

Relationships between leaf morphology and climate, Bolivia: implications for estimating paleoclimate from fossil floras

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Abstract.—Fossil floras are an important source of quantitative terrestrial paleoclimate data. Many paleoclimate estimates are based on relationships observed in modern vegetation between leaf morphology and climate, such as the increase in the percentage of entire-margined species with increasing temperature and the increase in leaf size with increasing precipitation. An important question is whether these observed relationships are universal or regional; for example, recent studies suggest that significant differences exist between floras from three domains: the Northern Hemisphere, New Zealand/Australia, and subalpine zones. Also, debate exists over which statistical models of modern data sets, univariate or multivariate, provide the most accurate estimates of paleoclimate. In this study, 12 foliage samples from living Bolivian forests are compared with data sets from different regions. Models based on data sets from North America and Japan, namely the Climate-Leaf Analysis Multivariate Program (CLAMP) data set of J. A. Wolfe, and from east Asia produce reasonably accurate estimates of temperature and precipitation, suggesting that the climate–leaf morphology relationships for Bolivian vegetation do not differ significantly from those for Northern Hemisphere vegetation. The mean leaf size for a given mean annual precipitation is smaller than for a data set from the Western Hemisphere and Africa, but this difference is most likely due to different sampling methods. As for estimating climate from fossil floras, these results, along with the analysis of four other regional data sets, imply that the most accurate climate estimates will be produced by the predictor data set with the most similar climate–leaf morphology relationships. Unfortunately, our present lack of understanding of why climate–morphology relationships vary between the North America/Japan, New Zealand/Australia, and subalpine domains makes it difficult to identify data sets similar to paleofloras. Until we learn more, it is probably best to compare fossil floras to predictor data sets from the same domain. The performance of the various statistical methods depends on the nature of the predictor data set. Multiple regression analysis tends to produce the most accurate estimates for small data sets with a narrow range of environmental variation that have similar relationships to the flora, and linear regression or canonical correspondence analysis for the larger and more varied CLAMP data set. If a similar predictor data set is not available, then nearest-neighbor analysis can still produce accurate paleoclimate estimates.

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Introduction

Ecologists and plant geographers have long noted that the leaf morphology of woody dicotyledons varies with climate, and that the first-order trends appear to be independent of species composition. For example, the percentage of species with entire margins tends to increase with increasing temperature, while leaf size tends to increase with increasing precipitation (Bailey and Sinnott 1915; Wolfe 1979, 1993; Givnish 1987). These relationships between leaf morphology and climate are of interest to neobotanists, because they can provide insight into the adaptive significance of leaf form. Also, as will be discussed in this study, these relationships

are of great interest to paleobotanists, because they can be used to infer the climate of fossil floras, providing one of the few quantitative measures of terrestrial paleoclimate for the Cretaceous to Recent period (Chase et al. 1998; Wolfe et al. 1998).

The observed trend in leaf size is thought to derive from the balance the leaf must strike between photosynthesis and transpiration (Parkhurst and Loucks 1972; Givnish 1979). Expanding leaf size raises leaf temperature, which in turn increases photosynthesis. However, expanding leaf size also increases transpiration, which requires a larger root system to maintain leaf hydration. In drier climates, the carbon “cost” of replacing a given water loss is greater than for more humid climates,

and thus smaller leaves are more efficient (Givnish 1979, 1984).

There is less known about the advantage conferred by other leaf morphologies. Some workers suggest that marked correspondence between margin type and temperature reflects the correspondence, as yet unquantified, between the evergreen habit and tropical climates. Givnish (1979) observes that evergreen leaves tend to be thicker than deciduous leaves; he argues that flow resistance decreases as leaves become thicker, allowing for more growth in the intercostal area, and thus smoothed margins. Roth et al. (1995) and Mosbrugger and Roth (1996) suggest that the formation of an entire margin requires a denser network of veins than the formation of a toothed margin. This dense network provides a better water supply but is more costly, and thus is more advantageous for evergreen leaves.

Alternatively, Baker-Brosch and Peet (1997) suggest that toothed margins may be advantageous in cooler climates because they provide loci for early-season photosynthesis for deciduous trees, while Wilf (1997) suggests the advantage might be in increased sap flow; this enhanced movement of water could compensate for lower transpiration rates in cooler climates.

Apex type appears to be related to environmental conditions during leaf expansion. Emarginate, or notched, apices are thought to be due to a shortage of water during leaf expansion (Wolfe 1993; Richards 1996). As discussed by Richards (1996), early workers suggested that elongate apices, or drip-tips, are common in warm, moist environments because they allowed water to drain quickly off the leaf surface, but later workers rejected this theory. Richards (1996) instead suggests that many plants in warm, humid environments have unprotected buds; if conditions are favorable during development, the leaf apex can grow rapidly and differentiate before the rest of the leaf has expanded, forming an elongate apex.

Stenophylls, or leaves with a large length-to-width ratio, are thought to be more common in riparian vegetation. Richards (1996) cites studies that suggest that a long, thin lamina is

advantageous because it reduces the amount of resistance to fast-flowing water. Wolfe (1993) suggests that the adaptation is instead to the dry, sunny conditions often found in streamside environments; a thin lamina reduces the likelihood of overheating, because no part of the lamina is far from the margin (Wolfe 1993).

With the goal of quantifying relationships between leaf morphology and climate, several data sets of modern leaf morphology and climate have been collected (Table 1). The largest is associated with the Climate-Leaf Analysis Multivariate Program (CLAMP) of Wolfe (1993, 1995). The most recent version of this data set, CLAMP 3A, which is available from J. A. Wolfe on request, has percentage occurrence data for 31 different leaf morphology character states from 173 sites, mostly in North America and Japan. The other leaf morphology data sets contain percentage of entire-margined species or data on mean leaf size for various geographical areas (Table 1).

An important question is whether there are differences in the relationships between leaf morphology and climate between different parts of the world. Stranks and England (1997) argue that we are unlikely to find relationships with the major climate variables, mean annual temperature and mean annual precipitation, that we can apply globally. They suggest that most relationships will only be regional, because leaf morphology character states do not solely depend on one parameter, but rather vary as a function of a number of environmental factors. For example, Jacobs (1999) looked at the correlation between climate and leaf morphology for 30 sites from equatorial Africa and found that the percentage of entire-margined species, a factor that typically correlates strongly with mean annual temperature, correlated significantly with precipitation during the wet season. Thus the relationship between margin type and temperature could vary between regions with different overall climate, for example a xeric region and a mesic region.

Also, leaf morphology is affected by factors other than climate, such as floristic composition and soils and other environmental factors. Floristic composition varies from region

TABLE 1. Data sets and statistical methods used to estimate climate from leaf morphology in this study. CLAMP refers to the Climate-Leaf Analysis Multivariate Program data set of Wolfe (1993, 1995). CLAMP 3A refers to the most recent version of the data set, which has percent occurrence data for 31 different leaf morphology character states from 173 sites. Most CLAMP 3A sites are from North America and Japan, with some sites from Caribbean and South Pacific islands. CLAMP 3B is a subset of CLAMP 3A that excludes 29 subalpine sites; these sites are known to be outliers (see text). CLAMP 3B, GSP < 222 cm is a subset of the CLAMP data set that excludes sites with a mean growing-season precipitation >222 cm, where the growing season is defined as the number of months with a mean warm-month temperature >10°C. n = number of samples in data set. Character states: for abbreviations, see Appendix. Method: CCA = canonical correspondence analysis; LRA = linear regression analysis; MRA = multiple regression analysis; NNA = nearest-neighbor analysis. ¹MAT = $1.36 + 0.275 \cdot \text{NoT}$, $r^2 = 76.8\%$, SE = 3.3°C, $F = 571$. ²MAT = $3.53 + 0.249 \cdot \text{NoT}$, $r^2 = 86.9\%$, SE = 2.2°C, $F = 948$. ³MAT = $1.14 + 0.306 \cdot \text{NoT}$, $r^2 = 98.3\%$, SE = 0.8°C, $F = 1901$. Equation calculated from caliper measurements by D. R. Greenwood of data published in Wolfe 1979. ⁴lnMAP = $1.78 + 0.484 \cdot \text{MinA}$, $r^2 = 61.2\%$, SE = 0.47, $F = 226$. ⁵GSP = $-45.2 + 1.60 \cdot \text{AAtm} + 280 \cdot \text{LW} 2-3:1$, $r^2 = 63.0\%$, SE = 27 cm, $F = 103$. ⁶lnMAP = $0.768 + 0.548 \cdot \text{MinA}$, $r^2 = 76\%$, SE = 0.36, $F = 152$, where MAT = mean annual temperature, MAP = mean annual precipitation, and GSP = mean growing-season precipitation.

