

When are leaves good thermometers? A new case for Leaf Margin Analysis

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Abstract.—Precise estimates of past temperatures are critical for understanding the evolution of organisms and the physical biosphere, and data from continental areas are an indispensable complement to the marine record of stable isotopes. Climate is considered to be a primary selective force on leaf morphology, and two widely used methods exist for estimating past mean annual temperatures from assemblages of fossil leaves. The first approach, Leaf Margin Analysis, is univariate, based on the positive correlation in modern forests between mean annual temperature and the proportion of species in a flora with untoothed leaf margins. The second approach, known as the Climate-Leaf Analysis Multivariate Program, is based on a modern data set that is multivariate. I argue here that the simpler, univariate approach will give paleotemperature estimates at least as precise as the multivariate method because (1) the temperature signal in the multivariate data set is dominated by the leaf-margin character; (2) the additional characters add minimal statistical precision and in practical use do not appear to improve the quality of the estimate; (3) the predictor samples in the univariate data set contain at least twice as many species as those in the multivariate data set; and (4) the presence of numerous sites in the multivariate data set that are both dry and extremely cold depresses temperature estimates for moist and nonfrigid paleofloras by about 2°C, unless the dry and cold sites are excluded from the predictor set.

New data from Western Hemisphere forests are used to test the univariate and multivariate methods and to compare observed vs. predicted error distributions for temperature estimates as a function of species richness. Leaf Margin Analysis provides excellent estimates of mean annual temperature for nine floral samples. Estimated temperatures given by 16 floral subsamples are very close both to actual temperatures and to the estimates from the samples. Temperature estimates based on the multivariate data set for four of the subsamples were generally less accurate than the estimates from Leaf Margin Analysis. Leaf-margin data from 45 transect collections demonstrate that sampling of low-diversity floras at extremely local scales can result in biased leaf-margin percentages because species abundance patterns are uneven. For climate analysis, both modern and fossil floras should be sampled over an area sufficient to minimize this bias and to maximize recovered species richness within a given climate.

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Introduction

Understanding global change requires knowledge of terrestrial as well as marine climates, both past and present. The marine record offers detailed paleotemperature data for approximately the past 100 million years, primarily from stable isotope ratios (e.g., Savin 1977; Zachos et al. 1994). On land, the morphologic characteristics of fossil plant assemblages, in particular the leaves of flowering plants, are considered to be useful sources of proxy data for past climates. The fossil record of flowering plants is temporally comparable to the marine isotope record, dating to the Early Cretaceous (e.g., Taylor and Hickey 1996), although leaf-climate relationships have undoubtedly changed through time. The

primary role of leaves as photosynthetic organs requires that their morphologies be climatically tuned for photosynthetic efficiency. Many correlations of the sizes and shapes of modern leaves to climatic conditions are statistically significant and have been used in a uniformitarian manner to quantify past climates (e.g., Wolfe 1993). How best to apply this uniformitarian procedure is still controversial.

Bailey and Sinnott (1915, 1916) observed a robust positive relationship between climatic warmth and the percentage of dicotyledonous species in a flora that have leaves with entire margins (i.e., untoothed, smooth edges), suggesting that this relationship be used as a paleothermometer that is independent of taxonomy. After a number of initial paleoclimatic

studies (Berry 1916; Chaney and Sanborn 1933; Wolfe and Hopkins 1967; Wolfe 1971, 1978), Wolfe (1979) published a linear regression of mean annual temperature (MAT) vs. the percentage of woody dicot species with entire margins in floral samples from eastern Asian forests. These samples are all from forests without significant moisture limitations, and only one sample has MAT \ll 10°C. Application of this regression to fossil floras to estimate past MAT is known as Leaf Margin Analysis (LMA).

Paleotemperature estimates from Leaf Margin Analysis have shown general agreement with other geologic proxies, such as marine temperature trends (Wolfe and Poore 1982; Parrish and Spicer 1988; Johnson and Hickey 1990; Stott and Kennett 1990; Huber and Watkins 1992; Johnson and Wilf 1996); diversity patterns for reptiles (Hutchison 1982); and stable oxygen isotope ratios of hematite encrustations on bones of fossil mammals (Koch et al. 1996).

The physiological basis of the MAT vs. leaf-margin correlation has never been adequately demonstrated. However, teeth are strongly associated with the movement of water out of leaves via transpiration and guttation (Haberlandt 1914; Bailey and Sinnott 1916; Canny 1990; Wilson et al. 1991; Wolfe 1993), which suggests that one of the functions of teeth in colder climates is to boost sap flow. Leaf teeth typically have large veins running directly to their apices and often contain conspicuous open pores, or hydathodes (e.g., Haberlandt 1914; Bailey and Sinnott 1916; Canny 1990). As spikes projecting from the leaf margin with veins running to the end of the 'spike,' teeth thin the boundary layer and create transpiration hot spots (Canny 1990). Tracer dyes rapidly move toward teeth (Canny 1990), and Wolfe has observed that leaf-clearing chemicals are forcibly ejected from many tooth apices (Wolfe 1993: p. 61). Toothed species are also uncommon in dry, saline, frigid or otherwise moisture-limiting environments (e.g., Bailey and Sinnott 1915, 1916). Givnish (1979) proposed that untoothed margins correlate to leaf thickness, and in turn to temperature, because the decreased flow resistance in thicker leaves allows more even growth be-

tween secondary veins, resulting in a smoother margin. Roth et al. (1995), in a hydrodynamic modeling study, suggested that some teeth are byproducts of differential expansion near large veins that run to the margin. This growth strategy may be cost-effective for the frequent leaf regeneration required of deciduous plants (Mosbrugger and Roth 1996).

Wolfe (1993) attempted to improve the precision of paleotemperature estimates and to provide a method for inference of other climatic variables, including seasonality of temperature and amount and seasonality of rainfall, with the Climate-Leaf Analysis Multivariate Program (CLAMP). This approach uses a multivariate data set, primarily from North American forests, of 29 leaf characters per sampling site, including leaf-margin type. Unlike the LMA data set, CLAMP contains a large number of samples from dry and severely cold areas. The CLAMP data set and accompanying meteorological data are ordinated onto two axes using correspondence analysis (Hill 1974). Quantitative climate estimates for a fossil flora are derived by scoring each species in the flora for all of the 29 CLAMP characters, ordinating the resulting vector along with the CLAMP data set to obtain the two axis scores for the fossil sample, and following a graphical procedure to correlate these scores to polynomial fits of the data set for each climate variable (see Wolfe 1993). A revised version of CLAMP that uses canonical correspondence analysis has been developed (Wolfe 1995), but the modified data set is not yet published.

The climatic significance of the majority of the CLAMP characters, other than leaf-margin type, remains largely speculative. The best-substantiated theories link moisture to leaf size (e.g., Webb 1968; Givnish 1979) and to the presence of drip-tips, which are attenuate, elongate leaf apices that appear to control the rate of water clearance (e.g., Dean and Smith 1978; Richards 1996). The relatively long and narrow drip-tip enables water flowing as a sheet to form droplets that are large enough to break the surface tension over this narrow area (H. Pfefferkorn personal communication 1997).

A series of studies have utilized the CLAMP

ordination approach to estimate past MAT and other climatic variables (Wolfe 1990, 1992, 1994a,b,c; Povey et al. 1994; Herman and Spicer 1996, 1997). The CLAMP data set has also been analyzed through multiple regression, which results in the elimination of the majority of the characters as statistically insignificant (Gregory and Chase 1992; Wing and Greenwood 1993; Gregory 1994; Greenwood and Wing 1995; Gregory and McIntosh 1996; but see Wolfe 1995: Fig. 2). A few tests of CLAMP-based multiple regressions in modern forests have, for the most part, resulted in poor estimates for temperature variables besides MAT and in overestimates of precipitation (Jacobs and Deino 1996; Wilf 1996, unpublished data; Burnham in press). Recently, Jordan (1996; see Wing and Greenwood 1996) has shown that the temperature signal in the CLAMP data set is statistically dominated by MAT and that CLAMP-derived estimates of cold-month mean temperature (CMM) are by-products of the modern correlation between MAT and CMM. The utility of the CLAMP data set for estimating variables besides mean annual temperature is therefore poorly substantiated.

