Pennsylvanian tropical rain forests responded to glacial-interglacial rhythms

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ABSTRACT

Pennsylvanian tropical rain forests flourished during an icehouse climate mode. Although it is well established that Milankovitch-band glacial-interglacial rhythms caused marked synchronous changes in Pennsylvanian tropical climate and sea level, little is known of vegetation response to orbital forcing. This knowledge gap has now been addressed through sequence-stratigraphic analysis of megafloral and palynofloral assemblages within the Westphalian D–Cantabrian Sydney Mines Formation of eastern Canada. This succession was deposited in a low-accommodation setting where sequences can be attributed confidently to glacio-eustasy. Results show that long-lived, low-diversity peat mires dominated by lycopsids were initiated during deglaciation events, but were mostly drowned by rising sea level at maximum interglacial conditions. Only upland coniferopsid forests survived flooding without significant disturbance. Mid- to late interglacial phases witnessed delta-plain progradation and establishment of high-diversity, mineral-substrate rain forests containing lycopsids, sphenopsids, pteridosperms, cordaites, and tree ferns. Renewed glaciation resulted in sea-level fall, paleovalley incision, and the onset of climatic aridity. Glacial vegetation was dominated by cordaites, pteridosperms, and tree ferns; hydrophilic lycopsids and sphenopsids survived in paleovalley refugia. Findings clearly demonstrate the dynamic nature of Pennsylvanian tropical ecosystems and are timely given current debates about the impact of Quaternary glacial-interglacial rhythms on the biogeography of tropical rain forest.

Keywords: Pennsylvanian ecology, coal measures, Milankovitch cycles, glacial-interglacial, Nova Scotia, sequence stratigraphy.

INTRODUCTION

Pennsylvanian terrestrial successions in North America and Europe contain spectacular remnants of early tropical rain forests (DiMichele et al., 2001). These strata are characterized by cyclic sedimentation patterns (sequences) that record Milankovitch-band glacial-interglacial rhythms (Cecil, 1990; Maynard and Leeder, 1992). Sequences were generated by coupled eustatic-climatic fluctuations (Tandon and Gibling, 1994), and modified by basin subsidence and sediment supply (Gastaldo et al., 1993; Leeder et al., 1998). Despite the known major impact of glacial-interglacial rhythms on Quaternary tropical biogeography (Harrison and Prentice, 2003), the response of Pennsylvanian rain forests to such phenomena remains unclear.

Previous studies have obliquely addressed this issue by analyzing the interglacial (coal bearing) components of sequences, where the fossil plant material is best preserved. This research has demonstrated that, following each glacial disturbance, compositionally stable ecosystems repeatedly reassembled (DiMichele et al., 1996, 2002; Pfefferkorn et al., 2000). In other studies, oscillations in plant assemblage composition have been recognized in Czech successions and attributed to glacial-interglacial rhythmicity (Havlena, 1971; Gastaldo, 1996). However, in the absence of a sequence stratigraphic context for these assemblages, such interpretations are speculative. In order to confidently analyze Pennsylvanian vegetation response to glacial-interglacial rhythms, plant assemblage data must be acquired through multiple, well-constrained sequences.

Earlier attempts at such sequence analysis in a high-accommodation setting at Joggins, Nova Scotia, were only partially successful (Falcon-Lang, 2003a) because the orbitally driven motif could not be disentangled from tectonic effects (Davies and Gibling, 2003). In this paper we describe the sequence-stratigraphic distribution of Pennsylvanian plant assemblages from the Sydney Mines Formation of Nova Scotia (Gibling et al., 2004). These strata were deposited in a stable cratonic setting where tectonic effects were minimal; consequently, the well-studied sequences that characterize this unit provide an unambiguous orbital framework (Tandon and Gibling, 1994). Fossil plant data acquired within this context confirm the repeated contraction and expansion of Pennsylvanian rain forests in response to glacial-interglacial rhythms.

