Community heterogeneity of Early Pennsylvanian peat mires

Robert A. Gastaldo*   Department of Geology, Colby College, Waterville, Maine 04901, USA
Ivana M. Stevanović-Walls   Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, Pennsylvania 19104-6316, USA
William N. Ware   1109 Wynterhall Land, Dunwoody, Georgia 30338, USA
Stephen F. Greb   Kentucky Geological Survey, University of Kentucky, Lexington, Kentucky 40506, USA

ABSTRACT

Reconstructions of Pennsylvanian coal swamps are some of the most common images of late Paleozoic terrestrial ecosystems. All reconstructions to date are based on data from either time-averaged permineralized peats or single-site collections. An erect, in situ Early Pennsylvanian forest preserved above the Blue Creek Coal, Black Warrior Basin, Alabama, was sampled in 17 localities over an area of >0.5 km^2, resulting in the first temporally and spatially constrained Pennsylvanian mire data set. This three-tiered forest was heterogeneous. Lycopsid and calamitean trees composed the canopy, and lepidodendrids, *Lepidophloios*, and sigillarians grew together at most sites. More juvenile than mature lycopsid biomass occurs in the forest-floor litter, indicating a mixed-age, multicohort canopy. Pteridophytes (tree fern) and pteridosperms (seed fern) dominated as understory shrubs, whereas sphenophyllaleans, pteridophytes, and pteridosperms composed the ground-cover and liana tier. The proportion of canopy, understory, and ground-cover biomass varied across the forest. Low proportions of ground-cover and liana taxa existed where canopy fossils accounted for $>60\%$ of the litter. There is a distinct spatial clustering of sites with more or less understory (or ground cover) where canopy contribution was $<60\%$. Where canopy biomass was low ($<50\%$), understory shrubs contributed more biomass, indicative of light interception and/or competition strategies. *Sphenopteris pottsvillea*, a ubiquitous ground-cover plant, is abundant in all sites except one, where pteridosperm creepers and lianas dominate the litter, interpreted to indicate total suppression of other ground-cover growth. Ecological wet-dry gradients identified in other Pennsylvanian swamps do not exist in the Blue Creek mire, with the interpreted wettest (*Lepidophloios*), driest (*Sigillaria*), and intermediate (*Lepidodendron* sensu latu) taxa coexisting in most assemblages.

Keywords: Carboniferous, coal, paleobotany, peat mire, wetland.

INTRODUCTION

Pennsylvanian peat-accumulating forests are one of the most intensively studied and often-reconstructed Phanerozoic ecosystems; models appeared soon after coal exploitation increased following demands that accompanied the Industrial Revolution. Unfortunately, most nineteenth and twentieth century reconstructions present a "family portrait" of these mires and mainly depict principal trees and understory plants. Although plant-growth architectures have been refined over the past century as insight was gained from both adpression and permineralized specimens, mire-ecosystem reconstructions remain coarse. The most plausible coal swamp reconstructions to date are based on permineralized plants from coal-ball assemblages taken from discrete stratigraphic horizons (e.g., DiMichele et al., 2002) supplemented, at times, with palynological data (Greb et al., 1999). However, even coal-ball assemblages do not provide an instantaneous snapshot of the mire community. Coal-ball floras represent time-averaged assemblages, consisting mainly of aerial plant parts (stems, branches, reproductive structures) with rarely preserved leaves (Gastaldo and Staub, 1999); these floras represent the resistant biomass contribution from several plant generations to the peat. Decay rates of aerial parts that fall to the surface of Holocene tropical mires are accelerated by high temperatures and rainfall as well as by fungal and detritovore activity; leaf half-life is often less than a few months (Gastaldo, 1994; Gastaldo and Staub, 1999). As competition for newly opened space following the death of a plant may change the systematic composition in the sample location, resistant plant parts that accumulate and are buried may represent a century or more of biomass contribution in any one coal ball. Hence, the most accurate reconstructions must be based on assemblages that were buried in a geologic instant, freezing the plant relationships in space and time. Such assemblages are found in some types of roof shale floras, where erect trees are preserved above the coal (Gastaldo et al., 1995; DiMichele et al., 1996; Calder et al., 1996). Such collections commonly are restricted to what is recoverable from one or two localities along a high wall (or to what can be seen from beneath in an underground mine), limiting recoverable rock volume, or from spoil piles, where samples from various horizons often are mixed. Although the data may be temporally constrained in these autochthonous assemblages, the spatial relationships often cannot be discerned because of logistical constraints.

