

Using fossil leaves as paleoprecipitation indicators: An Eocene example: Comment and Reply

COMMENT

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Wilf et al. (1998) analyzed leaf sizes in modern vegetation and concluded that leaf sizes accurately predict mean annual precipitation (MAP). However, we question the methods employed by these authors to derive leaf size; the modern samples are not comparable to one another or to fossil leaf assemblages, and the influence of temperature on leaf size is ignored.

Data for some samples were derived primarily from sizes cited in floral manuals, which cover the entire range of a species. Can this method produce even approximately valid size data? We compiled data for eight sites on the island of Yakushima in southern Japan. These sites were collected for CLAMP (Climate-Leaf Analysis Multivariate Program; Wolfe, 1993, 1995) samples; the full range of physiognomy, including leaf size, of each species of woody dicot was collected in limited areas analogous to areas represented by fossil leaf assemblages. Leaf sizes were calculated according to the method of Wilf et al.: The smallest and largest leaf sizes for species in the sample were based on two-thirds the length times the width for (1) the shortest and/or narrowest leaves and (2) the longest and/or broadest leaves; the resulting areas were converted to natural logs and then averaged to yield a mean natural log of the leaf area, which was then averaged for each sample. The same procedure was used for data taken from the pertinent floral manual (Ohwi, 1984). Obviously this procedure cannot validly delimit the smallest or the largest leaf sizes in every species, because in many instances, the shortest and narrowest measurements were not necessarily found on the same leaf, and likewise for the longest and widest measurements. In 25%–30% of the species analyzed, the low-end extreme measurements occurred on different leaves, as did the high-end extremes.

Leaf areas derived from actual samples are markedly smaller (Table 1) than those derived from Ohwi (1984). Comparison was also made for sizes of a sample from Ketchikan, Alaska, to data from the pertinent manual (Vierick and Little, 1972). These comparisons indicate that (1) manual-derived data have a different mean leaf size than sample-derived data from a restricted climate zone and (2) size relates poorly to MAP, especially for temperate, high rainfall samples. Using Wilf et al.'s equations and mean leaf sizes, predicted MAP for the Yakushima samples is ~113–133 cm, and for Ketchikan, 64 cm.

Neither the manual-derived plots nor the sample-derived plots for Yakushima fit Wilf et al.'s Figure 2 regression, and for Ketchikan, which has

milder winters than the two Pennsylvania samples used by Wilf et al., both manual- and sample-derived plots also deviate markedly from other plots. Regression of leaf size against MAP with the addition of the Yakushima and Ketchikan samples as in Wilf et al.'s Figure 2 reduces the r^2 to 0.35. Leaf sizes from manuals do not yield valid site-specific data; more work may be involved in obtaining actual samples, as in CLAMP, but clearly actual collections are needed for valid calibration of physiognomy to climate.

Leaf-size data employed by Wilf et al. from different samples are not comparable. Sarmiento (1972) measured only canopy leaves and Bongers and Popma (1990) measured only "sun-leaves" (presumably = canopy), and canopy and/or sun leaves are smaller than shade and/or subcanopy leaves (e.g., Richards, 1996). Only part of the flora was included in the size analyses, because subcanopy trees and shrubs were excluded. In contrast, data reported by Dolph and Dilcher (1980) represented all woody plants in a sample plot. The data compiled from Hall and Swaine (1981) were based on averages for each species of "leaves of mature plants not saplings" (p.105), although Hall and Swaine (p. 49) recognized that "the leaves of many species . . . are much larger . . . in the young sapling stage than in the canopy." Dolph and Dilcher's (1980) samples are comparable to what might be found in the fossil record, but the samples based on Hall and Swaine (1981) were derived from thousands of square kilometers.

Leaf size, as in the instances of many other physiognomic character states, cannot be correlated in an isolated, univariate fashion to any one environmental parameter. Large leaves require both high moisture and high heat (Richards, 1996, p. 100). For example, lowland Yakushima samples have a lower score in the mesophyll categories (~16%–24%) than do samples from Fiji (32%–59%), although lowland Yakushima has considerably higher MAP (~430 vs. 200–300 cm) than does Fiji. However, Fiji is warmer, with a MAT of ~25 °C as opposed to ~19 °C, and thus the climate is more conducive to large leaves.