Data set	n	Character state(s)	Method	Source
Temperature models				
CLAMP 3A	20 of 173	31 of Wolfe 1995	NNA	Stranks and England 1997
CLAMP 3A	173	NoT	LRA	This study ¹
CLAMP 3B	144	31 of Wolfe 1995	CCA	Wolfe 1995
CLAMP 3B	144	NoT, BRnd, LW < 1:1	MRA	Wiemann et al. 1998
CLAMP 3B	144	NoT	LRA	This study ²
CLAMP 3B	34	NoT	LRA	Wolfe 1979; Wing and Greenwood 1993 ³
Precipitation models				
CLAMP 3A	20 of 173	31 of Wolfe 1995	NNA	Stranks and England 1997
CLAMP 3B	144	31 of Wolfe 1995	CCA	Wolfe 1995
CLAMP 3B	144	MinA	LRA	This study ⁴
CLAMP 3B, GSP < 222 cm	121	AAtm, LW 2-3:1	MRA	This study ⁵
Western Hemisphere/Africa	50	MinA	LRA	Wilf et al. 1998 ⁶

to region because of differing geologic, climatic, and evolutionary histories. Selection has caused the development of physiognomically similar forest types with similar leaf morphology in areas of similar major climate parameters (Wolfe 1979; Givnish 1987). Thus we see the same first-order trends in leaf morphology from region to region, but it is possible that floristic composition could cause variation within these trends, especially in isolated environments. For example, Wolfe (personal communication 1999) suggests that the small number of species with lobed leaves in upland sites of Puerto Rico is due to the fact that uplift was recent, and there was no close-by source of microthermal clades such as Fagaceae, Aceraceae, Rosaceae, and Betulaceae to populate the highlands.

Several studies have suggested that Southern Hemisphere vegetation has a significantly different relationship between leaf morphology and climate from Northern Hemisphere vegetation. For example, data sets from east Asia and the Northern Hemisphere demonstrate a strong correlation between the percentage of entire-margined leaves and mean annual temperature (Table 1) while in contrast, a data set from New Zealand lacks a correlation between these variables (Kennedy 1998). Greenwood (1992) did see a correlation for eight sites from eastern Australia, but the 1%/°C increase in the percentage of entire-margined species with temperature is smaller than the 3%/°C observed for Wolfe's North American sites. Jordan (1997) found that multivariate analysis of the predominantly Northern Hemisphere CLAMP data set consistently overestimated the mean annual temperature of 13 sites from south eastern Australia and New Zealand.

As for South America, the only available data on leaf morphology are the percentages of entire-margined species for a site in Peru and a site in Bolivia (Wilf 1997); Halloy and Mark (1996) analyzed leaf morphology of six sites from South America, but they analyzed the full flora rather than just the woody dicotyledons; thus their sites are not comparable to sites in the CLAMP data set. With so few South American sites it is impossible to discern whether the relationships between leaf

morphology and climate are different from those of North American vegetation; one might suspect they are, given the differences observed for other floras with Gondwanan affinities.

Another important topic of debate is whether univariate or multivariate statistical models provide the most accurate estimates of paleoclimate from leaf morphology. Workers have proposed a variety of models to analyze the data sets in Table 1, including linear regression analysis, multiple regression analysis, correspondence analysis, use of a resemblance function combined with correspondence analysis, and canonical correspondence analysis.

In theory, nonlinear, multivariate methods such as correspondence analysis are more appropriate than linear, univariate methods such as linear regression because of the complex nature of plant response to environmental variables, though note that linear methods can be appropriate for data sets with a narrow range of environmental variation (ter Braak and Prentice 1988; Jacobs 1999). Wolfe (1995) proposed that canonical correspondence analysis, a nonlinear ordination technique, is the most appropriate statistical method to use for analysis of the CLAMP data set, which consists of data for 31 different leaf morphology character states.

Wilf (1997) and Wilf et al. (1998, 1999) contend that the approach of Wolfe (1995) is problematical. Wilf (1997) argues that the temperature signal from leaf morphology is dominated by the leaf-margin character state, thus the additional leaf morphological character states in the CLAMP data set do not improve the accuracy of temperature estimates as compared to univariate analysis. As for precipitation analysis, Wilf et al. (1998, 1999) argue that the samples in the CLAMP data set have too few species and are collected from areas that are too small, and as a result they are biased against large leaves. To correct these problems, Wilf et al. (1998) compiled a data set of average leaf site for sites from the Western Hemisphere and Africa (Wilf et al. 1998) (Table 1).

In turn, Wolfe and Uemura (1999) criticize the Western Hemisphere/Africa data set, noting that samples are mostly culled from the

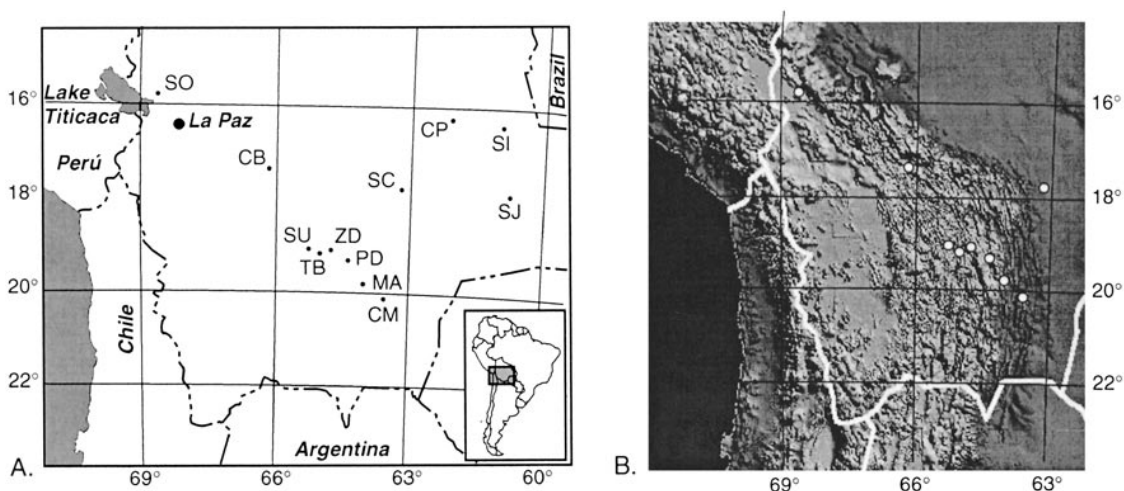


FIGURE 1. A, Location map, showing 12 vegetation sample sites. CB = Cochabamba, CM = Camiri, CP = Concepción, MA = Monteagudo, PD = Padilla, SC = Santa Cruz, SI = San Ignacio, SJ = San José, SO = Sorata, SU = Sucre, TB = Tarabuco, ZD = Zudañez. Shaded areas = water. B, The westernmost sample sites superimposed on USGS 30 arc-second DEM data for the Central Andes, as processed by the Cornell Andes Project.

literature, and that they represent a variety of sampling strategies and sample plot sizes (up to thousands of kilometers) and thus do not accurately reflect the leaf morphology of a given site-specific climate.

This study analyzes the leaf morphology of live foliage samples from Bolivia in order to (1) investigate whether the relationships between climate and leaf morphology in South American vegetation are different from those in other parts of the world, and (2) evaluate whether univariate or multivariate models produce more accurate climate estimates. Leaf morphology scores for the Bolivian sites are input into climate models based on a variety of data sets from different geographical regions, and the resulting climate estimates are analyzed in terms of their accuracy. Models which produce accurate estimates are assumed to be based on predictor data sets with similar morphologic relationships to the Bolivian samples. Also, the similarity of linear regression models for the various databases is evaluated using statistical techniques. The results are discussed in terms of their implications for estimating the climate of fossil floras.

Materials and Methods

Collection of Modern Vegetation Sites

Twelve leaf morphology samples were collected from the eastern slope of the Andes and

the eastern lowlands of Bolivia (Fig. 1). These sites were chosen because they had climate stations with at least a decade of good-quality records of temperature and precipitation (Table 2). The climate of the sites varies from tropical-dry to temperate-dry, with mean annual temperature (MAT) ranging from 12.5° to 25.5°C and the mean annual precipitation (MAP) ranging from 50 to 134 cm (Table 3), and the vegetation type varies from semideciduous tropical forest to páramo (Table 4). The climate of these sites is typical of equatorial regions, in that the difference between the shortest and longest days is no greater than three hours, and the daily variations of temperature are larger than the yearly variations (Beck et al. 1993). There is a marked dry season during the winter months.

For the sake of consistency, the samples were collected using the methodology of Wolfe (1993), in which foliage from at least 30 species of woody dicotyledons is collected from an area of 1–5 hectares, usually in a riparian zone, that is within 5 km of a climate station (Wolfe 1993); this sampling strategy was designed to mimic fossil floras from a single quarry. Ideally, sites should be undisturbed, but this is often not possible for areas close to a climate station. For example, for sites in the lowlands of the Precambrian shield (Concepción, San Ignacio de Velasco, and San

TABLE 2. Bolivian climate stations. Latitude and longitude given in decimal degrees. Z = elevation of station. Sources: GHCN = the Global Historical Climatology Network (Vose et al. 1992) (monthly temperature and precipitation data); SNM = SENAMI = Servicio Nacional de Meteorología, Bolivia (station averages of mean monthly temperature and precipitation data). L_t , L_p = length of temperature and precipitation records, respectively, in years.

