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Terrestrial–marine teleconnections in the Devonian: links between the evolution of land plants, weathering processes, and marine anoxic events

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The Devonian Period was characterized by major changes in both the terrestrial biosphere, e.g. the evolution of trees and seed plants and the appearance of multi-storied forests, and in the marine biosphere, e.g. an extended biotic crisis that decimated tropical marine benthos, especially the stromatoporoid-tabulate coral reef community. Teleconnections between these terrestrial and marine events are poorly understood, but a key may lie in the role of soils as a geochemical interface between the lithosphere and atmosphere/hydrosphere, and the role of land plants in mediating weathering processes at this interface. The effectiveness of terrestrial floras in weathering was significantly enhanced as a consequence of increases in the size and geographic extent of vascular land plants during the Devonian. In this regard, the most important palaeobotanical innovations were (1) arborescence (tree stature), which increased maximum depths of root penetration and rhizoturbation, and (2) the seed habit, which freed land plants from reproductive dependence on moist lowland habitats and allowed colonization of drier upland and primary successional areas. These developments resulted in a transient intensification of pedogenesis (soil formation) and to large increases in the thickness and areal extent of soils. Enhanced chemical weathering may have led to increased riverine nutrient fluxes that promoted development of eutrophic conditions in epicontinental seaways, resulting in algal blooms, widespread bottomwater anoxia, and high sedimentary organic carbon fluxes. Long-term effects included drawdown of atmospheric pCO₂ and global cooling, leading to a brief Late Devonian glaciation, which set the stage for icehouse conditions during the Permo-Carboniferous. This model provides a framework for understanding links between early land plant evolution and coeval marine anoxic and biotic events, but further testing of Devonian terrestrial–marine teleconnections is needed.

Keywords: land plants, weathering, paleosols, global climate change, root systems, extinctions

1. INTRODUCTION

The Devonian Period was characterized by major changes in both the terrestrial and marine biospheres. Terrestrial ecosystems were marked by large increases in biomass and complexity, evolution of trees and seed plants, appearance of multi-storied forests, and formation of deeply weathered soils (Beerbower *et al.* 1992). Rapid drawdown of atmospheric pCO₂ resulted in global cooling and, toward the end of the Devonian, continental glaciation (Caputo 1985; Berner 1992, 1994). In the marine realm, the late Middle and Late Devonian were characterized by widespread development of bottomwater anoxia, enhanced organic carbon burial rates, and an extended biotic crisis that decimated tropical marine benthos, especially stromatoporoid-tabulate coral reef communities ('Frasnian/Famennian mass extinction'; McGhee 1996). Although the biotic crisis and related marine events have been attributed to a range of factors, e.g. bolide impacts,

tectonism and climate change, oceanic overturn, and eustatic fluctuations (McLaren 1982; Wilde & Berry 1984; Johnson *et al.* 1985; Copper 1986; Geldsetzer *et al.* 1987; Etensohn *et al.* 1988a; Wang 1992), few if any of these proposals have attempted to link Devonian marine phenomena to coeval developments in the terrestrial realm.

Algeo *et al.* (1995) presented the hypothesis that the Middle-to-Late Devonian biotic crisis, and related events in the marine realm, were precipitated by the evolutionary development of vascular land plants. Although terrestrial floras probably appeared by the Middle Ordovician, early land plants were small, non-rooted or shallowly rooted, and limited ecologically to moist lowland habitats. The potential of these floras to interact with their physical substrates and, hence, to influence weathering processes and geochemical fluxes on a global scale was greatly enhanced by evolutionary innovations that appeared during the Devonian, e.g. arborescence (tree stature) and

seed habit. Arborescence, especially among progymnperms, markedly increased depths of root penetration, rhizoturbation, and seeds permitted colonization of previously inaccessible dry upland and harsh primary seasonal habitats. These developments are likely to have caused a transient intensification of global rates of chemical weathering and soil formation, and to have led to long-term changes in subaerial weathering processes, patterns of landscape stabilization, and riverine sediment and nutrient fluxes. Algeo *et al.*'s (1995) thesis emphasizes the importance of soils as a chemical interface between the lithosphere and atmosphere, and the fundamental role of plants in mediating weathering processes at this interface. Although supported by broad temporal correlations between terrestrial and marine events of Devonian age and by a plausible mechanism linking such events, further study will be required to substantiate or refute key aspects of the hypothesis. The primary goals of the present paper are to (1) develop further the mechanism linking terrestrial and marine events of Devonian age and (2) identify testable aspects of the hypothesis for further study.

EVOLUTIONARY INNOVATIONS AMONG EARLY VASCULAR LAND PLANTS

Colonization of land surfaces by vegetation is likely to have been a protracted process (Selden & Edwards 1989). Land plants at a probable bryophytic grade of evolution appeared in the Early or Middle Ordovician but were small, non-vascular, and thalloid (i.e. lacking morphological differentiation into roots, stems, and leaves: Thomas & Spicer 1987; Beerbower *et al.* 1992; Strother *et al.* 1996). Non-vascular (tracheid-bearing) plants evolved and began to diversify during the Late Silurian and Early Devonian (Selden & Andrews 1984, 1987; Gray 1985, 1993; Boucot & Edwards & Berry 1991), but these forms were small, shallowly rooted, and confined to moist, shaded habitats, thus having little effect on their physical environment (figure 1a). Plant-substrate interactions are likely to have increased substantially with the appearance and spread of arborescent vegetation between the Pragian and Givetian (figure 1b), and with the development of seeds in the Late Devonian (figure 1c; Banks 1980; Thomas & Spicer 1987; Beerbower *et al.* 1992). With regard to potential weathering effects, first appearances and early radiations of primitive plants were less significant than the increases in floral mass and geographic range that accompanied the development of arborescence, advanced root systems, and seed habit.

Arborescence

The maximum size of vascular land plants increased markedly during the Devonian (figure 2; Chaloner & Beerbower 1979; Knoll *et al.* 1984; Edwards & Berry 1991; Beerbower *et al.* 1992). By the Late Givetian, woody plants and medium-sized trees had appeared in several independent clades, including cladoxylalean ferns (e.g. *Cladosporochnus*), lepidosigillarioid lycopsids (e.g. *Eospermatia*), aneurophyte progymnosperms (e.g. *Rellimia* and *Xylopteris*), and archaeopterid progymnosperms (e.g. *Archaeopteris*; Scheckler 1974, 1986a; Banks 1980; Gensel &

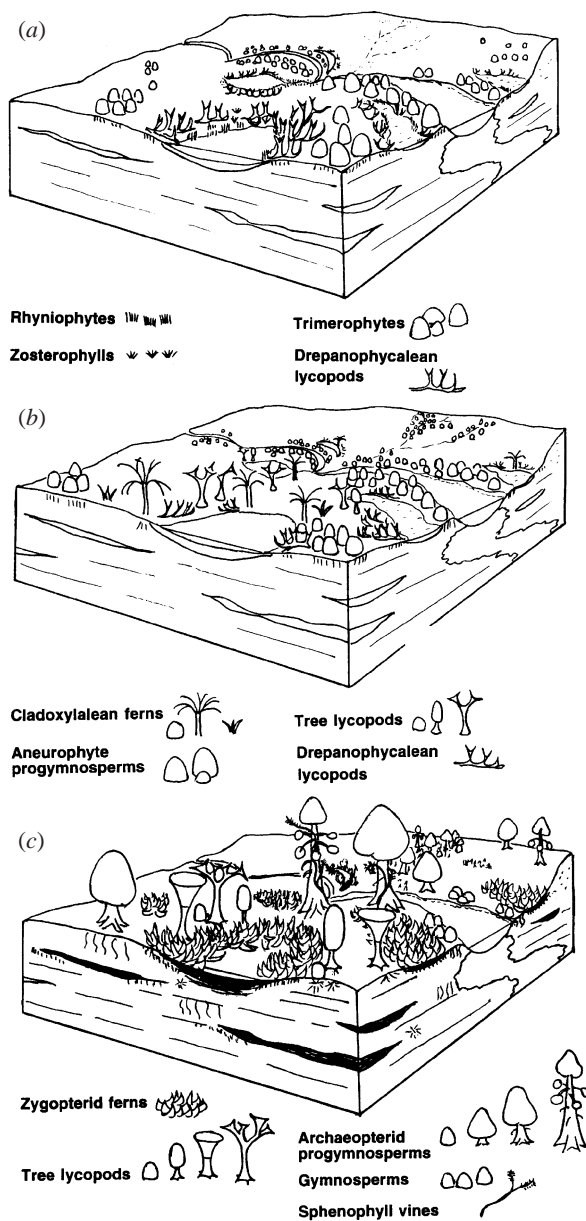


Figure 1. Palaeobotanical and palaeoecological reconstructions of (a) an Early Devonian (Siegenian/Pragian–Emsian) upland floodplain, (b) a Middle Devonian (Eifelian–Givetian) upland floodplain, and (c) a Late Devonian (Famennian) upland floodplain. Data from Scheckler & Basinger (1982), Scheckler (1986a,b,c, unpublished data), Gensel & Andrews (1984, 1987), and Hill *et al.* (1997).

