

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 ordines 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 PRECIPITATION¹

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 \times 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: $\ln(\text{MAP}) = 0.548 \text{ MlnA} + 0.768$, $r^2 = 0.760$, 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 $\ln(\text{MAP})$ 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).

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, mm ²) | 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, Ormo 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 site 16 | 365 | 8.75 | 18 |
| (46) Costa Rica site 18 | 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); China 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).

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

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).

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 mm²): 25, 225, 2025, 4500, 18225, 164025 (Raunkiaer-Webb); 19, 91, 392, 1420, 3516, 6226 (CLAMP).

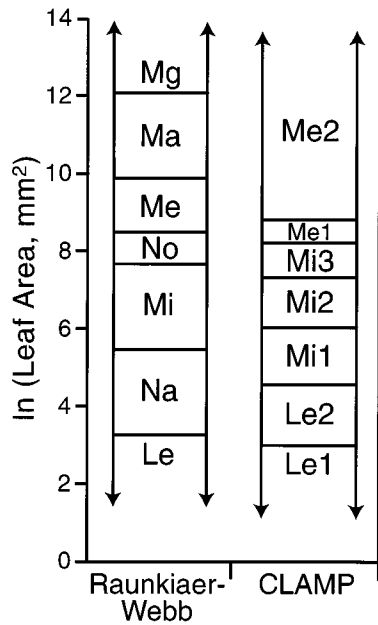
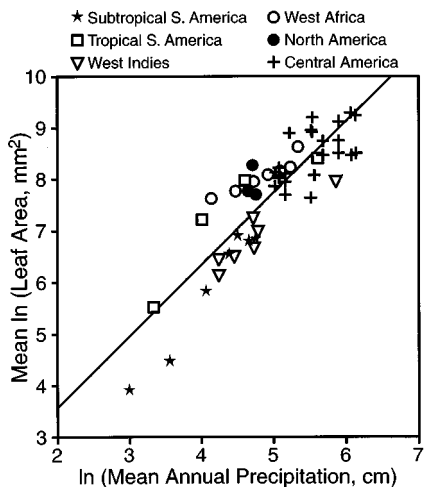


Figure 2. Mean natural log leaf area (MlnA) as a function of mean annual precipitation (MAP): $MlnA = 1.39 \ln(MAP) + 0.786$, $r^2 = 0.760$, standard error = 0.572, $F(1,48) = 152$, $p = 10^{-15}$. Data from Table 2.



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

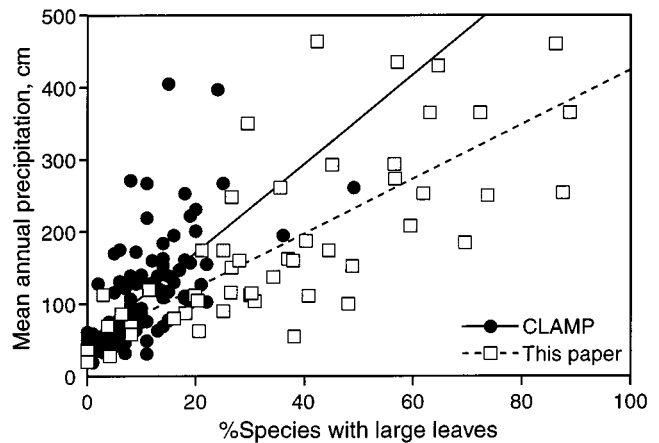


Figure 3. Regressions of mean annual precipitation (MAP) vs. percent of species with large leaves for CLAMP data set (Wolfe 1993) and leaf-area analysis data set of this paper (Table 2). For CLAMP: $MAP = 6.18(\%mesophyll\ 1 + \%mesophyll\ 2) + 47.5$, $r^2 = 0.439$. For leaf-area analysis: $MAP = 3.77(\%mesophylls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

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

| Flora (Ma)* | Wing and Greenwood (1993) | |
|------------------------|---------------------------|-------------------|
| | (cm) [†] | (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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REFERENCES CITED