GEOLoGIC SETTING

The Sydney Mines Formation is exposed in a near-continuous, 50-km-long sea-cliff section on the northeast coast of Cape Breton Island, Nova Scotia, eastern Canada (Fig. 1; lat 46°10’N, long 60°00’W). This Westphalian D–Cantabrian succession has an onshore thickness of 520 m, and was deposited in the paleo-equatorial Sydney Basin within the northeastern part of the Appalachian orogen (Pascucci et al., 2000). Stratal accumulation rates of ~173 m/m.y. (uncompacted) are low compared with many coeval basins in Europe and North America. The low accumulation rates are indicative of a modest subsidence rate and a cratonic style during the thermal-sag phase of basin evolution (Calder, 1998; Gibling et al., 2004).

Depositional sequences in the Sydney Mines Formation range in thickness from 12 to 83 m and, in general, compose a classic Exxon-type architecture of transgressive, highstand, and lowstand systems tracts (Fig. 2; Gibling et al., 2004). The glacial-interglacial origin of the sequences is supported by coupled fluctuations in climate and sea level (Tandon and Gibling, 1994): paleovalley incisions formed at lowstand laterally correlate with mature interfluve calcrites indicative of
The limestones that cap the transgressive system tracts, and contain the maximum flooding surface, exhibit rare charred coniferopsid woods. This diversity is mirrored in the palynofloral assemblages, which contain large spikes in the abundance of coniferopsid pollen (Florinites and Potoniesporites) in five of the sequences. Similar assemblages are associated with Pennsylvanian maximum flooding surfaces across Euramerica (Davies and McLean, 1996; Falcon-Lang, 2003a) and may record a distal signature from cordaite-conifer-dominated upland floras that survived the deglaciation-driven flooding of lowland environments (Falcon-Lang and Bashforth, 2004).

**Highstand Systems Tracts**

Highstand systems tracts comprise dominantly coarsening-upward successions that immediately overlie the transgressive system tracts and were formed as delta plains that prograded out into the basin during mid- to late interglacial highstand conditions. Gray mudstone units containing agglutinated foraminifera represent brackish bay-fill deposits and mark the onset of highstand conditions (Gastaldo et al., 1993). Gray mudstone successions containing ≤5-m-thick, fine- to medium-grained channel sandstones and sheet sandstones represent poorly drained delta-plain deposits (Gibling and Bird, 1994). Relatively thin (1–90 cm) coals at numerous intervals indicate establishment of short-lived mires in emergent delta-top environments.

Compressed plant assemblages are abundant and extremely diverse in the highstand systems tracts. Upright, sandstone-cast lycopsid trees are rooted in the thin coals, which represent the deposits of relatively short lived, forested peat mires (10^3–10^6 yr). Associated palynoflora and parautochthonous adpressed megaflora indicate that the longest-lived mires in the highstand systems tract setting were dominated by Lepidoptiloios harcourtii and Lepidodendron hickii (Dolby, 1988; Calder et al., 1996). More ephemeral, flood-disturbed mires were dominated by the lycopsids Sigillaria and Paralycopepodites brevifolius, together with medulosan pteridopsids.

Flood-basin mudstones contain parautochthonous megafloral compressions dominated by sigillarian lycopsids, alethopterid and neuropterid pteridopsids, cordaites, and pecopterid tree ferns. These assemblages represent the remains of highly diverse vegetation that occupied flood-disturbed mineral substrates. Channel-sandstone units contain allochthonous assemblages of similar composition, but show greater numerical dominance by cordaites, sphenopsids, and pecopterids. These assemblages contain mixtures of plants from a variety of low-elevation wetland settings, but are likely biased toward levee niches (Scheihing and Pfefferkorn, 1984), where cordaites, sphenopsids, and pteridopsids dominated.

