A Method of Obtaining Climatic Parameters from Leaf Assemblages

U.S. GEOLOGICAL SURVEY BULLETIN 2040

U.S. DEPARTMENT OF THE INTERIOR
MARCH 3, 1849

A Method of Obtaining Climatic Parameters from Leaf Assemblages

By Jack A. Wolfe

U.S. GEOLOGICAL SURVEY BULLETIN 2040

U.S. DEPARTMENT OF THE INTERIOR
MARCH 3, 1849

UNITED STATES GOVERNMENT PRINTING OFFICE, WASHINGTON : 1993

U.S. DEPARTMENT OF THE INTERIOR
BRUCE BABBITT, Secretary

U.S. GEOLOGICAL SURVEY
Robert M. Hirsch, Acting Director

For sale by
USGS Map Distribution
Box 25286, Building 810
Denver Federal Center
Denver, CO 80225

Library of Congress Cataloging-in-Publication Data

Wolfe, Jack A., 1936–
A method of obtaining climatic parameters from leaf assemblages / by Jack A. Wolfe.
p. cm.—(U.S. Geological Survey bulletin ; 2040)
Includes bibliographical references.
Supt. of Docs. no.: I 19.3:B2040
1. Vegetation and climate—Statistical methods. 2. Leaves—Morphology—Statistical methods. 3. Woody plants—Climatic factors—Statistical methods. 4. Vegetation and climate—North America—Statistical methods. 5. Leaves—North America—Morphology—Statistical methods. 6. Woody plants—North America—Morphology—Statistical methods. 7. Multivariate analysis. I. Title. II. Series.
QE75.B9 no. 2040
[QK754.5]
557.3 s—dc20
[572'.05'222]
92–27842
CIP

CONTENTS

PLATES

[Plates are in pocket]

FIGURES

TABLES

A Method Of Obtaining Climatic Parameters From Leaf Assemblages

By Jack A. Wolfe

ABSTRACT

Leaf samples of woody dicotyledons in modern vegetation were collected from a wide variety of vegetation types and climates of the Northern Hemisphere but principally from North America. Most sample sites are proximal to places where meteorological data have been recorded and are generally of limited geographic extent (1–5 hectares). Each of the 106 samples comprises at least 20 species (most more than 25 species) and typically includes both streamside and slope vegetation. The leaves of each species in each sample were scored for the full range of variation in 29 character states, including characters of the margin, size, apical and basal configurations, length to width ratios, and general foliar shape.

The total for each character state in a given sample is converted to percentages of the number of species in that sample that have that character state. These percentages for all samples are then subjected to a multivariate Correspondence Analysis. The resulting analysis indicates that approximately 70 percent of total physiognomic variation is accounted for by two principal axes. Axis 1 accounts for approximately 50 percent of the variation, and relative scores of the samples indicate that the axis approximately corresponds to temperature factors, especially mean annual temperature. Axis 2 accounts for approximately 20 percent of the variation and corresponds to water stress.

Meteorological data for the sample sites can be entered into the database as if the data represent physiognomic character states and show the relation of a given meteorological parameter to the samples. For example, when the sample scores are orthogonally projected to the vector derived from the score for percent no teeth, which forms almost the same vector as mean annual temperature, the samples are ranked according to mean annual temperature. This relative ranking is best fit by polynomial regressions; the regressions explain 96–97 percent of the residuals about the mean (residual mean squares of 0.8–1.4) and have standard errors of mean annual temperature of 0.7°C–1.0°C. Estimates of mean temperature of the cold month have standard errors of 1.5°C–2.0°C. Precipitation estimates have moderate to low accuracies; megathermal and mesothermal samples provide the most accurate estimates.

This Climate-Leaf Analysis Multivariate Program (CLAMP) offers an accurate (valid) and precise (repeatable) method for obtaining climatic parameters from an assemblage of leaves. Even assemblages of less than 20 species yield reasonably accurate estimates of temperatures, but estimates of precipitation are more inaccurate when less than 25 species are analyzed. Taphonomy samples were also collected from a few sites where CLAMP samples were collected; scoring of a given taphonomy sample produces climatic, especially temperature, estimates that are not significantly different from the estimates obtained from the CLAMP sample.

INTRODUCTION

The great complexity of land climates is mirrored by the complex relations between these climates and land organisms. Land climates have many more and wider ranges of environmental parameters than marine climates. Environmental parameters of marine climates are mean annual temperature, which fundamentally ranges from freezing to almost 30°C, means of the cold and warm months and the concomitant mean annual range of temperature, which varies from a few degrees to rarely more than 10°C, and water salinity and density, which are in large part functions of water depth. In marked contrast, environmental parameters of the atmosphere include mean annual temperature, which ranges from –40°C to 30°C, diurnal temperature ranges, which can produce daytime temperature of more than 50°C and nighttime temperatures of less than –60°C, warm- and cold-month mean temperatures and the concomitant mean annual range of temperature, which can exceed 50°C, atmospheric density (barometric pressure), which is mostly a function of altitude, and, most significantly, various parameters that relate to water. These last include relative humidity, pressure of water vapor, and precipitation, all of which can be highly variable throughout the year and some of which result from not just available moisture but also from temperature. Land organisms have a far more complex system of environmental factors than do marine organisms, and it is not surprising that far more is now known about marine paleoclimates than about land paleoclimates.

Indeed, since the 1960's, a vast body of data has accumulated on marine paleoclimates of the last 100, and especially the last 80, million years from the work of the Deep Sea Drilling Project (DSDP). These data are based mostly on the acceptance by scientists of certain tools for estimating various parameters of marine environments, especially oxygen-isotope and other geochemical analyses. These analyses are based on calibration for accuracy (validity) in modern environments and demonstration that these analyses are precise (repeatable). Combined with the development of a detailed biostratigraphy and magnetostratigraphy, many samples of known time placement have been readily available for analysis by a number of valid and precise methods. Yet, except for some generalities, the detailed paleoclimatic work based on DSDP samples has produced little information relative to land paleoclimates.

The most significant information on land paleoclimates is, of course, based on terrestrial plants. The close correlation between vegetational type and climate is obvious to even a casual observer, and indeed some climatologists used the distribution of vegetational types to map climates, especially many decades ago when meteorological data were sparse or lacking from many regions of the globe. Excepting areas of human influence, neither deserts nor grasslands develop in areas of high rainfall, and closed-canopy rain forests obviously indicate areas of high precipitation. Because the physical aspects of the overall vegetation type, such aspects as density and height of the crown and density of vegetative cover, are rarely directly evidenced in the fossil record, the task is to infer accurately and precisely from the preserved remains of plants what vegetation type is represented by a particular assemblage of fossils and, in turn, to infer paleoclimate. At this point, some lose sight of a critical distinction. As succinctly stated by the neobotanist Lyman Benson (*in* Benson and Darrow, 1980, p. 15), "Flora and vegetation are different. A [regional] *flora* is composed of species whose lineages have tended to stay together; the *vegetation* of a region is of a special form [physiognomy] tending to develop in a particular climate, regardless of its species composition and the flora from which it is developed." The loss of this distinction between vegetation and flora is to some extent understandable. As any gardener can testify, the distributions of plant species are strongly controlled by climate. No sensible gardener would plant a gardenia outside in Alaska and expect the plant to survive the winter, and European settlers in tropical areas find that most cherished native European plants will not survive in the tropics. Paleobotanists thus extended this valid relation between modern plant taxa and modern climates to fossil floras. This extension has, however, a major theoretical flaw (Wolfe and Schorn, 1989, p. 180):

> Assuming that a clade such as the angiosperms originated at a point in time and at a place that had a particular environment, then the present angiospermous flora has in the intervening time departed in varying degrees from that original set of environmental parameters and from the original habit. Further, the rates of departure might be different in different lineages, and the level of taxonomic differentiation may offer no clue as to the degree of ecologic digression.

To be sure, many fossil floras can have an association of taxa that appears to support the same climatic inferences, mostly because these taxa are still associated today. Here, however, a not too subtle identification factor can play a role.

The classification of the flowering plants (angiosperms) is almost entirely based on megascopic features of flowers, which are rare as fossils, rather than on leaves, pollen, and wood, which are the common fossils. For all the 19th and part of the 20th century, identification of the common Cretaceous and Tertiary angiosperm fossils depended on finding among living plants a close anatomical-morphological "match." These "matches" could be based on many characters or could be based on only a few characters, none of which might be taxonomically significant. In any case, because search had to be made through many thousands of extant plants (about 250,000 species comprise extant angiosperms) for "matches," the paleobotanist typically would narrow the search to plants that are now associated with taxa already identified in the fossil flora. This approach has resulted in some fossil associations that have spurious similarity to present-day associations, as in the instances, prior to the discovery of extant *Metasequoia*, to match numerous fossil assemblages with modern redwood (*Sequoia*) forest.

Identification of isolated organs of angiosperms has become more rigorous. Surveys of the anatomy-morphology of organs of the living angiosperms indicate which characters have evolved in parallel to floral characters; that is, which nonfloral characters are taxonomically significant. Even, however, if a fossil flora is 100 percent validly determined, inferences of paleoclimate remain problematic.

The theoretical flaw mentioned above is attested to by the fossil record. Although many younger Neogene floras are composed of taxa that are associated today, the older the flora the more taxa in the flora whose closest living relatives are not now associated. In Paleogene floras the similarities between fossil and modern associations are even more general, and the inclusion in Paleogene floras of many extinct genera can place floristic similarities between fossil and modern floras at tribal or subfamilial levels.

Two paleobotanists dealing with the same fossil flora can arrive at significantly different conclusions relative to paleoclimatic inferences. No rigorous methodology exists for weighting the various floristic elements in a fossil flora. If the closest living relatives of two or more taxa in a fossil flora now live in mutually exclusive climates, how can this seeming contradiction be resolved? If phylogenetic studies indicate that the fossil taxon represents an extinct sister-lineage to a surviving lineage, what paleoclimatic significance should be attributed to the extinct lineage; that is, to what extent does taxonomic-phylogenetic distance represent climatic distance? If an extant taxon such as *Cercidiphyllum japonicum* clearly represents a relict of a family that in the past was more diverse at both generic and specific levels, did all these extinct genera and species live in the same climatic regime as the sole surviving taxon? These and similar problems beset any attempt to base paleoclimatic inferences on the present-day climatic distribution of closest living relatives, and it is very understandable that the same list of fossil taxa will be interpreted differently by more than one paleobotanist. What this discussion highlights, however, is that this methodology lacks precision (repeatability) and has not demonstrated accuracy (validity) of paleoclimatic inferences based on extinct lineages. This floristic methodology of estimating paleoclimatic parameters can, at best, yield only general and possibly invalid estimates.

What is clearly needed is an accurate and precise methodology for deriving paleoclimatic estimates from fossil plants. The vegetative body, the wood and the leaves, of terrestrial plants should be adapted to the environment in which the plant lives. The overall physical aspects or physiognomy of all the species in a given vegetational type define that vegetational type. The gross characters of the leaves of all the species are an important element of the overall physiognomy, and foliar physiognomy should in theory show environmental adaptations.

Acknowledgments.—Since the initiation of work leading to CLAMP, A.L. Kraps has offered continual encouragement and has assisted in the collection of 51 samples and in the collection of the original samples from the South Pacific. R.A. Spicer (Oxford University) has made crucial comments and suggestions throughout the course of the study.

The Puerto Rican samples were supplied by members of the Sociedad de Estudiantes de Botanica under the supervision of Gary J. Breckon and Duane A. Kolterman (University of Puerto Rico, Mayaguez); these are crucial samples in representing the major part of the megathermal database. Howard E. Schorn (University of California, Berkeley) supplied two samples (Lakeport, Calif., and River Falls, Wis.) and assisted in the collection of seven additional samples. Bruce H. Tiffney (University of California, Santa Barbara) collected two samples from the Santa Barbara, Calif., area. K. Uemura (National Science Museum) supplied two critical samples from Japan. Robyn J. Burnham and Scott L. Wing (Smithsonian Institution) collected and allowed me to score a large sample from Barro Colorado Island, Panama. Cooperation of the National Park Service, Stanford University, and Kitt Peak National Observatory is gratefully acknowledged in obtaining samples from Grand Lake, Colo., Jasper Ridge, Calif., and Kitt Peak, Ariz., respectively.

Funding for the field work and to obtain samples from Puerto Rico was supplied mostly by the U.S. Geological Survey G.K. Gilbert Fellowship Program. The Yakushima sample was collected during the tenure of a Japan Society for the Promotion of Science Senior Fellowship and was made with the assistance of T. Tanai (then at the University of Hokkaido).

For offering comments and suggestions on the manuscript, I thank D.L. Dilcher (University of Florida), R.A. Spicer, B.H. Tiffney, K. Uemura, and S.L. Wing.

PHYSIOGNOMIC METHODOLOGY

The physiognomic methodology relies on the physical aspects of plants to determine paleoclimate. The methodology rests on the assumption, in some instances supported by theoretical reasoning and (or) experimental work, that foliar characters such as size, shape, and margin represent evolutionary strategies that have adapted the plants to their respective environments (see, for example, Givnish, 1979, and various papers in Givnish, 1986). If this assumption is valid, then analysis of foliar characters should produce estimates of at least some of the environmental parameters.

In the early part of the 20th century, Bailey and Sinnott (1915, 1916) showed that some characters of angiosperm leaves appeared to vary in marked correlation with climatic differences. Bailey and Sinnott did not emphasize that these physiognomic leaf characters had been used as part of the characterization of some vegetational units, but the recognition and demonstration of these general correlations of leaf physiognomy with climate was a major advance. These correlations were based on compilations of regional floras containing hundreds (if not thousands) of species. The most marked correlation was between an entire (untoothed) margin and mean annual temperature; most species in tropical climates had entire margins, but toothed leaves were overwhelmingly dominant in temperate regions.

Some paleobotanists accepted the general validity of the correlations proposed by Bailey and Sinnott and applied these correlations in a general fashion to the fossil record. Thus Chaney (1924) and Chaney and Sanborn (1933) documented the temperate character of the early Oligocene (current usage) Bridge Creek flora versus the subtropical character of the latest Eocene to earliest Oligocene Goshen flora. Chaney and Sanborn also showed that coriaceous texture (associated with an evergreen habit), attenuated apices (drip-tips), and large size (>10 cm long) are also indicative of a subtropical climate for the Goshen assemblage, in contrast to the thin texture, nonattenuated apices, and small size of the Bridge Creek leaves. In retrospect, some of these categories (for example, using only two size classes) appear primitive and their statistical basis in modern vegetation is meager, but these categories provided a significant basis for comparing fossil with modern vegetation and for comparing two fossil assemblages.

Other students and associates of Chaney continued to use leaf physiognomy as a paleoclimatic tool, especially Sanborn (1935), Potbury (1935), MacGinitie (1937, 1941, and subsequent publications), and Dorf (1942). The primary basis for the paleoclimatic inferences made by these workers was, however, floristic comparisons between fossil and present-day associations; the physiognomic comparisons were used primarily to bolster these floristic inferences. Physiognomic methodology was still calibrated in only a general manner with assemblages of modern leaves, and no numerical paleoclimatic parameters were proposed from physiognomic analyses.

The general correlation between temperature and the percentage of species that have entire-margined leaves was the correlation most emphasized by Bailey and Sinnott (1915, 1916). They, however, noted that relative physiologic dryness appeared to influence this character because the percentage increased in the Arctic and in middle-latitude alpine and subalpine floras. Bailey and Sinnott also noted two other anomalous situations: some dry, subtropical to tropical floras could have a high percentage of nonentire, spinose leaves, and warm temperate to subtropical areas of eastern North America had anomalously low percentages of entire-margined species relative to temperature.

In the 1960's and 1970's I initiated an attempt to calibrate the percentage of entire-margined species with the specific parameter of mean annual temperature in order to arrive at numeric estimates of mean annual temperature. Based on review of the literature and on my own experience, I (1971) suggested that the percentage of entire-margined species for a given fossil flora changed no more than 3 percent as new taxa were found after the flora had reached about 30 species total; this would be a measure of precision (repeatability) of the leaf margin analysis. The calibration (Wolfe, 1979) excluded dry (including Arctic and alpine-subalpine) vegetation and concentrated on humid to mesic vegetation of eastern Asia. Similar to Bailey and Sinnott's earlier compilation, my data were based on compilations from floral lists, and most data points were based on 50 or more species. The east Asian data indicated that in broad-leaved humid to mesic forests the percentage of entire-margined species increased at a linear rate of about 3 percent/°C.

In the humid coniferous forests of the Pacific Northwest, however, I (1979) found no apparent correlation between the percentage of entire-margined species and temperature. Moreover, the anomalous correlation in the broad-leaved deciduous forests of eastern North America still persisted, although I emphasized that in areas of comparable major temperature parameters in eastern Asia the vegetation was broad-leaved evergreen and not deciduous; the anomaly in some aspects of foliar physiognomy in eastern North America extended to the overall physiognomy of the vegetation.

