Dartmouth College
Dartmouth Digital Commons

Open Dartmouth: Faculty Open Access Articles

8-23-2016

Belowground Rhizomes in Paleosols: The Hidden Half of an Early Devonian Vascular Plant

Jinzhuang Xue
Peking University

Zhenzhen Deng
Peking University

Pu Huang
Peking University

Kangjun Huang
Peking University

Michael J. Benton
University of Bristol

See next page for additional authors

Follow this and additional works at: https://digitalcommons.dartmouth.edu/facoa

Part of the Geochemistry Commons, Paleobiology Commons, and the Plant Sciences Commons

Authors

Jinzhuang Xue, Zhenzhen Deng, Pu Huang, Kangjun Huang, Michael J. Benton, and Ying Cui

Belowground rhizomes in paleosols: The hidden half of an Early Devonian vascular plant

Jinzhuang Xue[a,b,1], Zhenzhen Deng[a], Pu Huang[a], Kangjun Huang[a], Michael J. Benton[c], Ying Cui[d], Deming Wang[a], Jianbo Liu[a], Bing Shen[a], James F. Basinger[e], and Shougang Hao[a]

[a]The Key Laboratory of Orogenic Belts and Crustal Evolution, School of Earth and Space Sciences, Peking University, Beijing 100871, People's Republic of China; [b]Key Laboratory of Economic Stratigraphy and Palaeogeography, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, People's Republic of China; [c]School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, United Kingdom; [d]Department of Earth Sciences, Dartmouth College, Hanover, NH 03755; and [e]Department of Geological Sciences, University of Saskatchewan, Saskatoon, SK S7N 5E2, Canada

The colonization of terrestrial environments by rooted vascular plants had far-reaching impacts on the Earth system. However, the belowground structures of early vascular plants are rarely documented, and thus the plant–soil interactions in early terrestrial ecosystems are poorly understood. Here we report the earliest rooted paleosols (fossil soils) in Asia from Early Devonian deposits of Yunnan, China. Plant traces are extensive within the soil and occur as complex network-like structures, which are interpreted as representing long-lived, belowground rhizomes of the basal lycopsid *Drepanophycus*. The rhizomes produced large clones and helped the plant survive frequent sediment burial in well-drained soils within a seasonal wet–dry climate zone. Rhizome networks contributed to the accumulation and pedogenesis of floodplain sediments and increased the soil stabilizing effects of early plants. Predating the appearance of trees with deep roots in the Middle Devonian, plant rhizomes have long functioned in the belowground soil ecosystem. This study presents strong, direct evidence for plant–soil interactions at an early stage of vascular plant radiation. Soil stabilization by complex rhizome systems was apparently widespread, and contributed to landscape modification at an earlier time than had been appreciated.

rhizome | paleosol | clonal growth | fluvial landscape | Devonian

The great radiation of vascular plants during the middle–late Paleozoic had profound impacts on the Earth system. The Silurian–Devonian periods witnessed a series of secular changes in Earth's atmosphere and surface, including decrease of concentration of atmospheric carbon dioxide, increasing prominence of meandering river facies with stabilized banks and muddy floodplains, and the increase of pedogenic sediments. These changes have been linked to the colonization of terrestrial landscapes by rooted plants (1–5). Previous studies have emphasized the effects of early trees and forests, which first appeared in the Middle Devonian (6–8), on enhanced chemical weathering rates and soil development (2, 9–11). However, the roles that vascular plants played in soil production and landscape stability before the evolution of trees and deep roots (the interval from ~420 to 390 Ma) are poorly understood. This issue is of significance particularly in light of the ecological importance of small, herbaceous plants with a clonal growth habit in modern ecosystems (12, 13).

Early vascular plants of the Late Silurian–Early Devonian, including rhyniopsids, zosterophyllopsids, lycopsids, and euphyllophytes, are small in aboveground stature (14, 15). Although the small aboveground size could suggest that the belowground components of these plants were similarly small and therefore limited in their impact on sediments, fossils of their belowground structures such as roots or rhizomes are rare and incomplete (16–23). Some species have been recorded as bearing shallow rooting systems (or root-like structures) (16–20), others as having surficial or shallowly subterranean rhizomatous axes with rhizoids (21–23). Thus, the geochemical effect of these plants on the substrate (or soils) was presumably limited (11), and their capacity for landscape stabilization was trivial. However,

because of a poor fossil record, it remains quite unclear how the "hidden half" ecosystem (24), with buried structures growing in soils, functioned during the early stage of vascular plant radiation. Such a knowledge gap hinders a deep understanding of the ecology of early plants and their roles in terrestrial environments.

In this article, we report well-preserved plant traces from the Lower Devonian Xujiachong Formation of Yunnan, China, which are interpreted as representing belowground rhizomes of the primitive lycopsid *Drepanophycus*. Paleobotanical, sedimentological, and geochemical studies reveal the ecology of this plant, the earliest known rooted paleosols (fossil soils) in Asia, and a mechanism for plant–soil interactions for early vascular plants.

