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 pCO$_2$ 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 pCO$_2$ 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; Ettenson 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
the seed habit. Arborescence, especially among progymnosperms, markedly increased depths of root penetration and rhizoturbation, and seeds permitted colonization of previously inaccessible dry upland and harsh primary successional habitats. These developments are likely to have caused a transient intensification of global rates of pedogenic weathering and soil formation, and to have resulted in long-term changes in subaerial weathering processes, patterns of landscape stabilization, and riverborne sediment and nutrient fluxes. Algeo et al.'s (1995) hypothesis emphasizes the importance of soils as a geochemical interface between the lithosphere and atmosphere/hydrosphere, as well as the fundamental role of land 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 critical 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.

2. 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). Vascular (tracheid-bearing) plants evolved and began to diversify during the Late Silurian and Early Devonian (Gensel & Andrews 1984, 1987; Gray 1985, 1993; Bocot 1990; Edwards & Berry 1991), but these forms were small, non-rooted or shallowly rooted, and confined to moist, lowland 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 seed plants (figure 1c; Banks 1980; Thomas & Spicer 1987; Beerbower et al. 1992). With regard to potential weathering effects, first appearances and early radiations of primitive land plants were less significant than the increases in floral biomass and geographic range that accompanied the development of arborescence, advanced root systems, and the seed habit.

(a) Arborescence

The maximum size of vascular land plants increased greatly during the Devonian (figure 2; Chaloner & Sheerin 1979; Knoll et al. 1984; Edwards & Berry 1991; Beerbower et al. 1992). By the Late Givetian, woody shrubs and medium-sized trees had appeared in several independent clades, including cladoxylacean ferns (e.g. Pseudopodoceras), lepidosigillarioid lycopsids (e.g. Eospermatopteris), aneuphyte progymnosperms (e.g. Retinia and Tetraylaria), and archaepocterid progymnosperms (e.g. Sothbaddafi; Scheckler 1974, 1986a; Banks 1980; Gensel & Andrews 1984; Mosbrugger 1990). Among arborescent taxa, archaepocterids 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 palaearlatitudes (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 archaepocterid remains are known from many Late Devonian (especially Middle- to Late Frasnian) terrestrial and marginal marine successions, and monospecific archaepocterid forests may have been common in floodplain habitats at that time (Beck 1964; Scheckler & Basinger 1982; Béiron-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 1986a,b; Beerbower et al. 1992); earliest seed plants (Fairon-Demaret 1986; Rothwell & Scheckler 1988); first appearance data (FAD) of 2° cortex (i.e. periderm) and progynnosperms (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 Strel (1986, 1992).
Figure 3. Diagram of the relative sizes, morphologies, and penetration depths of the root systems of selected Early, Middle, and Late Devonian plants. Abbreviations: rhy = rhyniophytes such as Agleophyton or Hornophyton; tri = trimerophytes such as Psilophyton; lyc-he = early herbaceous lycopsods such as Asterosylon or Drepasophytes; lyc-tr = early tree lycopsods such as Lepidostigma or Cyclostigma; prog-an = aneuphylate progymnosperms such as Tetrazylopteris; prog-arc = Archaeopteris progynomosperms; gym = early gymnosperms such as Elkinsia or Morenetia; and zyg = zygopterid ferns such as Rhacophyton. Scale bar, 1 m.

Scheckler 1986a,b,c; Thomas & Spicer 1987). The success of the archaeopterid progynomosperms may have been due to their ability to create and maintain favourable microenvironments. Mass-shedding of their leafy lateral branch systems (Beck 1964; Scheckler 1978) would have produced deep 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 aneuphylate progynomosperms, which were homosporous, did not shed branch parts, and may have been adapted to a more open canopy structure (Scheckler 1975, 1976; Taylor & Scheckler 1996; Hill et al. 1997).