Taking data from the literature on the flora of the Carolinas, Dolph and Dilcher (1979) considered that the overall relation between margin type (as well as other physiognomic characters) and climate was too general for use in paleoclimatological work and thus no calibrations were attempted. This conclusion, in part, rested on failure to use standard statistical techniques to determine the validity of comparisons between climate and physiognomic characters. Dolph (1979) arrived at the same conclusion based on Costa Rican samples, but some of his samples had few species (for example, one sample comprised a single species), which hardly provided a reliable statistical basis for his conclusions; again, no statistical tests were performed to determine degree of validity of possible correlations. Dolph and Dilcher (1979), however, emphasized that leaf sizes might offer significant paleoclimatic information (as Wolfe, 1972 and 1977, also emphasized).

In their analysis of Late Cretaceous leaf assemblages, Wolfe and Upchurch (1987) suggested that, because the percentage of entire-margined species showed a marked paleolatitudinal gradient during different parts of the Late Cretaceous, the relation between margin type and climate had evolved early in the evolution of the angiosperms. Emphasis was also placed on leaf sizes and on leaf apices, but, as with Dolph and Dilcher's (1979) work, these categories could not be translated into numeric paleoclimatic parameters.

Granted that some characters may be closely correlated with various climatic parameters, a major, unstated, problem with all these single-character analyses is: how closely does the physiognomy of a given fossil-leaf assemblage mirror the physiognomy based on compilations from large modern samples? Many fossil samples comprise 30 or fewer species, and no data had been presented that samples of 30 species of modern vegetation produce accurate numeric values of mean annual temperature.

Wolfe and Upchurch (1987) suggested that, using leaf physiognomy, Late Cretaceous climates at middle to lower paleolatitudes in North America generally were warm and subhumid but, using data from fossil woods, had precipitation well distributed throughout the year. These authors also suggested that the closest modern analogous vegetation to the North American Late Cretaceous vegetation might be found today in the South Pacific, in areas such as Fiji, New Caledonia, and eastern Australia. In an attempt to find this "lost world" of the Late Cretaceous, I visited the South Pacific in 1988 and collected leaf and wood samples of the present-day vegetation. The collection areas were of limited geographic extent, in order to make the modern samples comparable in size and area of origin to fossil samples. While collecting in the South Pacific, I became aware that two samples from geographically and meteorologically similar environments could markedly differ in a single physiognomic character set (for example, size or apical configuration). This suggested that single-character analyses such as margin type or leaf size could yield invalid paleoclimatic results.

Single-character analysis of these collections of modern South Pacific vegetation confirmed that these analyses had an accuracy that would yield only very general estimates of climatic parameters. On the other hand, if a number of characters in the samples were scored and then subjected to multivariate analysis, the analysis appeared correctly to place the samples relative to temperature and precipitation. With the addition of several samples from the Sonoran Desert of Arizona collected late in 1988, the multivariate analysis still indicated that this method could produce accurate and precise numeric estimates of paleoclimatic parameters. I thus began intensive sampling to enlarge the database to include samples from as wide a variety of present-day climates as possible. Early versions of the Climate-Leaf Analysis Multivariate Program (CLAMP) were used to interpret climatic changes across the Cretaceous-Tertiary boundary (Wolfe, 1990a) and to suggest some climatic parameters for Pliocene leaf assemblages (Wolfe, 1990b).

The current CLAMP database, excluding the 11 South Pacific samples, now totals 106 samples; an additional 10 samples of small size or that were not collected according to established standards assist in interpreting various physiognomic trends. As discussed in a later section of this report (p. 42–49), the samples are from a great variety of climates. The samples are from latitudes as low as 9° N. and as high as 62° N. and from altitudes as low as sea level and as high as 2,700 m. Thus, possible influences on leaf physiognomy such as light regime and atmospheric pressure are taken into account.

COLLECTION SITES

SAMPLING STRATEGY

Most samples were collected from a limited geographic area that might be comparable to an area that furnished an assemblage of fossil leaves; that is, most samples were collected from an area of 1–5 hectares. Ideally each sample should have been collected from slopes above a stream and should include the streamside taxa as well as slope taxa. Inclusion of streamside taxa is particularly important in areas of low precipitation because in these areas the composition of the streamside flora is typically very distinct from the slope flora; this distinction is less marked in areas of high precipitation. Fossil leaf assemblages, of course, have a moderate to large percentage of taxa that today occupy streamside habitats.

In some areas, however, the ideal sampling strategy could not be accomplished. Some of these areas have geographically limited areas of vegetation interspersed with cleared areas of human habitation and (or) cultivation. Such limited areas did not provide a sufficient number (at least 20 and preferably 25–30 or more) of species on which to base a sample, and thus more than one sampling site had to be selected to achieve the necessary diversity. In still other areas (for example, Alaska and mid-latitude subalpine areas) the vegetation has low diversity and typically more than one site had to be selected; accessibility of sampling sites was also a factor here. In one instance (Kitt Peak, Ariz.) no streams, even ephemeral, are in the sampled area.

The typical sampling strategy was to begin collecting along a stream; once specimens of all streamside species were collected, the sampling area was enlarged to include slope vegetation. The sampling area was continually enlarged until either specimens of at least 25–30 species had been collected or no new species were encountered in a 15-minute traverse. The voucher specimens collected may include a single herbarium-size voucher or may also include a second voucher specimen of the same species or single leaves encountered later in the day that display physiognomic variations not included in the original voucher. With this strategy, obviously both sun and shade leaves were collected for each species.

The latitudes and longitudes given in the following site descriptions refer to the approximate center of a sampled area.

CARIBBEAN

PANAMA

Barro Colorado Island.—Lat 9°9.50′ N., long 79°51′ W.; sample from 1 hectare plot on plateau at an altitude of 150 m; soil volcanic-derived; primarily high (30 m), closed-canopy rain forest; meteorological data from Smithsonian station (2 km northeast, altitude 75 m). Collected by R.J. Burnham and S.L. Wing, 1989; 139 species.

PUERTO RICO

Some of the Puerto Rican samples (fig. 1) were collected proximal to meteorological stations, but some are distant (>10 km) from meteorological stations, especially where temperature data have been recorded. In these instances, I have estimated temperatures for the samples by calculating terrestrial lapse rates. Figures 2 and 3 represent regression analyses for mean annual temperature versus altitude for the northern and southern slopes of Puerto Rico, respectively. Although data are sparse, they indicate that the terrestrial lapse rate is higher on the north

Figure 1. Sampling sites (solid circles) in Puerto Rico.

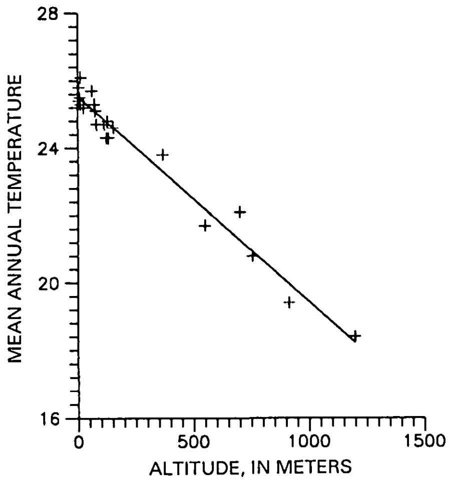

Figure 2. Linear regression for mean annual temperature (in °C) relative to altitude in northern Puerto Rico.

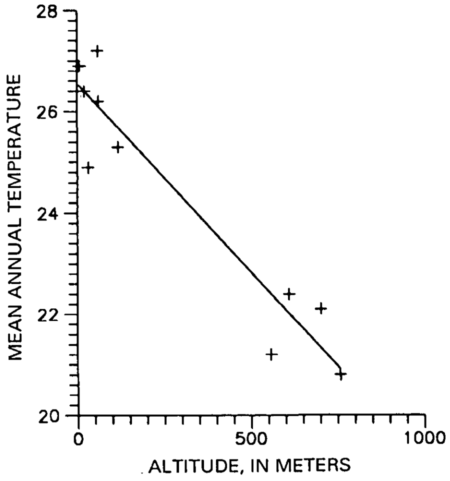

Figure 3. Linear regression for mean annual temperature (in °C) relative to altitude in southern Puerto Rico.

side of the island than on the south side. Meteorological stations are cited as in the publications of the National Oceanic and Atmospheric Administration and its predecessors; a designation such as "Arecibo 2 ESE" means that the data were recorded at a site approximately 2 miles east-southeast of the post office in the town of Arecibo.

Site and vegetation descriptions were furnished by G.J. Breckon and D.A. Kolterman (written commun., 1991).

Guanica.—Municipio Guanica. Lat 17°55′1″ N., long 66°54′36″ W.; Bosque Estatal de Guanica, about 100 m east of Bahia de Guanica at an altitude of about

10 m; shallow soil derived from limestone; semideciduous forest with scattered cacti; precipitation data from Ensenada (3 km west-northwest, altitude 8 m) and temperature data from Magueyes Island (15 km west, altitude 5 m). Where temperature data have been recorded from near sea level on the south coast (Magueyes Island and Aguirre), they indicate a mean annual temperature of 26.9°C. This value is, therefore, applied to the Guanica and Cabo Rojo samples. Collected by Breckon, Garcia, Kolterman, and Myatt, December 11, 1990; 33 species.

Cabo Rojo.—Municipio Cabo Rojo. Lat 17°56′45″ N., long 67°11′20″ W.; Bosque Estatal de Boqueron, north and northwest of lighthouse at an altitude of about 10 m; shallow soil on limestone; grasslands with scattered thickets of windswept low trees and shrubs; precipitation and temperature data from Magueyes Island (15 km east-northeast, altitude 5 m). Collected by Breckon, Kolterman, Garcia, and Caminero, June 21, 1991; 30 species.

Borinquen.—Municipio Guanica. Lat 17°58′20″ N., long 66°52′25″ W.; Bosque Estatal de Guanica, along highway 344 at about km 5.3 at an altitude of about 140 m; shallow soil and exposed limestone; plants sparse and shrubby; precipitation data from Ensenada (6 km west, altitude 8 m) and temperature data modified for altitudinal difference from Magueyes Island (18 km west, altitude 5 km). Collected by Garcia, Caminero, Kolterman, and Myatt, December 18, 1990; 41 species.

Cambalache.—Municipio Arecibo. Lat 18°27′15″ N., long 66°35′55″ W.; Bosque Estatal de Cambalache, gentle slopes of karst topography along western access road behind Job Corps facility near ranger station at an altitude of about 30–35 m; soil derived from limestone; semideciduous forest; meteorological data from Arecibo 2 ESE (9.5 km east-northeast, altitude 5 m). Collected by Breckon and Myatt, December 28, 1990; 37 species.

Susua Alta.—Municipio Yauco. Lat 18°04′20″ N., long 66°54′35″ W.; Bosque Estatal de Susua, along dirt road on east side of Quebrada Peces at an altitude of about 200 m; shallow, rocky, serpentine-derived soil; sclerophyllous evergreen forest with open, irregular canopy about 4–6 m high; precipitation data from Sabana Grande 2 ENE (5 km west, altitude 259 m), temperature data adjusted for altitude from San German 1 W (14 km west, altitude 116 m). Collected by Breckon, Garcia, Kolterman, and Myatt, December 4, 1990; 42 species.

Guajataca.—Municipio Planas. Lat 18°24′40″ N., long 66°58′ W.; karst topography along the Salome trail off route 446 at an altitude of about 250 m; soil derived from limestone; low evergreen forest; precipitation data from Guajataca Dam (4.50 km south-southeast, altitude 200 m) and temperature data adjusted for altitudinal difference from Quebradillas (7.5 km north-northeast, altitude 113 m). Collected by Breckon, Kolterman, and Myatt, January 2, 1991; 38 species.

Buena Vista.—Municipio Maricao. Lat 18°10′00″ N., long 66°59′40″ W.; Bosque Estatal de Maricao, along trail below hilltop on east side of highway 120 at km 17.9–18.0 at an altitude of about 655 m; shallow, rocky soil derived from serpentine; low Subtropical Wet forest; meteorological data adjusted for altitude from Maricao 2 SSW (5 km southwest, altitude 863 m). Collected by Caminero, Garcia, and Kolterman, May 31, 1991; 38 species.

Maricao.—Municipio Maricao. Lat 18°08′45″ N., long 66°58′50″ W.; Bosque Estatal de Maricao, north-facing slope on north side of highway 120 at km 14.0 across from observation tower at an altitude of about 850 m; lateritic soil derived from serpentine; Lower Montane Wet forest; meteorological data from Maricao 2 SSW (4 km southwest, altitude 863 m). Collected by Caminero, Garcia, and Kolterman, May 15, 1991; 35 species.

Monte Guilarte.—Municipio Adjuntas. Lat 18°09′24″ N., long 66°48′29″ W.; Guilarte Commonwealth Forest, northwest- to southwest-facing slopes along dirt road near summit at an altitude of 1,050–1,100 m; soil volcanic-derived; Lower Montane Rain forest; meteorological data adjusted for altitude from Garzas Dam (7 km east-southeast, altitude 757 m). Collected by Breckon, Caminero, Garcia, and Myatt, February 16, 1991; 33 species.

Toro Negro.—Municipio Jayuya. Lat 18°10′ N., long 66°34′17″ W.; Bosque Estatal de Toro Negro, north- and south-facing slopes of ridge on southeast side of Monte Jayuya at an altitude of about 1,270–1,300 m; soil volcanic-derived; dwarf forest; meteorological data adjusted for altitude from Cerro Maravilla (1.3–2 km east-southeast, altitude 1,200 m). Collected by Breckon, Bueno, Caminero, Garcia, and Reyes, December 1, 1990; 44 species.

EASTERN UNITED STATES

Most sampling sites in the Eastern United States (fig. 4) represent areas that were cut-over since settlement by Europeans. In most instances, however, the forests are either in late successional stage or have returned to "climax" stage. Attempts were made to collect as proximal as possible to meteorological stations, but this was generally not possible on the Coastal Plain because of heavy urbanization. The rolling to flat topography of the Coastal Plain, however, results in isotherms and isohyets that can be accurately estimated from available stations.

FLORIDA

Avon Park.—Polk County. Site 1 lat 27°41.6′ N., long 81°28.7′ W.; about 0.5 km south of Hickory Lake at an altitude of 30 m; soil sandy; closed- to open-canopy, short-statured evergreen sclerophyll forest, appearing to be moderately disturbed; site 2 lat 27°42.9′ N., long 81°28.5′ W.; 0.1–0.2 km south of Reedy Lake at an altitude of 25 m; soil

Figure 4. Sampling sites (solid circles) in the Eastern United States.

deep alluvial; closed-canopy, high-statured, mostly deciduous forest, appearing to be mostly undisturbed; precipitation and temperature data from Avon Park (10 km southeast of site 1 and 12 km south of site 2, altitude 25 m). Collected by J.A. Wolfe and A.L. Kraps, May 9, 1990; 31 species.

Orlando.—Osceola County. Site 1 lat 28°20.4′ N., long 81°18.3′ W.; about 1.5 km north of East Lake Tohopekaliga at an altitude of 30 m; soil sandy; open-canopy, short-statured woodland of *Pinus* and evergreen sclerophylls, appearing to be disturbed; site 2 lat 28°24.0′ N., long 81°19.9′ W.; immediately adjacent to property of Orlando Airport at an altitude of 15 m; soil sandy; very disturbed vegetation of widely spaced, short trees and shrubs that are mostly sclerophylls; site 3 lat 28°23.4′ N., long 81°19.4′ W.; along Boggy Creek on north side of Boggy Creek Swamp at an altitude of 20–25 m; wet-ground *Taxodium* swamp; meteorological data from Orlando Airport (9 km northwest of site 1, 3.5 km north of site 2, and 4 km north of site 3, altitude 25 m). Collected by J.A. Wolfe and A.L. Kraps May 10, 1990; 31 species.

Lake George.—Lake County. Lat 29°11.7′ N., long 81°32.2′ W.; within 1 km of Lake George at Zinder Point at an altitude of less than 5 m; soil sandy to boggy; vegetation disturbed to undisturbed, open-canopy sclerophyll scrub to closed-canopy mixed evergreen and deciduous forest; meteorological data from Deland 1 SSE (30 km southeast, altitude 8 m). Collected by J.A. Wolfe and A.L. Kraps, May 11, 1990; 30 species.

GEORGIA

Brunswick.—Glynn County. Lat 31°15.0′ N., long 81°26.6′ W.; along alluvial plain of tributary of Troup Creek at an altitude of 2–3 m; soil deep alluvial to sandy; vegetation includes undisturbed, high-statured, closed-canopy mixed evergreen and deciduous forest and low-statured second-growth deciduous forest with some *Pinus*; meteorological data from Brunswick FAA Airport (1.5 km northwest, altitude 5 m). Collected by J.A. Wolfe and A.L. Kraps, May 12, 1990; 34 species.

SOUTH CAROLINA

Beaufort.—Beaufort County. Site 1 lat 32°21.2′ N., long 80°49.6′ W.; along slopes of minor creeks about 2 km from coast at an altitude of 5 m; soil deep alluvial; mostly closed-canopy second-growth deciduous forest; site 2 lat 32°22.3′ N., long 80°49.6′ W.; on Lemon Island at an altitude of less than 2 m; soil sandy; disturbed open-canopy woodland of evergreen sclerophyllous and deciduous trees; meteorological data from Beaufort 7 SW (13 km northeast of site 1 and 6 km south of site 2, altitude 6 m). Collected by J.A. Wolfe and A.L. Kraps, May 13, 1990; 33 species.

