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ESTIMATION OF TEMPERATURE AND PRECIPITATION FROM MORPHOLOGICAL CHARACTERS OF DICOTYLEDONOUS LEAVES[1]

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The utility of regression and correspondence models for deducing climate from leaf physiognomy was evaluated by the comparative application of different predictive models to the same three leaf assemblages. Mean annual temperature (MAT), mean annual precipitation (MAP), and growing season precipitation (GSP) were estimated from the morphological characteristics of samples of living leaves from two extant forests and an assemblage of fossil leaves. The extant forests are located near Gainesville, Florida, and in the Florida Keys; the fossils were collected from the Eocene Clarno Nut Beds, Oregon. Simple linear regression (SLR), multiple linear regression (MLR), and canonical correspondence analysis (CCA) were used to estimate temperature and precipitation. The SLR models used only the percentage of species having entire leaf margins as a predictor for MAT and leaf size as a predictor for MAP. The MLR models used from two to six leaf characters as predictors, and the CCA used 31 characters. In comparisons between actual and predicted values for the extant forests, errors in prediction of MAT were 0.6°–5.7°C, and errors in prediction of precipitation were 6–89 cm (=6–66%). At the Gainesville site, seven models underestimated MAT and only one overestimated it, whereas at the Keys site, all eight models overestimated MAT. Precipitation was overestimated by all four models at Gainesville, and by three of them at the Keys. The MAT estimates from the Clarno leaf assemblage ranged from 14.3° to 18.8°C, and the precipitation estimates from 227 to 363 cm for MAP and from 195 to 295 cm for GSP.

Key words: canonical correspondence analysis; leaf morphology; leaf physiognomy; multiple linear regression; paleoclimate; simple linear regression.

The relationship between leaf morphology and climate was first documented by Sinnott and Bailey (1915), and since the publication of their findings leaf characters have been used to estimate temperature and precipitation. Bailey and Sinnott (1915) compared woody dicotyledonous species from four temperature regimes. They found that species that have entire-margined leaves predominate in frigid, subtropical, and tropical environments, whereas leaves with toothed margins are more frequent in temperate regions. Because of their small size, short life cycles, and ability to pass unfavorable periods underground or as seeds, herbs are more adaptable and variable than trees, and as a result the correlations between leaf margin and climate are weaker in herbs than in trees and large shrubs (Bailey and Sinnott, 1916).

Wolfe (1971) presented a comparison of mean annual temperature (MAT) and percentage of species with entire-margined leaves; for 19 modern floras, an increase from 10 to 86% of entire-margined species corresponded to an increase from 4° to 28°C in temperature. Wolfe's (1979) plot of MAT as a function of the percentage of entire-margined species in eastern Asian forests shows a remarkably strong correlation; similar plots presented by Greenwood (1992) for Australia show the same trend but with weaker correlations. Leaf length is also related to MAT; Carpenter et al. (1994) found a high correlation ($r = 0.88$) between MAT and the mean length of leaves collected from Australian leaf litter.

Studies in Australia (Webb, 1968), Ghana (Hall and Swaine, 1981), and worldwide (Dilcher, 1973) show that leaf size decreases with decreasing site rainfall. Givnish (1984) found that, among lowland tropical sites, leaves are narrower in drier environments. Wilf et al. (1998) found a strong ($r^2 = 0.760$) relationship between the logarithm of mean annual precipitation (MAP) and the logarithm of average leaf area. Dolph and Dilcher (1980a, b) found that leaf size also varies with temperature, with larger leaves found at warmer sites.

The relationships among environment and leaf anatomy and morphology can be used to predict climate from an assemblage of extant or fossil leaves. This physiognomic method is based on the similarity in morphology and anatomy of the constituent species in areas with similar climates, even if the floras have very different taxonomic compositions. Bivariate analyses may be used to determine climate measures from single leaf morphological characters. The relationships may be illustrated by

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plots or may be expressed as simple linear regression (SLR) equations. SLR assumes that the relationship between a response and a single predictor is a straight line. This assumption is good for site MAT vs. percentage of woody dicotyledonous species having entire-margined leaves, as can be seen by Wolfe's (1979, fig. 8) plot, which has a coefficient of determination of $r^2 = 0.983$ (Wing and Greenwood, 1993). Other relationships may be linear but much weaker; the plots of site MAP vs. percentage of dicotyledonous species with large leaves given by Wilf et al. (1998, fig. 3), which have coefficients of determination of $r^2 = 0.439$ and $r^2 = 0.554$, are examples.