Station	Lat.	Long.	Z (m)	Source	L_t	L_p
San José	-17.83	-60.75	~400	GHCN	13	29
Santa Cruz	-17.80	-63.17	414	GHCN	42	41
San Ignacio	-16.37	-60.95	413	GHCN	27	37
Concepción	-16.25	-62.01	497	GHCN	22	35
Camiri	-20.05	-63.57	914	GHCN	34	32
Monteagudo	-19.80	-63.95	1130	SNM	~17	~17
Padilla	-19.30	-64.30	2080	SNM	~44	~44
Cochabamba	-17.45	-66.10	2548	GHCN	45	43
Zudañez	-19.12	-64.70	2475	SNM	~41	~41
Sucre	-19.05	-65.22	2903	GHCN, SNM	19	~45
Sorata	-15.75	-68.68	2697	SNM	~38	~38
Tarabuco	-19.17	-64.90	3284	SNM	~41	~41

José de Chiquitos), riparian or valley areas are often disturbed by agricultural activity, and these samples were collected from small ridges or level ground. Also, even in what appear to be undisturbed stands, it is likely that species with valuable wood such as mahogany have been selectively logged. For the sites in the dry intermontane valleys (Cochabamba, Padilla, Sucre, Sorata, Tarabuco), it is also impossible to find areas close to climate stations that are completely undisturbed; most of these areas have been grazed or burned at some time in their history (Richards 1996: p. 435). The least disturbed-looking areas were chosen for sampling, but they were not free of human influence.

The size of the sampled area varied from

site to site, being much larger for the cool, dry, lower-diversity sites than for the warm, moist, higher-diversity sites. For example, in the cool, dry intermontane sites such as Tarabuco, live foliage was collected from every species found along watercourses over about a square kilometer, while for the lowland sites such as Santa Cruz, leaves were collected from strata between 0 and 3 m in an area of about 50 m × 50 m. Care was taken to sample the full range of physiognomic variability for each species; species were distinguished by differences in leaf venation, bark, and reproductive structures. Introduced or cultivated species were not collected.

Samples were pressed, dried, and scored for leaf morphology according to the CLAMP

TABLE 3. Climate data for the Bolivian climate stations. MAT = mean annual temperature (°C). WMMT = warm-month mean temperature (°C). MAP/GSP = mean annual precipitation (cm) and mean growing-season precipitation (cm), where growing season is defined by Wolfe (1993) as the number of months with a monthly mean temperature >10°C. For the Bolivian sites, the growing season thus defined is 12 months long, and thus MAP = GSP. WMP = wet-months precipitation; wet months defined by Jacobs (1999) as consecutive months with rainfall >5 cm. MMGSP = mean monthly growing-season precipitation (cm). 3WET = precipitation during the three wettest months (cm). 3DRY = precipitation during the three driest months.

Station	MAT	WMMT	MAP/GSP	WMP	MMGSP	3WET	3DRY
San José	25.5	27.8	92	71	7.7	43.7	6.6
Santa Cruz	24.5	26.9	134	130	11.2	51.2	17.7
San Ignacio	24.5	26.8	122	114	10.2	57.6	7.9
Concepción	24.3	26.6	117	107	9.7	50.6	9.3
Camiri	23.0	26.5	87	77	7.3	46.6	3.1
Monteagudo	20.1	23.6	79	71	6.6	38.4	3.8
Padilla	17.9	20.0	68	54	5.7	39.5	1.8
Cochabamba	17.6	20.3	50	39	4.2	32.0	0.9
Zudañez	16.2	17.8	55	43	4.6	35.6	0.8
Sucre	15.7	17.4	65	53	5.4	38.4	1.2
Sorata	15.4	16.6	80	73	6.7	46.1	2.3
Tarabuco	12.5	13.8	58	48	4.8	36.5	1.1

TABLE 4. Description of vegetation sample sites. n = number of species sampled. D = distance from climate station. ΔZ = elevation of sample site – elevation of climate station. Vegetation type from Rivera et al. 1996.

Site	n	D (km)	ΔZ (m)	Vegetation type	Soil	Location description
San José	43	3.5	+10	Semideciduous forest	Laterite	Flat ground
Santa Cruz	44	5	-5	Semideciduous forest	Very poor, sandy	Sandy floodplain of large river
San Ignacio	41	6	0	Semideciduous forest	Laterite	Top of small hill
Concepción	38	1	-15	Semideciduous forest	Laterite	Flat ground above small stream
Camiri	38	7	+40	Deciduous forest	Very poor, sandy	Banks of seasonal stream
Monteagudo	37	5	+30	Sub-Andean forest	Very poor, sandy	Banks of perennial stream
Padilla	32	0.5	0	Scrub	Very poor, sandy	Banks of seasonal stream
Cochabamba	22	~20	-65	Scrub	Poor, sandy	Arroyo with small perennial stream
Zudañez	40	4	-50	Scrub	Poor, sandy or rocky	Banks, bars of perennial river
Sucre	29	4	± 90	Scrub	Poor, rocky	Banks of seasonal stream and valley slopes
Sorata	30	2	-30	Páramo	Poor, sandy or rocky	Small canyon with perennial stream
Tarabuco	32	2	+60	Scrub	Poor, clayey	Small arroyos with seasonal streams
			-100			

system of Wolfe (1993) (Appendix). The samples will be archived, along with copies of the data sets used for analysis, at the Desert Laboratory, University of Arizona, Tucson.

Climate Data

Data on monthly mean temperature and precipitation were those of Vose et al. (1992), and station averages of mean monthly temperature and precipitation were obtained from the Bolivian National Meteorological Service (Table 2). From these data, the climate parameters used by the models in Table 1 were calculated for the Bolivian sites (Table 3).

There is some question of how best to define the mean growing-season precipitation, a climate parameter modeled in several of the studies listed in Table 1. Wolfe (1993) defines the length of the growing season for the CLAMP data set as the number of months with a mean warm-month temperature greater than 10°C; mean growing-season precipitation is thus the amount of rainfall during the growing season so defined. Using this definition, the Bolivian sites all have a 12-month growing season, and the mean growing-season precipitation is equal to the mean annual precipitation (Table 3).

This temperature-based definition of the growing season makes sense for CLAMP sites, which are mostly from middle to high latitudes where growth tends to be limited by temperature. However, for low-latitude sites, such as the Bolivian sites in this study, growth is more often limited by rainfall. Thus, it might be useful to also use a precipitation-based definition of the growing season when calculating the mean growing-season precipitation of the Bolivian sites.

Thus, I calculated the climate parameter mean wet-months precipitation, defined by Jacobs (1999) as the average sum of precipitation during wet months, where wet months are those months in which precipitation exceeds 5 cm (Table 3). Months with less than 5 cm precipitation are categorized as drought months in many climate classifications (Richards 1996), and growth is likely limited. This parameter can be used in comparison to mean growing-season precipitation as calculated for middle- and high-latitude sites. I did not cal-

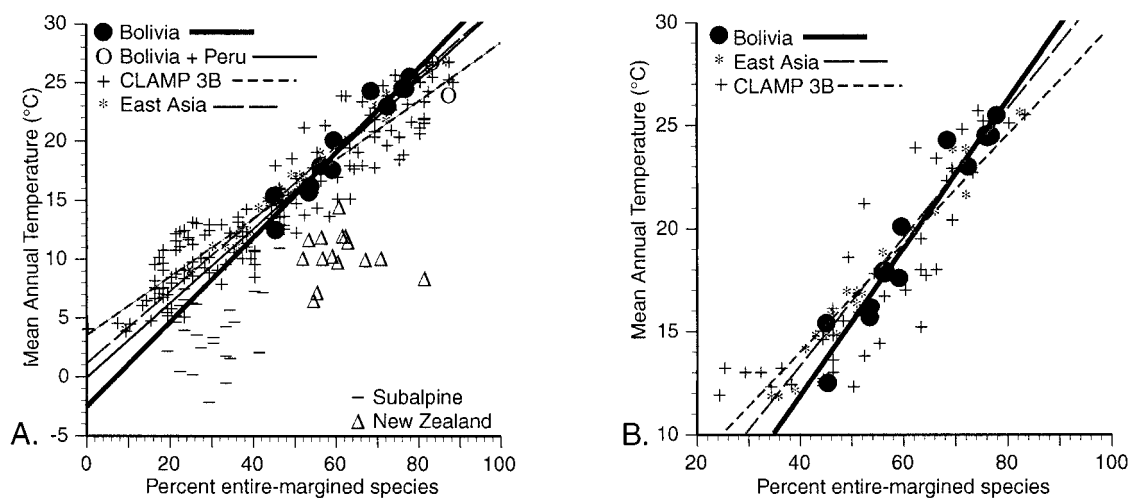


FIGURE 2. A, Mean annual temperature (MAT) vs. percentage of entire-margined species for different data sets: Bolivia (this study) ($\text{MAT} = -2.52 + 0.359 \cdot \text{NoT}$, $r^2 = 93\%$, $\text{SE} = 1.2^\circ\text{C}$, $F = 141$); Bolivia + Peru: this is the data set composed of the Bolivian sites from this study and two samples from Bolivia and Peru from Wilf (1997) ($\text{MAT} = -0.059 + 0.316 \cdot \text{NoT}$, $r^2 = 89\%$, $\text{SE} = 1.6^\circ\text{C}$, $F = 102$); CLAMP 3B; east Asia (for equations see Table 1); the subalpine sites from the CLAMP 3A data set; and the New Zealand sites of Kennedy 1998. B, Mean annual temperature vs. percentage of entire-margined species for the Bolivian sites, for a subset of the CLAMP 3B data set consisting of sites with the same range of MAT and mean growing-season precipitation as the Bolivian sites, and for a subset of the east Asian data set consisting of sites with the same range of MAT as the Bolivian sites.

culate wet-months precipitation for low-latitude sites in the CLAMP data set, such as the sites from Mexico, Panama, and Puerto Rico, because monthly mean data were not available.