Simmonsville.—Georgetown County. Lat 33°25.0′ N., long 79°09.7′ W.; east of Simmonsville about equidistant between Waccamaw River and Long Bay at an altitude of 5 m; soil sandy; second-growth closed-canopy forest of evergreen sclerophyllous and deciduous trees with some *Pinus*; meteorological data from Georgetown 2 E (9 km southwest, altitude 3 m). Collected by J.A. Wolfe and A.L. Kraps, May 14, 1990; 31 species.

NORTH CAROLINA

Kure Beach.—Brunswick County. Lat 34°00.0′ N., long 74°54.4′ W.; immediately east of Kure Beach at an altitude of less than 5 m; soil sandy; closed- to open-canopy second-growth forest of evergreen sclerophyllous and deciduous trees with some *Pinus*; meteorological data from Southport (12 km southwest, altitude 5 m). Collected by J.A. Wolfe and A.L. Kraps, May 15, 1990; 28 species.

MARYLAND

S.I.E.R.C.—Anne Arundel County. Lat 38°52.4′ N., long 76°35.3′ W.; Smithsonian Institution Environmental Research Center at an altitude of 30–50 m; soil deep, derived from sedimentary rocks; closed-canopy deciduous forest; meteorological data from Annapolis U.S. Naval Academy (15 km northeast, altitude 1 m). Collected by J.A. Wolfe and S.L. Wing, May 18, 1990; 32 species.

Battle Creek.—Calvert County. Lat 38°29.6′ N., long 76°35.6′ W.; Battle Creek Cypress Swamp State Park at an altitude of less than 10 m; mostly swamp soil; closed-canopy *Taxodium* swamp; meteorological data from Prince Frederick (4 km north, altitude 43 m). Collected by J.A. Wolfe and S.L. Wing, May 18, 1990; 28 species.

Frederick.—Frederick County. Lat 39°26.0′ N., long 77°28.4′ W.; east-facing slopes about 3 km northwest of Frederick at an altitude of 100 m; soil deep, derived from sedimentary rocks; closed-canopy second-growth deciduous forest; meteorological data from Frederick Police Barracks (2 km southeast, altitude 116 m). Collected by J.A. Wolfe, May 19, 1990; 28 species.

PENNSYLVANIA

Arendtsville.—Adams County. Lat 39°56.2′ N., long 77°18.1′ W.; west-facing slopes at an altitude of 220–230 m; soil deep, derived from sedimentary rocks; closed-canopy second-growth deciduous forest; meteorological data from Arendtsville (1.5 km south, altitude 146 m). Collected by J.A. Wolfe and A.L. Kraps, May 21, 1990; 30 species.

Stroudsburg.—Monroe County. Lat 40°58.6′ N., long 75°11.2′ W.; west-facing slopes just east of highway 191 at an altitude of 160 m; soil deep, derived from sedimentary rocks; closed-canopy deciduous forest with some *Pinus*; meteorological data from Stroudsburg (1 km north, altitude 146 m). Collected by J.A. Wolfe and A.L. Kraps, May 22, 1990; 30 species.

Tunkhannock.—Wyoming County. Lat 41°34.5′ N., long 75°52.4′ W.; east-facing slopes above Tunkhannock Creek at an altitude of 240–260 m; soil deep, derived from sedimentary rocks; second-growth closed-canopy deciduous forest; meteorological data from Dixon (3 km southwest, altitude 229 m). Collected by J.A. Wolfe and A.L. Kraps, May 23, 1990; 33 species.

Mt. Pocono.—Wayne County. Lat 41°14.2′ N., long 75°28.0′ W.; Gouldsboro State Park at an altitude of 580–600 m; soil deep, derived from sedimentary rocks; second-growth closed-canopy deciduous forest; meteorological data from Mt. Pocono 2 N (10 km southeast, altitude 584 m). Collected by J.A. Wolfe and A.L. Kraps, May 24, 1990; 28 species.

NEW YORK

Dannemora.—Clinton County. Lat 44°44.4′ N., long 73°40.7′ W.; alluvial plain of Canfield Brook at an altitude of 410–420 m; soil derived from sedimentary rocks, deep to boggy; second-growth closed-canopy deciduous forest; meteorological data from Dannemora (3.5 km southwest, altitude 408 m). Collected by J.A. Wolfe and A.L. Kraps, May 26, 1990; 30 species.

Wanakena.—St. Lawrence County. Lat 44°09.4′ N., long 74°55.3′ W.; east of State Highway 3 on land of Wanakena Ranger School at an altitude of 450–460 m; soil derived from sedimentary rocks, deep to boggy; closed- to open-canopy forest of conifers and deciduous trees and marshland; meteorological data from Wanakena Ranger School (2.5 km south, altitude 455 m). Collected by J.A. Wolfe, May 27, 1990; 29 species.

Lake Placid.—Essex County. Lat 44°17.5′ N., long 73°57.5′ W.; along State Highway 86 at an altitude of 550–580 m; soil derived from sedimentary rocks, deep to boggy; closed-canopy forest of conifers and deciduous trees and marshland; meteorological data from Lake Placid Club (2.5 km southwest, altitude 570 m). Collected by J.A. Wolfe, May 28, 1990; 24 species.

WISCONSIN

River Falls.—St. Croix County. Lat 44°52′05″ N., long 92°22′05″ W.; rolling hills above Rush River at an altitude of 295 m; soil deep, derived from pre-Wisconsin glacial drift; closed-canopy broad-leaved deciduous forest; meteorological data from River Falls (20 km east, altitude 274 m). Collected by H.E. Schorn, July 15, 1991; 22 species.

WESTERN UNITED STATES

Climates in the Western United States have great variability that is related to altitude and exposure. Thus, collecting samples proximal to meteorological stations and at approximately the same altitude is generally necessary.

The areas sampled in Arizona (fig. 5) represent undisturbed vegetation. In marked contrast, European settlement in New Mexico has greatly disturbed sites such as Tierra Amarilla and Jemez Springs. Extensive mining of coal in the Raton Mesa area in the early part of this century has produced second-growth and still-disturbed vegetation around Lake Maloya. Most Colorado sampling areas (fig. 5), however, are undisturbed or only slightly disturbed.

The degree of ecologic disturbance in California is variable. Samples from the coastal areas have been disturbed, but the Jasper Ridge sample is from a biological preserve. Samples from the foothills below an altitude of about 1,500 m in the Sierra Nevada typically represent highly disturbed vegetation; this disturbance began in the 19th century during the gold rush and has returned, especially in the last few decades, as a result of urbanization. Sampling areas above 1,500 m altitude are typically undisturbed.

In Oregon and Washington, many sampling areas were logged several to many decades ago, and the present vegetation is second growth. The Cape Blanco, Three Lynx, Rimrock Lake, Government Camp, and Laurel Mountain samples are notable exceptions, either because the timber was not commercially viable or the areas were protected from logging.

ARIZONA

Canyon Lake.—Maricopa County. Lat 33°02.3′ N., long 110°26.6′ W.; north-facing slopes from reservoir level to about 50 m above at southwestern corner of reservoir at an altitude of 506–555 m; soil derived from volcanic rocks; open desert with cacti and scattered trees and shrubs; meteorological data from Mormon Flat (1.2–1.5 km north, altitude 523 m). Collected by J.A. Wolfe and A.L. Kraps, March 5, 1990; 30 species.

Bartlett Reservoir.—Maricopa County. Site 1 lat 33°51.1′ N., long 111°38.1′ W.; from reservoir level to about 30 m above along southwestern shore of reservoir at an altitude of 533–563 m; soil derived from volcanic rocks; open desert of cacti and widely spaced small trees and shrubs; site 2 lat 33°57.7′ N., long 111°42.7′ W.; along alluvial flats of Verde River at an altitude of 580 m; soil deep alluvial; open-canopy woodland of trees as high as 10 m; meteorological data from Bartlett Dam (2 km

Figure 5. Sampling sites (solid circles) in the Western United States.

south of site 1 and 7 km southeast of site 2, altitude 580 m). Collected by J.A. Wolfe and A.L. Kraps, December 5, 1988; 20 species.

Castle Creek.—Yavapai County. Site 1 lat 33°58.8′ N., long 112°21.7′ W.; along ephemeral streambed in canyon of Castle Creek at an altitude of 630 m; soil deep alluvial in streambed and bare rocky slopes forming canyon; gallery vegetation and adjacent open desert; site 2 lat 33°58.1′ N., long 112°20.8′ W.; along ephemeral stream bed of Castle Creek at an altitude of 580 m; soil deep alluvial to shallow and derived from volcanic rocks; open desert; meteorological data from Castle Hot Springs (0.2 northwest of site 1 and 4 km northwest of site 2, altitude 640 m). Collected by J.A. Wolfe and A.L. Kraps, December 12, 1988, November 20, 1989, and November 18, 1991; 23 species.

Superior.—Pinal County. Site 1 lat 33°17.0′ N., long 111°05.4′ W.; along dry washes and adjacent west-facing slopes 1 km south of Superior along highway 177 at an altitude of 900–920 m; soil shallow, rocky, derived from metamorphic rocks; open desert; site 2 lat 33°16.6′ N., long 111°09.0′ W.; on floodplain of Queen Creek at an altitude of 810 m; soil deep alluvial; open-canopy gallery woodland; meteorological data from Superior (2 km north of site 1 and 5 km northeast of site 2, altitude 913 m). Collected by J.A. Wolfe and A.L. Kraps, December 6, 1989; 29 species.

Saguaro Lake.—Maricopa County. Site 1 lat 33°03.8′ N., long 111°32.7′ W.; in and along ephemeral streambeds 1 km west of Saguaro Lake at an altitude of 470–490 m; soil derived from granite; open desert; site 2 lat 33°03.4′ N., long 111°32.3′ W.; in floodplain of Salt River at an altitude of 450 m; soil deep alluvial; gallery vegetation; meteorological data from Stewart Mountain Dam (0.8 km east of site 1 and 0.6 km north of site 2, altitude 450 m). Collected by J.A. Wolfe and A.L. Kraps, November 30, 1988, March 16, 1990, and December 2, 1991; 24 species.

Roosevelt Lake.—Gila County. Site 1 lat 33°41.6′ N., long 111°10.8′ W.; on slopes and ephemeral streambeds from reservoir level to 50 m above at an altitude of 645–695 m; soil shallow, rocky, derived from volcanic rocks; open desert; site 2 lat 33°42.3′ N., long 111°12.5′ W.; in small canyon with perennial spring at an altitude of 690 m; soil deep alluvial; open-canopy gallery woodland; meteorological data from Roosevelt 1 WNW (3.5 km southeast of site 1 and 6.5 km southeast of site 2, altitude 671 m). Collected by J.A. Wolfe, March 16, 1989; 23 species.

Punkin Center.—Gila County. Site 1 lat 33°52.5′ N., long 111°20.3′ W.; along north-facing slopes and in adjacent ephemeral streambed of Reno Creek at an altitude of 740–780 m; soil shallow, rocky, derived from metamorphic rocks; ecotone between open desert and chaparral; site 2 lat 33°53.6′ N., long 111°18.4′ W.; on flats above Tonto Creek at an altitude of 725 m; soil shallow alluvial; open desert; site 3 lat 33°52.1′ N., long 111°18.6′ W.; on alluvial plain of Tonto Creek at an altitude of 710–715 m; soil deep alluvial; open-canopy gallery woodland; meteorological data from Punkin Center (2 km east of site 1, 2.5 km south of site 2, and 0.1–0.2 km west of site 3, altitude 716 m). Collected by J.A. Wolfe and A.L. Kraps, November 29, 1989, and April 1, 1991; 30 species.

Childs.—Yavapai County. Lat 34°20.7′ N., long 111°41.7′ W.; alluvial flats and adjacent slopes along canyon of Verde River at an altitude of 800–820 m; soil deep alluvial to rocky, volcanic-derived; open-canopy gallery woodland on alluvial flats adjacent to open desert of large cacti, which are intermixed within 10 m above flats with chaparral; meteorological data from Childs (0–0.1 km west, altitude 808 m). Collected by J.A. Wolfe and A.L. Kraps, November 29, 1989; 24 species.

Santa Rita.—Santa Cruz County. Lat 31°46.4′ N., long 110°50.6′ W.; ephemeral streambed and adjacent slopes north and west of work station and headquarters of Santa Rita Experimental Range at an altitude of 1,305–1,320 m; soil mostly shallow, rocky, sedimentary-derived; open-canopy woodland of *Quercus* adjacent to stream to steppe with widely spaced trees and shrubs on slopes; meteorological data from Santa Rita Experimental Range (less than 0.5 km east and south of sampled area, altitude 1,311 m). Collected by J.A. Wolfe and A.L. Kraps, November 14, 1991; 28 species.

Miami.—Gila County. Lat 33°22.9′ N., long 110°53.7′ W.; ephemeral streambed and adjacent slopes at an altitude of 1,100–1,150 m; deep alluvial soil in streambed, shallow, granitic-derived soil on slopes; open-canopy gallery woodland in streambed, chaparral on slopes; meteorological data from Miami (2.5 km northeast, altitude 1,098 m). Collected by J.A. Wolfe and A.L. Kraps, December 4, 1989; 21 species.

Sierra Ancha.—Gila County. Lat 33°48.2′ N., long 110°58.1′ W.; along Parker Creek and adjacent slopes at an altitude of 1,540–1,560 m; deep alluvial to rocky, volcanic-derived soil; open- to almost closed-canopy gallery forest along creek merging into chaparral on slopes; meteorological data from Sierra Ancha Research Station (0–0.2 km east, altitude 1,555 m). Collected by J.A. Wolfe and A.L. Kraps, November 15, 1989, and November 19, 1990; 27 species.

Yava.—Yavapai County. Lat 34°28.3′ N., long 112°53.4′ W.; floodplain of Kirkland Creek and adjacent slopes at an altitude of 1,010–1,080 m; deep alluvial soil in floodplain and shallow, rocky, metamorphic-derived soil on slopes; open-canopy gallery woodland on floodplain merging with chaparral on slopes; meteorological data from Hillside 4 NE (within sampled area to 2 km north, altitude 1,012 m). Collected by J.A. Wolfe, November 22, 1989, and November 28, 1990; 24 species.

Jerome.—Yavapai County. Site 1 lat 34°46.0′ N., long 112°06.8′ W.; in ephemeral streambed and adjacent slopes at an altitude of 1,570–1,620 m; deep alluvial soil in streambed and shallow, rocky, metamorphic-derived soil on slopes; open-canopy gallery woodland along stream merging with chaparral on slopes; site 2 lat 34°44.6′ N., long 112°07.5′ W.; on rocky slopes at an altitude of 1,600 m; soil shallow, rocky, metamorphic-derived; grassland with widely spaced shrubs; meteorological data from Jerome (0.8 km north of site 1 and 2 km southeast of site 2, altitude 1,599 m). Collected by J.A. Wolfe and A.L. Kraps, July 1, 1989, December 1, 1990, and April 19, 1991; 26 species.

Natural Bridge.—Gila County. Lat 34°19.5′ N., long 111°27.3′ W.; along Pine Creek and adjacent slopes at an altitude of 1,350–1,420 m; deep alluvial to rocky, volcanic-derived soil; open-canopy gallery woodland along creek merging with open-canopy sclerophyll woodland and chaparral; meteorological data from Natural Bridge (0.1–0.2 km south, altitude 1,404 m). Collected by J.A. Wolfe and A.L. Kraps, November 21, 1990; 28 species.

Canelo.—Pima County. Lat 31°32.6′ N., long 110°30.6′ W.; ephemeral to perennial streambed of Turkey Creek and adjacent slopes at an altitude of 1,515–1,585 m; soil deep to shallow, rocky, sedimentary-derived; open-canopy woodland of broad-leaved evergreen sclerophyllous trees and shrubs; meteorological data from Canelo 1 NW (0–3 km north and south, altitude 1,519 m). Collected by J.A. Wolfe and K. Gregory, November 12, 1991; 31 species.

Junipine.—Coconino County. Lat 34°59.8′ N., long 111°44.2′ W.; along alluvial flats of Oak Creek and adjacent west-facing slopes at an altitude of 1,540–1,600 m; soil deep alluvial along Oak Creek to shallow, rocky sedimentary-derived on slopes; closed-canopy deciduous gallery forest on flats merging with open-canopy deciduous forest on adjacent slopes, some sclerophyllous shrubs; meteorological data from Junipine (at center of sampled area, which has a 0.2-km radius, altitude 1,562 m). Collected by J.A. Wolfe and A.L. Kraps, July 1, 1989, and November 14, 1990; 27 species.

Payson.—Gila County. Lat 34°17.1′ N., long 111°20.3′ W.; along south- and north-facing slopes of Ash Creek (here an ephemeral stream) at altitude of 1,480–1,500 m; soil deep to shallow, rocky, volcanic-derived; open-canopy woodland of *Quercus* and *Cupressus*-chaparral; meteorological data from Payson (4.5 km south, altitude 1,498 m). Collected by J.A. Wolfe and A.L. Kraps, October 30, 1991; 28 species.

