



Paleoecology of Early Pennsylvanian vegetation on a seasonally dry tropical landscape (Tynemouth Creek Formation, New Brunswick, Canada)



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ABSTRACT

The distribution and community ecology of Early Pennsylvanian (middle Bashkirian, Langsettian) vegetation on a seasonally dry fluvial megafan is reconstructed from plant assemblages in the Tynemouth Creek Formation of New Brunswick, Canada. The principal motif of the redbed-dominated succession consists of degraded interfluvial surfaces overlain by coarsening-upward aggradational sequences, a pattern that expresses the approach of an active channel system over a part of the megafan where landscape stasis prevailed. Accrual under a (dry) subhumid tropical climate, typified by a protracted dry season and a short wet season with torrential rainfall, resulted in Vertisol-like paleosols, episodic discharge and sedimentation, shallow channels incised into partially indurated interfluvial strata, and scattered 'waterhole' deposits. Plant fossils, including many upright stumps, are preferentially preserved above paleosol-mantled interfluvial surfaces, recording the inundation of a vegetated landscape. Quantitative analysis of 41 census-sampled megafan assemblages collected in facies context indicates that a cordaitalean-rich flora dominated the dryland ecosystem. Less common was a wetland flora typical of tropical lowlands at coeval localities, comprising medullolean pteridosperms and calamitaleans with rare ferns and lycopsids. 'Enigmatic dryland' plants, taxa of ambiguous affinity including *Megalopteris*, *Pseudodianites*, and *Palaeopteridium*, were rare but surprisingly diverse. The taphonomic and sedimentologic context of fossiliferous horizons indicates that low-diversity, old-growth stands of gigantic cordaitaleans blanketed distal interfluvial and inactive parts of the megafan, environs marked by limited deposition and extended paleosol development. Small patches of the pteridosperm-dominated wetland flora were interspersed within the dense cordaitalean forest, restricted to landforms that acted as waterholes during the dry season, such as perennial lakes, stagnant ponds, and seasonally active interfluvial channels. In contrast, cordaitaleans and wetland plants formed mixed communities in disturbance-prone proximal interfluvial and fluvial tracts, where more flooding and sedimentation resulted in less moisture-stressed conditions and a wider range of habitable landforms. Dense calamitalean groves persisted alongside fluvial channels, and an array of wetland plants occupied seasonally active abandoned channels that retained water throughout the year (waterholes). Rare 'enigmatic dryland' species were more prevalent in flood-prone fluvial tracts, and were dispersed within cordaitalean-dominated and wetland communities rather than forming discrete, compositionally unique patches. Although frequently characterized as 'extrabasinal' or 'upland' elements, this study confirms that these unusual plants occupied Pennsylvanian tropical lowlands during episodes of climatic drying.

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1. Introduction

Pennsylvanian (323–299 Ma) plant communities of tropical Euramerica, broadly subdivided into wetland and dryland floras,

experienced dynamic evolution and reorganization in the face of climatic change. The distribution and extent of these ecosystems responded to fluctuations in sea level and attendant climate cycles of variable magnitude and tempo (DiMichele et al., 1996; Gastaldo et al., 1996; DiMichele et al., 2001; Falcon-Lang, 2004; Poulsen et al., 2007; DiMichele et al., 2009; Falcon-Lang and DiMichele, 2010; van Hoof et al., 2013), particularly as a result of the far-field effects of glacial cover at high southern latitudes on Gondwana (Frakes et al., 1992; Cecil et al., 2003; Fielding et al., 2008a,b; Rygel

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et al., 2008; Martin et al., 2012; Montañez and Poulsen, 2013). When climatic conditions ranged from perhumid (everwet) to subhumid with some seasonal dryness, the tropics were blanketed by luxuriant, hygrophite-dominated communities (wetland floras) in peat-forming mires and associated clastic wetlands (Table 1; Cecil et al., 1985; Cecil, 1990; DiMichele and Phillips, 1994). The bulk of knowledge about Pennsylvanian vegetation is derived from such wetland deposits, typified by grey, coal-bearing strata and gleyed paleosols, because the plant fossil record is strongly biased towards communities that inhabited wet to waterlogged substrates, where burial and long-term preservation is enhanced (DiMichele and Gastaldo, 2008; Gastaldo and Demko, 2010). In contrast, strata between coal-bearing intervals often contain calcic and vertic paleosols and redbeds incised by paleovalleys (Gibling and Bird, 1994; Tandon and Gibling, 1994), and may preserve the remains of tropical vegetation adapted to more intensely seasonal rainfall under subhumid to semiarid conditions (Table 1; DiMichele et al., 2008, 2010a). These dryland floras, inferred to have grown on moisture-deficient soils and thus susceptible to oxidative destruction, tend to be only rarely preserved and hence are not as well known as those from wetlands.

DiMichele et al. (2010a) reviewed the occurrence and composition of several types of Pennsylvanian seasonally dry (= dryland) flora, which typically are gymnosperm dominated and include derived taxa with mesic or xeric characters (Table 1; DiMichele and Aronson, 1992). Rarely encountered in wetland deposits, such assemblages have been termed 'upland' or 'extrabasinal' floras based on the premise that the plants were transported to basinal lowlands from better-drained, elevated habitats (e.g., Chaloner, 1958; Havlena, 1961; Cridland and Morris, 1963; Havlena, 1971; Leary and Pfefferkorn, 1977; Pfefferkorn, 1980; Dimitrova et al., 2011). However, the terms 'dryland' or 'seasonally dry' floras are more appropriate because such vegetation commonly grew within depocentres rather than being confined to marginal settings, with prior adaptation to moisture limitation enabling the plants to disperse into basinal lowlands during episodes of climatic drying (Moore et al., 1936; Gastaldo, 1996; Falcon-Lang et al., 2009; DiMichele et al., 2010a; Dolby et al., 2011; Falcon-Lang et al., 2011, 2012; van Hoof et al., 2013).