Climate Analysis

The morphologic scores for each site (Appendix) were input into existing models that estimate temperature and precipitation (Table 1); these models vary in both the data set and type of statistical analysis used.

Univariate Models.—The simplest temperature models are linear regression models of the percentage of entire-margined species character state versus MAT, such as the model of Wolfe (1979), which is based on east Asian humid to mesic floras described in the literature. I also calculated the regression of the percentage of entire-margined species versus MAT for the CLAMP 3A and 3B data sets of J. A. Wolfe. CLAMP 3A is the latest, unpublished version of the CLAMP data set and has data for 31 leaf morphology character states from 173 sites located primarily in North America (including Alaska and Mexico) and Japan (including sites from the east Asian data

set of Wolfe 1979), but also with some sites from the Caribbean, Fiji, and New Caledonia. CLAMP 3B is a subset of the CLAMP 3A data set that excludes 29 subalpine/subarctic sites, defined as those sites with a warm month-mean temperature less than 16°C and a cold-month mean temperature less than 3°C (Wolfe 1993). The subalpine sites have significantly higher percentages of entire-margined species for a given MAT than other cool-temperate sites (Fig. 2A) and plot in a distinct region of multivariate space from the other CLAMP samples (Wolfe 1993). If these outlier sites are excluded from the data set, more accurate estimates of MAT are derived for non-subalpine sites (Wolfe 1995). The subalpine subset of the CLAMP 3A data set had no correlation between percentage of entire-margined species and MAT, so a model relating MAT to acute bases was used instead.

Greenwood (1992) and Wilf (1997) collected data on the percentage of entire-margined species for floras from Australia and the Western Hemisphere, respectively, but because of the small size of these data sets (eight to nine samples), the regressions were not proposed for use with fossil floras and are thus not in-

cluded in this study. Stranks (1996) collected leaf morphology data for 32 sites in New Zealand (Fig. 2A); in an analysis of this data set, Kennedy (1998) did not find a significant correlation between the percentage of entire-margined species and MAT, and thus no regressions based on this data set are included in this study.

The simplest precipitation model, proposed by Wilf et al. (1998), relates the natural log of mean annual precipitation at a given site to the mean of the natural log leaf areas of the species present (MlnA). For comparison, I calculated this regression for the CLAMP 3B data set. The value for MlnA was determined for each CLAMP site after the equation of Wilf et al. (1998):

$$\text{MlnA} = \sum a_i p_i$$

where a_i = the means of the natural log areas of the size categories and p_i represents the proportion of species in each size category. Samples in the CLAMP data set were scored using the CLAMP leaf size classification system as opposed to the Raunkiaer-Webb system used by Wilf et al. (1998), thus a_i values had to be recalculated. The area of the CLAMP size categories were determined from the CLAMP size template of A. B. Herman and others (unpublished); values are given in the Appendix.

Multivariate Models.—Several statistical methods have been used to build multivariate models of temperature and precipitation from the CLAMP data set. Wolfe (1995) argues that canonical correspondence analysis is the most appropriate method to use because it allows for collinearity between variables and for nonlinear relationships between leaf morphology and climate. Canonical correspondence analysis is similar in concept to principal components analysis; both methods are ordination techniques, in which data are ordered according to axes chosen to explain the most variance in the data. However, canonical correspondence analysis differs from principal components analysis in that it is a constrained ordination, in which the axes must be linear combinations of environmental variables, and it assumes nonlinear as opposed to linear responses to environmental variables (ter Braak and Prentice 1988).

Following the approach of Wolfe (1995), the environmental variables used to constrain the axes of the canonical correspondence analysis in this study are: MAT, warm-month mean temperature, growing-season length, mean growing-season precipitation, mean monthly growing-season precipitation, mean precipitation during the three wettest months, mean precipitation during the three driest months, relative humidity, specific humidity, and enthalpy. Climate estimates are derived by orthogonally projecting the axis scores to the vector of the climate parameter of interest. These vector scores are then calibrated with the measured values of the climate parameter (Wolfe 1995).

As discussed above, Stranks and England (1997) argue that the relationships between leaf morphology and climate are probably regional rather than global. They proposed a method that uses a resemblance function to identify those sites in multivariate space closest to a chosen site, and then uses only these nearest neighbors to estimate the climate of the chosen site. First, samples in the CLAMP data set and the chosen site are ordered using correspondence analysis. Correspondence analysis is similar to canonical correspondence analysis, except that the axes are not constrained to be linear combinations of environmental variables (ter Braak and Prentice 1988). The distances of each site from the chosen site along the first three axes of variation are calculated in order to derive the Euclidean distance between each site and the chosen site. The distances along each axis for the closest sites are then related to climate via multiple regression, with the constant of the regression providing an estimate of the climate of the chosen site. Stranks and England (1997) found that using 20 nearest neighbors gave the most accurate results for the aforementioned data set of New Zealand floras.

Multiple regression analysis has been used to derive climate models both for precursors of the current version of the CLAMP data set (Wing and Greenwood 1993; Gregory and McIntosh 1996) and for the current version (Wiemann et al. 1998); only the models for the most current version (CLAMP 3A and 3B) were used in this study. I recalculated the model for

mean growing-season precipitation of Wiemann et al. (1998) because this model was derived from an older, uncorrected version of the CLAMP 3B data set in which several pairs of sites with the same MAT had their precipitation values switched. Stepwise regression was performed on a subset of the data set that excluded sites with mean growing-season precipitation >222 cm as outliers. Jacobs (1999) calculated multiple regression models for 30 sites from equatorial Africa, but these models were not used because Jacobs's leaf morphology scoring system differs from the system of Wolfe (1993), which was used in this study.

Models Using Bolivian Data.—New linear regression, multiple regression, canonical correspondence, and nearest-neighbor models were calculated for data sets derived by adding the Bolivian data to existing data sets, namely the CLAMP, east Asia, and Western Hemisphere/Africa data sets. The value of MlnA was calculated in two ways: (1) using the proportions of species in the CLAMP size categories, as described above, or (2) using the proportion of species in the Raunkiaer-Webb size categories after the method of Wilf et al. (1998). By calculating both values, the Bolivian sites could be added to both the CLAMP and Western Hemisphere/Africa data sets.

Also, I created a South American leaf-margin data set by adding the Bolivian sites to two sites of Wilf (1997: Tables 1, 3) from Peru and Bolivia. These two sites may not be strictly comparable because Wilf used a different sampling strategy; the samples represent trees with a diameter at breast height greater than 10 cm, while the Bolivian samples from this study represent all woody species, including shrubs and subshrubs.

The canonical correspondence analysis of these combined Bolivia + existing data sets was modified from the method of Wolfe (1995); relative humidity, specific humidity, and enthalpy were removed from the set of environmental variables used to constrain the axes of variation, because these parameters were not calculated for the Bolivian climate stations. Also, analyses were run using both the temperature-based and precipitation-based definitions of the growing season.

When using the precipitation-based definition, the number of wet months was substituted for growing-season length, and wet-months precipitation was substituted for mean growing-season precipitation for the Bolivian sites.

In addition, new linear regression and multiple regression models were calculated for the data set composed just of the Bolivian sites. Canonical correspondence analysis and nearest-neighbor analysis were not carried out because of the small number of sites.

For both the existing + Bolivia and Bolivia-only data sets, when applying these models to a specific Bolivian site, the site was removed from the data set.

Results of Climate Analysis

Temperature Analysis

The results when the leaf morphology character scores (Appendix) were plugged into the various climate models are given in Tables 5 and 6, reported in terms of the errors (estimated value – actual value), with the models in each subsection that yielded the most accurate estimates of temperature and precipitation for the Bolivian sites listed first.

The average absolute error is a measure of the average magnitude of error; it is reported both for the Bolivian sites and for the data set used to derive each model. As a measure of the accuracy of a model, this value is more illuminating than the average error, in which positive and negative errors cancel each other out. However, the average error is useful as an indication of systematic bias. It is calculated in Tables 5 and 6, along with the average error for two subsets of the Bolivian sites, one comprising the six sites with MATs above 20°C, and the other comprising the six sites with MATs below 18° (Table 3). These values indicate whether the models tend to over- or underpredict the mean annual temperature of the warm/moist/low-elevation sites versus the cool/dry/high-elevation sites.

Most of the models produced reasonably accurate estimates of MAT for the Bolivian sites. The average absolute errors ranged from 0.6°C for multiple regression analysis of the Bolivia-only data set to 3.0°C for canonical correspon-

TABLE 5. Comparison of mean annual temperature (MAT) estimate errors (estimated MAT – actual MAT) of models applied to the Bolivian sites (Table 1). Method: LRA = linear regression analysis, NNA = nearest-neighbor analysis, CCA = canonical correspondence analysis. Data sets on which methods were performed are divided into three groups: those from the literature (Existing), those formed by combining data sets from the literature with the Bolivian sites of this study (Existing + Bolivia); and the data set comprising only the Bolivian sites from this study (Bolivia only). When applying models to a specific Bolivian site, that site was removed from the analysis. AbsBO, AbsDB = average absolute error (°C) of method applied to Bolivian sites and to sites in the data set used to derive the model, respectively. AvgW, AvgC = average error (°C) of method for the six Bolivian sites with MAT >20°C and MAT <20°C, respectively (see Table 3). An asterisk indicates that the result varies depending on 20 nearest neighbors; asterisked values are estimated to be the same as AbsD for CCA analysis.

