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A CLIMATIC AND TAXONOMIC COMPARISON BETWEEN LEAF LITTER AND STANDING VEGETATION FROM A FLORIDA SWAMP WOODLAND¹

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One method to determine past climate has been the use of leaf morphological characteristics of fossil leaves quantified using modern climate and canopy leaf characteristics. Fossil assemblages are composed of abscised leaves, and climate may be more accurately determined by using leaves from leaf litter instead of the canopy. To better understand whether taphonomic processes make a difference in this relationship, a north-central Florida woodland was sampled to determine the morphologically based climate estimates from these leaves. Leaves from woody, dicotyledonous plants were collected and identified, then compared using presence/absence data and analyzed using several linear regression equations and the CLAMP data set. Although the majority of standing vegetation was reflected in leaf litter, some inconsistencies were observed, which may reflect plant community structure or sampling technique. Mean annual temperature (MAT) and growing season precipitation (GSP) were estimated from leaf litter morphological characters and living leaves. Overall, values for MAT estimated from litter and living leaves were cooler than actual MATs, although several accurate and high estimates were obtained depending on the predictive method used. Estimated GSP values were higher than actual GSPs. Statistically, no difference was observed between MAT and GSP estimates derived from leaf litter vs. estimates derived from living leaves, with one exception.

Key words: CLAMP; climate; leaf litter; dicotyledons; Florida; warm temperate woodland.

Assemblages of fossil leaves are often used to reconstruct aspects of their original environment. These aspects include climate estimates, forest composition and structure, and the environment itself (e.g., swamp, mixed forest, rain forest). How accurately an assemblage of fossil leaves reflects its environment has been the focus of numerous studies, including the accuracy of climate prediction (e.g., Jacobs and Deino, 1996; Wilf, 1997; Wilf et al., 1998; Kowalski and Dilcher, 2003; Royer et al., 2005), taphonomic bias (e.g., Roth and Dilcher, 1978; Spicer, 1981; Greenwood, 1992, 2005) and relationship of leaf litter to standing vegetation (e.g., Burnham, 1989, 1993b, 1994; Burnham et al., 1992; Greenwood, 1992). The latter of which have shown leaf litter to be an accurate representation of the species composition of the standing forest from which it is derived (e.g., Burnham, 1993b, 1994; Burnham et al., 1992). Most climate studies have focused on accuracy of climate predictions in a given area based on modern canopy leaves. These studies are important because the accurate determination of paleoclimate is necessary to determine both past climate regimes and to accurately model future climate scenarios. These studies have found leaf morphological characters to be accurate and

robust proxies for climate variables (e.g., Jacobs and Deino, 1996; Wilf, 1997; Wilf et al., 1998; Kowalski and Dilcher, 2003; Royer et al., 2005). Fallen leaves and leaf litter have been studied mostly taphonomically, though there have been some exceptions (e.g., Greenwood, 2005) that have looked at a climate reconstruction using both fallen and canopy leaves. Combining information about modern climate prediction from canopy and fallen leaves is important because knowing the accuracy with which the leaf litter reflects the composition of the canopy above it can allow for a more robust reconstruction of paleoenvironment based on fossil leaf assemblages. In addition, knowing whether assemblage-wide suites of leaf characteristics are consistent between the canopy and its resultant leaf litter (as determined by similar climate estimates) can help to determine whether predictive equations derived from modern leaf canopy and climate data are appropriate for determining paleoclimate from the morphology of fossil leaves that abscised from the tree and were subjected to taphonomic processes after leaving the canopy and before being deposited.

To better understand the relationship between standing vegetation, leaf litter, and climate prediction, a comparative study was carried out in Dilcher's Woods. This woodland plot is located in north-central Florida and is almost entirely within or adjacent to swampy areas. The plot was chosen because such areas have the potential to become sites for the preservation of fossil leaves (Spicer et al., 1987; Burnham, 1989, 1993a, 1994; Burnham et al., 1992). Leaf litter was collected and transects made in each of four microhabitats within the woodland. The leaf litter and transect leaves were compared to each other to determine similarity to each other as well as to a compilation of species living in the area, and both were scored for climate analysis. Mean annual temperature (MAT) and growing season precipitation (GSP) predictions for each collection were also compared. This study examined the following questions: How

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well or how poorly does leaf litter collected from the transect reflect the vegetation over the transect or the woodland as a whole? Are climate predictions based on leaf physiognomy from both litter and standing vegetation similar or do they differ in a predictable manner? Can predictive equations based on data from leaf morphology characters from the canopy be used with accuracy on leaf morphological characters from the litter?

