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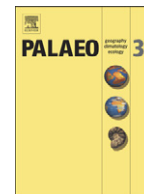
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Ecology and evolution of Devonian trees in New York, USA

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ABSTRACT

The first trees in New York were Middle Devonian (earliest Givetian) cladoxyls (*?Duisbergia* and *Wattieza*), with shallow-rooted manoxylic trunks. Cladoxyl trees in New York thus postdate their latest Emsian evolution in Spitzbergen. Progymnosperm trees (*?Svalbardia* and *Callixylon*–*Archaeopteris*) appeared in New York later (mid-Givetian) than progymnosperm trees from Spitzbergen (early Givetian). Associated paleosols are evidence that *Wattieza* formed intertidal to estuarine mangal and *Callixylon* formed dry riparian woodland. Also from paleosols comes evidence that *Wattieza* and *Callixylon* required about 350 mm more mean annual precipitation than plants of equivalent stature today, that *Wattieza* tolerated mean annual temperature 7 °C less than current limits of mangal (20 °C), and *Callixylon* could tolerate temperatures 14 °C less than modern mangal. Devonian mangal and riparian woodland spread into New York from wetter regions elsewhere during transient paleoclimatic spikes of very high CO₂ (3923 ± 238 ppmv), and subhumid (mean annual precipitation 730 ± 147 mm) conditions, which were more likely extrinsic atmospheric perturbations rather than consequences of tree evolution. For most of the Middle Devonian CO₂ was lower (2263 ± 238 ppmv), and paleoclimate in New York was semiarid (mean annual precipitation 484 ± 147 mm). Such transient perturbations and immigration events may explain the 40 million year gap between the late Emsian (400 Ma) evolution of trees and Famennian (360 Ma) CO₂ drawdown and expansion of ice caps.

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1. Introduction

The Devonian evolution of trees has been considered responsible for a cascade of global carbon sequestration culminating in the Late Paleozoic Ice Age (Bernier, 1997; Ward et al., 2006), and perhaps also Late Devonian (Frasnian–Famennian) mass extinction (Algeo and Scheckler, 1998; Algeo et al., 1995; Ward, 2009). This study of Middle Devonian paleosols aims at understanding the paleoclimate, including atmospheric CO₂, and paleoenvironment of fossil trees in the Catskill Mountains of upper New York State (Banks et al., 1985). Three specific problems have arisen from past study of these paleosols. First, many Devonian paleosols now known from New York and Pennsylvania are like pedocals of semiarid Utah (Driese and Mora, 1993; Retallack et al., 2009), too dry to have supported trees. Second, some Devonian trees in New York were intertidal, comparable with modern mangroves (Driese et al., 1997, 2000; Mintz et al., 2010), yet new paleogeographic reconstructions place New York at a paleolatitude of 35°S (J. Golonka for Joachimski et al., 2002), like Auckland today (37°S) where mangroves at the extreme southern margin of their mainly tropical distribution are only 1 m tall (Taylor, 1983). Third, large paleoclimatic variations from pedogenic carbonate evidence of varied atmospheric

CO₂ levels (Cox et al., 2001) may be coordinated with events of marked biotic overturn (Brett et al., 2009). Can such paleoenvironmental shifts or differing plant climatic ranges explain such discrepancies in the size, distribution and ecology of the earliest trees to reach North America?

These questions are addressed here with a compilation of data on fossil plants of New York and nearby Pennsylvania (Figs. 1 and 2), and with detailed studies of a sequence of paleosols in the Manorkill Formation near East Windham (Figs. 3 and 4). Climate, organisms, parent material, paleotopography and time for formation are not only soil forming factors, but also ecosystem defining factors (Jenny, 1980). In deep time these various factors can be inferred from paleosols, which represent long-term effects of ecosystems on their substrates (Retallack, 2001). Paleoprecipitation and paleotemperature, for example, can be interpreted from chemical weathering indices as well as depth to carbonate in soils (Retallack, 2005a,b; Sheldon, 2006; Sheldon and Tabor, 2009; Sheldon et al., 2002). Isotopic composition of pedogenic carbonate and depth to carbonate can be used to estimate atmospheric CO₂ levels (Cerling, 1991; Ekart et al., 1999; Retallack, 2009a). Degree of chemical weathering can be assessed from molar depletion of major elements and strain due to volume changes (Brimhall et al., 1992; Retallack and Mindszenty, 1994). This study of Middle Devonian (Givetian) soils from East Windham uses such proxies to evaluate paleoenvironmental controls on early communities with trees.

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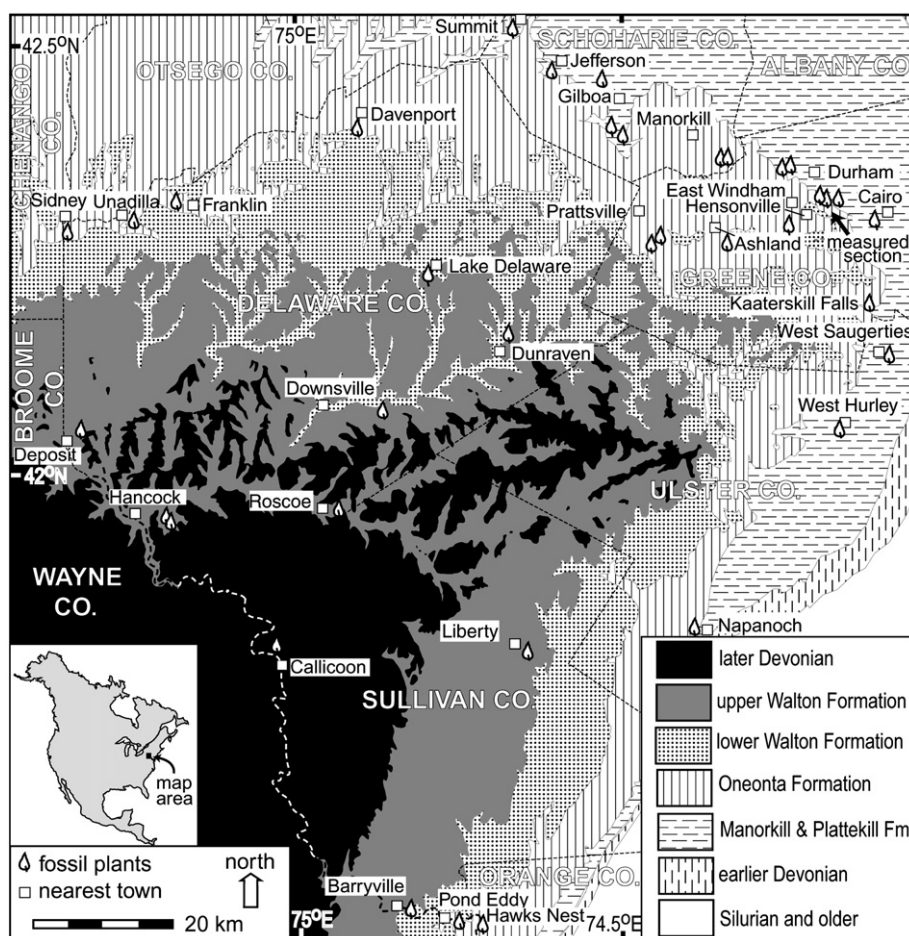


Fig. 1. Geological map and Devonian paleosol and plant fossil localities examined in upper New York State.

2. Geological setting

The Manorkill Formation in the Catskill Mountain Front records progradation of a coastal plain westward from uplift of the rising Acadian Mountains to the east. Marine gray siltstones of the Plattekill Formation are overlain by interbedded gray and red paleosols of the Manorkill Formation (Fig. 3), and then red paleosols of the Oneonta Formation (Sevon and Woodrow, 1985). Dark shales of Manorkill Formation in road cuts measured for this work (34 m in Fig. 4) have been correlated with the base of the upper Tully Limestone, using a combination of lithological correlations and fossil ostracods found within these exposures (Johnson and Friedman, 1969; Knox and Gordon, 1999). The Tully Limestone elsewhere has a marine fauna (Brett et al., 2009; Heckel, 1973), including ammonoids of the *Pharciceras amplexum* zone (Kirchgasser, 1985; Work et al., 2007), and conodonts of the *Polygnathus varcus* zone (Davis, 1975; Sparling, 1999), indicating late Givetian and 386 Ma in the time scale of Kaufmann (2006).

Vitrinite reflectance from fossil wood at East Windham (35 m in Fig. 4) has been used to estimate burial by 6.5 km of overburden (Friedman and Sanders, 1982). This conclusion has been disputed (Levine et al., 1983), but is supported by additional evidence from illite crystallinity, fluid inclusion homogenization temperatures, oxygen isotopic composition of fracture-filling carbonate cements, and conodont color alteration index (Mora et al., 1998; Sarwar and Friedman, 1995). This alteration has affected the grain size, mineral composition, and color of many of these paleosols: gray shales are silty with recrystallized illite–chlorite and red siltstones are purple with hematite (Retallack, 1985). Potash metasomatism is plausible

(Mora et al., 1998), but was limited, because maximum K_2O observed was 4.13 wt.% despite common feldspar (Fig. 5). Also affected was the thickness of beds, as indicated by ptgmatic folding of clastic dikes (sand filled mudcracks) in one paleosol (Fig. 3C: 50.6 m in Fig. 4), which average $72 \pm 8.4\%$ of their former assumed straightened thickness. This is comparable with 71% calculated using a standard compaction formula for calcareous soils (Eq. (1) for Aridisols of Sheldon and Retallack (2001) to obtain original thickness of soil (B_s in cm) from thickness of paleosol (B_p in cm) for a likely burial depth (K in km) of 6.5 km (Sarwar and Friedman, 1995), as follows.

$$B_s = B_p / \left[-0.62 / \left(\frac{0.38}{e^{0.17K}} - 1 \right) \right] \quad (1)$$

3. Materials and methods

A stratigraphic section near East Windham, New York, was measured in detail from Durso Corner overlook (N42.33667° W74.13333°) continuously through large road cuts to the top of the Manorkill Formation in August 1995 (Figs. 3 and 4). Different kinds of paleosols (pedotypes) were recognized (Tables 1 and 2), expanding an ongoing pedotype nomenclature for Devonian paleosols of New York and Pennsylvania (Retallack et al., 2009). Pedotype names refer to a particular kind of paleosol, not its location. Thus the Hyner pedotype was named from a type profile at Hyner (Retallack et al., 2009), but comparable paleosols occur also at East Windham (Fig. 4). In addition, a variety of paleoenvironmentally significant measures were taken from the paleosols (Fig. 5): Munsell hue, nodule size,

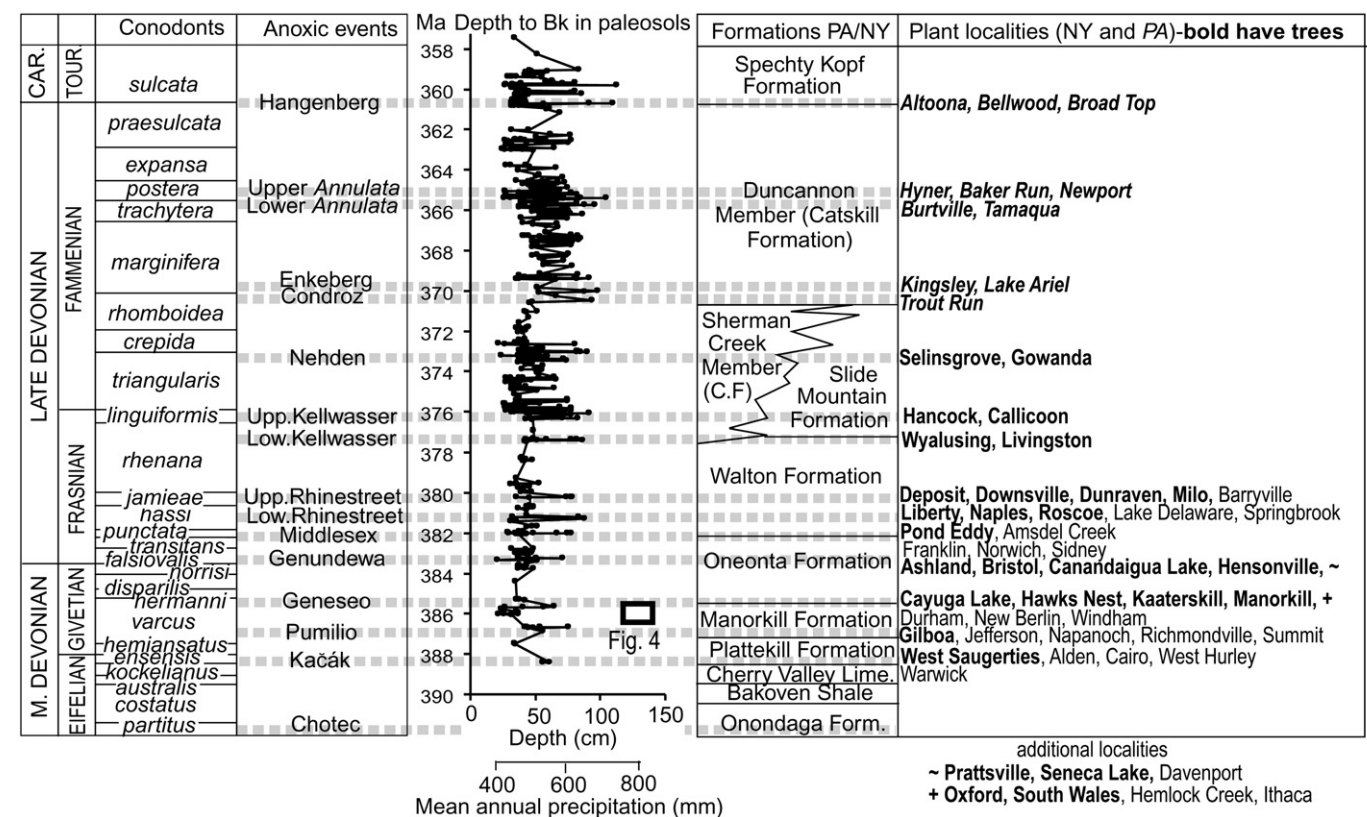


Fig. 2. Geological sequence and stratigraphic level of Devonian and Mississippian fossil plant localities in New York and Pennsylvania compared with a record of paleosol depth to Bk horizon (a proxy for mean annual precipitation, from Retallack, 2009a), used to correlate these sequences with marine anoxic events and conodont zonation (Kaufmann, 2006).