Method	Data set	AbsBO	AbsDB	AvgAll	AvgW	AvgC
<u>Existing</u>						
LRA	East Asia	1.0	0.8	0.3	-0.5	1.2
LRA	CLAMP 3B	1.6	1.8	-0.8	-2.2	0.6
LRA	CLAMP 3A	1.6	2.5	-1.4	-2.5	0.2
NNA	CLAMP 3A	1.9	1.5*	-0.9	-2.6	0.7
MRA	CLAMP 3B	2.2	1.6	-0.2	-2.4	1.9
CCA	CLAMP 3B	2.8	1.5	-1.4	-4.0	1.3
<u>Existing + Bolivia</u>						
LRA	East Asia + Bolivia	1.0	0.8	0.3	-0.6	1.1
LRA	Peru + Bolivia	1.2		-0.2	-1.1	0.6
LRA	CLAMP 3B + Bo.	1.6	1.8	-0.7	-2.1	0.7
NNA	CLAMP 3A + Bo.	2.2	1.7*	-1.6	-2.8	-0.4
CCA	CLAMP 3B + Bo.	3.0	1.7	-1.0	-3.9	2.0
<u>Bolivia only</u>						
MRA	Bolivia	0.6		-0.1	-0.2	0.1
LRA	Bolivia	1.1		0	-0.4	0.4

TABLE 6. Comparison of mean annual precipitation (MAP) or mean growing-season precipitation (GSP) estimate errors (estimated – actual) of models applied to the Bolivian sites (Table 1). Recall that MAP and GSP are equivalent for the Bolivian sites, but often differ in the CLAMP data set. For explanation of Method and Data set, see Table 5. When applying models to a specific Bolivian site, that site was removed from the analysis. AbsBO, AbsDB = average absolute error (cm) of method applied to Bolivian sites and to sites with MAP or GSP <135 cm (in order to be comparable with the Bolivian sites) in the data set used to derive the model, respectively. AvgW, AvgC = average error (cm) of method for the six Bolivian sites with MAT >20°C and MAT <20°C, respectively (see Table 3). One asterisk indicates a data set with GSP <222 cm. Two asterisks indicate that the result varies depending on 20 nearest neighbors; asterisked values are estimated to be the same as AbsD for CCA analysis.

Method	Data set	Variable	AbsBO	AbsDB	AvgAll	AvgW	AvgC
<u>Existing</u>							
LRA	CLAMP 3B	MAP	20	30	7	15	-2
NN	CLAMP 3A	GSP	20	21**	9	28	-10
MRA	CLAMP 3B*	GSP	23	24	-8	-9	-7
CCA	CLAMP 3B	GSP	25	21	17	34	1
LRA	Western Hem./Africa	MAP	27	30	-26	-27	-25
<u>Existing + Bolivia</u>							
LRA	CLAMP 3B + Bo.	MAP	20	32	6	14	-2
LRA	Western Hem./Africa + Bo.	MAP	20	30	-15	-15	-15
NN	CLAMP 3A + Bo.	GSP	22	19**	18	24	13
MRA	CLAMP 3B + Bo.*	GSP	23	20	-16	-27	-6
CCA	CLAMP 3B + Bo.	GSP	23	19	12	24	-1
<u>Bolivia only</u>							
LRA (Me1)	Bolivia	GSP/MAP	13		1	-3	4
LRA (MlnA)	Bolivia	GSP/MAP	16		-2	-7	3

dence analysis of the combined CLAMP 3B and Bolivia data set (Table 5).

In terms of data sets, models based on the Bolivian and east Asian data sets produced more accurate results than models based on the CLAMP data set. Note that adding the Bolivian data to the CLAMP data set made the nearest-neighbor and canonical correspondence analyses slightly less accurate than analysis of the CLAMP data set alone (Table 5). As for types of models, the linear regression models yielded more accurate estimates than the multivariate models of the CLAMP data set, while multivariate models yielded more accurate estimates for the Bolivia-only data set.

Most of the models tended to underestimate the MAT of sites with MATs above 20°C and to overestimate the MAT of sites with MATs below 18°C (Table 5). This tendency occurs because the slope of the regression of MAT as a function of percentage of entire-margined species is higher for the Bolivian data set than for all the other data sets (Fig. 2A); recall that this relationship is the strongest observed between MAT and leaf morphology. According to the slope equality test of Sokal and Rohlf (1995: p. 498), however, the slope of the Bolivian regression (3.6%/°C) is statistically indistinguishable ($p < 0.05$) from that of the other data sets.

It is possible that this comparison of regression lines is biased by the fact that the Bolivian data set has a much smaller range of MAT and mean growing-season precipitation than the CLAMP 3B data set, which includes sites with MATs from 4°C to 26.9°C and mean growing-season precipitation from 6 cm to 429 cm. Sites that are cooler or wetter than the Bolivian sites might have a different relationship between percentage of entire-margined species and MAT, thus making the regressions look the same, when in reality the relationships for that climate are different.

To test this idea, I calculated the regression for a subset of 42 sites from the CLAMP 3B data set for which MAT was between 12° and 26°C and mean annual precipitation was between 45 and 140 cm (Fig. 2B). I could limit the east Asian data set only in terms of temperature because precipitation data were not

available. The slope equality tests show that these regressions are also statistically indistinguishable ($p < 0.05$) from that of the Bolivian data set.

The comparison between slopes of the Bolivian and other regressions must also be viewed in the light of the small size of the Bolivian data set; the smaller the data set, the larger the potential effect of additional data points. For example, if the two samples of Wilf (1997) are added to the Bolivian data set, the resulting regression has a slope of 3.2%/°C, which is more similar to the other data sets.

The tendency to underpredict the MAT of warm sites and overpredict the MAT of cool sites is especially marked in the results from canonical correspondence analyses (Table 5). As can be seen in Figure 3A, the MAT vector score increases sharply as MAT increases for the CLAMP 3B data, but varies little for the Bolivian data. As a result, canonical correspondence analysis estimates that the MATs of the 12 Bolivian sites range only from 15.5° to 20.5°C, when in reality they range from 12.5° to 25.5°C.

Precipitation Analysis

The precipitation models all produced reasonably accurate estimates for the Bolivian sites; the average absolute errors ranged from 13 cm for linear regression analysis of the Bolivia-only data set to 27 cm for linear regression analysis of the Western Hemisphere/Africa data set (Table 6).

In terms of data sets, the models based on the Bolivia-only data set produced more accurate results than models based on any other data set; they had the lowest average absolute errors and the least amount of systematic bias. In contrast to the temperature models, when the Bolivian data were added to the CLAMP data set, the estimates from canonical correspondence analyses were no less accurate than when the CLAMP data set alone was used (Table 6).

As for types of models, the univariate and multivariate models of the CLAMP data set performed equally well. The comparison could not be made for the Bolivian data set, because no multiple regression models could

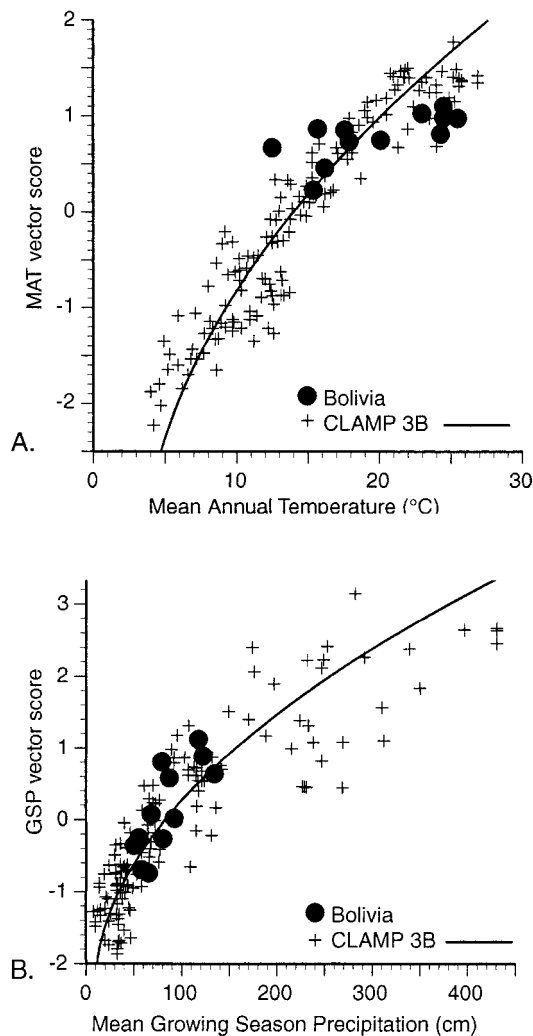


FIGURE 3. A, MAT vs. MAT vector score ($= -0.941 \times \text{axis 1 score} + 0.287 \times \text{axis 2 score}$) for canonical correspondence analysis of the CLAMP 3B + Bolivia data set. B, Mean growing-season precipitation vs. mean growing-season precipitation vector score ($= 0.038 \times \text{axis 1 score} + 0.972 \times \text{axis 2 score}$) for canonical correspondence analysis of the CLAMP 3B + Bolivia data set.

be found that were an improvement over linear models.