MATERIALS AND METHODS

The Dilcher's Swamp/Woods (Kowalski and Dilcher, 2003; Wagner et al., 2005) is located in a 25-ha warm temperate, broad-leaved woodland, 8.8 km east of central Gainesville, Florida (29°38' 41" N, 82°15' 10" W, 20 m a.s.l.). The Gainesville area has a mean annual temperature (MAT) of 21.0°C and a mean annual precipitation of 134 cm, based on weather data for 1951–1980 (NOAA, 1985). The weather station is at the same elevation, 4 km from the study area. Seven samples from four sites, representing four distinct habitats within the woodland were selected for sampling of leaf litter and nearby canopy leaves. The relative locations of these samples are shown in Fig. 1.

The first site, designated Peninsula, has three samples (1a, b, c) collected along the length of a peninsula of land 7 m wide and 100 m long; the peninsula extends into a mixed hardwood swamp (Ewel, 1990) and is elevated less than 1 m above the water. Samples 1a and 1b are 23 m apart; 1b and 1c are 62 m apart (Fig. 1).

The second site, designated Swamp, has two samples (2a, b) sampled along the edges of hydric swamps (Ewel, 1990). Sample 2a is 20 m from the water and 1 m above it; sample 2b is 5 m from the water and 0.33 m above it. Samples 2a and 2b are 15 m apart.

The remaining sites are elevated approximately 1 m above the water, but are much farther from the swampy areas than the previous two sites. The third site, Sand, a scrub community (Ewel, 1990), has one sample on a low-nutrient sugar sand lens dominated by *Quercus geminata* Small. This sample is 50 m from a swamp. The fourth site, designated Palmetto is located in a temperate, hardwood forest community (Ewel, 1990) and has one sample collected in a wet soil area 38 m from a nearby swamp and dominated by the palm *Serenoa repens* (Bartram) Small. Samples 3 and 4 are 12 m from one another.

For each litter sample, all the leaf litter in a randomly chosen 1-m² area was collected into plastic bags, labeled, and taken back to the laboratory for sorting and analysis. These leaves represent the sum total of leaves accumulated from the past one or two years because most of the leaves from earlier years were decomposed. The samples were collected in March, so included mainly leaves dropped in the previous autumn and winter, with a few leaves from previous years. Each sample was separated and the leaves identified to species (taxonomy of Radford et al., 1968; Godfrey, 1988), the number of leaves or identifiable leaf fragments of each species were counted. Before measurement and scoring, the leaves were soaked in water and pressed flat. Each litter collection plot also defined the center of a 10-m line transect, which was measured parallel to the swamp edge. Each tree, woody shrub, and vine species that overlay this line was recorded at 1-m intervals. Individual species that overlay the transect at more than one point were combined into one occurrence. The species identified from the leaf litter and line transects were compared to each other and with a vegetation list based on a comprehensive inventory begun in 1995 (Appendix 1; also see website http://www.flmnh.ufl.edu/paleobotany/swampwoods_leaves.htm for leaf images) of the woody plants growing in the entire 25-ha swamp forest and woodland.

The leaves of each species at each litter sample and transect were scored for the 31 characters described by Wolfe (1993, 1995) and Herman et al. (A. B. Herman, R. A. Spicer [The Open University, Milton Keynes, United Kingdom], J. A. Wolfe, and M. E. Collinson, 1996, unpublished pamphlet) (Table 1). The scores for leaf litter samples were based on whole and fragmentary leaves and leaflets. Measurable fragments that were once part of the same leaf were combined and made equivalent to a whole leaf. Species counts of fragmentary leaves or leaflets were based on base/petiole portions and apical portions. Purely marginal fragments were discarded. Fragmentary leaves were more prevalent in thin-textured species (i.e., *Acer rubrum* L.) in which base-petiole sections accounted for a large number of counts. Apical portions of leaves are present but always in lower numbers than base-petiole sections. Mature and juvenile leaves were counted and scored. Some species were scored based on limited samples (e.g., one leaf), and the number of leaves and species collected in each sample are given in Appendix 1. Scores for each species are based on all the leaves collected for that species in a given sample, with whole leaves

incorporating all characters, while character scores from fragmentary leaves are based on teeth, apex, and base. Representative samples of each species in leaf litter, covering all morphological variations, are archived in the Florida Museum of Natural History, Paleobotany/Palynology section.