Are leaves better thermometers when multivariate techniques based on the CLAMP data set are used, or is Leaf Margin Analysis, the simpler approach, at least as precise? I argue here for the latter. From both a theoretical and a practical standpoint, I examine whether including characters in addition to leaf-margin type improves MAT estimates. I analyze sources of noise in the CLAMP and LMA data sets that are related to the numbers of species scored per sample, sampling scale, the types of samples used, and the scoring process. I then use these analyses to predict how MAT estimates derived from the CLAMP data set should differ from LMA estimates and how MAT estimates using any method are expected to vary as a function of the number of species scored. The predictions are then tested on new data from living forests.

Materials and Methods: Living Forests

Nine Western Hemisphere floral samples were used in this study, seven tropical and two temperate, containing a total of 1445 spe-

cies. This figure is a maximum because some of the 62 taxa determined to be distinct species within samples, but not assigned to formal species names, may have been present in more than one sample (e.g., "*Trichilia* sp."). The median sample had 132 species. The nine floras were chosen because they are well studied, allowing the analysis of high numbers of species and the examination of leaf-climate data at more than one spatial scale. Also, the samples represent, albeit unevenly, a wide latitudinal range of about 55°, including two samples from South America, which has been little studied with regard to leaf-climate relationships (Halloy and Mark 1996). Desert sites and frigid sites with little rainfall during the growing season were avoided because the MAT vs. leaf-margin correlation is sensitive to dryness and extreme cold (Bailey and Sinnott 1915, 1916; Dilcher 1973; Wolfe 1979, 1993; Wing and Greenwood 1993; this paper). No preference was given to riparian vs. nonriparian habitats, or to whether or not vine data were available.

Sixteen floral subsamples were taken from the nine samples; the median subsample had 49 species. These subsamples were either field collections or species lists from previously published research plots. Basic data on the samples and subsamples are shown (Table 1), and short descriptions are given below.

All available species of native woody dicots were scored for leaf-margin type, whether trees, shrubs, or woody vines (Table 1), except for parasites, epiphytes, mangroves (because they typically grow in saline environments), cacti, cactus-like euphorbs, and many succulents. Three woody non-dicots (one *Gnetum*, two *Smilax*) that contribute dicot-like leaves to the forest litter were included.

Following Wolfe (1993), a species received a score of 0 if all of its leaves were toothed, a score of 0.5 if some leaves were toothed, and a score of 1 if all leaves were entire. A tooth was considered to be a vascularized extension of the leaf margin, with a corresponding sinus incised not more than one quarter the distance from margin to midrib. Spines were not counted as teeth, after Wolfe (1993), because they are unvascularized extensions of the leaf whose function may be defensive (Givnish

TABLE 1. Collection and meteorological data for the nine floral samples and 16 subsamples, subsample data in italics: (1) mean annual temperature, °C, (MAT); (2) mean annual precipitation, cm (MAP); (3) number of species scored; (4) area covered by samples or collection type of subsamples; and (5) vegetation sampled. See text for citations.

Sample or subsample	MAT	MAP	# Species	Collection area or type	Species scored
Beni Biodiversity Plots, Bolivia	27	180	104	4 ha	trees ≥ 10 cm dbh
<i>Plot 1</i>			43	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
<i>Plot 2</i>			49	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
<i>Plot 3</i>			44	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
<i>Plot 4</i>			9	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
Manu Biodiversity Plots, Peru	24.2	243	292	4.4 ha	trees ≥ 10 cm dbh
<i>Plot 1</i>			127	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
<i>Plot 2</i>			159	<i>1.4 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
<i>Plot 3</i>			101	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
<i>Plot 4</i>			64	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
Barro Colorado Island, Panamá	27.1	261	629	1560 ha	all woody species
<i>Burnham and Wing collection</i>			137	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
Bisley Watersheds, Puerto Rico	24.4	350	131	≈ 20 ha	all woody species
<i>Biodiversity Plot</i>			31	<i>1 ha plot</i>	<i>trees ≥ 10 cm dbh</i>
Guánica Commonwealth Forest, Puerto Rico	25.1	86	126	4016 ha	trees and shrubs
<i>subsample</i>			26	<i>limited local transects</i>	<i>trees and shrubs</i>
St. John, U.S. Virgin Islands, dry woodland	26.9	113	173	1730 ha	all woody species
<i>Biodiversity Plot</i>			48	<i>1 ha plot</i>	<i>trees ≥ 4 cm dbh</i>
St. John, U.S. Virgin Islands, moist forest	26.3	120	227	860 ha	all woody species
<i>L'Esperance</i>			35	<i>0.5 ha plot</i>	<i>all stems ≥ 5 cm dbh</i>
<i>Bordeaux</i>			57	<i>1 ha plot</i>	<i>all stems ≥ 5 cm dbh</i>
York County, Pennsylvania	11.8	104	132	2.35×10^5 ha	all woody species
<i>subsample</i>			56	<i>17 local transects</i>	<i>all woody species</i>
Allegheny National Forest area, Pennsylvania	7.2	116	74	$\approx 1.27 \times 10^5$ ha	all woody species
<i>subsample</i>			47	<i>28 local transects</i>	<i>all woody species</i>

1979) and not related to climate. Unvascularized crenulations or irregular edges were likewise not scored as teeth. Lobed leaves without teeth on the lobes were scored as entire. Except for the field-collected subsamples scored directly from specimens (Barro Colorado Island, Guánica Forest, York County, Allegheny National Forest), leaves were scored from manuals and from herbarium material at the National Herbarium (US) or the Herbarium of the Botany Department of the Academy of Natural Sciences (PH). Species with ambiguous or conflicting margin descriptions or poor figures in manuals were always herbarium-checked.

The four field-collected subsamples listed above were also scored (Table 2) for the CLAMP characters that were used as predictors in the following four regression models for estimating mean annual temperature (Gregory and McIntosh 1996): (1) all sites in

the CLAMP data set used as predictors, along with multiple characters; (2) all sites, but only the percentage of entire-margined species used as a predictor variable; (3) only relatively warm sites (CMM $< -2^\circ\text{C}$ [see Wing and Greenwood 1993]) used as predictors, multiple characters; and (4) only the warm sites, with just entire-margin percentage as a predictor variable. To avoid any circularity, regression coefficients were adjusted with the Barro Colorado Island (BCI) and Guánica Forest CLAMP sites removed from the predictor set. The former is the same as the BCI subsample in this paper, and the latter was collected near the site of the Guánica Forest subsample. The adjusted models (not shown) were nearly identical to the published models. Except for this adjustment specifically for the purpose of regression analysis of the subsamples, all calculations from the CLAMP data set in this article use the published version (Wolfe 1993).

TABLE 2. Physiognomic scores for multiple regression analysis, Barro Colorado Island (BCI), Guánica Forest, York County, and Allegheny National Forest subsamples, shown as proportions. The two rows for BCI show, respectively, the scores from Wolfe (1993; Table 2) and the rescaling of the same leaves for this paper. Scores for the proportions of entire-margined species (Table 4) were the same for both scorings of BCI. Characters scored following instructions in Wolfe (1993): (1) lobed leaf, (2) leptophyll 2 (size category), (3) emarginate apex (i.e. notched apex), (4) acute base, and (5,6) two categories of length : width ratios, <1 and 1–2.

Subsample	Lobed	Lepto 2	Apex em.	Base acute	L : w <1	L : w 1–2
BCI (Wolfe 1993)	0.02	0.01	0.12	0.66	0.03	0.18
BCI (this paper)	0.026	0.012	0.036	0.161	0.029	*
Guánica Forest	0	0.109	0.538	0.404	0.013	0.525
York County	0.232	0.018	0.054	0.277	0.098	0.491
Allegheny National Forest	0.202	0.011	0.043	0.106	0.096	0.386

* Not scored separately for BCI; 0.18 was used for regression.

All species lists generated for this contribution are available by request. Latitude-longitude coordinates are given at the precision available.