A data set from the Lower Pennsylvanian (Langsettian) Mary Lee Coal zone in the Black Warrior Basin provides the first temporally and spatially constrained perspective on Pennsylvanian peat-mire ecosystems at a community scale. Standing forests are preserved above each of the coals (Jagger, Blue Creek, Mary Lee, and Newcastle, in ascending stratigraphic order), as well as at five separate horizons between the Blue Creek and Mary Lee seams (Demko and Gastaldo, 1992). The most extensive in situ forest occurs above the Blue Creek Coal (Gastaldo et al., 1991) and consists of erect lycopsids, sphenopsids, pteridophytes (tree ferns), and pteridosperms (seed-bearing gymnosperms) rooted in the underlying coal. Cordaites pith casts are in the roof shale flora, yet no standing trees of this gymnosperm were encountered. Lycopsid trees occur to heights of 4.5 m, and all standing vegetation is preserved within and cast by tidalite deposits (Gastaldo, 1992; Gastaldo et al., 2004). Tidal rhythmites begin within the uppermost 0.5 cm of the coal, and are responsible for burial of the forest floor of the mire, preserving the leaf litter in exquisite detail. Gastaldo et al. (2004) argued that the only mechanism that can mold and cast erect forests in estuarine tidal deposits, and bury a nondegraded forest-floor litter, is rapid coseismic base-level subsidence. Rapid coseismic subsidence buried a peat forest by estuarine sedimentation during the Great Alaska earthquake of 1964. Subsurface peats in Turnagain Arm indicate recurrent coseismic subsidence and burial through time (Combellick, 1991).

LOCALITY AND METHODOLOGY

The roof shale flora was collected above the Blue Creek coal in the Drummond Brothers Cedrum mine, Townley, Walker County, Alabama (Fig. 1) during the last phase of excavation and exploitation of the Mary Lee interval in 1999. The mine was closed and reclaimed beginning in 2000. Mining opera-

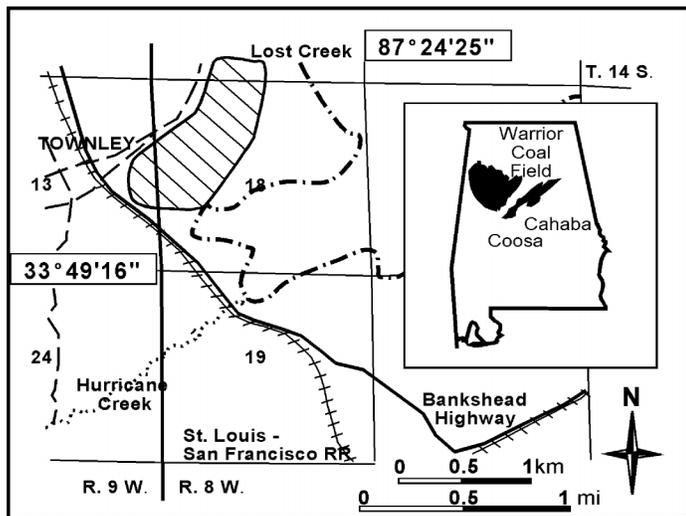*Corresponding author. E-mail: ragastal@colby.edu.

Figure 1. Locality map of Drummond Brother's Cedrum mine (Townley 7.5 U.S. Geological Survey Quadrangle Map, T. 14 S., R. 8 W., sec. 18, and T. 14 S., R. 9 W., sec. 13) in Warrior coal field, Alabama (inset). Ruled polygon indicates active exploitation area in which Blue Creek mire was investigated. RR—railroad.
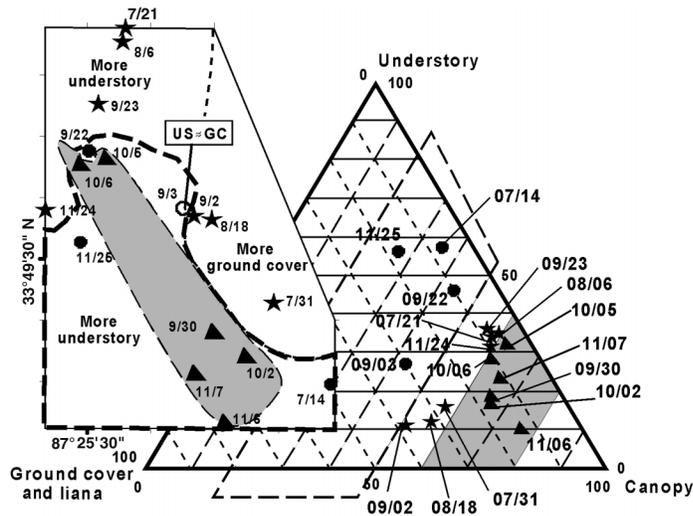

