Correlations of climate and plant ecology to leaf size and shape: potential proxies for the fossil record[1]

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The sizes and shapes (physiognomy) of fossil leaves are widely applied as proxies for paleoclimatic and paleoecological variables. However, significant improvements to leaf-margin analysis, used for nearly a century to reconstruct mean annual temperature (MAT), have been elusive; also, relationships between physiognomy and many leaf ecological variables have not been quantified. Using the recently developed technique of digital leaf physiognomy, correlations of leaf physiognomy to MAT, leaf mass per area, and nitrogen content are quantified for a set of test sites from North and Central America. Many physiognomic variables correlate significantly with MAT, indicating a coordinated, convergent evolutionary response of fewer teeth, smaller tooth area, and lower degree of blade dissection in warmer environments. In addition, tooth area correlates negatively with leaf mass per area and positively with nitrogen content. Multiple linear regressions based on a subset of variables produce more accurate MAT estimates than leaf-margin analysis (standard errors of ±2 vs. ±3°C); improvements are greatest at sites with shallow water tables that are analogous to many fossil sites. The multivariate regressions remain robust even when based on one leaf per species, and the model most applicable to fossils shows no more signal degradation from leaf fragmentation than leaf-margin analysis.

Key words: climate proxies; leaf economics; leaf mass per area; leaf physiognomy; paleobotany; paleoclimate; paleoecology; paleotemperature.

Paleontologists have long used the environmental sensitivity of plants to reconstruct paleoclimate from fossilized plant remains (Seward, 1892; see Parrish, 1998 for summaries). In particular, the size and shape (physiognomy) of leaves have been widely used as proxies for temperature and moisture variables (e.g., Bailey and Sinnott, 1915; Dilcher, 1973; Wolfe and Upchurch, 1987; Parrish and Spicer, 1988; Greenwood and Wing, 1995; Wolfe, 1995; Wing et al., 2000; Wilf et al., 2003). Leaf-margin analysis, the oldest and most reliable physiognomic technique, is based on the observation in present-day forests that the percentage of woody dicotyledonous species in a flora whose leaf margins are untoothed (here termed "margin percentage") correlates significantly with mean annual temperature (MAT) (Bailey and Sinnott, 1915, 1916; Wolfe, 1979; Wilf, 1997). Because leaf physiognomy reflects convergent responses to climate in different lineages (Wolfe, 1993; Greenwood et al., 2004), leaf-margin analysis can be used even when precise systematic placement of fossil leaf species is not possible (Spicer and Parrish, 1986; Wolfe and Upchurch, 1987; Parrish et al., 1998). The technique continues to be important in recent literature (e.g., Utescher et al., 2000; Wing et al., 2000; Wilf et al., 2003).

Despite its wide use, leaf-margin analysis is based on only one character state, the presence or absence of teeth. If leaf size and shape were more fully described, significant improvements should be possible. To this end, Wolfe (1993, 1995) developed a method involving 31 leaf character states, including margin percentage, called the Climate-Leaf Analysis Multivariate Program (CLAMP). This approach uses ordination techniques, such as canonical correspondence analysis, to correlate leaf character states with temperature and moisture variables. In theory, because leaf physiognomy is described more fully by CLAMP, more accurate predictions of MAT should result. However, in practice CLAMP, for considerably more effort, generally yields MAT predictions that are no more accurate than leaf-margin analysis (Jacobs and Deino, 1996; Wilf, 1997; Wiemann et al., 1998; Gregory-Wodzicki, 2000; Kowalski and Dilcher, 2001). This is because, at least in part, some of the CLAMP character states are not defined with sufficient precision, leading to variable scoring of the same leaves by different investigators (Wilf, 1997; Wiemann et al., 1998; Wilf et al., 1999).

In an attempt to improve upon leaf-margin analysis without the scoring imprecision of CLAMP, a new procedure for quantifying leaf physiognomy primarily based on computerized image analysis was introduced in a preliminary paper (Huff et al., 2003). This technique, known as digital leaf physiognomy, offers two important advantages over leaf-margin analysis and CLAMP. First, subjectivity and irreproducibility in the data collection process are largely removed because fixed algorithms process most of the measurements. Second, digital leaf physiognomy uses continuous variables, such as number of teeth and tooth area, in contrast to the discrete, usually binary character states native to leaf-margin analysis and CLAMP (Huff et al., 2003).

TABLE 1. Definitions of physiognomic and climatic variables used in study.

Variables	Definition (units)
Physiognomic variable, abbreviation	
Margin percentage, Margin	Percentage of untoothed species in a flora
Blade area, BladeArea	Area of leaf blade (cm^2)
Perimeter, Peri	Blade perimeter (cm)
Internal Perimeter, IntPeri	Perimeter after teeth are removed (cm)
Perimeter ratio, PeriRatio	Perimeter/internal perimeter (dimensionless)
Compactness, Comp	Perimeter^2/blade area (dimensionless)
Shape factor, ShapFact	$4\pi \times$ blade area/perimeter^2 (dimensionless)
Major axis length, MajLen	Longest measurable line across leaf blade (cm)
Minor axis length, MinLen	Longest measurable line perpendicular to the major axis (cm)
Feret diameter, FerDiam	Diameter of circle with same area as leaf (cm)
Feret diameter ratio, FerDiamRatio	Feret diameter/major axis length (dimensionless)
Tooth area, TA	Area of teeth (cm^2)
Tooth area : blade area, TABA	(dimensionless)
Tooth area : perimeter, TA : Peri	(cm)
Tooth area : internal perimeter, TA : IntPeri	(cm)
Number of primary teeth, 1° teeth	(count)
Number of secondary teeth, 2° teeth	(count)
Number of teeth, #Teeth	Number of primary and secondary teeth
Average tooth area, AvgTA	Tooth area/number of primary teeth (cm^2)
Number of teeth : perimeter, #Teeth : Peri	(cm^{-1})
Number of teeth : internal perimeter, #Teeth : IntPeri	(cm^{-1})
Climate variable, abbreviation	
Mean annual temperature, MAT	Average monthly temperature, Jan–Dec (°C)
Coldest month mean temperature, CMMT	Average daily temperature of the coldest month (°C)
Warmest month mean temperature, WMMT	Average daily temperature of the warmest month (°C)
Growing season length, GSL	Maximum number of consecutive frost-free days in a year (d)
Growing degree days, GDD	Mean daily temperature $-$ 10°C, summed over all days for a year when mean daily temperature exceeds 10°C base (°C)
Growing season degree days, GSDD	Growing degree days during the growing season (°C)
Mean annual precipitation, MAP	Sum of precipitation, Jan–Dec (cm)
Growing season precipitation, GSP	Sum of precipitation during the growing season (cm)

Huff et al. (2003) investigated two temperate floras and one humid tropical flora. Significant differences were apparent between the tropical and temperate sites for several character states, including the ratio of tooth area to blade area, shape factor (a modified area to perimeter ratio; see Table 1 for definition), and tooth count (which does not require computerized measurement), suggesting that the paleoclimatic potential of their new approach should be tested further. Because only three sites were investigated, Huff et al. did not quantify correlations among sites between physiognomy and climate.