Results

Geological Setting, Stratigraphy, and Sedimentary Environments. During the Early Devonian, the South China paleocontinent was located within the paleoequatorial region and far from Laurussia (25) (Fig. 1A). The Xujiachong Formation is well exposed near Qujing City, Yunnan Province (Fig. 1 B and C) (26) and consists of predominantly terrestrial deposits *ca.* 600 m to 900 m in thickness (27, 28). A late Pragian–early Emsian age has been proposed for the Xujiachong Formation in light of its plants, invertebrates, and spores (27). More recently, an early Pragian to ?earliest Emsian age has been determined for the upper part of this formation based on dispersed spore assemblages of the *polygonalis–emsiensis* Spore Assemblages Biozone of Laurussia (29). In this study, we focus on the lower to middle part of this formation, interpreted as Pragian in age (~411 to 408 Ma).

Significance

The roots and rhizomes of early vascular plants, and their interactions with soils, are poorly documented. Here we report on the complex, belowground rhizome systems of an Early Devonian plant, and their contribution to the formation of the earliest record of rooted red-bed soils in Asia. Our specimens predate the earliest trees with deep roots from the Middle Devonian by 20 million years. We propose that plant rhizomes have long functioned in terrestrial ecosystems, playing important roles in shaping Earth's environments by reducing soil erosion rates and thereby increasing the stability of land surface and resilience of plant communities.
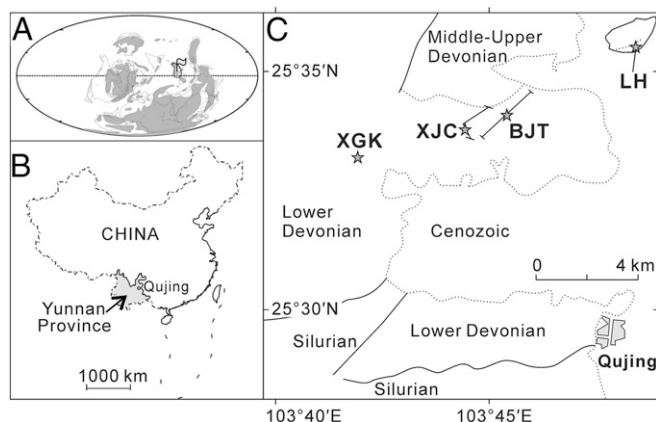
Fig. 1. Location and geologic map. (*A*) Early Devonian paleomap showing the location of South China (25). (*B* and *C*) Location (*B*) and geology (*C*) of the study area, near Qujing, Yunnan Province, China. The studied sections of the Lower Devonian Xujiachong Formation at Xujiachong (XJC), Xiaoguankou (XGK), Baojia Tunnel (BJT), and Longhua (LH) are indicated by stars.

Outcrops and specimens have been examined at the Xujiachong, Xiaoguankou, Baojia Tunnel, and Longhua sections of the Xujiachong Formation (Figs. 1*C* and 2 and *SI Appendix,* Figs. S1–S12). The Xujiachong section has been divided into 93 sedimentary cycles (28), and this scheme is followed here. Most of these cycles show repetitive facies associations comprising a lower conglomerate, medium to thickly bedded sandstone, thinly bedded sandstone and gray-green siltstone, and, at the top, red mudstone and gray-green siltstone/mudstone (Fig. 2 *A–D*). Each sedimentary cycle is interpreted to represent a river channel migration or episodic crevasse splay followed by floodplain development. Intraformational conglomerates (*SI Appendix,* Fig. S1), usually several centimeters thick, with abundant mud and some lithic clasts, are interpreted as basal lags of reworked floodplain deposits. Medium to thickly bedded gray sandstones, subarkosic arenitic, and quartz arenitic in composition, with trough and tabular cross-bedding, ripple lamination, and erosional base, are interpreted as fluvial channels and are typically found at or near the bases of some cycles (*SI Appendix,* Figs. S2 and S3). Couplets of thinly bedded sandstone and gray-green siltstone occur above medium-thickly bedded sandstones or near the bases of some other cycles (*SI Appendix,* Figs. S2*C* and S4*A*). Such heterolithic deposits provide strong evidence for deposition in a stabilized channel environment, as either laterally accreted point bars or crevasse splays (3, 4, 30, 31), although, in this instance, outcrop limitations do not permit a conclusive discrimination between these facies. Red mudstones (paleosols) with plant traces subsequently developed as floodplain deposits (Fig. 2 *A–G* and *SI Appendix,* Figs. S7–S9). Some sedimentary cycles include red-bed paleosols 2 to 4 times thicker than other lithofacies in the cycle (Fig. 2 *C, D,* and *G*), indicating a considerable time of landscape stability. In such cases, the sequence represents a mud-dominated, stabilized floodplain, and, at Xujiachong, for example, single beds of red mudstone average 2.4 m and their sum reaches 355 m, representing ca. 42% of the thickness of the entire formation (*SI Appendix,* Table S1).

