Pennsylvanian uplands were forested by giant cordaitalean trees

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ABSTRACT

The precise timing of when upland terrains first became forested is highly controversial. Pennsylvanian palynoflora and megaflores transported into marine highstand deposits imply that emergent topographic highs may have supported cordaitalean forests. The discovery of a new Pennsylvanian (Bolsovian) plant assemblage in southwest Newfoundland confirms this hypothesis and allows the architecture of these upland trees to be reconstructed in detail. The assemblage includes several hundred calcareously permineralized stumps, trunks, and branches, and represents the remains of shallowly rooted cordaitalean trees that were ≤48.5 m high when mature. The fossils occur in alluvial conglomerates that constitute a 10-km-diameter outlier on the margins of the paleoequatorial Variscan foreland. The paleogeographic setting together with plant taphonomic inferences strongly indicate that these giant trees were transported from nearby upland alluvial plains and deposited in an elevated intermontane basin. This interpretation is supported by analysis of rootstock morphology, which implies tree growth in thin soils consistent with an alluvial gravel substrate. This improved understanding of Pennsylvanian upland forests has important implications for geochemical modeling of the global carbon cycle.

Keywords: Pennsylvanian ecology, upland forests, fossil wood, carbon cycle, coal measures.

INTRODUCTION

When did upland terrains first become forested, and what was the composition of these ecosystems? These questions are highly important, not only because they relate to a significant event in the “greening of the Earth” (Falcon-Lang and Scott, 2000), but also because the colonization of upland environments would have exerted an enormous impact on continental weathering rates and hence on the global carbon cycle and climate (Algeo and Scheckler, 1998). However, as only lowland environments are preserved in the long-term geologic record, direct evidence for upland vegetation is scarce.

Many geologists accept that upland forests existed by latest Pennsylvanian (Cantabrian) time on the basis of the sudden appearance of morphologically advanced conifers in lowland settings coincident with the onset of climatic aridity (Cridland and Morris, 1963; Winston, 1983). They argue that these xeric floras evolved in upland areas before climate change caused them to expand down into the lowland depocenters (Frederiksen, 1972; DiMichele and Aronson, 1992).

In a classic paper, Chaloner (1958) provided insight into the nature of pre-Cantabrian upland communities. Reinterpreting palynological data from lower Pennsylvanian highstand marine deposits collected by Neves (1958), Chaloner reasoned that the palynofloras must have been derived from vegetation surviving in higher-altitude regions following widespread flooding of lowland forests. The “Neves effect,” as Chaloner termed his phenomenon, implied that early Pennsylvanian uplands were dominated by cordaitalean trees. Subsequent studies of palynoflora and megaflores in highstand sequences have generally supported this conclusion (Turner et al., 1994; Davies and McLean, 1996; Scott et al., 1997; Falcon-Lang, 2003).

In this paper a fossil plant assemblage is described from intermontane alluvial conglomerates in southwest Newfoundland. The assemblage provides the strongest evidence yet that Pennsylvanian uplands were dominated by cordaitaleans. Analysis of abundant and well-preserved remains allows detailed reconstruction of these gigantic upland trees at various ontogenetic stages.

GEOLOGIC SETTING

The cordaitalean remains occur in a 10-km-diameter outlier near Stephenville, Newfoundland (UTM 83757875, Map Sheet 12 B/10), that marks the northwest margins of the late Paleozoic Bay St. George Basin (Hyde, 1995; Fig. 1). The rocks of the Stephenville outlier belong to the Pennsylvania Barachois Group but have not yet been assigned to a formation. They unconformably overlie Proterozoic and lower Paleozoic basement and are of middle Pennsylvanian (Bolsovian) age, on the basis of megaflores and palynofloras assemblages (Hyde et al., 1991; Bashforth, 2004).

The only major exposure is along a 20–50-m-wide river valley called Blanche Brook, north of Stephenville, where there is a shallowly dipping (5°–16°ESE) succession ~115 m thick. Two facies associations are present: ≤4-m-thick units of very coarse grained, lithic sandstone and pebble conglomerate and ≤2.5-m-thick units of red mudstone, gray mudstone, and very thin, rare coals.

The coarse-grained units have subhorizontal erosive bases over tens of meters, contain trough cross-beds, and fine upward into medium-grained sandstones. Large-scale, low-angle strata, oriented subperpendicular to local paleoflow, and arcuate ridge-and-swale topography occur. Such facies characteristics are indicative of small sinuous gravel-bed streams, whereas intercalated mudstone units represent adjacent low-energy floodplains that periodically were sufficiently waterlogged for peat mires to develop.

