

# Biomass Allocation in Late Pennsylvanian Coal-Swamp Plants

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*Carbon allocation to different tissues and organs of Late Pennsylvanian-aged coal-swamp plants was determined for the first time through study of coal balls from the Calhoun coal of central Illinois. Coal balls are concretions that preserve the original peat fabric of the coal seam; they occur within the coal matrix and generally are permineralized with calcium carbonate. Coalified plant cell walls are preserved within the mineral matrix of the coal ball, entombed within the calcium carbonate. Relative carbon allocation was determined by separation of the mineral matrix and organic carbon. Carbon content was determined for replicates of tissues or organs of Psaronius tree ferns, Medullosa pteridosperms, the lycopsid Sigillaria approximata, the small fern Botryopteris forensis, and "whole peat". Unit volume results for tissues and organs were normalized for trunk sections 45 cm in diameter and 1 m long. Psaronius tree ferns were significantly "cheaper" than all other plants due to the large mantle of aerenchymatous roots that made up the bulk of the trunk. Medullosans and small ferns were most "expensive", with the arborescent lycopsid in between. Relative expense of construction closely parallels the inferred ecological role of each plant within ancient coal swamps, deduced from distributional patterns and indicators of habitat conditions. Tree ferns and lycopsids are colonists, medullosans are site occupying forms.*

## INTRODUCTION

Allocation of carbon to organs and tissues in plants is an important measure of the "cost" of a particular architecture or function within the context of life history. Differences in patterns of biomass allocation among species within a plant community also help establish patterns of

energy flow and constrain models of community dynamics. Studies, such as those at the Hubbard Brook research station (Bormann and Likens, 1979), have revealed complex relationships between nutrient flow and cycling within and through ecosystems, and depend partly on knowledge of the biomass distribution within the standing forest.

Biomass estimates in ancient ecosystems have been based largely on quantitative measures of biovolume or on relative counts of organs, such as leaves. Count methods are most common and have been applied largely to compression-impression fossil assemblages preserved in mudstones; the three most common methods either count individual leaves (Wing, 1984), point count leaves on bedding surfaces (Scott, 1978), or treat hand specimens as sampling quadrats (Pfefferkorn et al., 1975). Methods also have been designed specifically for the analysis of three-dimensionally preserved, petrified or permineralized plant debris, specifically peat concretions, or coal balls, of Pennsylvanian age (Phillips et al., 1977; Pryor, 1988).

All of these quantitative measures assume uniform carbon allocation to individual organs and tissues of different plant species. This assumption may be justified in some cases, perhaps best for analyses of angiosperm leaves. Actualistic studies on angiosperms have found low variance in carbon allocation among species, and strong correlations between leaf-litter abundance and basal stem diameters of individual trees and populations of trees (Burnham et al., 1992). However, compared to today or anytime since the mid-Cretaceous, dominant plants of Pennsylvanian-aged wetland ecosystems belonged to a much greater diversity of taxonomic and, hence, structural, groups. Four classes of plants were dominant in various habitats—ferns, lycopsids, sphenopsids, and two structurally distinct orders within seed plants. Consequently, assumption of uniformity of biomass allocation across taxa is unwarranted.

Because a clear means to compare patterns of "cost" of fossil plant tissues across time and taxa is lacking, it has been difficult to address issues such as evolutionary esca-

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lation (Vermeij, 1989) in an objective manner. Yet, the cost involved in constructing and maintaining a woody gymnosperm forest community in the Mesozoic lowlands must have been different from that for a largely parenchyma-based system dominated by lower vascular plants in the Pennsylvanian. How energy distribution patterns in either of these compare to flowering-plant dominated systems of the late Mesozoic and Cenozoic has yet to be explored. Thus, this paper represents the first attempt to measure directly carbon allocation among plant species of any extinct ecosystem.