In addition to paleoclimatic applications, fossil leaf morphology is also used as a paleoecological proxy. For example, based on analogies with living plants (Givnish, 1979; Richards, 1996; Wright and Westoby, 2002), thick fossil leaves, in combination with other characters, are associated with long leaf lifespan (e.g., Wilf et al., 2001). Also, a high frequency of drip tips in fossil floras has been used as evidence for tropical rainforest vegetation (e.g., Spicer, 1989; Johnson and Ellis, 2002). However, these ecological proxies are difficult to quantify accurately in fossils.

In living floras, there is growing recognition that leaf ecological traits such as lifespan, mass per area, and nitrogen content correlate with one another worldwide (Field and Mooney, 1986; Reich, 1992; Reich et al., 1992, 1997, 1999; Wright et al., 2004); like the leaf-climate correlations, these do not appear to be strongly influenced by phylogeny (Ackerly and Reich, 1999). Leaves with long lifespans tend to have a high mass per area, low nitrogen and phosphorus content, and low photosynthetic and dark respiration rate (e.g., Wright et al.,

2004). Insect herbivory also appears to be related to this trait array: feeding is more intense on leaves with short lifespans and high nitrogen contents, which are generally associated with low concentrations of qualitative defensive compounds and low leaf toughness (Coley, 1983, 1988; Coley et al., 1985; Lowman, 1992; Basset, 1994). The convergent relationships among these leaf ecological variables form what has been termed a "leaf economics spectrum" (Wright et al., 2004), running from "quick" to "slow" returns on nutrient investments.

An improved understanding of leaf economics in the geologic past would add an important dimension for interpreting ancient terrestrial ecosystems by comparison to modern analogs (Falcon-Lang, 2000; Wilf et al., 2001). However, proxies are lacking for leaf economic variables that cannot be directly measured in fossils, such as mass per area and nitrogen content. Leaf physiognomy represents a potential proxy for leaf economics because many of the selective filters that determine leaf economic traits, namely the optimization of carbon, water, and mineral nutrient fluxes (e.g., Wright et al., 2004), also influence leaf physiognomy (Webb, 1968; Vogel, 1970; Lewis, 1972; Parkhurst and Loucks, 1972; Givnish, 1979; Richards, 1996).

Here, we test the potential of digital leaf physiognomy as a proxy for climate and leaf economics at a statistically significant number of localities by expanding the Huff et al. (2003) pilot study from three to 17 sites. The primary objectives are to (1) develop regression models for predicting MAT using variables derived from digital leaf physiognomy, (2) investi-
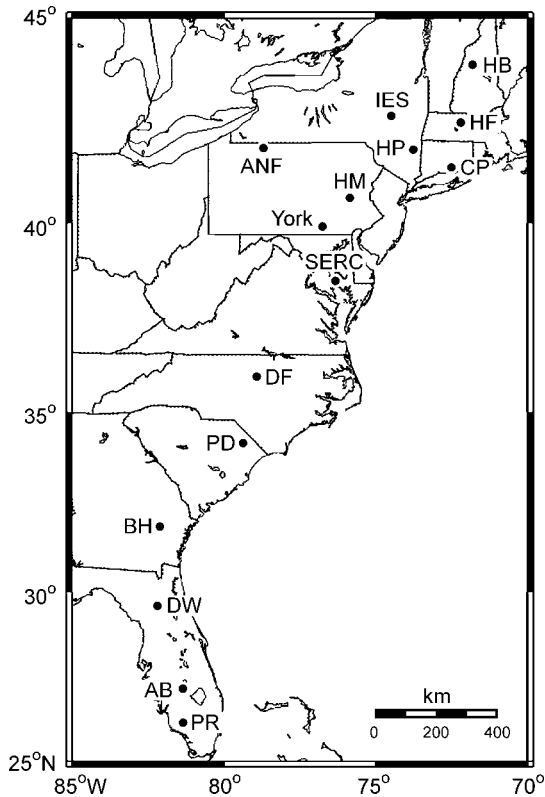
Fig. 1. Locations of floral sites used in study. One site, Barro Colorado Island (9°10′ N, 79°51′ W), is not shown. See Table 2 for further details of sites, including definitions of site abbreviations.

gate preliminary correlations between leaf physiognomy and leaf economics, and (3) assess the potential of these correlations as paleoclimatic and paleoecological proxies to be used on fossil floras. This assessment includes testing how many leaves per species and species per site are required to achieve reliable predictions, as well as evaluating the physiognomic variables that show the most potential for application to fragmentary fossil leaves. Finally, because both the climatic and ecological proxies are based on correlations with leaf physiognomy, we test their statistical independence.

MATERIALS AND METHODS

Seventeen living floras were sampled, resulting in 572 species-site pairs and 1423 photographed leaves (Fig. 1; Table 2). The sampled floras were derived from two sources, the first being 14 sites from eastern North America (Fig. 1). The MAT of these sites ranges from 5.6–25.8°C (Table 2). Between 15 and 31 native species of dicotyledonous trees and shrubs were sampled from each site by E. A. K. and D. L. D. between September and December of 1998, 2000, and 2001. Fifteen to 50 representative leaves per species were collected, pressed, and dried; the vouchers are housed at the Florida Museum of Natural History (see Kowalski and Dilcher, 2003 for details). A subsample of 3–6 leaves (or leaflets, in the case of compound leaves) from each species per site with completely or nearly completely intact margins was photographed digitally at 2048 × 1536 pixels resolution (Nikon Coolpix 995 camera, Nikon, Melville, New York, USA).

The second group of sampled floras was derived from the three sites presented in Huff et al. (2003) (italicized in Table 2), for which one digital image per species was available. Repository information is given in Huff et al. (2003). Two of the sites, Allegheny National Forest and York County, Pennsylvania, were derived from field transects as detailed in Wilf (1997) (see Fig.

1). Leaves from the third site, on Barro Colorado Island, Republic of Panama, were collected from a one hectare plot by R. Burnham (University of Michigan) and S. Wing (National Museum of Natural History, Smithsonian Institution), as described in Wilf (1997).

The digitized leaves were manipulated using Adobe Photoshop 8.0 (Adobe Systems, San Jose, California, USA) as described in Huff et al. (2003) and outlined here briefly. First, damaged margins were restored and shadows removed. The petiole was then removed so that it would not interfere with the subsequent measurements. Next, leaf teeth were selected; because no computer algorithm can reliably detect leaf teeth at the required resolution, teeth were selected manually before being measured by a computer. Tooth selection follows the protocols of Huff et al. (2003), except in a few cases when the protocols were found to be imprecise. New rules were developed to increase the reproducibility of tooth selection and are summarized in Appendix S1 (see Supplemental Data accompanying the online version of this article). Due to the minor revisions in tooth selection methods, all of the images from the Huff et al. (2003) study were reanalyzed. All leaf images studied here are available at servers linked from P. W.'s web site (www.geosc.psu.edu/~pwilf) or can be requested from D. L. R. or P. W. Authorities for binomial nomenclature are given by Croat (1978) for Barro Colorado Island and by USDA (2004) for all other sites.

For each photographed leaf, separate images were prepared of the petiole, leaf blade, leaf teeth, and leaf blade minus the leaf teeth. Image sizes were calibrated using the photographed scale. Image detection algorithms native to Sigma Scan Pro 5.0 (SPSS Science, Chicago, Illinois, USA) were then used to calculate the following variables: blade area, perimeter, internal perimeter, feret diameter, compactness, shape factor, major axis length, minor axis length, and tooth area (see Table 1 for definitions). These are the same variables measured by Huff et al. (2003) except for internal perimeter, which is new here. The number of teeth was determined visually. All other physiognomic variables (Table 1) were derived from these primary data.