DiMichele et al. (2010a) identified three main seasonally dry floras, which they inferred to intergrade along a less wet-to-dry gradient during the Early to Middle Pennsylvanian (Table 1). At the wettest end of the spectrum, forests dominated by gigantic cordaitaleans occupied habitats transitional between wetlands and strongly seasonal drylands, preferring well-drained floodplains, channel margins, and slopes bordering basinal

areas (Falcon-Lang and Scott, 2000; Falcon-Lang, 2003a,b; Falcon-Lang and Bashforth, 2004; Falcon-Lang et al., 2004; Falcon-Lang and Bashforth, 2005; Falcon-Lang, 2006a, 2007; Falcon-Lang et al., 2009, 2012). Floras typified by *Megalopteris* and *Lesleya*, along with other (pro)gymnosperms atypical of wetland assemblages (e.g., *Rhacopteridium*, *Palaeopteridium*, *Dicranophyllum*), make scattered appearances in the Early and Middle Pennsylvanian and may have occupied relatively drier, possibly alkaline soils, especially on limestone bedrock (Leary and Pfefferkorn, 1977; Leary, 1981). Given the variable and generally ambiguous affinities of these plants, and to differentiate them from cordaitalean-dominated and wetland floras, they are hereafter referred to as the 'enigmatic dryland' flora (Table 1). At the driest end of the spectrum were floras containing walcian conifers, with the facies context of rare (par) autochthonous finds confirming that the plants were centered in semi-arid climates (Galtier et al., 1992; Plotnick et al., 2009; Falcon-Lang et al., 2011). Although putative Early Pennsylvanian (Duckmantian) specimens attributed to conifer foliage (Scott and Chaloner, 1983) are now considered lycopsid remains (Hübers et al., 2011), unequivocal megafossil evidence of these xeric plants first appears as allochthonous elements in Middle Pennsylvanian strata (Lyons and Darrah, 1989; Falcon-Lang et al., 2009). However, palynological evidence implies that primitive conifers may have originated in the Late Mississippian (Stephenson et al., 2008; Utting and Giles, 2008), and that by Early Pennsylvanian times all three types of dryland flora were locally established across tropical basinal lowlands.

To help clarify the ecology and extent of dryland vegetation in tropical lowland settings during intervals of intensified seasonality, plant remains were studied from the Lower Pennsylvanian (middle Bashkirian) Tynemouth Creek Formation of Atlantic Canada. The redbed-dominated succession exhibits features consistent with accrual under strongly seasonal conditions (cf. Fielding et al., 2009; Allen et al., 2011; Fielding et al., 2011), including evidence for episodic fluvial discharge, degraded interfluvies mantled by vertic paleosols, shallow channels that cut into indurated floodplains, and scattered 'waterholes' that retained water during the dry season. Although the Tynemouth Creek Formation accumulated adjacent to an elevated margin (Plint and van de Poll, 1982; Nance, 1986, 1987), the recent discovery of a limestone containing an open-marine fauna in the basin fill (H.J. Falcon-Lang and P.K. Pufahl, unpublished data) confirms that deposition occurred in a lowland setting.

At first sight, the Tynemouth Creek Formation seems to hold little promise for unraveling the paleoecology of Pennsylvanian dryland floras. As in many redbed-dominated units, fossils first appear to be rare, apart

Table 1
Segregation of habitats, floral types, and main plant groups that existed in paleotropical Euramerica during the Pennsylvanian depending on seasonality of precipitation and climate. Note that vegetation present under a particular environmental regime is not immutable but an approximation, and that a gradation is presumed to exist between wetland and dryland settings. The Tynemouth Creek Formation is interpreted to have been deposited under a dry subhumid climate (3 to 5 'wet' months) with maximal seasonality of precipitation. 'Wet' months, precipitation regime, and seasonality adapted from Cecil (2003, table 1), whereas floral types adapted and modified from DiMichele et al. (2010a, table 1).

'Wet' months ^a	Precipitation regime	Seasonality	Habitat(s)	Floral type(s)	Main plant groups
<i>Dryland settings</i>					
0	Arid	Aseasonal	Desert	Xerophytes	Not known
1–2	Semiarid	Minimal	Drylands	Xerophytes	Walcian conifers, 'enigmatic dryland' flora ^b
3–5	Dry subhumid	Maximal	Drylands	Mesophytes to xerophytes	Gigantic cordaitaleans, 'enigmatic dryland' flora ^b
			Clastic wetlands	Mesophytes to hygrophytes	Pteridosperms, sphenopsids, gigantic cordaitaleans
<i>Wetland settings</i>					
6–8	Moist subhumid	Medial	Clastic wetlands	Hygrophytes to mesophytes	Lycopsids, ferns, sphenopsids, pteridosperms, low-stature cordaitaleans
			Rheotrophic mires	Higher-diversity hygrophytes (specialists)	
9–11	Humid	Minimal	Rheotrophic mires	Higher-diversity hygrophytes (specialists)	
			Clastic wetlands	Hygrophytes	
12	Perhumid	Aseasonal	Ombotrophic mires	Low-diversity hygrophytes (specialists)	Lycopsids, ferns

^a Consecutive months when rainfall exceeds evapotranspiration.

^b *Megalopteris/Lesleya* flora of DiMichele et al. (2010a).

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