Unlike the temperature models, which had a fairly consistent systematic bias, the trends for the precipitation models are mixed. Linear regression, nearest-neighbor, and canonical correspondence analysis of the CLAMP data set tend to overpredict the precipitation of the warmer/moister sites, while multiple regression models tend to underpredict the precipitation of these sites. Note that the canonical

correspondence analysis vector scores for the Bolivian data are more consistent with CLAMP 3B data for the precipitation analysis than for the temperature analysis (Fig. 3B).

The regression of MlnA versus mean annual precipitation (MAP) for the Western Hemisphere/Africa data set tends to underpredict precipitation for the Bolivian sites. Though the slope of the Bolivian regression is indistinguishable from this regression at the $p < 0.05$ level, we can see from Figure 4A that for a given MAP, mean leaf size tends to be larger in the Western Hemisphere/Africa data set than for the Bolivian and CLAMP 3B data sets. A t -test of those sites in the Bolivian and Wilf et al. (1998) data sets with similar MAPs (Fig. 4B) suggests that this difference is significant at the $p < 0.05$ level.

For the models that produced estimates of mean growing-season precipitation, namely multiple regression, canonical correspondence, and nearest-neighbor analysis, the results were calculated using both mean growing-season precipitation and wet-months precipitation of the Bolivian sites (Table 7). Recall that mean growing-season precipitation uses a temperature-based definition of the growing season, which may not be appropriate for the low-latitude Bolivian sites. The errors tended to be slightly larger for wet-months precipitation.

Discussion of Climate Analysis

Major Relationships with Climate

The regression of percentage of entire-margined species versus MAT for the Bolivian data set is indistinguishable from the regression for the CLAMP 3A, CLAMP 3B, and east Asian data sets, suggesting that Bolivian vegetation has a relationship between leaf margin and temperature similar to that of Northern Hemisphere vegetation.

In terms of trends with precipitation, the regression between mean natural log leaf size and natural log MAP is similar for the Bolivian and CLAMP 3B data sets; however mean leaf size for a given MAP tends to be smaller for the Bolivian data set than for the Western Hemisphere/Africa data set. Wolfe (1993) and Richards (1996) find that leaf size is smaller

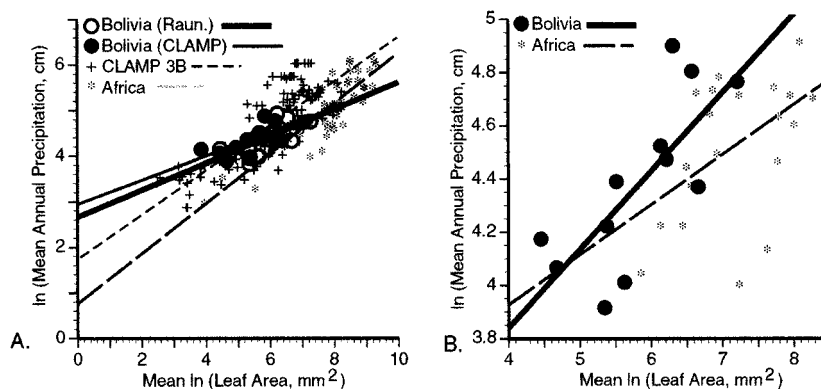


FIGURE 4. A, Natural log of mean annual precipitation (MAP) vs. the mean natural log leaf area (MlnA) for different data sets: Bolivia, as calculated using the Raunkiaer-Webb size categories ($\ln\text{MAP} = 2.64 + 0.298 \cdot \text{MlnA}$, $r^2 = 52\%$, $\text{SE} = 0.22$, $F = 12.7$); Bolivia as calculated using the CLAMP size categories; CLAMP 3B (CLAMP categories); and Western Hemisphere/Africa (Raunkiaer-Webb categories) (for equations see Table 1). B, Natural log of MAP vs. MlnA for the Bolivian sites (calculated using the Raunkiaer-Webb size categories) and for a subset of the Western Hemisphere/Africa data set consisting of sites with the same range of MAP as the Bolivian sites.

for forests growing on sandy, nutrient-poor soils; thus, the poorly developed and leached soils of the Bolivian samples could be a reason for the smaller leaf sizes.

However, Wilf et al. (1998, 1999) noted that samples in the CLAMP data set also tended to have smaller leaf sizes than samples in the Western Hemisphere/Africa data set. Recall that the Bolivian samples were collected from live forests using the methodology of Wolfe (1993) for collecting CLAMP samples, in which every species of woody dicotyledon is collected from a riparian area of limited geographical extent. In contrast, the 50 sites of Wilf et al. (1998) are mostly from the literature

and represent a variety of sampling methods. Some samples are from all woody species in a sample plot, and would thus be analogous to a CLAMP sample, but others are from floral manuals and regional ecology studies, which can represent up to thousands of square kilometers.

To test the effect of sampling strategy on leaf size, Wolfe and Uemura (1999) compared CLAMP samples with data taken from the corresponding floral manual for eight sites in southern Japan. They found that the leaf areas from the CLAMP samples were consistently smaller than those derived from the floral manual. They suggest that this trend occurs because a floral manual covers the entire range of a species, while the CLAMP samples are taken from a restricted climate zone. Thus, the smaller size of the Bolivian samples is most likely due to differences in sampling strategy rather than to differences in soils, or to a difference in the relationship between leaf morphology and climate.

Another interesting result from the precipitation analysis is that calculating wet-months precipitation, as opposed to mean growing-season precipitation, for the Bolivian sites did not result in smaller errors, even though using a precipitation-based measure of the growing season was thought to be more appropriate for the low-latitude Bolivian sites. Perhaps the es-

TABLE 7. Average absolute error of precipitation estimates for Bolivian sites, when compared with wet-months precipitation (WMP) (predicted GSP - measured WMP) and mean growing-season precipitation (GSP) (predicted GSP - measured GSP). An asterisk indicates a data set with GSP <222 cm.

Method	Data set	WMP	GSP
	<u>Existing</u>		
NN	CLAMP 3A	24	20
MRA	CLAMP 3B*	23	23
CCA	CLAMP 3B	30	25
	<u>Existing + Bolivia</u>		
NN	CLAMP 3A + Bo.	26	22
CCA	CLAMP 3B + Bo.	27	23
MRA	CLAMP 3B + Bo.	25	23
	<u>Bolivia only</u>		
LRA (Me1)	Bolivia	15	13

TABLE 8. Comparison of average absolute errors for mean annual temperature estimates from leaf margin analysis (LMA), canonical correspondence analysis (CCA), nearest-neighbor analysis (NNA), and multiple regression analysis (MRA), from analysis on some version of the CLAMP data set, and from analysis of data sets from the same leaf morphology domain. Data set = sites for which mean annual temperature was calculated. n = number of sites in data set. Model data set = data set(s) on which LMA, CCA, and MRA models were based. NNA based on CLAMP 3A + Bolivia, or CLAMP 1A + New Zealand data sets. Errors calculated by author except where noted. ¹Data from Jordan (1997: p. 539). ²Average absolute error for LMA calculated from data of Kennedy (1998: Table 6.8). Errors for CCA and NNA from Stranks and England (1997: pp. 21–22) stated on RMS misfit rather than the average absolute error. ³CCA analysis of Kennedy (1998: Table 6.8). An asterisk indicates best analysis for data set.

Data set	n	Model data set	Univariate		Multivariate	
			LMA	CCA	NNA	MRA
<u>CLAMP data set</u>						
Bolivia	12	CLAMP 3B + Bo.	1.6*	3.0	2.2	—
Subalpine	29	CLAMP 3A	4.9	3.8	2.5*	3.4
Australia + NZ ¹	14	East Asia, CLAMP 3B	9.4	8.2*	n/a	n/a
New Zealand ²	32	CLAMP 1A	8.9	3.0	2.1*	—
New Zealand ²	32	CLAMP 1A + N.Z.	6.2	4.8	2.3*	n/a
<u>Same domain</u>						
Bolivia	12	Bolivia	1.1	—	2.2	0.6*
CLAMP 3B	144	CLAMP 3B	1.8	1.5	1.4*	1.6
Subalpine	29	Subalpine	2.0	2.2	2.5	1.6*
New Zealand ³	32	New Zealand ³	—	1.0*	2.3	—

timates would be improved if wet-months precipitation were also calculated for low-latitude sites in the CLAMP data set.

Thus, overall, the major relationships between leaf morphology and climate are similar for the Bolivian and CLAMP 3B data sets. However, more sampling of Bolivian vegetation is needed to confirm this result.

Additional Relationships with Climate

For the MAT estimates, errors from multivariate CLAMP-based models are larger than those for linear regression analyses of the same data sets; for precipitation, results from univariate and multivariate modeling are similar. One might have expected that the additional climatic and leaf morphologic data used in the multivariate, CLAMP-based analyses would improve the accuracy of the temperature estimates.