Multivariate analyses, which simultaneously analyze multiple measurements, might be expected to improve the predictive ability of models. One commonly applied multivariate technique is multiple linear regression (MLR), in which a response is the function of more than one predictor variable. MLR models must be linear in the parameters, but may be linear (first-order) or curvilinear (higher than first-order) with respect to the predictors (Neter et al., 1996). Even though the bivariate relationships between the response and the individual predictors may not be linear, the relationship between the response and two or more (n) predictors taken together may be linear in ($n + 1$)-dimensional space. Thus an assumption of a linear bivariate relationship between response and individual predictors is not necessary to derive a valid multiple linear regression model.

Useful multivariate models may also be developed through ordination methods, which find weighted combinations that maximize the dispersion of the characters included in the ordination. Ordination methods include correspondence analysis (CA), which maximizes dispersion of the characters themselves, and canonical correspondence analysis (CCA), which integrates regression and ordination methods. As used in community ecology, CCA relates species abundances to explanatory variables, with no assumptions of linearity in the data. In CCA, ordination axes, which are linear combinations of the explanatory variables, are extracted from the data so as to maximize the dispersion among the species, with the constraint that the ordination axes must be uncorrelated with each other (i.e., they are orthogonal). Multiple regression can then be used to quantify the relationships between species abundances and scores on the ordination axes (ter Braak, 1986, 1987, 1988, 1995; Herman et al., 1996).

Wolfe (1993, 1995) developed ordination methods to estimate a number of temperature and precipitation variables based on the simultaneous use of multiple leaf characters. His original CLAMP (Climate-Leaf Analysis Multivariate Program) method used CA to predict climate based on 29 foliar characters related to margin, size, apex, base, and shape. Additional leaf characters, such as venation pattern (Dilcher, 1974), stomatal area (Davis and Taylor, 1980), or blade thickness (Roth, 1984), may also be related to environmental variables, but these are not included in Wolfe's database. Herman and Spicer (1996, 1997) used Wolfe's CLAMP database, with an additional two leaf size characters, to estimate paleotemperature and paleoprecipitation for four fossil assemblages using CCA. Kovach and Spicer (1996) also used Wolfe's data to calculate climate by CCA; they found that the method worked well for MAT in the range of 10°–20°C, but that temperatures above and below this range, as well as measures of annual, growing season, and dry season precipitation, could not be accurately estimated. They suggest that the inaccuracies at MAT $< 10°$C may be caused by an interaction of factors that affect leaf physiognomy only at low temperatures and that precipitation might not be in a form immediately available for plant use.

Wing and Greenwood (1993), Gregory (1994), and Gregory and McIntosh (1996) applied regression analysis to Wolfe's data and obtained regression equations that used from two to six characters as predictor variables. Jacobs and Deino (1996) used the equations derived by Wing and Greenwood (1993) to estimate modern climate at two sites in Uganda and paleoclimate at two sites in Kenya. Their estimates of MAT at the modern sites were within 1.1°C of the actual values, but MAP was overestimated by 96% at one site and 148% at the other.

The purpose of this study was to assess the ability of three types of models (SLR, MLR, and CCA) to predict climate and to estimate the paleoclimate of the Eocene Clarno Nut Beds. To do this we applied the relationships between leaf morphological characters and climate measures (temperature and precipitation) to assemblages of leaves from two extant forests in Florida and the extinct Clarno Nut Beds forest of Oregon. Leaf morphology was used to estimate MAT, MAP, and growing season precipitation (GSP) from models developed by other investigators, and to estimate MAT and GSP from regression models derived by us using Wolfe's data for 144 sites (CLAMP 3B database). We have used Wolfe's (1993) criterion for the calculation of GSP, which is the amount of precipitation that falls during those months in which the monthly mean temperature is at least 10°C. In the case of our two Florida sites, MAP is equal to GSP.