The species represented in the leaf litter plots were compared to the species identified in the line transects and in the woodland as a whole. The physiognomy of the modern leaves was measured from a leaf assemblage of 19 woody dicot species that were collected in Dilcher's Woods previously for use in other studies (Wiemann et al., 1998; Kowalski and Dilcher, 2003).

Mean annual temperature estimates (Table 2) were calculated for each transect, litter site, and the woodland as a whole using several simple linear and multiple linear equations (Table 3), as well as with canonical correspondence analysis (CCA) (CANOCO version 4, ter Braak and Smilauer, 1998) using the CLAMP data set (Wolfe, 1993; available at website <http://www.open.ac.uk/earth-research/spicer/CLAMP/Clampset1.html>), a multivariate method of comparing climate with leaf physiognomy. In addition, growing season length and growing season precipitation estimates (Table 2) were calculated using CCA with CLAMP. Because the standard error of each equation tested varies from 0.8°C to 3.6°C according to the number of sample data used to create that particular equation, we followed the convention of Wilf (1997) and adopted a minimum standard error for statistical MAT prediction of 2°C. Therefore, MAT estimates within 2°C of the actual MAT are considered to be accurate results. Growing season precipitation estimates that are within 32 cm (the published standard error, Spicer et al., 2005) of the actual growing season precipitation are likewise considered to be accurate. Estimates that exceed the accepted error as mentioned are distinguished in Table 2.

RESULTS AND DISCUSSION

Appendix 1 shows the results of the inventory of the 25-ha woodland where a total of 60 woody species is known. Of the 39 species encountered in this study, 29 (74%) were found in the leaf litter, 34 (87%) were found in the line transects, and 24 (62%) were found in both the leaf litter and line transects.

A total of 2324 leaves representing 18 species was found in the three combined Peninsula litter samples, 1764 leaves representing 16 species were found in the two combined Swamp litter samples, 925 leaves representing 15 species were found in the Sand litter sample, and 1046 leaves representing nine species were found in the Palmetto litter sample (Appendix 1). Only three species, *Gordonia lasianthus* (L.) Ellis, *Magnolia virginiana* L., and *Vitis rotundifolia* Michaux were found in all four areas (Appendix 1).

For individual samples, Fig. 2 shows that between 50 and 75% of the species seen in a line transect were found in its associated leaf litter site, whereas between 46 and 100% of the species in the leaf litter sites were seen in the associated line transect. At Palmetto, (sample 4) the inventory of the leaf litter was a faithful (100%) indicator of the line transect, whereas the other leaf litter samples only partially reflect the species found in the associated line transects. This lack of correlation between species in the transect and leaf litter is especially pronounced at the Sand site, whose leaf litter contained many leaves of *Liquidambar styraciflua* (32) and *Vaccinium corymbosum* (19) that were not found in its associated line transect (Appendix 1). This disjunct may be due in part to the leaves having been transported a considerable distance from their parent trees (Appendix 1) because the Sand site is in an open area through which wind can carry leaves from greater distances than is the case with any of the other sites. *Prunus* was similarly often present in the leaf litter sites and not in the associated line transects, possibly reflecting greater distance dispersal of leaves under the forest canopy or along the forest floor in a closed canopy forest. The presence of these leaves may also reflect the transect-sampling design, which could potentially miss trees close to the collection site that did not overlap the transect line.