depth to calcareous nodules, thickness of paleosol with nodules and depth of rooting (Retallack, 2001, 2005a). Samples were collected from a representative profile of each pedotype for laboratory analyses (Fig. 5): major and trace element geochemical analysis by XRF, ferrous iron by potassium dichromate titration (both by ALS Chemex of Vancouver, British Columbia), and bulk density determined from the weight suspended in air and then water of a paraffin-coated clod (following Blake and Hartge, 1986). Petrographic thin sections were cut from the same samples, and 500 points counted using a Swift automated point counter to determine grain size distribution and mineral composition (Fig. 5). These and other Devonian paleontological and stratigraphic data (available at website <http://www.uoregon.edu/~dogsci/directory/faculty/greg/about>) allow comparison with modern soil classifications (Food and Agriculture Organization, 1974; Isbell, 1996; Soil Survey Staff, 2001).

Additional observations and stratigraphic sections were made of numerous paleosols elsewhere in New York and Pennsylvania (Retallack, 1985; Retallack et al., 2009). Measurements were made of the following nodular paleosols (not carbonate beds) sampled for carbon isotope study by Cox et al. (2001): Dehli (N42.30105° W74.89786°), Toad Hollow (N42.33100° W74.48225°), Guilford (N42.34039° W75.40309°), East Unadilla (N42.35583° W75.25722°), Mount Hayden (N42.38918° W74.24403°), Potter Hollow (N42.43641° W74.24913°), Gulf Creek (N42.33111° W74.137222°) and Kaaterskill Creek (N42.275556° W74.100253°).

Two datasets relating the height of modern trees to modern environmental variables were also compiled for comparison with Devonian tree sizes. Height of 100 trees was measured using an Optilogic laser hypsometer at each of 10 sites with a soil profile also exposed along a rainfall gradient in western New South Wales, Australia (Table 3). Climatic data for each site was obtained online (www.bom.gov.au/climate/averages/ accessed 11/15/2008). Height

of intertidal fringe (not riverine or basinal) mangrove trees at sites of varied mean annual temperature (Table 4) were compiled from published ecological studies (Clarke and Hannon, 1967; Lacerda et al., 2002; Lin and Wei, 1983; Pool et al., 1977; Spenceley, 1983; Taylor, 1983), with climatic data supplemented from Müller (1982) and online (www.climate-charts.com accessed 8/17/2009).

Representative fossils collected during this work (Figs. 6 and 7) are archived in the Condon Collection, Museum of Natural and Cultural History, University of Oregon, Eugene. Work included compilation of published data on fossil plant diversity, stratigraphic levels, and size of stump casts (Table 5: Beck, 1964; Bridge and Nickelsen, 1985; Bridge and Willis, 1994; Driese and Mora, 1993, 2001; Driese et al., 1997; Elick, 2002; Gordon, 1988; Mintz et al., 2010; White, 1907).

4. Local soil and sedimentary setting

Road cuts along state highway 23 up the Catskill Front to East Windham have long been favored by university geology excursions for their clear exposures of estuarine and fluvial paleochannels, heterolithic cross stratification, and marsh deposits (Fig. 3D–E; Johnson and Friedman, 1969), as well as fossil plants, ostracods and clams (Friedman and Chamberlain, 1995; Friedman and Lundin, 1998; Knox and Gordon, 1999). Information from paleosols (Fig. 3A–B) can now be added to these lines of evidence for Middle Devonian paleoenvironments at East Windham (Fig. 8).

The Manorkill Formation is laterally equivalent to the Panther Mountain and other marine formations with brachiopods, trilobites and crinoids to the west (Brett et al., 2009; Heckel, 1973). It formed within a coastal plain west of the Acadian Mountains of metamorphic and igneous rocks of New Hampshire and Vermont (Sevon and Woodrow, 1985). This was the source of metamorphic rock fragments, quartz and feldspar, which dominate parent materials of

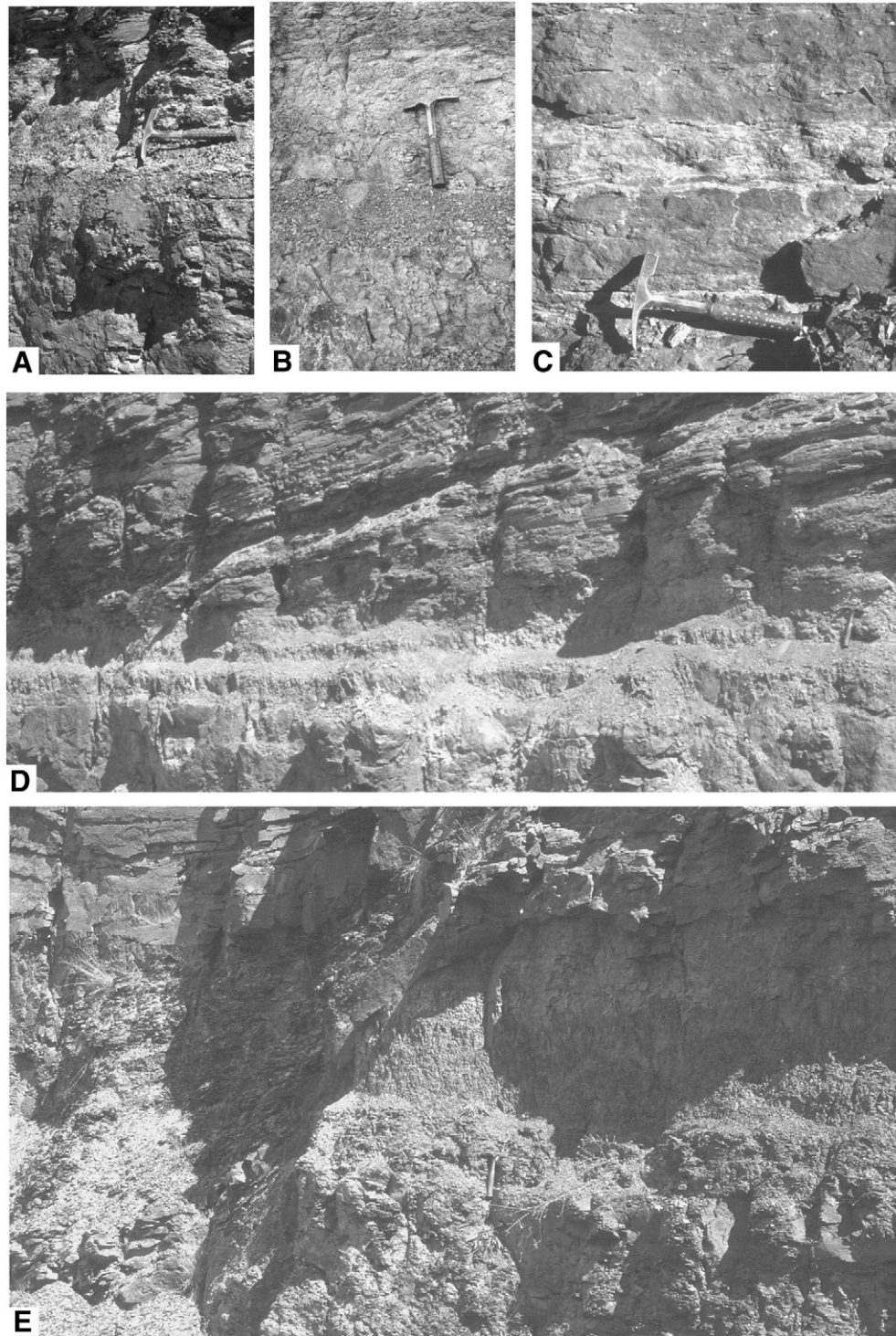


Fig. 3. Sedimentary facies and paleosols from East Windham: A, Farwell over Bucktail pedotype at 49.3 m in measured section; B, Windham pedotype at 33 m; C, prominent mud cracks in Gleasonton pedotype at 50.2 m; D, heterolithic cross strata overlying Sproul pedotype paleosols at 34 m; E, channel incision through Farwell, Bucktail and Sproul pedotypes from 49 to 44 m. Hammer handle for scale in each panel is 25 cm long.

the paleosols (Fig. 5). It was a flat coastal plain judging from steep cut-banks as found in meandering streams (Fig. 3E), low-angle heterolithic cross stratification as found in alluvial levees (Fig. 3D), and carbonaceous siltstones comparable with marsh deposits (Johnson and Friedman, 1969). Fossil ostracods may be evidence of limited marine influence (Friedman and Lundin, 1998; Knox and Gordon, 1999). Small archaenodont bivalves are found elsewhere in tidal flat

assemblages with other marine taxa, but the large (up to 22 cm long) shells of *Archanodon catskillensis* (Fig. 6A) from East Windham appear to have been the earliest known freshwater bivalves (Bridge et al., 1986; Friedman and Chamberlain, 1995). Among modern unionid bivalves, such large sizes are only attained at temperate latitudes (Bauer, 1992) and in large streams, comparable in drainage area with the Ohio and Mississippi Rivers (van der Schalie, 1938). Furthermore,

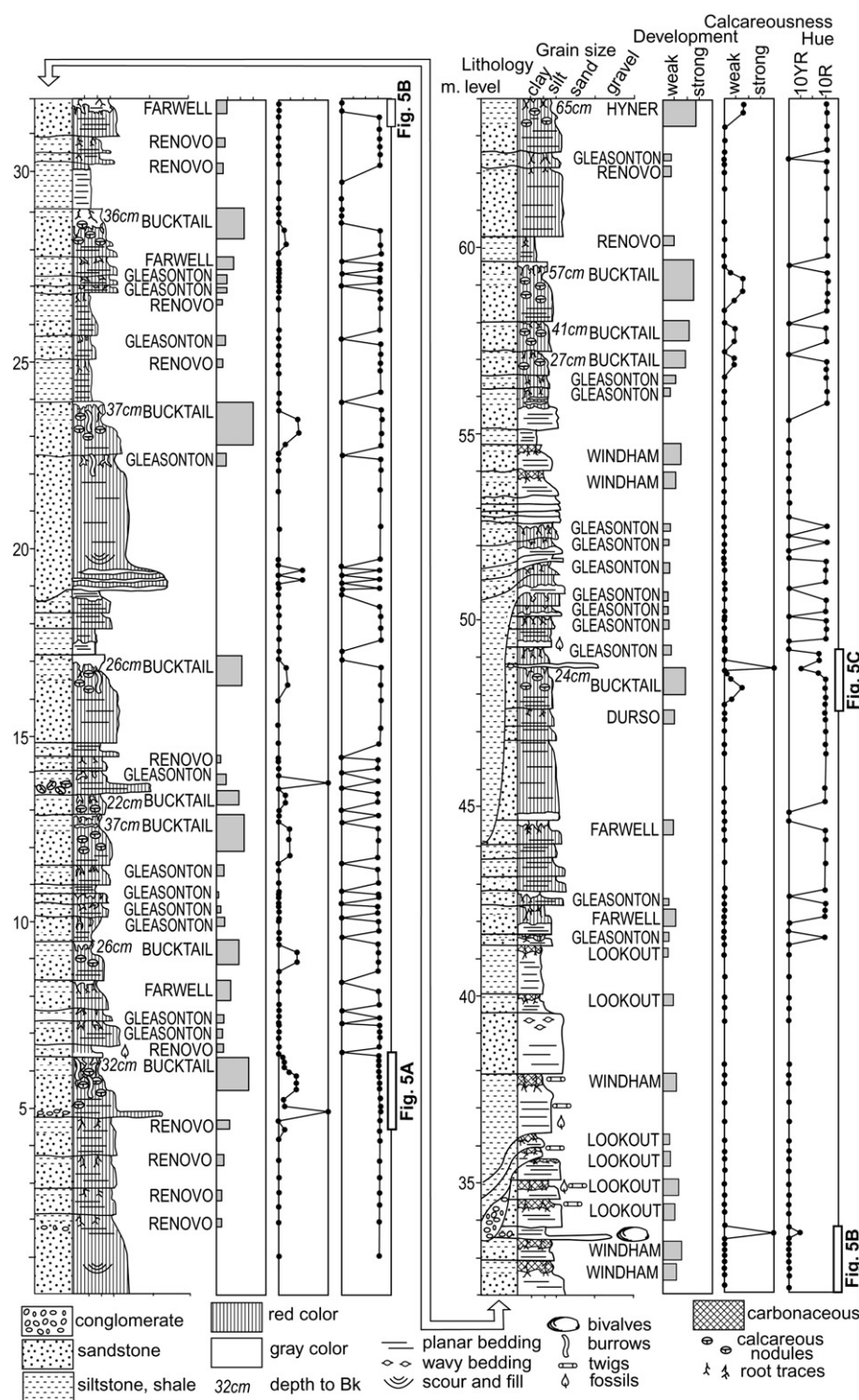


Fig. 4. A geological section of Devonian paleosols on the Catskill Front east of East Windham. Scales for degree of development of the individual paleosols and degree of reaction with HCl are after Retallack (2001).

preservation as molds and casts with corroded umbos (Fig. 6A) is evidence of acidic stream chemistry, and thus little influence of large lakes or shallow marine water.