(b) Root systems

Arborescence was accompanied by development of larger root systems that led 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 in herbaceous lycopsods (e.g. Asterosylon, Drepasophytes) 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 archaeopterid spread during the Frasnian–Famennian (figure 3; Beck 1953, 1967; Walker & Harms 1971; Snigirevskaya 1984a,b, 1988, 1995; Retallack 1983; L'Gueune 1986; Scheckler 1986a,b,c, 1995, and unpublished data; Beerbower et al. 1992). Some non-progynomosperms also developed extensive root systems, e.g. the tree lycopsods Cyclostigma and Lepidoselendrotaxis/Proto-stigmata, the cladoxylalean fern Pseudosporochclus, and the zygopterid fern Rhacophyton, but these were generally shallower than those of contemporaneous progynomosperms owing to growth in water-saturated soils (Leclercq & Banks 1962; Schweitzer 1969; Scheckler 1974, 1986a,c, Jenkins 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; Drye & Foreman 1991), which were generally of limited abundance owing to low rates of net primary productivity in algal-lichen (under 100 gm⁻² yr⁻¹) and bryophyte communities (below 1000 gm⁻² yr⁻¹) compared to modern forest and grassland ecosystems (600–6000 gm⁻² yr⁻¹), Longton 1988; Comeau & Kimmins 1989; Retallack 1992a; Viles & Pentecost 1994). Root growth accounts for 40–85% of 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, progynomosperms 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 progynomosperms 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.

(e) **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 peridiphytic 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 archeoepidendrogymnosperms (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 & Scheikler 1988; D’Michele et al. 1989; Bateman & D’Michele 1994). The development of seeds freed land plants from dependence on aseptic 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; Scheikler 1986e; Thomas & Spicer 1987; Rothwell & Scheikler 1988; Beerbower et al. 1992). The earliest known seeds are Middle to Late Famennian in age, e.g. Moresnetia zaleskiiy, Dorinnotheca streedi, and Elkinsia polymorpha (lower VCg spore zone; Fa2c), followed by Archaeosperma arnoldii, Aglostoma quadrivariata, Spermolithus devonicus, Kerryia mantelli, and Xenotheca devonica (LV-LN spore zones; Fa2d-basal Tu1b; Chaloner et al. 1977; Gillespie et al. 1981; Fairon-Demaret 1986, 1996; Fairon-Demaret & Scheikler 1987; Rothwell & Scheikler 1988; Rothwell et al. 1989; Rothwell & Wight 1989; Steer & Scheikler 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 & Scheikler 1988; Beerbower et al. 1992). Because gymnosperms had the same types of advanced root systems as the older progymnosperms (figure 4d; Scheikler 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 Orдовician 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 Orдовician, 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; Ettenson 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 calcareous rhizocreations 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 progynnosperms (e.g. *Archaeopteris*) or early gymnosperms (e.g. *Morenetia* or *Durnrothaea*). (b) Horizontal view of the same palaeosol block showing in cross-section the large vertical rhizocreations and the smaller branching root traces attached to them. Large (2–5 cm diameter) prismatic soil peds are visible. Both the calcareous rhizocreations 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 *Phil. Trans. R. Soc. Lond. B* (1998).

(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; Johnson 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. 1968; 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 & Kimmis 1989; Retallack 1992a); and (2) a greater (three-dimensional volumetric) contact area of roots 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 (Veld 1985; Singer & Muns 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 K2O/Na2O 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 evaporative 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 evaporative 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. 230–350 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 progynosperm tree Archaeopteris, showing numerous lateral rootlets (UAPC 84630). 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 84631b). 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 oxeath main root (Callixylon petryi, specimen UAPC S2883-10A) 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 (e) (specimen UAPC 84630-2aL). Visible at the top, where the main root is cut in near-radial LS, is a near-medial 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.
particulate fluxes during the Middle-to-Late Devonian (Algeo et al. 1995). However, sediment yields are largely a function of local relief, and global clastic fluxes mainly reflect weathering rates in upland areas (Stallard 1985; Summerfield 1991), which probably intensified with the spread of gymnosperms during the Late Devonian.

(d) Atmospheric pCO₂ and global climate change

Elevated 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 CO₂ levels. Estimates of atmospheric pCO₂ 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). Imprecision in pre-Devonian estimates is mainly due to uncertainty regarding the relative weathering efficiencies of vascular and non-vascular plants (see above; Berner 1993, 1994). Palaeoatmospheric CO₂ levels may be independently determined through C-isotopic analysis of soil rhizoliths in vertisols and carbonaceous impurities in hardpan Fe oxyhydroxides (Mora et al. 1991, 1996; Yapp & Potts 1992, 1996), and these studies have yielded pCO₂ 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 0.7–1.0 PAL for the Early Permian (figure 5a).