Prescott Airport—Yavapai County. Site 1 lat 34°37.6′ N., long 112°25.9′ W.; along ephemeral stream and adjacent flats at an altitude of 1,530–1,540 m; soil shallow, granitic-derived; open-canopy sclerophyllous woodland and grassland; site 2 lat 34°36.9′ N., long 112°24.9′ W.; along alluvial flats of Granite Creek and adjacent lower slopes at an altitude of 1,520–1,540 m; soil deep alluvial to shallow, rocky, granitic-derived; open-canopy deciduous gallery forest on flats to chaparral on slopes; meteorological data from Prescott WB AP (3 km north of site 1 and 4 km north of site 2, altitude 1,528 m). Collected by J.A. Wolfe and A.L. Kraps, July 2, 1989, and November 12, 1990; 30 species.

Crown King.—Yavapai County. Lat 34°12.4′ N., long 112°20.1′ W.; along ephemeral streams and adjacent lower slopes at an altitude of 1,820–1,870 m; soil shallow, rocky, granitic-derived; open-canopy forest dominated by *Pinus ponderosa* with evergreen sclerophyllous and deciduous small trees and shrubs; meteorological data from Crown King (at center of sampled area, which has a 0.5-km radius, altitude 1,829 m). Collected by J.A. Wolfe and A.L. Kraps, July 4, 1989, and November 10, 1990; 25 species.

Kitt Peak.—Pima County. Lat 31°57.5′ N., long 111°35.7′ W.; on upper slopes of Kitt Peak at an altitude of 2,050–2,070 m; soil shallow, rocky, granitic-derived; open-canopy woodland of broad-leaved evergreen sclerophyllous trees and shrubs; meteorological data from Kitt Peak (within sampled area, which has a radius of about 1 km, altitude 2,070 m). Collected by J.A. Wolfe and A.L. Kraps, November 12, 1991; 23 species. No streams, even ephemeral, occur on Kitt Peak above about 1,500 m altitude; this sample thus contains no fluviatile or wet-ground vegetation.

Hasayampa.—Yavapai County. Site 1 lat 34°27.5′ N., long 112°27.5′ W.; along Wolf Creek and adjacent lower slopes at an altitude of 1,920–1,960 m; soil deep to shallow and rocky granitic-derived; open- to closed-canopy forest of *Pinus ponderosa* with mostly deciduous trees and shrubs below canopy; site 2 lat 34°26.3′ N., long 112°26.7′ W.; along Hasayampa River and adjacent lower slopes at an altitude of 1,820–1,840 m; soil and vegetation as at site 1; meteorological data from Groom Creek (2 km northeast of site 1 and 4.5 km northeast of site 2, altitude 1,859 m). Collected by J.A. Wolfe and A.L. Kraps, July 2, 1989, and November 12, 1990; 22 species.

NEW MEXICO

Jemez Springs.—Sandoval County. Lat 35°45.8′ N., long 106°41.2′ W.; valley of Jemez River from alluvial flats to east- and west-facing slopes about 40 m above river at an altitude of 1,840–1,950 m; soil deep to shallow and rocky granitic-derived; open-canopy deciduous gallery woodland along river to low, open-canopy woodland of *Juniperus* and evergreen sclerophyllous and deciduous trees and shrubs on slopes; meteorological data from Jemez Springs (at center of sampling area, which has a radius of 3 km, altitude 1,859 m). Collected by J.A. Wolfe and A.L. Kraps, June 30, 1989, and September 8, 1990; 24 species.

Los Alamos.—Los Alamos County. Lat 35°53.8′ N., long 106°19.1′ W.; southeast-trending ravine in northwestern part of town of Los Alamos at an altitude of

2,260–2,280 m; soil deep, volcanic-derived; open- to closed-canopy forest dominated by *Pinus ponderosa*; meteorological data from Los Alamos (1 km south, altitude 2,259 m). Collected by J.A. Wolfe and A.L. Kraps, September 9, 1990; 25 species.

Lake Maloya.—Colfax County (part of sampled area is in Las Animas County, Colorado). Lat 36°59.8′ N., long 104°21.9′ W.; alluvial flats and adjacent slopes north of Lake Maloya at an altitude of 2,289–2,350 m; soil shallow to deep sedimentary-derived and moist meadow; open- to closed-canopy second-growth forest dominated by *Pinus ponderosa* and deciduous *Quercus*, with thickets of *Salix* on flats; meteorological data from Lake Maloya (1 km south, altitude 2,256 m). Collected by J.A. Wolfe and A.L. Kraps, September 12, 1990; 20 species.

Tierra Amarilla.—Rio Arriba County. Site 1 lat 36°44.3′ N., long 106°32.3′ W.; along alluvial flats of Rio Brazo at an altitude of 2,260 m; soil deep alluvial; open-canopy gallery woodland of deciduous trees and shrubs; site 2 lat 36°39.3′ N., long 106°33.6′ W.; near top of hill along highway 84 at an altitude of about 2,370 m; soil shallow, rocky, sedimentary-derived; open-canopy forest dominated by *Juniperus*, *Pinus ponderosa*, and deciduous *Quercus*; site 3 lat 36°42.5′ N., long 106°34.8′ W.; along small creek south of highway 112 at an altitude of 2,250 m; soil deep alluvial; gallery shrubs in an area of grassland; meteorological data from Tierra Amarilla 4 NNW (0.5 km southeast of site 1, 9 km north of site 2, and 5 km northeast of site 3, altitude 2,263 m). Collected by J.A. Wolfe and A.L. Kraps, September 7, 1990; 21 species.

Red River.—Taos County. Lat 36°42.6′ N., long 105°39.7′ W.; alluvial flats of Red River and Malrette Creek and adjacent slopes to about 20 m above at an altitude of 2,620–2,660 m; soil deep to shallow metamorphic-derived; open- to closed-canopy forest dominated by *Picea* and *Pinus*; meteorological data from Red River (1.5–2.0 km southeast, altitude 2,645 m). Collected by J.A. Wolfe and A.L. Kraps, September 10, 1990; 29 species.

COLORADO

Cheesman.—Jefferson County. Site 1 lat 39°13.0′ N., long 105°16.5′ W.; along northeast ern shore of reservoir to 30 m above at an altitude of 2,085–2,115 m; soil shallow, metamorphic-derived; open-canopy forest dominated by *Pinus ponderosa*; site 2 lat 39°14.6′ N., long 105°16.0′ W.; alluvial flats of Wigwam Creek at an altitude of 2,050–2,060 m; soil deep alluvial; mostly dense thickets dominated by *Salix*; meteorological data from Cheesman (0.5–1.5 km south of site 1 and 3.5 km south of site 2, altitude 2,096 m). Collected by J.A. Wolfe, August 23, 1990; 27 species.

Estes Park.—Larimer County. Lat 40°22.9′ N., long 105°32.8′ W.; along alluvial flats of Fall River and adjacent lower slopes to 20 m above river at an altitude of 2,350–2,370 m; soil deep alluvial to shallow, metamorphic-derived; thickets of *Salix* along river to open-canopy forest of *Pinus ponderosa* on lower slopes; meteorological data from Estes Park (2–3 km east, altitude 2,285 m). Collected by J.A. Wolfe and A.L. Kraps, August 1, 1990; 30 species.

Nederland.—Boulder County. Lat 39°59.2′ N., long 105°29.5′ W.; along alluvial flats of North Boulder Creek and adjacent lower slopes to 30 m above creek at an altitude of 2,500–2,530 m; soil deep alluvial to shallow, rocky metamorphic-derived; mostly thickets of *Salix* on flats and open-canopy forest of *Pinus contorta* and *Picea* on slopes; meteorological data from Nederland 2 ENE (1 km southwest, altitude 2,512 m). Collected by J.A. Wolfe and A.L. Kraps, August 3, 1990; 26 species.

Allens Park.—Boulder County. Lat 40°11.6′ N., long 105°31.4′ W.; creeks and slopes of varying exposures within 1.5 km of Allens Park at an altitude of 2,550–2,600 m; soil deep alluvial to shallow, rocky metamorphic-derived; flats with thickets of *Salix* along streams to open-canopy forest dominated by *Pinus contorta* on lower slopes; meteorological data from Allens Park (within sampled area, which has a radius of 1.5 km, altitude 2,591 m). Collected by J.A. Wolfe and H.E. Schorn, August 27, 1991; 27 species.

Wolf Creek.—Mineral County. Lat 37°28.5′ N., long 106°51.4′ W.; along alluvial flats of Wolf Creek and adjacent lower slopes to 50 m above creek at an altitude of 2,850–2,900 m; soil deep to shallow, volcanic-derived; some thickets of *Salix* along creek but mostly open- to closed-canopy forest dominated by *Picea*; meteorological data from Wolf Creek Pass 4 W (recording equipment at center of sampled area, which has a radius of 1 km, altitude 2,873 m). Collected by J.A. Wolfe and A.L. Kraps, September 6, 1990; 20 species.

Tahosa Creek.—Larimer County. Lat 40°16.9′ N., long 105°32.8′ W.; along alluvial flats of Tahosa Creek and adjacent lower slopes to 70 m above creek at an altitude of 2,730–2,800 m; soil deep alluvial to shallow, rocky, metamorphic-derived; thickets of *Salix* on flats to open- to closed-canopy forest of *Pinus contorta* and *Picea* on slopes; meteorological data from Longs Peak (at center of sampled area, which has a radius of 1 km, altitude 2,730 m). Collected by J.A. Wolfe and A.L. Kraps, August 7, 1990; 20 species.

Lake Granby.—Grand County. Site 1 lat 40°11.2′ N., long 105°52.3′ W.; within 0.5 km of north shore of lake at an altitude of 2,530–2,550 m; soil deep alluvial to shallow, metamorphic-derived; thickets of *Salix* along creeks bounded by steppes dominated by *Artemesia* to open-canopy forest dominated by *Pinus contorta*; site 2 lat 40°12.0′ N., long 105°53.6′ W.; along ephemeral creeks and slopes northwest of lake at an altitude of 2,530–2,580 m; soil as at site 1; sparse thickets of *Salix* and steppe; meteorological data from Grand Lake 6 SW (0.1 km south of site 1 and 1.5–2.5 km southeast of site 2, altitude 2,526 m). Collected by J.A. Wolfe and A.L. Kraps, August 29, 1990; 22 species.

Dillon.—Summit County. Site 1 lat 39°37.8′ N., long 106°03.7′ W.; along alluvial flats of Strait Creek and adjacent north-facing slopes to 60 m above creek at an altitude of 2,750–2,810 m; soil mostly shallow, rocky metamorphic-derived; thickets of *Salix* along creek and open-canopy forest dominated by *Pinus contorta* on slopes; site 2 lat 39°38.1′ N., long 106°02.3′ W.; on southwest-facing slopes above Dillon Reservoir at an altitude of 2,780 m; soil as at site 1; steppe; meteorological data from Dillon 1 E (2 km east-northeast of site 1 and <1 km north of site 2, altitude 2,763 m). Collected by J.A. Wolfe and H.E. Schorn, August 29, 1991; 26 species.

Grand Lake.—Grand County. Site 1 lat 40°15.2′ N., long 105°47.9′ W.; along lower reaches of Tonahutu Creek at an altitude of 2,600 m; soil rocky metamorphic-derived; sparse gallery shrubs; site 2 lat 40°17.7′ N., long 105°50.3′ W.; along alluvial flats of Colorado River and adjacent slopes to 30 m above river (Kawuneeche Valley) at an altitude of 2,660–2,670 m; soil glacial outwash to shallow, rocky metamorphic-derived; thicket of *Salix*, open meadows, and *Artemesia*-dominated steppe on flats giving way to open- to closed-canopy forest dominated by *Pinus contorta* and *Picea* on slopes; meteorological data from Grand Lake 1 NW (2.2 km northwest of site 1 and 1.5–6.5 km south of site 2, altitude 2,646 m). Collected by J.A. Wolfe and A.L. Kraps, August 30, 1990; 28 species.

UTAH

Red Fleet.—Uintah County. Lat 40°33.0′ N., long 109°19.6′ W.; hills and valleys north and east of Red Fleet Reservoir at an altitude of 1,610–1,710 m; soil mostly shallow, sedimentary-derived but some deep alluvial soil in one valley drained by perennial stream; thickets of *Salix* and *Betula* along stream giving way to woodland of widely spaced *Juniperus* intermixed with *Artemesia*-dominated steppe; meteorological data from Vernal (5–8 km south and southwest, altitude 1,609 m). Collected by J.A. Wolfe and A.L. Kraps, June 25, 1990; 24 species.

CALIFORNIA

Camp Pardee.—Calaveras County. Site 1 lat 38°15.7′ N., long 120°51.6′ W.; slopes of varying exposure above Pardee Reservoir at an altitude of 170–240 m; soil deep alluvial to shallow, rocky volcanic-derived; open-canopy gallery woodland along perennial streams slopes with chaparral to open-canopy woodland of evergreen sclerophyllous and deciduous trees; site 2 lat 38°13.4′ N., long 120°54.0′ W.; along Bear Creek southwest of Burson at an altitude of 180 m; soil deep alluvial; open-canopy gallery woodland; meteorological data from Camp Pardee (at center of site 1, which has radius of 7 km, and 10 km northeast of site 2, altitude 201 m). Collected by J.A. Wolfe, July 14, 1990; 27 species.

Auburn.—Placer County. Site 1 lat 38°54.5′ N., long 121°01.2′ W.; north-facing ravine above Middle Fork of American River along State Highway 49 at an altitude of 390–400 m; soil shallow, rocky, volcanic-derived; open- to almost closed-canopy woodland of broad-leaved evergreen and deciduous trees and shrubs; site 2 lat 38°52.5′ N., long 121°01.1′ W.; shallow depression just south of Highway 49 along ephemeral waterway at an altitude of 420 m; soil deep alluvial; open-canopy gallery woodland; meteorological data from Auburn (1.5 km west-southwest of site 1 and 4 km west-northwest of site 2, altitude 394 m). Collected by J.A. Wolfe, July 15, 1990; 29 species.

Colfax.—Placer County. Site 1 lat 39°06.4′ N., long 120°56.6′ W.; east-facing ravine leading to American River immediately south of Interstate 80 at an altitude of 730–740 m; soil deep alluvial; open- to closed-canopy woodland of broad-leaved evergreen and deciduous trees and shrubs; site 2 lat 39°06.4′ N., long 120°58.1′ W.; in valley and adjacent slopes at an altitude of 700–720 m; soil deep alluvial; open-canopy woodland of broad-leaved evergreen and deciduous trees and shrubs; meteorological data from Colfax (0.5 km west of site 1 and 2 km east of site 2, altitude 737 m). Collected by J.A. Wolfe, July 21, 1990; 27 species.

Jasper Ridge.—Santa Clara County. Lat 37°24.4′ N., long 122°14.0′ W.; valleys and hills of varying exposure in Stanford University Jasper Ridge Biological Preserve at an altitude of 30–50 m; soil deep alluvial along creeks to shallow, rocky serpentine-derived on slopes; open- to closed-canopy gallery woodland along creek and either chaparral or woodland of widely spaced trees in grassland on slopes; meteorological data from Jasper Ridge (0.1–2 km northeast, altitude 30 m). Collected by J.A. Wolfe and H.E. Schorn, May 20, 1991; 32 species.

Lakeport.—Lake County. Lat 39°05′ N., long 122°56′ W.; along alluvial flats of Scotts Creek and adjacent plain at an altitude of 410 m; soil deep alluvial, sedimentary-derived; open-canopy gallery woodland along stream and open-canopy woodland of broad-leaved deciduous and evergreen sclerophyllous trees; meteorological data from Lakeport (6 km south-southeast, altitude 411 m). Collected by H.E. Schorn, October 17, 1990; 21 species.

Santa Cruz.—Santa Cruz County. Site 1 lat 36°58.7′ N., long 121°55.3′ W.; on hills in and immediately south of New Brighton State Beach at an altitude of 2–40 m; soil deep alluvial; open- to closed-canopy forest of *Pinus radiata*; site 2 lat 36°58.2′ N., long 121°54.1′ W.; on sea bluffs in Seacliff State Beach; soil deep alluvial; coastal scrub; meteorological data from Santa Cruz (5 km west of site 1 and 7 km west of site 2, altitude 0 m). Collected by J.A. Wolfe and H.E. Schorn, May 18, 1991; 25 species.

Placerville.—El Dorado County. Site 1 lat 38°42.8′ N., long 120°45.6′ W.; along Weber Creek and slopes above where crossed by State Highway 49 at an altitude of 520–530 m; soil deep alluvial; mostly closed-canopy gallery forest of broad-leaved evergreen and deciduous trees and shrubs; site 2 lat 38°47.5′ N., long 120°48.8′ W.; in Texas Canyon east of State Highway 193 at an altitude of 600 m; soil shallow, rocky, volcanic-derived; open-canopy woodland and scrub with many sclerophyllous evergreen shrubs; site 3 lat 38°45.0′ N., long 120°46.4′ W.; immediately north of U.S. Highway 50 at an altitude of 610 m; soil deep alluvial; open- to closed-canopy gallery forest; meteorological data from Placerville (3 km northeast of site 1, 6 km south-southeast of site 2, and 2.5 km west of site 3, altitude 576 m). Collected by J.A. Wolfe and H.E. Schorn, July 20, 1990; 24 species.