Species means for each physiognomic variable were calculated based on the 1–6 images captured per species. Site means were then derived from the species means. For variables involving teeth, untoothed species were removed to retain normal distributions of data (Huff et al., 2003). Site medians, minima, maxima, means with the 5% tails removed (±2 SD), and natural logs of means were also computed.

The resulting physiognomic data were correlated with climate variables (Table 2) using single and multiple linear regression (SPSS 12.0; SPSS Science) and canonical correspondence analysis (Canoco 4.5; Microcomputer Power, Ithaca, New York, USA; see Ter Braak, 1987). Two criteria were used to select multivariate models: all predictor variables were required to be significant at the $\alpha = 0.05$ level and not to show a high degree of collinearity with the other predictor variables (variance inflation factor <10; Sokal and Rohlf, 1995). Correlations with rainfall variables were not pursued because of their limited range at the test sites (Table 2).

Computer code was developed in Mathematica 5.0 (Wolfram Media, Champaign, Illinois, USA) to subsample the physiognomic data randomly many times ($N = 10\,000$ adopted here) at a designated number of leaves per species or of species per site. This program was used to test the sensitivity of MAT predictions to sample size.

All leaf economic data were derived from the eastern North American transect discussed earlier (14 sites; 338 species-site pairs; 1185 leaves). Leaf mass per area was calculated from the dry mass and area of the leaf blade, including the petiole (Cornelissen et al., 2003). Nitrogen content was determined for one leaf per species per site. Approximately 3.5 mg of dry leaf tissue were cored from the leaf center and measured for % nitrogen on a Carlo Erba 1108 elemental analyzer (Thermo Electron, Milan, Italy). The nitrogen content analyses should be considered preliminary because they are based on leaves collected near the end of their growing seasons (September–December), when foliar nutrient concentrations typically decline (Chapin and Kedrowski, 1983; Reich et al., 1992).

RESULTS

Physiognomic correlations with climate—Strong univariate correlations are evident between the site means of many phys-

TABLE 2. Details of field sites. Italicized sites were studied in Huff et al. (2003). Most climate data are from the National Climatic Data Center (downloaded from website cdo.ncdc.noaa.gov/CDO/cdo, March 2004) and are based on hourly or daily summaries from at least 16 yrs (mean = 50 yrs); numbers in parentheses refer to National Weather Service Cooperative Station Network IDs. For those sites with independently operated climate stations, website from which data were downloaded is provided. All climate stations are located within 20 km of the sites (mean = 7.5 km). Climate data vary slightly at some sites compared to Wilf (1997) and Kowalski and Dilcher (2003). Number of species also varies at some sites compared to Kowalski and Dilcher (2003) because only native species with completely or nearly completely intact margins were selected here (see text). Abbreviations of climate variables are defined in Table 1.

Floral site, state or country (site abbreviation)	Species used	MAT (°C)	CMMT (°C)	WMMT (°C)	GSL (d)	GDD (°C)	GSDD (°C)	MAP (cm)	GSP (cm)	Climate station
Hubbard Brook Experimental Forest, New Hampshire (HB)	15	5.6	−9.1	18.9	150	937	889	131	56	Hubbard Brook (hubbardbrook.org)
Allegheny National Forest, Pennsylvania (ANF)	47	7.0	−6.9	19.0	119	1056	873	114	44	Bradford Central Fire Station (360867)
Harvard Forest, Massachusetts (HF)	27	7.2	−7.4	20.2	144	1130	1045	107	45	Harvard Forest (harvardforest fas.harvard edu)
E. N. Huyck Preserve and Biological Research Station, New York (HP)	24	7.6	−7.2	20.6	131	1212	1044	88	39	West Berne (309100)
Institute for Ecosystem Studies, New York (IES)	31	9.5	−4.2	22.0	146	1458	1309	109	48	IES (www.ecostudies.org)
Cockaponset State Forest, Connecticut (CP)	26	10.2	−2.7	22.3	188	1478	1435	121	58	Groton (063207)
Hawk Mountain Sanctuary, Pennsylvania (HM)	24	10.8	−3.1	23.5	177	1717	1632	116	64	Hamburg (363632)
York County, Pennsylvania (York)	56	11.9	−1.7	24.2	167	1933	1740	103	52	York 3 SSW Pumping Station (369933)
Smithsonian Environmental Research Center, Maryland (SERC)	25	12.8	0.1	25.0	214	2037	1976	113	65	SERC (www.serc.si.edu)
Duke Forest, North Carolina (DF)	27	15.2	3.5	26.0	205	2543	2337	111	66	Durham (312515)
Little Pee Dee State Park, South Carolina (PD)	27	16.9	5.6	27.1	223	2930	2669	115	77	Dillon (382386)
Big Hammock Natural Area and Wildlife Management Area, Georgia (BH)	26	19.5	9.4	28.0	270	3622	3355	119	92	Glennville (093754)
Dilcher's Woods lowland, Florida (DWl)	24	20.6	11.7	27.5	286	3942	3627	126	103	Gainesville Regional Airport (083326)
Dilcher's Woods upland, Florida (DWu)	22	20.6	11.7	27.5	286	3942	3627	126	103	Gainesville Regional Airport (083326)
Archbold Biological Station, Florida (AB)	18	22.3	15.2	27.5	300	4538	4082	132	120	Archbold Biological Station (080236)
Florida Panther National Wildlife Refuge, Florida (PR)	18	24.3	18.6	28.5	363	5239	5239	150	150	Pompano Beach (087254)
Barro Colorado Island, Republic of Panama (BCI)	135	25.8	24.7	26.9	365	5810	5810	264	264	Barro Colorado Island (www.stri.org)

iognomic character states and MAT (Fig. 2; see also Appendix; for raw data and correlation matrix of climatic and physiognomic variables, see Appendices S2–3 in Supplemental Data with online version of this article). Most notably, significant relationships exist for number of teeth ($r^2 = 0.79$; $P < 0.001$), perimeter ratio ($r^2 = 0.74$; $P < 0.001$), and shape factor ($r^2 = 0.73$; $P < 0.001$), as well as the traditional variable, margin percentage ($r^2 = 0.80$; $P < 0.001$) (see Table 1 for definitions of variables). Some of these relationships are significant even within individual species (e.g., Fig. 3). Correlations with growing season length, growing degree days, and growing season degree days are comparable to the correlations with MAT: r^2-values for these climate variables vs. physiognomy are within 0.05 units of one another.

Generally, alternatives to site means such as medians, minima, maxima, natural log of means, and means with 5% tails removed do not improve the correlations with MAT (see Ap-

pendix). One exception is tooth area, which shows considerable improvements relative to the site means for medians, means with 5% tails removed, and natural log of means (see Appendix). This is due to the non-Gaussian distribution of tooth area, which is partially corrected by the transformations.