Figure 2. Ternary diagram on which proportions of canopy, understory, and ground-cover and liana biomass are plotted for each sample quadrat. Biomass proportion is based on 32 identified biological taxa. Sites are subdivided into three clusters according to proportion of canopy biomass: >60% (triangle), >50% but <60% (star), and <50% (circle). Clusters are identified in inset map of Cedrum mine, where spatial position is indicated by global positioning system readings of latitude and longitude. Shaded areas on distribution map correlate with ternary diagram. Sample site 9/3 is where there is equal proportion of understory (US) and ground-cover (GC) biomass.

tions cleared overburden down to the fossiliferous horizon, which ranged from <5 to >15 cm in thickness depending upon locality, in 17 sampled sites within the mine (Fig. 1). A 10 m^2 bedding surface was cleaned and used as the sampling quadrat for each site, allowing for identification of lycopsid trees in the sample area. (Systematic assignment of lycopsids cannot be made on either juvenile or mature leaves because all higher taxa produced the same structures. Hence, it is necessary to identify lycopsids on leaf-scar patterns found on the bark, requiring larger than the standard 1 m^2 quadrats used in Holocene studies.) An identification booklet was developed to assist in systematic assignment to assure taxonomic consistency among investigators. Split blocks of overburden exposed sequential bedding surfaces from which taxon presence or absence was recorded. Collection curves were constructed to maximize recovery efforts, resulting in samples ranging from 134 to 393 identified specimens (average 281) per locality.

Field identifications of 47 form taxa were made from plant debris consisting of randomly oriented trunks, stems, and branches of lycopsids (club mosses) and calamiteans (horsetails); juvenile (Kosanke, 1979) and mature foliage of lycopsids and calamiteans with or without attached reproductive cones (a juvenile-to-mature lycopsid-leaf ratio was calculated for each site); mature foliage and dehisced stems or branches of ferns and pteridosperms (seed ferns); disseminated reproductive structures of lycopsids, calamiteans, and pteridosperms; small-diameter axes with attached leaves assignable to sphenophyllaleans (horsetails), ferns, and pteridosperms (lyginopterids, medullosans, and ?callistophytaleans); and unidentifiable, decorticated stems and branches (Stevanović-Walls, 2001; Ware, 2001). Form taxa were condensed within recognized biological taxa, where applicable, allocating the dispersed canopy detritus proportionally to known biological affinities. For example, where two or more lycopsid stem taxa were identified in a site, the numbers of leaves, leaf-bearing branches, strobili, etc., were apportioned proportionately based on the number of each identified stem taxon. Hence, if *Lepidodendron aculeatum* was identified three times and *Lepidophloios laricinus* was found seven times at the collection site, then 30% and 70% of the total number of vegetative and reproductive parts were transferred to these taxa, respectively. This placement of form taxa within a parent taxon resulted in an interpretation that 32 biological taxa contributed to the mire (Gastaldo et al., 2004). These were categorized relative to their growth form and include a canopy (lycopsids, calamiteans, cordaites), an understory or subcanopy (tree ferns and pteridosperms), and ground-cover and liana tier (ferns and pteridosperms); the latter two categories are based solely on sterile foliage leaf architecture, frond size, and diameter of parent stem, where available (e.g., Gastaldo and Boersma, 1983). As in modern ecosystems, many ground-cover plants that develop along a rhizome or prostrate stem can grow as a vine into the canopy. Therefore, taxa considered to be creepers can occupy either or both positions within the forest, depending upon space, light, and plant density. The systematic composition between sample locations was compared by using the biological data set with χ^2 statistics to determine forest homogeneity or heterogeneity, and the growth-habit proportions for each locality were plotted on a ternary diagram.