Beni Biosphere Reserve, Bolivia.—Leaves were scored from photocopied mini-herbaria and plot lists in Dallmeier et al. (1991a,b) for Beni Biosphere Reserve Biodiversity Plots 1–4, along and near the Curiraba River, near San Borja, Bolivia (14°30'S,66°18'W). The four plots combined comprised the sample, the individual plots the subsamples. Climate data are given by Dallmeier et al. (1991a), who report a six-month dry season. The plots lie in tropical moist forest (Plots 1–3) and tropical savanna (Plot 4).

Manu Biosphere Reserve, Peru.—Leaves were scored from photocopied mini-herbaria and plot lists in Dallmeier et al. (1993a,b) for Manu Biosphere Reserve Biodiversity Plots 1–4, along and near the Manu River, adjacent to Pakitza Station, Peru (11°55'48"S,71°15'18"W). The four plots combined comprised the sample, the individual plots the subsamples. Climate data from the Cocha Cashu Biological Station, upriver from Pakitza at 11°54'S,71°22'W (Terborgh 1990), were supplied by J. Terborgh and M. Jarrell. The area is in tropical moist forest, with about five drier months.

Barro Colorado Island, Panamá.—All woody species listed and described in Croat (1978) comprised the sample. The subsample was a collection of BCI leaves made by R. Burnham and S. Wing in 1989 at 9°10'N,79°51'W from a single hectare of the 50-ha permanent forest plot of Hubbell and Foster (1983). These were the same leaves used as the BCI sample in the CLAMP data set (Wolfe 1993), and they are

housed in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution. My rescaling of these leaves was a test of the repeatability of the scores; the new scores were used for the regression analyses. Climate for BCI is reported in Windsor (1990); the forest type is tropical moist forest. The dry season lasts approximately four and a half months.

Bisley Experimental Watersheds, Luquillo Experimental Forest, Puerto Rico.—Woody dicot species were those listed in Chinaea et al. (1993). The subsample was Bisley Biodiversity Plot 13 (18°18'N,65°50'W), scored from the photocopied mini-herbarium in Dallmeier, Kabel et al. (1991). Precipitation data are as reported in Scatena (1989); the area lies within montane subtropical wet forest, with little rainfall seasonality (Lugo 1986). Temperature data were derived by linear altitudinal interpolation from Brown et al. (1983).

Guánica Commonwealth Forest, Puerto Rico.—Woody species in the sample are those listed in Little and Wadsworth (1964) and Little et al. (1974) as present in Guánica Commonwealth Forest (Lugo et al. 1997). These manuals primarily list tree species but also include many shrubs. Limited transects collected in May, 1995, within a 0.5-km radius of the forest office, at 17°58'27"N,66°52'09"W, comprised the subsample. A full physiognomic range of each species encountered was included. Voucher specimens are housed in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution. Climate data are from Ensenada, 17°58'N,66°56'W (Murphy and Lugo 1990). Guánica Forest is a subtropical dry forest. There are two significant

dry periods per year, totaling seven to eight months; high temperature and low precipitation make Guánica Forest the driest of the nine samples. One of Wolfe's (1993) CLAMP sites was also from this area. The Ensenada data used here indicate MAT almost 2°C lower than reported in Wolfe (1993).

St. John, United States Virgin Islands.—Two vegetational zones were scored: dry evergreen woodland and moist forest (Woodbury and Weaver 1987; Acevedo-Rodríguez 1996). Species lists for the zones given in Woodbury and Weaver (1987) were revised following Acevedo-Rodríguez (1996). Three research plots comprised the subsamples. St. John Biodiversity Plot 1 (Dallmeier, Comiskey, and Ray 1993) on Caneel Hill, Virgin Islands National Park (18°21'N, 64°44'W), lies within the dry evergreen formation. The two moist forest sites were Bordeaux Mountain and L'Esperance in the central part of the island (Reilly et al. 1990). Climate data are from Cruz Bay, near Caneel Hill, for dry woodland, and from Lameshur Bay, south of Bordeaux Mountain, for moist forest (Woodbury and Weaver 1987). The dry season throughout St. John is about four months.

Pennsylvania: York County and Allegheny National Forest.—Species lists of trees, shrubs, and woody vines for the York County and Allegheny National Forest (ANF) floral samples were generated by A. Rhoads from the computerized version of the Pennsylvania Flora Database (Rhoads and Klein 1993). For ANF, the query was a latitude-longitude grid containing all of western McKean County, northwestern Pennsylvania, which includes the National Forest. The species list for York County, southeastern Pennsylvania, was generated by the county name. The query areas were large in order to capture adequate numbers of species for analysis from these low-diversity floras.

Although temperature varies within these regions, effects on the analysis were minimized by selecting climate stations as close as possible to the latitudinal and altitudinal centers of the sampled areas. For York County and ANF respectively, these were York SSW3 Pumping Station, at 39°55'N, 76°45'W, 118 m elevation, and Bradford 4 SW Reservoir 5, 41°53'31"N, 78°42'52"W, 503 m. Climate data

were supplied by P. Knight. The York County area has even precipitation throughout the year, while for ANF there is a slight drop in precipitation in January and February; ANF is the coldest sample, with a January mean temperature of -5.8°C. The York County and Allegheny National Forest study areas respectively belong to the Appalachian oak forest and Allegheny hardwood forest types.

The York County and Allegheny National Forest subsamples were each collected in October, 1995, at the respective times of maximum abscission, within a range of less than 250 m of altitude and less than 15' of latitude. Both subsamples were composed of multiple transects for leaf collection, with 28 transects for ANF and 17 in the eastern portion of York County. Ten of the ANF transects and seven of the York County transects were collected along rivers and streams, the rest on slopes and ridge crests. Each transect consisted of three parallel linear subtransects, 40 m in length and spaced 10 m apart. Individual parautochthonous assemblages of fossil leaves from single quarry sites are thought to represent a similar source area of vegetation, so these transects were spatially analogous to such sites (Burnham et al. 1992; Wing and DiMichele 1995). For each transect, I collected the full physiognomic range found for the leaves of all species encountered on the transect lines. Leaves were collected both from litter, to include the physiognomy of canopy leaves, and directly from live twigs, to maximize the number of species and facilitate identification. *Betula alleghaniensis* Britton (toothed) and *Cephalanthus occidentalis* L. (entire) were encountered but not included in the subsample list. Leaves of the former had dried and disintegrated prior to abscission, and no leaves of the latter could be found. Voucher specimens and field maps are housed in the Botany Department of the Morris Arboretum, University of Pennsylvania. All species-locality data have been submitted for inclusion in the Pennsylvania Flora Database.

The Importance of Leaf-margin Type

Analysis.—The proportion of entire-margined species is the CLAMP character that explains, by far, the most variance in estimated MAT. This character offers important addi-

tional advantages in that its relationship to temperature is well documented, and it is easily and unambiguously scored for nearly all modern leaves and for all but the most poorly preserved fossils. There is also no taphonomic bias in this character that has been rigorously substantiated (Roth and Dilcher 1978; Greenwood 1992; Burnham 1994).

The CLAMP ordination itself provides the clearest evidence of the dominance of leaf-margin type in the temperature signal from leaves. The MAT and no-teeth vectors are so coincident that Wolfe projected directly to the no-teeth vector in his bivariate plots used to estimate MAT (Wolfe 1993: Fig. 11, Plate 4).

The dominance of margin type is also clear in multiple regression analyses of the CLAMP data set. The Gregory and McIntosh (1996) multiple regression for MAT based on the 74 CLAMP sites with cold-month mean temperature greater than -2°C has a standard error of 1.5°C ($r^2 = 0.92$, $F = 170$, $p < 0.0005$). Re-running this multiple regression as specified and examining the standardized coefficients for the predictor variables shows that the proportion of entire-margined leaves controls 67% of the MAT signal (standardized coefficient of 0.67). The univariate MAT vs. leaf-margin regression in the same table, using the same subset of 74 sites, has only 0.6°C more standard error, 2.1°C ($r^2 = 0.84$, $F = 390$, $p < 0.0005$).