Gray siltstones associated with paleochannels (marsh deposits of Johnson and Friedman, 1969) include fossil twigs, but also contain common carbonaceous root traces, in paleosols here designated the Windham pedotype (Table 1). Such wetland soils are formed by a combination of continuing increments of sedimentation, organic carbon accumulation and bioturbation by roots and aquatic inverte-

brates. Munsell value of 4 in Windham pedotype paleosols corresponds to an organic carbon content of about 2% by weight for Appalachian Devonian shales (Hosterman and Whitlow, 1981), and plant compressions are too sparsely distributed to qualify as peat. Bioturbation is the most prominent of these processes in formation of the Windham pedotype, which has little trace of sedimentary bedding. For these same reasons, these paleosols are classified as gleyed Inceptisol (Aquept of Soil Survey Staff, 2001), rather than a peaty soil (Histosol) or alluvial soil (Entisol). Histosols were not found

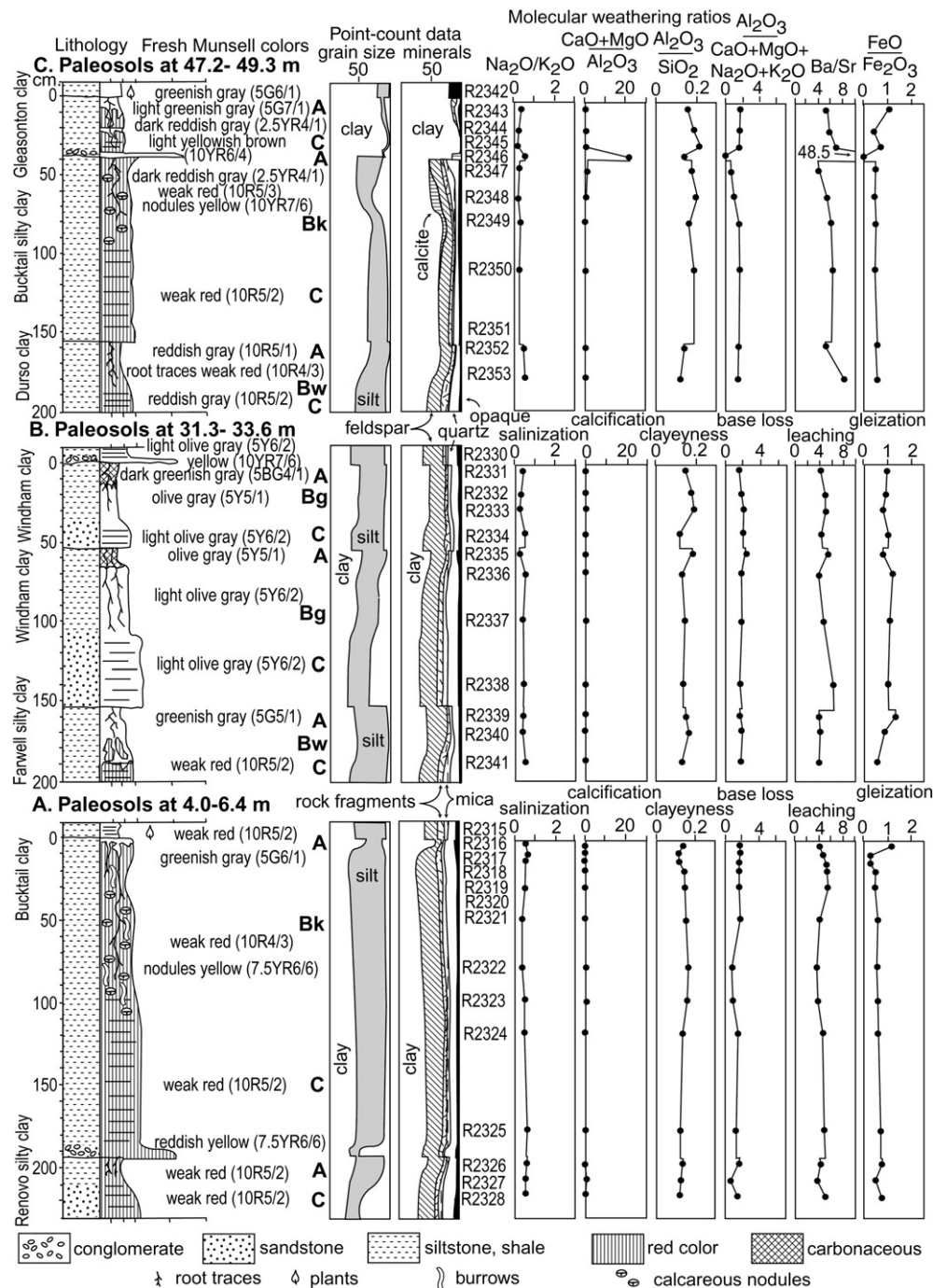


Fig. 5. Petrographic and geochemical data on pedotypes of Devonian paleosols from the East Windham section. Grain size and mineral data is from point counting petrographic thin sections. Molecular weathering ratios are designed as proxy for a variety of weathering reactions.

at East Windham, but green-gray Entisols with well preserved fossil plants (Aquents) are here designated the Lookout pedotype (Table 1), after nearby Point Lookout. The unoxidized Windham and Lookout pedotypes reflect low-lying parts of the coastal plain in which water table was close to the surface throughout the year. Root penetration of up to 81 cm (calculated from observed 58 cm using Eq. (1)) in one Windham pedotype paleosol is evidence that water table fell at least that deep during a dry season. Such water table fluctuations also explain the blocky ped structure and large amount of very decayed organic matter within the Windham pedotype, as also interpreted for comparable Middle Devonian (Givetian) paleosols from Alberta, Canada (Williams et al., 1996).

Other paleosols are red with hematite and reflect well drained parts of the landscape, which had a measurable relief of at least 9.2 m (calculated from observed 6.6 m using Eq. (1)) at the paleochannel cut bank (Fig. 3E, 50.6 m in Fig. 4). Formerly good drainage of these paleosols also is indicated by deeply penetrating root traces and probable millipede burrows (*Beaconites antarcticus* of Gordon, 1988), clay skins in petrographic thin sections, and hydrolytic weathering revealed by chemical base loss (Fig. 5). Many of these paleosols (Hyner, Bucktail, Gleasonton and Farwell pedotypes, but not Durso and Renovo pedotypes) have drab mottles in surficial layers and haloes around root traces down into the reddish matrix lower in the profile. Such features are widespread in red paleosols and interpreted

Table 1
Classification of Devonian pedotypes from East Windham, New York.

Pedotypes	Diagnosis	U.S soil taxonomy (Soil Survey Staff, 2001)	Food and Agriculture Organization (1974)	Australian classification (Isbell, 1996)
Bucktail	Red siltstone with drab-haloed root traces (A) blocky peds, and shallow (<65 cm) calcareous nodules (Bk) over red siltstone (C)	Calcicid	Calcic Xerosol	Calcic Calcarosol
Durso	Red siltstone with red clayey root traces (A) passing down into red siltstone with blocky peds (Bw) over bedded red siltstone (C)	Ochrept	Chromic Cambisol	Red-Orthic Tenosol
Farwell	Red siltstone with drab haloed root traces (A) over slickensided red siltstone (Bw) and bedded siltstone (C)	Ochrept	Chromic Cambisol	Red-Orthic Tenosol
Gleasanton	Red siltstone with drab-haloed root traces (A) over bedded red siltstone (C)	Aquent	Eutric Fluvisol	Oxyaquic Hydrosol
Hyner	Red siltstone with drab-haloed root traces (A) and deep (>65 cm) calcareous nodules (Bk) over bedded red siltstone (C)	Ustert	Chromic Vertisol	Red Vertosol
Lookout	Dark gray shale (O) over green-gray siltstone with carbonaceous root traces (A) over gray siltstone	Fluvent	Humic Gleysol	Sapric Organosol
Renovo	Red siltstone with root traces (A) over bedded red siltstone (C)	Fluvent	Eutric Fluvisol	Stratic Rudosol
Windham	Dark gray shale (O) over green-gray siltstone with carbonaceous root traces (A) over bedded gray siltstone	Aquept	Eutric Fluvisol	Oxyaquic Hydrosol

as burial gleization, a process in which microbial chemical reduction of iron oxides is fueled by consumption of organic matter at the surface of a soil once it has been freshly buried and subsided to near the water table (Retallack, 2001). The alternative explanation of surface-water gleization (chemical reduction by surface ponding) is not favored in this case, because petrographic study (Fig. 5) reveals no discontinuities in clay content or porosity, which would create a perched water table. Hyner, Bucktail, Gleasanton and Farwell pedotypes were thus well drained, lowland soils of alluvial levees and terraces, and stream margins tributary to estuarine and wetland basins with Windham and Lookout pedotypes.

With the exception of the Durso pedotype, other red and mottled pedotypes are based on type profiles in the Late Devonian (Famennian) Duncannon Member of the Catskill Formation near Hyner, Pennsylvania (Retallack et al., 2009). These red and mottled pedotypes are differentiated by degree of disruption of primary bedding and size and depth of carbonate nodules. Sedimentary lamination and ripple marks are obvious between the red-clayey root traces in Renovo and Gleasanton pedotype paleosols, as in comparable alluvial soils of young sedimentary surfaces (Fluvents of Soil Survey Staff, 2001). Such original sedimentary structures are extensively disrupted by blocky ped structure in Durso and Farwell pedotypes, as in alluvial soils that have been forming for a longer period of time (Ochrepts of Soil Survey Staff, 2001). Bucktail and Hyner pedotypes also show clear soil structures including a well differentiated horizon of calcareous nodules with the calcareous micritic calclasepic-porphroskelic petrographic texture, replacive caries texture and displacive fabrics of pedogenic nodules, as opposed to groundwater or

marine nodules (Retallack, 2001). This horizon is shallower than 65 cm in the Bucktail pedotype, as in desert soils (Aridisols of Soil Survey Staff), but deeper than 65 cm in the Hyner pedotype, which also include slickensided shearing characteristic of swelling clay soils (Usterts of Soil Survey Staff, 2001). The calcite of East Windham calcareous nodules is also isotopically light for carbon ($-7.2 \pm 1.2\%$ vs PDB) and oxygen ($-17.7 \pm 1.2\%$ vs PDB analyses of Cox et al., 2001). A cross-plot of carbon vs oxygen isotopic composition of East Windham pedogenic carbonates forms a linear trend, as is typical for soils (Knauth et al., 2003), paleosols (Ufnar et al., 2008) and “meteoric diagenesis” (Knauth and Kennedy, 2009), but unlike unaltered lacustrine or marine carbonate (Railsback et al., 2003).

Relative degree of paleosol development can be quantified from the diameter (S in mm) of calcareous nodules with the petrographic and physical character of pedogenic nodules, which in modern soils is related to soil age (A in ka) by Eq. (2) (with $R^2 = 0.57$; S.E. = ± 1.8 ka from Retallack, 2005a).

$$A = 3.92 \cdot S^{0.34} \quad (2)$$

Application of this equation to East Windham paleosols gives average duration of soil formation of 11 individual Bucktail paleosols of 4.6 ± 1.8 ka (2.6–7.2 ka), and 6.3 ± 1.8 ka for the single Hyner paleosol at the top of the measured section (Fig. 4). These were the oldest and best drained landforms of the Middle Devonian coastal plain. By comparison, very weakly developed paleosols (Lookout, Renovo, Gleasanton pedotypes) represented less than 100 yr of soil formation,

Table 2
Interpretation of Devonian pedotypes from East Windham, New York.