RESULTS

When the biomass of a tier in each locality is compared to the average tier proportion for the forest, there is a statistical difference among collection sites (canopy $\chi^2 = 40.82$, df [degrees of freedom] = 16, $p = 0.0005$; understory $\chi^2 = 114.14$, df = 16, $p = 7.3 \times 10^{-7}$; ground cover $\chi^2 = 102.76$, df = 16, $p = 1.1 \times 10^{-14}$). Hence, the Blue Creek mire is a heterogeneous forest. A ternary diagram depicts the forest-structure variation, and the spatial distribution is highlighted on a sample-site map (Fig. 2). Six sites delimit a central southeast trend where canopy elements compose ~60% of the biomass; the understory varies from 10% to 40%, and the remainder consists of ground cover and liana (Table 1). Here, the canopy is most diverse systematically and dominated by a mix of lepidodendrids, *Lepidophloios*, sigillarians, and abundant calamiteans. The ratio of mature-to-immature lycopsid-leaf biomass indicates a high contribution from juvenile

TABLE 1. FOREST CHARACTERISTICS OF SAMPLE SITE CLUSTERS

	C > 60%	C > 50% U > 30%	C > 50% G > 25%	C < 50% U > 40%	C < 50% U = G
Canopy (average %)	66	58	55	36	43
Understory (average %)	22	35	13	52	27
Ground cover (average %)	12	7	32	11	30
Canopy taxa (N)	7	6	6	5	6
Understory taxa (N)	6	5	8	7	8
Ground cover taxa (N)	6	6	9	6	8
Immature:mature lycopsid-leaf ratio	19:1	9:1	14:1	18:1	16:1

Note: Sample site clusters are delimited from the plot of canopy (C) : understory (U) : ground cover (G) ratios on the ternary diagram (Fig. 2). The average proportion of biomass from each tier is provided in addition to the number of taxa responsible for the contribution on the basis of identified "biological" taxa. A juvenile:mature lycopsid leaf ratio is calculated from raw field data.

trees. The understory is dominated by pteridosperms, including *Eusphenopteris* and *Neuralethopteris*, and has a small proportion of small ferns (*Sphenopteris brongniartii*). The ground-cover pteridosperm *Sphenopteris pottsvillea* (Gastaldo, 1988) is ubiquitous, and only the ground-cover and liana lyginopterid vine, *Lyginopteris hoeninghausii*, occurs in abundance. Other ground-cover taxa are rare.

In areas where there is >50% but <60% canopy biomass, two distinct floral assemblages exist (Table 1). One group (Fig. 2) is characterized by >30% biomass of ground-cover and liana taxa and a low proportion of understory. This canopy is dominated by *Lepidophloios* and *Sigillaria* as well as calamiteans, and the ratio of lycopsid-leaf biomass indicates a high contribution from juveniles. Understory taxa are rare ferns and pteridosperms—*Cardiopteridium*, *Eremopteris*, *S. brongniartii*, *Alethopteris*—with a *S. pottsvillea* ground cover. The ground-cover and liana taxa *Lyginopteris*, *Palmatopteris*, *Sphenopteris pseudocristata*, and *Sphenopteris schatzlarensis* each may compose ~5% of the biomass. The second group averages 35% understory biomass and shows very low proportions (~10%) of ground cover and liana. Here, *Lepidophloios*, *Sigillaria*, and *Calamites* contribute biomass, and the juvenile:mature leaf ratio is lowest in the forest (Table 1). Pteridosperms conspicuously dominate the understory, which contains abundant *Neuralethopteris* but a near absence of *Alethopteris*, and there is a minor *Eusphenopteris* contribution. As elsewhere, *S. pottsvillea* is very abundant, along with small ground creepers and/or vines (*Palmatopteris*, *Sphenopteris*, and *Sphenophyllum*). No sampling sites exist intermediate between these two extremes.