MATERIALS AND METHODS

We computed correlation coefficients and their significance levels among leaf morphological characters, MAT, and GSP, using data from Wolfe's CLAMP 3B database. CLAMP 3B is a tabulation of data on 31 leaf characters and ten meteorological parameters from 144 sites located in temperate and tropical America, and Japan. The correlations were run using SAS Release 6.04. Although previous versions of CLAMP included MAP, the latest version does not. This is because winter precipitation at sites with less than a 12-mo growing season is not significant to the plants (J. Wolfe, personal communication).

In order to test the ability of various models to predict temperature and precipitation, two validation sites with 30-year climate records were chosen to provide leaf samples for analysis. One site, ''Dilcher's Florida Woods,'' is a 25-ha woodland located 3 km east of Gainesville, Florida (29.6° N latitude, 82.2° W longitude, 20 m elevation). The MAT, MAP, and GSP of the site are, respectively, 21.0°C, 134 cm, and 134 cm, measured over the period 1951–1980 (NOAA, 1985) at Gainesville Airport. The species from the other site, located in the southern Florida Keys (24.7° N latitude, 81.4° W longitude, <2 m elevation), were collected on No Name Key, Big Pine Key, and Little Torch Key. The MAT, MAP, and GSP of the closest weather station, on Key West (24.5° N, 81.7° W), are, respectively, 25.4°C, 100 cm, and 100 cm, also for the period 1951–1980 (NOAA, 1985). Samples of living leaves, representing both sun and shade conditions, were collected from trees on the sites and preserved in a herbarium press. When a species was represented by more than one tree, the leaves of that species were combined. Only leaves of woody dicots were included in the sample; herbaceous

TABLE 1. Leaf physiognomic characters, abbreviations used in MLR equations (in parentheses), and correlation coefficients of each character with MAT and GSP. Correlation coefficients were computed from Wolfe's 144 sites (CLAMP 3B database) and are significant at the 0.01 level unless marked ns. Percentage of leaf types given for assemblages from the Clarno Nut Beds (74 fossil leaf types), Gainesville (24 extant species), and the southern Florida Keys (30 extant species).

Leaf character (and abbreviaton)		Correlation with		Percentage of leaf types		
		MAT	GSP	Clarno	Gainesville	Keys
Lobing	lobed (lobed)	−0.74	−0.37	5	19	0
Teeth	no teeth (none)	0.93	0.16 ns	45	58	98
	regular	−0.90	−0.10 ns	44	21	1
	close	−0.91	−0.27	29	4	1
	round	−0.40	−0.21 ns	39	23	2
	acute	−0.86	−0.07 ns	16	19	0
	compound	−0.86	−0.21 ns	3	2	0
Size	nano	0.47	−0.29	0	0	0
	lepto I	0.45	−0.34	0	0	1
	lepto II (leptII)	0.32	−0.55	0	3	13
	micro I	0.02 ns	−0.34	1	14	24
	micro II (micrII)	−0.46	0.32	25	31	38
	micro III	−0.41	0.44	23	25	13
	meso I	−0.27	0.39	25	18	6
	meso II (mesoII)	−0.04 ns	0.28	13	6	2
	meso III	0.05 ns	0.29	13	4	2
Apex	emarginate (emarg)	0.76	−0.12 ns	5	0	35
	round	0.62	−0.34	39	33	70
	acute	−0.71	−0.30	42	58	27
	attenuate (atten)	−0.29 ns	0.61	19	10	3
Base	cordate (Bcord)	−0.68	−0.35	13	13	9
	round (Brnd)	−0.16 ns	−0.02 ns	35	4	23
	acute (Bacut)	0.65	0.29	52	83	68
L:W ratio	<1:1 (<1:1)	−0.77	−0.38	2	6	3
	1–2:1 (1–2:1)	−0.41	−0.57	34	28	43
	2–3:1 (2–3:1)	0.50	0.68	46	51	44
	3–4:1 (3–4:1)	0.50	0.42	14	13	12
	>4:1	0.39	−0.19 ns	3	1	1
Shape	obovate	0.60	−0.33	17	33	38
	elliptic	−0.20 ns	0.67	66	53	57
	ovate	−0.36	−0.53	17	14	5

species were excluded because their leaves do not fall off and contribute to leaf litter (Gregory, 1994) and because the correlations between their leaf characters and climate are weak (Bailey and Sinnott, 1916). Whether or not a species contributes to the leaf litter is important in paleoclimate determination by foliar physiognomy because litter is most likely the source of fossil leaves. The leaf assemblages, which contained 24 species for the Gainesville site and 30 species for the Florida Keys site, were used to compare the results of various methods of climate estimation to actual climate.

