Using fossil leaves as paleoprecipitation indicators: An Eocene example

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ABSTRACT

Estimates of past precipitation are of broad interest for many areas of inquiry, including reconstructions of past environments and topography, climate modeling, and ocean circulation studies. The shapes and sizes of living leaves are highly sensitive to moisture conditions, and assemblages of fossil leaves of flowering plants have great potential as paleoprecipitation indicators. Most quantitative estimates of paleoprecipitation have been based on a multivariate data set of morphological leaf characters measured from samples of living vegetation tied to climate stations. However, when tested on extant forests, this method has consistently overestimated precipitation. We present a simpler approach that uses only the mean leaf area of a vegetation sample as a predictor variable but incorporates a broad range of annual precipitation and geographic coverage into the predictor set. The significant relationship that results, in addition to having value for paleoclimatic reconstruction, refines understanding of the long-observed positive relationship between leaf area and precipitation. Seven precipitation estimates for the Eocene of the Western United States are revised as lower than previously published but remain far wetter than the same areas today. Abundant moisture may have been an important factor in maintaining warm, frost-free conditions in the Eocene because of the major role of water vapor in retaining and transporting atmospheric heat.

INTRODUCTION

Fossil leaves are a rich source of information about past rainfall because the morphologies of living leaves, and leaf size in particular, are greatly influenced by available moisture (Raunkiaer, 1934; Richards, 1996). Because leaves transpire water into the atmosphere and have a high ratio of surface area to volume, plants in drier climates tend to have smaller leaves because they cannot afford the elevated water loss required to maintain large leaves (Givnish, 1984). Available water, which is controlled by many factors including precipitation, evapotranspiration, temperature, seasonality, and soil conditions, appears to be the primary control on the size of an average leaf (Givnish, 1984; Richards, 1996). Mean annual precipitation is a proxy for available water that is both readily available from climate stations and applicable to a wide variety of research. The emphasis of this paper is therefore on the correlation between mean annual precipitation (MAP) and leaf morphology.

Recent paleoprecipitation estimates have been based on Wolfe's (1993) Climate Leaf-Analysis Multivariate Program (CLAMP), which ordinates a multivariate data set of leaf-morphologic characters scored from modern vegetational samples that are associated with climate stations to provide a quantitative framework for estimating climatic variables. The CLAMP samples are primarily from North American forests, and few are from the moist tropics. Estimates of MAP and other variables such as growing season precipitation have been derived either using CLAMP (Wolfe, 1994; Herman and Spicer, 1996, 1997) or multiple regression analysis of the CLAMP data set (Wing and Greenwood, 1993; Greenwood, 1996; Gregory and McIntosh, 1996). Most of these authors have noted the approximate nature of the statistical fits and urged caution when interpreting results. Only the multiple regression approach has been tested on living forests, with the result that both mean annual and growing season precipitation are consistently overestimated (Table 1).

An alternative to methods based on CLAMP is a reexamination of the positive univariate relationship between leaf area and annual precipitation (Webb, 1968; Dilcher, 1973; Dolph and Dilcher, 1980a, 1980b; Hall and Swaine, 1981; Givnish, 1984). Givnish (1984) quantified this relationship for a broad range of forest types in South America, Costa Rica, and Australia and found it to be significant. Preliminary tests of Givnish's equations with new data gave promising results, leading to the revised and expanded analysis presented here.

TABLE 1. PRECIPITATION IN LIVING FORESTS, ESTIMATED FROM MULTIPLE REGRESSION ANALYSIS OF THE CLAMP DATA SET

Forest	Estimated (cm)	Actual (cm)
(1) Uganda, woodland	243*; 164[†]	124*; 60.5[†]
(2) Uganda, Mpanga rain forest	338*; 298[†]	136*; 45.9[†]
(3) Costa Rica, Santa Rosa National Park	212*; 207[§]	161*[§]
(4) Panamá, Barro Colorado Island	494*[§]	261*[§]
(5) Puerto Rico, Guánica Forest	162*[§]	86.0*[§]
(6) Pennsylvania, York County	260[§]	104*
(7) Pennsylvania, Allegheny National Forest	258[§]	116*

Notes: Uganda data from Jacobs and Deino (1996); Costa Rica data from Burnham (1997). Estimates (1-3) used multiple regression models of Wing and Greenwood (1993). Estimates (4-7) are from "subsamples" of Wilf (1997), multiple regression model of Wilf (1996).
*Mean annual precipitation.
[†]Three-month growing-season precipitation.
[§]Total growing season precipitation. For the Pennsylvania samples, mean annual precipitation is therefore estimated as > 258 cm.