Plant Traces Produced by *Drepanophycus*. Plant traces preserved as sediment-filled casts, molds, and/or rhizohaloes [diffuse, chemically altered zones (2, 10, 11)] occur in all lithofacies (Fig. 2 and *SI Appendix, Detailed Description of Plant Traces* and Figs. S4 *C–H,* S5 *C–F,* S6 *A* and *B,* and S7–S11), but are most common in red and gray-green mudstone/siltstone paleosols in the four examined sections. Vertical traces are found throughout a 15.5-m-thick bed of red mudstone at Xiaoguankou (Fig. 2 *F* and *G* and *SI*

Appendix, Fig. S7), and similarly in cycles 33 and 35 of the Xujiachong section (Fig. 2 *C* and *D* and *SI Appendix,* Fig. S8*A*). The traces are more or less consistent in density and morphology through the vertical profiles, with the most common type of trace 5.9–18 mm wide (average 10.5 mm; $n = 90$), and interpreted as rhizomes of the extinct, basal lycopsid *Drepanophycus*. By "rhizome," we mean vegetative extensions produced by means of axis elongation and branching either above or within the substrate. The second type is much thinner and less common, and is interpreted as traces of adventitious roots of *Drepanophycus* (*SI Appendix,* Figs. S4 *G* and *H* and S6 *A* and *B,* arrows). Numerous traces show multiple occurrences of H- or K-shaped branchings (Fig. 2 *H* and *I* and *SI Appendix,* Fig. S13), typical of the rhizomes of many zosterophyllopsids and early lycopsids (17, 18, 32, 33). Typically, a parent rhizome divides to produce a lateral branch at nearly 90°, and, after a short distance, this lateral trace divides to produce two daughter traces that diverge at a wide angle (K-shaped) to almost 180° (H-shaped); during this process, the trace width changes little. These K- or H-shaped branchings are morphological expressions of the same developmental pattern, and therefore for simplicity, we refer to this pattern only as H-branching. Some traces tend to extend horizontally (*SI Appendix,* Figs. S6 *A* and *B* and S8 *B* and *C*), whereas, in other examples, vertical traces bend to become horizontal and appear to represent impressions of aerial plant axes (Fig. 2 *I* and *J*). Lateral, millimeter-scale projections can be seen on these traces (Fig. 2*K*), indicative of leaves. The number of trace transections on a bedding surface ranges from 800 to as high as 1,300 per square meter (*SI Appendix,* Figs. S8 *D* and *E,* S10, and S11 and Table S2), and the total length of rhizomes per cubic meter of sediment is estimated to be 800 m to 1,300 m. Nearest-neighbor analysis for point pattern (34) shows a statistically significant clustering (nonrandom distribution) of trace transections on a sampled bedding surface [$P_{(random)} \ll 0.001$].

Although traces are found in both green and red beds, gray-green mudstone/siltstone has a greater preservational potential for plant remains and may preserve coalified material (*SI Appendix,* Figs. S4 *F–H* and S6 *C–H*). In many green beds, remains of *Drepanophycus qujingensis* are preserved as densely arranged parallel axes (*SI Appendix,* Fig. S6 *C* and *F*), indicative of effects of water currents in aligning aerial parts of the plant. The microphyllous aerial axes of *Drepanophycus* are characterized by dichotomous and pseudomonopodial branching (*SI Appendix,* Fig. S6 *D, E,* and *G*), and appear to differ from the rhizomes on which H-branching occurs, although rhizomes may have occurred either as aerial scrambling stems or as subterranean organs. Pseudomonopodial branching means a pattern with a distinct main axis and subordinate, thinner, lateral branches (*SI Appendix,* Fig. S6*G*), and further divisions of the lateral branches usually do not diverge with a wide angle or with opposite directions, as they do in H-branching. The width of rhizomes and their traces (average 10.5 mm) is somewhat less than that of the aerial axes of *Drepanophycus* (average 15.9 mm) (*SI Appendix,* Fig. S14).

Paleosol Morphology and Geochemistry. Red mudstone facies (Munsell color 7.5R4/4, 10R4/2, 10R6/4) with abundant plant rhizome traces (5PB4/4, 7.5PB4/2, 7.5BG8/2), and some with scattered carbonate nodules, are classified as protosols or calcisols (35). Some beds of gray-green mudstone/siltstone (7.5G7/2, 10B5/2), also showing plant traces (5PB4/2, 10BG1/2) and red mottling but lacking carbonate nodules (Fig. 2*I*), are assignable to protosols. Carbonate nodules are subangular to rounded in shape (*SI Appendix,* Fig. S9 *D* and *E*), and, in chemical components, may show a sharp boundary or diffuse pattern of carbon and calcium (*SI Appendix,* Fig. S12). Nodules in paleosols at Xujiachong and Xiaoguankou are 1.8 mm to (6.7 mm) to 25.1 mm in long dimension (most commonly 3 to 9 mm; *SI Appendix,* Fig. S15 and Table S3) and show no discernable trend in size distribution versus profile depth (Fig. 2 *C, D,* and *G*). Although some

Fig. 2. Stratigraphy of the Xujiachong Formation. (*A*, *C*, and *D*) Lithological columns with representative sedimentary cycles of the Xujiachong section. Cycle numbers, lithofacies, and contained fossil plants are based on ref. 28 and our reexamination. (*B*) Typical sedimentary sequence at Xujiachong. (*E*) Polished vertical section of red mudstone (at Xujiachong), with drab-haloed plant traces and scattered carbonate nodules (arrows). (*F*) Red mudstone with green vertical plant traces at Xiaoguankou. (*G*) Stratigraphy of the Xiaoguankou section. (*H–K*) Specimens from the Baojia Tunnel section. (*H*) Gray-green vertical traces in red mudstone, with K- or H-shaped branching and horizontal extension (arrows). (*I*) Vertical traces in green mudstone with red mottling. Traces bend to horizontal on upper surface, the edge of which is indicated by arrows. (*J*) Upper surface of the rock in *I*. Traces with horizontal extensions (weak contrast with the matrix) and transections (black circles). (*K*) Vestige of axes with lateral projections (arrows). (Scale: coin in *H* and *J*, 20 mm.)

nodules occur within, or very close to, rhizohaloes, and some nodules appear to occur within distinct beds (but free from one another), most are scattered in the matrix (*SI Appendix,* Fig. S9 *A–D*). Nodules are usually associated with local reduction of iron within the adjacent matrix. These carbonate nodules belong to developmental stage II, as measured by the criteria of Machette (nodules common, 5 mm to 40 mm in diameter) (36). The thickest exposed paleosol is 15.5 m, and as much as 17.0–19.4 m in original thickness, assuming a burial depth of 1–3 km (37), and, except for some vague and discontinuous beds of carbonate nodules (*SI Appendix,* Fig. S9 *A* and *B*), such paleosols show no soil profile development and seem to be aggradational (cumulate soils), lacking evidence of internal bedding or erosion.