Andrews 1984; Mosbrugger 1990). Among arborescent taxa, archaeopterids achieved the greatest size (trunk diameters greater than 1.5 m, maximum heights more than 30 m; Beck 1981), and became increasingly dominant during the Late Devonian, ranging from tropical to boreal palaeolatitudes (figure 2; Beck 1981; Cross 1983; Gensel & Andrews 1984; Scheckler 1986a,b; Thomas & Spicer 1987; Snigirevskaya 1988, 1995; Edwards & Berry 1991; Trivett 1993). 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; Scheckler & Basinger 1982; Fairon-Demaret 1986;

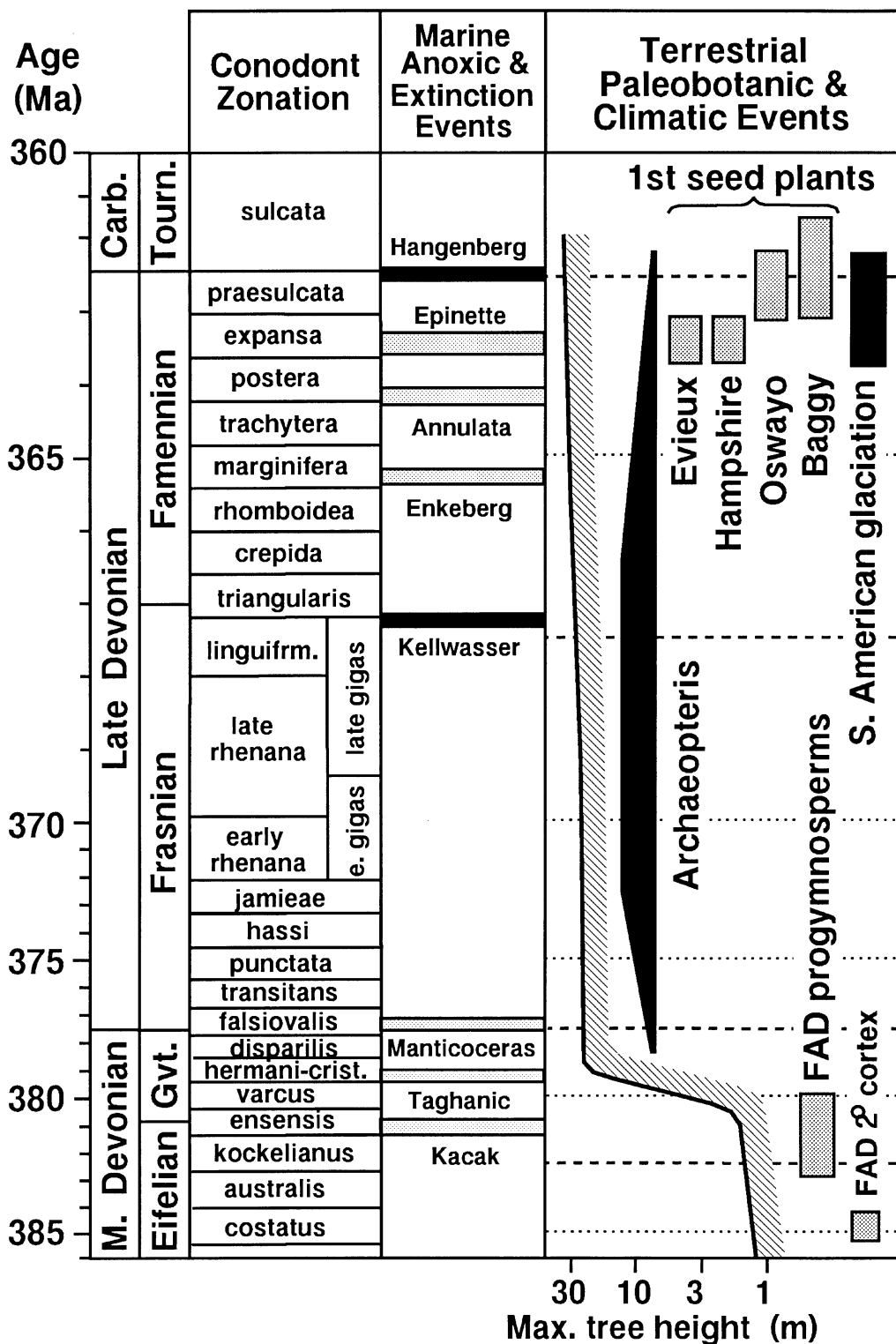


Figure 2. Middle-to-Late Devonian terrestrial and marine events. Sources: time-scale (Harland *et al.* 1990); conodont zonation (Ziegler & Sandberg 1984, 1990); marine anoxic/extinction horizons (Algeo *et al.* 1995, 1997); maximum tree heights (Chaloner & Sheerin 1979; Gensel & Andrews 1984; Mosbrugger 1990); range and epibole of *Archaeopteris* (Beck 1964; Scheckler 1986*a,c*; Beerbower *et al.* 1992); earliest seed plants (Fairon-Demaret 1986; Rothwell & Scheckler 1988); first appearance data (FAD) of 2° cortex (i.e. periderm) and progymnosperms (Scheckler & Banks 1974; Chaloner & Sheerin 1979; Banks 1981; Gensel & Andrews 1984; Thomas & Spicer 1987; Stewart & Rothwell 1993; Taylor & Taylor 1993); late Famennian continental glaciation (Caputo 1985; Caputo & Crowell 1985); age constraints from Streele (1986, 1992).

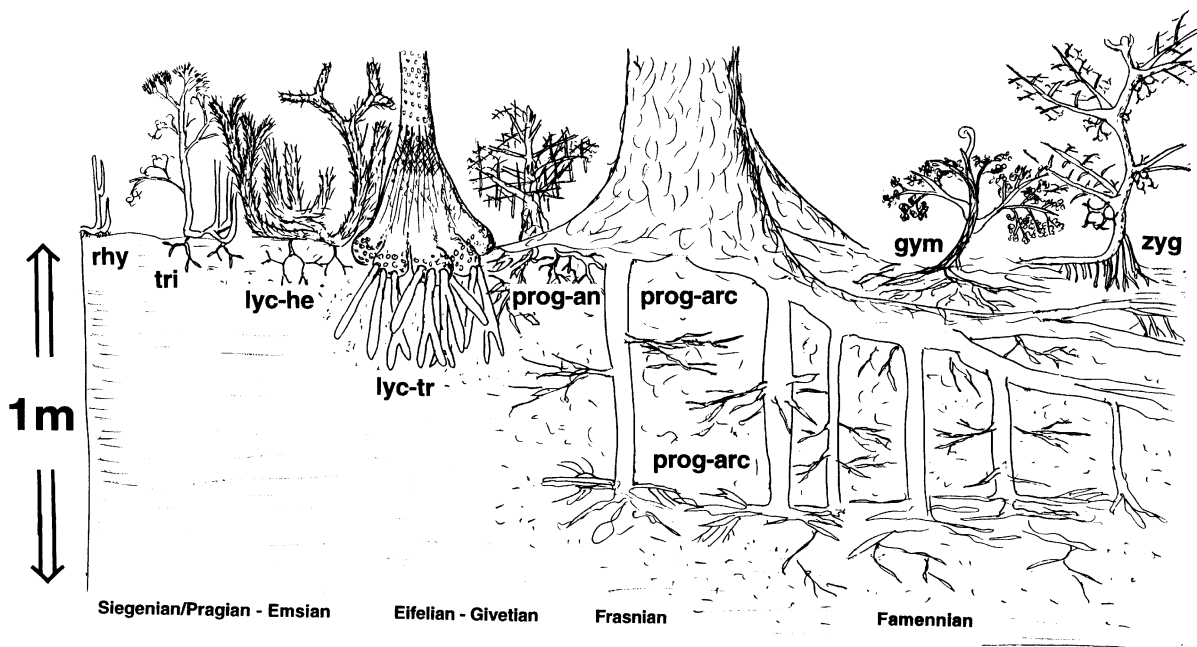


Figure 3. Diagram of the relative sizes, morphologies, and penetration depths of the root systems of selected Early, Middle, and Devonian plants. Abbreviations: rhy=rhyniophytes such as *Aglaophyton* or *Horneophyton*; tri=trimerophytes such as *Psilophyton*; lyc-he=early herbaceous lycopods such as *Asteroxylon* or *Drepanophycus*; lyc-tr=early tree lycopods such as *Lepidosigillaria* or *Cyclostigma*; prog-an=aneurophyte progymnosperms such as *Tetraxylopteris*; prog-arc=*Archaeopteris* progymnosperms; gym=early gymnosperms such as *Elkinsia* or *Moresnetia*; and zyg=zygopterid ferns such as *Rhacophyton*. Scale bar, 1 m.

