Early Forest Soils and Their Role in Devonian Global Change

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A paleosol in the Middle Devonian Aztec Siltstone of Victoria Land, Antarctica, is the most ancient known soil of well-drained forest ecosystems. Clay enrichment and chemical weathering of subsurface horizons in this and other Devonian forested paleosols culminate a long-term increase initiated during the Silurian. From Silurian into Devonian time, red clayey calcareous paleosols show a greater volume of roots and a concomitant decline in the density of animal burrows. These trends parallel the decline in atmospheric carbon dioxide determined from isotopic records of pedogenic carbonate in these same paleosols. The drawdown of carbon dioxide began well before the Devonian appearance of coals, large logs, and diverse terrestrial plants and animals, and it did not correlate with temporal variation in volcanic or metamorphic activity. The early Paleozoic greenhouse may have been curbed by the evolution of rhizospheres with an increased ratio of primary to secondary production and by more effective silicate weathering during Silurian time.

Forest ecosystems of the mid-Paleozoic have been viewed as engines of past global change. Devonian lignin, trees, and swamps have been proposed as sinks for atmospheric CO_2 that terminated an earlier Paleozoic greenhouse (1, 2). Large roots of trees would have promoted more thorough weathering than before, including increasingly clayey subsurface horizons and increased consumption of carbonic acid during weathering (3, 4). In addition, forest habitats would have provided new niches for adaptive radiations of animals and plants (5). These ideas concerning the first forests can now be tested against a fossil record of soils (6). Here, I describe the geologically most ancient paleosol thought to have supported well-drained forest, and evaluate its importance within the context of other Paleozoic paleosols.

Like many ancient red beds, the Aztec Siltstone of Antarctica contains numerous paleosols (7, 8). The Rosemary pedotype (7) (Figs. 1 and 2) is a profile on the steep ridge 3 km southeast of Mount Crean, Victoria Land (77° 52.4′S, 159° 32.0′E). The Rosemary paleosol is 91 m above the local base of the Aztec Siltstone (9), corresponding to the *Bothriolepis kohni* fossil fish biozone (10). Both fossil fish and pollen at this level have been correlated with the later Middle Devonian *Schmidtognathus hermanni–Polygnathus cristatus* and *Polygnathus varcus* conodont zones of the Givetian (11), dated at 377 to 379 million years ago (12).

The Rosemary paleosol shows several features comparable to well-drained forest soils. Root traces are stout (up to 11 mm in diameter) and penetrate deeply (1.5 m into the paleosol). The root traces are finely striated

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and surrounded by drab haloes typical for woody roots in paleosols (4). The surface of the paleosol also has common, large (20 cm), irregular sandy patches (arrow in Fig. 1A) comparable to disruption created by tree fall (7). Their local ragged extensions preclude interpretation as load casts or other forms of soft sediment deformation. The paleosol includes a thick subsurface horizon enriched in clay to such an extent (Fig. 1, B and D, and Fig. 2) that it qualifies as both a Bt horizon and an argillic horizon (13). The argillic horizon has a blocky angular ped structure defined by slickensided clay skins, as well as

deeply penetrating sand-filled cracks. The argillic horizon also is evident from subsurface alumina enrichment (high alumina/silica ratios in Fig. 2). There is chemical evidence of good drainage (low ferrous/ferric iron ratios in Fig. 2) and moderate base depletion (low but nonzero alkaline earths/alumina ratios and moderate alumina/bases ratios). These chemical criteria allow identification of the Rosemary paleosol with Alfisols (13) and Luvisols (14).