Major and trace elemental compositions of four paleosols, three within cycles 33, 35, and 37 at Xujiachong (9.0, 7.8, and 4.4 m thick, respectively) and one at Xiaoguankou (15.5 m), were analyzed to evaluate pedogenesis. The homogeneity of these paleosols is verified by the molecular weathering ratio, including [Ca+Mg]/Al, Al/Si, Al/[Ca+Mg+K], and Ba/Sr (Fig. 3 and *SI Appendix,* Fig. S16), which have been commonly used to identify calcification, clayeyness, base loss, and leaching of paleosols, respectively (2). No discernable trend is exhibited in the values of these ratios versus profile depth. The Ti/Al ratios fall within the range of mudstone-parented, weakly to moderately developed soils (38). The average weight percentage (wt%) of CaO and MgO reaches 7.48% and 4.87%, respectively, in these red-bed paleosols, and thus the calcification values are high throughout the profiles, although showing slight fluctuation that indicates some change in abundance of carbonates. Paleosol samples from the red-bed facies and two samples from adjacent green siltstone facies are similar in molecular ratios and REE (rare earth elements) abundance (*SI Appendix,* Figs. S16 and S17).

Stable isotope values of micrites of carbonate nodules ($\delta^{13}C_{carb}$ and $\delta^{18}O_{carb}$), as well as carbon isotope values of organic matter within the paleosols ($\delta^{13}C_{OM}$), show no discernable change throughout the profiles, and no significant difference between the Xiaoguankou and Xujiachong paleosols (Fig. 3 and *SI Appendix,* Figs. S16 and S18). Relative to the Vienna Pee Dee Belemnite standard, the values range from −8.16 to −5.12‰ for $\delta^{13}C_{carb}$, −9.51 to −7.24‰ for $\delta^{18}O_{carb}$, and −25.28 to −23.38‰ for $\delta^{13}C_{OM}$; the difference between $\delta^{13}C_{carb}$ and $\delta^{13}C_{OM}$, $\Delta^{13}C_{carb–OM}$, averages 17.73‰.

Discussion and Conclusions

The Xujiachong Formation presents an exceptional example of the contribution of early vascular plant vegetation to terrestrial sedimentation. Most sedimentary cycles within this formation began with a basal conglomerate or sandstone body deposited most probably by channel migration or episodic crevasse splay, followed by floodplain development. *Drepanophycus* appears to have been an immediate colonizer of the newly formed alluvium, as evidenced by autochthonous or parautochthonous preservation of abundant compression remains and plant traces in sandstone−siltstone couplets. We propose that continuous growth of *Drepanophycus* via their rhizomes, and sequential burial in fine sediments, may

have conferred erosion resistance to floodplains and contributed to the establishment of red-bed paleosols. Although *Drepanophycus* is characterized by limited xylem and wide cortex tissues (16, 32, 33), the rhizomatous growth of this plant could produce dense vegetation cover (*SI Appendix,* Fig. S19), which alone would have protected the substrate against surface erosion while increasing trapping of fine particles (4, 39), as has been demonstrated in numerous studies of the erosion-reducing effects of modern plants (5, 39). Perhaps more importantly, belowground rhizomes of *Drepanophycus* formed complex networks as a result of belowground growth as well as sequential burial of aerial stems and rhizomes, which had the potential to bind sediments in a reinforced matrix, thereby increasing soil aggregate stability. Analogous cases are common in modern environments, where, for example, the angiosperms *Psammochloa villosa* and *Sporobolus virginicus* form dense rhizomatous networks that are subject to frequent burial and efficiently stabilize mobile sand dunes (13, 40). Other factors may have contributed to stabilization, including decomposition of *Drepanophycus* rhizomes, a source of organic matter that would increase the soil structure, and, in some cases, contribute to formation of rhizocretions (*SI Appendix,* Fig. S10 *B* and *D*) to provide additional resistance against erosion.

Quantifying the effects of roots (or rhizomes) on soil erosion rate is difficult, due to the diversity of root architectures and soil structures. However, root volume and root length per unit volume of sediment (RLD) are two variables that can be compared across communities and can be obtained from the fossil record (but only in rare cases, as in this study). Experiments have shown that bank sediments with 16 to 18% roots by volume can have 20,000 times more resistant to erosion than those without vegetation (41). For reference, in this study, rhizomes of *Drepanophycus* are estimated to have occupied 6.9 to 11.3% by volume of sediment (*SI Appendix,* Table S7). Root length density (RLD) has been found to correlate well with the soil detachment ratio (SDR) (*SI Appendix, Quantifying the Erosion-Reducing Potential of Drepanophycus Rhizomes*) (39). The rhizome length density within the Xujiachong paleosols is estimated to be 0.8–1.3 km/m³, a value at the lower end of the range for modern plant roots (39), and, by using the nonlinear regression function between RLD and SDR resulting from concentrated flow (39), weak to modest effects of rhizomes in reducing soil erosion can be expected (*SI Appendix,* Table S8).