One potential shortcoming of digital leaf physiognomy is that some variables, such as number of teeth and tooth area, require leaves with wholly intact margins. The fossil leaf record, however, is dominated by incomplete specimens (see discussion in Huff et al., 2003). Importantly, many of the variables that can be measured on portions of leaf margins, and therefore do not require a complete outline, also correlate well with MAT, such as the ratio of the number of teeth to internal perimeter, the ratio of tooth area to internal perimeter, and perimeter ratio (Fig. 2; see also Appendix). In general, the correlations with MAT for these derived variables are not appreciably different from their primary counterparts (e.g., the
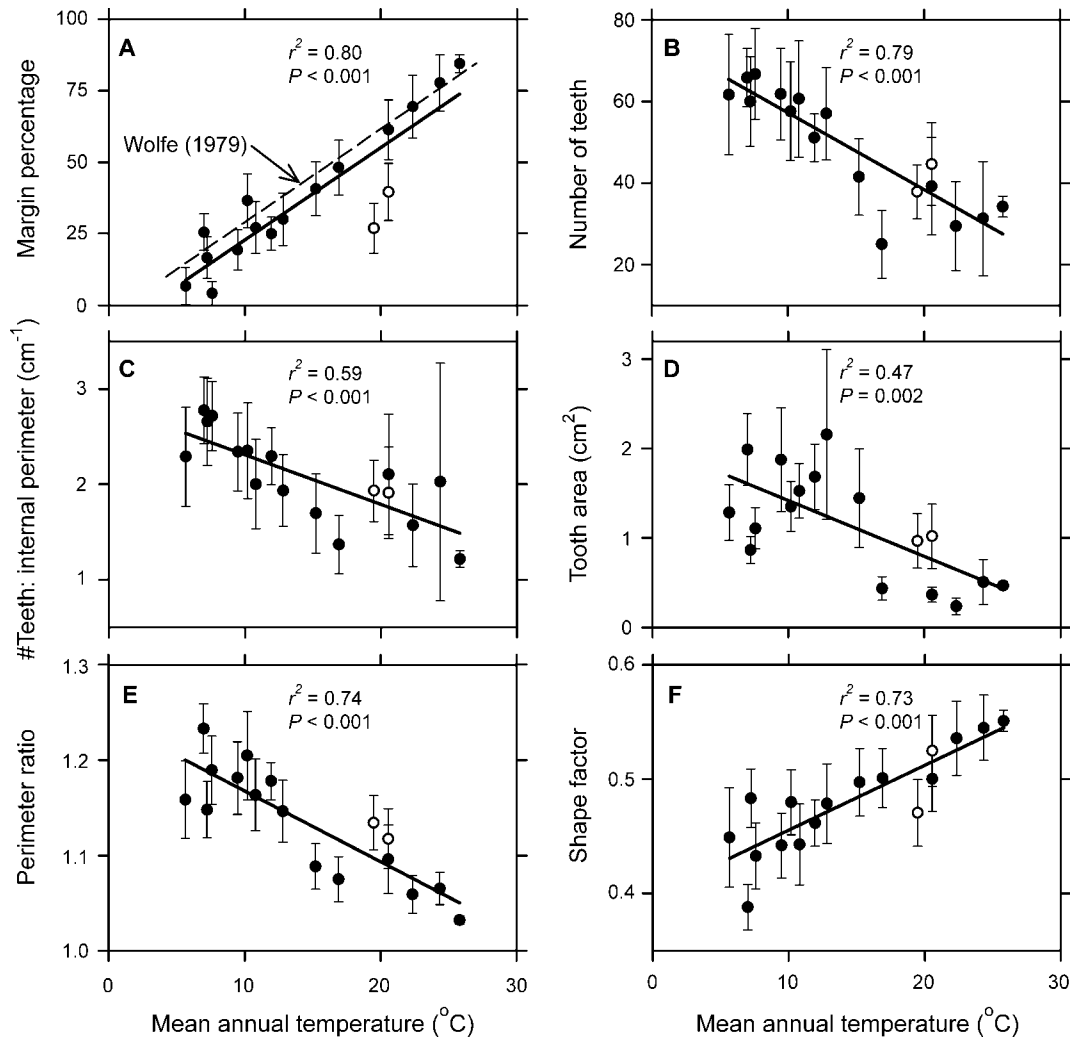
Fig. 2. Relationships between site means of physiognomic variables and mean annual temperature at the 17 test sites. Open symbols correspond to wet sites with shallow water tables (Kowalski and Dilcher, 2003). Standard errors of the means for each site are plotted. Linear regression fits and associated r^2 and P values are given in each panel (see also Appendix). In panel (A), the relationship between margin percentage and mean annual temperature from Wolfe (1979) for east Asia, as quantified by Wing and Greenwood (1993), is also given (dashed line). Standard errors of margin percentage character are calculated after Eq. 1 in Wilf (1997). Physiognomic variables are defined in Table 1.

ratio of tooth area to internal perimeter vs. tooth area; see Appendix).

Multiple linear regressions result in more significant models for MAT prediction relative to the univariate regressions (Table 3, Fig. 4). Two classes of multivariate models were investigated, based either on the inclusion of all physiognomic variables or on the inclusion of only those variables that are potentially applicable to leaf fragments. The standard error of the most significant multiple linear regression based on all available variables is $\pm 1.8°C$ ("overall"; $r^2 = 0.95$; $P = 10^{-7}$), and the standard error of the most significant model based on variables that can be applied to fragments is $\pm 2.0°C$ ("fossil"; $r^2 = 0.93$; $P = 10^{-7}$; Table 3, Fig. 4; in the fossil regression, untoothed leaves are represented by the margin percentage character state). In contrast, the most significant univariate regression, based only on margin percentage (i.e., leaf-margin analysis), has a standard error of $\pm 3.0°C$ ($r^2 = 0.80$; $P = 10^{-6}$; Table 3, Fig. 4). One attractive alternative to multiple linear regression for leaf-climate correlations is canonical correspondence analysis (CCA) (e.g., Wolfe, 1993, 1995). How-

ever, the accuracy of MAT predictions using CCA here was considerably poorer in all models relative to the linear regressions, probably because the second axis of environmental variation in the ordination, rainfall, is of minor importance in this data set (Table 2).