Can Additional Variables Increase Precision?—While the extra 0.6°C of resolution predicted by multivariate analysis is possible in theory, it may not yet be attainable in practice. Small errors in any of the scores used in multivariate models (Table 2), whether caused by scoring methodology or taphonomy, can easily affect the value of the temperature estimate by more than 0.6°C ; for example, a 7% error in the score for leptophyll 2 is sufficient in the model based on the 74 warm CLAMP sites of Gregory and McIntosh (1996). Accurate scoring of the size distributions of leaves in fossil floras is especially problematic because large leaves are preferentially removed during transportation, and a precise correction method has not been found (Roth and Dilcher 1978; Greenwood 1992). Also, the CLAMP scoring procedures specified in Wolfe (1993) have nev-

er been tested for consistency among investigators and may not be reproducible at the precision needed, even for modern samples. The rescaling of the BCI subsample for this paper differed substantially from the published scores in Wolfe (1993) for both acute bases and emarginate apices (Table 2), but not for the proportion of entire-margined species. In an informal experiment, I asked eight paleontologists, five of them paleobotanists, to score, independently, voucher specimens of the same six randomly chosen species from the Barro Colorado Island subsample for presence or absence of an acute base. The instructions were to follow exactly the definition given in Wolfe (1993: p. 28): "a base is acute if the most basal fourth of the lamina has a straight or concave margin." There was 100% agreement for two species, 75% agreement for three species, and 63% agreement for one species. The participants reported that the complexity of basal curvatures exhibited by the specimens was greater than the definition could accommodate, leading to uncertainty in scoring, for example, if there were both concave and convex portions of the margin of the basal fourth.

Expected Differences between CLAMP and LMA Estimates.—The dominance of leaf-margin type predicts that differences among estimated MATs from different data sets primarily depend on the fits of MAT vs. leaf-margin percentage in those data sets. Linear regressions are shown (Fig. 1) for the following: Leaf Margin Analysis (Wolfe 1979); the full CLAMP data set of Wolfe (1993); the warm CLAMP subset, containing only sites with CMM greater than -2°C ; and the samples scored for this paper. The presence of numerous dry and cold sites in the CLAMP data set but not in the LMA data set explains much of the difference between the CLAMP and LMA regressions. Dry and cold sites have the same margin percentages as warmer, moister sites. For example, the 32 CLAMP sites with CMM less than -2°C , most of which receive very little moisture during the growing season, have an average of 25.4% entire-margined species, which gives an averaged estimated MAT from Leaf Margin Analysis of 8.9°C . The actual average MAT for these sites, however, is only 4.5°C . The effect of the cold outliers is to pull

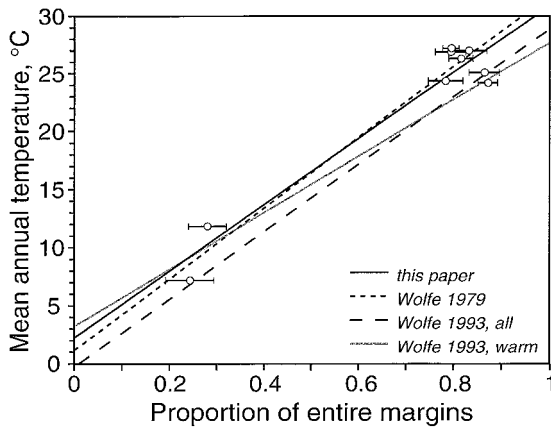


FIGURE 1. Fits of mean annual temperature vs. the proportion of entire-margined species, with plots of the nine floral samples scored in this paper. The solid line is the regression using the nine samples: $\text{MAT} = 28.6P + 2.24$ ($r^2 = 0.94$, $\text{SE} = \pm 2.0^\circ\text{C}$, $F = 102$, $p < 0.0005$), where P is the observed proportion of entire-margined species. The dashed line is from the Wolfe (1979) East Asian data set: $\text{MAT} = 30.6P + 1.14$ ($r^2 = 0.98$, $\text{SE} = \pm 0.8^\circ\text{C}$, F not available, $p < 0.001$). The dotted line is from the CLAMP data set (Wolfe 1993): $\text{MAT} = 29.1P - 0.266$ ($r^2 = 0.76$, $\text{SE} = \pm 3.4^\circ\text{C}$, $F = 333$, $p < 0.0005$), and the gray line is from the CLAMP data set when the 32 sites with the coldest winter temperatures are removed prior to regression: $\text{MAT} = 24.4P + 3.25$ ($r^2 = 0.84$, $\text{SE} = \pm 2.1^\circ\text{C}$, $F = 384$, $p < 0.0005$). Error bars are one standard deviation (eq. 1).

down the regression line from the CLAMP data set on the left side; when removed (gray line in Fig. 1), the vertical-intercept becomes higher and the slope lower than for all of the other fits shown, and standard error decreases significantly.

The regression lines for the warm subset and for LMA cross at 34% entire margins (Fig. 1). Multivariate MAT estimates that use all sites in the CLAMP data set as predictors, and estimates derived from the warm subset for floras with more than about 34% entire-margined species should be, on average, cooler than MAT estimates from the same leaves estimated with LMA. Floras with less than about 34% entire margins will generally give higher multivariate MAT estimates than Leaf Margin Analysis if the warm subset is used.

Quantification of Sampling Error

Analysis.—Leaf-margin type is essentially a binomial character. Only a small percentage of species bear both toothed and entire leaves, creating a third outcome (3.7% of the species

scored for this study). Assuming random sampling of leaf margins, binomial probability predicts that the standard deviation of an observed leaf-margin percentage is a function of the number of species scored, just as the standard deviation of the outcome of a weighted coin-toss experiment is a function of the number of trials.

Suppose that r species are selected at random from an unlimited species pool, and a proportion P , $0 < P < 1$, of the r species have entire margins. After repeating this experiment many times, the standard deviation of P , $\sigma[P]$, will be

$$\sigma[P] = \sqrt{\frac{P(1-P)}{r}} \quad (1)$$

which is the equation for the standard deviation of binomially distributed outcomes (see also Raup 1991). The equation for Leaf Margin Analysis, based on the Wolfe (1979) data set, is (Wing and Greenwood 1993)

$$\text{LMAT} = 30.6P + 1.14 \quad (2)$$

where LMAT is the *leaf-estimated mean annual temperature*. Constants have no variance, so if c and d are constants, then

$$\sigma[cP + d] = c\sigma[P]. \quad (3)$$

Combining equations (1), (2), and (3), the standard deviation of LMAT, in degrees C, is

$$\sigma[\text{LMAT}] = c \sqrt{\frac{P(1-P)}{r}} \quad (4)$$

where c is the slope of the MAT vs. leaf-margin regression in the data set used. In this paper, $c = 30.6$, from equation (2), will be applied. The standard deviation that is the output of equation (4) will be referred to as the “sampling error” or the “binomial sampling error” (Fig. 2). Equation (4) also applies to multivariate estimates of MAT because margin type is the dominant character in predicting MAT, even in multivariate models. For 50% entire margins, binomial sampling error is near 3°C at 26 species and near 2°C at 59 species. The 80% or 20% entire-margins case is more generous, with 17 species required for 3°C of sampling error and 37 for 2°C . For most fossil floras, sampling error exceeds the standard errors of published methods for estimat-

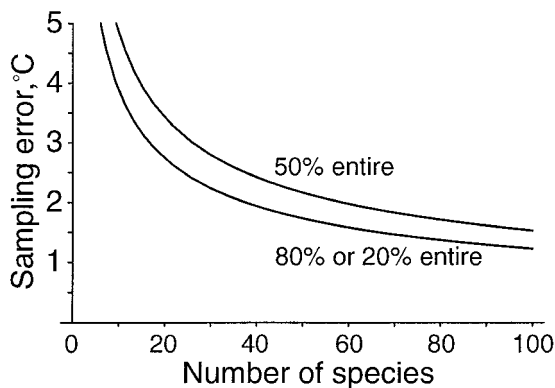


FIGURE 2. Sampling error for Leaf Margin Analysis as a function of the number of species scored. Plotted from equation (4), using $P = 0.5$ (50% entire-margined species) and $P = 0.8$ (80% or 20% entire).