Drawdown of atmospheric pCO₂ during the Devonian had far-reaching climatic consequences, contributing to global cooling and a short Late Eamennian 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 δ¹⁸O 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; Dunn 1988; Lohmann 1988; Brand 1989). About 0.5% of this shift in marine carbonate δ¹⁸O values may be attributable to growth of continental ice sheets (Crowley & Baum 1991), but the remaining 3.5% is likely to reflect cooling of tropical surface waters by ca. 14 °C, i.e. from ca. 40 °C in the Devonian to near-modern temperatures of ca. 25–28 °C in the Carboniferous (Craig 1965; Veizer et al. 1986). Temperature control of Devonian–Carboniferous marine carbonate δ¹³C values is strongly favoured owing to the link it provides between changes in organic carbon burial rates, atmospheric CO₂ levels, and coeval continental glaciation (Algeo et al. 1997). Late Eamennian glaciation is evidenced by diancritics in Brazil containing striated and polished pebbles, rhythmites containing dropstones, erratic boulders, and striated pavements in Brazil and, possibly, by correlative deposits in North Africa and Argentina (Caputo 1985; Caputo & Crowell 1985). This event has been dated to the Strunian (equivalent to the Middle and Upper prasulcata conodont zones, or the Late Eamennian) on the basis of miospores (Streel 1986, 1992), making it roughly correlative with the spread of the earliest seed plants as well as with the Hangenberg marine anoxic event (see below).
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 1986a).

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 δ13C values reflect elevated 12C/13C ratios in the ocean surface ΣCO2 reservoir as a consequence of enhanced fixation and burial of 13C-depleted organic matter (Kump 1991; Joachimski & Buggisch 1993). Devonian marine carbonates exhibit little C-isotopic variation during the Lochkovian–Eifelian (less than ±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 5b; 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 613C excursions (e.g. figure 5b), 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 (Bernier 1978; Berner & Raiswell 1983), and the Late Devonian is characterized by high burial rates of 34S-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 5c; 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 Protoeustinia, 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 1986c). 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. Strel & 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).
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
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 (arborecence), 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 CO₂ 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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diverse floras, the constituents of which varied with the formation and its horizons as follows.

(i) Strathcona Fiord Formation (Eifelian): consisted largely of anephyte progymnosperms similar to *Rellinia* and *Aneurophyton*, but with some *Pseudosporochmus*-like cladosyleante ferns.

(ii) Fram Formation (Early to Mid Frasnian): in its lower parts had mostly axes of *Callixylon* sp. and branches of the progymnosperm *Archaeopteris* *fisilis*, but in its upper parts had these plus *Archaeopteris obtusa*, a possible anephyte, and tree lycopsids that included *Leptophloeoium thombeicum*.

(iii) Nordstrand Point Formation (Mid to Late Frasnian): had the most diverse flora with abundant *Callixylon* sp., *Archaeopteris fisilis*, *A. obtusa*, and *A. macilentia*, the early zygopterid fern *Ellesmeris sphenopetrides*, strobili of *Bairrophtyon* sp., a tree lycopod, 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 anephyte progymnosperms similar to *Rellinia* and in its upper part had *Callixylon* sp. and *Archaeopteris fisilis*.

(ii) Hell Gate Fm (Mid Frasnian): consisted mostly of the progymnosperms *Callixylon* sp., *Archaeopteris fisilis*, and *A. obtusa*, but also had a tree lycopod, and strobili of *Bairrophtyon cirilliforme*.

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. Scheckler & 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

S. E. SCHECKLER. 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 estimation of upland and lowland vegetation comes primarily from two sets of studies: one is our ongoing survey (e.g. Scheckler et al. 1990; Hill et al. 1997) of the beds of the Franklinian Geosyncline as exposed on the High Arctic islands of Canada; the other is our work with Famennian beds in Appalachian USA (e.g. Scheckler 1986a; Strel & Scheckler 1990).

 Beds of the Middle to Late Devonian Okse Bay Group of Franklinian Geosyncline are exposed at Bird Fiord and Sor Fiord of southern Ellesmere Island and elsewhere. They are the Strathcona Fiord (Eifelian), Hecla Bay (Eifelian/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 (Emby 1988, 1991; Embry & Klovon 1969; Rice 1962) as nearly continuous terrestrial deposition of meandering streams (Strathcona Fiord, Fram, and Nordstrand Point Fms) or braided streams (Hecla Bay and Hell Gate Fms) facies complexes. Based on these depositional models and our own observations, we conclude that the meandering stream facies (characterized by thick palaeosol 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 (with stacked, high energy channels that exhibit conglomeratic lag deposits of pebbles, rip-up clasts, and logs and that have high angle, trough cross-stratification of 10 cm to 1 m thick bed sets) represent upland sedimentation regimes.

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