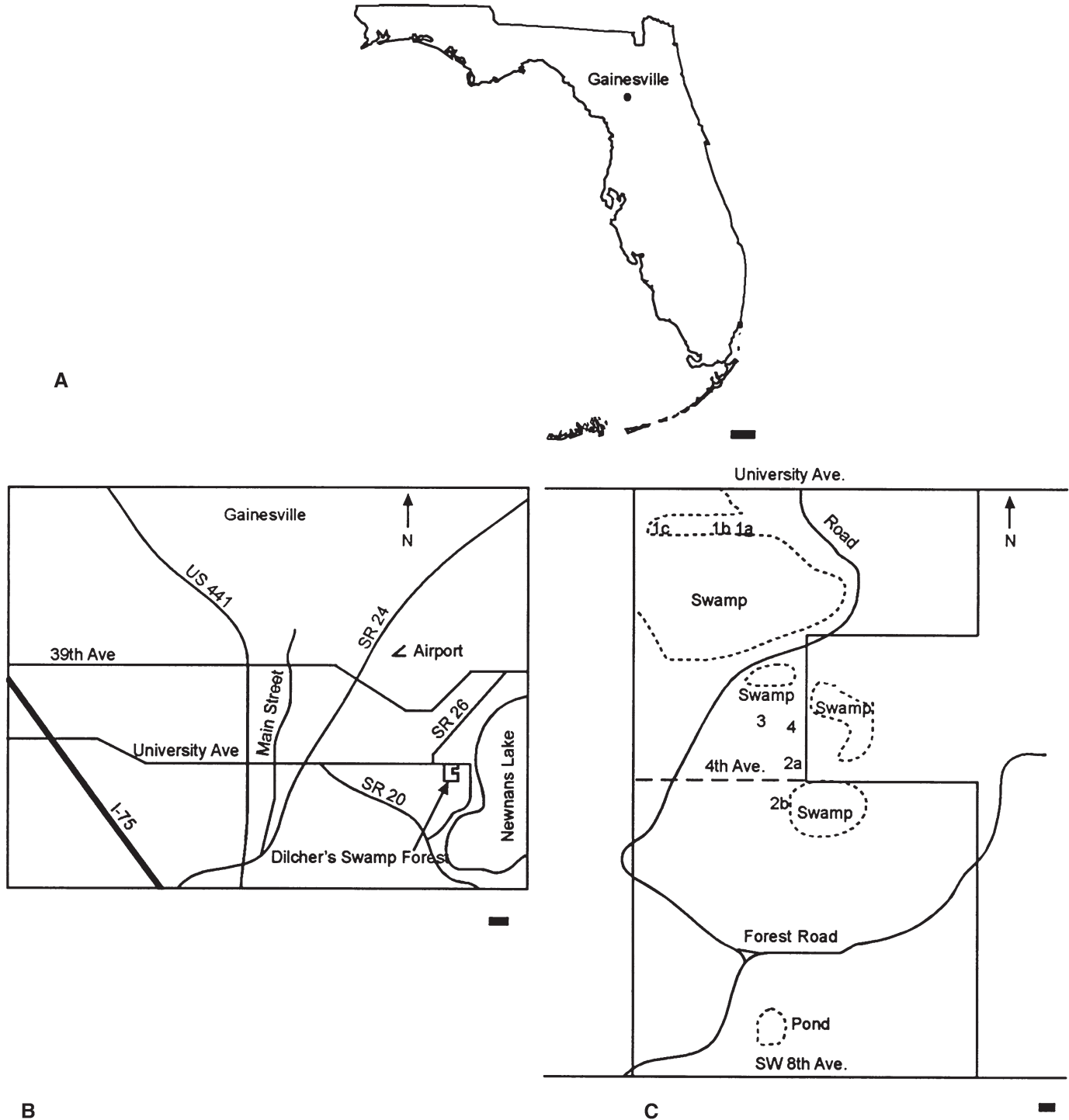


Fig. 1. Maps of study area. (A) Florida, USA. Scale bar = 50 km. (B) Gainesville, Florida. Scale bar = 1 km. (C) Study area east of Gainesville, Florida. Scale bar = 20 m. Sample sites: 1a–c = Peninsula, 2a, b = Swamp, 3 = Sand, 4 = Palmetto.

Species most likely to be identified in the line transects but not found in the leaf litter sites were shrubs, *Leucothoe*, *Vaccinium* (except Sand), *Lyonia*, and *Myrica* (except Peninsula). The absence of shrub leaves in the leaf litter may reflect the low number of leaves produced by individual plants, such as *Leucothoe*, or the nature of the leaves shed. For example, *Myrica* sheds numerous leaves that wither quickly and do not disperse

far from the parent plant. Species represented by high numbers of leaves in litter samples, such as *Quercus nigra* L. (Swamp, 1085), *Myrica cerifera* (Peninsula, 752), and *Acer rubrum* (Peninsula, 558), correspond to a high transect occurrence (Appendix 1). In general, the species abundance in leaf litter sites reflects the relative abundance and composition of the standing forest.

TABLE 3. Simple linear (SLR) and multiple linear regression (MLR) equations used to predict mean annual temperature (MAT) for each set of combined litter and canopy samples in Dilcher's Swamp/woods.