The mud-dominated beds of the Xujiachong Formation are interpreted as the result of long-term development of floodplain deposits, where an individual aggradational paleosol sequence may reach up to 20 m thick and contain abundant plant traces and carbonate nodules of stage II development of Machette (36). Episodic overbank flooding, with high aggradation rates of 10–40 mm·y⁻¹, has been proposed as a dominant mechanism in forming these types of alluvial deposits on floodplains (42). If such depositional activity was sustained, an active pedogenesis zone 2 m thick would have a residence time of only 50–200 y. During aggradation, plants appear to have recovered from the buried plant body, given the vertical continuity of the *Drepanophycus* traces. The lifespan of a *Drepanophycus* clone may have been on the order of decades or even centuries, if this fossil plant was
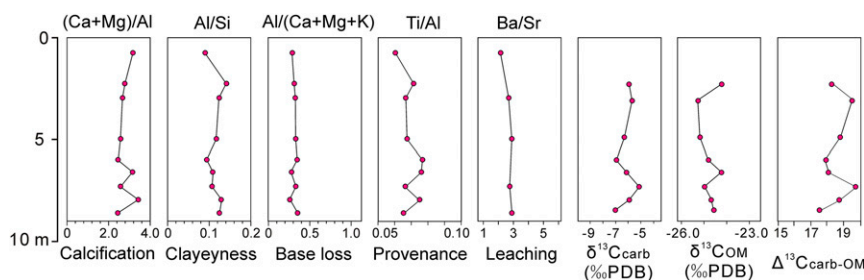
Fig. 3. Geochemical characteristics of a paleosol of the Xujiachong Formation (cycle 33 at Xujiachong; see Fig. 2*D* for lithology; data in *SI Appendix,* Tables S4–S6); $\delta^{13}C_{carb}$, stable carbon isotope values of carbonate nodules; $\delta^{13}C_{OM}$, stable carbon isotope values of organic matter within the paleosol; $\Delta13C_{carb–OM}$, the difference between $\delta^{13}C_{carb}$ and $\delta^{13}C_{OM}$.

similar in its clonal growth to the related extant lycopsid *Lycopodium* or the fern *Pteridium* (*SI Appendix*, Table S9). However, the stage II carbonate nodules within these paleosols imply a much greater residence time of 10,000–200,000 y (43). Thus, multiple generations of *Drepanophycus* clones likely grew within the beds, with periodic deposition by episodic flooding events and very long intervals of active pedogenesis with little deposition.

Paleosols of the Xujiachong Formation and their pedogenic carbonates document the earliest record of plant-associated pedogenesis in Asia (44), and our findings are consistent with this earlier report. These paleosols were aggradational, with poor horizonation [protosols, comparable to modern entisols or inceptisols (35)], some bearing a high proportion of carbonate nodules [calcisol (35)]. Geochemical proxies for calcification ([Ca+Mg]/Al), clayeyness (Al/Si), base loss (Al/[Ca+Mg+K]), and leaching (Ba/Sr) confirm their homogeneity, deposited under a seasonal, wet–dry climate as indicated by the presence of pedogenic carbonate (44, 45). The abundance of carbonate, in terms of calcification [Ca+Mg]/Al index, is 10 times higher than most of the Middle Devonian forest soils of New York (10). Such high concentrations of Ca^{2+} and Mg^{2+} indicate carbonate accumulation on a geomorphologically stable landscape over a long time, i.e., at least thousands of years (36).

The $\delta^{13}C_{carb}$ values of the carbonate nodules from the Xujiachong paleosols (−8.16 to −5.12‰) are similar to those of the North American Bloomsburg Formation (Silurian) and Catskill Formation (Upper Devonian), implying a strong contribution of ^{13}C-rich atmospheric CO_2 to the carbonate $\delta^{13}C$ (46) and, thus, a well-drained soil (47). The organic matter within the Xujiachong paleosols has a $\delta^{13}C_{OM}$ value of −25.28 to −23.38‰, consistent with the $\delta^{13}C$ of early vascular plants (48). The consistently high $\Delta^{13}C_{carb-OM}$ values through the profile depth, averaging 17.73‰ and larger than values for the supposed equilibrium difference between carbonate and soil organic matter (12.2 to 15.8‰), indicate low soil productivity during the formation of the pedogenic carbonates (49).

The new knowledge of plant traces and paleosols of the Xujiachong Formation contributes to the interpretation of some previous records. Extensive traces preserved as casts in alluvial deposits of the Lochkovian–Pragian of South Britain, some also seemingly with H-branching, were interpreted as produced by the fungus *Prototaxites* (50). Some of the large plant traces from the Battery Point Formation (Emsian) of Gaspé, Canada, were described as roots and rhizomatous extensions extending downward into the substrate nearly 1 m, and were interpreted as evidence of deep rooting (although the parent plant is unknown, *Drepanophycus* has been suggested as one of the candidates) (51). Evidence from the Xujiachong Formation suggests that the traces do not represent downwardly extended roots but rather belowground rhizomes of *Drepanophycus* and progressive burial of a long-lived plant body. We speculate that a similar explanation may account for the remains in South Britain and Canada, where compression remains of *Drepanophycus* are also encountered (50, 51). Paleosols are abundant in the Upper Silurian and Lower Devonian of Laurussia, for example, in Lower Old Red Sandstone facies of Britain (31, 52). Although most British profiles clearly show soil horizon development (e.g., vertisols), some resemble the Xujiachong paleosols in the presence of vertically aligned drab haloes and stage II carbonate nodules (31).