Scheckler 1986*a,b,c*; Thomas & Spicer 1987). The success of archaeopterid progymnosperms may have been due to their ability to create and maintain favourable microenvironments. Mass-shedding of their leafy lateral branches (Beck 1964; Scheckler 1978) would have produced litter mats that affected soil moisture, pH, and humic content. In turn, such soil conditions may have selected in favour of the archaeopterids' free-sporing heterosporous reproduction to the potential detriment of other plants, such as aneurophyte progymnosperms, which were homosporous, did not shed branch parts, and may have been restricted to a more open canopy structure (Scheckler 1975; Taylor & Scheckler 1996; Hill *et al.* 1997).

Root systems

Arborescence was accompanied by development of more extensive root systems that left distinctive 'signatures' in contemporaneous palaeosols. Rooting by higher terrestrial plants began only in the late Pragian (mid-Early Devonian) with the appearance of short, forked roots/rhizomes of herbaceous lycopods (e.g. *Asteroxylon*, *Drepanophycus*) and trimerophytes (e.g. *Psilophyton*; figure 3). The first large root systems coincided with the advent of arborescent vegetation in the Middle and Late Devonian. Soil penetration depths were shallow (less than 20 cm) during the Eifelian-Givetian but increased to 80–100 cm as archaeopterids spread during the Frasnian-Famennian (figure 3; Beck 1953, 1967; Scheckler & Harms 1971; Snigirevskaya 1984*a,b*, 1988, 1995; Retallack 1985; LeJeune 1986; Scheckler 1986*a,b,c*, 1995, unpublished data; Beerbower *et al.* 1992). Some non-archaeopterid progymnosperms also developed extensive root systems, such as the tree lycopods *Cyclostigma* and *Lepidodendropsis/Protolobaria*, the cladoxylalean fern *Pseudosporochnus*, and the

zygopterid fern *Rhacophyton*, but these were generally shallower than those of contemporaneous progymnosperms owing to growth in water-saturated soils (Leclercq & Banks 1962; Schweitzer 1969; Scheckler 1974, 1986*a,c*; Jennings *et al.* 1983).

The increasing size of root systems was important with regard to changes in weathering rates and processes. In the pre-Devonian, pedoturbation (soil mixing) was effectuated largely or entirely through burrowing by invertebrates (Retallack 1985; Feakes & Retallack 1988; Driese & Foreman 1991), which were generally of limited abundance owing to low rates of net primary productivity in algal-lichen (under $100 \text{ gm}^{-2} \text{ yr}^{-1}$) and bryophyte communities (below $1000 \text{ gm}^{-2} \text{ yr}^{-1}$) compared to modern forest and grassland ecosystems ($600\text{--}6000 \text{ gm}^{-2} \text{ yr}^{-1}$; Longton 1988; Comeau & Kimmins 1989; Retallack 1992*a*; Viles & Pentecost 1994). Root growth accounts for 40–85% of net primary productivity in modern ecosystems dominated by vascular plants, and an even higher proportion is put into rootlets in harsh environments (Keyes & Grier 1981). This suggests that as early land plants began to colonize marginal new habitats, an important physiological adaptation may have been larger root systems. Among Middle-to-Late Devonian arborescent taxa, progymnosperms exhibited the greatest rhizoturbational effectiveness due to innovations in root structure: (1) the presence 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 re-penetrate a given volume of soil (figure 4; Scheckler 1995, 1997). Later gymnosperms possessed much the same type of root system as progymnosperms and were probably equally effective

with regard to rhizoturbation. The effect of these innovations in root structure was to permit colonization and exploitation of previously underused or vacant habitats, increasing both the depth and geographic distribution of thick, mature soil profiles.

(c) *Seed habit*

New reproductive modes that evolved during the Devonian led to adaptation of land plants to existence in harsher upland and primary successional habitats. Early land plants had a pteridophytic reproductive mode (i.e. free-living gametophytes grew from dispersed spores and produced sperm that swam over moist plant or soil surfaces to egg-bearing archegonia of the same or other gametophytes), constraining them to moist lowland habitats (figure 1a; Kenrick 1994; Remy *et al.* 1993; Remy & Hass 1996). Following the development of heterospory (i.e. two different sizes of spores with reduced internal gametophytes) in several clades, including archaeopterid progymnosperms (figure 1b), further differential growth led to the appearance of seeds, in which a single spore matures into a megagametophyte within a nutrient-bearing and protective ovule, the shape and orientation of which aid capture and transfer of microgametophytes (i.e. pollen; Chaloner & Sheerin 1979; Rothwell & Scheckler 1988; DiMichele *et al.* 1989; Bateman & DiMichele 1994). The development of seeds freed land plants from dependence on aqueous sperm dispersal, permitting occupation of previously closed habitats such as drier upland areas, and resulted in greater adaptability to diverse ecological conditions, allowing colonization of harsh primary successional stages in floodplain and delta environments (figure 1c; Scheckler 1986c; Thomas & Spicer 1987; Rothwell & Scheckler 1988; Edwards & Berry 1991). As stress-resistant propagules, seeds also reduced the risk of gametophyte desiccation, improved the rate of successful sexual unions by pollination, and allowed rapid early growth of seedlings under unfavourable conditions, e.g. in bare primary successional as well as in shaded forest understory environments.

The seed habit was an important factor in the rapid spread and diversification of gymnosperms during the Late Devonian and Early Carboniferous (figure 2; e.g. Scheckler 1986c; Thomas & Spicer 1987; Rothwell & Scheckler 1988; Beerbower *et al.* 1992). The earliest known seeds are Mid-to-Late Famennian in age, e.g. *Moresnetia zalesskyi*, *Dorinnotheca streelii*, and *Elkinsia polymorpha* (lower VCo spore zone; Fa2c), followed by *Archaeosperma arnoldii*, *Aglosperma quadripartita*, *Spermolithus devonicus*, *Kerryia mattenii*, and *Xenotheca devonica* (LV-LN spore zones; Fa2d-basal Tn1b; Chaloner *et al.* 1977; Gillespie *et al.* 1981; Fairon-Demaret 1986, 1996; Fairon-Demaret & Scheckler 1987; Rothwell & Scheckler 1988; Rothwell *et al.* 1989; Rothwell & Wight 1989; Streel & Scheckler 1990; Hilton & Edwards 1996; see Richardson & McGregor (1986) and Richardson & Ahmed (1988) for spore zonation). Seed plants diversified during the Early Mississippian, filling ecological niches in floodplain and upland forest environments previously occupied by the progymnosperm *Archaeopteris* (Rothwell & Scheckler 1988; Beerbower *et al.* 1992). Because gymnosperms had the same types of advanced root systems as the older progymnosperms

(figure 4d; Scheckler 1995, 1997), changes in pedogenic processes that had been initiated in the Middle Devonian continued into the Carboniferous with even greater ecological amplitude.

3. EFFECTS ON SOILS, WEATHERING PROCESSES, THE HYDROLOGIC CYCLE, AND GLOBAL CLIMATE

The evolutionary development of vascular land plants during the Devonian is likely to have resulted in intensified pedogenesis, and to have precipitated major changes in weathering processes, the hydrologic cycle and sediment yields, and global climate.

(a) *Soils*

Pre-Devonian land surfaces may have consisted largely of barren rock and thin microbial proto-soils (Retallack 1985, 1986, 1990, 1992a,b; Feakes & Retallack 1988), similar to modern 'desert crusts' formed by cyanobacterial mats (Campbell 1979; Whitford & Freckman 1988; Watson 1992). Primitive land plants of the Silurian–Early Devonian had shallow or non-existent root systems that contributed little to soil formation or stabilization (figure 2; Banks 1985). With the advent of trees and seed plants in the Middle and Late Devonian, a transient acceleration of pedogenesis may have occurred, yielding rapid increases in the depth and geographic extent of deeply weathered soils. Pedogenesis may have accelerated due to (1) accumulation of humus in soils, increasing the rate of recycling of organic detritus by soil fungi and bacteria and permitting greater standing floral biomass, and (2) positive feedback between floral biomass and soil formation rates (Thomas & Spicer 1987; Klepper 1987; Retallack 1990). Positive plant–soil feedbacks of this type may account for the approximately synchronous development of arborescence among a number of plant clades in the late Middle Devonian (Mosbrugger 1990).