The climate models used to compare predicted with actual MAT, MAP, and GSP at the validation sites were also used to determine paleoclimate at a fossil site. This site, the Nut Beds of the middle Eocene Clarno Formation, is known for its well-preserved silicified fruits, seeds, leaves, and wood (Scott, 1954; Scott and Wheeler, 1982; Manchester, 1994) and is located 3 km east of Clarno, Oregon, at 44.9° N latitude, 120.4° W longitude and ~550 m elevation. An assemblage collected by S. R. Manchester of >500 fossil leaf specimens, representing 74 distinct leaf types, was used to estimate paleoclimate. The leaf assemblage from the Clarno Nut Beds has not been fully described (Manchester, 1981), but is available for study at the Florida Museum of Natural History. The Nut Beds site is ~44 million years old, based on fission-track (43.6 and 43.7 ± 10%; Vance, 1988) and Ar/Ar (43.76 ± 0.29; Turrin, in Manchester, 1994, p. 13) dating of pumice fragments collected from the fossil-bearing tuff.

The leaves in the living and fossil assemblages were examined for the presence or absence of each of 31 morphological characters, described by Wolfe (1993) and Herman et al. (1996), and listed in Table 1. The character ''no teeth'' is the same as ''margin entire'' of Bailey and Sinnott (1916) except that spinose leaves are included in the ''no teeth'' category. The percentage occurrences of the characters, shown in Table 1 for each of the assemblages, were used to calculate climate using SLR, MLR, and CCA models developed by other researchers and using MLR models derived by us using Wolfe's CLAMP 3B database. The SLR models used absence of teeth on leaf margins as the predictor variable for MAT and the presence of large leaves as the predictor variable for MAP. The models were derived from plots of MAT vs. percentage entire-margined species published by Wolfe (1979, fig. 8) for species of eastern Asia, Greenwood (1992, fig. 12) for species of Australia, and Wilf (1997, fig. 1) for species of temperate and tropical America, and from the plot of MAP vs. percentage large-leaved species published by Wilf et al. (1998, fig. 3) based on Wolfe's CLAMP database. Converting the plots into linear equations gives

$\text{MAT} = 1.14 + 0.306 \times (\%\ \text{entire})$ (Wolfe, 1979; Wing and Greenwood, 1993)
$\text{MAT} = 4.4 + 0.22 \times (\%\ \text{entire})$ (Greenwood, 1992)
$\text{MAT} = 2.24 + 0.286 \times (\%\ \text{entire})$ (Wilf, 1997)
$\text{MAP} = 47.5 + 6.18 \times (\%\ \text{large leaves})$ (Wilf et al., 1998)

In these equations, (% entire) is the percentage of leaves in an assemblage that have entire (untoothed) margins, and (% large leaves) is the percentage of leaves in an assemblage that are size mesophyll I or larger (i.e., area $\geq$33 cm^2)

We also calculated climate from the MLR equations published by Wing and Greenwood (1993), Gregory (1994), and Gregory and McIntosh (1996), which are based on Wolfe's data or subsets of Wolfe's data. They used angular transformations in their regression analyses of leaf characters to estimate climate variables.

In order to reduce multicollinearity, Wing and Greenwood (1993)

TABLE 2. MAT, MAP, and GSP for Clarno Nut Beds, Gainesville, and the southern Florida Keys, calculated from simple linear regression (SLR), multiple linear regression (MLR), and canonical correspondence analysis (CCA) models.