The fact that the additional data made the estimates no more accurate suggests that the additional leaf morphology character states either (1) contribute more noise than information (Wilf 1997) or (2) have a different relationship with climate for the Bolivian sites, that is, reflect a region effect. Regarding the former possibility, Wilf (1997) found that while his rescaling of the Barro Colorado Is-

land CLAMP sample had the same proportion of entire-margined species as the scoring of the same leaves by Wolfe (1993), his scores varied for more-subjective character states, such as apex acute. Wiemann et al. (1998) also reported problems with reliable scoring of some character states. Thus, errors in scoring procedure may exceed the signal of some leaf morphology character states.

In some cases, however, the additional character states do contribute information. For example, multivariate analysis produces smaller temperature errors than linear regression analysis for the Bolivia-only data set and the CLAMP 3B data set (Table 8). However, in both cases samples are compared with a data set that was scored by the same worker and thus do not address the question of whether the climate signal is greater than scoring error.

Implications for Estimating Climate from Fossil Floras

Choosing a Predictor Data Set

The analysis of the Bolivian samples provides insight into how one can derive the most accurate paleoclimate estimates for fossil floras. The results indicate that choosing an appropriate predictor data set is important, be-

cause the closer its relationships between leaf morphology and climate to those of the site to be analyzed, the more accurate the climate estimates will be.

As of now, it appears that we can divide the globe into three domains based on similar leaf morphology: (1) the CLAMP domain, which includes North America, the Caribbean, Bolivia, Japan, Fiji, and New Caledonia; (2) Australia/New Zealand; and (3) subalpine zones. The differences in leaf morphology observed between these domains can be due to differences in the climate, environmental conditions, floristic composition, or scoring style.

For some of these areas, workers have proposed causes for the observed region effect; in the case of New Zealand floras, Kennedy (1998) suggests that their distinct leaf morphology is probably due to the isolation of New Zealand since the mid-Cretaceous. Thus we can suspect that post-middle Cretaceous floras from New Zealand should be compared with modern New Zealand floras.

In the case of subalpine floras, their distinct nature is probably due to extreme cold (Wolfe 1993), and the most accurate estimates of temperature for fossil subalpine floras would most likely be based on a data set of modern subalpine floras. However, subalpine floras can be difficult to identify in the fossil record. As of now, the most quantitative estimates of paleoelevation are derived from climate analysis of fossil floras (Chase et al. 1998; Forest et al. 1999), which poses a problem of circular reasoning.

Wolfe (1993) suggests that subalpine floras can be identified in the fossil record by plotting axis scores derived from correspondence analysis; subalpine sites plot in a distinct nest away from the rest of the CLAMP sites on graphs of axis 1 scores versus axis 3 scores. It is possible that other sites with a different relationship between MAT and the percentage of entire-margined species can be identified using this method. For example, the New Zealand sites of Stranks and England (1997) also plot in a distinct nest away from the rest of the CLAMP sites.

There are problems with this approach, however. The axis scores of each site change with each new site added to the data set, and

what was formerly an outlier can become less so as more sites are added. For example, the separation of the subalpine sites from the rest of the CLAMP 3B data set disappears when the Bolivian sites are added. Also, the fact that a site is an outlier does not mean it has different relationships than the CLAMP sites; some of the Bolivian sites plot away from the CLAMP sites yet respond quite well to univariate analysis.

Another possible way to identify fossil subalpine sites would be to look at the number of subalpine sites among the 20 nearest neighbors identified by the resemblance function of Stranks and England (1997); 27 of the 29 subalpine sites identified by Wolfe (1993) have at least 10 subalpine nearest neighbors. Of course, this criterion might also change as more sites are added to the data set.

As for the CLAMP leaf morphology domain, one would suspect that fossil floras from this area should be compared with the CLAMP 3B + Bolivia data set. However, we must be cautious because we do not yet understand the causes of the region effect; there are likely to be many exceptions to this broad generalization. For example, Cretaceous and early Tertiary high-latitude vegetation, which grew under warm, low-light conditions, has no modern analogue (Herman and Spicer 1997); so even though the CLAMP 3B data set contains modern samples from Alaska, it is not necessarily appropriate for comparison. Another question is whether South American vegetation truly belongs in the CLAMP domain. The data set is small and from a limited region; additional sites are needed to confirm the observed relationships.

In all these cases, the assumption is that the relationships between leaf morphology and climate have not changed significantly since the late Cretaceous, and thus that modern floras can be compared with fossil floras. This is probably a reasonable conjecture because the relationships are based on physiology rather than systematics. Also, the fact that modern vegetations from widely separated areas have similar relationships suggests that the relationships between leaf morphology and climate have not changed significantly over time.

One also makes the assumption that taph-

onomic bias does not significantly affect the leaf morphology of fossil floras. However, some studies suggest that the processes associated with fossilization, such as leaf fall, transport, and deposition, can discriminate against larger leaves (Roth and Dilcher 1978; Greenwood 1992). A small study by Wolfe (1993) suggests that this bias does not have a large effect on climate estimates, but more work is needed.

In summary, choosing an appropriate data set for comparison with a fossil flora is complicated by the fact that we do not understand why there are different correlations between climate and leaf morphology in different regions. We can suspect that in some cases, floras from a given leaf morphology domain should be compared with modern floras from that same domain, but this will not always be true. To make more intelligent choices of predictor data sets, we need (1) additional collections of modern floras, which would help define leaf morphology domains and uncover the causes of their distinct nature; (2) taphonomic studies, which would help discover any biases in comparing fossil with modern samples; and (3) independent climate estimates from other quantitative indicators, such as stable isotopes (e.g., Bao et al. 1999), which would help verify the climate estimates from leaf morphology.

Univariate versus Multivariate Models

After one has chosen an appropriate predictor data set for a fossil flora, then one must choose a type of statistical analysis. To get a better idea which analysis techniques produce the smallest residuals, data sets from all three leaf morphology domains were analyzed using models based on some version of the CLAMP data set and a data set from the same domain (Table 8). From this analysis, one cannot make a general recommendation about which analytical method is best, because the results vary with the nature of the predictor data set.

If the data set is small and from a fairly limited geographical region, and the site to be analyzed has similar relationships, then multiple regression or canonical correspondence analysis appears to be the best method to use. For

example, multiple regression produced the most accurate temperature and precipitation results for the Bolivian sites from the Bolivia-only data set and for the subalpine sites from the subalpine-only data set, and canonical correspondence analysis produced the most accurate temperature results for the New Zealand sites from the New Zealand-only data set (Table 8). Note, however, that the raw data were not available for this latter data set, so a multiple regression model could not be developed.

For the CLAMP data set, which is a fairly large data set from a varied region, nearest-neighbor analysis tends to give the best temperature results, especially if the CLAMP data set has different relationships than the site to be analyzed. The Bolivian sites are an exception to this generalization, because univariate models provided more accurate temperature results than any of the multivariate models of the CLAMP data set. As discussed above, the smaller residuals from univariate analysis could reflect scoring errors or a small region effect. For precipitation, at least for the Bolivian data set, univariate and multivariate analyses achieved similar results.

The results for the New Zealand, Australian, and subalpine floras suggest that if none of the modern data sets are considered appropriate for comparison—for example, in the case of the Early Tertiary high-latitude floras—then the nearest-neighbor method is the best technique to use. The results from this analytical technique are robust in the sense that fairly accurate results can be obtained using a data set that has different relationships between leaf morphology and climate than the site to be analyzed. For example, nearest-neighbor analysis produces the best results when the subalpine and New Zealand sites are compared with the CLAMP data set. However, with the exception of the CLAMP data set, this method results in less accurate results than if one chooses an appropriate data set and applies another statistical method.

One caution with the nearest-neighbor method is that in this study, both temperature and precipitation estimates became slightly less accurate when the Bolivian sites were

added to the CLAMP data set. Stranks and England (1997) obtained a similar result for New Zealand floras; nearest-neighbor estimates were slightly less accurate for the CLAMP 1A + New Zealand data set than for the CLAMP data set alone. One would think that the addition of similar sites would improve estimates. The fact that it does not suggests that building a larger predictor data set may not necessarily improve paleoclimate estimates from this method; thus, to obtain accurate results, it may be necessary to select among the predictor sites.

Of course, all these recommendations are based on the analysis of only a few data sets; more analyses are needed to further explore the question of which statistical methods produce the best results. What this study does demonstrate is that the discussion over univariate versus multivariate models cannot be separated from a discussion of data sets.

Conclusions

The comparison of 12 living foliage samples from Bolivia with data sets from other regions suggests the following conclusions:

1. We can divide climate–leaf morphology data sets into three domains: (1) CLAMP, which includes North America, the Caribbean, Japan, Fiji, and New Caledonia; (2) Australia/New Zealand; and (3) subalpine zones. Differences in the relationships between climate and leaf morphology occur between these domains because of differences in climate, environmental factors, floristics, and/or the scoring style of investigators.

2. Bolivian vegetation and vegetation in the CLAMP 3B data set appear to have similar relationships between the percentage of entire margined species and mean annual temperature and between mean leaf size and mean annual precipitation. Thus, Bolivian vegetation should be considered part of the CLAMP leaf morphology domain. However, the fact that canonical correspondence analysis produces the largest errors of any of the statistical analysis methods suggests either scoring errors in the other leaf character states or a small region effect.

3. The mean leaf size of the Bolivian sam-

ples is smaller than the mean leaf size of samples from the Western Hemisphere/Africa data set of Wilf et al. (1998). This difference is more likely the result of worker-related differences in sampling strategy than to differences in the relationship between size and precipitation.