The role of vegetation in soil formation has been assessed through comparison of subtropical alluvial fan palaeosols of Ordovician to Carboniferous age (Retallack 1985). Younger palaeosols exhibit increases in clay content, soil structuring (i.e. ped formation), and profile maturity (i.e. horizonation) that correlate with increases in the depth of root penetration (i.e. 0 cm in the Late Ordovician, 25 cm in the Late Silurian, and 100 cm in the Late Devonian). Also, a number of soil types associated predominantly with temperate-zone forests, e.g. alfisols, ultisols, spodosols, and vertisols, either first appeared or increased markedly in abundance during the Late Devonian and Early Carboniferous, attesting to widespread afforestation of land surfaces at that time (Retallack 1986, 1990, 1992b; Wilding & Tessier 1988; Mack & James 1992). Horizonation patterns typical of these soils, e.g. translocation of clays and iron to form a pale, leached 'A' horizon and a purple, illuviated 'B' horizon, first developed in wet lowland soils in the Early Frasnian and in dry upland soils in the Early Carboniferous (Retallack 1985), which is consistent with the ecological ranges of arborescent progymnosperms and gymnosperms, respectively. Overall, deeply rooted palaeosols increased in frequency during the Devonian (e.g. Allen 1986; Driese & Mora 1993) and again during the Carboniferous (e.g. Wright 1987; Ettensohn *et al.* 1988b; Wright & Robinson 1988;

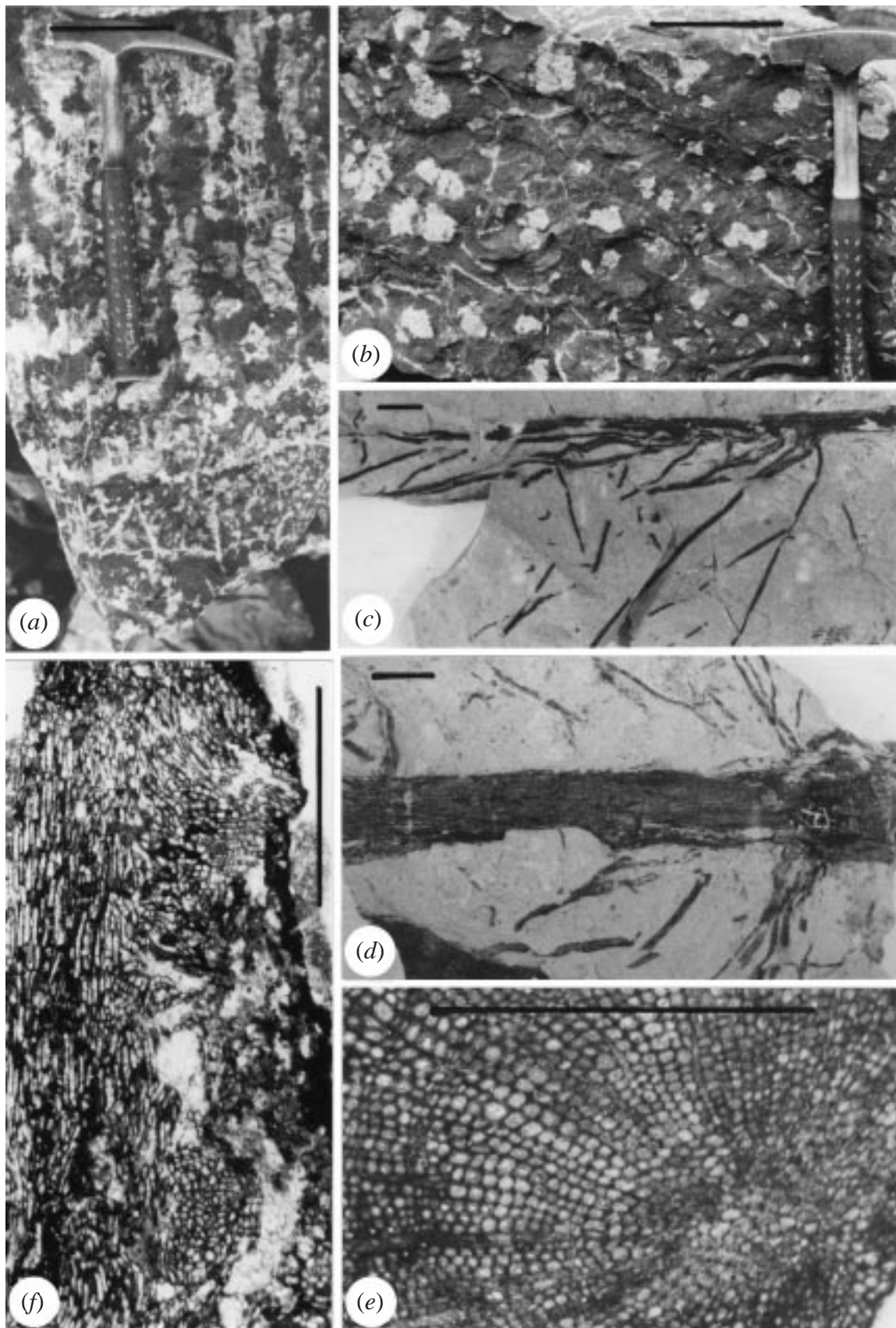


Figure 4. Late Devonian root systems. (a) Vertical profile of a palaeosol horizon, the upper part of which contains large rhizocretions typical of those formed around major roots of *Archaeopteris* in semi-arid environments, and the lower part of which contains small root traces typical of the multi-branched root systems of either young progymnosperms (e.g. *Archaeopteris*) or early gymnosperms (e.g. *Moresnetia* or *Dorrinotheca*). (b) Horizontal view of the same palaeosol block showing in cross-section the large vertical rhizocretions and the smaller branching root traces attached to them. Large (2–5 cm diameter) prismatic peds are visible. Both the calcareous rhizocretions and the peds are indicative of a deeply weathered soil subject to periods of wetness and dryness. Palaeosols in (a) and (b) are from the Mid-Famennian Evieux Formation of the Dinant Synclinorium of

Vanstone 1991; Driese *et al.* 1994; Retallack & Germán-Heins 1994; Gill & Yemane 1996).

(b) *Weathering processes*

The spread of forests and associated deeply rooted soils is likely to have effectuated major changes in weathering processes. Chemical weathering in the soil environment occurs mainly within microenvironments created by higher plants, and is due to organic acids released through root mycorrhizae, humic and fulvic acids produced through bacterial decay of complex organic compounds, and carbonic acid generated through oxidation of decaying organic matter in soils (Knoll & James 1987; Johnsson 1993; Drever 1994). Higher land plants are thought to weather substrates more intensively than non-vascular plants: studies of weathering on fresh volcanic rocks and of soil- and river-water chemistry (Cawley *et al.* 1969; Drever & Zobrist 1992; Cochran & Berner 1993, 1997) suggest a weathering efficiency ratio of about 7:1 (Berner 1994). The greater weathering efficiency of vascular plants is due to (1) greater acid production as a function of higher net primary productivity (Longton 1988; Comeau & Kimmins 1989; Retallack 1992a); and (2) a greater (three-dimensional volumetric) contact area of rootlets and root hairs with soils relative to the (two-dimensional surficial) contact area of algae and lichens (Russell 1977; Fogel 1985). 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 & Volk 1989; Keller & Wood 1993; Horodyski & Knauth 1994).

The spread of higher plants is likely to have changed the residence time of material in the soil environment and the texture and mineralogy of pedogenic weathering products (Drever 1994). In the absence of interwoven root mats, weathering products are rapidly swept from hill slopes, accumulating as immature sediments in alluvial fans and braided streams. Development of a densely rooted vascular plant cover stabilized land surfaces, allowing more time for weathering of surface materials to a finer-grained, compositionally more mature product (Schumm 1968, 1977; Stallard 1985; Johnsson 1993; Drever 1994). This process may account for secular changes in the compositional maturity of fluvial clastics (Cotter 1978) and in the clay mineralogy of shales (Weaver 1967, 1989). Smectite and kaolinite are produced in large amounts under conditions of moderate-to-strong soil leaching in temperate and tropical climates, respectively (Velde 1985; Singer & Munns 1991), and the

abruptness of the mid-Palaeozoic transition from illite-chlorite to smectite-kaolinite-dominated clay-mineral assemblages implicates changes in primary weathering processes rather than progressive diagenetic transformation (Algeo *et al.* 1997). Other products of intense pedogenic weathering also first become abundant during the Late Devonian and Carboniferous, e.g. bauxites and laterites (Nicholas & Bildgen 1979; Retallack 1986, 1990, 1992b). Furthermore, secular changes in sediment chemistry may have resulted from selective weathering by plants of minerals containing essential nutrients (Newman & Andrews 1973). Pre-Silurian clastic sediments are richer in chemically labile K-feldspars and have higher K_2O/Na_2O ratios than equivalent younger facies, suggesting more complete pedogenic decomposition of K-bearing minerals from the mid-Palaeozoic onwards (Basu 1981; Maynard *et al.* 1982; Holland 1984; Nesbitt *et al.* 1996).