Equation type	Equation	Reference
SLR	$30.6E + 1.14$	Wolfe, 1979; Wing and Greenwood, 1993
SLR	$0.363E + 2.223$	Kowalski and Dilcher, 2003
MLR	$17.372E + 2.896AE - 8.592W + 2.536$	Wing and Greenwood, 1993
MLR	$0.207E - 0.058BR - 0.202W + 9.865$	Wiemann et al., 1998

Notes: Regression equations to determine MAT (mean annual temperature) and GSP (growing season precipitation) from CCA (canonical correspondence analysis) using CLAMP (Climate-Leaf Analysis Multivariate Program) are available at <http://www.open.ac.uk/earth-research/spicer/CLAMP>. Abbreviations: *E* = percentage of leaves with entire margins, *AE* = percentage of leaves with emarginated apex, *BR* = percentage of leaves with a round base, *W* = percentage of leaves with a length to width ratio of <1. The MLR from Wing and Greenwood (1993) requires transforming each percentage value before the regression by taking the arcsine in degrees of the square root of the proportion.

woodland are shown in Table 1. The results of the MAT and GSP predictions for each of these sites and from the entire woodland are shown in Table 2. All the MAT predictions derived from the equations by Wing and Greenwood (1993) and Wiemann et al. (1998) and from CCA are underestimates, as are 60% of the predictions from the simple linear regression equation (Table 2). The MAT predictions using the equation from Kowalski and Dilcher (2003) are overestimated in 50% of the sites. The remaining 50% of the sites predicted with the Kowalski and Dilcher (2003) and 40% of the sites predicted using the simple linear regression were estimated accurately, within 2°C.

MAT estimates derived from leaves collected from the canopy and those derived from leaf litter were estimated to within 2°C of each other for each site, with the exception of the Sand site. The large percentage of overlapping species between litter and canopy samples present at each site probably accounts for this consistency in estimates. The exception, Sand, had 15 species scored for physiognomy in the litter site, but only seven species from the canopy. While totals for both species are lower than the 20 species recommended for statistical temperature prediction (Wolfe, 1993), the total of seven canopy species from Sand is exceptionally low and should not be expected to result in an accurate MAT prediction. In addition, the canopy and litter samples from the Sand site have a 24% difference in the proportion of species with an entire margin (Table 1), due to the high species total disjunct. This would explain the major difference in MAT estimates between litter and canopy samples at the Sand site, because MAT predictive equations and CCA using CLAMP weigh the entire margin character (no teeth in Table 1) most heavily of all the leaf physiognomic characters. The remaining sites have a proportion of entire margin leaves that differs less than 3% between canopy and litter samples (Table 1).

The results of the GSP predictions were expected to be lower than the actual mean annual precipitation (MAP) total used as a comparison, because the growing season in Gainesville is approximately 9.6 mo (Martin and Jokela, 2004), but rainfall continues throughout the year. However, GSP was overestimated for all samples except the Palmetto litter sample, although in two of these samples (Swamp litter and Palmetto canopy) the overestimates are within the 32 cm error using CCA with