4. The most accurate climate estimates for a fossil flora will be produced by the predictor data set with the most similar climate–leaf morphology relationships. However, because we do not understand why leaf morphology varies between domains, it is difficult to choose such data sets. For now, it is probably best to compare fossil floras with modern floras from the same leaf morphology domain; however, more work is needed to improve on this simplistic strategy.

5. One cannot make a definitive statement about whether univariate or multivariate methods produce more accurate temperature estimates, because their performance depends on the nature of the predictor data set. However, one can generalize that (1) multiple regression analysis tends to produce the most accurate estimates for small data sets with a narrow range of environmental variation that have similar relationships to those of the fossil flora, (2) linear regression or canonical correspondence analysis produces the most accurate estimates for the larger and more varied CLAMP data set of J. A. Wolfe, and (3) nearest-neighbor analysis produces the most accurate results if the leaf-climate relationships in the predictor data set are different from those in the site to be analyzed.

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Appendix

CLAMP scores for each sample site. The current version of CLAMP is scored for 31 character states, which are organized into 13 categories numbered from 1 to 13 in the leaf margin character states (LMCS) column. Some categories, such as "No teeth" and "Apex emarginate," have only one character state. They receive a score of 1 if the character state is present, a score of 0.5 if partly present, and a score of 0 if absent. Other categories, such as "Size," contain several character states. If present, these character states receive a score of 1 divided by the total number of character states present in the category; if partly present, they receive a score of 0.5 divided by the number of character states present in the category, and if absent, they receive a score of 0. For example, a species in the Mi1-2 size category with toothed leaves and with rounded, emarginate apices would be scored NoT = 0; Mi1 = $\frac{1}{2}$ = 0.5; Mi2 = $\frac{1}{2}$ = 0.5; AEmg = 1; ARnd = 1. Species scores are then added for each character state and divided by total number of forms to derive the morphologic score. See Wolfe 1993 for details of scoring and definitions. The value for MlnA (R-Webb) was determined for each site after the equation of Wilf et al. (1998): $MlnA = \sum a_i p_i$ where a_i = the means of the natural log areas of the Raunkiaer-Webb size categories and p_i represents the proportion of species in each size category. MlnA (CLAMP) values were calculated using the CLAMP leaf-size classification system. Because these size categories differ from the Raunkiaer-Webb size categories, a_i values had to be recalculated. The size of the CLAMP size categories was measured from the CLAMP size template of A. B. Herman et al. (unpublished) and are as follows: Nan = 0-5 mm², Le1 = 5-25 mm², Le2 = 25-80 mm², Mi1 = 80-400 mm², Mi2 = 400-1400 mm², Mi3 = 1400-3600 mm², Me1 = 3600-6400 mm², Me2 = 6400-10,400 mm², Me3 = 10,400+ mm². Note that these values differ from those in Forest et al. 1999, in which Me2 and Me3 were measured incorrectly. The measured values were used to calculate the value of a for each size category: 0.80, 2.41, 3.80, 5.19, 6.62, 7.72, 8.48, 9.01, and 9.61, with the exception that the lower size limit of Nan was changed to 1 mm² instead of 0 mm² because the natural log of 0 cannot be calculated, and the upper size limit of Me3, which is not given in the latest CLAMP size template, was set at 21,280 mm². This value was calculated by following the general size progression of the CLAMP size categories, in which each leaf size increases in length by ~4 cm and in width by ~1.8 cm, and by calculating two size classes larger than the Me3 size category. Typically, there are very few leaves in the Me3 size category; thus the number chosen for the upper limit has little effect on the value of MlnA. Abbreviations: LMCS = leaf morphologic character state; TLob = teeth lobed; NoT = no teeth; TRg = teeth regularly spaced; TCl = teeth closely spaced; TRnd = teeth round; TAct = teeth acute; TCmp = teeth compound; Nan = nanophyllous; Le1,2 = leptophyllous 1,2; Mi1,2,3 = microphyllous 1,2,3; Me1,2,3 = mesophyllous 1,2,3; AEmg = apex emarginate; ARnd = apex round; AAct = apex acute, AAtn = apex attenuate, BCd = base cordate, BRnd = base round, BAct = base acute, LW = length-to-width ratio, SOb = shape obovate, SElp = shape elliptical, SOv = shape ovate, SJ = San José de Chiquitos, SC = Santa Cruz, SI = San Ignacio de Velasco, CP = Concepción, CM = Camiri, MA = Monteagudo, PD = Padilla, CB = Cochabamba, ZD = Zudañez, SU = Sucre, SO = Sorata, TB = Tarabuco.

LMCS	SJ	SC	SI	CP	CM	MA	PD	CB	ZD	SU	SO	TB
TLob (1)	2.3	3.4	4.9	2.6	2.6	4.1	6.3	0.0	7.5	1.7	0.0	7.8
NoT (2)	77.9	76.1	76.8	68.4	72.4	59.5	56.3	59.1	53.8	53.4	45.0	45.3
TRg (3)	15.1	18.2	14.6	22.4	14.5	28.4	27.3	21.6	33.1	27.6	44.2	23.4
TCl (4)	4.7	4.5	1.2	9.2	5.9	8.1	1.6	15.9	6.3	12.1	27.5	6.3
TRnd (5)	15.1	11.9	13.4	27.0	14.5	28.4	10.9	28.4	31.9	37.1	29.2	25.0
TAct (6)	7.0	11.9	9.8	4.6	13.2	12.2	32.8	12.5	14.4	9.5	25.8	29.7
TCmp (7)	5.8	2.3	4.9	9.2	5.3	5.4	4.7	6.8	4.4	5.2	10.0	3.1
Size (8)												
Nan	9.3	8.0	9.1	2.2	5.3	5.4	9.1	10.2	7.6	14.9	5.6	7.8
Le1	7.0	6.4	3.5	2.2	2.6	3.4	8.3	11.7	6.3	19.8	13.4	12.2
Le2	10.0	12.0	6.9	8.1	11.6	7.5	20.8	20.8	11.7	25.3	16.2	25.5
Mi1	18.9	21.0	14.6	10.7	28.7	17.7	28.2	29.9	29.0	26.7	20.4	37.2
Mi2	24.9	19.8	24.2	17.4	28.7	27.4	21.2	15.9	30.8	10.6	24.4	14.8
Mi3	19.1	13.4	19.5	23.1	12.3	18.6	9.0	11.4	9.9	1.7	11.6	1.6
Me1	8.0	10.6	14.8	18.5	5.0	12.3	1.7	0.0	3.6	0.9	5.4	0.8
Me2	2.1	5.4	6.7	11.1	2.4	5.2	1.7	0.0	0.5	0.0	2.3	0.0
Me3	0.8	3.4	0.6	6.7	3.3	2.4	0.0	0.0	0.5	0.0	0.7	0.0
AEmg (9)	37.2	13.6	22.0	21.1	21.1	16.2	0.0	9.1	5.0	3.4	6.7	15.6
Apex (10)												
ARnd	59.7	43.2	46.7	54.4	57.0	45.9	42.2	52.3	40.0	48.3	44.4	48.4
AAct	32.9	45.5	33.3	28.1	38.6	40.5	57.8	47.7	58.8	51.7	54.4	51.6
AAtn	7.4	11.4	19.9	17.5	4.4	13.5	0.0	0.0	1.3	0.0	1.1	0.0
Base												
BCd	24.0	11.4	18.7	23.7	9.2	12.2	3.1	4.5	12.5	0.0	3.3	0.0
BRnd	43.8	46.6	51.6	51.3	50.0	55.4	43.8	45.5	50.0	46.6	46.7	51.6
BAct	32.2	42.0	29.7	25.0	40.8	32.4	53.1	50.0	37.5	53.4	50.0	48.4
LW (12)												
LW < 1:1	4.7	1.1	3.3	1.3	6.6	1.4	0.0	0.0	2.5	0.0	0.0	0.0
LW 1-2:1	50.8	28.0	45.9	44.7	26.8	34.0	12.5	21.2	25.4	16.7	32.8	26.0
LW 2-3:1	30.6	31.4	36.2	38.2	43.4	37.2	45.3	37.9	30.8	30.5	37.2	28.6
LW 3-4:1	8.5	18.9	11.0	10.5	17.1	16.9	20.3	26.5	22.1	25.3	18.9	22.4
LW > 4:1	5.4	20.5	3.7	5.3	6.1	10.6	21.9	14.4	19.2	27.6	11.1	22.9

Appendix. Continued.

LMCS	SJ	SC	SI	CP	CM	MA	PD	CB	ZD	SU	SO	TB
Shape (13)												
Sob	11.6	14.4	11.8	7.9	10.5	13.5	10.9	13.6	11.3	6.9	6.7	14.1
SElp	54.7	61.0	58.1	59.2	61.8	62.2	65.6	50.0	48.8	63.8	53.3	57.8
Sov	33.7	24.6	30.1	32.9	27.6	24.3	23.4	36.4	40.0	29.3	40.0	28.1
MlnA (CLAMP)	5.67	5.82	6.21	7.08	5.85	6.33	4.92	4.64	5.37	3.86	5.28	4.43
MlnA (R-Webb)	6.14	6.30	6.57	7.21	6.20	6.66	5.37	5.34	5.62	4.45	5.51	4.68