Half Moon Bay.—San Mateo County. Site 1 lat 37°25.9′ N., long 122°26.2′ W.; along coastal plain at Miramontes Point at an altitude of 10–20 m; soil deep alluvial; coastal scrub with scattered groves of *Cupressus*; site 2 lat 37°21.7′ N., long 122°23.8′ W.; valley of Tunitas Creek where crossed by State Highway 1 at an altitude of 10 m; soil deep alluvial; some open-canopy gallery woodland along stream and dense thickets of shrubs on slopes; site 3 lat 37°24.3′ N., long 122°24.7′ W.; on Purissima Creek east of Highway 1 at an altitude of 50 m; soil deep alluvial; open-canopy gallery woodland of broad-leaved evergreen and deciduous trees and shrubs; meteorological data from Half Moon Bay (3 km north of site 1, 11 km north of site 2, and 6 km north-northwest of site 3, altitude 19 m). Collected by J.A. Wolfe and H.E. Schorn, May 19, 1991; 25 species.

Nevada City.—Placer County. Site 1 lat 39°15.9′ N., long 121°02.4′ W.; along State Highway 49 and south-facing slopes above at an altitude of 750–780 m; soil deep, volcanic-derived; open- to closed-canopy woodland of sclerophylls mixed with *Pinus ponderosa*; site 2 lat 39°16.0′ N., long 121°00.2′ W.; along Deer Creek and slopes above at an altitude of 760–770 m; soil deep alluvial; open-canopy gallery woodland; meteorological data modified from Nevada City (2–3 km east-southeast of site 1 and 1 km west-southwest of site 2, altitude 768 m). Collected by J.A. Wolfe, July 23, 1990; 21 species. Although long-term temperature data recorded from Nevada City produce a mean annual temperature of 11.5°C, the recording instruments used must be in error. Strawberry Valley (altitude 1,161 m) and De Sabla (altitude 827 m) are both well north of Nevada City and have mean annual temperatures of 11.3°C and 12.9°C, respectively. To the south of Nevada City, Grass Valley (altitude 732 m), which is only 6 km from Nevada City, and Colfax (altitude 737 m) have mean annual temperatures of 15.0°C and 15.1°C, respectively.

Blue Canyon.—Placer County. Site 1 lat 39°16.9′ N., long 120°41.4′ W.; along creek (North Fork of American River) and adjacent slopes at an altitude of 1,600 m; soil shallow, granitic-derived; area had been heavily logged within the last few years but originally was coniferous forest with some chaparral on slopes above; site 2 lat 39°16.0′ N., long 120°58.1′ W.; canyon along North Fork of American River at an altitude of 1,560 m; soil deep alluvial; closed-canopy conifer forest except thickets of *Salix* along river; meteorological data from Blue Canyon WSMO (1 km west of site 1 and 1 km north of site 2, altitude 1,609 m). Collected by J.A. Wolfe, July 22, 1990; 23 species.

Bowman Dam.—Nevada County. Lat 39°26.6′ N., long 120°39.3′ W.; alluvial flats of Canyon Creek and adjacent slopes to 30 m above creek at altitude of 1,620–1,650 m; soil shallow, rocky granitic-derived; thickets of *Salix* along creek and open- to closed-canopy forest dominated by *Calocedrus* and *Pseudotsuga* on slopes; meteorological data from Bowman Dam (recording equipment at center of sampled area, which has a radius of 0.2 km, altitude 1,630 m). Collected by J.A. Wolfe, July 19, 1990; 31 species.

Lake Spaulding.—Nevada County. Lat 39°19.3′ N., long 120°38.0′ W.; slopes above south side of lake including perennial stream at an altitude of 1,530–1,600 m; soil deep alluvial along creek to mostly shallow, rocky granitic-derived; open- to closed-canopy forest dominated by *Abies* and *Pseudotsuga*; meteorological data from Lake Spaulding (at center of sampled area, which has a radius of 0.2 km, altitude 1,572 m). Collected by J.A. Wolfe and H.E. Schorn, July 21, 1990; 31 species.

Sierraville.—Sierra County. Lat 39°33.6′ N., long 120°21.4′ W.; along alluvial flats of Cold Stream and adjacent slopes to 20 m above creek at an altitude of 1,520–1,560 m; soil deep alluvial to shallow, rocky volcanic-derived; open- to closed-canopy forest dominated by *Abies*, *Pinus*, and *Pseudotsuga* (some logged) on east-facing slope and widely scattered trees and low shrubs on west-facing slope; meteorological data from Sierraville Ranger Station (3–4 km north-northwest, altitude 1,516 m). Collected by J.A. Wolfe, July 17, 1990; 30 species.

Donner Lake.—Nevada County. Lat 39°19.1′ N., long 120°14.0′ W.; alluvial flats of Cold Creek south of lake and adjacent north-facing slopes up to 50 m above lake at an altitude of 1,810–1,860 m; soil deep alluvial along creek and rocky volcanic-derived on slopes; thickets of *Salix* along creek and shores of lake giving way to mostly closed-canopy forest dominated by *Abies* and *Pinus*; meteorological data from Truckee Ranger Station (4 km east-northeast, altitude 1,827 m). Collected by J.A. Wolfe, July 16, 1990, 28 species.

Soda Springs.—Nevada County. Site 1 lat 39°19.3′ N., long 120°21.7′ W.; south-facing slope from shore of Lake Van Norden up to 20 m above at an altitude of 2,050–2,070 m; soil shallow, rocky granitic-derived; mostly evergreen sclerophyllous scrub with widely spaced trees of *Abies*; site 2 lat 39°19.7′ N., long 120°22.9′ W.; along upper valley of Yuba River and adjacent north-facing slopes at an altitude of 2,060–2,080 m; thickets of *Salix* along river and open- to closed-canopy forest dominated by *Abies* on slopes; meteorological data from Soda Springs (2 km west-northwest of site 1 and 0.2–0.5 km north of site 2, altitude 2,057 m). Collected by J.A. Wolfe, July 18, 1990; 27 species.

OREGON

Powers.—Coos County. Site 1 lat 42°53.9′ N., long 124°05.3′ W.; along banks above Coquille River at an altitude of 60–70 m; soil rocky, sedimentary-derived; open-canopy woodland of conifers and mostly broad-leaved deciduous trees and some thickets of *Salix* along river; site 2 lat 42°54.5′ N., long 124°06.6′ W.; along alluvial flats of Coquille River at junction with Baker Creek at an altitude of 60 m; soil deep alluvial; closed-canopy conifer forest; meteorological data from Powers (1 km east-southeast of site 1 and 4 km east-southeast of site 2, altitude 70 m). Collected by J.A. Wolfe, June 21, 1991; 33 species.

Troutdale.—Multnomah County. Site 1 lat 45°33.6′ N., long 122°26.4′ W.; on alluvial flats of Columbia River at an altitude of 10 m; soil deep alluvial; thickets of *Salix*; site 2 lat 45°31.4′ N., long 122°19.2′ W.; along Sandy River and west-facing slopes above river at an altitude of 10–70 m; soil deep, volcanic-derived; mostly closed-canopy, second-growth conifer forest; site 3 lat 45°30.9′ N., long 122°19.0′ W.; on bluffs above Sandy River at an altitude of 60 m; soil deep, volcanic-derived; closed-canopy, second-growth conifer forest; meteorological data from Troutdale Substation (3 km east of site 1, 4 km northwest of site 2, and 4 km north-northwest of site 3, altitude 9 m). Collected by J.A. Wolfe, August 27, 1989, and June 20, 1991; 30 species.

Port Orford.—Curry County. Site 1 lat 42°45.0′ N., long 124°30.2′ W.; flats immediately southeast of Garrison Lake at an altitude of 10 m; soil sandy; low, windswept forest of *Pinus contorta* and evergreen sclerophyllous trees; site 2 lat 42°44.6′ N., long 124°29.2′ W.; slopes between Port Orford and Hubbard Creek and on alluvial flats of Hubbard Creek at an altitude of 5–30 m; soil deep alluvial to sedimentary-derived; thickets of *Salix* along creek to closed-canopy conifer forest (some logged) on slopes; meteorological data from Port Orford (0.5 km east of site 1 and 0.5–2 km west-northwest of site 2). Collected by J.A. Wolfe, June 22, 1991; 31 species.

North Bend.—Coos County. Site 1 lat 43°25.0′ N., long 124°14.9′ W.; hills above airport at an altitude of 3–20 m; soil sandy to deep, sedimentary-derived; coastal scrub to closed-canopy conifer forest with broad-leaved evergreen small trees and shrubs; site 2 lat 43°26.3′ N., long 124°12.5′ W.; north- and south-facing slopes above Coos Bay near Glasgow at an altitude of 5–20 m; soil deep, sedimentary-derived; closed-canopy, second-growth conifer forest with mostly broad-leaved deciduous small trees and shrubs; meteorological data from North Bend FAA AP (<0.5 km north of site 1 and 4 km southwest of site 2, altitude 2 m). Collected by J.A. Wolfe, June 25, 1991; 26 species.

Bandon.—Curry County. Site 1 lat 43°07.9′ N., long 124°23.9′ W.; on river banks of Coquille River near mouth at an altitude of 2–5 m; soil deep alluvial; remnant open- to closed-canopy gallery forest; site 2 lat 43°07.9′ N., long 124°23.0′ W.; on gentle slopes above cranberry bogs at an altitude of 20–30 m; soil sandy; open- to closed-canopy conifer forest with mostly broad-leaved deciduous small trees and shrubs; meteorological data from Bandon 1 E Bates Bog (1.5 km east-southeast of site 1 and 1–2 km south of site 2). Collected by J.A. Wolfe, June 24, 1991; 27 species.

Hood River.—Hood River County. Site 1 lat 45°42.6′ N., long 121°32.7′ W.; on slopes above Columbia River in western part of town of Hood River at an altitude of 170 m; soil deep, volcanic-derived; closed-canopy, second-growth conifer forest; site 2 lat 45°41.2′ N., long 121°31.0′ W.; along creek incised into plain west of experiment station at an altitude of 140 m; soil deep alluvial; open-canopy gallery woodland and thickets of *Salix* along creek; site 3 lat 45°39.2′ N., long 121°32.7′ W.; in valley of Hood River where crossed by State Highway 35 at an altitude of 140–150 m; soil sandy to rocky, volcanic-derived; meteorological data from Hood River Experimental Station (4 km southeast of site 1, 0.1 km east of site 2, and 5 km northeast of site 3, altitude 152 m). Collected by J.A. Wolfe, August 23, 1989, and July 6, 1991; 32 species.

Cape Blanco.—Curry County. Site 1 lat 42°50.0′ N., long 124°32.9′ W.; on bluffs 1–2 km east of Cape Blanco lighthouse at an altitude 10–65 m; soil sandy; open- to closed-canopy, short-statured, windswept conifer forest and coastal scrub; site 2 lat 42°50.4′ N., long 124°31.0′ W.; on banks of Sixes River at an altitude of 1–5 m; soil deep alluvial; thickets of *Salix* along river and coastal scrub; meteorological data from Cape Blanco (1–2 km west of site 1 and 2 km west-southwest of site 2, altitude 64 m). Collected by J.A. Wolfe, June 22 and 23, 1991; 25 species.

Three Lynx.—Clackamas County. Lat 45°07.6′ N., long 122°04.7′ W.; on north- and south-facing slopes of valley of Clackamas River from river level up to 30 m above at an altitude of 320–350 m; soil deep, volcanic-derived; thickets of *Salix* along river to closed-canopy (some second-growth) coniferous forest on slopes; meteorological data from Three Lynx (within sampled area, which has a 0.5-km radius, altitude 341 m). Collected by J.A. Wolfe, August 26, 1989, and July 1, 1991; 30 species.

Parkdale.—Hood River County. Site 1 lat 45°30.8′ N., long 121°34.0′ W.; on gentle west-facing slopes at and adjacent to Tollbridge County Park above Hood River from river level to as much as 30 m above at an altitude of 450–480 m; soil deep alluvial to deep, volcanic-derived; thickets of *Salix* and groves of *Populus* along river merging with closed-canopy, second-growth coniferous forest; site 2 lat 44°29.3′ N., long 121°34.0′ W.; on alluvial flats west of Hood River; soil deep alluvial; closed-canopy coniferous forest; meteorological data from Parkdale 2 SSE (2 km northwest of site 1 and 4 km north of site 2, altitude 442 m). Collected by J.A. Wolfe, August 23, 1989, and July 5, 1991; 35 species.

Laurel Mountain.—Lincoln County. Lat 44°55.4′ N., long 123°34.9′ W.; south- and west-facing slopes of Laurel Mountain at an altitude of 1,000–1,090 m; soil deep, sedimentary-derived; closed-canopy coniferous forest interspersed with meadows and one small perennial, boggy, creek; meteorological data from Laurel Mountain (within sampled area, which extends 1.5 km west, altitude 1,094 m). Collected by J.A. Wolfe, July 4, 1991; 24 species.

Government Camp.—Clackamas County. Site 1 lat 45°18.9′ N., long 121°44.8′ W.; on gentle north-facing slopes of Multorpor Mountain at an altitude of 1,220–1,250 m; soil deep, volcanic-derived; closed-canopy coniferous forest; site 2 lat 45°17.5′ N., long 121°41.3′ W.; along creek and on gentle east-facing slope immediately north of U.S. Highway 26 at an altitude of 1,170–1,200 m; soil deep, volcanic-derived; closed-canopy coniferous forest interspersed with meadows; meteorological data from Government Camp (0.5 km north of site 1 and 2.5 km northwest of site 2, altitude 1,213 m). Collected by J.A. Wolfe, August 29, 1989, and July 5, 1991; 29 species.

WASHINGTON

Wind River.—Skamania County. Lat 45°48.3′ N., long 121°56.4′ W.; along alluvial flats of Trout Creek at an altitude of 350 m; soil deep alluvial; closed-canopy coniferous forest; meteorological data from Wind River (0.5–3 km southwest, altitude 351 m). Collected by J.A. Wolfe, August 21, 1989, and July 6, 1991; 30 species.

Rimrock Lake.—Yakima County. Lat 46°39.1′ N., long 121°08.4′ W.; along south-facing slopes rising from north shore of Rimrock Lake along U.S. Highway 12 at an altitude of 890–900 m; soil mostly shallow, rocky, volcanic-derived; open- to closed-canopy coniferous forest; meteorological data from Rimrock Tieton Dam (0.1–2 km east and south, altitude 832 m). Collected by J.A. Wolfe, August 25, 1989; 25 species.

Republic.—Ferry County. Lat 48°38.8′ N., long 118°44.6′ W.; east-, west-, and north-facing slopes in valley of North Fork of Sanpoil River at an altitude of 750–800 m; soil deep alluvial to shallow, rocky, volcanic-derived; closed- to open-canopy, second-growth coniferous forest with thickets of deciduous shrubs along river; meteorological data from Republic (0.5–1.5 km east and northeast, altitude 793 m). Collected by J.A. Wolfe, June 28, 1991; 28 species.

Bumping Lake.—Yakima County. Lat 46°51.9′ N., long 121°17.6′ W.; flats along southeast shore of Bumping Lake at an altitude of 1,050 m; soil shallow, rocky, and volcanic-derived to boggy; open- to closed-canopy, second-growth coniferous forest; meteorological data from Bumping Lake (1–2 km north and west, altitude 1,049 m). Collected by J.A. Wolfe, August 25, 1989; 26 species.

ALASKA

Except for slight human disturbance, most Alaskan areas (fig. 6) sampled show no evidence of disturbance. Some logging has occurred around Seward and much around Ketchikan, but many stands of virgin forest remain.

Ketchikan.—Lat 55°19.4′ N., long 131°35.7′ W.; along southwest-facing slopes from beach-level up to 60 m above at an altitude of 1–60 m; soil deep, boggy to shallow and rocky, metamorphic-derived; closed-canopy coniferous forest interspersed with bogs and meadows; meteorological data from Ketchikan (0–5 km northwest, altitude 24 m); collected by J.A. Wolfe, August 22, 1991; 26 species.

Seward.—Site 1 lat 60°07.5′ N., long 149°21.5′ W.; along flats and southwest-facing slopes rising above northeast shore of Resurrection Bay at an altitude of 1–20 m; soil deep alluvial and boggy to mostly shallow, rocky, metamorphic derived; flats with dense thickets of *Salix* and slopes with closed-canopy coniferous forest; site 2 lat 60°07.0′ N., long 149°26.3′ W.; steep east-facing slopes rising above Seward at an altitude of 2–20 m; soil shallow, rocky, metamorphic-derived; closed-canopy coniferous forest; site 3 lat 60°11.1′ N., long 149°24.1′ W.; boggy shores of small lake at an altitude of 120 m; soil deep, boggy; meadow; meteorological data from Seward

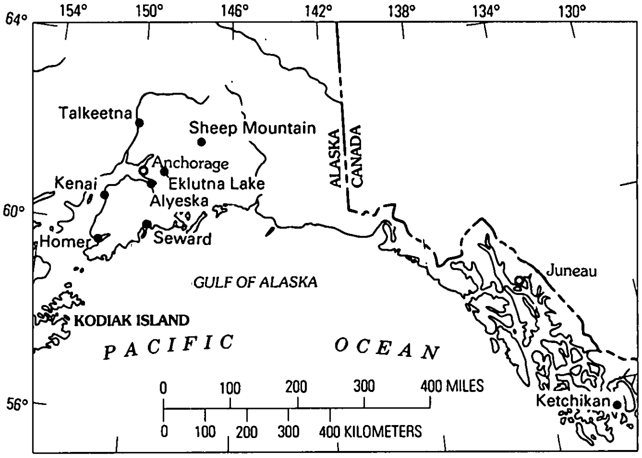

Figure 6. Sampling sites (solid circles) in Alaska.