Modern soils comparable to the Rosemary pedotype are common in the Indo-Gangetic plain of northern India (15). Such soils now support monsoon forests of sal [*Shorea robusta* (16)]. The Aztec Siltstone has yielded unidentified fossil wood, generally similar to that of the progymnosperm *Callixylon-Archaeopteris* (7), a plant known to have produced the spores *Geminospora lemurata* also found in the upper Aztec Siltstone (17). Such vegetation is compatible with the stout root traces of the Rosemary paleosol. A subhumid seasonal paleoclimate like that of northern India is indicated by the depth and nature of calcareous nodules and ferruginous concretions in the Rosemary profile (Fig. 1, C and E). The depth of calcareous nodules in modern soils is related to mean annual rainfall and biological productivity, and (after correction for burial compaction) it gives an estimated mean annual rainfall of 779 ± 141 mm for the Rosemary paleosol (7). The rooting, depth of ferruginization, and weathering of minerals in these profiles are suggestive of a warm climate, probably subtropical to tropical. The paleo-
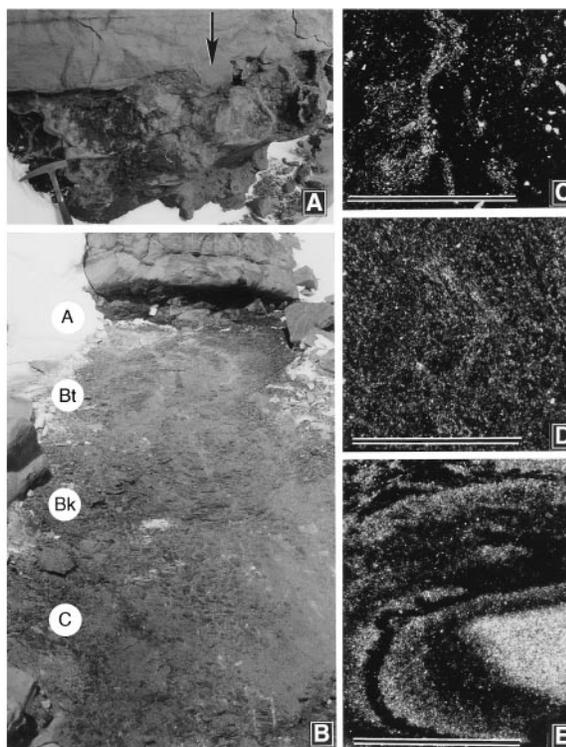
Fig. 1. Field photographs (**A** and **B**) and photomicrographs under crossed nicols (**C** to **E**) of the Middle Devonian Rosemary paleosol at Mount Crean, southern Victoria Land, Antarctica, showing (A) drab-haloed root traces, large root disruptions (at arrow), and sand-filled cracks in the surface; (B) complete profile with interpreted soil horizons [A, surface mineral and organic; Bt, subsurface clay enriched; Bk, subsurface calcareous; and C, weathered parent material (13)] (hammer in horizon Bt); (C) rhizoconcretion in horizon Bk; (D) clinobimasepic plasmic fabric in horizon Bt; and (E) part of ferruginous concretion in horizon Bt. Hammer in (A) and (B), 25 cm; scale bars in (C) to (E), 1 mm.

magnetically determined paleolatitude of the Rosemary paleosol during the middle Devonian was about 40° ± 14° (18). A seasonal paleoclimate can be inferred from calcareous rhizoconcretions (Fig. 1C) together with ferruginized concretions (Fig. 1E), growth rings in fossil wood, and abundant sand-filled cracks within the paleosols (7). Like comparable soils of northern India, paleosols of the Aztec Siltstone were part of a large alluvial plain of quartzofeldspathic composition (8).

Numerous similar fossil Alfisols are known from Late Devonian red beds of the United States and Britain, and they are common in every subsequent geological period (4). The oldest known forest paleosols, like the profile from Antarctica described here (Figs. 1 and 2), were probably fertile soils (Alfisols and Inceptisols), judging from their mineral and chemical compositio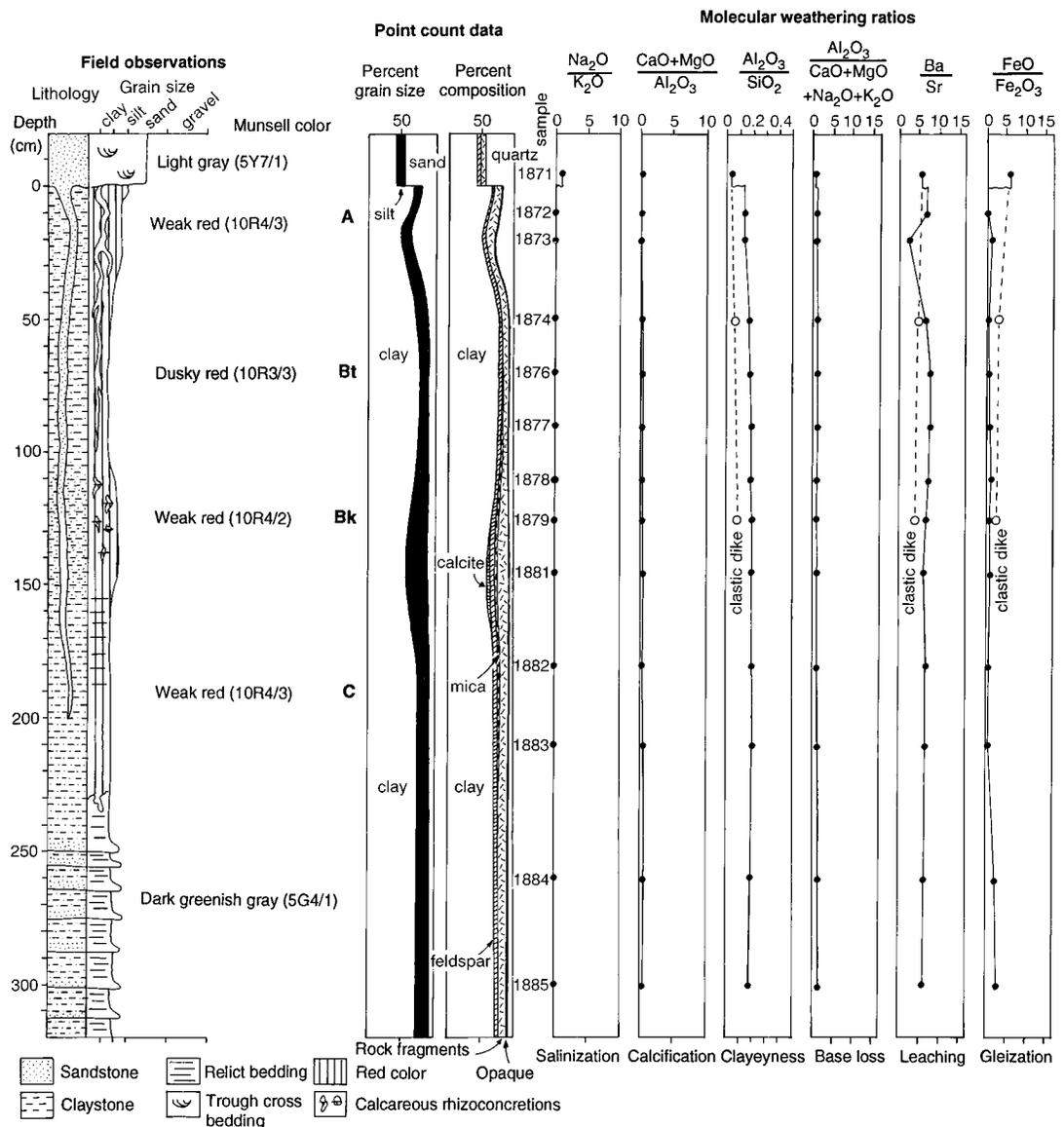n. This was also true of the oldest forested clastic swamps, represented by the well-known Gilboa fossil forests of New York (6). Oligotrophic woodlands and forests in deeply weathered clays (Ultisols and Oxisols), in quartz sands (Spodosols, Dystrochrepts, and Quartzipsamments), and forming woody peats (Histosols) evolved later in geological time. All are known by the mid-Carboniferous (6, 19). Adaptation of trees and their rhizospheres to such infertile substrates was thus geologically delayed.

Devonian Alfisols like the Rosemary paleosol culminate a mid-Paleozoic rise in the degree of weathering of red clayey calcareous paleosols in fluvial facies (Fig. 3A). Early Paleozoic red calcareous paleosols are most clayey and weathered at the surface, whereas mid-Paleozoic and later paleosols with large woody root traces show the pattern of subsurface maxima of chemical weathering and clay content found in modern Alfisols (13) and Luvisols (14).

In another long-term trend, root trace density and rooting depth increase as burrows decline in abundance in red calcareous paleosols of Silurian to Carboniferous age (Fig. 3B). This may indicate a long-term increase in the ratio of primary to secondary productivity in soils through time. Such an interpretation is supported by $\delta^{13}C$ isotopic evidence for near modern levels of soil respiration in an Ordovician paleosol (20). Because small nonvascular plants of Ordovician paleosols are unlikely to have matched the root respiration of modern forests, much of the inferred respiration was that of animals and other secondary producers. Both burrows (21) and trackways (22) like those of millipedes are known from Late Ordovician nonmarine red beds. Compared with Devonian and later forest soils, Ordovician soils may have lost a greater proportion of

Fig. 2. Field and laboratory data on the Middle Devonian Rosemary paleosol at Mount Crean, showing a measured section, Munsell colors, grain size, mineral composition, and selected molecular weathering ratios calculated from chemical analyses. Clastic dikes in the paleosol consist of compositionally and texturally distinct sands that fell down cracks in the soil, as indicated by chemical and textural analysis of separate samples.

primary production to consumption.