- Acevedo-Rodríguez, P., 1996, Flora of St. John, U.S. Virgin Islands: *Memoirs of the New York Botanical Garden*, v. 78, p. 1–581.
- Acevedo-Rodríguez, P., and Woodbury, R. O., 1985, Los bejucos de Puerto Rico, Volumen 1: U.S. Department of Agriculture, General Technical Report, v. SO-58, p. 1–331.
- Bigg, G. R., 1996, *The oceans and climate*: Cambridge, Cambridge University Press, 266 p.
- Bongers, F., and Popma, J., 1990, Leaf characteristics of the tropical rain forest flora of Los Tuxtlas, Mexico: *Botanical Gazette*, v. 151, p. 354–365.
- Bongers, F., Popma, J., Meave del Castillo, J., and Carabais, J., 1988, Structure and floristic composition of the lowland rain forest of Los Tuxtlas, Mexico: *Vegetatio*, v. 74, p. 55–80.
- Burnham, R. J., 1997, Stand characteristics and leaf litter composition of a dry forest hectare in Santa Rosa National Park, Costa Rica: *Biotropica*, v. 29, p. 384–395.
- Cain, S. A., and Castro, G. M. de O., 1959, *Manual of vegetation analysis*: New York, Harper and Row, 325 p.
- Cain, S. A., Castro, G. M. de O., Pires, J. M., and Silva, N. T. da, 1956, Application of some phytosociological techniques to Brazilian rain forest: *American Journal of Botany*, v. 43, p. 911–941.
- Chinae, J. D., Beymer, R. J., Rivera, C., Sastre de Jesús, I., and Scatena, F. N., 1993, An annotated list of the flora of the Bisley Area, Luquillo Experimental Forest, Puerto Rico 1987 to 1992: U.S. Department of Agriculture, General Technical Report, v. SO-94, p. 1–12.
- Croat, T. B., 1978, *Flora of Barro Colorado Island*: Stanford, California, Stanford University Press, 943 p.
- Dilcher, D. L., 1973, A paleoclimatic interpretation of the Eocene floras of southeastern North America, in Graham, A., ed., *Vegetation and vegetational history of northern Latin America*: Amsterdam, Elsevier, p. 39–59.
- Dolph, G. E., and Dilcher, D. L., 1980a, Variation in leaf size with respect to climate in Costa Rica: *Biotropica*, v. 12, p. 91–99.
- Dolph, G. E., and Dilcher, D. L., 1980b, Variation in leaf size with respect to climate in the tropics of the Western Hemisphere: *Bulletin of the Torrey Botanical Club*, v. 107, p. 154–162.
- Givnish, T. J., 1984, Leaf and canopy adaptations in tropical forests, in Medina, E., Mooney, H. A., and Vázquez-Yanes, C., eds., *Physiological ecology of plants of the wet tropics*: The Hague, Junk, Tasks for Vegetation Science, Volume 12, p. 51–84.
- Greenwood, D. R., 1992, Taphonomic constraints on foliar physiognomic interpretations of Late Cretaceous and Tertiary paleoclimates: Review of Palaeobotany and Palynology, v. 71, p. 149–190.
- Greenwood, D. R., 1996, Eocene monsoon forests in central Australia?: *Australian Systematic Biology*, v. 9, p. 95–112.
- Gregory, K. M., and McIntosh, W. C., 1996, Paleoclimate and paleoelevation of the Oligocene Pitch-Pinnacle flora, Sawatch Range, Colorado: *Geological Society of America Bulletin*, v. 108, p. 545–561.
- Hall, J. B., and Swaine, M. D., 1981, Distribution and ecology of vascular plants in a tropical rain forest: *Forest vegetation in Ghana*: The Hague, Junk, 383 p.
- Herman, A. B., and Spicer, R. A., 1996, Palaeobotanical evidence for a warm Cretaceous Arctic Ocean: *Nature*, v. 380, p. 330–333.
- Herman, A. B., and Spicer, R. A., 1997, New quantitative paleoclimate data for the Late Cretaceous Arctic: Evidence for a warm polar ocean: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 128, p. 227–251.
- Holdridge, L. R., Grenke, W. C., Hatheway, W. H., Liang, T., and Tosi, J. A., Jr., 1971, *Forest environments in tropical life zones: A pilot study*: Oxford, Pergamon Press, 747 p.