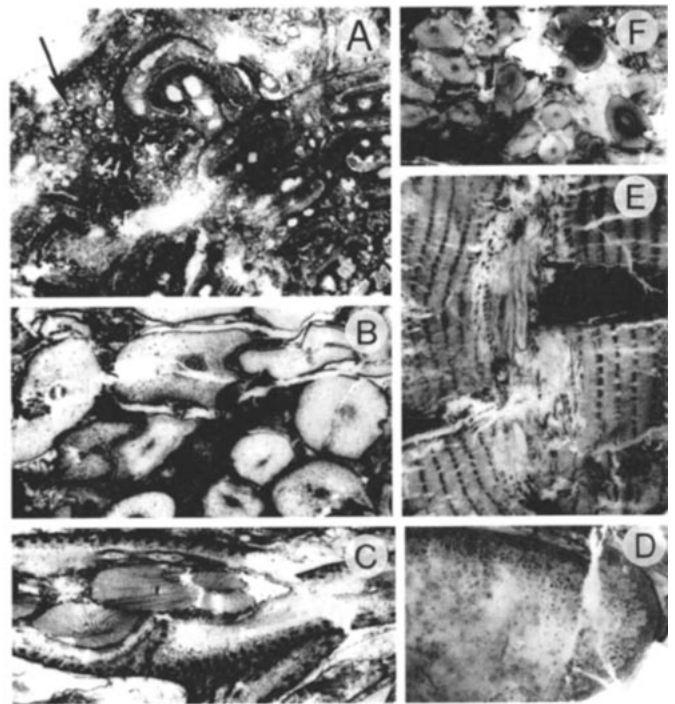
#### MATERIALS AND STUDY SITE

The fossil plants used in this study are preserved in coal balls, which are concretions that preserve permineralized peat stages of the original coal seam and occur within the coal matrix. Samples were collected from the Calhoun coal of Illinois, specifically from the Berryville locality in east central Illinois (Mamay and Yochelson, 1962; Phillips et al., 1985). The Calhoun coal is a Late Pennsylvanian (Stephanian) coal seam between 300 and 305 million years old (Hess and Lippolt, 1986; Klein, 1990). Phillips et al. (1985) report that the flora of the Calhoun coal is dominated by marattialean tree ferns of the genus *Psaronius*, which form up to 74% of the peat biomass. Subdominant tree groups include medullosan seed ferns and sphenopsids, with sigillarian lycopsids locally abundant. Tree fern dominance is typical of most mid-continent coal floras of Late Pennsylvanian age; in contrast, Middle Pennsylvanian coals are dominated by a diversity of tree lycopsids.

Coal balls from the Calhoun coal are permineralized with calcium carbonate. There are several models for the formation of calcium carbonate coal balls, which occur in over 50 coal seams of Pennsylvanian age in Europe and North America (Stopes and Watson, 1909; Mamay and Yochelson, 1962; Perkins, 1976; DeMaris et al., 1983; Scott and Rex, 1985). All agree that coal balls form very early after peat inundation by marine waters, before significant compaction or coalification has ensued.

For this initial study we decided to restrict our sample to a single coal where depositional and coalification history were relatively constant, removing potential bias that could be introduced by differences in rank between coals. Although the entombing minerals of the coal balls protect the original plant cell walls from further compression, they do not prevent some changes in cell-wall chemistry, in some instances resulting in coalification of cell walls to the same rank as the surrounding coal (Lyons et al., 1985). Comparison of carbon allocation to different tissues and organs from the same coal seam, therefore, is relative rather than absolute. Establishment of a larger data base using specimens of the same species from different coals is needed to estimate the effects of different coal-seam histories, and to develop a means of calibration if needed.

The specimens were collected by Sergius H. Mamay and Ellis L. Yochelson in 1954. All collections and voucher acetate peels reside in the Paleobotanical collections of the National Museum of Natural History, Smithsonian Insti-



**FIGURE 1**—Example specimens used in destructive analysis. (A) *Psaronius blickleis* stem. Some part of the inner root mantle are adherent (at arrow). USNM 489626 (B) *Psaronius* sp. outer roots. USNM 489627 (C) *Medullosa* sp. stem showing vascular bundles and surrounding cortical and epidermal tissues, including sclerenchyma and resin bodies. USNM 489628 (D) *Medullosa* rachis showing scattered vascular bundles, sclerenchyma and resin bodies. USNM 489629 (E) *Sigillaria approximata* periderm. Large dark areas are aerating strands. USNM 489630 (F) *Botryopteris forensis* axes. USNM 489631. All specimens in transverse or oblique section. All magnifications 1×.

tution, Washington, DC. Specimens used in this study bear the following numbers: USNM 489626–489645, and 489750.