(4–5 km south and west-southwest of site 1, 0.5 km east of site 2, and 8 km south-southwest of site 3, altitude 11 m). Collected by J.A. Wolfe, August 19, 1991; 22 species.

Homer.—Site 1 lat 59°38.4′ N., long 151°28.8′ W.; along gentle slopes rising above Kachemak Bay adjacent to airport at an altitude of 5–15 m; soil deep, sedimentary derived; closed-canopy coniferous forest interspersed with meadows; site 2 lat 59°39.5′ N., long 151°29.7′ W.; along moderate to steep slopes rising above Homer at an altitude of 20–100 m; soil deep, sedimentary-derived; closed-canopy coniferous and broad-leaved deciduous forest; meteorological data from Homer WSO (within site 1, which has a radius of 1 km, and 2–5 km south and southwest of site 2, altitude 27 m). Collected by J.A. Wolfe, August 15, 1991; 24 species.

Alyeska.—Site 1 lat 60°57.7′ N., long 149°06.7′ W.; west-facing slopes north and south of Alyeska at an altitude of 70–100 m; soil deep to shallow, rocky, metamorphic-derived; closed-canopy coniferous forest interspersed with meadows; site 2 lat 60°59.0′ N., long 149°06.0′ W.; east-facing slopes at an altitude of 80–90 m; soil and vegetation as at site 1; meteorological data from Alyeska (within site 1, which has a radius of 0.5 km, and 2.5–3 km south of site 2, altitude 76 m). Collected by J.A. Wolfe, August 20, 1991; 22 species.

Kenai.—Site 1 lat 60°33.3′ N., long 151°12.8′ W.; flats within 1 km of airport at an altitude of 10 m; soil deep, sedimentary-derived and glacial outwash; open- to closed-canopy, short-statured coniferous and broad-leaved deciduous forest interspersed with meadows; site 2 lat 60°33.2′ N., long 151°16.4′ W.; on bluffs above Cook Inlet at an altitude of 10 m; soil and vegetation as at site 1; meteorological data from Kenai (1 km west of site 1 and 0.5 km east of site 2, altitude 26 m). Collected by J.A. Wolfe, August 16, 1991; 24 species.

Talkeetna.—Site 1 lat 62°18.6′ N., long 150°06.6′ W.; on alluvial flats of Susitna River and plain above river at an altitude of 105–120 m; soil deep alluvial to glacial outwash; closed-canopy coniferous and broad-leaved deciduous forest interspersed with meadows; site 2 lat 62°15.4′ N., long 150°04.9′ W.; gentle slopes surrounding Fish Lake at an altitude of 140 m; soil deep and boggy; bog vegetation with widely spaced *Picea*; meteorological data from Talkeetna (1–3 km north and west of site 1 and 7 km north-northwest of site 2, altitude 105 m). Collected by J.A. Wolfe, August 17, 1991; 29 species.

Eklutna Lake.—Lat 61°25.0′ N., long 149°09.7′ W.; south-facing slopes rising above northeast part of Eklutna Lake at an altitude of 870–900 m; soil deep alluvial to shallow, rocky, metamorphic-derived; open- to closed-canopy coniferous and broad-leaved deciduous forest interspersed with meadows; meteorological data from Eklutna Lake (within sampled area, which has a radius of 3 km, altitude 268 m). Collected by J.A. Wolfe, August 21, 1991; 31 species.

Sheep Mountain.—Lat 61°48.0′ N., long 147°35.8′ W.; south- and north-facing slopes within 0.5 km of Glenn Highway at an altitude of 700–720 m; soil deep and boggy to shallow, rocky, metamorphic-derived; low-statured, open-canopy coniferous and broad-leaved deciduous forest interspersed with meadows and bogs; meteorological data from Sheep Mountain (within sampled area, which extends about 1.5 km east and west, altitude 707 m). Collected by J.A. Wolfe, August 18, 1991; 28 species.

JAPAN

The anomaly between the vegetation of certain areas of Japan and the Eastern United States was mentioned earlier (p. 4; see also Wolfe, 1979). In eastern Asia, areas that have a cold-month mean temperature between −2°C and 1°C have a large, although not dominant, broad-leaved evergreen element, and areas that have a cold-month mean temperature above 1°C have dominantly broad-leaved evergreen vegetation. In the Eastern United States, however, areas of similar temperature parameters are occupied by vegetation that is overwhelmingly broad-leaved deciduous, except along the very narrow coastal strip from North Carolina south; even in this coastal strip, broad-leaved deciduous trees and shrubs play a significant role in the vegetation. Obtaining some samples from eastern Asia (especially Japan; fig. 7) was necessary to compare aspects of leaf physiognomy other than evergreen versus deciduous. I am especially grateful to K. Uemura for collecting two samples, and the Yakushima sample, although not collected according to the normal CLAMP standards, is also included because of the paucity of Asian samples in the database.

Yakushima.—Yakushima Prefecture. This sample was collected prior to the initiation of sampling for CLAMP and was not collected according to the normal standards. The plants comprising this sample were collected at five principal sites. One site (4 species) is on the east side of the island in lowland (<5 m altitude) broad-leaved evergreen second-growth rain forest in the Nabeyama National Forest and includes low-statured vegetation between the beach and the rain forest. A second site (10 species) is at the waterfall north of Kurio along the west side of the island at an altitude of 20 m; vegetation, which is disturbed, is broad-leaved evergreen in successional stage. A third site (7 species) is along the road from Kurio to Nagata at an altitude of approximately 300 m on the west side of the island; the mostly undisturbed vegetation represents Notophyllous Broad-leaved Evergreen forest. The fourth site (6 species) on the road to the Yaksugi National Forest at an altitude of 300–400 m on the east side of the island and also represents notophyllous vegetation. The fifth site (2 species) is southwest of Miyanoura at an altitude of 200 m also represents notophyllous forest. Meteorological data from Yakushima represent conditions in the

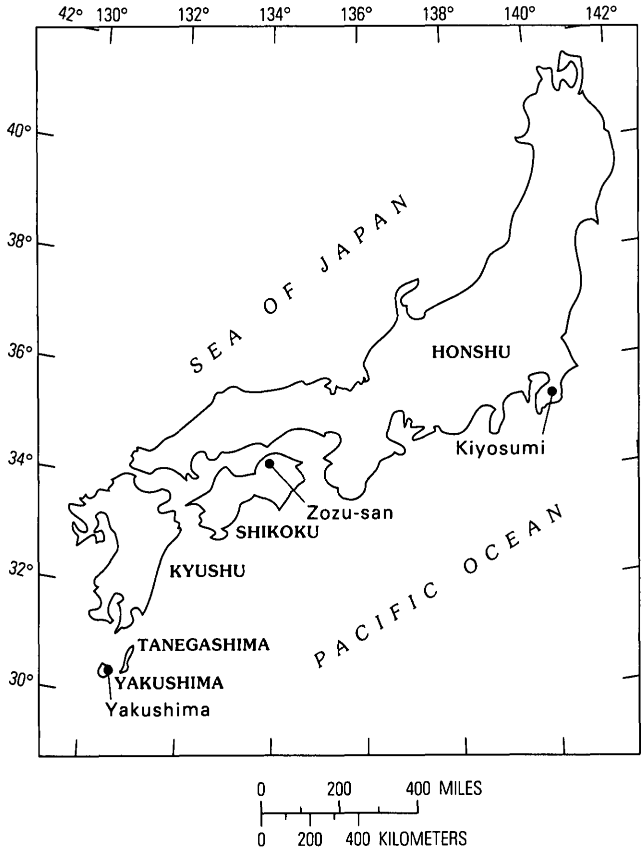

Figure 7. Sampling sites (solid circles) in Japan.

lowlands, and the temperature estimated for this sample reflect an altitudinal adjustment as if the sample was from about 150–200 m altitude. Collected by J.A. Wolfe and T. Tanai, October 1 and 2, 1986; 29 species.

Zozu-san.—Kagawa Prefecture. Lat 34°11′ N., long 133°48.7′ E.; slopes above Zozu-san temple at an altitude of 250 m; soil deep, sedimentary-derived; closed-canopy, broad-leaved evergreen forest; temperature data from Saita (5 km south, altitude 195 m) and precipitation data from Takamatsu (30 km northeast, altitude 32 m; because precipitation generally increases at higher altitudes in this area of Japan, the precipitation on Zozu-san must be higher than at Matsuyama). Collected by K. Uemura, January 3, 1991; 35 species.

Kiyosumi.—Chiba Prefecture. Lat 35°9.5′ N., long 140°9.6′ E.; Tokyo University Forest Reserve at an altitude of 300 m; soil deep, sedimentary-derived; closed-canopy, broad-leaved evergreen and coniferous forest; temperature data from Kiyosumi Tokyo University Forest (in sampled area, altitude 300 m; record of 10 years) and Kiyosumi (15 km east, altitude 380 m) and precipitation data from Yokohama (40 km northwest, altitude 39 m). Collected by K. Uemura, November 3, 1990; 32 species.

METEOROLOGICAL DATA

The meteorological data used in this report are, for most stations, based on various published reports of the National Oceanic and Atmospheric Administration (NOAA), or its predecessors. This organization does not publish reports received from all stations; Sellers and Hill (1974), however, published data for all stations in Arizona, and Leslle (1989) published data for all stations in Alaska, basing these compilations on data files in NOAA's National Climatic Center. Data for Barro Colorado Island were published by Windsor (1990), and data for Jasper Ridge, Calif., were furnished by Stanford University. Japanese data are from various publications of the Japan Meteorological Agency, Tokyo Astronomical Observatory, and Kaji (1975).

The meteorological data are of variable quality relative to length of observation, although the great majority of stations are represented by 30 or more years of record. Because I attempted to sample vegetation in climates as varied as possible (plate 1), some short-term (<30 years) data are included. At any given meteorological station, meteorological data can show variation in both temperature and especially precipitation means from one 10-year interval to the next, and the data listed in table 1 represent observations during different decades or groups of decades. Many stations for which data are regularly reported by National Oceanic and Atmospheric Administration have "normals" established, the "normals" being the means reported during a 30-year period ending with the last complete decade. I have, however, generally disregarded such "normals" and have used means for the total period of record for each station; such longer records probably more closely approach a woody plant's longevity than do the "normals."

Other variables in the meteorological data set are introduced because the data for the various stations were not taken at a standard distance above the ground or using exactly the same make and model of instrument. Some stations, moreover have been moved in distance and (or) altitude over the years; such movements could affect the reported means. The introduction of such variables indicates that, although the temperature means are given to one decimal and the precipitation means are given to one centimeter, such precision is probably not justified. However, the exact level of imprecision is unknown.

Perhaps temperature and precipitation means for the immediate decade preceding the collection of the samples might best reflect the environment to which the plants became adapted. Some samples, however, were collected proximal to stations that no longer record meteorological data. Further, the period of climatic change necessary to induce response in foliar physiognomy is unknown. I have, for example, compiled meteorological data for a two-year period preceding sample collection for stations still operating, and these data showed much less correspondence to relative placement of samples from the multivariate analysis than did long-term data.

CHARACTER SCORING

SELECTION OF CHARACTER STATES

None of the character states selected for scoring is probably totally independent of some, perhaps considerable, genetic control. At first thought, leaf size, because of its variability on even a single organism or variability during different growth stages of the plant, might be thought to be totally independent of genetic control, but this cannot be valid. Take, for example, the very small leaves of most plants living on the Sonoran Desert. If the plants responded to the relatively abundant precipitation that occurs in March (when much new foliage is produced) by producing large leaves, these large leaves would be nonadaptive during the very dry and hot period in May and June. A similar situation relative to leaf size is true for plants in the California chaparral, where abundant rain falls during the spring, when the new leaf crop is produced, followed by extreme summer drought. The plants must produce leaves that are adaptive to the entire growing season, and this production must, therefore, be genetically controlled.

The characters selected typically show considerable variation on a given plant or between plants of the same species. Despite some genetic control, these characters are also apparently environmentally influenced. Most of these characters are gross characters and are readily described and (or) measured on the leaves of the modern samples and are generally readily scored from fossil-leaf impressions, even if preservation is poor. The characters scored fundamentally are those of the outline of the leaf.

During one stage of this study I expanded the character set to include about 20 character states additional to those discussed later in this section. Judging from eigenvalues and percent of total variance accounted for, these characters either added nothing or even lowered both eigenvalues and percent variance and are thus no longer scored. For example, as an attempt to determine evergreen versus deciduous habit, I scored the evergreen habit and whether the margin was inrolled and (or) thickened; inrolling or thickening of the margin might be thought to occur with leaf thickness and thus in turn to indicate an evergreen habit. The correlation between an evergreen habit and inrolling or thickening of the margin was low. Among other characters scored but now excluded are teeth pointing abmedially versus apically, teeth small versus large, relative widths of apices and bases, three additional leaf sizes, palmatifid versus pinnatifid, and palmately compound versus pinnately compound.

Bailey and Sinnott (1916) suggested that the compound leaf might have climatic significance. I scored the samples for the palmately compound, pinnately compound, and noncompound character states. Subjecting the database of 29 character states to multivariate analysis and adding (1) the three character states just listed or (2) only the compound versus simple character states indicated that these character states were not significant in grouping samples and that the character states occurred in no meaningful pattern in the sample set.

Spinose leaves are particularly common in dry mesothermal vegetation, which is typically chaparral and (or) open-canopy woodland. The multivariate analysis gives the spinose-leaved character state a moderately high score (>1.1) on axis 1, which suggests that this character state could be climatically significant. However, R.A. Spicer (oral commun., August 1991) suggested that spinose leaves were primarily a defense against herbivory by mammals. Spinose leaves are rare in Late Cretaceous leaf assemblages, even assemblages inferred to represent dry mesothermal woodland; most large Late Cretaceous herbivores were large dinosaurs that had a massive chewing apparatus that would probably have been able to handle spinose leaves. Removal of the spinose-leaved character state from the database results in no significant change to scores for other character states or scores for samples.

DEFINITIONS OF CHARACTER STATES SCORED

Lobed.—A species receives a score of 0 if no leaves are lobed, a score of 0.5 if some leaves are lobed and some are unlobed, and a score of 1 if all leaves are lobed. Lobing can be either pinnately lobed (for example, many *Quercus*) or palmately lobed (for example, many *Acer*). Both pinnately and palmately lobed (figs. 8*A*–*C*) were scored separately but were later combined because separate scoring appeared to produce no refinement. In order to be pinnately lobed, a lamina must be incised so that a line connecting the sinuses between the lobes is approximately parallel to the midrib; in some *Quercus* leaves, however, a line connecting the sinuses is parallel to a line connecting the apices of the laminar segments, which, therefore, are classed as teeth rather than lobes. In palmately lobed leaves, the lobes are entered by a major (primary) vein that originates at or near the base of the leaf.