- Howard, R. A., 1969, The ecology of an elfin forest in Puerto Rico, 8. Studies of stem growth and form and of leaf structure: *Journal of the Arnold Arboretum*, v. 50, p. 225–261.
- Jacobs, B. F., and Deino, A. L., 1996, Test of climate-leaf physiognomy regression models, their application to two Miocene floras from Kenya, and $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the late Miocene Kapturo site: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 123, p. 259–271.
- Little, E. L., Jr., and Wadsworth, F. H., 1964, *Common trees of Puerto Rico and the Virgin Islands*: U.S. Department of Agriculture, Agriculture Handbook 249, 548 p.
- Little, E. L., Jr., Woodbury, R. O., and Wadsworth, F. H., 1974, *Trees of Puerto Rico and the Virgin Islands, Volume 2*: U.S. Department of Agriculture, Agriculture Handbook 449, 1024 p.
- Loveless, A. R., and Asprey, G. F., 1957, The dry evergreen formations of Jamaica. I. The limestone hills of the south coast: *Journal of Ecology*, v. 45, p. 799–822.
- MacGinitie, H. D., 1969, The Eocene Green River flora of northwestern Colorado and northeastern Utah: *University of California Publications in Geological Sciences*, v. 83, p. 1–140.
- Raunkiaer, C., 1934, *The life forms of plants and statistical plant geography*: Oxford, Clarendon, 632 p.
- Richards, P. W., 1939, Ecological studies on the rain forest of southern Nigeria. I. The structure and floristic composition of the primary forest: *Journal of Ecology*, v. 27, p. 1–61.
- Richards, P. W., 1996, *The tropical rain forest*, (second edition): Cambridge, Cambridge University Press, 575 p.
- Roehler, H. W., 1993, Eocene climates, depositional environments, and geography, Greater Green River Basin, Wyoming, Utah, and Colorado: U.S. Geological Survey Professional Paper 1506-F, p. 1–74.
- Sarmiento, G., 1972, Ecological and floristic convergences between seasonal plant formations of tropical and subtropical South America: *Journal of Ecology*, v. 60, p. 367–410.
- Sloan, L. C., Walker, J. C. G., and Moore, T. C., Jr., 1995, Possible role of oceanic heat transport in early Eocene climate: *Paleoceanography*, v. 10, p. 347–356.
- Sokal, R. R., and Rohlf, F. J., 1995, *Biometry* (third edition): New York, W. H. Freeman, 887 p.
- Webb, L. J., 1959, A physiognomic classification of Australian rain forests: *Journal of Ecology*, v. 47, p. 551–570.
- Webb, L. J., 1968, Environmental relationships of the structural types of Australian rain forest vegetation: *Ecology*, v. 49, p. 296–311.
- Wilf, P., 1996, How good are dicot leaves as thermometers?: Santa Barbara, California, International Organization of Paleobotany Quadrennial Conference Abstracts, v. 5, p. 112.
- Wilf, P., 1997, When are leaves good thermometers?: A new case for Leaf Margin Analysis: *Paleobiology*, v. 23, p. 373–390.
- Wing, S. L., and Greenwood, D. R., 1993, Fossils and fossil climate: The case for equable continental interiors in the Eocene: *Philosophical Transactions of the Royal Society of London ser. B*, v. 341, p. 243–252.
- Wolfe, J. A., 1993, A method of obtaining climatic parameters from leaf assemblages: *U.S. Geological Survey Bulletin*, v. 2040, p. 1–71.
- Wolfe, J. A., 1994, Alaskan Palaeogene climates as inferred from the CLAMP database, in Boulter, M. C., and Fisher, H. C., eds., *Cenozoic plants and climates of the Arctic*: NATO ASI Series, Series I, v. 27, p. 223–237.
- Wolfe, J. A., and Upchurch, G. R., 1987, North American nonmarine climates and vegetation during the Late Cretaceous: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 61, p. 33–77.

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