Pedotype	Paleoclimate	Paleovegetation	Former animals	Paleotopography	Parent material	Time for formation
Bucktail	MAT $11.7^\circ \pm 4.4^\circ \text{C}$ MAP 484 ± 147 mm MARF 94 ± 22 mm	Arid shrubland judging from root traces and profile: no plant fossils	<i>Beaconites antarcticus</i>	Dry floodplain	Quartzofeldspathic silts	2–5 kyr
Durso	No indication	Riparian shrubland judging from root traces and profile: <i>Wattieza</i> sp. cf. <i>W. casatii</i>	No trace or body fossils	Fluvial levee	Quartzofeldspathic silts	1–2 kyr
Farwell	No indication	Riparian shrubland judging from root traces and profile: <i>Wattieza</i> sp. cf. <i>W. casatii</i>	No trace or body fossils	Fluvial levee	Quartzofeldspathic silts	0.1–1 kyr
Gleasanton	Subhumid warm-temperate	Early successional scrub judging from root traces and profile: no plant fossils	No trace or body fossils	Fluvial levee	Quartzofeldspathic silts	0.01–0.1 kyr
Hyner	MAT 730 ± 147 mm MARF 80 ± 22 mm	Subhumid woodland judging from root traces and profile: no plant fossils	No trace or body fossils	Dry floodplain	Quartzofeldspathic silts	2–8 kyr
Lookout	No indication	Early successional shrubland judging from root traces and profile: <i>Leclercquia complexa</i> , <i>Tetraxylopteris schmidtii</i>	<i>Archanodon catskillensis</i>	Oxbow lake margin	Quartzofeldspathic silts	1–2 kyr
Renovo	No indication	Dry early successional scrub judging from root traces and profile: no plant fossils	No trace or body fossils	Point bar swales and chutes	Quartzofeldspathic silts	0.01–0.1 kyr
Windham	No indication	Marsh: <i>Wattieza</i> sp. cf. <i>W. casatii</i>	No trace or body fossils	Oxbow lake margin	Quartzofeldspathic silts	0.1–0.2 kyr

Table 3

Stations for observations of modern tree height in N.S.W., Australia.

Locality	Coordinates	Common species	Weather station	Mean annual precipitation (mm)	Mean height (m)	Tallest plant (m)	A horizon thickness (cm)	Depth to Bk (cm)
Gunbar	S33.95894 E145.12595	<i>Sclerolaena tricuspidis</i>	Hay/Hillst.	202.5	0.3 ± 0.1	1.42	16	16
Booligal	S34.03244 E144.82653	<i>Chenopodium nitrarium</i>	Hay/Ivan.	203.9	1.0 ± 0.3	1.54	17	21
L. Mungo	S33.74500 E143.08167	<i>Atriplex nummularia</i>	L. Mungo	225.9	0.3 ± 0.08	0.52	9	23
Damara	S34.154190 E143.32983	<i>Eucalyptus incrassata</i>	Balr./L. M.	273.8	7.4 ± 1.5	10.7	30	35
Goolgowi	S34.00914 E145.66322	<i>Callitris columellaris</i>	Wya./Hills.	299	11.1 ± 2.5	16.1	27	34
Balranald	S34.55142 E143.58503	<i>Eucalyptus socialis</i>	Balranald	321.7	7.5 ± 1.5	11.24	12	37
Maude	S34.465468 E144.32517	<i>Eucalyptus largiflorens</i>	Hay	363.7	10.3 ± 2.1	13.9	30	37
Back Cr.	S33.86613 E147.35642	<i>Casuarina cristata</i>	Wyalong	476	15.7 ± 2.8	19.8	23	65
Narrandera	S34.75156 E146.50253	<i>Eucalyptus melliodora</i>	Narrandera	482.5	14.7 ± 2.6	21.1	17	52
Bland Cr.	S33.76181 E147.51970	<i>Eucalyptus bridgesiana</i>	Marsden	506.5	13.9 ± 3.2	20.9	32	60

Note: Climate data www.bom.gov.au/climate/averages/ accessed 11/15/2008.

and weakly developed paleosols (Windham, Durso, Farwell pedotypes) represented not much more than 1000 yr. This was a youthful landscape compared with coasts of plate-tectonic passive margins, such as the modern coastal plain of the southeastern US, where soils 500-kyr-old are widespread (Markewich et al., 1990). A better modern analog is the Indus river of Pakistan, where soil development is limited by high sedimentation rate from Himalayan sources (Ahmad et al., 1977). Summing the durations of paleosols indicated earlier for the 64 m measured section at East Windham gives a rock accumulation rate of 0.90 mm yr⁻¹, which can be converted to a sediment accumulation rate (using Eq. (1)) of 1.27 mm yr⁻¹. These estimates support the idea of synorogenic deposition of the Manorkill Formation (Barrell, 1913; Sevon and Woodrow, 1985), although its mountainous source was not of Himalayan scale.

5. Paleoprecipitation

Paleosols are archives of former mean annual precipitation and mean annual range of precipitation from depth to, and spread of, calcareous nodules, and from intensity of chemical weathering of clayey matrix. Depth to carbonate nodules in soils (D_o in cm) increases with mean annual precipitation (R in mm following Eq. (3) with

$R^2 = 0.52$, and standard error ± 147 mm from Retallack, 2005a). Thickness of soil with carbonate, or distance between lowest and highest nodule in the profile (H_o in cm), also increases with mean annual range of precipitation, which is the difference in monthly mean precipitation between the wettest and driest month (M in mm: using Eq. (4) with $R^2 = 0.58$; S.E. = ± 22 mm recalculated from Retallack, 2005a).

$$R = 137.24 + 6.45D_o - 0.013D_o^2 \quad (3)$$

$$M = 0.79H_o + 13.71 \quad (4)$$

Depths in paleosols could have been compromised by surficial erosion under paleochannels (Cotter and Driese, 1998) or vertic displacement (Miller et al., 2007; Nordt et al., 2006), but these are not problems for paleosols of East Windham, where calcic paleosols are remote from paleochannels and paleosol surfaces are defined by drab-haloed root traces showing no sign of microrelief formed by vertic displacement (Figs. 3–5). Higher than modern atmospheric CO₂ may increase depth to carbonate nodules in soils, but an increase from 280 to 3080 ppmv modeled by McFadden and Tinsley (1985) increased depth to pedogenic carbonate only 5 cm, so this correction is not made here. However,

Table 4

Stations for observations of mangrove height.

Location	Coordinates	Weather station	Mean annual temperature (°C)	Mangal height (m)	Source
Isla Juan Venado, Nicaragua	N12.357853 W87.008156	Managua	27.3	14	Lacerda et al. (2002)
Aguirre, Puerto Rico	N17.943494 W66.272989	San Juan	26.9	12	Pool et al. (1977)
Punta Gorda, Puerto Rico	N17.928202 W66.936783	San Juan	26.9	7	Pool et al. (1977)
Santa Rosa, Costa Rica	N10.851256 W85.794653	Puntarenas	26.9	10	Pool et al. (1977)
Laguna de Cosinetas, Venezuela	N11.840074 W71.340535	Maracaibo	27.4	7	Lacerda et al. (2002)
Morrocoy, Venezuela	N10.878871 W68.222421	Maracaibo	27.4	11	Lacerda et al. (2002)
Tacarigua, Venezuela	N10.536077 W66.107568	Maracaibo	27.4	9.5	Lacerda et al. (2002)
Ceiba, Puerto Rico	N18.275888 W65.629059	San Juan	26.9	8.5	Pool et al. (1977)
Estero Pargo, Mexico	N18.743834 W91.550332	Merida	25.8	6	Lacerda et al. (2002)
Majana, Cuba	N22.686655 W82.793074	Havana	25.1	10	Lacerda et al. (2002)
Townsville, Australia	S19.272357 E146.835756	Townsville	24.2	8	Spenceley (1983)
Marismas, Mexico	N22.243437 W97.8000030	Tampico	24.3	5.2	Lacerda et al. (2002)
Ten Thousand Islands, Florida	N25.788165 W81.424294	Miami	23.9	7.3	Pool et al. (1977)
Agua Brava, Mexico	N22.175036 W105.616030	Acapulco	27.7	7.5	Lacerda et al. (2002)
Lechuguilla, Mexico	N25.659523 W109.384900	Mazatlan	24.2	4.5	Lacerda et al. (2002)
Sipacate, Guatemala	N13.919239 W91.81699	San Salvador	22.8	9	Lacerda et al. (2002)
Sepetiba, Brazil	S25.055224 W43.935970	Rio de Janeiro	22.7	6.1	Lacerda et al. (2002)
Ilha Comprida, Brazil	S24.681684 W47.436396	Rio de Janeiro	22.7	8.6	Lacerda et al. (2002)
Tiandong, Hui-an, China	N25.086640 W118.875029	Jinjiang	20.4	0.65	Lin and Wei (1983)
Sucuo, Hui-an, China	N24.897865 W118.687102	Jinjiang	20.4	0.8	Lin and Wei (1983)
Dongyuan, Hui-an, China	N25.016863 W118.942799	Jinjiang	20.4	0.57	Lin and Wei (1983)
Xiyuan, Hui-an, China	N24.937631 W118.902517	Jinjiang	20.4	0.6	Lin and Wei (1983)
Kaitaia, New Zealand	S35.000128 E173.260196	Kaitaia	19.6	8	Taylor (1983)
Wooloware Bay, Australia	S34.004229 E151.156549	Sydney	17.4	6	Clarke and Hannon (1967)
Auckland, New Zealand	S36.798133 E174.765230	Auckland	15.2	1	Taylor (1983)

Note: Climate data from Müller (1982); Pool et al. (1977), Lin and Wei (1983), and www.climate-charts.com accessed 8/17/2009.

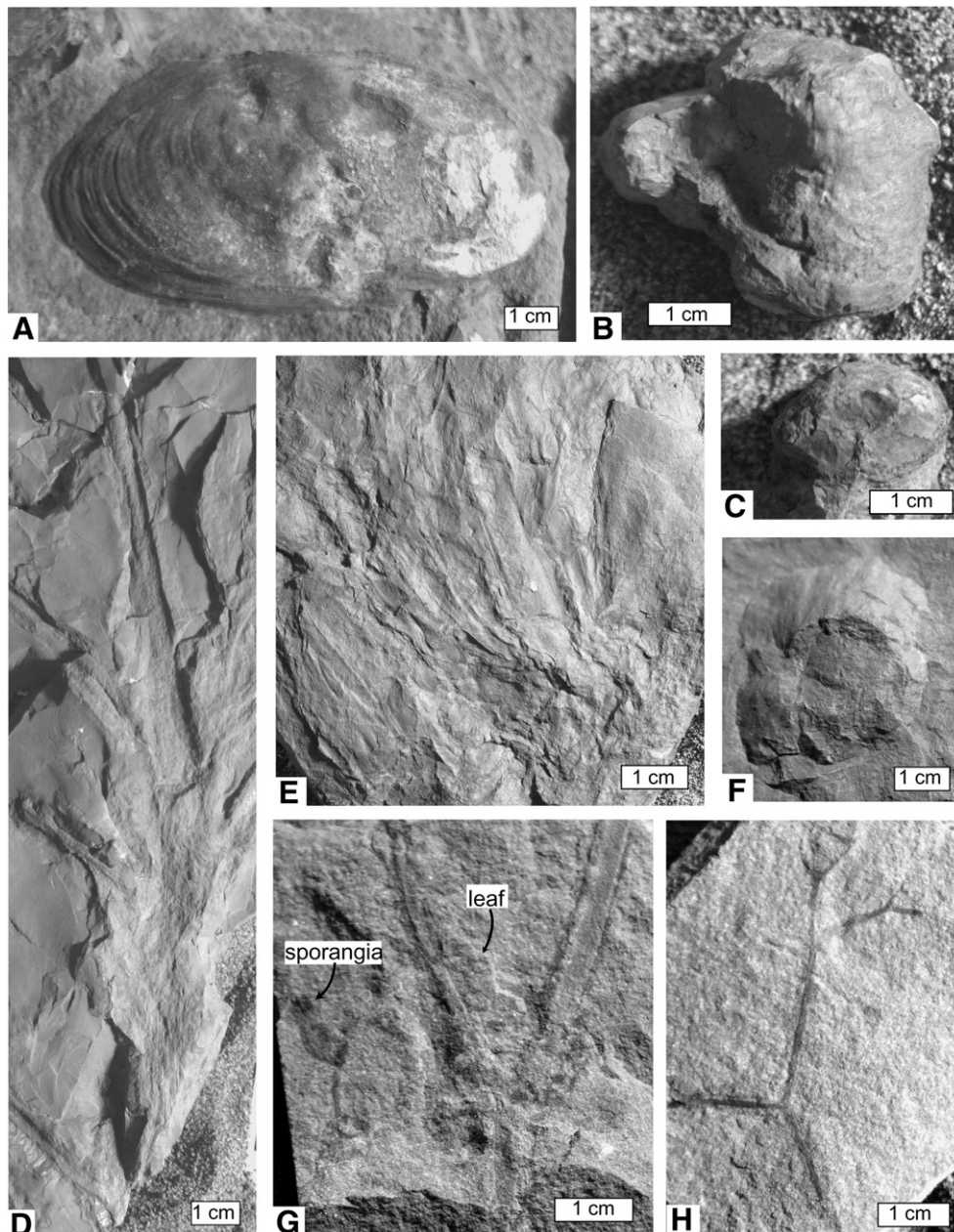


Fig. 6. Fossil plants and mollusc from road cuts east of East Windham, New York: A, *Archaeonodon catskillensis* from 33.5 m in measured section; B–C, lateral and basal views stem base from 22.3 m; D, deciduous branch from 49.3 m; E–F, stem apex and base in growth position with deciduous branches from 6.6 m; G–H, *Leclercqia complexa* partly decorticated leafy stem, from 36.5 m; G–H, *Rellimia thomsoni*, sporangia (G to left) and branches (H), from 36.5 m. Specimens in Condon Collection, University of Oregon are F112798A (A), F112807 (B–C), F112805 (D), F112795A (E), F112794B (F), F112803A (G), and F112800B (H).

allowance does need to be made for burial compaction of depth to Bk and thickness of soil with nodules, using Eq. (1) described earlier.