#### TAXA ANALYZED

Four taxa and a variety of tissue types were used in the analysis (Table 1). Tissues are illustrated in Figure 1. Periderm was analyzed from *Sigillaria approximata* (Delevoryas, 1957), an arborescent lycopsid; periderm is the main support tissue of the arborescent lycopsids and accounts for the bulk of the stem tissues. Wood of the *Sigillaria* rhizomorph, or stigmarian root system (Eggert, 1972), was used instead of stem wood.

Stems and rachises of the pteridosperm *Medullosa noei* were analyzed separately. Anatomy of these organs prevented segregation of cellularly uniform tissue; small vascular bundles are dispersed in the rachises, and the complex cortex includes a variety of cell types. *M. noei* is a form species and may encompass more than one natural species.

Several types of tissues and organs make up the complex aerial trunk and crown of the marattialean tree fern

TABLE 1—Biomass of taxa and tissues analyzed.

Taxon-tissue	Mean gm C/cc	n
Whole peat	0.075 ± 0.018 s.d.	6
<i>Psaronius</i> trunk	0.076 ± 0.002 s.d.	7
<i>Psaronius</i> inner root	0.103 ± 0.011 s.d.	5
<i>Psaronius</i> outer root	0.024 ± 0.002 s.d.	5
<i>Medullosa</i> stem	0.049 ± 0.007 s.d.	5
<i>Medullosa</i> rachis	0.051 ± 0.008 s.d.	7
<i>Botryopteris</i> axis	0.045 ± 0.005 s.d.	4
<i>Sigillaria</i> periderm	0.041 ± 0.007 s.d.	6
Stigmarian wood	0.052	1

*Psaronius blicklei* (Morgan, 1959; Ehret and Phillips, 1977). We analyzed specimens of stems, inner root mantles, outer root mantles, and rachises.

One species of ground-cover fern was examined, *Botryopteris forensis*, a primitive filicalean (Phillips, 1974). Tissue types were not segregated separately due to the small size of the plants.

Several "whole peat" samples also were analyzed; these were coal balls containing a mixture of organs, taxa, and dispersed humic matter.

#### ANALYTICAL AND STATISTICAL METHODS

Replicate samples of each tissue or organ, with the exception of stigmarian wood, were prepared to permit analysis of intrataxon variability and to facilitate statistical evaluation of differences in biomass patterns. Only a single sample of stigmarian wood was analyzed, limiting the statistical treatment of that tissue type.

Coal balls were cut into slices approximately 2 cm thick on a diamond-blade cutting saw using Almag oil as a lubricant. Each slice was washed to remove the oil, and air dried. Slices were etched in a 5% dilution of concentrated hydrochloric acid, which dissolved away a small amount of the calcium carbonate matrix, exposing the edges of the cell walls. The surfaces of the coal ball slices then were flooded with acetone and a cellulose acetate peel was made of the cut surface (Joy et al., 1956; Phillips et al., 1976).

Slices that contained large areas of pure tissue or organ types without macroscopically visible mineral-filled cracks were identified. Cubes of pure tissue/organ, approximately 1 cm on a side, were cut from the identified slices using a water-lubricated diamond-blade cutting saw. Volume of the cube was determined by displacement in water and the mass of the cube was measured. The cube was crushed in a mortar to coarse size pieces; when ground too finely, the material floated in subsequent acid treatment. The crushed material was macerated in a 10% dilution of concentrated hydrochloric acid to remove the calcium carbonate; the final solution was titrated to a neutral pH.

The macerate solution was filtered through a weighed filter paper under vacuum; the residue contains carbon

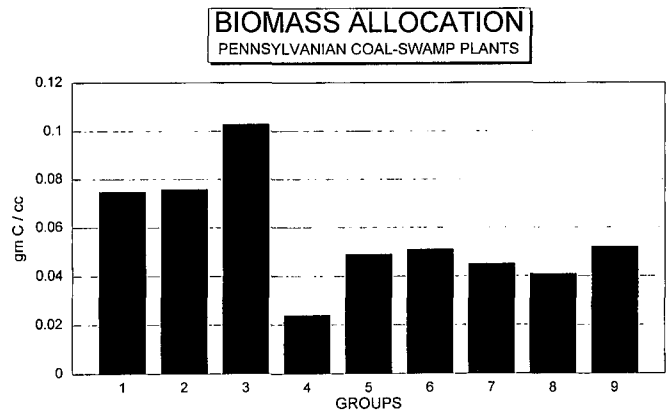


FIGURE 2—Carbon biomass allocation of selected tissues and organs from Late Pennsylvanian coal swamp plants. (1) Whole Peat (2) *Psaronius* stem (3) *Psaronius* inner root (4) *Psaronius* outer root (5) *Medullosa* stem (6) *Medullosa* rachis (7) *Botryopteris* axis (8) *Sigillaria* periderm (9) *Sigillaria* stigmarian wood.