The extension of rhizomes to produce large clones seems to have been well established in Silurian–Devonian floras (Fig. 4*A*) (53). The rhizomatous clonal habit of *Drepanophycus* has been demonstrated by previous studies, and the belowground rhizomes of this plant spread out and colonized space via repeated H-branching as the plant grew (32, 33). We show that such rhizomes developed in vertical profiles, within unexpected thicknesses in a setting of prolonged accumulation of sediment. The existence of clonal growth similar to that of *Drepanophycus* is known to have occurred

among Pragian zosterophyllopsids, and has been demonstrated clearly for *Bathurstia* (17, 18). Rhizomatous habit also occurred in the Early Devonian rhyniopsids (21, 22), early euphyllophytes, and other groups (14). Most Rhynie Chert plants of Early Devonian age have rhizoid-based rhizomatous axes, which are either surficial or shallowly subterranean at a millimeter-scale depth (22, 23). Large woody rhizomes of aneurophytalean progymnosperms have been found in the Middle Devonian of New York, alongside cladoxylopsid and lycopsid trees (7). Rhizomes characterized many Late Devonian plants, including fern-like clades (15). For plants with small and ephemeral aboveground structures, rhizomatous clonal growth contributes to robustness, as evidenced here in *Drepanophycus*, and survival in disturbed environments, in particular, where they are subject to frequent sediment burial.

The Lower Devonian Xujiachong paleosols and plant traces provide strong, direct evidence for plant−soil interactions during the Early Devonian. Predating the earliest trees, the rhizomes of early vascular plants such as *Drepanophycus* would have contributed to stabilization of fluvial sediments and floodplains, and, in some cases, formed a deep soil ecosystem that would have served as an important carbon sink and a place for the diversification of terrestrial invertebrates. The proportion of meandering river facies, with stabilized banks, muddy floodplains, rooted sediments, and pedogenic carbonate nodules, increased steadily in the geological record from the Late Silurian (Fig. 4*B*), reflecting a secular change in fluvial geomorphology (3–5). This change in terrestrial landscapes paralleled the evolution of vascular plants and the expansion of vegetation cover (Fig. 4*C*). We propose that, underlying these processes, belowground rhizomes
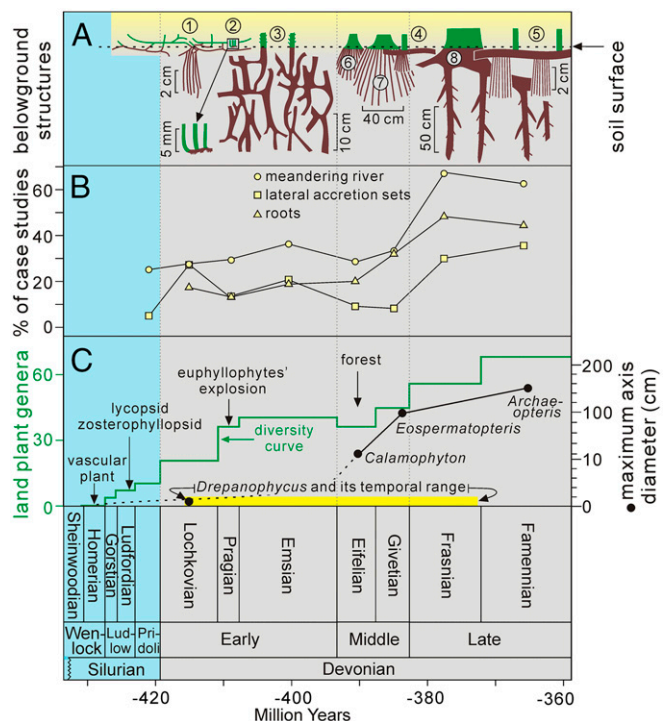
Fig. 4. Vascular plant and geomorphological evolution during the Silurian–Devonian. (*A*) Belowground structures of representative plants; most are characterized by rhizomes [1, *Zosterophyllum* (19); 2, *Rhynia* (22); 3, *Drepanophycus* (Pragian in this study, but widespread in Early Devonian); 4, aneurophytalean (7); 5, fern-like plants (15)], whereas some are trees with roots [6 and 7, pseudosporochnalean (7, 8); 8, archaeopteridalean (9)]. (*B*) Percentage of fluvial successions with meandering river facies, lateral accretion sets, and plant rooting structures (3). (*C*) Plant diversity (54), key evolutionary events, maximum size of plant axes (6), and temporal range of *Drepanophycus*.

EARTH, ATMOSPHERIC, AND PLANETARY SCIENCES

PLANT BIOLOGY

of early plants such as *Drepanophycus* were one of the biological agents working on landscape evolution by moderating soil erosion. Plant rhizomes persisted as a strategy into later geologic periods, as evidenced by the Middle Devonian aneurophytalean forests with woody rhizomes [Gilboa, New York (7)], and they continue to play critical roles in modern ecosystems (12, 13).