		Site						
		Clarno			Gainesville		Keys	
Model	Source	MAT (°C)	MAP (cm)	GSP (cm)	MAT (°C)	MAP = GSP (cm)	MAT (°C)	MAP = GSP (cm)
SLR	Wolfe (1979)	14.9	—	—	18.9	—	31.1	—
	Greenwood (1992)	14.3	—	—	17.2	—	26.0	—
	Wilf (1997)	15.1	—	—	18.8	—	30.3	—
	Wilf et al. (1998)	—	363	—	—	221	—	109
MLR	Wing and Greenwood (1993)	14.7	227	—	15.4	159	27.7	94
	Gregory (1994)	18.8	—	—	16.1	—	30.0	—
	Gregory and McIntosh (1996)	17.9	—	—	21.8	—	30.6	—
	Wiemann et al. (this paper)	16.8	—	195	20.4	172	28.2	112
CCA	Wolfe; Herman et al. (1996)	17.0	—	295	18.9	223	28.7	146
Actual	NOAA (1985)	—	—	—	21.0	134	25.4	100

eliminated some of the potential regressors, selecting from the characters in Table 1 one character from each leaf form category that had low correlation with the other characters and reasonably high correlation with the climate variable of interest. They used only 74 sites, eliminating those with very low (less than −2.0°C) cold-month mean temperatures. Their multiple regression models for MAT and MAP are as follows.

$$\mathrm{MAT} = 2.536 + 17.372(\mathrm{none}) + 2.896(\mathrm{emarg}) - 8.592(<1{:}1) \qquad r^2 = 0.863$$

$$\mathrm{MAP} = 11.489 + 167.948(\mathrm{atten}) + 377.735(\mathrm{mesoII}) \qquad r^2 = 0.497$$

Gregory (1994) used 29 of the 31 characters listed in Table 1; she deleted the characters ‘‘teeth regular’’ and ‘‘teeth close’’ because of their high collinearity with ‘‘no teeth.’’ She used 84 of the 86 sites that were included in Wolfe's database at that time, eliminating the two coldest sites because of their anomalous residuals. Her stepwise regression included quadratic functions of the character frequencies. Her leaf size leptophyll III corresponds to leptophyll II as defined by Herman et al. (1996) (K. Gregory, Lamont-Doherty Earth Observatory of Columbia University, personal communication). We use leptophyll II in this paper, and have made the substitution in her equation, given below.

$$\mathrm{MAT} = 15.32 + 10.34(\mathrm{none})^2 + 5.48(\mathrm{emarg}) - 15.32(<1{:}1)^2 - 15.29(\mathrm{leptII}) - 5.79(\mathrm{micrII}) \qquad r^2 = 0.938$$

Gregory and McIntosh (1996) used the same 29 characters to derive models that did not use quadratic functions. They derived two MLR models, one based on all 106 sites included in Wolfe's CLAMP database at that time and another based on only the sites with a cold month mean temperature of at least −2°C. We have used the model based on the larger database for two reasons: we have already chosen one model derived from the reduced database, the Wing and Greenwood (1993) model discussed above, and we wanted to examine models that were as inclusive as possible so that if a flora comes from a cold site it can be legitimately evaluated. The Gregory and McIntosh (1996) model for MAT, based on all 106 sites, follows.

$$\mathrm{MAT} = -11.262 + 10.282(\mathrm{lobed}) + 23.258(\mathrm{none}) - 12.211(\mathrm{leptII}) + 7.022(\mathrm{Bacut}) - 16.099(<1{:}1) + 11.484(1\text{–}2{:}1) \qquad r^2 = 0.893$$

For the models derived by Wing and Greenwood (1993) and Gregory (1994), the quantities indicated in parentheses represent the arcsines (in radians) of the square roots of the proportions of leaves in the assemblage having the indicated characters, which are summarized in Table 1. For the model derived by Gregory and McIntosh (1996), 0.005 was added to each proportion before taking the arcsine of the square root.

In addition to the models developed by other researchers, we used Wolfe's CLAMP 3B data to develop our own multiple linear regression models using the STEPWISE function in SAS Release 6.04. The untransformed data from all 144 sites and 31 morphological characters were used to derive MLR models for MAT and GSP at significance levels of $\alpha = 0.001$ for the F statistics.

The CCA model used the CANOCO Version 3.12 program developed by C. J. F. ter Braak and available from Microcomputer Power; we used Wolfe's data from 144 sites (CLAMP 3B) to establish the ordinations. The method for doing this using leaf physiognomic data is described by Herman et al. (1996). The leaf character percentages for the Gainesville, Florida Keys, and Clarno assemblages were entered as passive samples (i.e., without climate data). The Axis 1 and 2 scores from the CANOCO output were used to calculate MAT, and the Axis 2 and 5 scores were used to calculate GSP, from power functions furnished by J. Wolfe.