Another example of the influence of temperature on leaf size is subalpine (including subarctic) mesic vegetation relative to non-subalpine mesic vegetation (Table 2). The reduction in leaf size in subalpine vegetation is surely not the result of reduction in MAP, because these subalpine samples have higher MAP, and this reduction cannot be attributed to winter cold, because these subalpine samples have higher CMMT (cold-month mean temperature). Low heat during, and brevity of, the growing season are major features of subalpine climates and reduce average leaf size; fossil assemblages that display physiognomy characteristic of subalpine vegetation are found in the Paleogene of Idaho and Colorado (Wolfe et al., 1998) and in the Miocene of Alaska and Kamchatka (Wolfe, 1994). The complexity of the interactions of various environmental parameters that produces various compromises in physiognomic adaptations demands a more sophisticated approach than presented by Wilf et al.

TABLE 1. COMPARISONS OF LEAF SIZES DERIVED FROM FLORAL MANUALS TO ACTUAL SIZES IN AN ALTITUDINAL TRANSECT ON YAKUSHIMA AND AT KETCHIKAN

Sample	No. spp.	Manual mean natural log	Actual mean natural log	% large leaves	MAP (cm)
Yakushima 10 m	52	7.31	7.18	23	~430
Yakushima 10 m	41	7.23	6.87	16	~430
Yakushima 260 m	40	7.53	7.14	24	~670
Yakushima 420 m	40	7.37	7.00	21	~760
Yakushima 700 m	35	7.46	6.92	14	~860
Yakushima 800 m	32	7.23	7.02	18	~880
Yakushima 1080 m	26	7.34	6.93	11	~920
Yakushima 1350 m	17	7.42	7.11	13	~950
Ketchikan, Alaska	24	6.19	5.60	16	~405

Note: Large leaves are in the mesophyll 1 (or larger) size of Wolfe (1993).

TABLE 2. COMPARISON OF THREE HOKKAIDO NON-SUBARCTIC SAMPLES TO THREE SUBARCTIC/SUBALPINE SAMPLES FROM WESTERN UNITED STATES

Sample	No. spp.	CMMT (°C)	MAP (cm)	% small leaves
Kogawa, Hokkaido	43	-10.1	135	2
Teshio, Hokkaido	26	-10.4	138	2
Nukabira, Hokkaido	29	-10.7	160	3
Ketchikan, Alaska	24	0.5	405	38
Laurel Mtn., Oregon	24	2.5	271	22
Gov't Camp, Oregon	29	-1.5	219	22

Note: Small leaves are in the leptophyll 2 (or smaller) size of Wolfe (1993).

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REPLY

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We feel Wolfe and Uemura's criticisms are inaccurate and do not offer a serious challenge to our paper.

(1) Leaf size was approximated from published length:width minima and maxima for only five of our 50 modern samples (numbers 10, 19, 22, 39, and 43). If these five samples are removed, the effect on the correlation in our Figure 2 is not significant (r^2 increases from 0.760 to 0.783, slope from 1.39 to 1.41, p remains at 10^{-15}). Thus, contrary to Wolfe and Uemura's claim, the few data derived in this way did not compromise the relationship between leaf size and precipitation that we detected. Furthermore, the Eocene paleoprecipitation estimates that we presented were all derived from minimum/maximum areas for each fossil species, measured from actual specimens, and are not subject to any problems potentially introduced by approximation from the literature.

(2) As we noted (p. 205), leaf size appears to decrease, not increase, at extreme mean annual precipitation (MAP). The nine sites listed in Wolfe and Uemura's Table 1 are as wet to more than twice as wet as the rainiest sites in our data set. Contrary to their claim, the small leaf sizes recorded by Wolfe and Uemura do not invalidate our correlation, which is based on less extreme rainfall values. The data they cite from Ohwi corroborate the pattern of leaf size decline with very high precipitation in both warm and cool climates (but see point 5b regarding the CLAMP samples).