In sites averaging ~40% canopy biomass, one cluster of three sites is characterized by >50% understory biomass, and one locality has a near-equal contribution from both ground cover and understory that is spatially intermediate (Fig. 2; Table 1). Canopy constituents are mainly lepidodendrons and calamiteans, although *Lepidophloios* occurs in all but one site. Pteridosperms (*Neuralethopteris*) dominate the understory in the former group, whereas a mix of pteridosperms and ferns (*Neuralethopteris*, *Alethopteris*, and sphenopterids) accounts for the low biomass contribution in the latter. Where the proportion of ground-cover and liana taxa is highest (sample 9/3; Fig. 2), *Lyginopteris* dominates along with high proportions of other lianas (*Alloiopteris* and *Sphenophyllum*), and there is a pronounced absence of *S. pottsvillea*. This is the only collection site where *S. pottsvillea* was absent.

DISCUSSION

There is a considerable range of vegetational heterogeneity in the forest-floor litter of the Blue Creek mire, reflecting contribution from three forest tiers. Most localities are dominated by canopy biomass with varying contributions from understory and ground cover (Fig. 2; Table 1). Overall, juvenile lycopsids were intermixed with a few mature trees, and calamiteans were ubiquitous. Where the greatest proportion of canopy-biomass exists, juvenile lycopsids grew as pole trees, enveloped by linear leaves up to 1 m in length (Kosanke, 1979), generally with an understory of scattered tree ferns and abundant pteridosperms along with an omnipresent ground cover of *Sphenopteris pottsvillea*. Here, there are scattered to abundant occurrences of taxa capable of a liana growth habit (i.e., *Lyginopteris*, *Sphenophyllum*), and an average of 12 other taxa beneath the canopy, many of which are encountered rarely (<2.5%). Hence, tree density in these sites probably limited systematic diversity owing to space competition.

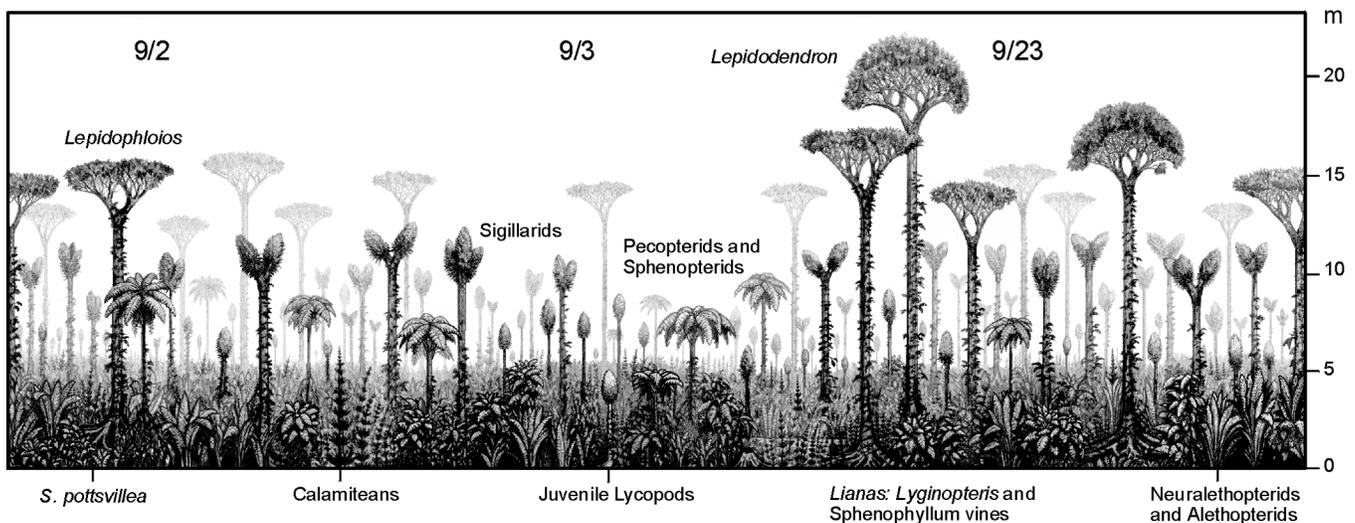When canopy detritus is <60% of the biomass, there is more systematic diversity in the