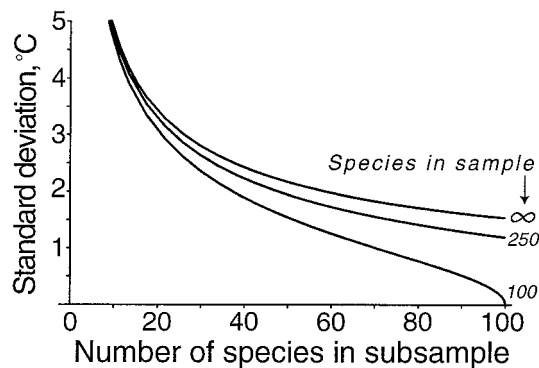


FIGURE 3. The standard deviations of temperatures estimated from Leaf Margin Analysis of subsamples when the means are temperatures estimated from Leaf Margin Analysis of samples. Combined plots from equation (6), using 50% entire margins and samples of 100, 250, and ∞ species.

ing paleotemperature (Wing and Greenwood 1993; Wolfe 1993; Gregory and McIntosh 1996).

Suppose that a subsample of r species is taken from a particular floral sample. If the sample contains m entire and n toothed species, and P is now the observed proportion of entire margins in the subsample, the standard deviation of P is

$$\begin{aligned} \sigma_{m+n}[P] &= \sigma(m, n, r) \\ &= \frac{1}{m+n} \sqrt{\frac{mn(m+n-r)}{r(m+n-1)}}. \end{aligned} \quad (5)$$

For the derivation and demonstration of the convergence of equation (5) to equation (1) as $m+n \rightarrow \infty$, see Appendix 1. The standard deviation of LMAT of the subsample from the LMAT of the sample is then

$$\sigma_{m+n}[\text{LMAT}] = \frac{c}{m+n} \sqrt{\frac{mn(m+n-r)}{r(m+n-1)}}. \quad (6)$$

The standard deviation function of equation (6) is shown (Fig. 3) for $m = n$ (50% entire margins) and samples of $m+n = 100, 250$, and ∞ species. The latter value gives the same curve as equation (4), with $P = 0.5$. As the number of species in the subsample approaches the number in the sample, ever fewer combinations of species are possible, and the standard deviation goes to zero.

Application of the Sampling Error Model to MAT Estimation.—The equation for binomial sampling error (eq. 4) makes the conservative,

worst-case assumption that the flora being sampled has infinite species richness. There are two major reasons why this is a practical assumption. First, it is difficult, even in the most fortunate situations, to make better than an order-of-magnitude estimate of the true diversity of the regional flora from which any fossil assemblage was drawn (e.g., Anderson et al. 1996). By assuming an infinite flora, this issue is moot. Second, the difference between the standard deviations for the “infinite” vs. “finite” cases is negligible (Fig. 3), except for the unusual case of depauperate floras that have been exceptionally well sampled.

The appropriate error placed on a particular estimate of past MAT is the larger of the two error figures given by binomial sampling error and the standard error on the regression used. For the latter, unfortunately, it is not yet clear what value to apply. The LMA regression of Wolfe (1979) has a standard error of $\pm 0.8^\circ\text{C}$ (Wing and Greenwood 1993). This extremely low value is unlikely to be reproduced in other data sets. For example, an individual sample, using 25% entire margins, would have to contain 274 species just for its binomial sampling error to be this low. Standard error for an LMA-type regression using the full CLAMP data set is $\pm 3.4^\circ\text{C}$; with the coldest sites removed it is $\pm 2.1^\circ\text{C}$ (Fig. 1). Standard error for MAT vs. leaf-margin regression using the nine floral samples scored for this study is $\pm 2.0^\circ\text{C}$. Until additional speciose

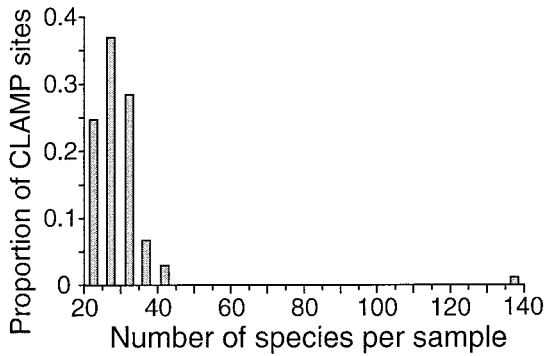


FIGURE 4. Distribution of the number of species per sample for the 106 samples in the CLAMP database (Wolfe 1993). The single outlier is the collection from Barro Colorado Island, Panamá.

data sets are published from mesic forests without extreme winter temperatures, the distribution of standard error values will be unknown. On the basis of the regression from nine samples, I suggest a provisional minimum error for paleotemperature estimates of $\pm 2^\circ\text{C}$, to be used when binomial sampling error is less than 2°C .

Range of Temperature in Data Sets.—Construction of leaf-margin data sets that are statistically robust requires a range of temperature among samples such that there is an adequate ratio of temperature range to database noise. In county-scale studies in the Carolinas (Dolph and Dilcher 1979) and Indiana (Dolph 1984), no strong correlation between leaf-margin type and temperature was found. However, both areas have limited temperature ranges that are close to the 4°C ($\pm 2^\circ\text{C}$) suggested minimum noise level (Carolinas: about 6°C ; Indiana: about 3°C).

Relative Noise among Data Sets.—The equation for binomial sampling error (eq. 4) can be used to approximate the relative amount of statistical noise in the LMA and CLAMP data sets. Most of the samples that comprise the LMA data set contain more than 50 species (Wolfe 1993: p. 4), whereas the CLAMP data set has a median of 28 species per sample (Fig. 4). If 50% of the flora has entire margins, then sampling error is less than 2.2°C for more than 50 species, but for 28 species, it is 2.9°C (Fig. 2), a noise gap of more than 0.7°C . For this reason, combining leaf-margin data from

TABLE 3. Leaf-margin data for the nine floral samples: (1) proportion of entire-margined species; (2) leaf-estimated mean annual temperature (LMAT), in $^\circ\text{C}$; (3) error of the estimate, LMAT – actual MAT; and (4) binomial sampling error, in $^\circ\text{C}$ (eq. 4).

Sample	Entire	LMAT	Error of estimate	Sampling error
Beni Biodiversity Plots	0.832	26.6	-0.4	1.1
Manu Biodiversity Plots	0.872	27.8	3.6	0.6
Barro Colorado Island	0.797	25.5	-1.6	0.5
Bisley Watersheds	0.782	25.1	0.7	1.1
Guánica Forest	0.864	27.6	2.5	0.9
St. John, dry woodland	0.795	25.5	-1.4	0.9
St. John, moist forest	0.822	26.3	0.0	0.8
York County	0.280	9.7	-2.1	1.2
Allegheny National Forest	0.243	8.6	1.4	1.5

CLAMP and LMA into a single database is not recommended.

Results and Discussion: Living Forests

Leaf Margin Analysis: Floral Samples.—Results are shown in Table 3. The samples were sufficient to generate a statistically robust MAT vs. leaf-margin relationship (Fig. 1). This nine-sample regression is much closer to the fit for Leaf Margin Analysis than to the fits of the CLAMP data set (Fig. 1), although all four regression lines are broadly similar.

Leaf Margin Analysis: Floral Subsamples.—The subsamples performed well as thermometers in comparison to the samples (Table 4). Four of the subsamples gave better temperature estimates (negative error difference in Table 4), and five subsamples gave LMAT that was the same or only 0.1°C worse than the samples (error difference = 0 or 0.1). Excluding Beni 4, a subsample of only nine species, the subsamples correlated nearly as well as the samples in MAT vs. leaf-margin regression ($r^2 = 0.84$, $SE = \pm 2.4^\circ\text{C}$, $F = 71$, $p < 0.0005$).