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LEAF AREA AND PRECIPITATION[1]

We selected fifty vegetation samples from living forests for our predictor set (Table 2), encompassing a wide variety of climates and vegetation. No samples were included from areas with few climate data, extreme winter cold and dry growing seasons, severe human modification, high salinity, or marked nutrient deficiencies. Samples with fewer than 16 species were excluded because above this value regression statistics were highly similar, but below about 16 species the fit deteriorated. Plants that were not native, dicotyledonous, woody, and leaf-bearing were excluded whenever they could be identified as such from species lists, as were mangroves, which typically inhabit saline environments. Ground herbs were uniformly excluded.

The mean of the natural logarithms of the species' leaf areas (MlnA) was estimated for each sample in either of two ways: directly from leaf-area measurements when possible, for seven samples, or, for the other 43 samples, from the proportions of species reported in each of the traditional Raunkiaer-Webb size categories (Raunkiaer, 1934; Webb, 1959; Fig. 1; Table 2). For compound leaves, leaflets were used instead of leaves. If two size classes were originally merged into one, separate values for the two size classes were log-interpolated.

For the direct measurement approach, we used either actual measurements of leaf area or length and width data from manuals, supplemented with U.S. National Herbarium material. For the latter, area values for each species were calculated as the mean of the natural log areas of the smallest and largest leaves, where leaf area was approximated as two-thirds length × width (Cain and Castro, 1959). The MlnA for the 43 samples scored with size categories was MlnA $= \sum a_i p_i$, where a_i represents the seven means of the natural log areas of the size categories (2.12, 4.32, 6.51, 8.01, 9.11, 10.9, and 13.1), and p_i represents the proportions of species in each category. Because the size classes are mostly a geometric series with a factor of nine, the lower bound of leptophyll was taken as the upper bound divided by nine, and the upper bound of megaphyll as the lower bound multiplied by nine (Givnish, 1984). This computation is similar to Givnish's "average width" (Givnish, 1984) and to the leaf size index (LSI) of Wolfe and Upchurch (1987). As a cross check, we converted the directly measured samples to Raunkiaer-Webb categories; changes in derived MlnA were small (maximum of 0.24).

The highly significant fit of MlnA as a function of mean annual precipitation is shown in Figure 2. The fit can be inverted for paleoclimatic purposes so that MAP is the dependent variable: ln(MAP) = 0.548 MlnA + 0.768, $r^2 = 0.760$, standard error = 0.359, $F (1,48) = 152, p = 10^{-15}$. We will refer to the application of the preceding as leaf-area analysis. The quality of fit is lower when ln(MAP) is regressed against LSI ($r^2 = 0.720, F = 124$).

We also compared the slope of the relationship of MAP as a function of the percentage of species with large leaves in our data set to that in the CLAMP data set of Wolfe (1993; Fig. 3). Because the percentages of species in the two largest size categories in CLAMP (Fig. 1) are values closely associated with moisture (Wolfe, 1993), a steeper slope in the CLAMP data set than in ours might explain the consistent pattern of overestimated MAP seen in Table 1. For the CLAMP data set, the percentage of large leaves was taken as the summed percentage of mesophylls 1 and 2 (Fig. 1) and for our data set as the summed percentage of mesophylls, macrophylls, and megaphylls. The comparison is not exact because the CLAMP mesophyll 1 category includes the upper part of the Raunkiaer-Webb notophyll category (Fig. 1). The result of this mismatch should be that most CLAMP sites have a higher percentage of species with large leaves at a given MAP than do our sites, and that the slope in question is lower in the CLAMP data set than in our data set. Instead, the reverse is true: the slope within CLAMP is significantly higher (Fig. 3). We suggest that this steep slope causes overestimated mean annual precipitation (Table 1).

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[1]All supporting data and an overlay for measuring leaves are available from Wilf.