RESULTS

Examination of the correlation coefficients between the climate variables and the leaf characters (Table 1) shows that leaf morphology has a stronger relationship with temperature than with precipitation. Whereas nine of the characters have correlation coefficients >0.7 with MAT, none of the correlation coefficients with GSP are this high. The five characters most highly correlated with MAT all relate to leaf margin. In contrast, leaf margin characters correlate poorly with GSP. The leaf characters most strongly correlated with GSP include L:W ratio, leaf shape, presence of an attenuate apex, and leaf size.

The STEPWISE procedure, using the untransformed data from CLAMP 3B, gave the following MLR models.

$$\mathrm{MAT} = 9.865 + 0.207(\mathrm{none}) - 0.058(\mathrm{Brnd}) - 0.202(<1{:}1) \qquad r^2 = 0.898$$

$$\mathrm{GSP} = 31.6 - 3.393(\mathrm{leptII}) + 2.400(\mathrm{atten}) - 2.671(\mathrm{Bcord}) + 2.360(2\text{–}3{:}1) + 3.122(3\text{–}4{:}1) \qquad r^2 = 0.796$$

The quantities indicated in parentheses represent the percentages of leaves in an assemblage having the characters summarized in Table 1.

The character most strongly correlated with MAT, leaf margin with no teeth, is less abundant in the fossil assemblage than in the extant assemblages (Table 1), suggesting that Eocene Clarno was cooler than present-day Florida. Using this character alone, estimation of MAT by SLR gave values ranging from 14.3° to 15.1°C for Clarno, compared with values ranging from 17.2° to 18.9°C for Gainesville (actual = 21.0°C) and from 26.0° to 31.1°C for the Keys (actual = 25.4°C) (Table 2).

The leaves in the fossil assemblage are larger than those in the extant assemblages: 51% of them are in the mesophyll categories, whereas only 28% of the species in the Gainesville assemblage and 10% in the Keys assemblage have leaves this large (Table 1). This suggests that Clarno was probably wetter than present-day Florida. Another character that is significantly correlated with precipitation, leaf apex attenuate ($r^2 = 0.37$), is more abundant in the fossil assemblage, also indicating that Clarno was wetter than Florida. Estimation of MAP by the single character ''large leaves,'' using the model of Wilf et al. (1998), gave a value of 363 cm for Clarno, 221 cm for Gainesville (actual = 134 cm), and 109 cm for the Keys (actual = 100 cm) (Table 2).

Use of several characters and MLR gave MAT estimates of 14.7°–18.8°C for Clarno, 15.4°–21.8°C for Gainesville, and 27.7°–30.6°C for the Keys. The estimates obtained using all 31 characters and CCA are 17.0°C for Clarno, 18.9°C for Gainesville, and 28.7°C for the Keys (Table 2).

For Clarno, MAP was estimated as 227 cm using Wing and Greenwood's (1993) MLR equation, whereas GSP was estimated as 195 cm using our MLR equation and 295 cm using CCA. For Gainesville, the corresponding values are 159, 172, and 223 cm, respectively, and for the Keys they are 94, 112, and 146 cm, respectively (Table 2).

The SLR, CCA, and three of the four MLR models underestimated MAT at Gainesville—the SLR models by 2.1°–3.8°C, the CCA model by 2.1°C, and the MLR models by 0.6°–4.9°C; the other MLR model overestimated it by 0.8°C. The opposite trend was found for the Keys, where MAT was overestimated by every model; the SLR models by 0.6°–5.7°C, the CCA model by 3.3°C, and the MLR models by 2.3°–5.2°C. All four precipitation models overestimated MAP in Gainesville (by 19–66%). Three of them overestimated it in the Keys (by 9–46%), and one of them underestimated it, but by only 6%.

DISCUSSION

Because MAT was underestimated by seven of the eight models at Gainesville and overestimated by all eight models in the Keys, the errors in estimation are probably due, at least in part, to characteristics of the floras. Examination of the estimates of precipitation show that it was overestimated by all four models at Gainesville and by three of the four models in the Keys. Only one model underestimated precipitation, and that error was only 6%. Thus, the errors in estimation of precipitation may be due to characteristics of the floras, or it may be that the models are biased. In their investigation of the usefulness of CCA for paleoclimate determination, Kovach and Spicer (1996) found that precipitation variables were skewed, and they used logarithmic transformations to compensate. Wilf et al. (1998) showed an approximately linear relationship between the logarithm of leaf area and the logarithm of MAP. Therefore, more valid models might be obtainable by using logarithmic functions for precipitation models.