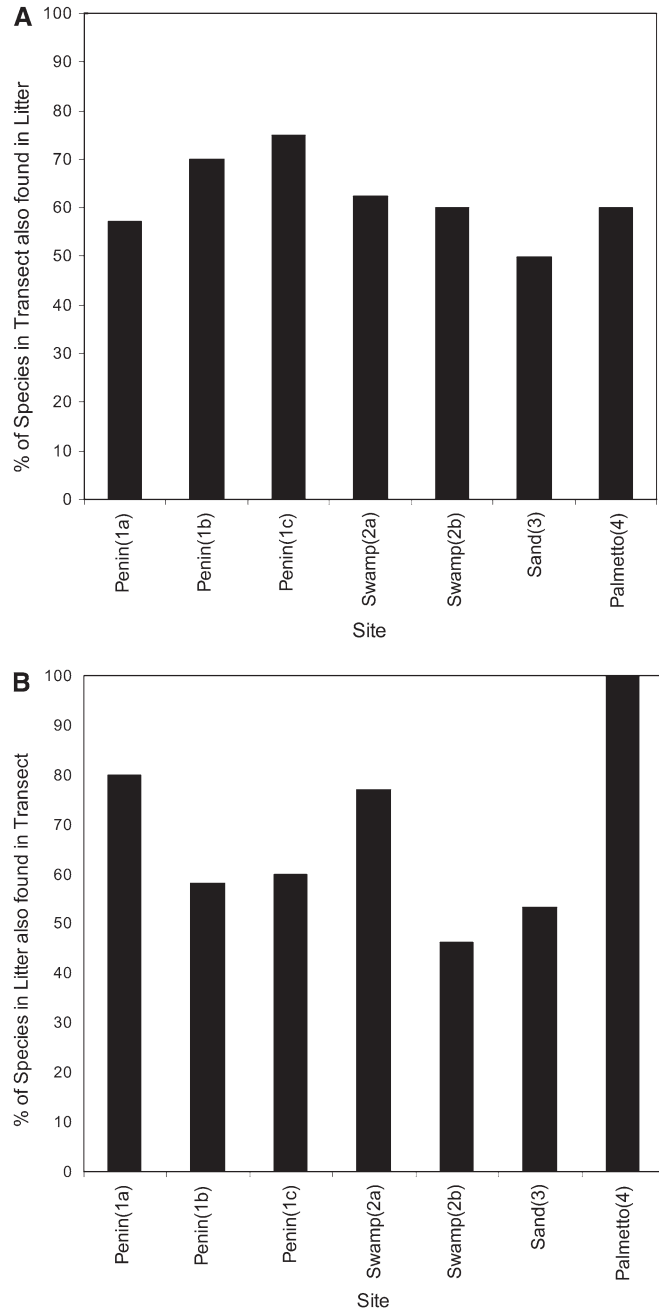


Fig. 2. Line transect and leaf litter charts for sites in Dilcher's Swamp/woods, Gainesville, Florida. (A) Percentage of species found in the line transect and also the leaf litter. (B) Percentage of species found in the leaf litter and also the line transect. (See Fig. 1 for names and locations of sites.)

CLAMP (Spicer et al., 2005) (Table 2). In addition, although CLAMP overestimated the growing season length for Gainesville at two sites (Table 2), the remaining six sites, as well as the litter and canopy as a whole, had growing season lengths that were underestimated by CLAMP by as much as 1.6 mo. Given these estimates, MAP totals (the GSP estimate plus off-season precipitation) would be even higher.

At each site, canopy samples produce higher precipitation estimates than litter samples. However, only the Sand and

Palmetto sites have precipitation estimates that differ by more than the 32 cm standard error. The differences between estimates derived from litter and the canopy, though small, are possibly due to the lower percentage of large leaves in the litter samples as compared to the canopy samples (Table 1) because leaf size is the physiognomic character weighted most heavily in precipitation estimates using CCA with CLAMP (Wolfe, 1993). The higher percentage of larger leaf sizes in canopy samples vs. leaf litter samples has also been noted in Australian samples (Greenwood, 1992) and Indiana (Roth and Dilcher, 1978) and may be the result of the physical deterioration of the larger shade leaves prior to deposition or larger surface area allowing the shade leaves to travel further from the canopy as it falls to the ground. This loss has also been discussed by Spicer et al., (2005) who noted that, surprisingly, loss of large leaf sizes does not affect the estimate of GSP considerably using CCA in at least one test sample.

In summary, we have gained new and important messages from this study. (1) Leaf litter and canopy leaves give similar MAT predictive results, suggesting that predictive equations derived from canopy leaf morphology may be used with accuracy to determine MAT of fossil deposition sites. These results are not necessarily expected because leaf litter composition is not a complete mirror of the canopy's composition. However, this is not the case for GSP, because although GSP predictive results for both canopy and leaf litter are overestimates, the canopy consistently gives higher GSP predictions than the leaf litter, and (2) the use of a line transect does show a reasonable match with the leaf litter and species composition of a lower diversity forest. Therefore, a fossil collection site the size of the litter sample presented here potentially could show us the nature of ancient forests with considerations to proximity of the source and the nature of the transport to the site of deposition. The heterogeneity of the litter collection presented here and the number of species that are unique to single collection sites underscores the need for multiple fossil collections to truly reconstruct fossil depositional environments. A continuation of this study might be to calculate climate estimates based on the leaf morphologic characters from leaves at subfossil deposition sites, which would further examine the accuracy of using predictive equations based on canopy characters for determining climate parameters from leaves at fossil deposition sites.