### Lowstand to Early Stage Transgressive Systems Tracts

Lowstand systems tracts are characterized, in three of the sequences, by paleovalleys deeply incised into the underlying highstand systems tracts (as much as 5 m basal relief in outcrop). They correlate laterally with meter-thick calcretes that represent mature (10^6 yr old) interfuvle soils formed under semiarid conditions. Together, these phenomena define the sequence boundary and record a major fall in sea level forced by the renewed onset of glaciation (Tandon and Gibling, 1994). Paleovalley fills comprise multistory coarse-grained channel bodies, 300 m thick and >7 km wide, one exhibiting glaucony (Gibling and Wightman, 1994; Batson and Gibling, 2002). Overlying stratal successions comprise units of red, vertisol-bearing mudstone, 2-m-thick sheet sandstone, and ≤5-m-thick channel sandstone. These deposits are assigned to the early stage transgressive systems tract and record valley filling and subsequent vertical aggradation of seasonally dry alluvial-plain deposits during mid- to late glacial phases.
Basal paleovalley fills contain calcite-permineralized, ≤20–30-cm-diameter trunks, in one example adjacent to the basin margin (Cald-er et al., 1996), and 1-cm-diameter charred blocks of wood in two examples. All woods conform to Dadoxylon materiarium Dawson and derived from large cordaites (Falcon-Lang et al., 2004). This allochthonous assemblage was likely fluvially transported from upland forested regions (Falcon-Lang and Bashforth, 2004). Rare upright, sandstone-cast lycopid trees, locally rooted in thin coals between al-luvial stories in one paleovalley, indicate that peat-forming wetland rain forests persisted through dry glacial phases within isolated valley refugia.

Overlying alluvial-plain deposits contain extremely rare megafaunal impressions. The sparse nature of the floral record at this point in the base-level transit cycle is likely taphonomic (linked to predominantly oxidizing soil conditions) rather than reflective of originally sparse vegetation. Immature red (locally vertic) paleosols contain complex, extensive, horizontal root traces that exhibit more than four orders of branching, and are locally connected to mud-cast upright trunks (≤13 cm diameter). Paraautochthonous megafossil assemblages in over-lying splay-deposited siltstone and sandstone sheets consist of either Cordaites, Alethopteris, Neuropteris, or Pecopteris, indicating a range of possible affinities for the facies-associated autochthonous remains. Channel facies, especially mud-filled abandonments, contain Cordaites. Levee-deposited sandstones contain upright, sandstone-cast calamitean stems and paraautochthonous Annularia and Sphenophyllum impres-sions. Palyno/loral assemblages contain only tree ferns, cordaites, and rare lycopsids. Collectively, data indicate that glacial lowlands outside paleovalleys were dominated by cordaites, pteridosperms, and tree ferns, together with sphenopsids and lycopsids, probably in riparian niches (Falcon-Lang et al., 2004).

**IMPLICATIONS OF VEGETATION RESPONSE**

Plant assemblages in the Sydney Mines Formation demonstrate that Pennsylvanian tropical rain forests contracted and expanded in response to glacial-interglacial rhythms (Fig. 3). Peat-forming, lycopid-dominated, lowland rain forest held sway during interglacial phases, and especially during deglaciation, but contracted into isolated paleovalley refugia during glacial phases. Dry glacial lowland environments were dominated by gymnosperms and tree ferns, the plant groups best adapted to better drained conditions (DiMichele and Phil- lips, 1994). Upland coniferopsid forests existed during both interglacial and glacial phases, but may have expanded down to lower altitudes during glacial phases, as inferred from the incursion of large cordait logs into lowland paleovalleys.

Precisely this kind of biogeographic response to glacial-interglacial rhythms is also seen in Quaternary time, the first major icehouse episode to affect Earth since the Pennsylvanian Period (DiMichele et al., 1996). Palynological data from well-dated lacustrine cores indicate that Asian and African rain forests underwent significant contraction and fragmentation during the cool, dry Last Glacial Max-imum (LGM), being replaced by drought-adapted savanna vegetation (Heaney, 1991; Prentice and Jolly, 2000). Even in South America, where the picture is least clear, the lowland Amazon rain forest appears to have exhibited some marginal contraction during the LGM (Hooghiemstra and van der Hammen, 1998; Colinvaux et al., 2000) or was, perhaps, partially replaced by upland elements (Colinvaux et al., 1996).

The findings of this paper are significant because they overturn previous conjecture that the Pennsylvanian tropical biome was a rather static system (DiMichele et al., 1996), and replace this image with a more dynamic model. The results further emphasize the importance of studying fossil plants in their sequence-stratigraphic context (Gastaldo
et al., 1993), an approach that highlights the significance of poorly preserved redbed plant assemblages (Falcon-Lang, 2003b).

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REFERENCES CITED

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