The estimates of MAT at Clarno ranged from 14.3° to 18.8°C, a difference of 4.5°C among models. The models were derived from data based on measurements of leaves sampled directly from living plants (Wolfe, 1993), which may not accurately represent leaf litter or, consequently, fossil leaves. The composition of assemblages of fossil leaves is also affected by the processes of transport, degradation, and burial, and these may introduce additional biases. Therefore, the use of these models to deduce paleoclimate may be in error at least in part due to differences in the characteristics of fossil and living leaves. Greenwood (1992) found that litter is dominated by leaves from the canopy trees, and that leaves were smaller in the litter than in the canopy. Roth and Dilcher (1978) found that leaves deposited in an Indiana lake bottom were smaller than leaves from the surrounding forest and that fewer entire-margined species were recovered from the lake. Untransported, undecayed leaf litter reflects the forest tree composition in temperate forests (Burnham, 1993; Burnham, Wing, and Parker, 1992), but not in subtropical and tropical forests, probably due to the high species richness of these forests (Burnham 1989, 1993, 1994). Burnham (1997) used the Wing and Greenwood (1993) MLR model to calculate MAT of Santa Rosa National Park in Costa Rica based on leaf litter collections. She found that it underestimated MAT by more than 7°C; however, the same model also gave an estimate of MAT for Clarno that was 2.1°–4.1°C cooler than those obtained by the other multivariate models (Table 2), indicating that the low estimates may be due at least in part to bias in the model. Greenwood and Wing (1995) state that calculation of paleoclimate using their MLR approach yields MAT estimates 2°–3°C cooler than estimates based on leaf margins or nearest living relatives because it is sensitive to the low proportions of species in Eocene floras with emarginate apices, and because of deciduousness induced by light rather than temperature seasonality. In deciduous forests, leaves with L:W = 1:1 predominate, whereas in evergreen forest the predominant ratio is L:W > 3:1 (Greenwood and Basinger, 1994). However, for the Clarno assemblage, the result from using Wing and Greenwood's (1993) model (MAT = 14.7°C), which was based on leaf margin, apex, and length-to-width ratio, was not much different from the SLR results (MAT = 14.3°–15.1°C) (Table 2), which are based only on leaf margin; furthermore, Gregory's (1994) model, which also included emarginate apex and length-to-width ratio, gave the highest estimate of any model (MAT = 18.8°C).

It is not clear which, if any, of the models shown in Table 2 give more accurate climate determinations. The only model to estimate MAT to within 3°C at both validation sites was the MLR model that we derived based on untransformed leaf physiognomy data. Our precipitation model also gave reasonably close estimates (within 30%) of GSP at the two sites. However, because both sites were in Florida, possible biases in the models might not have been evident; validation sites that are considerably colder and wetter need to be sampled.

At the two validation sites, SLR seemed to be as good at predicting MAT as some of the multivariate models, although the errors exceeded 3°C in at least one site for each SLR model. Wilf (1997) calculated MAT at tropical and temperate sites using SLR and MLR and also found that SLR was at least as precise as MLR; he maintains that using additional characters beyond leaf margin con-

TABLE 3. Number of leaf characters in MAT model and range in errors in predicted MAT at the two validation sites (absolute values) for each model.

Model	Source	Number of characters	Range in errors (°C)
SLR	Wolfe (1979)	1	2.1°–5.7°
	Greenwood (1992)	1	0.6°–3.8°
	Wilf (1997)	1	2.2°–4.9°
MLR	Wing and Greenwood (1993)	3	2.3°–5.6°
	Wiemann et al. (this paper)	3	0.6°–2.8°
	Gregory (1994)	5	4.6°–4.9°
	Gregory and McIntosh (1996)	6	0.8°–5.2°
CCA	Wolfe; Herman et al. (1996)	31	2.1°–3.3°