CORDAITALEAN TREES

More than 200 calcareously permineralized stumps, trunks, and branches of cordaitaleans are exposed along Blanche Brook. They occur within the basal lags of the gravel-bed stream deposits at ~11 stratigraphic intervals. Almost all cordaitalean specimens are prostrate, although one stump specimen is preserved up-
right (Fig. 2A). They are facies associated with compressions of Sigillaria and Calamites. Detailed thin-section analysis of wood anatomy demonstrates that the material represents a single taxon. A cordaitalean affinity is indicated by a combination of features, including the presence of a septate Artisia pith cavity, pycnoxylic wood referable to Dadoxylon materiarium Dawson, and branches bearing the helically arranged bases of large leaves (Rothwell, 1988); 127 specimens are sufficiently well preserved to identify from which part of the tree they were derived.

Specimens of Basal Parts of Trees

The basal parts of the trees are represented by 36 specimens. These consist of stumps with attached roots and, in some examples, as much as the lower 7 m of the trunk. Stumps have a marked flare, typically increasing in diameter by an additional 50%–120% over the basal 20–45 cm of the trunk (Figs. 2A, 2B). At the point of maximum flare, stump diameters range from 22 to 192 cm (mean 79.16 cm), with values ranging from 16 to 117 cm (mean 46.56 cm) immediately above the flared zone. All the stump wood has a characteristic ropy texture, as commonly seen in the buttresses of modern confers. In the largest stumps the septate pith cavity has apparently been lost, having been replaced by a large, subconical, sandstone-cast cavity ≤19 cm in diameter and ≤38 cm high (Fig. 2A).

The gross morphology of the cordaitalean root system is complex and variable, its characteristics apparently highly dependent on ontogenetic age. The smallest, and hence presumably the most juvenile stumps (<15 cm diameter), have a mass of fine, densely arranged, vertically oriented roots (<1–2 cm diameter) that extend to depths as great as 30 cm. Middle-sized stumps (15–40 cm diameter) are typically dominated by a single, sub-vertically oriented tap root, which may be ≤20 cm in diameter at its broadest end and ≤1 m long (Fig. 2C). The largest stumps (≤1.92 m) are characterized by subhorizontally oriented roots, ≤10–43 cm in diameter, that show at least three orders of bifurcation and have a preserved radius of ≤1.7 m, although originally the root system would have extended much further (Figs. 2A, 2B). None of the rootstock specimens observed preserved attached fragments of the original soil.

Specimens of Upper Parts of Trees

A further 91 specimens clearly represent upper parts of the trees because they lack attached stumps. These specimens consist of ≤7.5-m-long monopodial trunks, 6–84 cm in diameter (mean 30.61), that bear small, sparsely distributed lateral branches. Where the septate pith cavity is preserved, it is always skewed from the center of the trunk by 44%–60% (n = 5) (Fig. 2D). This is not a taphonomic artifact, as indicated by cross-sectional views of complete trunks bearing bark. Nor are these skewed pith cavities part of a lateral branch system, because they follow a perfectly trunk-parallel orientation for >1.5 m.

Lateral branches are only attached to the smallest-diameter trunks (7–36 cm diameter; n = 9) and never occur associated with specimens exhibiting attached stumps, even where ≤7 m of the lower trunk is preserved. Branches are 2.5–10 cm in diameter (mean 4.85 cm; n = 13) and circular to oval in cross section; they project upward from the vertical trunk at an angle of 31°–50°. They are arranged either in opposite pairs or in irregular whirls with ≤4–7 branches at a particular level (Fig. 2E), and each branch tier is spaced ≥2 m apart. Some branch scars are partially or completely overgrown by subsequent trunk expansion.

Pith casts of several branches preserve the position of departing leaf traces as vertically oriented oval projections on the exterior of the cast (10–11 mm high, 4–5 mm wide). These data show that leaves were helically arranged (17–19 mm apart measured around the helix) with an angular spiral of 48°–53° and a phylloxylogy approximating a 1/8 arrangement.

Although leaves were never found attached to the branches, devolatized compressions of Cordaites are facies associated with the permineralized woody remains in the alluvial channel deposits, but leaves of this type have never been found in intercalated flood-basin mudstone facies despite detailed targeted searches (Bashforth, 2004). These are large, coriaceous, strap-like leaves, 18–45 mm wide and >30 cm long (complete leaves were never observed).