Additional indications of paleoprecipitation come from chemical index of alteration without potash ($A = 100\text{mAl}_2\text{O}_3 / (\text{mAl}_2\text{O}_3 + \text{mCaO} + \text{mMgO} + \text{mNa}_2\text{O})$, in moles), which increases with mean annual precipitation (R in mm) in modern soils (Eq. (5) with $R^2 = 0.72$; S.E. = ± 182 mm from Sheldon et al., 2002).

$$R = 221e^{0.0197A} \quad (5)$$

These two distinct methods of obtaining paleoprecipitation are needed because depth to Bk is highly correlated with plant productivity as well as mean annual precipitation in modern soils (Retallack, 2009c), and lower productivity vegetation before the evolution of trees may have produced shallower Bk horizons than today for the same

precipitation and degree of chemical weathering. Data from paleosols of the Manokill Formation at East Windham do not support a bias of Bk estimates lower than chemical estimates of paleoprecipitation. The two different estimates of paleoprecipitation are statistically indistinguishable: 401 ± 147 mm from depth to Bk and 528 ± 182 mm from chemistry of a Bucktail paleosol at 48.8 m, and 477 ± 147 mm from depth to Bk and 642 ± 182 mm from chemistry of another Bucktail paleosol at 6.3 m (Fig. 4). Middle Devonian paleosols were also comparable in weathering with Miocene paleosols of comparable paleoclimate (Retallack, 1991). Comparability of paleoprecipitation estimates from chemical weathering and Bk depth also hold for Silurian, paleosols, with the expected productivity bias first noticeable during the Ordovician (Retallack, 1997a, 2008a).

Average estimates of 484 ± 147 mm mean annual precipitation and 94 ± 22 mm mean annual range of precipitation come from 11

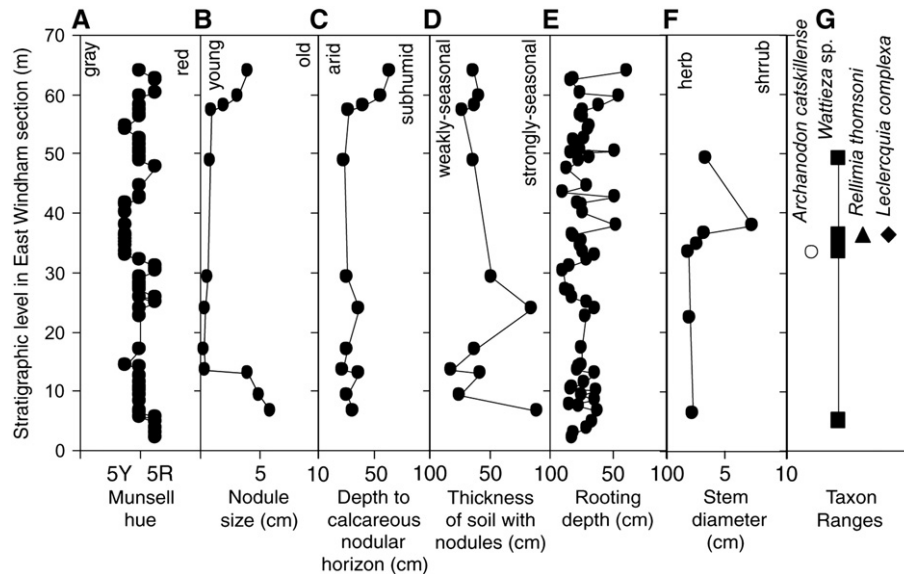


Fig. 7. Paleoclimatic and paleoecological proxies from a measured section of paleosols near East Windham, New York.

Bucktail pedotype Bk horizons. In contrast, the Hyner pedotype paleosol at 64 m in the East Windham section has a Bk depth indicative of 730 ± 147 mm mean annual precipitation and Bk spread indicative of 80 ± 22 mm mean annual range of precipitation. This contrast between common shallow-calcic (Bucktail pedotype) and occasional deep-calcic (Hyner pedotype) paleosols is characteristic of Devonian paleosols of Pennsylvania and New York (Fig. 9B). Deep-calcic paleosols such as the Hyner pedotype, occur at irregular intervals that are longer than Milankovitch scale (>100 ka) variation in depth to carbonate (Retallack et al., 2009), and can be used as marker beds for correlation (Retallack, 2009a,b). These calculations thus confirm the semiarid nature of most Catskill paleosols, as proposed by Barrell (1913), but not his interpretation that these were monsoonal soils (mean wet month-dry month precipitation difference of more than 100 mm: Retallack, 2005a). Nevertheless, both Hyner and Bucktail paleosols at Manorkill are evidence of stronger seasonality of precipitation than other Devonian paleosols of New York and Pennsylvania (Fig. 9A).

6. Paleotemperature

Deriving paleotemperature from isotopic composition of oxygen ($\delta^{18}\text{O}_c$) in soil carbonate (Dworkin et al., 2005) is unreliable for these paleosols because of metamorphic alteration of oxygen isotopic composition (Mora et al., 1998). Better paleotemperature proxies for paleosols are alkali index ($N = (\text{K}_2\text{O} + \text{Na}_2\text{O})/\text{Al}_2\text{O}_3$ as a molar ratio) or chemical index of clayeyness ($I = \text{Al}_2\text{O}_3/\text{SiO}_2$, as a molar ratio), which is related to mean annual temperature (T in $^\circ\text{C}$) in modern soils by Eqs. (6) and (7) respectively ($R^2 = 0.37$; S.E. = ± 4.4 $^\circ\text{C}$ for Eq. (6), and $R^2 = 0.96$; S.E. = ± 0.6 $^\circ\text{C}$ for Eq. (7)). Eq. (6) applies over many kinds of modern soils (Sheldon et al., 2002), but Eq. (7) is only for Inceptisols (Sheldon, 2006).

$$T = -18.5N + 17.3 \quad (6)$$

$$T = 46.94I + 3.99 \quad (7)$$

Both estimates are useful because of potential illitization (Mora et al., 1998), which would effect Eq. (6) but not (7). Low potash and high feldspar content is evidence against extensive illitization (Fig. 5), and so is the comparable paleotemperature from two Bucktail paleosols

chemically analyzed: 11.7 ± 4.4 $^\circ\text{C}$ using Eqs. (6) and 11.8 ± 0.6 $^\circ\text{C}$ using Eq. (7). These results are evidence that Devonian paleoclimate of New York was temperate, not tropical as proposed by Barrell (1913). Thus Bucktail paleosols are evidence of paleotemperature compatible with a modern climate at latitude 35°S , which is the paleolatitude proposed for Late Devonian New York by J. Golonka for Joachimski et al. (2002). Hyner paleosols on the other hand, are evidence of unusually warm paleoclimates at that paleolatitude (Retallack et al., 2009).

7. Paleo- CO_2

Estimates of atmospheric CO_2 from Devonian paleosols have been used to argue for long-term drawdown of atmospheric CO_2 after the advent of woodlands (Cox et al., 2001; Mora et al., 1996; Retallack, 1997a), but both climatic and CO_2 estimates now reveal considerable variation, particularly in the early stages of woodland evolution (Fig. 9). No new carbon isotopic analyses are presented here, but the results of Cox et al. (2001) have been revised for subsequently discovered refinements in estimating atmospheric isotopic composition, temperature-dependent fractionations and soil productivity effects (Retallack, 2009c).

Paleosol-based estimates of past atmospheric CO_2 (P_a in ppmv) come from the balance between isotopically light soil CO_2 ($\delta^{13}\text{C}_s$) compared with isotopically heavy atmospheric CO_2 ($\delta^{13}\text{C}_a$) of Eq. (8) (Ekart et al., 1999). A variety of terms in the governing equation are derived from other analyses and transfer functions. The isotopic composition of soil CO_2 ($\delta^{13}\text{C}_s$) comes from that of pedogenic carbonate ($\delta^{13}\text{C}_c$) using temperature (T in $^\circ\text{C}$) dependent fractionation from Eq. (9) ($R^2 = 0.93$, S.E. = $\pm 0.28\%$: Romanek et al., 1992). The isotopic composition of associated soil organic matter ($\delta^{13}\text{C}_o$) is used as a proxy for respired soil CO_2 ($\delta^{13}\text{C}_r$) and also to calculate the isotopic composition of atmospheric CO_2 ($\delta^{13}\text{C}_a$) following Eq. (10) ($R^2 = 0.34$, S.E. = $\pm 0.0039\%$: Arens et al., 2000). Finally, partial pressure of respired CO_2 in soil (P_r) is derived from its known relationship with depth to carbonate nodules (D_o , corrected for compaction in paleosols using Eq. (1)) in modern soils expressed in Eq. (11) ($R^2 = 0.80$, S.E. = ± 893 ppmv: Retallack, 2009c).

$$P_a = P_r \cdot \frac{(\delta^{13}\text{C}_s - 1.0044 \cdot \delta^{13}\text{C}_r - 4.4)}{(\delta^{13}\text{C}_a - \delta^{13}\text{C}_s)} \quad (8)$$

Table 5
Diameters, heights and paleoclimate of Devonian wood from New York.

Taxon	Preservation style	No.	Locality	Reference	Stratigraphic level (m)	Stem diameter at breast height (cm)	Paleosol Bk depth (cm)	Paleosol Al ₂ O ₃ /SiO ₂ molar ratio	Estimated tree height (m)	Mean annual precipitation (mm)	Mean annual temperature (°C)
<i>Wattieza</i>	C	1	Pond Eddy	Herein	1066	18	46		4.7 ± 0.9	595 ± 147	
<i>Wattieza</i>	S	1	Wyalusing	Elick (2002)	858.6	26.6	75		6.7 ± 0.9	790 ± 147	
<i>Wattieza</i>	S	2	Kaaterskill	Bridge and Nickelsen (1985)	661.7	24.5	71		6.2 ± 0.9	757 ± 147	
<i>Wattieza</i>	S	4	Prattsville	Herein	592.3	12	42		3.3 ± 0.9	559 ± 147	
<i>Wattieza</i>	C	5	Manorkill	Stein et al. (2007)	336	45	65		10.7 ± 0.9	730 ± 147	
<i>Wattieza</i>	C	4	Windham	Herein	320.8	3.3	24	0.2028	1.0 ± 0.9	401 ± 147	13.5 ± 0.6
<i>Wattieza</i>	C	5	Windham	Herein	289.2	1.8	26	0.1386	0.6 ± 0.9	421 ± 147	10.5 ± 0.6
<i>Wattieza</i>	P	3	Windham	Herein	284.9	2	37	0.1386	0.7 ± 0.9	522 ± 147	10.5 ± 0.6
<i>Wattieza</i>	P	8	Windham	Herein	278.7	2.2	32	0.1386	0.7 ± 0.9	477 ± 147	10.5 ± 0.6
<i>Wattieza</i>	S	61	Gilboa	Bridge and Willis (1994)	196.3	36	76		8.8 ± 0.9	793 ± 147	
<i>?Duisbergia</i>	S	20	W. Saugerties (1)	Mintz et al. (2010)	— 39	6.8	61		2.4 ± 0.9	705 ± 147	
<i>Callixylon</i>	S	1	Newport	Driese and Mora (1993)	1232	6	42	0.0840	1.8 ± 0.9	569 ± 147	7.9 ± 0.6
<i>Callixylon</i>	S	1	Livingston	Gordon (1988)	1162	9	53		2.5 ± 0.9	648 ± 147	
<i>Callixylon</i>	S	1	Trout Run	Driese et al. (1997)	1086	30	98		7.4 ± 0.9	884 ± 147	
<i>Callixylon</i>	C	1	Deposit	Beck (1964)	1068	15	74		4.0 ± 0.9	775 ± 147	
<i>Callixylon</i>	S	1	Wyalusing	Elick (2002)	858.6	14	75		3.8 ± 0.9	790 ± 147	
<i>Callixylon</i>	S	1	Hancock	Retallack (1985)	384.1	15	73		4.0 ± 0.9	766 ± 147	
<i>Callixylon</i>	C	1	Hancock	Herein	381.4	30	92	0.2072	7.4 ± 0.9	854 ± 147	13.7 ± 0.6
<i>Callixylon</i>	S	1	Kaaterskill	Gordon (1988)	336	15	65	0.2028	4.0 ± 0.9	730 ± 147	13.5 ± 0.6
<i>Callixylon</i>	S	2	E. Windham	Mintz et al. (2010)	336	12.6	65		3.4 ± 0.9	730 ± 147	
<i>?Svalbardia</i>	S	6	W. Saugerties (2)	Mintz et al. (2010)	196	10.5	70		2.9 ± 0.9	760 ± 0.9	
<i>Lepidosigillaria</i>	C	1	Naples	White (1907)	1068	19	79		4.9 ± 0.9	795 ± 147	
<i>Lepidosigillaria</i>	S	1	Selinsgrove	Driese and Mora (2001)	1034	17	74		4.5 ± 0.9	795 ± 147	

Note: Preservation styles include stump casts (S), organic log compression (C), inorganic log impression (I), and pyretic permineralized log (P). No. is the number of stumps and stems observed.

$$\delta^{13}C_s = \frac{\delta^{13}C_c + 1000}{\frac{11.98 - 0.12 \cdot T}{1000} + 1} - 1000 \quad (9)$$

$$\delta^{13}C_a = \frac{(\delta^{13}C_o + 18.67)}{1.1} \quad (10)$$

$$P_r = 66.7D_o + 588 \quad (11)$$

Standard error of estimates of atmospheric CO₂ using Eq. (8) was calculated by Gaussian error propagation of the five component standard errors (following Retallack, 2009c). The largest component of error comes from respired soil CO₂ partial pressure ($P_r \pm 893$ ppmv), but propagated error is less than that in proportion to averages of 10,685 ppmv respired CO₂ in 3 individual Hyner paleosols, and 7110 ppmv CO₂ in 4 Bucktail paleosols. Of the various carbon isotopic compositions ($\delta^{13}C$) needed for Eq. (8), the isotopic composition of carbonate ($\delta^{13}C_c$) was from Cox et al. (2001). Two other quantities ($\delta^{13}C_a$ and $\delta^{13}C_r$) were derived from carbon isotopic composition of coexisting organic matter ($\delta^{13}C_o$) taken as -27.2% for the Catskill Formation in Pennsylvania (Mora et al., 1996), which is lower than usual for Late Devonian plants (Peters-Kottig et al., 2006). Paleotemperature was calculated using Eq. (6), and paleoproductivity using Eq. (11), for Bk depths corrected for compaction using Eq. (1).