To examine whether LMAT changes in a predictable fashion with sample size, equation (6) was applied to each subsample to generate a standard deviation, which was compared to the observed deviation of subsample LMAT from sample LMAT (Table 4, Fig. 5). Observed deviations, in absolute value, are less than standard deviations for 14 of the 16 subsamples, or 88%, more than the expected value of 68% associated with one standard deviation. The subsample LMATs are therefore more like

TABLE 4. Leaf-margin data for the 16 floral subsamples and comparisons with corresponding data from full samples: (1) proportion of entire-margined species; (2) leaf-estimated mean annual temperature (LMAT) (eq. 2), °C; (3) error of the estimate, $LMAT - MAT$; (4) sampling error, °C (eq. 4); (5) error difference between each subsample and its sample, calculated as $|LMAT(\text{subsample}) - MAT| - |LMAT(\text{sample}) - MAT|$, some apparent discrepancies due to rounding; (6) observed deviation of the estimate, $LMAT(\text{subsample}) - LMAT(\text{sample})$; (7) the expected estimate difference of one standard deviation between subsamples and samples, °C (eq. 6); and (8) the percentage of the species in the sample represented by the subsample.

Subsample	Entire	LMAT	Error of estimate	Sampling error	Error difference	Observed deviation	Standard deviation	% Species
<i>Beni Biodiversity Plot 1</i>	0.860	27.5	0.5	1.6	0.1	0.9	1.3	41.3
<i>Beni Biodiversity Plot 2</i>	0.857	27.4	0.4	1.5	0.0	0.8	1.2	47.1
<i>Beni Biodiversity Plot 3</i>	0.807	25.8	-1.2	1.8	0.8	-0.8	1.3	42.3
<i>Beni Biodiversity Plot 4</i>	0.667	21.5	-5.5	4.8	5.1	-5.1	3.7	8.7
<i>Manu Biodiversity Plot 1</i>	0.862	27.5	3.3	0.9	-0.3	-0.3	0.7	43.5
<i>Manu Biodiversity Plot 2</i>	0.868	27.7	3.5	0.8	-0.1	-0.1	0.5	54.5
<i>Manu Biodiversity Plot 3</i>	0.871	27.8	3.6	1.0	0.0	0.0	0.8	34.6
<i>Manu Biodiversity Plot 4</i>	0.891	28.4	4.2	1.2	0.6	0.6	1.1	21.9
<i>Barro Colorado Island</i>	0.807	25.8	-1.3	1.0	-0.3	0.3	0.9	21.8
<i>Bisley Biodiversity Plot</i>	0.823	26.3	1.9	2.1	1.2	1.2	2.0	23.7
<i>Guánica Forest</i>	0.846	27.0	1.9	2.2	-0.5	-0.5	1.8	20.6
<i>St. John Biodiversity Plot</i>	0.927	29.5	2.6	1.1	1.2	4.0	1.5	27.7
<i>St. John, L'Esperance</i>	0.829	26.5	0.2	1.9	0.2	0.2	1.8	15.4
<i>St. John, Bordeaux</i>	0.816	26.1	-0.2	1.6	0.2	-0.2	1.3	25.1
<i>York County</i>	0.277	9.6	-2.2	1.8	0.1	-0.1	1.4	42.4
<i>Allegheny National Forest</i>	0.245	8.6	1.4	1.9	0.0	0.0	1.2	63.5

the sample LMATs than expected from random sampling of margin type.

Leaf Margin Analysis vs. CLAMP-based Regression.—When both LMA and the CLAMP data set were used to estimate MAT from four subsamples (Table 5), Leaf Margin Analysis results had less total error than any of the four CLAMP-based models. The maximum LMA error was 2.5°C, while each CLAMP-derived regression model generated at least one error

figure greater than 3°C. The multivariate CLAMP-based estimates were not more accurate in absolute sum than their univariate counterparts, despite their lower standard errors (Gregory and McIntosh 1996), and multivariate maximum errors were greater. The sum of errors row in Table 5 shows a distinct negative bias in the CLAMP-based scores, principally from the severe underestimates for Barro Colorado Island.

The differences between the estimates for “univariate all,” “univariate warm,” and LMA (Table 5) are the result of the different regression lines used (Fig. 1). “Multivariate warm” results, in identical fashion to the “univariate warm” estimates, are cooler than LMA for the tropical sites and warmer than LMA for the temperate sites. The “multivariate all” estimates, like “univariate all”, are lower than the LMA estimates, except for York County and ANF. Six of the eight multivariate estimates therefore are higher or lower than the LMA estimates as predicted by the leaf-margin character alone, a reasonable percentage given that the latter controls about 70% of the temperature signal.

The poor multivariate results for BCI probably reflect the lack of moist tropical sites in the CLAMP data set. For example, the char-

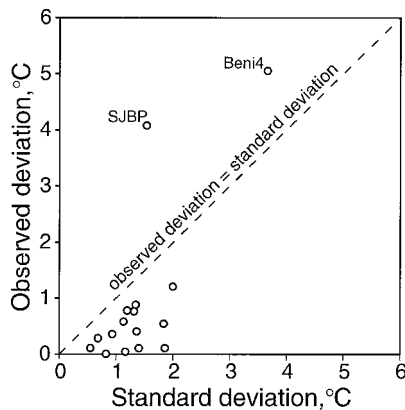


FIGURE 5. Observed deviations vs. standard deviations of leaf-estimated mean annual temperature (LMAT) for the 16 floral subsamples in relation to the samples containing them. Data from Table 4, in absolute value. Labeled outliers: Beni Biodiversity Plot 4 (Beni4) and St. John Biodiversity Plot (SJB).

TABLE 5. Errors of regression estimates (estimate – actual) from four subsamples for mean annual temperature, in °C, using both Leaf Margin Analysis and the CLAMP data set. Predictor data used for estimates, from left to right: (1) Leaf Margin Analysis data set; (2) all CLAMP sites, multiple predictor variables; (3) all CLAMP sites, one predictor; (4) the “warm” CLAMP sites with CMM > –2°C, multiple predictors; and (5) “warm” sites, one predictor. Column totals shown both as sums and as sums of absolute values.

Subsample	LMAT – MAT	(MAT estimated from CLAMP data set) – MAT			
		Multivariate, all	Univariate, all	Multivariate, warm	Univariate, warm
BCI	–1.6	–7.7	–4.2	–6.1	–4.4
Guánica Forest	2.5	–0.6	–0.8	–0.3	–1.3
York County	–2.1	0.7	–3.8	0.0	–1.6
Allegheny National Forest	1.4	1.8	–0.2	3.1	2.2
Sum of errors	0.1	–5.8	–9.0	–3.3	–5.1
Sum of absolute errors	7.6	10.8	9.0	9.5	9.5

acter for emarginate (notched) apices is highly correlated with MAT in CLAMP and is included in the regression models used here. A leaf cannot have both an emarginate apex and a drip-tip at the same time. Therefore, in tropical forests with high drip-tip percentages, like BCI, the percentage of species with emarginate apices is likely to be lower than in drier climates with the same MAT. If few wet tropical forests are in the predictor set, MAT will probably be underestimated for warm floras with a high percentage of drip-tips.

Effects of Nonrandom Species Abundance Patterns: Pennsylvania Transects.—Plant species in natural communities generally do not occur

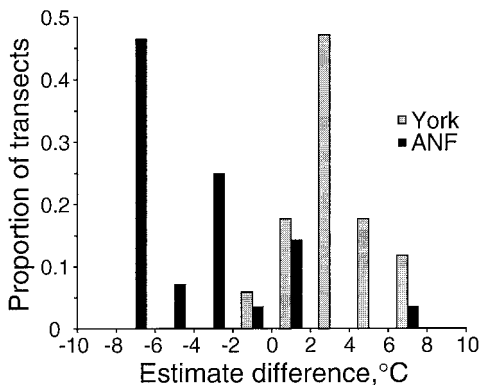


FIGURE 6. Estimated mean annual temperatures, using Leaf Margin Analysis, derived from each of 45 Pennsylvania transects (Appendix 2) minus the estimated temperatures given by the corresponding York County and Allegheny National Forest samples (York, ANF) (Table 3), shown as proportional distributions. Individual transects in these floras tend to have leaf-margin percentages that are greater (York) or less (ANF) than the leaf-margin percentages of the samples containing them, reflecting the biases of local patterns of species abundance.

with equal abundance. The probability of sampling a margin type will rarely equal the proportion of species in the source flora having that margin type. The leaf-margin percentage of the species present in a local area will differ both from the regional flora and from nearby sampling locations (Gentry 1969; Dolph 1971, 1979; Burnham 1994). The smaller the collection area and the fewer species present, the more significant the possible leaf-margin bias.