DISCUSSION

Leaf-area analysis, a univariate method, is more significant and has an r^2 close to or greater than those of various multivariate models based on the CLAMP data set (Wing and Greenwood, 1993; Gregory and McIntosh, 1996; Herman and Spicer, 1996). The benefits of using data from more than one major area are clear (Fig. 2). None of the six subsets of data covers the

TABLE 2. SUMMARY DATA FOR PREDICTOR SAMPLES

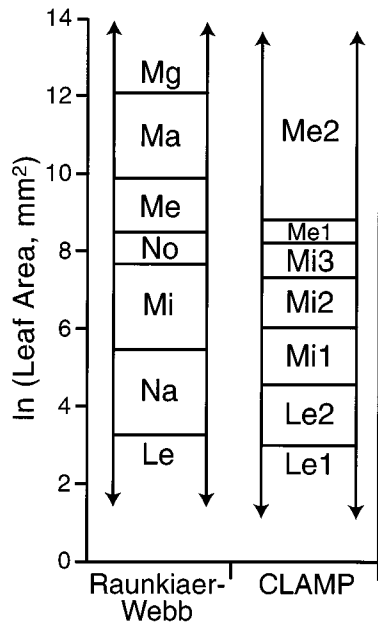| Sample	Mean annual precipitation (cm)	Mean ln (leaf area, mm²)	Number of species measured
(1) SSA, Monte scrub	10-30	3.94	
(2) TSA, Thorn scrub	15-40	5.53	
(3) SSA, Arid Chaco woodland	30-40	4.50	
(4) TSA, Thorn forest	40-70	7.23	
(5) SSA, Western Chaco forest	45-70	5.85	
(6) Ghana, rainfall zone 1	50-75	7.62	17
(7) Jamaica, Cactus scrub	69	6.13	17
(8) Jamaica, Evergreen bushland	69	6.44	55
(9) SSA, Central Chaco forest	70-90	6.56	
(10) Puerto Rico, Guánica Forest	86	6.49	126
(11) Ghana, rainfall zone 2	75-100	7.77	94
(12) SSA, Transition forest	80-100	6.92	
(13) TSA, Deciduous forest	80-120	8.00	
(14) Pennsylvania, York County	104	7.79	56
(15) SSA, Eastern Chaco forest	90-120	6.82	
(16) Maryland, Smithsonian Environmental Research Center	111	8.27	27
(17) Jamaica, Dry evergreen thicket	112	7.23	58
(18) Ghana, rainfall zone 3	100-125	7.95	309
(19) St. John, woodland	113	6.63	173
(20) SSA, Gallery forest	100-130	6.86	
(21) Pennsylvania, Allegheny Ntl. Forest	116	7.72	47
(22) St. John, moist forest	120	6.95	227
(23) Ghana, rainfall zone 4	125-150	8.08	457
(24) Costa Rica site 7	151	7.86	30
(25) Costa Rica, Taboga	153	8.13	19
(26) Costa Rica site 5	160	8.02	25
(27) Costa Rica site 6	160	8.22	37
(28) Ghana, rainfall zone 5	150-175	8.15	495
(29) Costa Rica site 28	174	7.69	19
(30) Costa Rica site 29	174	7.95	16
(31) Costa Rica site 27	174	8.10	27
(32) Costa Rica site 25	185	8.90	23
(33) Ghana, rainfall zone 6	175-<200	8.23	375
(34) Nigeria, Omo Forest Reserve	208	8.62	
(35) Costa Rica site 32	248	7.64	30
(36) Costa Rica site 3	250	8.95	19
(37) Costa Rica site 22	253	8.91	21
(38) Costa Rica site 4	254	9.20	24
(39) Panamá, Barro Colorado Island	261	8.07	627
(40) Brazil, Mucambo, Belém	273	8.41	139
(41) Costa Rica site 21	293	8.46	20
(42) Costa Rica site 20	294	8.74	23
(43) Puerto Rico, Bisley Watersheds	350	7.95	131
(44) Costa Rica site 7	365	8.50	19
(45) Costa Rica site16	365	8.75	18
(46) Costa Rica site18	365	9.12	27
(47) Costa Rica, Osa secondary	430	9.29	18
(48) Costa Rica, Osa ridge	435	8.47	18
(49) Costa Rica site 2	460	9.24	29
(50) Mexico, Los Tuxtlas	464	8.50	64