To test the two new multivariate models, temperatures were estimated at each site using regressions based on the remaining 16 sites. As with the original regressions, the standard errors for the two multivariate models in this independent test are smaller than for leaf-margin analysis (Table 4). Improvements over previous methods come at two sites with shallow water tables (italicized rows in Table 4; open symbols in Fig. 2; see Kowalski and Dilcher, 2003). Leaf-margin analysis underestimates MAT at these sites (mean error = $-7.0°C$), whereas errors are minimized in the multiple linear regressions (mean errors = $-2.4°C$ and $-4.1°C$ for the overall and fossil regressions, respectively). Although CLAMP is a multivariate technique, it also underestimates MAT greatly at these sites (mean error = $-8.3°C$ using CCA; Kowalski and Dilcher, 2003).
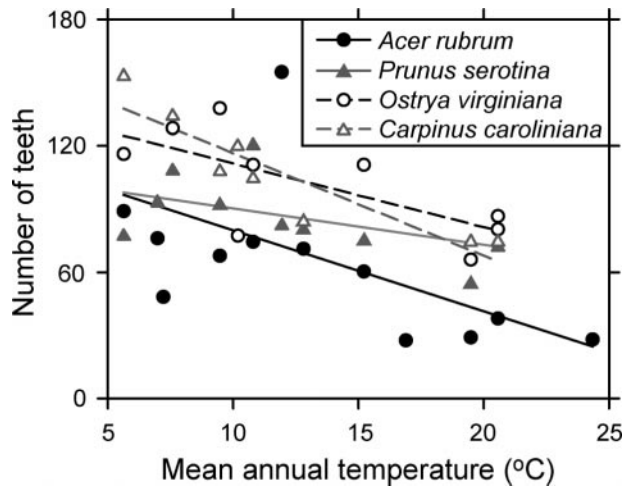
Fig. 3. Correlation between number of teeth and mean annual temperature for individual species appearing at multiple sites. Each data point represents a mean of 1–6 leaves. Least-squares fits are also shown ($P < 0.05$ for all species except *Prunus serotina*). Species were chosen based on their wide distributions within the 17 test sites.
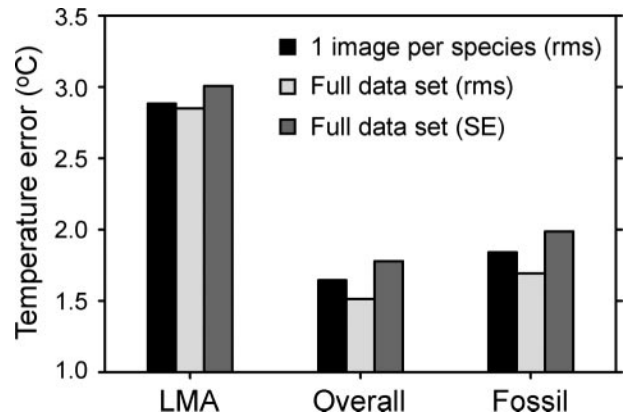
Fig. 4. Mean root mean squares (rms) of mean annual temperature (MAT) residuals for leaf-climate models based on either one image per species, each species randomly and simultaneously resampled 10 000 times from the full data set, or the full data set (1–6 images per species). Standard errors (SE) of MAT predictions for full data set are also plotted to facilitate visual comparison with root mean squares. Leaf-climate models: LMA = leaf-margin analysis; Overall = most significant multiple linear regression based on digital leaf physiognomy character states; Fossil = most significant multiple linear regression based on digital leaf physiognomy character states that are applicable to fragmentary leaves.

The leaf-climate models presented here are based on 1–6 leaves per species per site (typically 3–6). Results of computerized resampling indicate that errors in MAT predictions based on one leaf per species are only 0.1–0.2°C larger than errors based on the full data set (Fig. 4). For number of species sampled per site, resampling indicates a similar sensitivity for leaf-margin analysis and the fossil multivariate model: the precision of MAT predictions is similar at a given number of species sampled (Fig. 5). The overall multivariate model shows a different pattern: at warm sites it is comparable with the other two models (Fig. 5C), but at cool sites a greater number of species is required to achieve a similar precision in MAT predictions relative to the other models (Fig. 5A, B).

To quantify the sensitivity of MAT predictions to leaf fragmentation in both the fossil model and leaf-margin analysis, the distal quarter (based on midvein length, cut perpendicular to midvein) of one leaf image per species in each of the 17 floras was digitally removed; for perimeter measurements, the cut portion of the perimeter was subtracted. The distal portion was chosen because, in our experience, the base of a fossil leaf usually has more diagnostic characters than the apex; fossil leaves preserved only as apices are much more likely to be binned as indeterminates and thus not be used in paleoclimate analyses. Temperature was estimated for the 17 test sites from these altered leaves using the regressions in Table 3, and then compared to estimates based on intact leaves. The fragmentation caused a loss of precision of 1.0°C and 0.8°C (root mean square, rms) for the fossil model and leaf-margin analysis, respectively. Next, we performed a more extreme test, removing the distal half of the same original images. Errors increased for both models, but the loss of precision was more severe for leaf-margin analysis (rms relative to intact leaves = 2.2°C) than the fossil model (rms = 1.7°C). These tests do not address all taphonomic issues typical for fossil leaves, such as damaged teeth and irregularly preserved margins, but they degrade all leaves in a straightforward and uniform way that expedites processing and comparisons of results.

Physiognomic correlations with leaf economic variables—The site means of several physiognomic character states cor-

TABLE 3. Three regression models for predicting mean annual temperature based on the 17 test sites (Table 2). LMA = leaf-margin analysis; Overall = most significant multiple linear regression based on digital leaf physiognomy character states; Fossil = most significant multiple linear regression based on digital leaf physiognomy character states that are applicable to fragmentary leaves. Variables are defined in Table 1.

Regression model	Variable	Coefficient	r^2	SE (°C)	F	P
LMA	Margin percentage	0.250	0.80	3.01	61.4	10^{-6}
	Constant	5.19				
Overall	Shape factor	104.9	0.95	1.78	51.4	10^{-7}
	Feret diameter ratio	−82.00				
	Tooth area : blade area	250.2				
	Number of teeth : internal perimeter	−3.59				
	Constant	15.50				
Fossil	Margin percentage	0.155	0.93	1.99	54.3	10^{-7}
	Perimeter ratio	−84.56				
	Tooth area : blade area	313.0				
	Constant	94.95				

TABLE 4. Predictions of mean annual temperature (MAT) for the 17 test sites based on regressions derived from the remaining 16 sites. Italicized rows represent wet sites with shallow water tables that greatly underpredict MAT when using leaf-margin analysis (Kowalski and Dilcher, 2003). r^2 values and standard errors (SE, in °C) of the three models, as determined by regressing the 17 MAT predictions against actual MAT, are given at the bottom. Overall = most significant multiple linear regression based on digital leaf physiognomy character states; Fossil = most significant multiple linear regression based on digital leaf physiognomy character states that are applicable to fragmentary leaves. Full names of sites are given in Table 2.

Site	Leaf-margin analysis		Overall		Fossil	
	Predicted MAT (°C)	Error (°C)	Predicted MAT (°C)	Error (°C)	Predicted MAT (°C)	Error (°C)
Hubbard Brook	7.2	1.5	7.1	1.4	8.0	2.4
ANF	11.9	4.9	10.9	3.9	10.5	3.5
Harvard Forest	9.6	2.4	8.2	1.0	8.6	1.4
Huyck Preserve	5.9	−1.7	4.3	−3.3	4.8	−2.8
IES	10.1	0.6	7.4	−2.1	7.9	−1.5
Cockaponset	14.6	4.4	13.1	2.9	10.0	−0.2
Hawk Mountain	12.0	1.2	9.8	−1.0	10.5	−0.3
York	11.4	−0.5	13.6	1.7	12.7	0.8
SERC	12.7	−0.1	13.0	0.2	12.7	−0.1
Duke Forest	15.4	0.2	16.1	0.9	20.5	5.3
Pee Dee	17.2	0.3	21.0	4.1	17.9	1.0
Big Hammock	*11.3*	*−8.2*	*15.1*	*−4.3*	*15.2*	*−4.3*
DW lowland	*14.7*	*−5.9*	*20.1*	*−0.5*	*16.7*	*−3.9*
DW upland	20.5	−0.1	21.8	1.2	21.2	0.6
Archbold	22.6	0.3	21.8	−0.6	21.7	−0.7
Panther Refuge	24.8	0.4	22.8	−1.5	25.3	1.0
BCI	26.5	0.7	23.6	−2.2	23.9	−1.9
r^2	0.77		0.87		0.86	
SE	2.9		2.3		2.4	

relate significantly with leaf mass per area and nitrogen content. Specifically, the ratio of tooth area to perimeter gives the most robust correlations (Fig. 6; for raw data, see Supplemental Appendix S2). Most other significant correlations are also related to tooth area, such as the natural log of tooth area ($r^2 = 0.69$, $P < 0.001$ for leaf mass per area; $r^2 = 0.33$, $P = 0.03$ for nitrogen content) and the ratio of tooth area to blade area ($r^2 = 0.30$, $P = 0.04$; and $r^2 = 0.43$, $P = 0.01$). In contrast to the site means, no significant correlations between physiognomy and leaf economic variables are evident at the species level ($N = 335$ species-site pairs; $r^2 \leq 0.13$ for all comparisons).