Figure 3. Reconstruction of three-locality transect in central position within mire. Vegetation at 9/2 (far left) consists of 51% canopy with high proportion of understory contribution; canopy tier represents only 43% of assemblage at 9/3 (middle), whereas canopy contributes 53% of biomass to site 9/23 (far left). Mire forest consists of more juvenile than mature lycopsid trees with abundant calamiteans. Well-developed understory of seed-fern shrubs and rare tree ferns allowed for nearly ubiquitous ground cover by *S. pottsvillea*. Reduced light penetration in these sites limited other ground-cover and liana taxa abundance. Vertical scale in meters applies to foreground plants.

other two tiers (Table 1). Where understory contribution is greater than ground-cover biomass, 11 other taxa occur and are similar to the diversity noted here. But, where ground-cover plants contributed more biomass, there are at least 17 taxa that resided beneath the canopy, equally distributed between understory and ground-cover and liana growth strategies. Diversity in these sites probably was controlled by light penetration because of either lower plant density or a more juvenile lycopsid canopy.

The forest had a better-developed understory where there is the least canopy contribution, but this biomass originated from the same number of taxa as found in the remainder of the forest. The number of ground-cover and liana taxa equals that of the understory, and *S. pottsvillea* was abundant across the forest floor. In only one site is *S. pottsvillea* absent; here the biomass is dominated by the liana or ground creeper *Lyginopteris*. This relationship indicates a near-total cover of the forest floor by lianas, preventing the growth of ground cover. Such high proportions of ground-cover and liana biomass are associated with very open areas within modern forests, as the result of either canopy-tree death or blow-down that allows light penetration (Oliver and Larson, 1990).

A reconstructed transect through the Blue Creek mire at the time of its burial depicts a mixed-age, multicohort forest (Oliver and Larson, 1990) consisting of more juvenile than mature trees in an open-canopy configuration (Fig. 3). At one extreme where the densest canopy formed, more understory than ground-cover biomass was produced, indicating limited light penetration to the forest floor. The understory seed-fern and tree-fern taxa grew to sizes that maximized light interception, limiting the establishment of a well-developed and diverse ground-cover tier. At the other extreme where there was minimal canopy biomass, understory taxa dominated except in one site, where there is an equal contribution from both understory and ground-cover tiers. Intermediate between these extremes are areas in which either understory or ground cover contributed more biomass to the litter.

Previous mire reconstructions have emphasized a soil-moisture gradient in Pennsylvanian swamps on the basis of lycopsid distribution (DiMichele et al., 1985; Gastaldo, 1987; DiMichele and Phillips, 1994). The wettest extreme was interpreted as a monoculture of *Lepidophloios*; the driest extreme was dominated by *Sigillaria*; lepidodendrids grew within intermediate sites. The spatial resolution of the Blue Creek mire data allows a test of this hypothesis wherein the previously interpreted gradient is not present. Rather, the current data indicate that these lycopsids had

a wider range of environmental tolerances and commonly grew in close proximity within the same Histosol. Hence, the ecological partitioning interpreted in Late Pennsylvanian mires either may be a sampling artifact, an ecophysiological adaptation of these plants to changing climatic conditions (Gastaldo et al., 1996), or increasing habitat specialization as peat mires become more extensive in the Late Pennsylvanian.

REFERENCES CITED

Calder, J.H., Gibling, M.R., Eble, C.F., Scott, A.C., and MacNeil, D.J., 1996, The Westphalian D fossil lepidodendrid forest at Table Head, Sydney Basin, Nova Scotia: Sedimentology, paleoecology, and floral response to edaphic conditions: International Journal of Coal Geology, v. 31, p. 277–313.

Combellick, R.A., 1991, Paleoseismicity of the Cook Inlet region, Alaska: Evidence from peat stratigraphy in Turnagain and Knik Arms: Alaska Department of Natural Resources, Division of Geological and Geophysical Surveys, Professional Report 112, 52 p.

Demko, T.M., and Gastaldo, R.A., 1992, Paludal environments of the Lower Mary Lee coal zone, Pottsville Formation, Alabama: Stacked clastic swamps and peat mires: International Journal of Coal Geology, v. 20, p. 23–47.

DiMichele, W.A., and Phillips, T.L., 1994, Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 106, p. 39–90.

DiMichele, W.A., Phillips, T.L., and Peppers, R.A., 1985, The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants, *in* Tiffney, B.H., ed., Geological factors and the evolution of plants: New Haven, Connecticut, Yale University Press, p. 223–256.