These points are demonstrated by the transect data from York County and Allegheny National Forest (Fig. 6, Appendix 2). The differences in LMAT for individual transects and whole samples are not evenly distributed; neither distribution in Figure 6 has a mean or mode near zero. While inconsistent LMAT from such species-poor collections is expected, each set of transects has a bias that reflects the species abundance patterns of the two floras. All but one of the 17 York County transects is more entire than the York sample as a whole, resulting in higher LMAT (mean difference = 3.3°C, σ of differences = 1.9°C). In contrast, all but five of the 28 ANF transects are more toothed than the ANF sample, giving lower LMAT (mean difference = –4.4°C, σ of differences = 3.6°C). The modal percentage of entire-margined species for the ANF transects is 0.

The frequencies of occurrence of individual species further illustrate the nonrandom patterns of species distribution in these Pennsylvania floras (Appendix 3). In the York County sample, many entire-margined species are ubiquitous in transects, but this margin type

makes up a minority of the total woody species (28.0%; Table 3). In the ANF area, the toothed species are both ubiquitous and a majority of the species (24.3% entire; Table 3). The ubiquity of entire-margined species in the York transects causes the right-shift of the distribution of estimate differences in Fig. 6, while for ANF, the ubiquity of toothed species results in a left-shift.

These Pennsylvania transects are spatially, if not depositionally, analogous to the source areas of single quarry sites containing fossil leaves deposited in low-transport environments (Burnham et al. 1992; Wing and DiMichele 1995), illustrating that leaf-margin percentages of fossil samples that are highly localized and also have low species richness can be affected by uneven species abundance patterns as well as by sampling error. The latter can always be quantified using the methods in this paper, even in a fossil assemblage. However, the possibility of nonrandom sampling of margin types from the source flora (Fig. 6) is much more difficult to evaluate in fossil floras and is best countered at a particular stratigraphic level by maximizing recovered diversity, number of replicate samples, transect length, and number of facies types sampled (Burnham 1989).

Similarly, modern predictor samples should be collected over an area large enough to account for site-to-site physiognomic variation in the vegetation being sampled and to be spatially analogous to multiple rather than single quarry sites of fossils. Special care must be taken when sampling is spatially restricted, for example, to a close radius around a climate station. In such a case, the investigator should demonstrate, by examining the vegetation in surrounding areas, that the gain in microclimatic resolution is greater than the loss to sampling error and local bias in margin type. The "finite flora" method (eq. 5) can be used to evaluate the latter by comparing observed deviations vs. standard deviations of the leaf-margin percentages of vegetational subsamples in relation to a corresponding sample. Also, the distribution of the leaf-margin percentages of subsamples relative to that of the sample can be examined for unidirectional biases (Fig. 6).

This study also points out a hazard of inferring climate from the proportion of *leaves* possessing physiognomic characters, rather than the proportion of *species* (Greenwood 1992). The former is highly influenced by abundance patterns that may have no climatic significance.

Conclusions

Estimates of mean annual temperature based on Leaf Margin Analysis are at least as precise as those derived from the CLAMP data set. Leaf-margin type dominates the temperature signal in dicot leaf physiognomy and, in mesic and nonfrigid climates, the proportion of species in a flora that have untoothed margins is an excellent thermometer. Use of the additional characters from CLAMP contributes little information about temperature. These characters probably can not be scored reliably enough to make use of this additional information, either in modern or fossil floras.

The number of species per sample has a major effect on the precision of MAT estimates, both in predictor data sets and in fossil samples for which an MAT estimate is desired. This sampling error can be quantified, if sampling is random with respect to margin type, using a simple equation based on the standard deviation of binomially distributed outcomes. The minimum error placed on an MAT estimate using either LMA or the CLAMP data set should be about $\pm 2^\circ\text{C}$, or the binomial sampling error when the latter is greater.

In practice, the assumption of random sampling of margin types from a regional flora will usually be violated because species abundance patterns are uneven. The effects of nonrandom sampling in fossil floras are best overcome by maximizing the number of species, the number of facies, and the transect length sampled per stratigraphic level. Predictor data sets should be collected over a sufficient area to minimize local biases caused by species abundance patterns and to maximize the number of species scored within a given climate.

Leaf Margin Analysis remains the most effective, unambiguous, and simply applied method for estimating past land temperatures, providing an invaluable complement to

the marine stable isotope record. In the future this method and new multivariate approaches may be improved considerably by (1) constructing new predictor data sets that contain highly speciose samples and cover a wide temperature range, especially in the Southern Hemisphere, and (2) physiological studies to determine the biological bases of the correlations of leaf physiognomy to climatic variables.

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Appendix 1

Derivation of equation (5) and proof of its convergence to equation (1) as $m + n \rightarrow \infty$.

Given m entire and n toothed leaves, we choose r leaves. The probability $\text{Prob}(m, n, r, j)$ that exactly j entire leaves are chosen is

$$\text{Prob}(m, n, r, j) = \frac{\binom{m}{j} \binom{n}{r-j}}{\binom{m+n}{r}}$$

because the right side is the number of ways of choosing j entire leaves from m , times the number of ways of choosing $r - j$ toothed leaves from n , divided by the total number of outcomes. Hence, the average proportion of entire leaves that will be chosen is clearly

$$\frac{m}{m+n}.$$

The variance of the proportion of leaves chosen that are entire, i.e., the variance of j/r , is then

$$\begin{aligned} \sigma^2 &= \sum_j \left(\frac{j}{r}\right)^2 \text{Prob}(m, n, r, j) - \left(\frac{m}{m+n}\right)^2 \\ &= \sum_j \frac{j^2}{r^2} \frac{\binom{m}{j} \binom{n}{r-j}}{\binom{m+n}{r}} - \left(\frac{m}{m+n}\right)^2 \\ &= \frac{mn(m+n-r)}{r(m+n)^2(m+n-1)}. \end{aligned}$$

The standard deviation of the proportion of entire leaves chosen is therefore

$$\sigma(m, n, r) = \frac{1}{m+n} \sqrt{\frac{mn(m+n-r)}{r(m+n-1)}}$$

which is equation (5).

Consider a limiting situation for the standard deviation above. Assume that m , the number of entire leaves, is equal to $P(m+n)$ (i.e., a fixed proportion of the total number of leaves), where P is a fixed constant, i.e., that $m = Pn/(1-P)$. Now, let $n \rightarrow \infty$. We find, from equation (5), that

$$\lim_{n \rightarrow \infty} \sigma \left(\frac{Pn}{1-P}, n, r \right) = \sqrt{\frac{P(1-P)}{r}}$$

which is equation (1).

Appendix 2

Species richness, leaf-margin data, and locality information for transects. “Y” transects from York County; “M” transects from Allegheny National Forest (McKean County, Pennsylvania). Shown for each transect: transect number; location ($\pm 2''$, ± 10 m); number of species; proportion of entire-margined species; leaf-estimated mean annual temperature (LMAT) (eq. 2), °C. Actual MAT's are 11.8°C for York County and 7.2°C for ANF (Table 1).