1. Berner RA (1997) The rise of plants and their effect on weathering and atmospheric CO_2. *Science* 276(5312):544–546.
2. Retallack GJ (1997) Early forest soils and their role in Devonian global change. *Science* 276(5312):583–585.
3. Davies NS, Gibling MR (2010) Paleozoic vegetation and the Siluro-Devonian rise of fluvial lateral accretion sets. *Geology* 38(1):51–54.
4. Davies NS, Gibling MR (2010) Cambrian to Devonian evolution of alluvial systems: the sedimentological impact of the earliest land plants. *Earth Sci Rev* 98(3-4):171–200.
5. Gibling MR, Davies NS (2012) Palaeozoic landscapes shaped by plant evolution. *Nat Geosci* 5(2):99–105.
6. Meyer-Berthaud B, Soria A, Decombeix AL (2010) The land plant cover in the Devonian: A reassessment of the evolution of the tree habit. *Geol Soc Lond Spec Publ* 339: 59–70.
7. Stein WE, Berry CM, Hernick LVA, Mannolini F (2012) Surprisingly complex community discovered in the mid-Devonian fossil forest at Gilboa. *Nature* 483(7387):78–81.
8. Giesen P, Berry CM (2013) Reconstruction and growth of the early tree *Calamophyton* (Pseudosporochnales, Cladoxylopsida) based on exceptionally complete specimens from Lindlar, Germany (Mid-Devonian): Organic connection of *Calamophyton* branches and *Duisbergia* trunks. *Int J Plant Sci* 174(4):665–686.
9. Algeo TJ, Scheckler SE (1998) Terrestrial-marine teleconnections in the Devonian: Links between the evolution of land plants, weathering processes, and marine anoxic events. *Philos Trans R Soc Lond B Biol Sci* 353(1365):113–128.
10. Retallack GJ, Huang CM (2011) Ecology and evolution of Devonian trees in New York, USA. *Palaeogeogr Palaeoclimatol Palaeoecol* 299(1-2):110–128.
11. Morris JL, et al. (2015) Investigating Devonian trees as geo-engineers of past climates: Linking palaeosols to palaeobotany and experimental geobiology. *Palaeontology* 58(5):787–801.
12. Eilts JA, Mittelbach GG, Reynolds HL, Gross KL (2011) Resource heterogeneity, soil fertility, and species diversity: Effects of clonal species on plant communities. *Am Nat* 177(5):574–588.
13. Yu FH, Dong M, Krüsi B (2004) Clonal integration helps *Psammochloa villosa* survive sand burial in an inland dune. *New Phytol* 162(3):697–704.
14. Hao SG, Xue JZ (2013) *The Early Devonian Posongchong Flora of Yunnan* (Science, Beijing).
15. Taylor TN, Taylor EL, Krings M (2009) *Paleobotany: The Biology and Evolution of Fossil Plants* (Academic, Amsterdam).
16. Li CS, Edwards D (1995) A reinvestigation of Halle's *Drepanophycus spinaeformis* Göpp. from the Lower Devonian of Yunnan Province, southern China. *Bot J Linn Soc* 118:163–192.
17. Kotyk ME, Basinger JF (2000) The Early Devonian (Pragian) zosterophyll *Bathurstia denticulata* Hueber. *Can J Bot* 78(2):193–207.
18. Gensel PG, Kotyk ME, Basinger JF (2001) Morphology of above- and below-ground structures in Early Devonian (Pragian–Emsian) plants. *Plants Invade the Land: Evolutionary and Environmental Perspectives*, eds Gensel PG, Edwards D (Columbia Univ Press, New York), pp 83–102.
19. Hao S, Xue J, Guo D, Wang D (2010) Earliest rooting system and root : shoot ratio from a new *Zosterophyllum* plant. *New Phytol* 185(1):217–225.
20. Matsunaga KKS, Tomescu AMF (2016) Root evolution at the base of the lycophyte clade: Insights from an Early Devonian lycophyte. *Ann Bot (Lond)* 117(4):585–598.
21. Edwards DS (1986) *Aglaophyton major*, a nonvascular land plant from the Devonian Rhynie Chert. *Bot J Linn Soc* 93:173–204.
22. Edwards D (2004) Embryophytic sporophytes in the Rhynie and Windyfield cherts. *Trans R Soc Edinb Earth Sci* 94(4):397–410.
23. Kenrick P, Strullu-Derrien C (2014) The origin and early evolution of roots. *Plant Physiol* 166(2):570–580.
24. Waisel Y, Eshel A, Kafkafi U (1991) *Plant Roots: The Hidden Half* (Marcel Dekker, New York).
25. Scotese CR (2001) Paleogeography, Atlas of Earth History, PALEOMAP Project, Vol 1. Available at www.scotese.com. Accessed April 22, 2014.
26. Hao SG, Xue JZ, Liu ZF, Wang DM (2007) *Zosterophyllum* Penhallow around the Silurian-Devonian boundary of northeastern Yunnan, China. *Int J Plant Sci* 168(4): 477–489.
27. Wang DM, Hao SG, Liu ZF (2002) Researches on plants from the Lower Devonian Xujiachong Formation in the Qujing district, eastern Yunnan. *Acta Geol Sin-Engl* 76(4):393–407.
28. Liu ZF, Hao SG, Wang DM, Liu JB (2004) Study on the Xujiachong Formation section of non-marine Lower Devonian of eastern Yunnan, China. *Professional Papers of Stratigraphy and Palaeontology*, ed Chinese Academy of Geological Sciences (Geol Publ House, Beijing), Vol 28, pp 61–88.