Notes: SSA = subtropical South America; TSA = tropical South America (Sarmiento 1972). When a range of annual precipitation was given, the midpoint value was analyzed (187.5 for Ghana zone 6). Number of species given when precisely known. Numbered Costa Rica sites correspond to site numbers in Dolph and Dilcher (1980a), climate data from Holdridge et al. (1971). Leaf areas for samples 10, 16, 19, 22, 39, 43, and 50 calculated from direct measurements; otherwise from size categories. Samples 14 and 21 are "subsamples" of Wilf (1997); samples 10, 19, 22, 39, and 43 are "samples" of Wilf (1997). Ghana data: Hall and Swaine (1981); Jamaica: Loveless and Asprey (1957); Puerto Rico: Little and Wadsworth (1964); Little et al. (1974); Acevedo-Rodríguez and Woodbury (1985); Chinea et al. (1993); Maryland: unpublished data furnished by G. Parker; St. John: Acevedo-Rodríguez (1996); Costa Rica samples 25, 47, 48: Gentry (1969); Dolph and Dilcher 1980b; Nigeria: Richards (1939, 1996); Panamá: Croat (1978); Brazil: Cain et al. (1956); Mexico: Bongers et al. (1988); Bongers and Popma (1990).
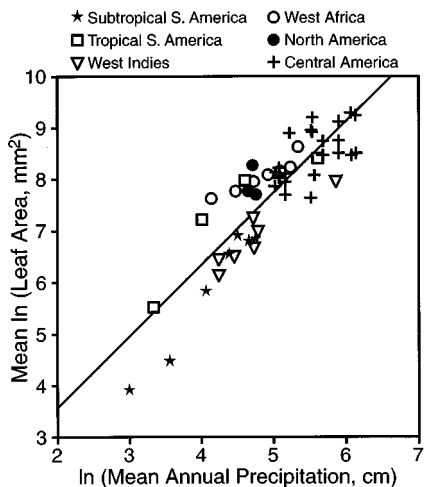
entire range of either axis, but the subtrends are subparallel. All but the Central American subset are primarily either above or below the trendline, which reflects some combination of differences in primary data collection and real variation among forests. For example, the low MlnA of the West Indian samples may result from the drying and destructive effects of high winds. The overall trend is probably not linear for the driest or the wettest climates, where biological stresses are maximized. At the dry end, MlnA appears to decline abruptly off the regression line (Fig. 2). Very wet climates typical of cloud forests were not sampled. Cloud forest leaves can be much smaller than leaves at lower and drier elevations in the same region (e.g., Howard, 1969). The lack of extreme values of MAP in our data set should therefore be noted by ecologists, but this omission is probably unimportant in the context of paleoprecipitation because desert and cloud forest floras are very rare in the fossil record.

The scatter in the regression (Fig. 2) mandates that leaf-area analysis be used with caution. Estimates based on several contemporaneous fossil samples are preferable to those from single samples. We strongly advise the use of supplemental data, including the distributions and characteristics of coals, clays, red-beds, and evaporites and the judicious analyses of fossil flora and fauna belonging to large extant clades with narrow moisture tolerances. Care must be taken with samples of fossil leaves to account for taphonomic removal of large leaves prior to deposition (Greenwood, 1992).

EOCENE EXAMPLE

Geological data have long indicated that the early to early middle Eocene of the U.S. Western Interior was much warmer than today, with generally frost-free winters (e.g., Roehler, 1993). Proxy paleoprecipitation data are critical for improving understanding of this unusual time period. Wing and Greenwood (1993) presented MAP estimates based on the CLAMP data set for six early and middle Eocene floras from the Western Interior and one from the West Coast, using two predictors, the percentages of species having (1) drip-tips and (2) leaves in the mesophyll 2 category (Fig. 1). The size categorizations were made from a data set of length and width measurements of the fossil leaves. Using these same data, we derived MlnA and reestimated paleo-MAP for the fossil samples with leaf-area analysis.