One potential concern is that independent reconstructions of leaf economics and climate may be impaired because both are based on correlations with leaf physiognomy. Using partial correlation to control for the influence of MAT, correlations with the ratio of tooth area to perimeter remain significant for both leaf mass per area ($r^2 = 0.60$, $P = 0.002$) and nitrogen content ($r^2 = 0.45$, $P = 0.01$). Moreover, the ratio of tooth area to perimeter is not a component in either of the two multivariate leaf-climate models presented here (Table 3). Other variables that correlate well with leaf mass per area and nitrogen content, such as average tooth area, also do not correlate significantly with MAT or most of the character states included in the multivariate models (Supplemental Appendix S3). These results suggest that independent reconstructions of leaf economics and climate are possible.

DISCUSSION

Digital leaf physiognomy as a paleoclimate proxy—This study marks the first application of digital leaf physiognomy at a statistically significant number of sites, and the results are consistent with the preliminary assessment of Huff et al. (2003). Not only are plant species that grow in colder environments more likely to have teeth (Fig. 2A), as long known,

but they are also likely to have more teeth (Fig. 2B), larger tooth areas (Fig. 2D), and more dissected blades (Fig. 2E, F). This information about climatic selection of leaf shape cannot be recovered with other methods, highlighting a major strength of digital leaf physiognomy. Two new multiple linear regressions based on a suite of continuous, reproducible physiognomic character states show significant improvements over leaf-margin analysis for predicting MAT (Table 3, Fig. 4).

A weakness of leaf-margin analysis and CLAMP is their underestimation of MAT in riparian and wet soil environments, which typically host a disproportionate number of species with teeth compared to adjacent forests with the same climate (MacGinitie, 1953; Burnham et al., 2001; Kowalski and Dilcher, 2003). This effect is important because many fossil floras represent similarly wet, disturbed habitats (e.g., Wing and DiMichele et al., 1992). Digital leaf physiognomy appears to be less sensitive to this "wet soil" bias because temperature errors at two sites with shallow water tables are reduced on average by over 3°C compared to leaf-margin analysis (Table 4; see also Fig. 2), and over 5°C compared to CLAMP (Kowalski and Dilcher, 2003). This suggests that digital leaf physiognomy could yield significantly more accurate paleotemperature estimates for fossil floras derived from riparian or wet soil habitats.

The resampling results indicate that one leaf per species is sufficient for precise MAT predictions (Fig. 4). This is good news for paleobotanists: although a higher number of replicates is always desirable, sometimes only one fossil specimen of a species is available, for example with rare species or small museum collections. The overall and fossil regressions show a similar sensitivity to leaf-margin analysis for number of species used (Fig. 5; but see discussion later). Typically, at least 20, and preferably many more woody dicotyledonous species are required for robust MAT predictions with leaf-margin analysis (Wolfe, 1993; Wilf, 1997; Burnham et al., 2001); a similar
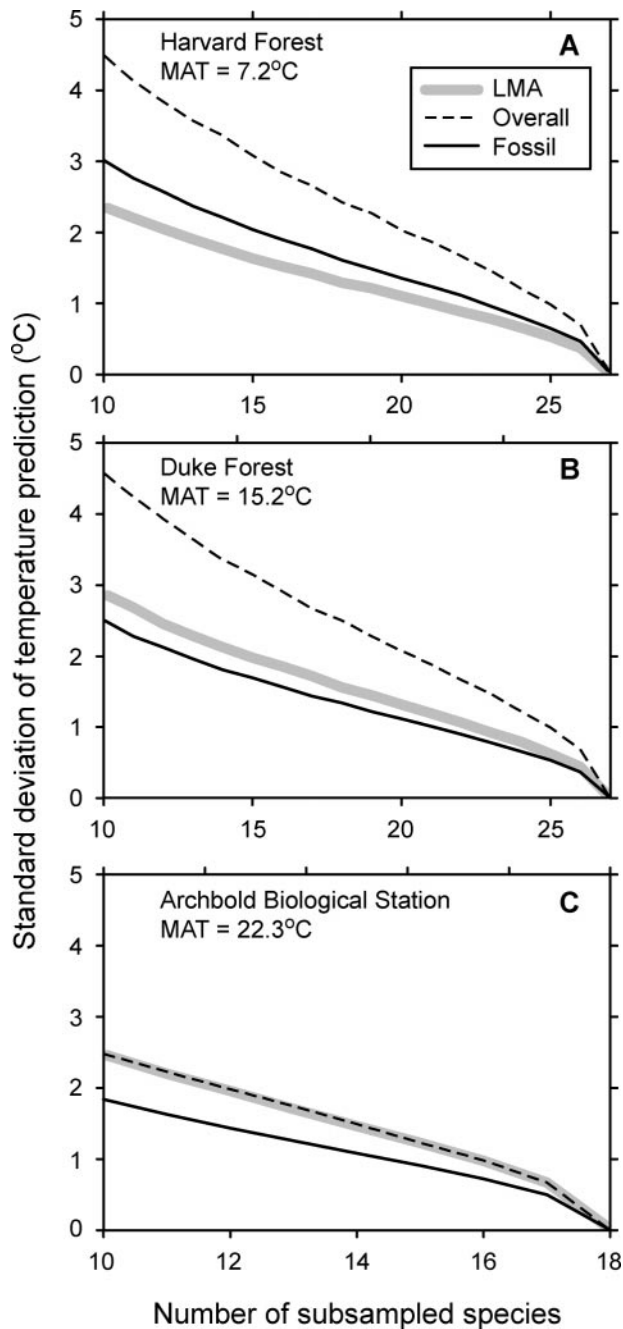
Fig. 5. Sensitivity of mean annual temperature (MAT) predictions to number of species for the three leaf-climate models. Plotted are the standard deviations of MAT predictions based on the number of species on the horizontal axis, randomly resampled 10 000 times. Standard deviations for leaf-margin analysis approximate a binomial distribution (Eq. 6 in Wilf, 1997). Three test sites are shown here, chosen to span a large range in MAT; results from the other sites are similar (not shown). MAT predictions based on <10 species are not shown. Abbreviations of leaf-climate models are defined in Fig. 4 caption.