No teeth.—A species receives a score of 0 if teeth are present on all leaves, a score of 0.5 if some leaves are toothed and some are not, and a score of 1 if no leaves are toothed; the scores, when converted to percentages, for no teeth, teeth rounded and (or) appressed, and teeth acute will total approximately 100 for a single sample. The no teeth character state is basically that of the entire margin as proposed by Bailey and Sinnott (1915, 1916); a major

Table 1. Meteorological data for samples.
[All figures are based on means. Sample locations described in text]

	Temperature (°C)			Precipitation (centimeters)			
Sample	Annual	Warm month	Cold month	Annual	Growing season	Growing season, monthly	Three consecutive driest months
Barro Colorado Is., Panama	27.2	27.8	26.7	261	261	22	20
Guanica P.R.	26.9	28.3	25.2	75	75	6	6
Cabo Rojo, P.R.	26.9	28.3	25.2	71	71	6	6
Borinquen, P.R.	25.6	27.8	24.7	75	75	6	6
Cambalache, P.R.	25.4	26.9	23.4	147	147	12	35
Susua Alta, P.R.	25.2	24.5	21.2	129	129	11	7
Guajataca, P.R.	24.0	25.2	21.9	195	195	16	27
Avon Park, Fla.	22.8	28.1	17.2	140	140	12	14
Orlando, Fla.	22.4	28.1	15.8	122	122	10	14
Buena Vista, P.R.	22.0	23.8	21.1	267	267	22	23
Canyon Lake, Ariz.	21.8	33.0	11.6	35	35	3	2
Maricao, P.R.	21.7	22.9	20.2	267	267	22	23
Lake George, Fla.	21.3	27.3	14.4	139	139	12	18
Bartlett Reservoir, Ariz.	21.3	32.2	11.4	33	33	3	3
Castle Creek, Ariz.	21.1	32.2	11.4	38	38	3	2
Superior, Ariz.	20.5	30.3	11.2	45	45	4	4
Saguaro Lake, Ariz.	20.5	32.2	10.2	31	31	3	2
Roosevelt Lake, Ariz.	19.8	31.5	8.7	37	28	3	3
Brunswick, Ga.	19.6	27.7	10.7	130	130	11	20
Monte Guilarte, P.R.	19.0	20.5	17.0	231	231	20	24
Beaufort, S.C.	18.7	27.1	9.5	127	119	11	19
Punkin Center, Ariz.	18.6	30.7	7.3	43	31	3	4
Yakushima, Japan	18.4	26.2	10.6	397	397	33	60
Childs, Ariz.	18.1	29.9	7.7	46	36	4	5
Simmonsville, S.C.	18.1	26.9	8.4	130	104	12	24
Toro Negro, P.R.	17.9	19.7	16.6	222	222	19	25
Kure Beach, N.C.	17.9	26.9	8.8	139	109	15	28
Santa Rita, Ariz.	17.8	26.5	9.0	50	46	4	3
Miami, Ariz.	17.1	28.7	6.7	48	33	4	4
Camp Pardee, Calif.	16.2	25.8	7.4	41	33	3	1
Auburn, Calif.	15.6	25.1	7.1	88	41	5	2
Sierra Ancha, Ariz.	15.3	25.5	5.9	63	36	5	5
Yava, Ariz.	15.3	26.7	6.6	35	22	3	3
Colfax, Calif.	15.1	25.3	6.9	122	40	5	2
Zozu-san, Japan	14.9	27.0	4.0	130	101	14	33
Jerome, Ariz.	14.9	25.7	5.1	48	31	4	5
Jasper Ridge, Calif.	14.7	22.0	9.1	56	27	3	1
Natural Bridge, Ariz.	14.5	25.1	5.1	59	35	5	6
Lakeport, Calif.	13.9	23.3	5.7	76	13	2	1
Kiyosumi, Japan	13.8	24.4	3.8	160	118	15	42
Canelo, Ariz.	13.8	23.2	5.2	44	32	5	3
Santa Cruz, Calif.	13.7	17.4	9.4	74	57	5	1
Nevada City, Calif.	13.5	23.0	5.7	139	28	4	2
S.I.E.R.C., Md.	13.3	25.3	1.6	111	70	9	33
Placerville, Calif.	13.3	23.1	5.1	94	20	3	0
Battle Creek, Md.	13.1	24.4	1.4	108	65	8	32
Junipine, Ariz.	13.1	23.7	3.9	70	33	5	9
Payson, Ariz.	13.1	24.2	3.6	53	30	4	5
Prescott Airport, Ariz.	12.9	24.2	2.8	33	20	3	4
Crown King, Ariz.	12.8	21.8	2.6	71	34	5	6
Half Moon Bay, Calif.	12.5	15.2	10.2	64	64	5	2
Frederick, Md.	12.4	24.2	–0.4	103	64	9	28
Kitt Peak, Ariz.	12.4	21.2	5.1	61	34	5	11
Powers, Oreg.	11.8	17.8	6.3	157	38	5	8
Troutdale, Oreg.	11.7	19.6	3.0	118	63	9	5
Port Orford, Oreg.	11.5	15.4	8.2	201	60	10	10

Table 1. Meteorological data for samples—Continued.
[All figures are based on means. Sample locations described in text]

	Temperature (°C)			Precipitation (centimeters)			
Sample	Annual	Warm month	Cold month	Annual	Growing season	Growing season, monthly	Three consecutive driest months
Arendtsville, Pa.	11.2	23.7	–0.8	109	64	9	28
North Bend, Oreg.	11.2	15.4	7.2	155	51	7	7
Jemez Springs, N. Mex.	11.1	22.3	0.5	40	26	4	7
Bandon, Oreg.	10.8	14.4	7.4	153	51	7	6
Hood River, Oreg.	10.3	19.3	0.9	78	15	3	4
Cape Blanco, Oreg.	10.2	12.7	7.7	195	78	11	9
Blue Canyon, Calif.	10.2	20.2	2.8	172	24	4	4
Hasayampa, Ariz.	10.2	20.4	1.2	59	31	5	12
Three Lynx, Oreg.	9.8	17.9	1.9	184	43	7	11
Stroudsburg, Pa.	9.8	22.3	–2.6	122	62	10	31
Bowman Dam, Calif.	9.7	19.3	2.2	170	26	4	6
Los Alamos, N. Mex.	9.0	20.2	–1.6	45	32	5	10
Wind River, Wash.	8.9	17.7	–0.1	253	51	10	10
Lake Spaulding, Calif.	8.7	17.7	1.2	175	25	4	5
Tunkhannock, Pa.	8.6	21.1	–3.3	102	52	9	27
Parkdale, Oreg.	8.5	17.3	–0.9	117	15	3	5
Sierraville, Calif.	8.0	18.1	–1.6	68	8	2	3
Ketchikan, Alaska	7.6	14.8	0.5	405	102	26	67
Cheesman Reservoir, Colo.	7.6	18.9	–2.6	41	24	5	17
Red Fleet, Utah	7.3	21.8	–8.4	19	8	2	5
Mt. Pocono, Pa.	7.2	18.7	–5.7	128	48	8	38
Rimrock Lake, Wash.	6.9	17.4	–3.4	65	9	2	5
Lake Maloya, N. Mex.	6.9	17.6	–3.3	57	34	7	24
River Falls, Wis.	6.8	21.9	–11.7	77	57	10	24
Laurel Mountain, Oreg.	6.7	13.6	2.5	271	3	1	16
Tierra Amarilla, N. Mex.	6.3	18.1	–6.0	39	22	4	14
Dannemora, N.Y.	6.2	20.2	–8.4	84	42	7	24
Estes Park, Colo.	6.2	16.8	–2.6	35	18	5	15
Republic, Wash.	5.9	17.4	–6.5	41	15	3	2
Donner Lake, Calif.	5.8	16.2	–3.4	80	5	1	4
Government Camp, Oreg.	5.6	14.1	–1.5	219	27	9	16
Nederland, Colo.	5.3	15.8	–5.3	50	20	5	11
Wanakena, N.Y.	5.2	18.4	–8.8	107	50	10	29
Bumping Lake, Wash.	4.8	14.7	–4.8	116	11	3	6
Allens Park, Colo.	4.8	15.8	–4.3	52	20	5	11
Lake Placid, N.Y.	4.6	17.8	–9.6	98	46	9	27
Soda Springs, Calif.	4.4	14.8	–3.4	131	6	2	3
Seward, Alaska	4.1	13.4	–4.6	161	39	11	27
Red River, N. Mex.	3.7	14.7	–6.8	48	22	6	18
Wolf Creek, Colo.	3.5	14.6	–6.8	128	31	10	22
Tahosa Creek, Colo.	3.0	13.1	–5.4	55	19	6	19
Homer, Alaska	2.6	11.6	–6.2	63	12	6	12
Alyeska, Alaska	2.3	13.2	–7.3	163	25	8	25
Lake Granby, Colo.	2.2	14.5	–10.2	35	11	4	11
Dillon, Colo.	1.9	13.4	–8.8	37	11	4	11
Grand Lake, Colo.	1.7	13.3	–9.2	51	15	5	15
Kenai, Alaska	0.6	12.3	–12.1	49	15	5	15
Talkeetna, Alaska	0.3	14.5	–13.1	69	27	9	27
Eklutna Lake, Alaska	–0.4	12.8	–15.2	31	11	4	11
Sheep Mountain, Alaska	–2.0	11.7	–14.6	32	14	5	14

difference, however, is that spinose leaves (leaves that have a fimbrial vein forming abmedial projections) are included in the no teeth category.

Regularity of tooth spacing (teeth regular).—A species receives a score of 0 if no teeth are present, a score of 0.25 if the teeth are both regular and irregular and some leaves have teeth and others do not, a score of 0.5 if the teeth are only regular and some leaves have teeth and others do not, a score of 0.5 if the teeth are both regular and irregular and all leaves are toothed, and a score of 1 if all teeth are regular and all leaves are toothed. Teeth are considered to be regularly spaced if the lengths of the basal flanks of two adjacent teeth differ by less than one-third (fig. 8*E*).

Closeness of teeth (teeth close).—A species receives a score of 0 if no teeth are present, a score of 0.25 if the teeth are both close and distant and some leaves have teeth and others do not, a score of 0.5 if the teeth are only close and some leaves have teeth and others do not, a score of 0.5 if the teeth are both close and distant and all leaves are toothed, and a score of 1 if all teeth are close and all leaves are toothed. Teeth are considered to be closely spaced if the basal flanks of the teeth are no longer than three times the apical flanks (fig. 8*G*).

Teeth rounded and (or) appressed.—A species receives a score of 0 if no teeth are present, a score of 0.25 if the teeth are both rounded (or appressed) and acute and some leaves have teeth and others do not, a score of 0.5 if the teeth are only rounded (or appressed) and some leaves have teeth and others do not, a score of 0.5 if the teeth are both rounded (or appressed) and acute and all leaves are toothed, and a score of 1 if all teeth are rounded (or appressed) and all leaves are toothed. Teeth are rounded if they have convex apical and basal flanks and the convexity extends to the tip of the tooth (fig. 8*H*). Teeth are appressed if the apical flank is concave, the basal flank is convex, and the tooth is curved toward the lamina (fig. 8*I*); such teeth are typically glandular. The two states of rounded teeth and appressed teeth were scored and run separately, but combining the two states produced both higher eigenvalues and percent variance.

Teeth acute.—A species receives a score of 0 if no teeth are present, a score of 0.25 if the teeth are both

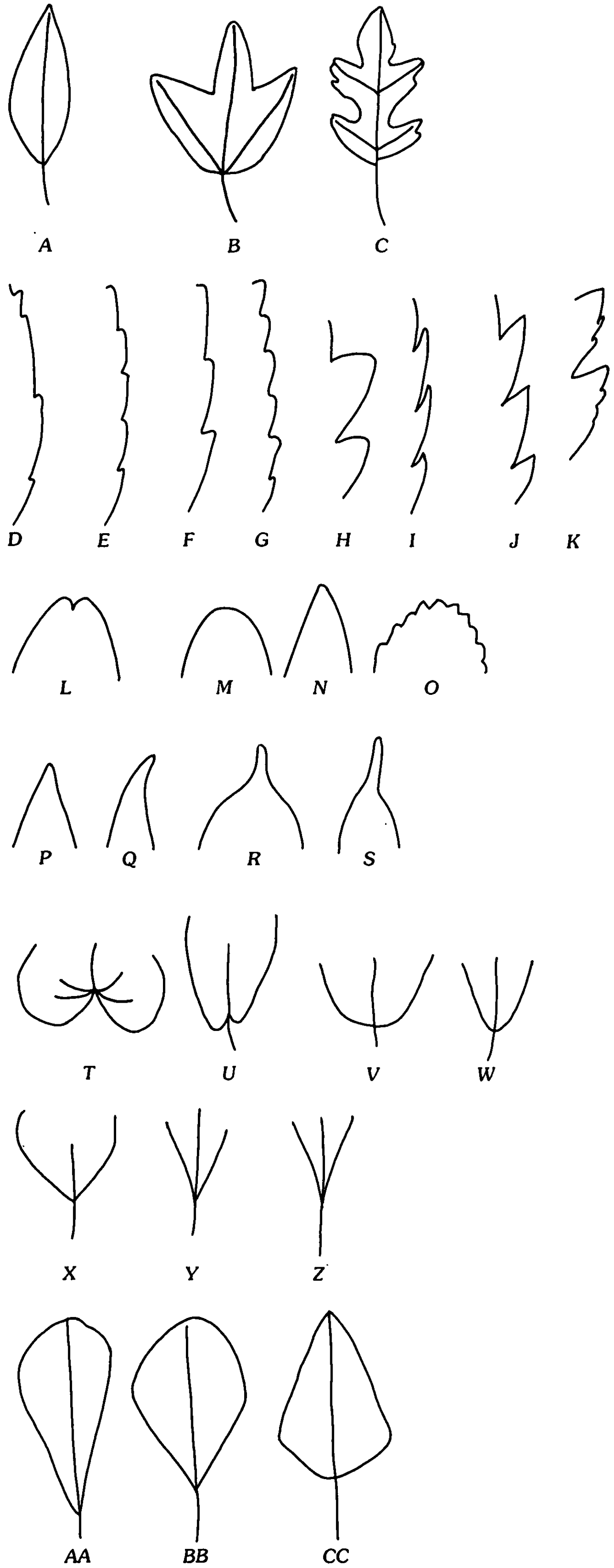

Figure 8 (facing column). Character states other than size. *A*, Unlobed, untoothed leaf. *B*, Palmately lobed, untoothed leaf. *C*, Pinnately lobed, toothed leaf. *D*, Teeth irregularly spaced. *E*, Teeth regularly spaced. *F*, Teeth distantly spaced. *G*, Teeth closely spaced. *H*, Teeth rounded. *I*, Teeth appressed. *J*, Teeth acute. *K*, Teeth compound. *L*, Apex emarginate. *M–O*, Apex rounded. *P*, *Q*, Apex acute. *R*, *S*, Apex attenuate. *T*, *U*, Base cordate. *V*, *W*, Base rounded. *X– Z*, Base acute. *AA*, Shape obovate. *BB*, Shape elliptic. *CC*, Shape ovate.

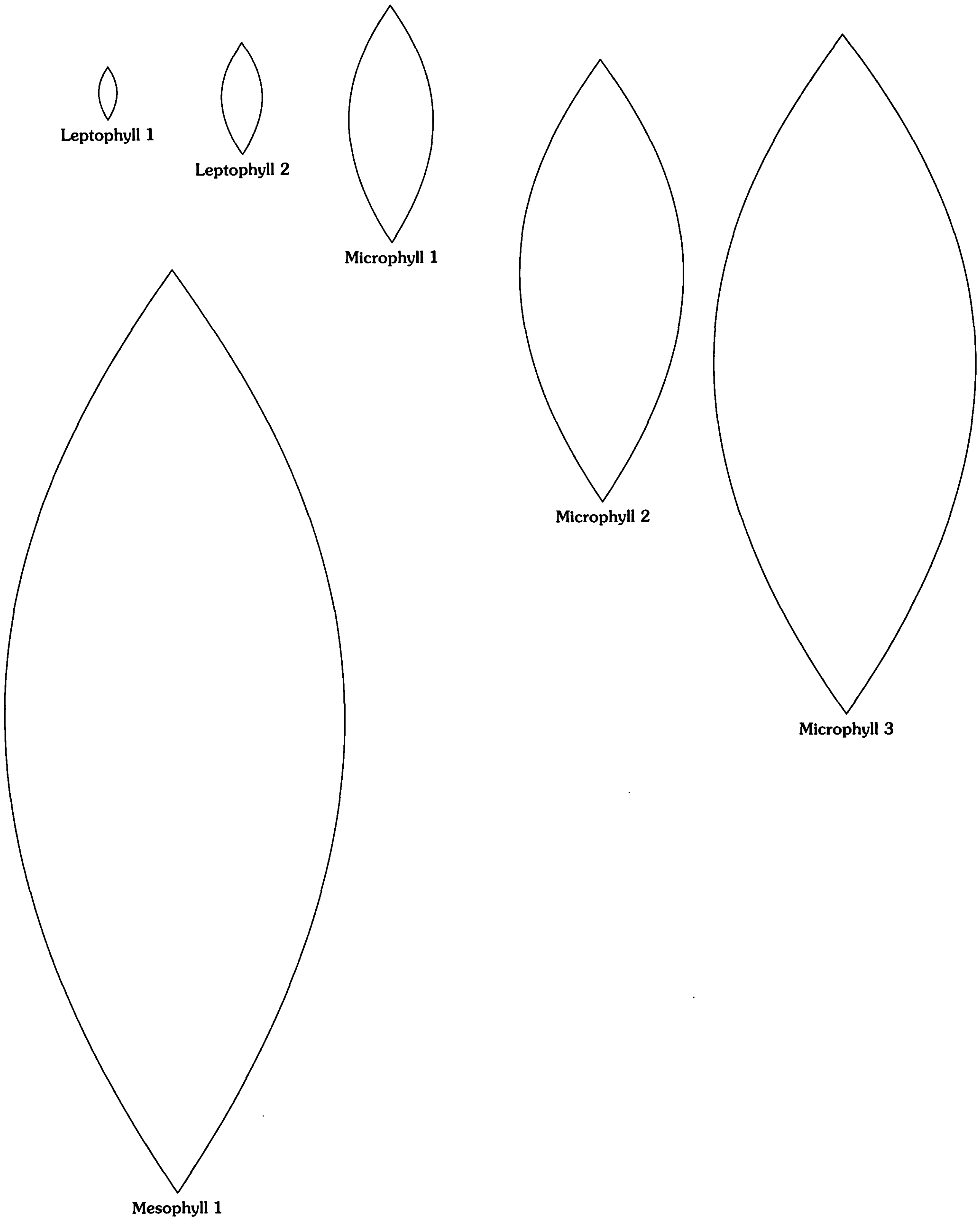

Figure 9. Leaf-size character states.