tributes little information and may increase error because scoring procedures for many of the characters are subjective, making it difficult to score them reliably. Although we concur with his contention that difficult-to-score characters may increase error and have experienced the same scoring problems that he described in determining the presence or absence of an acute base (Wilf, 1997, p. 379), we are inclined to agree with Wolfe (1995) that multiple characters might provide more information than a single character alone, especially considering the interactions between temperature and precipitation. Furthermore, use of additional characters might act as a ‘‘buffer’’ to reduce the effect of an anomalously high or low frequency of a single character in an assemblage of leaves. A comparison of the number of characters used in the models with the accuracy of prediction of MAT is illustrative of this point. As can be seen in Table 3, the largest error (5.7°C) was found in a model that used only one character. In contrast, the model that used all 31 characters had a maximum error of only 3.3°C, even though many of the characters may have poor correlation with MAT.

Angular transformations and use of quadratic functions did not improve the ability of a model to predict climate at the Florida sites. The best overall models were our MLR, which predicted MAT within 2.8°C, and CCA, which predicted MAT within 3.3°C (Table 3); neither of these used a transformation or power function of the raw data. The unjustified use of power functions may be especially serious. If the relationships between MAT and the frequencies of occurrence of leaf characters are in fact approximately linear, then relatively small biases in the floras can result in relatively large errors in estimation due to the effects of exponentiation. Fitting a curve to data can result in a high coefficient of determination even if the true fit is a straight line, but the resulting model will not represent the phenomenon well and its application to new data may give large errors. An example is Gregory’s (1994) model, which uses quadratic functions and has a coefficient of determination of 0.938, but which underestimated MAT by 4.9°C at the Gainesville site and overestimated it by 4.6°C at the Keys site.

Including too many independent variables in a model can have the same effect as fitting a curve when the actual phenomenon is linear. Inclusion of variables that do not belong decreases a model’s descriptive abilities and increases the problem of roundoff errors; on the other hand, omitting important variables can lead to serious bias (Neter et al., 1996). Keeping in mind the difficulty of accurately and consistently evaluating leaf base shape (Wilf, 1997), the contribution of the character ‘‘base round’’ to our MLR model for MAT should be examined to rule out the possibility that its inclusion is just an artifact of the data and the STEPWISE procedure, particularly because its correlation with MAT is non-significant. The other two characters in this model, ‘‘leaf with no teeth’’ and ‘‘length less than width,’’ in contrast, can be rigorously defined and easy to evaluate, and they have high correlations with MAT. Our MLR model for GSP includes two characters that measure leaf shape: ‘‘length 2–3 times greater than width’’ and ‘‘length 3–4 times greater than width.’’ Their highly significant correlation coefficient is +0.49, and it would seem that one or the other of them might profitably be eliminated from the analysis.

CONCLUSIONS

1) Some of the leaf morphological characters are difficult to score reliably, and more accurate models might be developed if these characters are not used.

2) Some characters are unimportant in climate prediction, and others duplicate information. These might profitably be deleted to simplify scoring and to reduce ‘‘noise.’’

3) Multiple character models as they are presently formulated may not be any better than single character models.

4) Angular transformations of character data do not seem to improve models.

5) The precipitation models gave biased estimates; a logarithmic transformation of precipitation data may be appropriate to derive improved models.

6) Leaf size is one of the most important predictors of precipitation. It may, however, be worth exploring measurements of size that are not based on categories, since the ones presently defined for the CLAMP databases may not be optimum for climate determination, and it is often difficult to decide which category a leaf falls into, especially if it has a shape that does not correspond to one of the template choices. On the other hand, an advantage of using size categories determined by use of a template is ease of use, especially for the measurement of fossils.

RECOMMENDATIONS FOR FUTURE MODEL DERIVATION AND TESTING

1) Have several individuals score the same assemblages of leaves to determine which leaf characters can be evaluated consistently, and eliminate those that cannot.

2) Compare the correlation coefficients among leaf characters to determine which ones may be superfluous due to collinearity.

3) Verify whether data manipulation, such as the use of angular or logarithmic transformations, yields models with increased predictive capacity.

4) Use STEPWISE regression procedures at various F levels to compile a list of leaf characters to be used as potential predictor variables.

5) Derive regression and correspondence analysis models based on a more limited number of well-defined, easy-to-evaluate leaf characters.

6) Test models using validation sites from a wide range of climates to determine which models give the best predictions and to evaluate the precision of leaf physiognomy as a climate estimator.

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