and insoluble inorganic residues. The mass of the residue and filter paper were determined after drying, which permits calculation of the original calcium carbonate mass of the cube. The residue and filter paper were placed in a low temperature ashing oven at 500° C, which destroyed the carbon residue and the filter paper and left the inorganic residue. Mass of the inorganic residue was determined.

The carbon content of the original cube was determined by subtracting the combined mass of calcium carbonate and inorganic residue from the original mass of the cube. This was then normalized to mass of carbon per cubic centimeter.

All statistical analyses were performed in Systat for Windows, version 5 (Wilkinson et al., 1992). The mean carbon masses of each tissue or organ type were compared in a one-way ANOVA; medullosan stem and rachis samples were combined, and the one sample of stigmarian wood was not included. Normality of each data set was assessed with normal probability plots and, although deviations from normality were detected for some sets, we considered these minor and not serious enough to compromise the statistical test. The ANOVA results were evaluated with post-hoc pairwise tests: Tukey's Honest Significant Difference method, Scheffé's method, and the Tukey-Kramer or Dunnett test. All methods returned the same results, and only results from Dunnett's test are reported. These methods and their relationship to unbalanced ANOVA designs are discussed in Sokal and Rohlf (1981). Wilkinson et al. (1992) argue that Tukey's HSD and the Scheffé method can be applied to unbalanced designs using the adjustments in Systat.

Using the mean biomass of each tissue or organ type for the trees, we estimated the biomass of a hypothetical axis segment 45 cm in diameter and 1 m long.

#### RESULTS

Table 1 and Figure 2 summarize the results of the analyses by taxon and by tissue or organ type. Results of the

**TABLE 2**—One-way ANOVA and Dunnett's multiple comparison test of differences between seven tissue and taxonomic groups. Medullosan stem and rachis samples combined.

Source	Sum-of-squares	DF	Mean-square	F-ratio	P		
Group	0.023	6	0.004	35.126	0.00		
Error	0.004	38	0.000				
Dunnett's Test, with one-sided probabilities							
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1) Whole Peat	1.000	0.000	0.000	0.000	0.000	0.000	0.000
(2) <i>Psaronius</i> trunk	0.500	1.000	0.000	0.000	0.000	0.000	0.000
(3) <i>Psaronius</i> inner root	0.000	0.000	1.000	0.000	0.000	0.000	0.000
(4) <i>Psaronius</i> outer root	0.000	0.000	0.000	1.000	0.000	0.000	0.000
(5) <i>Medullosa</i> stem & rachis	0.000	0.000	0.000	0.000	1.000	0.435	0.181
(6) <i>Botryopteris</i> axis	0.000	0.000	0.000	0.011	0.467	1.000	0.492
(7) <i>Sigillaria</i> periderm	0.000	0.000	0.000	0.021	0.207	0.488	1.000

ANOVA and post-hoc tests indicate significant differences among the taxa and tissue types (Table 2). Dunnett's test provides details of the differences among the sample groups. Organs of the tree fern *Psaronius* (stem, inner roots and outer roots) differ significantly from each other and from all other organ and tissue types. Examination of Figure 2 indicates that stems and inner roots of *Psaronius* are more carbon rich per unit volume than other kinds of tissues and organs, whereas outer roots are significantly lower in carbon per unit volume than other tissues and organs examined. *Medullosa* pteridosperms, the filicalean fern *Botryopteris*, and the tree lycopsid *Sigillaria*, do not differ significantly from one another. *Medullosa* stem and rachis segments were nearly identical in carbon per unit volume and were combined in the ANOVA.

Table 3 summarizes the estimated biomass for axis slices of *Sigillaria*, *Psaronius*, and *Medullosa*, accounting for the complex organization of the stems. When normalized to a standard axis size, *Psaronius* is cheapest, *Medullosa* most expensive, and *Sigillaria* intermediate in carbon cost.