	Latitude (N), longitude (W), elevation (m)	# Species	Entire	LMAT		Latitude (N), longitude (W), elevation (m)	# Species	Entire	LMAT
Y1.1	39°50'20",76°22'27",220	15	0.4	13.4	M4.2	41°53'59",78°49'33",650	6	0.25	8.8
Y1.2	39°50'23",76°22'27",210	12	0.375	12.6	M4.3	41°53'59",78°49'33",650	4	0	1.1
Y1.3	39°50'16",76°22'30",220	11	0.409	13.7	M5.1	41°42'25",78°49'26",470	7	0	1.1
Y1.4	39°50'09",76°22'29",200	18	0.361	12.2	M5.2	41°42'30",78°49'18",470	8	0.125	5.0
Y1.5	39°50'13",76°22'27",190	16	0.375	12.6	M5.3	41°42'33",78°49'08",470	6	0	1.1
Y2.1	39°52'42",76°23'02",60	10	0.25	8.8	M6.1	41°42'39",78°49'38",480	7	0.071	3.3
Y2.2	39°53'02",76°22'53",50	14	0.429	14.3	M6.2	41°42'39",78°49'38",480	6	0	1.1
Y2.3	39°53'22",76°22'54",50	12	0.5	16.4	M6.3	41°42'46",78°49'22",550	4	0	1.1
Y3.1	40°00'38",76°39'23",260	7	0.5	16.4	M6.4	41°42'48",78°49'25",580	5	0.2	7.3
Y3.2	40°00'42",76°38'54",280	13	0.308	10.6	M7.1	41°46'30",78°53'01",440	9	0.167	6.2
Y3.3	40°00'37",76°38'59",270	14	0.429	14.3	M7.2	41°46'29",78°52'59",440	12	0.125	5.0
Y4	40°03'11",76°36'56",170	13	0.385	12.9	M8.1	41°46'21",78°51'23",410	5	0	1.1
Y5	40°02'48",76°33'40",70	13	0.346	11.7	M8.2	41°46'43",78°50'32",420	10	0	1.1
Y6.1	39°50'37",76°21'22",180	13	0.346	11.7	M8.3	41°45'41",78°44'11",460	11	0	1.1
Y6.2	39°50'32",76°21'16",150	16	0.375	12.6	M8.4	41°45'41",78°44'11",460	8	0.125	5.0
Y7.1	39°50'29",76°21'08",60	12	0.417	13.9	M9.1	41°39'44",78°55'13",560	8	0	1.1
Y7.2	39°50'45",76°21'05",60	12	0.375	12.6	M9.2	41°39'20",78°54'50",580	4	0	1.1
M1	41°51'42",78°52'22",650	11	0.455	15	M10	41°39'43",78°53'33",480	6	0.167	6.2
M2.1	41°53'37",78°53'09",440	12	0.25	8.8	M11.1	41°52'08",78°48'33",540	5	0	1.1
M2.2	41°54'10",78°52'29",450	5	0	1.1	M11.2	41°52'09",78°48'35",540	5	0.1	4.2
M3.1	41°53'33",78°53'24",410	4	0.25	8.8	M11.3	41°52'10",78°48'37",540	5	0	1.1
M3.2	41°53'33",78°53'20",410	7	0.143	5.5	M12	41°54'50",78°46'15",630	6	0.167	6.2
M4.1	41°53'59",78°49'33",650	6	0.25	8.8					

Appendix 3

Leaf-margin scores, following procedure in text, and frequencies of occurrence for leaves of species collected in 17 York County transects, $f(\text{York})$, and 28 Allegheny National Forest transects, $f(\text{ANF})$. Species scored as collected in area, resulting in one discrepancy (*Rubus idaeus*). *Rhus typhina* L. was collected at roadside in York County but not in a transect—it is included in the subsample for York County but not in this list.

Species	Margin	$f(\text{York})$	$f(\text{ANF})$	Species	Margin	$f(\text{York})$	$f(\text{ANF})$
<i>Acer negundo</i> L.	0.5	6		<i>Comptonia peregrina</i> (L.)			
<i>Acer pensylvanicum</i> L.	0		6	Coult.	1		1
<i>Acer rubrum</i> L.	0	10	12	<i>Cornus amomum</i> Mill.	1	4	4
<i>Acer saccharinum</i> L.	0	5		<i>Cornus florida</i> L.	1	1	
<i>Acer saccharum</i> Marsh.	0		19	<i>Crataegus</i> sp.	0		1
<i>Acer spicatum</i> Lam.	0		2	<i>Dirca palustris</i> L.	1		1
<i>Alnus serrulata</i> (Ait.) Willd.	0	1		<i>Fagus grandifolia</i> Ehrh.	0	7	24
<i>Amelanchier laevis</i> Wieg.	0	1	1	<i>Fraxinus americana</i> L.	0.5	6	6
<i>Amorpha fruticosa</i> L.	1	2		<i>Hamamelis virginiana</i> L.	0	1	4
<i>Aronia arbutifolia</i> (L.) Ell.	0	1		<i>Hydrangea arborescens</i> L.	0	1	
<i>Asimina triloba</i> (L.) Dunal	1	8		<i>Ilex verticillata</i> (L.) Gray	0	1	
<i>Betula lenta</i> L.	0	6	1	<i>Kalmia latifolia</i> L.	1	4	1
<i>Betula nigra</i> L.	0	2		<i>Lindera benzoin</i> (L.) Blume	1	13	
<i>Carpinus caroliniana</i> (Walt.)	0		17	<i>Liriodendron tulipifera</i> L.	1	15	1
<i>Carya cordiformis</i> (Wang.)				<i>Magnolia acuminata</i> L.	1		6
K. Koch	0	2		<i>Nyssa sylvatica</i> Marsh.	1	1	
<i>Carya glabra</i> (Mill.) Sweet	0	5		<i>Ostrya virginiana</i> (Mill.)			
<i>Carya laciniata</i> (Michx.) Loud	0	2		K. Koch	0		1
<i>Carya ovalis</i> (Wang.) Sarg.	0	2		<i>Parthenocissus quinquefolia</i>			
<i>Carya ovata</i> (Mill.) K. Koch	0	1	1	(L.) Planch	0	1	
<i>Carya tomentosa</i> Nutt.	0	4		<i>Platanus occidentalis</i> L.	0	5	
<i>Castanea dentata</i> (Marsh.)				<i>Populus grandidentata</i> Michx.	0	1	3
Borkh.	0	3		<i>Populus tremuloides</i> Michx.	0		3
<i>Celtis occidentalis</i> L.	0	2		<i>Prunus serotina</i> Ehrh.	0	8	23
<i>Clematis virginiana</i> L.	0		3	<i>Prunus virginiana</i> L.	0		1

Appendix 3. Continued.

Species	Margin	f(York)	f(ANF)	Species	Margin	f(York)	f(ANF)
<i>Quercus alba</i> L.	1	5	1	<i>Salix nigra</i> Marsh.	0	4	1
<i>Quercus coccinea</i> Muenchh.	0	10		<i>Salix sericea</i> Marsh.	0		6
<i>Quercus prinus</i> L.	0	9	1	<i>Salix</i> sp.	0	2	
<i>Quercus rubra</i> L.	0	2	5	<i>Sambucus canadensis</i> L.	0	1	1
<i>Quercus velutina</i> Lam.	0.5	6		<i>Sambucus pubens</i> Michx.	0		1
<i>Rhododendron maximum</i> L.	1		1	<i>Sassafras albidum</i> (Nutt.) Nees	1	11	1
<i>Rhododendron nudiflorum</i> (L.) Torr.	1	1		<i>Smilax rotundifolia</i> L.	1	4	
<i>Rhus typhina</i> L.	0		2	<i>Tilia americana</i> L.	0	1	6
<i>Robinia pseudo-acacia</i> L.	1	4		<i>Ulmus americana</i> L.	0	4	4
<i>Rubus allegheniensis</i> Porter	0	10	5	<i>Ulmus rubra</i> Muhl.	0		2
<i>Rubus idaeus</i> L.	0.5	5		<i>Vaccinium angustifolium</i> Ait.	0		1
<i>Rubus idaeus</i> L.	0		4	<i>Vaccinium corymbosum</i> L.	0.5	1	
<i>Rubus occidentalis</i> L.	0		1	<i>Vaccinium myrtilloides</i> Michx.	1		1
<i>Rubus</i> sp.	0	2		<i>Viburnum acerifolium</i> L.	0	3	
<i>Salix discolor</i> Muhl.	0		2	<i>Viburnum cassinoides</i> L.	1		1
<i>Salix eriocephala</i> Michx.	0		1	<i>Viburnum recognitum</i> Fern.	0	2	1
<i>Salix lucida</i> Muhl.	0		1	<i>Vitis aestivalis</i> Michx.	0	1	
				<i>Vitis vulpina</i> L.	0	7	