A marked decline in atmospheric CO_2 from the Ordovician to the Carboniferous is indicated by the isotopic composition of carbonate in red calcareous paleosols (Fig. 3D). A decrease in tectonic degassing of CO_2 does not explain this trend. Oceanic and continental volcanic rocks, as well as metamorphic rocks, increased in volume from the Ordovician to the Carboniferous (23). The increased abundance of trees (2), peat (24), or marine black shales (2) was also unlikely to have curbed the Early Paleozoic greenhouse; the timing of these carbon sinks is such that they would have contributed during the final phases of CO_2 decline (Fig. 3, C to E). Also postdating most of the decline in the early Paleozoic greenhouse is the marked rise in tree trunk and root diameter (Fig. 3F) and the increase in diversity of land plants and animals (Fig. 3G). These fossil records may lag the CO_2 decline because many of the fossils are preserved in gray shales (25), not red clayey paleosols.

Evidence presented here from red calcareous paleosols (Fig. 3, A and B) indicates widespread carbon-hungry ecosystems in well-drained soils by Silurian time (4). A useful working hypothesis is that the early Paleozoic greenhouse was curbed by an increased ratio of primary to secondary productivity on land. A plausible mechanism for this change is the evolution of herbivore-suppressant toxins such as flavonoids (26) or of refractory materials such as lignin in early land plants (1). Such chemical and microbial changes on dry land are better reflected in paleosols than in the sedimentary and fossil records. Distinctive early Paleozoic ecosystems of well-drained soils with low biomass but high soil respiration included posterlands of nonvascular plants and brakelands of extinct spore-bearing plants (27). In the coevolutionary arms race between plants and animals, early herbaceous plants may have been heavily cropped by animals and other secondary producers during an Ordovician greenhouse. By Silurian time, rhizospheres were impressively dense and deep (27, 28). By Devonian time, woody plants and primary productivity became dominant, leading to even greater carbon consumption and bringing on the late Paleozoic ice ages (29).
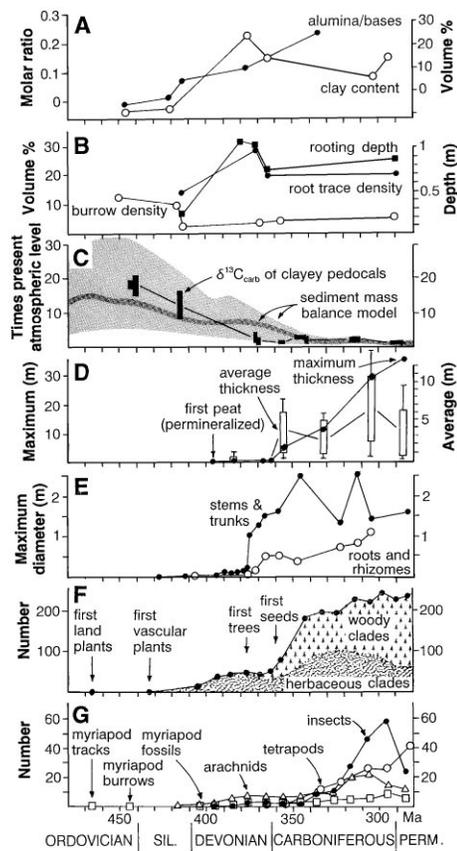

Fig. 3. Secular changes in paleosol features and coeval changes in the surface environments during mid-Paleozoic time (12). (**A**) Indices of soil differentiation, including enhanced subsurface silicate weathering [molar weathering ratios of alumina/bases in subsurface minus surface horizons (4, 28, 30, 31)] and enhanced subsurface clay accumulation [volume percent clay in subsurface minus surface horizons (4, 28, 31, 32)] in red clayey calcareous paleosols only. (**B**) Indices of bioturbation, including proportion of a line transect of hand specimens occupied by burrows and by roots (volume percent) (4, 28, 30, 33) and rooting depth (meters) (4, 28, 30, 33) in red clayey calcareous paleosols only. (**C**) Atmospheric partial pressure of CO_2 (times present atmospheric level) estimated from $\delta^{13}C$ of pedogenic carbonate (boxes) (34, 35) from red clayey calcareous paleosols, and from a sediment mass balance model [shaded area (3)]. (**D**) Coal thickness, including thickest coal seam and thickest average seam in successions of coals (36). (**E**) Maximum diameter of fossil stems and trunks and of roots and rhizomes (37, 38). (**F**) Diversity of plants, expressed as numbers of species (39, 40). (**G**) Diversity of myriapods, arachnids, insects, and tetrapods, expressed as numbers of families (41). Ma, million years ago.

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