RECONSTRUCTION OF CORDAITALEAN TREES

On the basis of the abundant and unusually well preserved specimens, it is possible to reconstruct the cordaitalean trees in detail at various ontogenetic stages. Application of Niklas’s (1994) empirically derived, biomechanical relationship between basal trunk diameter (D) and tree height (H) for woody plants permits the maximum buckling height of the trees to be inferred:

\[
\log_{10} H = 1.59 + 0.39(\log_{10} D) - 0.18(\log_{10} D)^2. \tag{1}
\]

Inputting cordaitalean basal (stump) diameter into equation 1 indicates that tree heights ranged from 18.02 to 48.53 m (mean 33.81 m; n = 36). The most mature cordaitaleans were therefore probably among the tallest trees in the Pennsylvanian tropical zone, apparently dwarfing the lepidodendrons, which in comparison attained a maximum height of only 35 m (Niklas, 1994).

As the cordaitalean trees matured, support was evidently provided through the expansion of the stump buttress zone and development of the rooting system. Small juvenile trees were initially anchored by a vertically oriented mass of shallow fibrous roots. Further matu-
Figure 2. Permineralized cordaitalean remains transported in alluvial conglomerates. A: Large, upright stump showing bifurcating roots and expanded basal cavity. Hammer is 38 cm long. B: Very large, prone trunk showing basal flare and attached roots (submerged). Hammer is 38 cm long. C: Stump showing single vertical tap root; specimen is horizontally disposed. Hammer is 38 cm long. D: Upper monopodial trunk showing skewed septate pith; scale bar represents 10 cm. E: Upper monopodial trunk showing several branch scars arranged in irregular whorl; tape case is 10 cm across.

EVIDENCE FOR UPLAND ECOLOGY

Several pieces of evidence strongly indicate that the Stephenville cordaitalean remains were derived from upland communities. Whereas previous inferences about Pennsylvanian upland floras have primarily been based on interpretation of distally deposited assemblages in marine highstand units, this paper presents much more informative data from terrestrial units within the proximal foothills of the Variscan mountains.

Basin Analysis and Paleogeography

The Stephenville outlier is preserved just beyond the margins of the main Bay St. George Basin, immediately downstream of the inferred location of the Variscan mountains. Regional mapping indicates that this Pennsylvanian succession unconformably overlies Proterozoic–lower Paleozoic basement (Williams, 1985). Field relationships imply that Pennsylvanian units infilled an ~200-m-deep and 10-km-wide valley on the basement complex (Palmer et al., 2002), flanked to the northwest and northeast by upland zones and open to the southwest, as indicated by coeval alluvial successions underlying St. George’s Bay and paleocurrent data (Langdon and Hall, 1994; Bashforth, 2004).

Given that Pennsylvanian units blanket ~200 m of paleorelief, it is highly unlikely that they were deposited at or close to sea level, but rather in topographically elevated, intermontane foothills. This interpretation is supported by the very coarse grained nature of the sedimentary rock and the complete absence of paralic, brackish-bay facies that are widespread in Pennsylvanian units elsewhere in eastern Canada (Archer et al., 1995).

Cordaitalean Taphonomy and Architecture

The allochthony of the cordaitalean remains is indicated by their prostrate orientation in channel deposits. The single upright stump is also allochthonous, as demonstrated by its facies context; upright orientation represented the most hydrodynamically stable position for this tree (cf. Fritz, 1980). However, it is unlikely that the cordaitalean remains in the Stephenville outlier have been transported more than a few kilometers. This short distance is
inferred from the relatively small size of the sinuous alluvial channels (probably ≤3–4 m deep), which would have had limited transport potential, and from the unusual preservation of abundant cordaitalean specimens with intact rootstocks.

The occurrence of abundant rootstock specimens indicates that trees entered the alluvial channels by lateral cutbank erosion of forested flood-basin soils upstream. Forest assemblages catastrophically destroyed by storms, fires, or flood are dominated, in contrast, by trunk and crown remains (Ash and Creber, 2000). The presence of abundant rootstock specimens therefore indicates that the cordaitalean trees were growing immediately adjacent to laterally migrating alluvial channels.

The cordaitalean rootstock ontogeny indicates that the trees were rooted in thin soils, which inhibited vertical root development. This morphology favors the hypothesis that the trees grew on thin alluvial gravels that likely blanketed the hinterland rather than on successions of unconsolidated fine-grained aluvium in the basin. This hypothesis is further supported by the skewed position of the pith in several trunks, which may imply growth on a significant gradient.

The fossil assemblage discovered in the Stephenville outlier therefore appears to confirm the existence of cordaitalean forests in the Pennsylvania uplands previously inferred primarily from palynological data (Chalonor, 1958). However, the exceptional preservation of large tree fossils additionally allows the architectural reconstruction of these upland trees for the first time and permits insight into their ontogeny.

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