Atmospheric CO₂ levels calculated using these equations from a single Hyner pedotype paleosol is 3923 ± 415 ppmv, but for 14 individual Bucktail paleosols is 2263 ± 238 ppmv. Thus CO₂ levels were generally high but showed excursions of an additional 1700 ppmv at times of unusually warm and wet paleoclimate (Fig. 9C). This result is very similar to Late Devonian (366 Ma) paleosols from Hyner, Pennsylvania (Retallack et al., 2009), where atmospheric CO₂ levels calculated using these equations from 3 individual Hyner paleosols

were 3742 ± 320 ppmv, and from 4 Bucktail paleosols were 2009 ± 258 ppmv. These estimates are comparable with those of Cox et al. (2001), and were elevated compared with 700–1275 ppmv calculated by Mora et al. (1996) for shallow-calcic paleosols of the Duncannon Member of the Catskill Formation. These data support the supposition of long term drawdown of CO₂ in shallow calcic paleosols (Bucktail) from Middle Devonian levels of ca. 2200 ppmv to late Devonian levels of ca. 1000 ppmv based on data of low temporal resolution (Cox et al., 2001; Mora et al., 1996; Retallack, 1997a,b,c). The refined stratigraphic sampling presented here now resolves long-term decline into a sequence with long episodes of low CO₂ punctuated by transient warm–wet climatic spikes, when CO₂ soared to ca. 3800 ppmv. These greenhouse climatic spikes align in time with named marine anoxic events (Fig. 9), and are also marked in marine rocks by pyritic black shales and major overturns in invertebrate faunas (Brett et al., 2009).

8. Carbon sequestration

The advent of trees has been considered a boost to carbon sequestration of terrestrial (Berner, 1997; Retallack, 1997a), and marine ecosystems (Algeo and Scheckler, 1998). Carbon sequestration in soils was promoted by increased silicate weathering consuming carbonic acid, and exporting through groundwater to the sea bicarbonate and nutrient cations, which promoted carbonate precipitation (now limestone), algal productivity, anoxia and carbon burial (now black shale) at sea. Carbon burial in peaty soils (now coals) also played a role, although woody (vitrinite-rich) peats appear only in the Late Devonian (Frasnian: Scheckler, 1986; Retallack et al., 1996), and other kinds of peat such as the Rhynie Chert (Rice et al., 1995) and Barzass Coal (Krassilov, 1981) were formed in marshes of Early Devonian herbaceous plants.

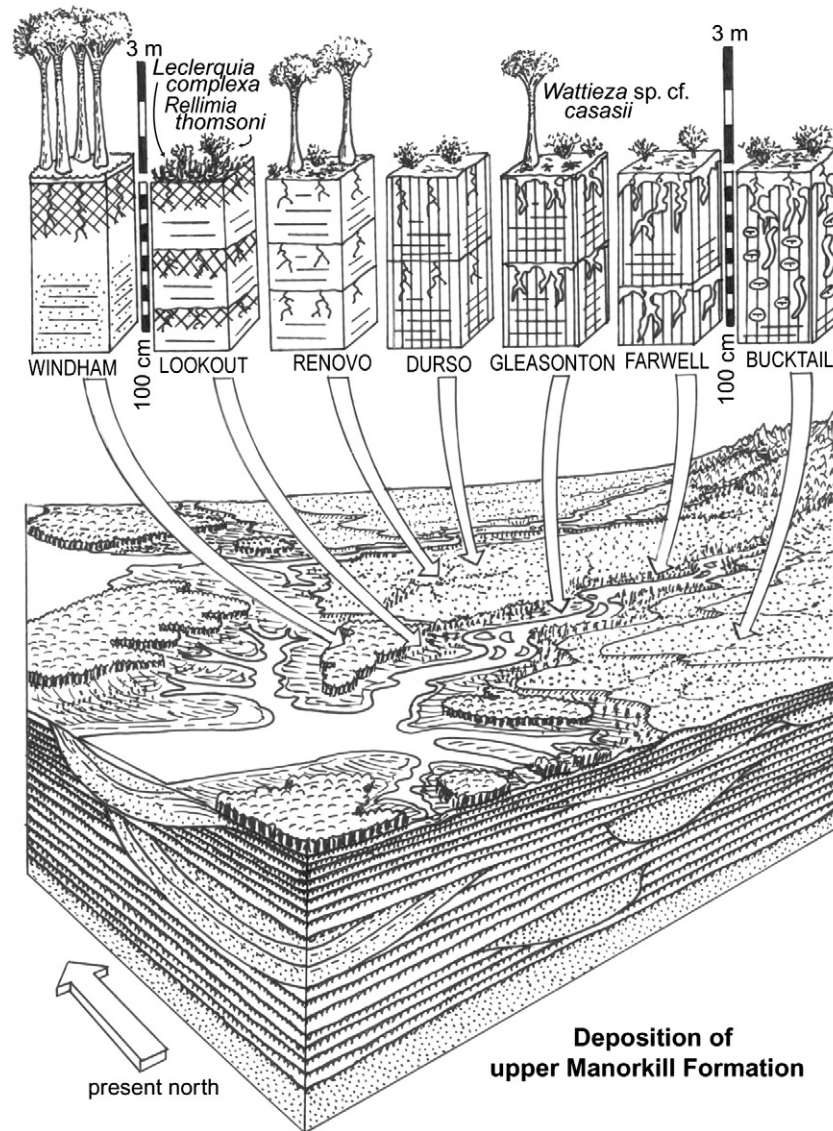


Fig. 8. A reconstruction of Middle Devonian landscapes, vegetation and soils in New York.

The mass transfer of elements in a soil at a given horizon (τ_{wj} in moles) can be calculated from the bulk density in the soil (ρ_w in g cm^{-3}) and in the parent material (ρ_p in g cm^{-3}) and from the chemical concentration of the element in soils ($C_{j,w}$ in weight %) and parent material ($C_{j,p}$ in weight %), and from the strain indicated by an immobile element in soil (such as Ti used here) compared with parent material ($\varepsilon_{i,w}$ as a fraction), using Eqs. (12) and (13) (Brimhall et al., 1992; Sheldon and Tabor, 2009).

$$\tau_{j,w} = \left[\frac{\rho_w \cdot C_{j,w}}{\rho_p \cdot C_{j,p}} \right] [\varepsilon_{i,w} + 1] - 1 \quad (12)$$

$$\varepsilon_{i,w} = \left[\frac{\rho_p \cdot C_{i,p}}{\rho_w \cdot C_{i,w}} \right] - 1 \quad (13)$$

Parent materials of paleosols in the Manokill Formation are sedimentary rocks derived from erosion of soils, and so are not as ideal for this kind of analysis as paleosols developed on crystalline rocks (Retallack and Mindszenty, 1994). Nevertheless, the strain and elemental mass transfer of Devonian paleosols from East Windham can be compared with that of dry-woodland paleosols from the

Miocene Dhok Pathan Formation of Pakistan (Retallack, 1991). The degree of silicate weathering of Devonian and Miocene alluvial paleosols is comparable (Fig. 10), and by inference so was productivity and carbon sequestration (Berner, 1997). The analyzed paleosols from East Windham appear to have supported shrublands (<2 m tall) rather than woodlands (Tables 2 and 5), and chemical weathering in Devonian and Silurian shrubland precursors of dry woodlands of calcareous soils was comparable with modern arid shrublands (see also Retallack, 1997a). The geographic spread and increased thickness of woody peats during the Late Devonian (Frasnian to Famennian) is another likely cause of long-term CO_2 drawdown and global cooling which culminated in Famennian ice-caps in Brazil (Isaacson et al., 2008), and Tournaisian montane glaciers in Pennsylvania and Maryland (Brezinski et al., 2008). These events postdate the latest Emsian appearance of trees in Spitzbergen (Schweitzer, 1999), and may represent long-term geographic expansion of swamps and dry woodlands, despite numerous reversals.

9. Sizes of Devonian trees

Devonian trees are represented in New York by compressed and permineralized wood and stump casts (*Callixylon*), sterile and fertile

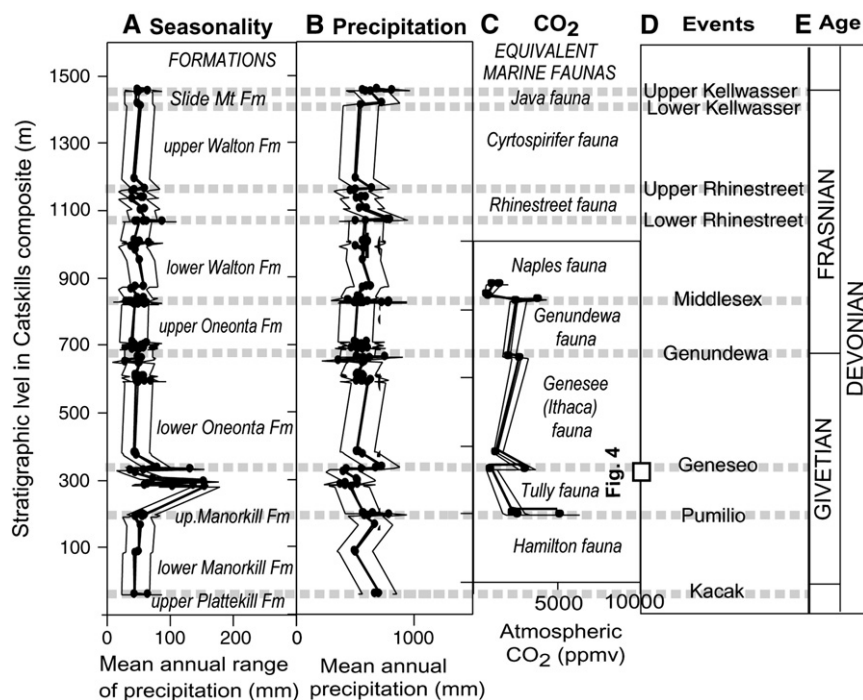


Fig. 9. Paleoclimatic and pCO₂ estimates from Middle (Givetian) to Late (Frasnian) Devonian paleosols of the Catskill Mountains, New York.

leafy shoots (*Archaeopteris*; Banks et al., 1985) of progymnosperms, and large compressions of lycopsids (*Lepidosigillaria*; White, 1907) and cladoxylaleans (*Wattieza*, including well known “Gilboa trees”: Stein et al., 2007). The very different architecture of these plants may reflect ecological differences: *Callixylon* has strongly tapering, deeply penetrating and spreading basal roots (Meyer-Berthaud et al., 1999), whereas *Wattieza* has a bulbous basal trunk that is rounded with spreading fine adventitious roots (Stein et al., 2007). Ecological differences have been investigated using evidence from fossil soils,

which suggest well drained alluvial soils (Psamments, Dystrochrepts, and Usterts) for *Callixylon*, and poorly drained mangrove soils (Aquepts and Sulfaquepts) for *Wattieza* (Driese et al., 1997; Mintz et al., 2010; Retallack, 1985).