29. Wellman CH, et al. (2012) Spore assemblages from the Lower Devonian Xujiachong Formation from Qujing, Yunnan, China. *Palaeontology* 55(3):583–611.
30. Turner BR, Eriksson KA (1999) Meander bend reconstruction from an Upper Mississippian muddy point bar at Possum Hollow, West Virginia, USA. *Spec Publ Int Assoc Sedimentol* 28:363–379.
31. Morris JL, Wright VP, Edwards D (2012) Siluro-Devonian landscapes of southern Britain: The stability and nature of early vascular plant habitats. *J Geol Soc London* 169(2):173–190.
32. Schweitzer HJ (1980) Uber *Drepanophycus spinaeformis* Göppert. *Bonner Palaeobot Mitt* 7:1–29. German.
33. Rayner RJ (1984) New finds of *Drepanophycus spinaeformis* Göppert from the Lower Devonian of Scotland. *Trans R Soc Edinb Earth Sci* 75(4):353–363.
34. Davis JC (1986) *Statistics and Data Analysis in Geology* (John Wiley, New York).
35. Mack GH, James WC, Monger HC (1993) Classification of paleosols. *Geol Soc Am Bull* 105(2):129–136.
36. Machette MN (1985) Calcic soils of the southwestern United States. *Soils and Quaternary Geology of the South West United States*, ed Weide DL, Geological Society of America Special Papers (Geol Soc Am, Boulder, CO), Vol 203, pp 1–21.
37. Sheldon ND, Retallack GJ (2001) Equation for compaction of paleosols due to burial. *Geology* 29(3):247–250.
38. Sheldon ND, Tabor NJ (2009) Quantitative paleoenvironmental and paleoclimatic reconstruction using paleosols. *Earth Sci Rev* 95(1-2):1–52.
39. Vannoppen W, et al. (2015) A review of the mechanical effects of plant roots on concentrated flow erosion rates. *Earth Sci Rev* 150:666–678.
40. Balestri E, Lardicci C (2013) The impact of physical disturbance and increased sand burial on clonal growth and spatial colonization of *Sporobolus virginicus* in a coastal dune system. *PLoS One* 8(8):e72598.
41. Smith DG (1976) Effect of vegetation on lateral migration of anastomosed channels of a glacier meltwater river. *Geol Soc Am Bull* 87(6):857–860.
42. Shen ZX, et al. (2015) Episodic overbank deposition as a dominant mechanism of floodplain and delta-plain aggradation. *Geology* 43(10):875–878.
43. Wright VP, Marriott SB (1996) A quantitative approach to soil occurrence in alluvial deposits and its application to the Old Red Sandstone of Britain. *J Geol Soc London* 153(6):907–913.
44. Boucot AJ, et al. (1982) Devonian calcrete from China: Its significance as the first Devonian calcrete from Asia. *Can J Earth Sci* 19(7):1532–1534.
45. Breecker DO, Sharp ZD, McFadden LD (2009) Seasonal bias in the formation and stable isotopic composition of pedogenic carbonate in modern soils from central New Mexico, USA. *Geol Soc Am Bull* 121(3-4):630–640.
46. Mora CI, Driese SG, Colarusso LA (1996) Middle to Late Paleozoic atmospheric CO_2 levels from soil carbonate and organic matter. *Science* 271(5252):1105–1107.
47. Gastaldo RA, Knight CL, Neveling J, Tabor NJ (2014) Latest Permian paleosols from Wapadsberg Pass, South Africa: Implications for Changhsingian climate. *Geol Soc Am Bull* 126(5-6):665–679.
48. Beerling DJ, et al. (2002) Carbon isotope evidence implying high O_2/CO_2 ratios in the Permo-Carboniferous atmosphere. *Geochim Cosmochim Acta* 66(21):3757–3767.
49. Montañez IP (2013) Modern soil system constraints on reconstructing deep-time atmospheric CO_2. *Geochim Cosmochim Acta* 101:57–75.
50. Hillier RD, Edwards D, Morrissey LB (2008) Sedimentological evidence for rooting structures in the Early Devonian Anglo-Welsh Basin (UK), with speculation on their producers. *Palaeogeogr Palaeoclimatol Palaeoecol* 270(3):366–380.
51. Elick JM, Driese SG, Mora CI (1998) Very large plant and root traces from the Early to Middle Devonian: Implications for early terrestrial ecosystems and atmospheric p(CO_2). *Geology* 26(2):143–146.
52. Marriott SB, Wright VP (1993) Palaeosols as indicators of geomorphic stability in two Old Red Sandstone alluvial suites, South Wales. *J Geol Soc London* 150:1109–1120.
53. Tiffney BH, Niklas KJ (1985) Clonal growth in land plants: A paleobotanical perspective. *Population Biology and Evolution of Clonal Organisms*, eds Jackson JBC, Buss LW, Cook RE (Yale Univ Press, New Haven, CT), pp 35–66.
54. Cascales-Miñana B (2016) Apparent changes in the Ordovician-Mississippian plant diversity. *Rev Palaeobot Palynol* 227:19–27.