minimum is suggested here for digital leaf physiognomy. However, in colder environments more species may be required to achieve comparable precision to leaf-margin analysis, particularly for the overall regression (Fig. 5). This degradation in colder climates is probably due to the greater variability of character states such as tooth area (Fig. 2D) and
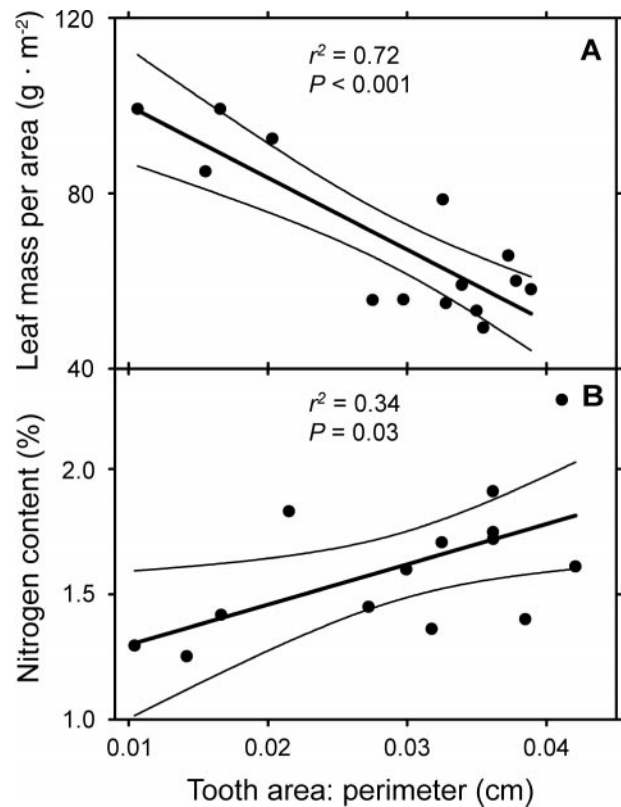

Fig. 6. Relationship of the ratio of tooth area to perimeter to (A) leaf mass per area and (B) nitrogen content at 14 of the test sites. Each data point represents a site mean of 4–25 toothed species (mean = 15 species). Curved lines denote 95% confidence intervals of linear regressions.

perimeter ratio (Fig. 2E) at cold sites relative to warm sites (see also Appendix).

Fragmented leaves are typical in the fossil record and inevitably lead to less precise climate estimates. Leaf-margin analysis and the fossil model are associated with similar signal losses for leaves that are 75% intact (0.8 vs. 1.0°C, respectively; $t_{16} = -0.71$; $P = 0.25$), whereas leaf-margin analysis produces greater errors for leaves that are 50% intact (2.2 vs. 1.7°C; $t_{16} = 1.9$; $P = 0.04$). The loss of precision in leaf-margin analysis is due to leaves that had teeth only in the distal quarter or half that consequently were scored as being untoothed. Failed tooth preservation in incomplete fossil leaves is probably a common, conventionally overlooked problem that can seriously affect paleotemperature estimates, especially in low-diversity samples with singleton species. Digital leaf physiognomy may help to mitigate this by increasing the number of reproducible character states.

One potential weakness of all MAT proxies based on leaf physiognomy is that the computation of MAT is equally weighted by all days in a year, including those when plant growth is negligible. Given this confounding factor, it is probable that climate variables other than MAT are more closely linked with plant growth, and by extension leaf physiognomy. Growing season length (GSL), growing degree days (GDD), and growing season degree days (GSDD) are three climate variables often invoked as having a close association with plant growth (e.g., Johnson et al., 2000; see Table 1 for definitions). However, these variables also correlate strongly with MAT (Fig. 7; Supplemental Appendix S3; see also Wolfe et
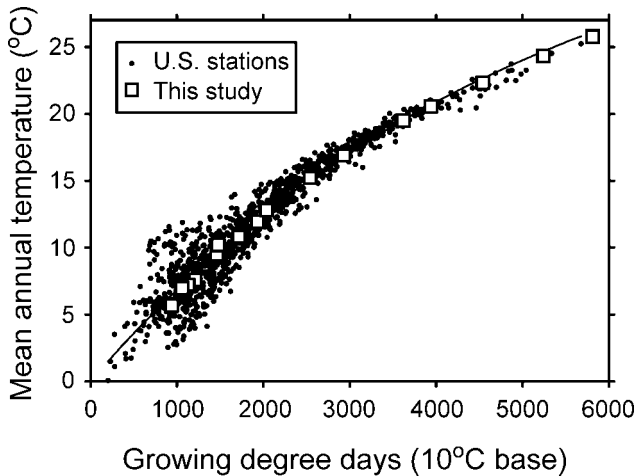
Fig. 7.   Correlation between growing degree days and mean annual temperature for 1217 U.S. climate stations. Large open squares represent climate stations used for the 17 test sites. Thin black line is an exponential fit to data ($r^2 = 0.91$; linear fit: $r^2 = 0.90$). Data compiled from National Climatic Data Center (downloaded from website cdo.ncdc.noaa.gov/CDO/cdo, April 2004).
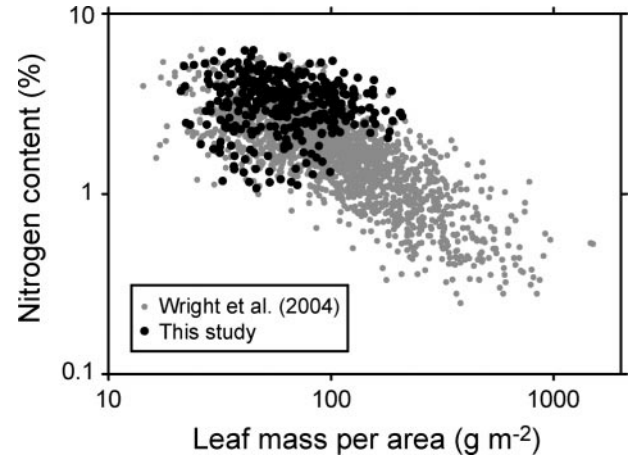

Fig. 8.   Relationship between leaf nitrogen content and leaf mass per area for individual leaves (toothed and untoothed) at 14 of the test sites. Also plotted are nitrogen content and leaf mass per area data from the worldwide compilation of Wright et al. (2004). Nitrogen contents from this study, which are based on aged leaves collected during autumn, have been adjusted uniformly by a factor of two to facilitate comparison with the Wright et al. data set, which is based on recently matured leaves (Chapin and Kedrowski, 1983; Reich et al., 1992).

al., 1995), indicating that even if a variable such as GDD is more causally linked to leaf physiognomy than MAT, in practice MAT can be reliably predicted from fossils, providing the relationship between MAT and GDD has not changed. Furthermore, both univariate and multivariate correlations between physiognomy and climate are no stronger (difference in r^2 values < 0.05) when based on MAT vs. the alternative climate variables GSL, GDD, GSDD, and MAT.

Digital leaf physiognomy as a paleoecological proxy—The site means of several tooth area variables correlate significantly with leaf mass per area and nitrogen content, including the ratio of tooth area to perimeter (Fig. 6), tooth area, and average tooth area. Importantly, the ratio of tooth area to perimeter and average tooth area can probably be measured accurately in fossil leaf fragments (see preceding discussion). This is the first time that relationships between leaf physiognomy and leaf economic variables have been quantified, and they have a plausible underlying explanation. The development of large teeth is only possible if leaf expansion is rapid (Roth et al., 1995; Mosbrugger and Roth, 1996), and fast growth correlates with high nitrogen content, low leaf mass per area, and other variables on the "quick" end of the leaf economics spectrum (Wright et al., 2004). This mechanistic link may also explain why correlations with character states not related to tooth area (e.g., number of teeth) are not as strong.