The measured section of paleosols (Fig. 4) at East Windham is stratigraphically above the first known New York occurrence of cladoxyls such as *Wattieza* and progymnosperms such as *Callixylon*–*Archaeopteris* (Fig. 11). The oldest cladoxyl stumps (West Saugerties locality 1 of Mintz et al., 2010) are intermediate between *Wattieza* and

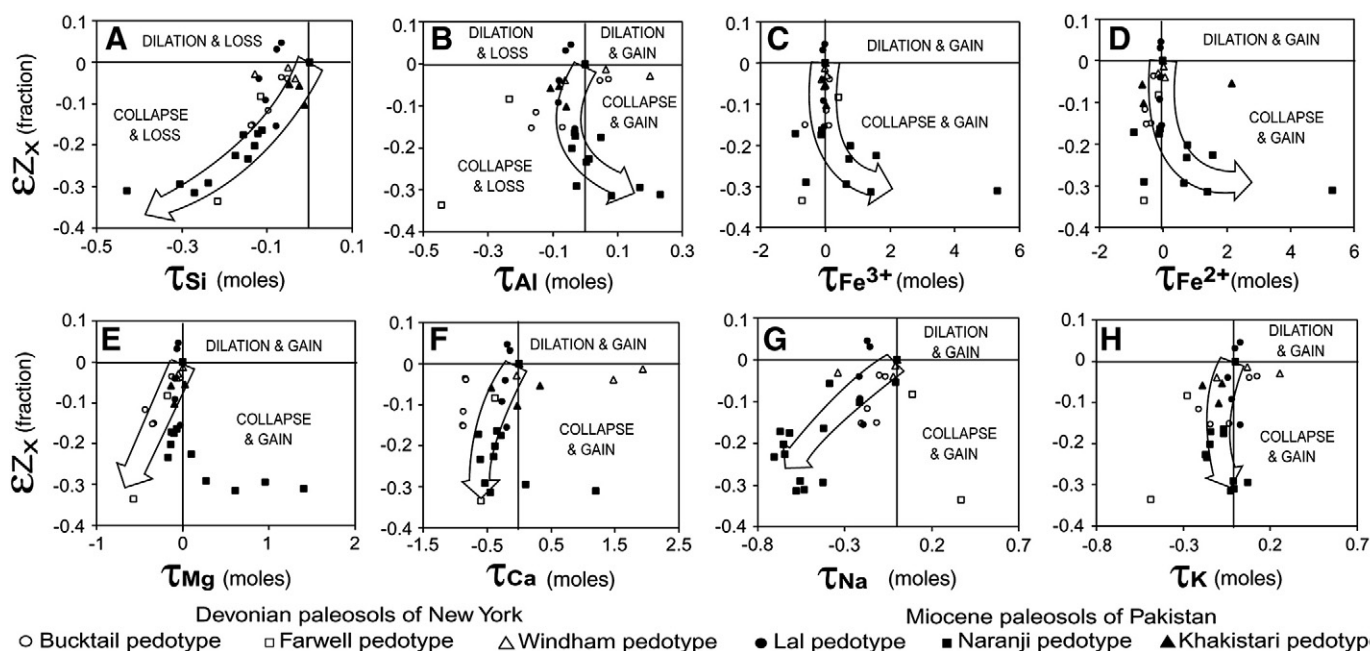


Fig. 10. Mass transport and strain (deviation from origin) within paleosols from East Windham, New York. Strain in soils (y axis) is usually collapse (negative) of volume, but dilation (positive) is possible with eolian or fluvial additions. Mass transfer (x axis) in soils is generally loss (negative), especially of nutrient elements, but can be gain (positive) of insoluble oxides (such as Al and Fe) is also common.

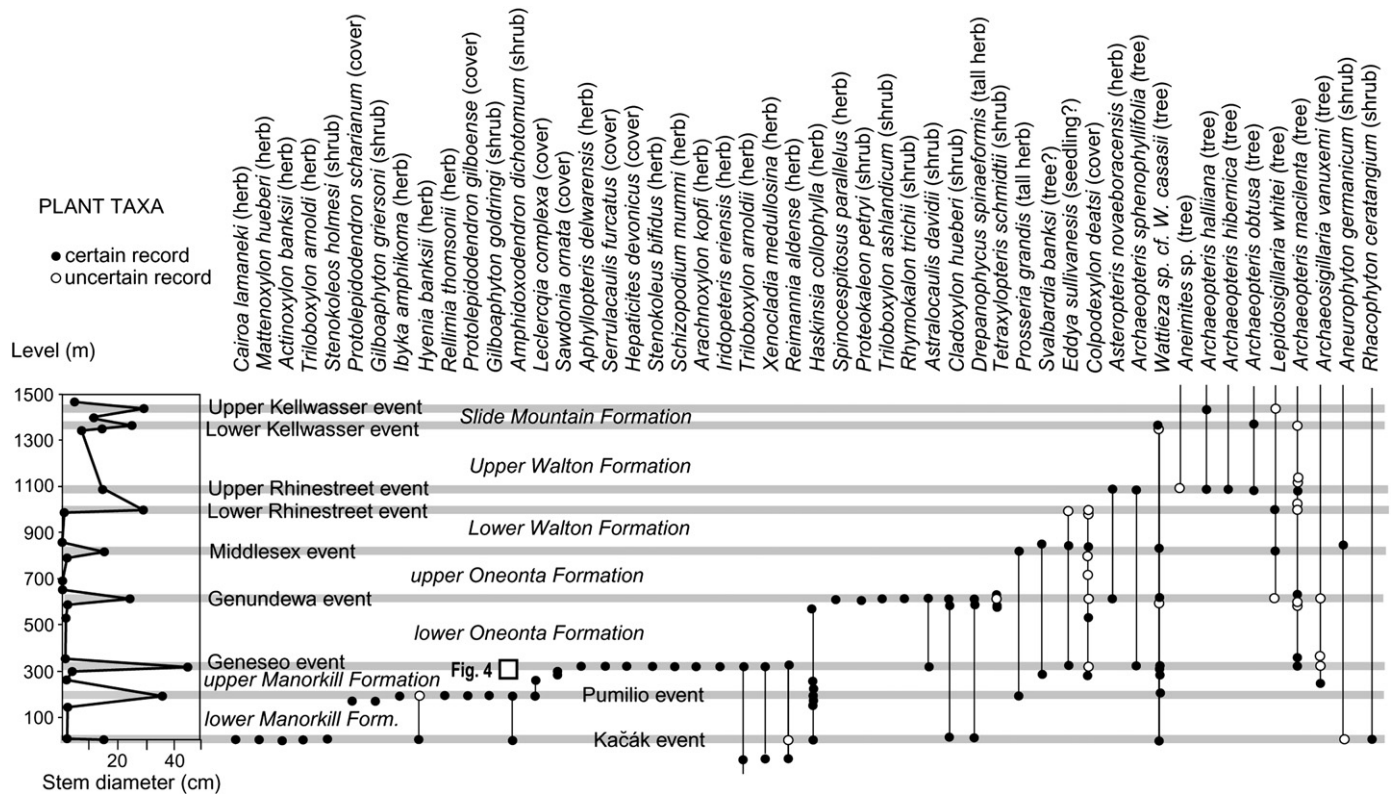


Fig. 11. Middle Devonian fossil plant ranges and stem diameters in New York.

Callixylon in showing a bowl-shaped base and large roots (as in the cladoxyl *Duisbergia* Schweitzer and Giesen, 2002), and are from near the base of the Manorkill Formation, 343 m below the detailed section (Fig. 4). Better known is the cladoxyl *Wattieza* from the Gilboa fossil forest (Mintz et al., 2010; Stein et al., 2007), at a stratigraphic level of 122 m (Johnson and Friedman, 1969) below the detailed section (Fig. 4). Other early *Wattieza* stump fields near Gilboa are known from 45 m and 105 m below our measured section (Fig. 3). The oldest progymnosperm stumps in New York are from locality 2 at West Saugerties (of Mintz et al., 2010), which is at the same stratigraphic level as the uppermost Gilboa fossil forest. These stumps more likely to belonged to *Svalbardia* than *Callixylon*–*Archaeopteris*, considering known ranges of these plants (Edwards et al., 2000). The oldest securely identified leaves and trunks of *Callixylon*–*Archaeopteris* in New York are from quarries near Durham, Manorkill and South Mountain, which also contain very large *Wattieza* sp. cf. *W. casatii* (Berry, 2000; Stein et al., 2007), 3–7 km northeast of the measured section, and at a stratigraphic level roughly equivalent to the Hyner pedotype paleosol at the top of the detailed section (Fig. 4).

The basal Oneonta Formation at South Mountain quarry near Manorkill yielded a complete compression of a cladoxyl tree trunk up to 1.2 m basal diameter and 8 m tall, with diameter at breast height (ca 1.2 m) of 45 cm (Stein et al., 2007). The 8 tree stumps at Gilboa measured by Driese et al. (1997), have basal diameters of 15–55 cm, or 41.5 ± 13 cm. Bridge and Willis (1994) illustrate a tall Gilboa stump with diameter at breast height of 36 cm. In the Manorkill tree of Stein et al. (2007) diameter at breast height (1.2 m) above the base of *Wattieza* was a factor of 0.34 ± 0.08 smaller than the swollen base. Assuming similar proportions for Gilboa trees measured by Driese et al. (1997) gives diameter at breast height of 2.4–22 cm diameter, or 14.8 ± 6 cm. Progymnosperm trunks tapered less from their stumps, as shown by a specimen of *Callixylon trifiliuvi* (Snigirevskaya, 1984), with roots converging to a stump 60 cm diameter and a diameter at

breast height of 25 cm: a factor of 0.42 smaller. Diameter at breast height scales with plant height in living trees, and the following relationship (Eq. (14) with $R^2 = 0.95$ and S.E. = ± 0.9 m from Niklas, 1994) between diameter at breast height (B in m) and tree height (H in m) for 670 living species of all kinds. Of all the equations provided by Niklas (1994), Eq. (14) best predicted the observed height (a little more than 8 m) of the near-complete Manorkill tree (of Stein et al., 2007).

$$H = 21.9B^{0.896} \quad (14)$$

Eq. (14) gives an earliest Givetian cladoxyl at West Saugerties (locality 1) some 2.4 m tall, and mid-Givetian *Wattieza* at Gilboa some 8.8 m tall and progymnosperms at West Saugerties (locality 2) some 2.9 m tall (Table 5). Forests are more than 10 m tall, woodlands 2–10 m, and shrublands less than 2 m (Retallack, 1992). Remarkably, none of the fossil plants found in the detailed section at East Windham (Fig. 4) was greater than 4 cm in diameter, and all are predicted using Eq. (14) to have been less than 1 m tall (Table 5). These include fossils comparable with *Wattieza* sp. cf. *W. casatii* (Fig. 6B–F) in Durso, Farwell and Windham pedotype paleosols, which formed shrublands. Other shrublands are represented by twigs and sporangia comparable with the shrubby progymnosperm *Rellimia thomsonii* (Fig. 6G–H). Leafy stems of the prostrate ground-covering lycopsid *Leclercqia complexa* (Fig. 6G) were found in a Lookout paleosol at 36.5 m in the measured section (Fig. 4). The big trees did not grow in the pedotypes found at East Windham, but rather in Sulfaquepts (un-named pedotype of Driese et al., 1997), Dystrochrepts (Peas Eddy pedotype) and Usterts (Hyner pedotype), which had limited distribution in time and space (Retallack, 1985, 2009a). These pedotypes moreover correspond with warm-wet CO₂-greenhouse spikes evident from paleosols (Fig. 9) and marine anoxic events (Fig. 2). At other drier, cooler and lower CO₂ times, vegetation was a mosaic of shrublands with wetland and riparian pole

woodland (Fig. 8). The advent of cladoxyl trees in New York coincides with the Kačák black shale event (earliest Givetian). Progymnosperm trees and large *Wattieza* reappeared during the Pumilio Black Shale event (mid-Givetian), at a time of a warm wet greenhouse spike encouraging their spread from elsewhere.

Big plants evolved earlier in more humid climates elsewhere in the world, such as Germany, where Early Devonian paleosols are common and non-calcareous (Stets and Schäfer, 2009; Retallack personal observations). A large cladoxyl (*Duisbergia mirabilis*) from Wuppertal, in the mid-Eifelian (AD Mac or *velatus-langi* zone: Edwards et al., 2000), Brandenburg Schichten, had a diameter at breast height of 23 cm (Schweitzer and Giesen, 2002), corresponding to a height of 5.9 ± 0.9 m (from Eq. (14)). Another large cladoxyl (*Protocephalopteris praecox*) from the uppermost Emsian to mid-Eifelian, Grey Hoek and Wijde Formations of Spitzbergen, had a diameter at breast height of 30 cm (Schweitzer, 1999), corresponding to a height of 7.5 ± 0.9 m (from Eq. (14)). These are earlier than the first large cladoxyls of earliest Givetian age in New York (Table 5). In Spitzbergen, progymnosperms (*Svalbardia polymorpha* and its spore *Geminospore lemurata*) with stems 12.5 cm in diameter, corresponding to plants 3.4 ± 0.9 m tall (from Eq. (14)), first appear in the Mimerdalen Formation of early Givetian age (predating appearance of *Chelinospore concinnus* and *Cristatisporites triangulatus*: Schweitzer, 1999; Marshall et al., 2007), earlier than mid-Givetian in New York (Table 5). Paleoclimatic limits to the size and immigration of cladoxyls and progymnosperms in New York can now be reassessed from their paleosols.