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Leaf sample	Angiosperm taxa	Percentage of litter										Percentage of occurrences in transect																
		Peninsula			Swamp			Sand			Palmetto			Peninsula			Swamp			Sand			Palmetto					
		1a	1b	1c	1abc	2a	2b	2ab	2c	2d	1a	1b	1c	1abc	2a	2b	2ab	2c	2d	1a	1b	1c	1abc	2a	2b	2ab	2c	2d
1	<i>Acer rubrum</i> L. *	43.6	19.8	15.0	24.0		3.5	1.5		11.0	12.5	18.0	9.8	13.7	2.6	3.3	2.9										5.1	
7	<i>Bignonia capreolata</i> L.																											
8	<i>Carpinus caroliniana</i> Walt.				0.4		0.2																				1.0	
9	<i>Carya glabra</i> (Mill.) Sweet *				12.8		7.6	10.3																				
11	<i>Cephalanthus occidentalis</i> L.																										1.3	
14	<i>Crataegus flava</i> Ait.							0.1																				
16	<i>Gaylussacia tomentosa</i> (A. Gray) Small																										3.8	
17	<i>Gelsemium sempervirens</i> (L.) Jaume St. Hil.	6.2	7.5		4.0																							
18	<i>Gordonia lasianthus</i> (L.) Ellis *	2.8	7.1	10.1	7.2		18.1	7.7	0.2	20.0	10.4	4.0	3.6	3.6	1.7	13.3	4.6										26.6	
19	<i>Hamelis virginiana</i> L.																											
20	<i>Ilex cassine</i> L. *																										3.8	
23	<i>Ilex opaca</i> Ait. *		1.5		0.5				1.6																		6.7	
25	<i>Leucothoe racemosa</i> (L.) Gray																										6.7	
26	<i>Liquidambar styraciflua</i> L. *																										5.1	
27	<i>Lyonia ferruginea</i> (Walt.) Nutt. *		0.1	0.1	0.1																						5.1	
28	<i>Lyonia lucida</i> (Lam.) K. Koch				0.04																						2.5	
29	<i>Magnolia grandiflora</i> L. *																										13.9	
30	<i>Magnolia virginiana</i> L. *	7.5	0.3	2.9	3.3		0.3	0.9	0.2	2.1																	3.8	
31	<i>Morus rubra</i> L.																											
32	<i>Myrica cerifera</i> L. *	2.6	31.3	51.6	32.4																						8.9	
33	<i>Nyssa sylvatica</i> Marsh. *	2.3	18.0	1.8	7.0																						5.1	
34	<i>Osmanthus americanus</i> (L.) A. Gray *		5.0		1.5																						10.6	
35	<i>Ostrya virginiana</i> (Mill.) K. Koch *																											
36	<i>Persea palustris</i> (Raf.) Sarg.	1.0	0.1	0.5	0.5		0.4	1.1	0.7	0.4	6.3	4.0	2.4	4.3	5.2	21.7	1.9										1.3	
37	<i>Prunus serotina</i> Ehrh. *		0.1	0.1	0.1		0.1																					
38	<i>Prunus umbellata</i> Ell.			0.3	0.1																							
40	<i>Quercus geminata</i> Small *																										17.3	
41	<i>Quercus hemisphaerica</i> Bart. ex Willd.																										5.8	
43	<i>Quercus laurifolia</i> Michx.	0.2			0.04		0.2	0.1	0.2																			
46	<i>Quercus nigra</i> L. *	21.5		9.1	9.6		62.5	60.1	61.5	32.4	12.5		4.3	4.3	18.3	10.0	15.4										11.4	
47	<i>Quercus virginiana</i> Mill.						4.9	7.0	5.8																			
50	<i>Rubus</i> sp.																											
52	<i>Tilia caroliniana</i> L.																											
53	<i>Toxicodendron radicans</i> (L.) Kuntze																											
55	<i>Vaccinium arboreum</i> Marsh. *																											
56	<i>Vaccinium corymbosum</i> L.																										2.5	
57	<i>Vaccinium myrsinites</i> Lam.			0.3	0.1																							
58	<i>Vaccinium stamineum</i> L.			0.1	0.04																						2.9	
	Number of leaves																											
	Number of occurrences	10	12	15	19	13	13	16	15	9	14	10	12	21	16.0	10	21	16	15	16	9	14	10	12	21	16.0	10	15
	Number of species																											