(c) *The hydrologic cycle and sediment yield*

The spread of terrestrial vegetation is likely to have altered the hydrologic cycle substantially. The effect of forests is to promote evapotranspirative recirculation of atmospheric water, increasing precipitation through changes in land surface albedo and atmospheric turbulence (Shukla & Mintz 1982; Sud *et al.* 1993). Vegetation also has a large effect on surface water runoff. At a given level of precipitation, a dense vegetative cover reduces runoff, total discharge, and peak discharge during floods (Schumm 1968, 1977). Although evapotranspirative recirculation of water (and, therefore, precipitation) is greater in a vegetated world, surface runoff is generally reduced owing to the increase in storage capacity of soils associated with dense vegetative covers.

The spread of terrestrial vegetation is also likely to have reduced sediment yields, owing to a combination of lower runoff and landscape stabilization. Higher plant covers serve as windbreaks and sediment binders, physically stabilizing land surfaces (Moore 1984). Sediment yields in the modern world peak in semi-arid environments at an annual precipitation of *ca.* 250–350 mm yr⁻¹, but in the absence of a higher plant cover, sediment yields may have increased monotonically with increases in precipitation (Schumm 1968, 1977; Summerfield 1991). Reduced sediment yields and landscape stabilization may be evidenced by secular changes in fluvial morphology during the Silurian, e.g. a shift from dominantly braided streams to mixed braided-meandering streams (Cotter 1978; Beerbower *et al.* 1992). Floodplain stabilization in the Silurian might appear to be inconsistent with evidence of elevated

Belgium; scale bars, 10 cm. (c) Compressed young root system (*Callixylon petryi*) of the progymnosperm tree *Archaeopteris*, showing numerous lateral rootlets (UAPC S4630). Petrified parts of this specimen (f) demonstrate that the lateral rootlets were endogenous. (d) Compressed older root system of *Archaeopteris* showing clusters of adventitious lateral rootlets (specimen UAPC S4631b). Specimens in (c) and (d) are from the lower Frasnian Yahatinda Formation of Alberta, Canada; scale bars, 1 cm. (e) Cross-section of a petrified octarch main root (*Callixylon petryi*, specimen UAPC S2585-10A) of *Archaeopteris* showing the secondary xylem (with portions of four growth layers) produced by its perennial bifacial vascular cambium. (f) Longitudinal section (LS) of a petrified portion of the young root of *Archaeopteris* seen in (c) (specimen UAPC S4630-2aL). Visible at the top, where the main root is cut in near-radial LS, is a near-median longitudinal view of an endogenous lateral rootlet (note the cell arrangement at its point of attachment to the tetrarch main root) and at bottom, where the main root is cut in near-tangential LS, is a cross-sectional view of a diarch endogenous lateral rootlet. Specimens in (e) and (f) are from the lower Frasnian Yahatinda Formation of Alberta, Canada; scale bars, 1 mm. UAPC=University of Alberta Paleobotany Collection.

culate fluxes during the Middle-to-Late Devonian (e.g. *et al.* 1995). However, sediment yields are largely a function of local relief, and global clastic fluxes mainly of weathering rates in upland areas (Stallard 1985; Merfield 1991), which probably intensified with the spread of gymnosperms during the Late Devonian.

Atmospheric $p\text{CO}_2$ and global climate change

Reduced rates of pedogenic weathering of silicate minerals and of organic carbon burial in marine shales (see below) resulted in major perturbations to the global carbon cycle during the Devonian, including a rapid drawdown of atmospheric CO_2 levels. Estimates of atmospheric $p\text{CO}_2$ based on carbon cycle modelling suggest a decrease from pre-Devonian concentrations of 4–20 PAL (present atmospheric level, generally taken as a pre-industrial value of 270 ppmv) to mid-Carboniferous concentrations of about 1 PAL (figure 5a; Berner 1994). Precision in pre-Devonian estimates is mainly due to uncertainty regarding the relative weathering efficiencies of vascular and non-vascular plants (see above; Berner 1994). Palaeoatmospheric CO_2 levels may be independently determined through C-isotopic analysis of soil lithols in vertisols and carbonate impurities in iron-bearing Fe oxyhydroxides (Mora *et al.* 1991, 1996; Yapp & Berner 1992, 1996), and these studies have yielded $p\text{CO}_2$ estimates that are in good agreement with Berner's carbon cycle model, i.e. 13–18 PAL for the Late Ordovician–Late Silurian, 3–5 PAL for the Late Devonian, and 1.0 PAL for the Early Permian (figure 5a).

The drawdown of atmospheric $p\text{CO}_2$ during the Devonian had far-reaching climatic consequences, contributing to global cooling and a short Late Famennian glacial episode (figure 2) and setting the stage for icehouse conditions during the Permo-Carboniferous Gondwanan Ice Age.

Climatic cooling is evidenced by a large increase in marine carbonate $\delta^{18}\text{O}$ values, i.e. from less than or equal to 5‰ to ca. -1‰ PDB (figure 5d), that occurred during a geologically short interval of some 7–15 Ma around the Devonian–Carboniferous boundary (Popp *et al.* 1986; Berner 1988; Lohmann 1988; Brand 1989). About 0.5‰ of shift in marine carbonate $\delta^{18}\text{O}$ values may be attributed to growth of continental ice sheets (Crowley & Baum 1992), but the remaining 3.5‰ is likely to reflect cooling of oceanic surface waters by ca. 14 °C, i.e. from ca. 40 °C in the Devonian to near-modern temperatures of ca. 25–30 °C in the Carboniferous (Craig 1965; Veizer *et al.* 1986). The temperature control of Devonian–Carboniferous marine carbonate $\delta^{18}\text{O}$ values is strongly favoured owing to the tight coupling it provides between changes in organic carbon burial, atmospheric CO_2 levels, and coeval continental glaciation (Algeo *et al.* 1997). Late Famennian glaciation is evidenced by diamictites in Brazil containing striated and rounded pebbles, rhythmites containing dropstones, and glacial boulders, and striated pavements in Brazil and elsewhere, probably by correlative deposits in North Africa and Antarctica (Caputo 1985; Caputo & Crowell 1985). This event has been dated to the Strunian (equivalent to the Middle and Upper *praesulcata* conodont zones, or the Late Famennian) on the basis of miospores (Streel 1986, 1992), linking it roughly correlative with the spread of the first seed plants as well as with the Hangenberg and Frasnian anoxic event (see below).

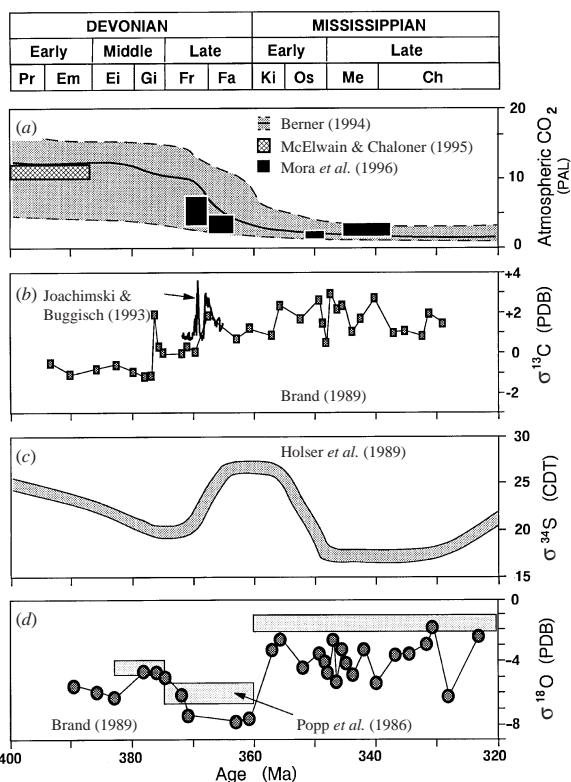


Figure 5. Devonian–Mississippian geochemical records: (a) atmospheric $p\text{CO}_2$ relative to present atmospheric level (PAL), based on global carbon cycle modelling (Berner 1994) and C-isotopic studies of soil carbonates (Mora *et al.* 1991, 1996), and stomatal indices of fossil plants (McElwain & Chaloner 1995); (b) marine carbonate $\delta^{13}\text{C}$ (Brand 1989; Joachimski & Buggisch 1993); (c) marine sulphate $\delta^{34}\text{S}$ (Holser *et al.* 1989, 1996); (d) marine carbonate $\delta^{18}\text{O}$ (Popp *et al.* 1986; Brand 1989).