All seven revised estimates are lower (Table 3). The greatest change is for Bear Paw, which drops by more than half and is the only case where standard error bars of the original and revised estimates do not overlap; Bear Paw has the highest percentage of species with drip-tips (50%). The revised estimates rank in a logical fashion. Chalk Bluffs, California, emerges as the wettest sample, which is consistent with its being the only site near the coast. Green River, the youngest sample, ranks driest in both analyses, in accord with floristic evidence and vast evaporitic deposits in parts of the Green River Formation indicating intermittent dry periods (MacGinitie, 1969; Roehler, 1993). The Bear Paw, Sepulcher, Kisinger Lakes, and Wind River samples are intermediate both in age and in estimated MAP between

Figure 1. Two systems of leaf-area classification, shown on natural log scale: Raunkiaer-Webb (Webb, 1959) and CLAMP (Climate Leaf-Analysis Multivariate Program: Wolfe, 1993). CLAMP sizes were measured from Wolfe (1993, p. 25) using digitizing tablet. Abbreviations: Le = leptophyll, Na = nanophyll, Mi = microphyll, No = notophyll, Me = mesophyll, Ma = macrophyll, Mg = megaphyll (Le1 = "leptophyll 1," etc.). Cutoff values (in mm^2): 25, 225, 2025, 4500, 18225, 164025 (Raunkiaer-Webb); 19, 91, 392, 1420, 3516, 6226 (CLAMP).
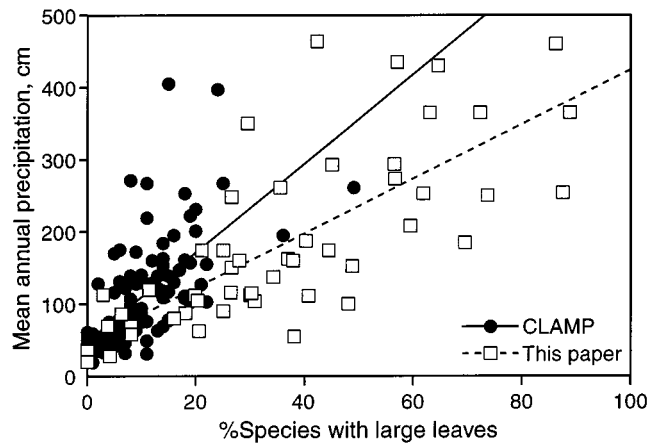

Figure 3. Regressions of mean annual precipitation (MAP) vs. percent of species with large leaves for CLAMP data set (Wolfe 1993) and leaf-area analysis data set of this paper (Table 2). For CLAMP: MAP = 6.18(%mesophyll 1 + %mesophyll 2) + 47.5, $r^2 = 0.439$. For leaf-area analysis: MAP = 3.77(%mesophylls + %macrophylls + %megaphylls) + 47.0, $r^2 = 0.554$. Difference in slope is significant at $p < 0.001$ level, using equality test of Sokal and Rohlf (1995, p. 498).

Figure 2. Mean natural log leaf area (MlnA) as a function of mean annual precipitation (MAP): MlnA = 1.39 ln(MAP) + 0.786, $r^2 = 0.760$, standard error = 0.572, $F(1,48) = 152$, $p = 10^{-15}$. Data from Table 2.

TABLE 3. ESTIMATED MEAN ANNUAL PRECIPITATION
FOR SEVEN EARLY AND MIDDLE EOCENE FLORAS

Flora (Ma)*	Wing and Greenwood (1993) (cm)[†]	This paper (cm)[§]
Bear Paw (49–51)	277	130 +56.1,–39.2
Sepulcher (50–51)	195	136 +58.8,–41.0
Camels Butte (53–55)	162	157 +67.6,–47.2
Chalk Bluffs (50–52)	241	160 +68.9,–48.1
Green River (45–48)	116	84 +36.2,–25.3
Kisinger Lakes (49–50)	129	110 +47.4,–33.1
Wind River (50–51)	149	104 +44.8,–31.3

*Age estimates from Wing and Greenwood (1993).
[†]Standard error is ±58.0 cm.
[§]Single standard errors shown are asymmetrical because they were converted from logarithmic units.

the older Camels Butte and the younger Green River samples, possibly indicating a regional drying trend.

The revised estimates, although lower, all indicate much more humid conditions than are found at basinal elevations of the same areas today. Water vapor is the most significant of the greenhouse gases, contributing two to three times the atmospheric heat retention of carbon dioxide in the modern atmosphere (e.g., Bigg, 1996). Water vapor is also the agent of latent heat transport, a possible mechanism of continental warming in the early Eocene (Sloan et al., 1995). High humidity may help to explain the frost-free nature of early to middle Eocene climates in the western United States.

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