## DISCUSSION

*Psaronius* tree ferns were the most cheaply constructed trees in Late Pennsylvanian coal swamps. However, their

**TABLE 3**—Stem biomass calculated for an axis segment 45 cm in diameter and 1 m in length.

Taxon	Tissues—radius	GM C/Axis
<i>Psaronius</i>	stem, 3 cm	4514.8
	inner roots, 3 cm	
	outer roots, 16.5 cm	
<i>Sigillaria</i>	wood, 3 cm	6275.3
	periderm, 19.5 cm	
<i>Medullosa</i>	wood and cortex, 22.5 cm	7793.1

construction was complex. The small primary stem and thin inner root mantle of *Psaronius* were the most expensive tissues/organs of those tested. In contrast, the massive, stem-supporting, outer root mantle typical of late Middle and Late Pennsylvanian *Psaronius* was the most cheaply constructed of all tissue types analyzed; these outer roots had a central stele surrounded by a trabeculum of parenchyma cells, resulting in a cortical area composed mostly of air spaces. Lesnikowska (1989) noted that most Middle Pennsylvanian *Psaronius* were small trees with thin root mantles. Large trees did not become common until the later part of the Middle Pennsylvanian, and these differed from the older, smaller trees largely by the addition of the massive root mantle. Thus, tree habit, particularly large size, in *Psaronius* was attained with a minimal input of structural tissue. Although some components were quite expensive, the average carbon cost of a *Psaronius* tree was relatively small. *Psaronius* species have been inferred to have been opportunists and colonizers (Lesnikowska, 1989). This inference is strongly supported by inexpensive construction in combination with the production of massive numbers of isospores on large fronds, evidence of wide distribution, and tolerance of a wide range of nutrient conditions.

*Medullosa* is the most expensive of the trees examined on an axis-segment basis. Cortical tissues in particular are rich in resin bodies, sclerenchyma, and, in the petioles and rachises, numerous small vascular bundles. Although stems could be quite massive, the leaves were the principal organs in most *Medullosa* species and could be many meters in length (Wnuk and Pfefferkorn, 1984; Pfefferkorn et al., 1984; Laveine, 1986). Foliage was thick in many species and has been suggested to be indicative of preference for open, high-light conditions (Mickle and Rothwell, 1982; Beeler, 1983; Schabillion and Reihman, 1985).

*Sigillaria approximata* was a moderate-sized tree lycopsid. Based on occurrences in coals and mineral-substrate environments, species of this genus preferred clastic and,

hence, nutrient-enriched habitats. Sigillarians were polycarpic; a single tree reproduced several times during its life. They apparently were dominants in a number of environmental settings (DiMichele and Nelson, 1989; DiMichele and Phillips, 1994). The principal support tissue in these plants was periderm, which proves to be of moderate carbon constructional cost. Lycopoid trees of several genera appear to have been colonizers of open, disturbed spaces, where they rapidly attained sexual maturity (Phillips and DiMichele, 1992).

The largest plants of the Carboniferous forests were lycopsids, which were intermediate in unit-volume cost, if *Sigillaria* can be taken as a standard-bearer for the entire group. The most expensive plants, medullosans, were significantly smaller in stature than lycopsids and tree ferns, but some species produced enormous fronds. These two groups occupied different parts of Carboniferous wetlands, the lycopsids largely in standing water or on saturated substrates strongly depleted in mineral nutrients. In contrast, the medullosans characteristically dominated mineral-substrate habitats through most of the Pennsylvanian, occurring in peat swamps in areas of high clastic influx, where nutrient availability was relatively high. Cheaply constructed tree ferns do not become a prominent part of the landscape until the end of the Middle Pennsylvanian, and then mostly as interstitial opportunists in a wide variety of habitats. Their construction and opportunistic life history may have been key in their rise to dominance in tropical wetlands following environmentally induced extinctions at the end of the Middle Pennsylvanian.

This study is an initial step in the establishment of a baseline from which to evaluate evolution within the lineages of plants that occupied Pennsylvanian wetlands for over 20 million years. Carbonate concretions preserving organics occur in the Mississippian, throughout the Pennsylvanian and into the Permian, offering the opportunity for extensive longitudinal study of late Paleozoic tropical plants. Permineralized plants also occur at other times in the geological record, such as the Eocene-age Princeton chert of British Columbia (Basinger et al., 1977). To the extent that such deposits preserve original organics, they offer the opportunity to examine changes in patterns of resource allocation in dominant plants and in plant communities through geologic time.

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