DiMichele, W.A., Eble, C.F., and Chaney, D.S., 1996, A drowned lycopsid forest above the Mahoning coal (Conemaugh Group, Upper Pennsylvanian) in eastern Ohio, U.S.A.: International Journal of Coal Geology, v. 31, p. 249–276.

DiMichele, W.A., Phillips, T.L., and Nelson, W.J., 2002, Place vs. time and vegetational persistence: A comparison of four tropical mires from the Illinois Basin during the height of the Pennsylvanian ice age: International Journal of Coal Geology, v. 50, p. 43–72.

Gastaldo, R.A., 1987, Confirmation of Carbonifer-

ous clastic swamp communities: Nature, v. 326, p. 869–871.

Gastaldo, R.A., 1988, The frond architecture of *Sphenopteris pottsvillea* (White) Gastaldo and Boersma: Journal of Paleontology, v. 62, p. 982–991.

Gastaldo, R.A., 1992, Regenerative growth in fossil horsetails (*Calamites*) following burial by alluvium: Historical Biology, v. 6, p. 203–220.

Gastaldo, R.A., 1994, The genesis and sedimentation of phytoclasts with examples from coastal environments, *in* Traverse, A., ed., Sedimentation of organic particles: Cambridge, Cambridge University Press, p. 103–127.

Gastaldo, R.A., and Boersma, M., 1983, A reinvestigation of Early Pennsylvanian species of *Mariopteris* from the Appalachian region. I. *Karinopteris*, *Mariopteris* and the 'Pottsvillea Complex': Review of Palaeobotany and Palynology, v. 38, p. 185–226.

Gastaldo, R.A., and Staub, J.R., 1999, A mechanism to explain the preservation of leaf litter lenses in coals derived from raised mires: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 149, p. 1–14.

Gastaldo, R.A., Demko, T.M., and Liu., Y., 1991, A mechanism to explain persistent alternation of clastic and peat-accumulating swamps in Carboniferous sequences: Bulletin de la Société Géologique de France, v. 162, p. 299–305.

Gastaldo, R.A., Pfefferkorn, H.W., and DiMichele, W.A., 1995, Taphonomic and sedimentologic characterization of "roof-shale" floras, *in* Lyons, P., et al., eds., Historical perspective of early twentieth century carboniferous paleobotany in North America: Geological Society of America Memoir 185, p. 341–352.

Gastaldo, R.A., DiMichele, W.A., and Pfefferkorn, H.W., 1996, Out of the icehouse into the greenhouse: A late Paleozoic analogue for modern global vegetational change: GSA Today, v. 10, no. 10, p. 1–7.

Gastaldo, R.A., Stevanović-Walls, I., and Ware, W.N., 2004, In situ, erect forests are evidence for large-magnitude, coseismic base-level changes within Pennsylvanian cyclothems of the Black Warrior Basin, USA, *in* Pashin, J.C., and Gastaldo, R.A., eds., Coal-bearing strata: Sequence stratigraphy, paleoclimate, and tectonics: American Association of Petroleum Geologists, Studies in Geology, v. 51, p. 219–238.

Greb, S.F., Eble, C.F., Chesnut, D.R., Jr., Phillips, T.L., and Hower, J.C., 1999, An in situ occurrence of coal balls in the Amburgy coal bed, Pikeville Formation (Duckmantian), central Appalachian Basin, U.S.A.: Palaios, v. 14, p. 433–451.

Kosanke, R.M., 1979, A long-leaved specimen of *Lepidodendron*: Geological Society of America Bulletin, v. 90, p. 431–434.

Oliver, C.D., and Larson, B.C., 1990, Forest stand dynamics: New York, McGraw-Hill, 467 p.

Stevanović-Walls, I.M., 2001, A paleontological study of an Early Pennsylvanian forest preserved above the Blue Creek Coal seam, Pottsville Formation, northwestern Alabama [M.S. thesis]: Auburn, Alabama, Auburn University, 98 p.

Ware, W.N., 2001, A paleoecological study of an in situ peat-forming Carboniferous forest in the Black Warrior Basin, Alabama [M.S. thesis]: Auburn, Alabama, Auburn University, 81 p.