(3) Wolfe and Uemura state that the effect of temperature on leaf size was ignored, noting that temperature has a large negative effect on leaf area in subalpine vegetation. However, we avoided subalpine areas in our data set for this very reason (p. 204) and also discussed the role of temperature in our introduction.

(4) The point that the samples in our database "are not comparable" is partially true but not important. Differences in leaf size calculation and data collection should introduce noise into the dataset and reduce the significance of the correlation between leaf size and precipitation shown in our Figure 2, thus biasing against our conclusions. The fact that a highly significant correlation remains is evidence that the variation in methods did not overwhelm the powerful signal.

TABLE 1. PERCENT LARGE LEAVES* IN CLAMP SAMPLES VS. COMPARABLE FIELD-COLLECTED SAMPLES

	CLAMP [†]	This Reply [‡]
(1) Barro Colorado Island, Panamá	49	59
(2) Guánica Forest, Puerto Rico	10	17
(3) Smithsonian Environmental Research Center, Maryland	18	51
(4) Southern Pennsylvania	14	49
(5) Northern Pennsylvania	19	40

*%Mesophyll 1 + % Mesophyll 2, as directed by Wolfe (1993).
[†]Data from Wolfe (1993): (4) = Arendtsville; (5) = Tunkhannock.
[‡](1) = same leaves as CLAMP sample (see Wilf, 1997); (2) = "subsample" of Wilf (1997); (3) our sample #16; (4 and 5) = York and Allegheny "subsamples" of Wilf (1997)- climates nearly identical to the corresponding CLAMP samples selected (Wolfe, 1993; Wilf, 1997).

(5) Wolfe and Uemura state that many of our size data are not "valid" for comparison with precipitation because they include leaves collected over too large an area. They argue that local samples, such as those in the CLAMP database (Wolfe, 1993), are more appropriate because they are "analogous" to fossil assemblages. We disagree.

(a) Fossil assemblages vary greatly in their diversity, the area they sample, and presumably the fidelity with which they represent the original source vegetation. They also have undergone various types and amounts of taphonomic alteration and have been collected with varying intensities (e.g., Behrensmeier and Hook, 1992). The strategy of very local sampling of living vegetation mimics some fossil assemblages. However, this procedure also results in a poor representation of the physiognomic range of living vegetation and has an unquantified effect on correlations of leaf size and shape with climate. The goal for baseline studies of living plants should be to sample as completely and carefully as possible so that the correlations between leaf physiognomy and climate can be known with the greatest precision. We should, correspondingly, be sampling fossils more thoroughly and trying to approximate the original leaf size spectrum of ancient source forests, not degrading modern samples in ways that may or may not match the taphonomic alteration and spatial limitation of fossil assemblages.

(b) The CLAMP samples clearly miss the larger leaves that are present in vegetation, as shown in our original Figure 3. It is probably this omission, and not the drawbacks of scoring from manuals as stated by Wolfe and Uemura, that results in manual-derived leaf area being higher than that of the CLAMP samples in their Table 1. The failure of CLAMP samples to include large leaves also can be demonstrated by comparing samples that are in the CLAMP database with our field-collected samples from the same locations or from climatically equivalent areas in the same region (Table 1). Most telling is the sample from Barro Colorado Island, Panama, for which Wolfe (1993) reports 10% fewer large leaves than we found, even though the same leaves were measured.

(6) With regard to the suitability of a univariate approach, we acknowledge that a method that simultaneously considers the effects on leaf size and shape of many variables such as precipitation, temperature, seasonality, soil characteristics, etc. might be more desirable. However, the accuracy of such an approach needs to be tested on a robust database. Unfortunately, CLAMP samples, in general, have too few species, are collected from areas that are too limited, and do not adequately represent the physiognomy of the vegetation that they are intended to sample (see also Wilf, 1997). Therefore, for the time being, we feel that the strong univariate correlation we demonstrated is a useful index of paleoprecipitation when used with the cautions given in our paper. We hope that it will be superceded by improved methodologies based on well-sampled field collections of living vegetation from a wide variety of continents and climates.

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