Drawdown of atmospheric $p\text{CO}_2$ and attendant global cooling ultimately were limited by strong negative feedbacks on silicate weathering rates. The feedback mechanisms involved (1) reduced availability of atmospheric CO_2 for transfer to soils and (2) lower rates of CO_2 utilization in weathering reactions at cooler temperatures (figure 6a,b; Berner & Rye 1992; Caldeira 1992; Berner 1994). Nonetheless, geologically rapid changes in atmospheric $p\text{CO}_2$ are possible owing to much larger time constants for CO_2 sources (i.e. volcanic and metamorphic degassing) than for sinks (i.e. silicate weathering and organic carbon fixation). Because a short-term increase in the rate of CO_2 uptake by land plants cannot be balanced by source fluxes, it must be counteracted by a decrease in atmospheric $p\text{CO}_2$ and/or global temperature. Such changes will yield a new equilibrium state in which globally integrated weathering rates are comparable to those prior to the disturbance, but in which atmospheric $p\text{CO}_2$ and/or global temperature are maintained dynamically at reduced levels through active ‘ CO_2 pumping’ by plants (i.e. transfer of CO_2 from the atmosphere to soils in the form of dead plant matter and exudates; figure 6c). Owing to stronger dependence of silicate weathering rates on temperature than on soil $p\text{CO}_2$ (Velbel 1993; Gwiazda & Broecker 1994), global cooling probably served as the

primary feedback mechanism on Devonian weathering rates. These considerations dictate that the intensification of weathering rates associated with the rapid spread of higher land plants in the Middle-to-Late Devonian was a transient phenomenon.

4. TERRESTRIAL–MARINE TELECONNECTIONS

Although the Devonian Period is characterized by far-reaching changes in both terrestrial and marine environments, connections between these realms are not well understood. The key to understanding terrestrial–marine teleconnections during the Devonian may lie in the role of soils as a geochemical interface between the lithosphere and the atmosphere/hydrosphere, and in the role of land plants as a mediator of weathering intensity at that interface (Algeo *et al.* 1995). A critical link may have been the flux of solutes (especially biolimiting nutrients) from soils, which would have increased as a consequence of enhanced pedogenesis, e.g. through mineral leaching and fixation of nitrogen by symbiotic root microbes. Elevated riverine nutrient fluxes would have promoted eutrophication of semi-restricted epicontinental seas, stimulating algal blooms and causing bottomwater oxygen depletion, as in many modern coastal and restricted marine environments (Kuparinen & Heinänen 1993; Lyons *et al.* 1993; Turner & Rabalais 1994). Another factor contributing to enhanced marine productivity may have been a large flux of terrestrial plant litter containing labile carbon compounds, promoting development in riparian and paralic habitats of complex food webs of detritivores, bacteria, and fungi; these, in turn, would have yielded soluble growth factors capable of enhancing marine primary productivity (Tappan 1980, 1982; Scheckler 1986*a*).

This model invokes a combination of enhanced preservation of organic matter and enhanced primary productivity to account for widespread deposition of organically rich marine black shales during the Middle-to-Late Devonian (figure 2). Preservation of organic matter was enhanced by episodic development of bottomwater anoxia over wide areas (e.g. Canfield 1994), leading to elevated rates of organic carbon burial. A record of secular changes in organic carbon burial is provided by marine carbonate C-isotopes, i.e. higher $\delta^{13}\text{C}$ values reflect elevated $^{13}\text{C}:^{12}\text{C}$ ratios in the ocean surface ΣCO_2 reservoir as a consequence of enhanced fixation and burial of ^{13}C -depleted organic matter (Kump 1991; Joachimski & Buggisch 1993). Devonian marine carbonates exhibit little C-isotopic variation during the Lochkovian–Eifelian (less than $\pm 1\%$; e.g. Hladikova *et al.* 1994), but show an increase of *ca.* 4% between the Givetian (0.5% PDB) and the Late Carboniferous (*ca.* 4.5% PDB; figure 5*b*; Popp *et al.* 1986; Lohmann 1988; Brand 1989; Holser *et al.* 1996). Well-studied sections of this age contain a series of large-amplitude (2–3%) positive $\delta^{13}\text{C}$ excursions (e.g. figure 5*b*), suggesting that the 4% net Devonian–Carboniferous increase may have occurred in a stepwise manner, probably in association with individual episodes of black shale deposition (figure 2; Buggisch 1991; Halas *et al.* 1992; Joachimski & Buggisch 1993; Wang *et al.* 1996). High organic C fluxes are generally associated with the production and burial of reduced S as Fe-sulphides (Berner 1978; Berner & Raiswell 1983), and the

Late Devonian is characterized by high burial rates of ^{34}S -depleted sulphide S as shown by (1) strong C–S covariance in marine sediments (Leventhal 1987; Berner & Canfield 1989), and (2) an 8–10% positive excursion in the marine evaporite S-isotopic record between the Givetian and Mid-Mississippian (figure 5*c*; Holser *et al.* 1989, 1996). On the other hand, evidence for increases in marine primary productivity during the Middle-to-Late Devonian is tentative, e.g. (1) high proportions of marine algal matter in black shales of this age (Maynard 1981; Robl *et al.* 1990), and (2) the wide geographic but restricted stratigraphic distribution of enigmatic fossils such as *Protosalvinia*, which may record opportunistic algal blooms in response to surface water eutrophication (Schopf & Schwietering 1970). Regardless of whether preservation or productivity factors controlled organic matter accumulation, black shale horizons of this age were generally correlative with extinction events (figure 6), implying that bottomwater anoxia or a correlative factor (e.g. seawater cooling or trophic chain disruption) was responsible for severe environmental stresses within tropical marine ecosystems (Algeo *et al.* 1995; McGhee 1996). The Middle-to-Late Devonian biotic crisis comprised some 810 separate extinction rate peaks over a *ca.* 20 Ma or so long interval (figure 2; e.g. House 1985; Walliser 1996), including the Frasnian–Famennian extinction event, which decimated the tropical stromatoporoid-tabulate coral reef community and eliminated *ca.* 20–25% of families and 70–82% of extant species (Bambach 1985; Sepkoski 1986, 1996; Raup & Boyajian 1988).

5. TESTING THE HYPOTHESIS

The hypothesis that the spread of vascular land plants during the Devonian resulted in major changes in terrestrial weathering processes and precipitated marine anoxic and extinction events may be investigated through studies of (1) terrestrial palaeoecology, (2) palaeopedology, (3) terrestrial–marine correlations, (4) black shale geochemistry, and (5) marine isotopic records. The nature and timing of compositional changes in terrestrial floras are poorly documented, and quantitative data on terrestrial ecosystem changes are needed (e.g. Scheckler 1986*c*). The timing of major palaeopedological changes (e.g. depth of rooting and degree of textural and chemical horizonation) is also in need of better documentation (e.g. Retallack 1985). Temporal relations between terrestrial and marine events require examination at a higher level of stratigraphic resolution than is possible using epoch-interval data sets (e.g. this paper). Terrestrial successions are limiting in this regard, and improved correlations with better-dated marine successions should be emphasized (e.g. Streeck & Scheckler 1990). At the existing level of resolution, potentially significant correlations may exist, e.g. between the appearance of seeds, widespread marine anoxia, and continental glaciation during the Late Famennian (Algeo *et al.* 1995). Geochemical studies of black shales would assist in analysis of productivity versus preservation controls on organic matter accumulation and in constraining organic carbon accumulation rates (e.g. Jaminski *et al.* 1997). Finally, high-resolution isotopic studies are needed to refine the magnitude and timing of geochemical changes in the atmospheric–oceanic system (e.g. Dunn 1988).