10. Paleoprecipitation constraints on early trees

Modern trees need a minimum amount of rainfall, and their stature declines steadily with declining mean annual precipitation. In many aridlands, the relationship between trees and precipitation is

obscured by intervening sod-grassland ecosystems with their distinctive soils (Mollisols), which evolved since the Miocene (Retallack, 2008b), but Australian aridlands retain more ancient kinds of non-mollic soils (Aridisols) in comparable climatic zones (McKenzie et al., 2004). Rather than a patchwork of open and wooded grassland, Australian trees decline in stature to a distinctive kind of pole woodland called “mallee” (Noble and Bradstock, 1989). This decline of tree stature with depth to Bk in paleosols and with mean annual precipitation has been measured in New South Wales (Fig. 12B, Table 3) for comparison with Devonian trees. Depth to Bk in paleosols with fossil trees has been measured in New York and Pennsylvania, and these depths can be used to estimate former mean annual precipitation (using Eq. (3)), once allowances have been made for burial compaction of the paleosols (using Eq. (1)).

The decline in stature of trees with declining mean annual precipitation is evident from both modern and Devonian trees (Fig. 12B) with the difference that the ecotone between woodland and shrubland (2 m height) in modern communities is predicted at the 250 ± 46 mm isohyet, whereas for Devonian *Wattieza* this vegetation break was at 571 ± 72 mm and for *Callixylon* at 611 ± 46 mm mean annual precipitation. These standard errors from an inverse regression to that shown in Fig. 12B are evidence that *Callixylon* and *Wattieza* were not statistically different in their tolerance of aridity. Devonian trees (>2 m high) required at least ca. 350 mm more mean annual precipitation than modern trees. In addition, Devonian trees gained stature less rapidly with increased precipitation, so that the ecotone between woodland and forest (10 m height) in modern communities is predicted at the 361 ± 46 mm isohyet, whereas for Devonian *Wattieza* this vegetation break was at 761 ± 72 mm and for *Callixylon* at 943 ± 46 mm mean annual precipitation. Only two examples of *Lepidosigillaria* are known for this analysis, and both plot with *Callixylon* (Fig. 12B).

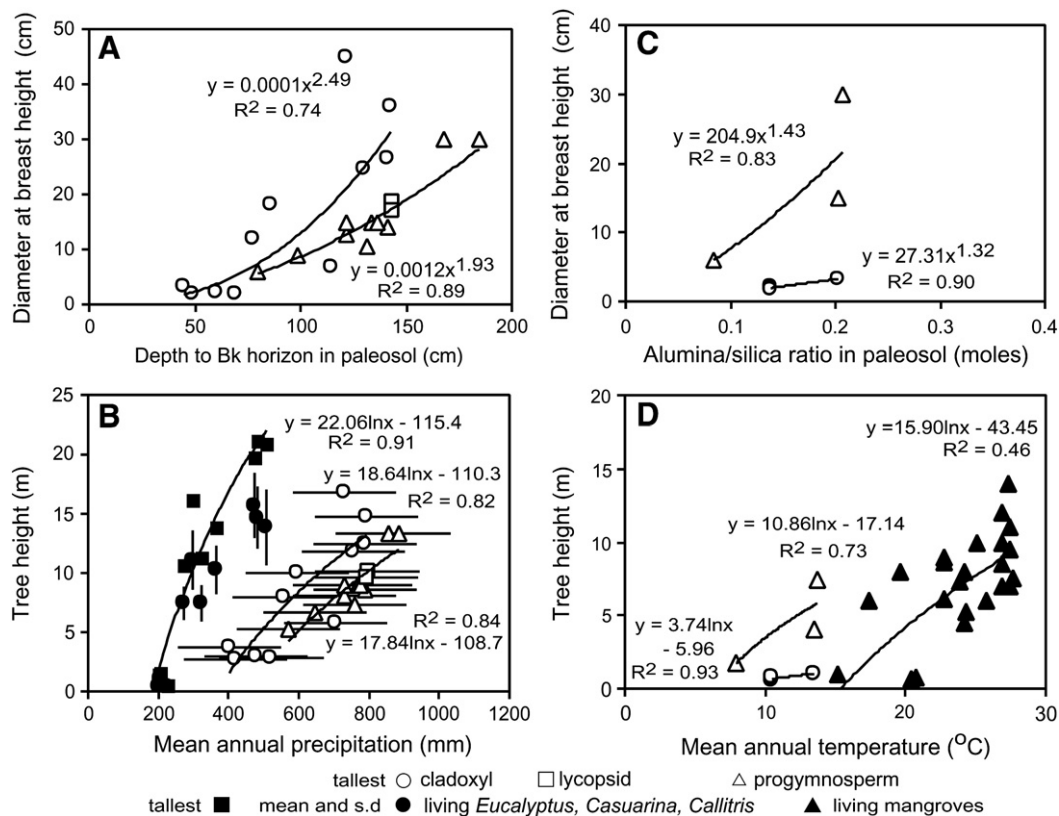


Fig. 12. Correlations between observed stem diameters of Devonian trees and depth to Bk horizon (A) and molar ratio of alumina/silica in paleosols (C), and inferred relationship between tree height and mean annual precipitation (B) and between mangrove height and mean annual temperature (D) during the Devonian compared with today.

These results lend support to the view that Devonian plants were limited in their colonization of dry soils compared with modern seed plants because they reproduced with spores and so needed water during reproduction on exposed ephemeral gametophytes (Niklas, 1997). This does not mean to say that Early Devonian and older plants were restricted to waterlogged soils, where they are best preserved (DiMichele and Hook, 1992): a well known taphonomic artefact for fossil plants of all ages (Retallack, 1998). Aridlands are often awash with floodwaters (Westbrooke and Florentine, 2005) and support a wide variety of pteridophytes, lichens and cyanobacteria (Noble and Bradstock, 1989). Devonian trees in well drained, calcareous soils (Aridisols) receiving as little as 570 mm mean annual precipitation are unlikely to have been limited completely by reproduction. Another explanation for smaller than modern Devonian trees could be moisture-limited nutrient acquisition by soil microbiota, but comparison of Devonian and Miocene paleosols does not show significant differences in weathering of nutrient cations (Fig. 10). A more promising explanation is the documented reduction in the ratio of stelar surface area to stelar volume in Silurian and Devonian plants (Niklas, 1997), which is particularly marked in cladoxyls (narrow steles of *Xenocladia* compared with wider steles of *Pseudosporochnus* and *Wattieza*: Stein and Hueber, 1989) and progymnosperms (lobed stele of *Rellimia* compared with cylindrical *Callixylon*: Matten and Banks, 1967). These changes increased transpiration efficiency to increasingly elaborate plagiotropic photosynthetic shoots (Niklas, 1997), but remained less efficient than for plants with large thick leaves appearing during the Mississippian (Beerling et al., 2001).

11. Paleotemperature constraints on early trees

Modern mangroves (*Avicennia*, *Rhizophora*, and *Kandelia*) form tall forests in tropical regions, but bushes only 1 m high at higher latitudes, such as Auckland harbor, New Zealand (Taylor, 1983) and Hui'an, China (Lin and Wei, 1983). At latitudes higher than 37°, intertidal vegetation is entirely herbaceous, salt marsh, including salt grasses (*Spartina* and *Distichlis*) and saltworts (*Arthrocnemum* and *Salicornia*: Chapman, 1960). In order to investigate whether this temperature control acted on the Devonian mangal plant *Wattieza* (Bridge and Willis, 1994; Driese et al., 1997), data was compiled on modern intertidal mangroves (Table 3) and the likely mean annual temperatures (using Eq. (7)) of Devonian trees from associated paleosols (Table 5).

Temperature constraints on modern mangroves and Devonian trees are broadly similar, but the minimal mean annual temperature requirement of each is different. Inverse regression (to Fig. 12D) predicts minimum mean annual temperature of 20.2 ± 2.6 °C for modern mangroves, which is similar to their limit in China (20.4 °C), but not New Zealand (15.2 °C). Minimum mean annual temperature of 13.1 ± 0.5 °C is predicted for *Wattieza* and 6.2 ± 2.6 °C predicted for *Callixylon*.

The lower temperature limit for *Callixylon* is unsurprising, because *Callixylon* has never been found in intertidal paleosols and so should not be under comparable constraints. Even within mangroves, trees are larger in inland, low-salinity groundwaters, such as the 39 m tall riparian mangroves (*Avicennia germinans*) of Belém, Brazil, where intertidal fringing mangroves are only 9 m tall (Lacerda et al., 2002).

The broadly comparable temperature limits of *Wattieza* and living mangroves is surprising because of their very different architecture and reproduction. *Wattieza* was similar to fossil lycopsid mangroves such as *Pleuromeia hataii* (Retallack, 1997b). Both genera had a columnar habit like living mangrove palm (*Nypa fruticans*) and a pteridophytic reproductive system like the mangrove fern (*Acrostichum aureum*: Duke, 1992). Most living mangroves have a different branching woody growth habit and large seeds, comparable with Carboniferous cordaitan mangroves, such as *Nucellangium glabrum* and *Cardiocarpus spinatus* (Raymond and Phillips, 1983), or Cretaceous angiosperm

mangroves, such as *Pabiana variabilis* (Retallack and Dilcher, 1986; Upchurch and Dilcher, 1990), although neither of these had viviparous water-dispersed propagules like many modern mangroves (Duke, 1992). These observations suggest that habit and reproductive system are not temperature-limiting features of modern or fossil mangal plants. A more likely limiting feature is frost sensitivity (Inouye, 2000), because many mangrove plants are similar to palms and cacti in having succulent stems with large frost-sensitive terminal meristems.

12. Conclusions

The earliest woodland trees in Middle Devonian coastal plains of New York were cladoxyl pteridophytes (?*Duisbergia*). They appeared during the earliest Givetian at a time of high CO₂ and a warmer and wetter climate (Fig. 9), coincident with the Kačák black shale event and faunal overturn in marine invertebrate communities (Brett et al., 2009). Before and after this transient episode of coastal afforestation, climate was too dry and cool for these trees (Fig. 12) and vegetation consisted of a mosaic of shrublands and low pole woodlands (Fig. 8). Presumably cladoxyls migrated during warm–wet paleoclimatic spikes from warmer and wetter regions such as Germany (Schweitzer and Giesen, 2002) or Spitzbergen (Schweitzer, 1999), where geologically older large cladoxyl trees have been found.

Large cladoxyl trees (*Wattieza* of the “Gilboa forest”) appeared during the mid-Givetian, in sulfidic intertidal soils (Sulfaquept) and so formed mangal vegetation (Driese et al., 1997). Their immigration coincided with another CO₂-greenhouse spike of warm–wet climate (Fig. 9), at the time of the Pumilio marine anoxic event and faunal overturn (Brett et al., 2009). At about the same time there also appeared in well drained, non-marine soils (Vertisols) the earliest progymnosperm trees (?*Svalbardia*) in New York, again later than early Givetian progymnosperm trees in Spitzbergen (Schweitzer, 1999). Progymnosperms were more limited by precipitation than temperature (Fig. 12), so may have migrated from higher altitudes or latitudes. Large *Wattieza* and *Callixylon* trees returned during subsequent CO₂-greenhouse spikes (Genesee, Genundewa, Middlesex, Rhinestreet and Kellwasser events of Figs. 2 and 9). *Wattieza* mangal did not survive the Frasnian–Famennian (Kellwasser) mass extinction, but *Callixylon*–*Archaeopteris* woodlands continued into the Late Devonian (Fig. 11), again in unusually warm–wet times and places (Retallack et al., 2009).

This complex history may explain the 40 million year lag between the latest Emsian (400 Ma) appearance of trees in Spitzbergen (Schweitzer, 1999) and the late Famennian (360 Ma) Ice Age in Appalachia (Brezinski et al., 2009) and South America (Isaacson et al., 2008), for which trees are considered responsible because of mitigation of an earlier Devonian CO₂ greenhouse by means of enhanced silicate weathering on land, oceanic fertilization and carbon burial (Berner, 1997). Trees expanded their range during transient CO₂-greenhouse crises, but were limited in distribution by temperature and precipitation at other times.

The evolution of “killer trees” (Algeo and Scheckler, 1998) or “Medea forests” Ward (2009) has been blamed for Devonian marine mass extinctions, using the argument that enhanced weathering would have delivered more nutrients to the ocean and thus encouraged planktic productivity and marine anoxia. Purely biological expansion of trees would result in a new equilibrium of lower CO₂, temperature and precipitation, not multiple transient expansions. Expansions of woodland at times of transient and large increases in atmospheric CO₂, paleotemperature and paleoprecipitation suggest another common cause (Fig. 9). These CO₂-greenhouse crises are comparable with other transient extrinsic perturbations to the atmosphere such as massive volcanic eruptions and meteorite impacts (Retallack, 2005b; Retallack and Jahren, 2008; Retallack et al., 2009). These events may have been short lived because newly evolved woodlands expanded to consume carbon in growth and

weathering, and promote oceanic carbon sequestration, thus restoring pre-existing cooler and drier conditions, in contradiction to biocidal hypotheses (Algeo and Scheckler, 1998; Ward, 2009). By Late Devonian to Mississippian time, trees colonized drier climates and infertile peaty substrates worldwide (Retallack, 2001), oxygenating the atmosphere and initiating the Carboniferous ice age (Bernier, 1997). This long-term coevolutionary transformation (Retallack, 2004) can be contrasted with Milankovitch and other extrinsic volcanic and bolide perturbations, which were repaired by woodland expansion.

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Appendix A. Supplementary data

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