Recommendations—This study establishes correlations in living plants that link quantitative leaf physiognomy to climate and leaf economics, and it lays a foundation for using digital leaf physiognomy to quantify both climatic and leaf economic variables from fossil plants. There is potential for refinements in these correlations; most critically, increased sampling of modern test sites is needed to increase species counts (see Fig. 5), geographic and climatic coverage (see Fig. 8), and the number of leaf economic variables (e.g., leaf lifespan). The test sites used here do not differ appreciably in precipitation, except for Barro Colorado Island (Table 2). An expansion to sites with larger differences in rainfall would potentially allow

for calibrations with precipitation variables and further increase the usefulness of the approach.

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APPENDIX. Site means ($\bar{x}$) and standard errors of the means (SE) of physiognomic variables, where means are based on species averages (1–6 leaves per species). r^2 values of variables vs. mean annual temperature (MAT) are given in the row labeled 'Mean'. r^2 values are also given for various transformations of the raw data vs. MAT (see text for definitions); values in boldface represent improved correlations relative to the standard 'Mean' correlation. Physiognomic character states and site abbreviations are defined in Tables 1 and 2, respectively.

Site	Margin (%) $\bar{x}$	SE	PeriRatio $\bar{x}$	SE	Comp $\bar{x}$	SE	ShapFact $\bar{x}$	SE	FerDiamRatio $\bar{x}$	SE	TA (cm²) $\bar{x}$	SE	TABA $\bar{x}$	SE	TA : Peri (cm) $\bar{x}$	SE	TA : IntPeri (cm) $\bar{x}$	SE	#Teeth $\bar{x}$	SE	AvgTA (cm²) $\bar{x}$	SE	#Teeth : Peri (cm⁻¹) $\bar{x}$	SE	#Teeth : IntPeri (cm⁻¹) $\bar{x}$	SE
HB	6.7	6.4	1.158	0.041	33.8	4.4	0.449	0.043	0.672	0.030	1.28	0.31	0.030	0.004	0.033	0.006	0.039	0.008	61.6	14.7	0.037	0.010	1.95	0.46	2.29	0.52
ANF	25.5	6.4	1.233	0.026	37.4	2.4	0.388	0.020	0.606	0.018	1.99	0.40	0.046	0.005	0.047	0.007	0.058	0.009	65.8	7.1	0.096	0.034	2.22	0.27	2.78	0.35
HF	16.7	7.2	1.148	0.029	28.7	1.9	0.483	0.025	0.672	0.018	0.87	0.15	0.025	0.004	0.028	0.005	0.033	0.006	59.9	10.9	0.028	0.007	2.24	0.39	2.66	0.46
HP	4.2	4.1	1.189	0.036	33.3	2.9	0.433	0.029	0.662	0.021	1.11	0.23	0.033	0.004	0.030	0.004	0.037	0.005	66.7	11.1	0.029	0.009	2.21	0.27	2.72	0.36
IES	19.4	7.1	1.181	0.038	32.7	2.2	0.442	0.028	0.656	0.021	1.88	0.58	0.032	0.005	0.038	0.007	0.047	0.009	61.7	11.2	0.085	0.033	1.91	0.32	2.34	0.41
CP	36.5	9.4	1.205	0.046	29.4	2.1	0.480	0.028	0.656	0.019	1.35	0.28	0.036	0.006	0.039	0.008	0.048	0.010	57.6	12.0	0.060	0.019	1.80	0.33	2.35	0.50
HM	27.1	9.1	1.163	0.037	36.7	5.4	0.443	0.035	0.641	0.022	1.53	0.30	0.031	0.005	0.035	0.007	0.042	0.008	60.5	14.2	0.059	0.014	1.65	0.39	2.00	0.47
York	25.0	5.8	1.178	0.020	31.1	1.8	0.461	0.020	0.647	0.016	1.69	0.36	0.043	0.005	0.041	0.005	0.051	0.007	51.1	5.8	0.068	0.018	1.93	0.25	2.29	0.30
SERC	30.0	9.2	1.146	0.033	33.7	5.0	0.478	0.035	0.656	0.015	2.16	0.95	0.032	0.006	0.037	0.008	0.046	0.011	57.0	11.4	0.097	0.048	1.69	0.33	1.93	0.38
DF	40.7	9.5	1.088	0.024	29.3	2.6	0.497	0.030	0.655	0.020	1.45	0.55	0.032	0.008	0.036	0.011	0.042	0.014	41.5	9.3	0.076	0.030	1.50	0.35	1.70	0.42
PD	48.1	9.6	1.075	0.024	29.3	3.9	0.501	0.026	0.591	0.018	0.44	0.13	0.020	0.005	0.016	0.005	0.018	0.006	25.0	8.3	0.052	0.030	1.27	0.29	1.37	0.31
BH	26.9	8.7	1.134	0.029	34.0	6.2	0.470	0.028	0.637	0.017	0.97	0.30	0.045	0.007	0.034	0.008	0.040	0.009	37.8	6.6	0.044	0.015	1.69	0.27	1.93	0.32
DWl	39.6	10.0	1.117	0.032	27.6	1.9	0.500	0.028	0.601	0.020	1.02	0.36	0.034	0.007	0.033	0.009	0.038	0.011	44.6	10.1	0.044	0.015	1.65	0.40	1.91	0.48
DWu	61.4	10.4	1.096	0.036	26.6	2.1	0.525	0.031	0.596	0.018	0.37	0.08	0.030	0.009	0.017	0.003	0.019	0.004	39.2	12.0	0.023	0.012	1.88	0.57	2.11	0.63
AB	69.4	10.9	1.059	0.020	25.8	2.2	0.536	0.032	0.594	0.023	0.24	0.10	0.018	0.004	0.011	0.004	0.012	0.004	29.4	10.9	0.009	0.003	1.46	0.40	1.57	0.43
PR	77.8	9.8	1.065	0.017	24.4	1.4	0.545	0.028	0.591	0.023	0.51	0.25	0.026	0.006	0.020	0.007	0.022	0.008	31.3	14.0	0.031	0.011	1.87	1.15	2.03	1.25
BCI	84.4	3.1	1.032	0.003	25.0	1.6	0.551	0.009	0.580	0.008	0.47	0.04	0.012	0.001	0.014	0.001	0.015	0.001	34.2	2.6	0.021	0.002	1.16	0.08	1.22	0.09
r^2 (vs. MAT)																										
Mean	0.80***		0.74***		0.55**		0.73***		0.64***		0.47**		0.22		0.48**		0.51**		0.79***		0.22		0.46**		0.59***	
ln(Mean)	N/A		0.73***		**0.71*****		0.71***		0.61***		**0.50***		0.08		0.26*		0.32*		0.64***		0.10		0.37*		0.45**	
Median	N/A		0.54**		**0.58*****		0.56***		0.46**		**0.64*****		0.22		**0.58*****		**0.64*****		0.44**		0.18		0.21		0.27*	
Minimum	N/A		0.12		0.31*		0.02		0.10		0.20		0.05		0.11		0.11		0.09		0.03		0.01		0.02	
Maximum	N/A		0.74***		0.06		0.33*		0.26*		0.17		0.10		0.23*		0.24*		0.65***		0.18		0.25*		0.33*	
5% tails removed	N/A		**0.68*****		**0.64*****		**0.74*****		**0.66*****		**0.65*****		0.18		**0.53*****		**0.61*****		0.74***		0.20		**0.52****		**0.64*****	

Notes: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. N/A = not applicable.