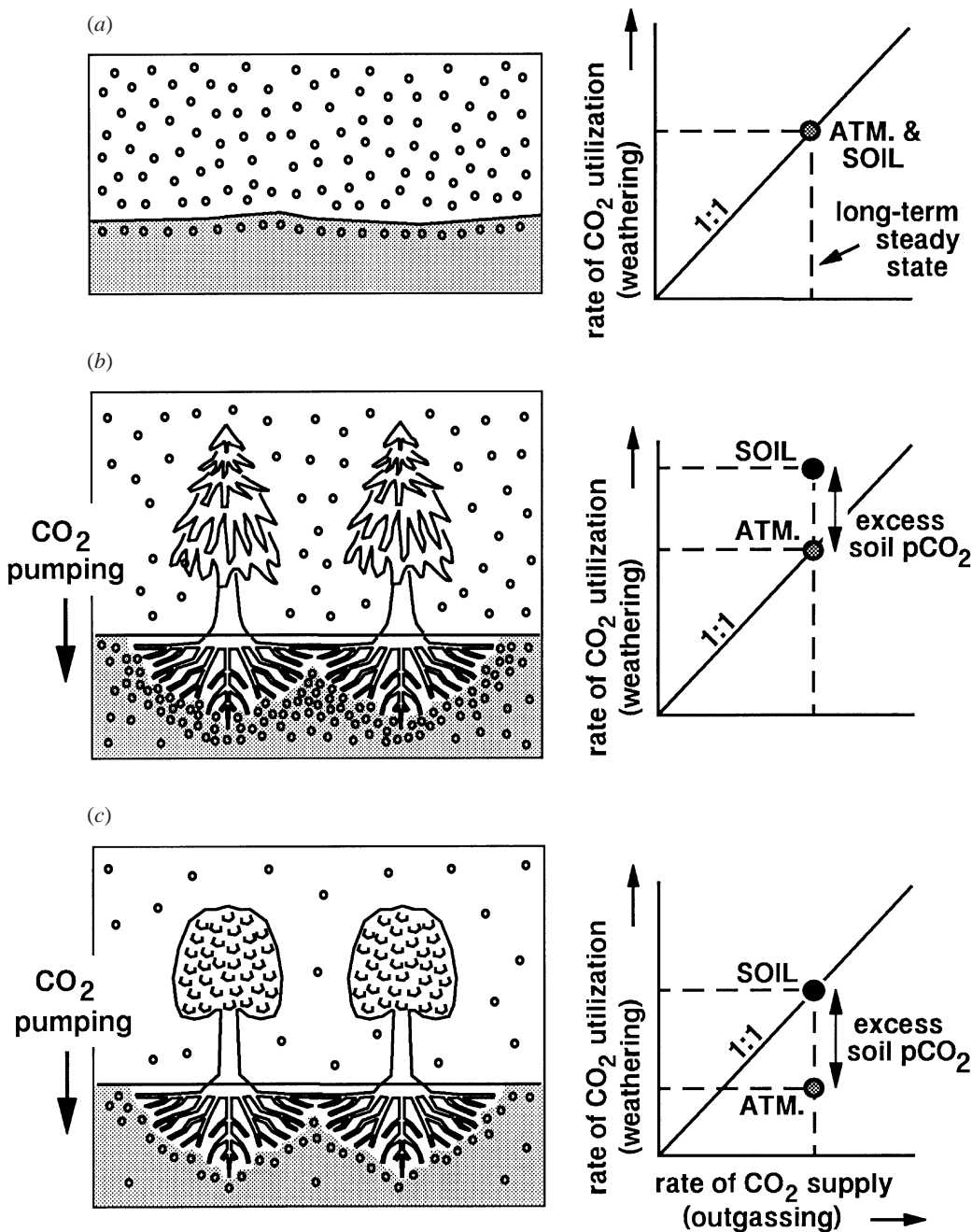


Figure 6. Changes in atmospheric and soil pCO₂ as a function of the spread of vascular land plants during the Devonian. (a) In the unvegetated pre-Devonian world, atmosphere and soil CO₂ levels were similar; (b) during the Devonian (and accelerating in the Late Devonian), atmospheric pCO₂ was drawn down through active 'CO₂ pumping' by land plants, leading to elevated soil CO₂ levels; (c) in the post-Devonian, terrestrial floras dynamically maintain low atmospheric pCO₂ via the CO₂ pumping mechanism; soil CO₂ levels are approximately equal to those prior to the spread of land plants owing to quasi-steady-state CO₂ input from volcanic and metamorphic sources and the requirement for long-term flux balance. As a consequence, silicate weathering rates were comparable in the pre- and post-Devonian, but experienced a transient maximum during the Devonian.

Stable isotope records have an inherent advantage over palaeobotanical, palaeopedological, and sedimentological records, in which strong spatial heterogeneity makes recognition of global changes difficult. Should causal relationships between Middle-to-Late Devonian terrestrial and marine phenomena be established, marine geochemical records will determine the level of resolution at which coeval terrestrial events ultimately may be dated.

6. CONCLUSIONS

The evolution of trees and seed plants, the appearance of multi-storied forests in the terrestrial biosphere, and the development of an extended biotic crisis that decimated the stromatoporoid-tabulate coral reef community in the marine biosphere may have been causally linked. The key to understanding Devonian terrestrial-marine

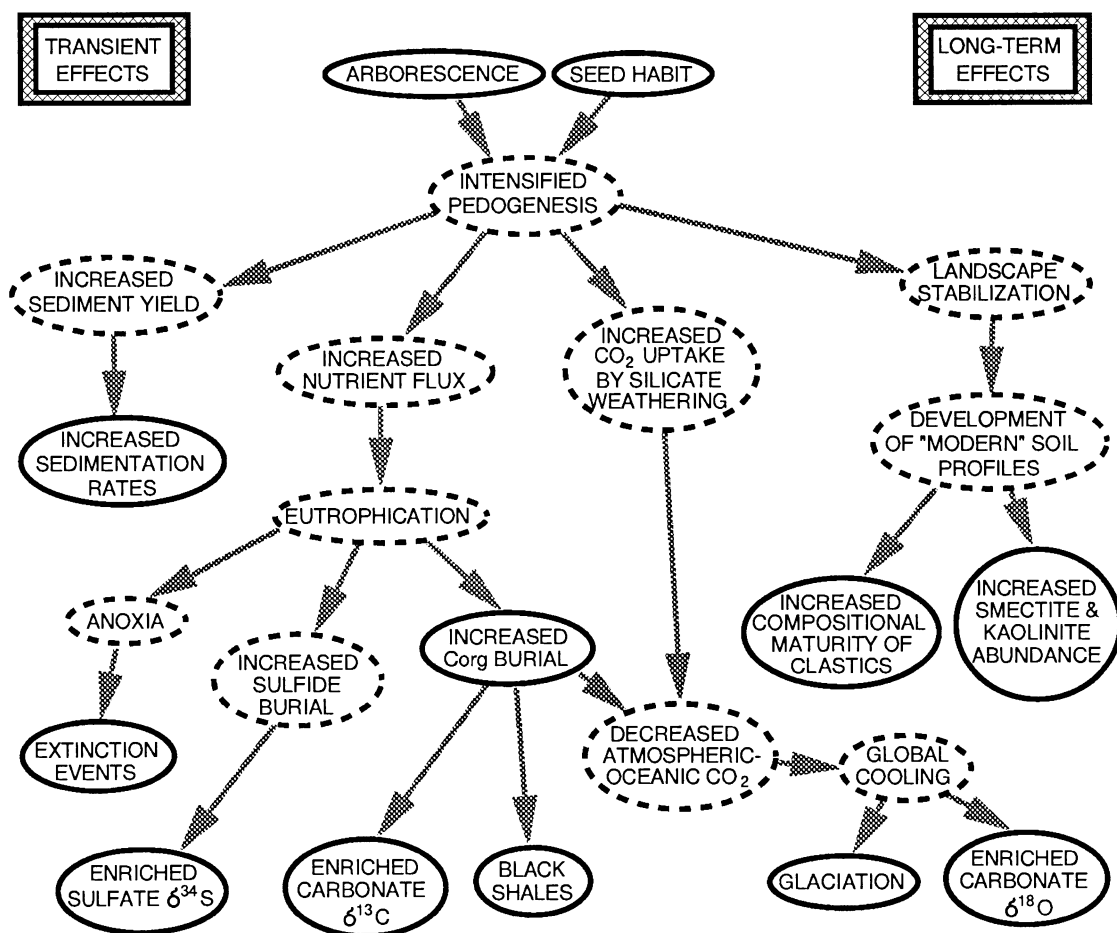


Figure 7. Flow-chart model linking the development of arborescence and the seed habit among vascular land plants during the Devonian to coeval terrestrial and marine events. Events are arrayed by relative duration with transient effects on the left and long-term effects on the right. Solid outlines indicate documented geological records; dashed outlines indicate processes inferred to link records (see text for discussion).

teleconnections may lie in the role of soils as a geochemical interface between the lithosphere and atmosphere/hydrosphere, and the role of land plants in mediating weathering processes at this interface. The effectiveness of Devonian terrestrial floras as weathering agents was significantly enhanced by increases in size (arborescence), which increased maximum depths of root penetration and rhizoturbation, and the advent of the seed habit, which allowed colonization of drier upland areas. These innovations resulted in a transient intensification of pedogenesis (soil formation) and to large increases in the thickness and areal extent of soils. Enhanced chemical weathering may have led to increased riverine nutrient fluxes that promoted development of eutrophic conditions in epicontinental seaways, resulting in algal blooms, widespread bottomwater anoxia, and high sedimentary organic carbon fluxes. Long-term effects included drawdown of atmospheric pCO₂ and global cooling, leading to a brief Late Devonian glaciation, and setting the stage for icehouse conditions during the Permo-Carboniferous. This model provides a framework for understanding links between early land plant evolution and coeval marine anoxic and biotic events, but further testing of Devonian terrestrial-marine teleconnections is needed.

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Discussion

1. SCOTT (*Geology Department, Royal Holloway University London, UK*). You talked about the presence of an upland flora in the late Devonian. Can you please provide evidence for this. It has long been recognized that the spread of land plants to a wide variety of lowland habitats took place by the end of the Devonian but it has been generally believed that there was no significant upland vegetation of, for example, tree size (Scott 1980, references therein). Our earliest evidence of upland floras comes from the Upper Carboniferous (Leary 1975; DiMichele *et al.* 1995; Scott *et al.* 1997). Do you believe that there was extensive forest vegetation in upland areas in the Late Devonian and if so what evidence should be sought to demonstrate its existence?

