Name	LEAF MORPHOLOGY
Material Needed	Fossil flora with at least 20-30 dicot morphospecies
Variables measured	31 leaf morphology character states, including margin type, size
Climate variables and precision	Mean annual temperature (± 2°C) Growing Season Precipitation (± 50 cm), among others
Time range	Middle Cretaceous - present
Advantages	Estimates not dependent on correct species indentifications
Errors	Fossil floras generally riparian, assemblages subject to taphonomic bias
Significance	Currently provides some of the most precise estimates of terrestrial paleoclimate for the Tertiary.
Principal Reference	Wolfe, 1993; 1995

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, that is, smooth 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).

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 hydrature. 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-Brosh 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.

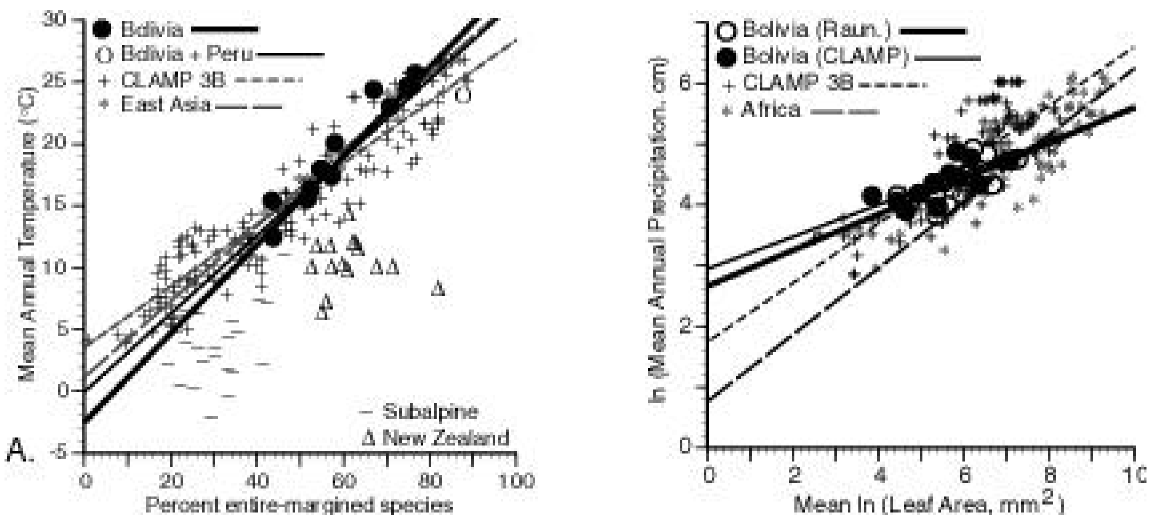
With the goal of quantifying relationships between leaf morphology and climate, several data sets of modern leaf morphology and climate have been collected (Table 1). The largest is associated with the Climate-Leaf Analysis Multivariate Program (CLAMP) of Wolfe (1993, 1995). The most recent version of 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).

Because these relationships are based on physiology, rather than the ecological tolerance of species, one should be able to use this method on fossil vegetation. Because it is based on angiosperms, it can be used for the Cenozoic.

It is difficult to estimate the errors for this method when applied to fossil floras; because it is one of the most quantitative terrestrial indicators, there are few indicators with which it can be compared. If we take errors for the modern database as a model, mean annual temperature can be estimated within ± 2 °C, and the growing season precipitation to withing ± 50 cm.

Current controversies include which statistical methods are most appropriate (univariate vs. multivariate), whether the method tends to systematically underestimate mean annual temperature, and whether the relationships between leaf morphology and climate vary between the North and South Hemisphere.



A, Mean annual temperature (MAT) vs. percentage of entire-margined species for different data sets: Boivia; Bolivia + Peru; CLAMP 3B; east Asia; the subalpine sites from the CLAMP 3A data set; and New Zealand. B. 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; Bolivia as calculated using the CLAMP size categories, CLAMP 3B (CLAMP categories); and Western Hemisphere/Africa (Raunkiaer-Webb categories). From Gregory-Wodzicki, 2000.

References: