

The evolutionary development and spread of vascular land plants during the Middle and Late Devonian may have been an important factor in coeval marine anoxic and extinction events. Although taxonomically diverse, pre-Middle Devonian terrestrial floras had little effect on their physical environment because of shallow root systems and narrow habitat ranges. According to the "Devonian plant hypothesis," the influence of land plants on pedogenic weathering processes and global geochemical cycles

increased substantially during the Middle and Late Devonian with the advent of arborescence (tree-sized stature), which increased depths of rooting and pedogenesis, and the seed habit, which freed plants from reproductive dependence on moist lowland habitats and allowed colonization of drier upland areas. These developments resulted in a transient increase in rates of pedogenesis and in large permanent increases in the thickness and areal extent of deeply weathered soil profiles. Accelerated pedogenesis led to increased sediment yields through episodic disturbance of developing soils and to increased riverine nutrient fluxes through enhanced rates of pedogenic chemical weathering and soil microbial nitrogen fixation. Elevated nutrient fluxes and bacterial or fungal breakdown of plant detritus during aqueous transport produced eutrophic conditions in semirestricted epicontinental seaways, stimulating algal blooms and causing development of widespread anoxia. Enhanced rates of silicate mineral weathering and organic carbon burial drew down atmospheric pCO_2, resulting in changes in marine carbonate equilibria, the C- and O-isotopic composition of the oceanic ΣCO_2 reservoir and marine carbonates, and global climate.

Temporal correlations provide circumstantial evidence in favor of terrestrial–marine teleconnections: (1) rapid increases in the maximum size of vascular land plants and onset of episodic marine anoxia during the Eifelian–Givetian, (2) advent of large, deeply rooted progymnosperms and increases in the frequency and intensity of marine anoxic events during the late Givetian, (3) a peak in the abundance of archaeopterid forests during the mid Frasnian to mid Famennian, which may or may not have been related to the Frasnian–Famennian boundary Kellwasser Event, and (4) the appearance and rapid diversification of seed plants during the late Famennian, probably less than 1 million years prior to the Devonian–Carboniferous boundary Hangenberg Event. Correlativity of Middle and Late Devonian black shales with extinction horizons implicates bottomwater anoxia or a related environmental parameter (e.g., increased turbidity

or seawater cooling) as the proximate cause of the biotic crisis among tropical-marine invertebrates. The Middle-to-Late Devonian spread of vascular land plants and consequent changes in pedogenic weathering processes and global geochemical fluxes may have been the ultimate cause for coeval marine anoxic and extinction events and for coeval changes in global climate.

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