SHECKLER. Professor Scott is quite correct to point out how little we know of upland vegetation during the Devonian. Studies of Middle to Late Devonian floras of North America, at least, are still quite preliminary. Our understanding of upland and lowland vegetation comes primarily from two sets of studies: one is our ongoing study (e.g. Scheckler *et al.* 1990; Hill *et al.* 1997) of the evolution of the Franklinian Geosyncline as exposed on the northern Arctic islands of Canada; the other is our work on Famennian beds in Appalachian USA (e.g. Scheckler *et al.*; Strel & Scheckler 1990).

Bedrock units of the Middle to Late Devonian Okse Bay Group within the Franklinian Geosyncline are exposed at Bird Fiord and Hell Gate Fiord of southern Ellesmere Island and elsewhere. These include the Strathcona Fiord (Eifelian), Hecla Bay (Eifel-Givetian to Early Frasnian), Fram (Early to Mid Frasnian), Hell Gate (Mid Frasnian), and Nordstrand Point (Mid to Late Frasnian) Formations. These formations are interpreted (Embry 1988, 1991; Embry & Klovan 1976; Embry 1982) as nearly continuous terrestrial deposition of a meandering stream (Strathcona Fiord, Fram, and Hell Gate Fms) or braided stream (Hecla Bay and Nordstrand Point Fms) facies complexes. Based on these depositional models and our own observations, we conclude that meandering stream facies (characterized by thick lag deposit sequences cut by low velocity, sinuous stream channels with low angle, trough cross-stratification of 1–10 cm thick bed sets) preserve a portion of mostly lowland floodplain vegetation. Whereas the braided stream facies (characterized by stacked, high energy channels that exhibit conglomerate lag deposits of pebbles, rip-up clasts, and logs and have high angle, trough cross-stratification of 10 cm to 1 m thick bed sets) represent upland sedimentation environments.

During two field seasons (1988–1989) we examined approximately 33 km of outcrop (Scheckler *et al.* 1990), and made hundreds of collections for floristic and sedimentological studies. The beds of meandering stream facies (Strathcona Fiord, Fram, and Nordstrand Point Fms) produced more

diverse floras, the constituents of which varied with the formation and its horizons as follows.

- (i) Strathcona Fiord Formation (Eifelian): consisted largely of aneurophyte progymnosperms similar to *Rellimia* and *Aneurophyton*, but with some *Pseudosporochnus*-like cladoxylean ferns.
- (ii) Fram Formation (Early to Mid Frasnian): in its lower parts had mostly axes of *Callixylon* sp. and branches of the progymnosperm *Archaeopteris fissilis*, but in its upper parts had these plus *Archaeopteris obtusa*, a possible aneurophyte, and tree lycophytes that included *Leptophloeum rhombicum*.
- (iii) Nordstrand Point Formation (Mid to Late Frasnian): had the most diverse flora with abundant *Callixylon* sp., *Archaeopteris fissilis*, *A. obtusa*, and *A. macilenta*, the early zygopterid fern *Ellesmeris sphenopteroides*, strobili of *Barinophyton* sp., a tree lycophyte, and several other plants.

But, the beds of braided streams facies (Hecla Bay and Hell Gate Fms) also had an abundant flora of similar kind, summarized as follows.

- (i) Hecla Bay Formation (Eifelian/Givetian to Early Frasnian): in its lower parts had mostly aneurophyte progymnosperms similar to *Rellimia* and in its upper part had *Callixylon* sp. and *Archaeopteris fissilis*.
- (ii) Hell Gate Fm (Mid Frasnian): consisted mostly of the progymnosperms *Callixylon* sp., *Archaeopteris fissilis*, and *A. obtusa*, but also had a tree lycophyte, and strobili of *Barinophyton citrulliforme*.

From this sample we conclude that upland vegetation for the Eifelian–Givetian and Frasnian was similar to that from lowland environments, but was possibly less diverse.

Our second suggestion of an upland vegetation comes from our studies of then Mid–Late Famennian Hampshire Formation in West Virginia and Virginia and is based on three sets of observations. One, is that where stacks of braided stream channels occur (along US Route 33 near the WV/VA border and indicated as site 11 in figure 1 of Scheckler (1986a)), in the otherwise predominantly floodplain/palaeosol sequences, the lag deposits contain abundant logs of *Callixylon* in addition to quartz pebbles, cobbles, and mud rip-up clasts.

Another, is that the high energy, upper flow regime sediments at Valley Head, WV (Locality D of Scheckler (1986a)) contain many branches of *Archaeopteris halliana* and *A. hibernica* as well as abundant foliar members of *Rhacophyton ceratangium*.

The third observation is based on the correspondence of variance of macrofossil versus microfossil data from the same beds used by Scheckler (1986a) to reconstruct a portion of the vegetation of Late Devonian floodplains and coastal marshes. Strel & Scheckler (1990) were able to characterize separate upstream from downstream vegetation environments. In what at first seem anomalous, the upstream samples yield a more diverse miospore assemblage than do the downstream sites. But this is easily understood when one considers that our downstream sites (e.g. at Elkins, WV) were autochthonous *Rhacophyton*-dominated wetlands in which the miospore assemblage closely reflected the *Rhacophyton* community and the

presence of nearby tree lycopods and the progymnosperm *Archaeopteris*. Whereas the upstream sites (e.g. at Rawley Springs, VA) included both autochthonous *Rhacophyton*-dominated wetlands and allochthonous crevasse splays as a result of periodic flash floods that brought in a more diverse palynoflora, the mother plants of which are unknown and grew remote from the deposition sites so that the megafossil floral recovery is substantially different from the miospore assemblage.

Furthermore, by comparing these upstream and downstream terrestrial miospore assemblages with contemporaneous (Vco) nearshore marine assemblages from Belgium, Strel & Scheckler (1990) were able to demonstrate that the latter have an over-representation of upstream elements similar to the situation in modern Corsica where Richelot & Strel (1985) were able to show that most of the recent pollen deposited in the nearshore Mediterranean sediments originated from an upland hinterland through periodic violent floods.

Together, these data support the notion that was an upland vegetation during Middle and Late Devonian and that it might not have differed much from lowland vegetation, including the presence of lycopod and progymnosperm trees and shrubs, except by lesser megafossil diversity of the former and differences of relative abundance. In our samples from Rawley Springs, however, there are some upstream miospores (e.g. *Retusotriletes* cf. *coniferus*, *Punctatisporites minutus*, and *Grandispora gracilis* that together are over 90% of these samples) that apparently represent taxa other than the megafossil dominants (*Rhacophyton*, a *Protolepidodendropsis*-like lycopod, and *Archaeopteris*) that have not yet been found and that may represent additional components of an as yet only partly recognized upland vegetation.

Also important to potential upland colonization are plant innovations, especially of roots, that commenced in the Middle and Late Devonian (Algeo *et al.* 1995; Scheckler 1986b). The hollow 'stigmairian rootlets' of early tree lycopods (e.g. Middle Devonian *Eospermatopteris* (see text) and Late Devonian *Lepidosigillaria*, *Leptophloeum*, and *Cyclostigma*) and their *in situ* occurrences in wetland (peat and non-peat accumulating) palaeosols suggest that these were predominantly restricted to wetland and fluvial habitats. Progymnosperm roots (both aneurophytes and archaeopterids), however, had perennating cambial activity and produced extensive lateral rootlet systems by endogenous and adventitious growth (figure 4, this paper; figure 19, Algeo *et al.* 1998; Scheckler 1995) that were capable of deep and thorough soil penetration.

Roots of *Archaeopteris* are known to have penetrated over 1 m of palaeosols that are interpreted as indicative of semi-arid climates (e.g. figure 4a,b, this paper; Embry 1988, 1991; LeJeune 1986). Such depth and extent of soil penetration by *Archaeopteris*, as one example, might have permitted this forest component to substantially ameliorate local microclimate and successfully invade drier upland sites. The ubiquitous occurrence of logs of *Callixylon* (the woody remains of *Archaeopteris*) in the channel lags of Frasnian and Famennian braided stream deposits suggests that this plant may have formed streamside gallery forests in the uplands similar to, but smaller than, those reconstructed for lowlands (Beck 1964; Snigirevskaya 1995) of this time.

Likewise, the abundant occurrences of aneurophyte progymnosperms in Eifelian–Givetian braided stream deposits suggests that these shrubby and apparently xeric-adapted plants (Scheckler *et al.* 1990; Scheckler & Banks 1971a,b) may formed a Mediterranean/Chaparral-like community in both uplands and lowlands of Middle Devonian time.

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