																LOBED
																NO TEETH
																TEETH REGULAR
																TEETH CLOSE
																TEETH ROUND
																TEETH ACUTE
																TEETH COMPOUND
																LEPTO I
																LEPTO II
																MICRO I
																MICRO II
																MICRO III
																MESO I
																MESO II
																APEX EMARG
																APEX ROUND
																APEX ACUTE
																APEX ATTEN
																BASE CORDATE
																BASE ROUND
																BASE ACUTE
																L:W < 1:1
																L:W 1-2:1
																L:W 2-3:1
																L:W 3-4:1
																L:W >4:1
																SHAPE OBOVATE
																SHAPE ELLIPTIC
																SHAPE OVATE

rounded (or appressed) and acute and some leaves have teeth and others do not, a score of 0.5 if the teeth are only acute and some leaves have teeth and others do not, a score of 0.5 if the teeth are both rounded (or appressed) and acute and all leaves are toothed, and a score of 1 if all teeth are acute and all leaves are toothed. Teeth are acute if the apical and basal flanks of the teeth form a sharp point (fig. 8*J*).

Teeth compound.—Species that have at least 50 percent teeth that are compound receive a score of 1, species that have some but less than 50 percent teeth that are compound receive a score of 0.5, and species that have no compound teeth receive a score of 0. A compound tooth is a tooth that has smaller teeth on (typically) its basal flank (fig. 8*K*).

Leaf size.—A species is scored for its full range of variation in leaf size. A species that has leaves of only one size category receives a score of 1 in that category. If a species ranges through two categories, it receives a score of 0.5 in both categories, if it ranges through three categories it receives a score of 0.33 in each category, and so forth. The leaf size (or area) categories (fig. 9) are defined differently than the categories proposed by Raunkiaer (1934), as modified by Webb (1959), although the division between the microphyll 3 and mesophyll 1 categories approximately corresponds to the division between Webb's (1959) notophyll and mesophyll categories. Raunkiaer's (1934) original categories were defined by him based on examination of a large number of herbarium specimens. In sizing leaves early in the development of CLAMP, I observed that many species tended to have leaves concentrated in certain sizes that represented categories intermediate between two of Raunkiaer's categories, and thus I developed the system proposed here. Note that if a lobed leaf is dissected more than half the distance from the apex of the lobe to the base of the lamina or to the midrib, the unit area scored is an individual lobe.

During development of CLAMP, three additional size categories were scored. One was smaller than the leptophyll 1 category and two were larger than the mesophyll 2 category. In all three instances, the multivariate analysis produced character-state scores that were almost the same as the scores for the adjacent leaf-size character states. These similarities in scores indicated that no significant information was being added, and deletion from the database of the duplicate character states produced somewhat higher eigenvalues and had little effect on sample scores.

Figure 10 (facing page). Score sheet for character states. Each species in a sample is scored for its full range of variation relative to lobing, toothing, size, apical configuration, basal configuration, length to width ratio, and general shape. The totals for each column are then added and converted to percentages. See text for detailed instructions.

Apex emarginate.—A species receives a score of 1 if some leaves are emarginate and a score of 0 if no leaves are emarginate. An apex is emarginate if the most apical part of the lamina convexly curves toward the base of the lamina (fig. 8*L*). Insect-related damage can cause a somewhat similar notched apex that tends to have irregular sides and is excluded from the emarginate category.

Apex round.—This and the two following categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. An apex is round if the most apical fourth of the lamina has a margin that convexly curves and the two sides meet to form a curve (figs. 8*M–O*).

Apex acute.—This and the two adjacent categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. An apex is acute if the most apical fourth of the lamina has a margin that is straight and the two sides form a point (figs. 8*P, Q*). Note that this definition of acute does not depend on the angle formed by the two laminar sides.

Apex attenuate.—This and the two preceding categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. An apex is attenuate if, in the most apical fourth of the lamina, the margin on both sides changes from a linear or convex margin to a concave margin and the concave margin extends for a distance of at least 1 cm (figs. 8*R, S*). The necessity in the attenuate category for both sides to change curvature thus excludes many falcate laminae, which typically have a change of curvature on only one side (fig. 8*Q*) and are considered to have acute apices.

Base cordate.—This and the two following categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. A base is cordate if the basal parts of the lamina extend basally (below) beyond the juncture of the petiole with the lamina (figs. 8*T, U*).

Base round.—This and the two adjacent categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. A base is round if the most basal fourth of the lamina has a convex margin (figs. 8*V, W*).

Base acute.—This and the two preceding categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. A base is acute if the most basal fourth of the lamina has a straight or concave margin (figs. 8*E–G*).

Length to width ratio.—The five categories of length to width have a total score of 1 for each species. A species is scored for its full range of variation in length to width. A species that has leaves of only one length to width category receives a score of 1 in that category. If a species ranges through two categories, it receives a score of 0.5 in each category, if it ranges through three categories it receives a score of 0.33 in each category, and so forth.

Shape obovate.—This and the two following categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. A leaf is obovate if it is widest in the most apical third of the lamina (fig. 8*AA*).

Shape elliptic.—This and the two adjacent categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. A leaf is elliptic if it is widest in the medial third of the lamina (fig. 8*BB*).

Shape ovate.—This and the two preceding categories have a total score of 1 for each species. A species can have a score of 0.33 in each category if each category is represented, a score of 0.5 in two categories if two categories are represented, and a score of 1 in one category if only one category is represented. A leaf is ovate if it is widest in the most basal third of the lamina (fig. 8*CC*).

RESULTS OF SCORING

Each species of a given sample is scored for the character states just described. The number of leaves of a given species that is scored is basically irrelevant because the goal is to score the full physiognomic variation for each character state. Then, the numbers in each column of the score sheet (fig. 10) are added, and the sum is converted to a percentage of the total number of species in the sample. The percentages of each character state for each sample are then entered into a tabular database (table 2). Note that conversion to percentages can be somewhat different for fossil samples (p. 65).

MULTIVARIATE ANALYSIS

CHOICE OF METHOD

A number of methods of multivariate analysis have been proposed for ordinating categories that are assumed to be mutually dependent variables. Among these methods, those which might be most appropriate are Discriminant Analysis, Principal Components Analysis, and Correspondence Analysis. All three methods lead to determination of those variables most significant in placing a sample in a particular position relative to other samples. Both Discriminant Analysis and Principal Components Analysis were developed in areas of the social sciences. The algorithms of Correspondence Analysis (called "Reciprocal Averaging" by Hill, 1973) were, in contrast, developed to analyze the distribution of terrestrial plant species along environmental gradients.

Discriminant Analysis operates on the basic assumption that a sample belongs to one of two or more categories that are known to be distinct. In order to perform the analysis, dividing points for each variable must be selected; dividing points are selected based on the assumption that each category has the same amount of variance for a given variable. Thus, the distribution of each variable is assumed to be "normal"; that is, the distribution can be represented by a bell-shaped curve, and skewed variable distributions increase the total error rate (Afifi and Clark, 1990). Discriminant Analysis, moreover, results in a single two-dimensional plot.

Application of Discriminant Analysis to the database of leaf physiognomy character states would be inappropriate. Vegetation represents a multidimensional continuum that we have arbitrarily (and not necessarily validly) divided into units. Assumptions should not be made relative to "normal" distributions of any particular character state, which could have a highly skewed distribution. Indeed, examination of table 2 indicates that most physiognomic character states have skewed distributions.

Principal Components Analysis, on the other hand, is an exploratory method that makes no assumptions relative to the existence of discrete categories or the distribution of the variables. The method combines information of the original variables in a linear fashion into new, presumably uncorrelated, variables termed principal components. These principal components are portrayed as axes, and the original variables and the samples receive scores on each axis; thus the variables (character states) and samples are considered in a multidimensional framework. The transformation of the original into the new variables is performed by calculating a similarity matrix of the variables, which has an advantage of showing which variables are correlated most closely to other variables.

Correspondence Analysis (Hill, 1973, 1979) operates in a similar manner as Principal Components Analysis and

Table 2. Character-state percentages for CLAMP database.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Barro Colorado Is.	Guanica	Cabo Rojo	Borinquen	Cambalache	Susua Alta	Guajataca	Avon Park	Orlando	Buena Vista	Canyon Lake	Maricao
Lobed	2	2	0	0	0	1	0	5	7	0	2	0
No teeth	81	86	90	83	87	79	74	69	66	80	78	79
Teeth regular	9	3	7	6	10	2	13	16	16	8	7	10
Teeth close	6	6	7	9	4	5	8	13	17	7	10	4
Teeth round	15	9	10	15	12	21	17	13	30	18	18	21
Teeth acute	4	5	0	2	1	0	9	18	4	1	3	0
Teeth compound	0	3	2	2	3	4	4	2	3	3	0	0
Leptophyll 1	1	7	13	6	6	12	2	7	9	4	67	0
Leptophyll 2	1	17	16	21	6	20	4	9	14	12	17	1
Microphyll 1	11	29	24	29	15	26	11	26	16	23	9	11
Microphyll 2	12	25	26	27	30	18	20	32	33	32	6	33
Microphyll 3	26	13	15	14	26	12	27	16	22	18	0	29
Mesophyll 1	33	5	6	2	12	5	21	8	6	9	0	15
Mesophyll 2	16	5	2	2	5	7	15	2	1	2	0	10
Apex emarginate	12	76	53	71	35	55	21	42	39	47	23	49
Apex round	31	89	84	87	57	72	54	55	55	72	77	74
Apex acute	28	9	13	9	12	23	11	26	30	17	23	9
Apex attenuate	40	2	3	5	31	4	35	19	15	11	0	17
Base cordate	8	8	18	9	4	11	4	5	15	8	12	4
Base round	27	53	52	62	61	52	63	21	27	42	43	73
Base acute	66	39	30	29	35	37	33	74	58	50	45	23
L:W <1:1	3	0	3	1	0	0	0	0	3	1	2	0
L:W 1–2:1	18	61	59	65	46	67	41	44	34	51	46	60
L:W 2–3:1	62	30	27	29	43	23	44	31	39	36	26	32
L:W 3–4:1	15	5	5	2	7	6	10	16	21	8	16	6
L:W >4:1	2	4	5	2	4	4	5	9	4	4	9	2
Shape obovate	15	33	33	26	22	25	28	38	33	29	23	25
Shape elliptic	62	44	41	44	51	45	45	46	45	55	50	41
Shape ovate	23	23	26	31	27	30	28	17	22	16	27	34

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Lake George	Bartlett Reservoir	Castle Creek	Superior	Saguaro Lake	Lake Roosevelt	Brunswick	Monte Guilarte	Beaufort	Punkin Center	Yakushima	Childs
Lobed	12	0	2	2	4	0	9	0	17	7	6	6
No teeth	53	80	78	69	75	74	63	71	50	73	54	63
Teeth regular	22	10	9	16	13	11	21	11	26	8	26	19
Teeth close	12	8	11	16	15	16	18	8	33	13	24	19
Teeth round	38	10	19	26	22	21	24	29	29	22	37	27
Teeth acute	8	10	3	5	3	5	13	0	21	5	9	10
Teeth compound	3	5	0	5	2	2	3	2	8	5	4	6
Leptophyll 1	2	50	53	55	49	54	6	2	0	36	0	40
Leptophyll 2	8	24	20	18	22	23	9	5	2	19	1	20
Microphyll 1	22	18	16	17	17	13	24	18	17	30	6	18
Microphyll 2	29	6	9	9	11	8	33	29	31	12	35	10
Microphyll 3	28	2	1	2	1	2	18	27	28	2	33	6
Mesophyll 1	12	0	0	0	0	1	8	14	15	1	16	4
Mesophyll 2	3	0	0	0	0	0	2	6	6	0	8	3
Apex emarginate	20	35	30	17	23	22	32	18	18	13	15	17
Apex round	46	91	82	81	81	71	49	64	47	68	26	76
Apex acute	23	6	15	16	18	25	27	10	27	31	20	18
Apex attenuate	31	3	3	2	1	4	23	26	26	1	54	5
Base cordate	12	10	10	5	23	10	12	12	27	16	19	12
Base round	37	53	47	47	44	47	24	58	31	46	46	53
Base acute	52	38	43	48	33	43	65	30	42	39	35	35
L:W <1:1	3	0	2	2	3	2	3	3	9	7	0	8
L:W 1–2:1	33	54	43	41	48	50	38	57	37	41	24	47
L:W 2–3:1	44	25	28	29	28	25	39	32	42	25	52	31
L:W 3–4:1	14	12	17	13	10	12	18	8	8	14	17	8
L:W >4:1	6	10	11	15	10	12	2	1	4	14	7	6
Shape obovate	27	31	38	32	31	32	34	17	32	25	22	35
Shape elliptic	47	36	29	39	27	32	49	43	39	40	36	40
Shape ovate	27	33	33	30	42	36	18	40	29	35	42	25

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Simmons-ville	Toro Negro	Kure Beach	Santa Rita	Miami	Camp Pardee	Auburn	Sierra Ancha	Yava	Colfax	Zozu-san	Jerome
Lobed	23	0	9	13	5	11	14	6	4	19	14	14
No teeth	61	68	50	64	60	52	50	63	60	48	50	48
Teeth regular	19	18	25	19	17	16	27	19	25	22	36	23
Teeth close	16	10	21	23	19	18	25	26	27	20	27	23
Teeth round	21	18	40	29	33	41	41	27	30	38	21	38
Teeth acute	18	14	10	7	7	7	9	10	10	14	30	14
Teeth compound	5	6	4	5	2	6	5	7	6	6	10	10
Leptophyll 1	5	0	0	30	24	8	4	15	41	4	0	26
Leptophyll 2	11	5	8	16	22	20	13	16	20	7	2	17
Microphyll 1	21	20	26	23	31	28	29	24	24	23	9	26
Microphyll 2	27	34	37	23	16	29	31	28	10	30	39	20
Microphyll 3	20	23	21	6	4	12	15	12	4	22	33	10
Mesophyll 1	8	13	7	2	3	2	7	3	1	9	12	0
Mesophyll 2	8	6	1	0	0	1	1	2	0	4	4	0
Apex emarginate	36	21	36	29	29	30	35	7	13	33	17	27
Apex round	61	55	51	66	65	59	77	67	72	64	33	73
Apex acute	37	20	37	30	29	34	13	26	22	32	30	23
Apex attenuate	2	25	12	5	6	7	11	7	6	4	37	4
Base cordate	11	10	9	26	12	15	17	13	8	22	20	19
Base round	24	50	27	58	62	63	74	69	63	53	51	47
Base acute	65	40	64	17	26	22	9	19	29	26	29	34
L:W <1:1	5	0	4	6	7	4	10	4	2	15	11	2
L:W 1–2:1	42	44	39	38	53	46	56	51	59	40	38	55
L:W 2–3:1	41	46	43	33	18	25	23	27	17	27	39	25
L:W 3–4:1	10	10	13	17	10	12	7	14	13	12	12	13
L:W >4:1	2	1	0	6	12	14	4	4	10	6	0	6
Shape obovate	41	22	25	16	18	19	24	20	32	17	9	24
Shape elliptic	49	48	57	25	48	41	44	39	32	48	57	38
Shape ovate	10	30	18	59	34	41	32	41	36	35	34	38

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Jasper Ridge	Natural Bridge	Lakeport	Kiyosumi	Canelo	Santa Cruz	Nevada City	S.I.E.R.C.	Placerville	Battle Creek	Junipine	Payson
Lobed	11	9	21	8	11	8	19	23	15	18	15	5
No teeth	42	55	48	47	60	44	41	36	31	27	32	46
Teeth regular	31	25	20	42	22	31	26	50	34	57	33	25
Teeth close	32	30	20	34	23	35	30	38	33	48	49	25
Teeth round	48	30	35	25	30	40	42	22	59	38	33	43
Teeth acute	11	15	17	28	9	16	17	42	10	36	35	11
Teeth compound	16	16	5	16	10	16	25	19	15	21	20	14
Leptophyll 1	5	7	4	3	20	3	6	0	3	0	6	14
Leptophyll 2	14	13	13	9	19	5	5	4	9	5	10	22
Microphyll 1	27	27	29	20	27	21	17	14	28	19	24	28
Microphyll 2	33	35	26	34	25	41	31	33	32	32	33	24
Microphyll 3	15	12	16	22	5	22	29	31	18	26	18	10
Mesophyll 1	7	3	7	10	3	7	13	14	9	14	7	2
Mesophyll 2	0	2	4	2	2	2	0	4	1	4	2	1
Apex emarginate	28	14	19	6	13	8	33	3	13	4	11	18
Apex round	73	55	60	28	58	70	53	28	72	22	50	65
Apex acute	22	33	36	30	37	28	34	47	25	52	34	27
Apex attenuate	5	12	5	42	6	2	13	25	4	26	16	8
Base cordate	16	17	17	6	21	22	26	17	10	16	14	19
Base round	61	56	60	58	53	62	57	59	71	59	56	62
Base acute	23	27	24	36	26	16	17	23	19	25	30	19
L:W <1:1	6	11	12	4	7	10	10	13	2	13	9	7
L:W 1–2:1	61	49	54	39	43	53	51	57	58	43	53	49
L:W 2–3:1	16	25	12	46	27	25	25	27	24	39	26	27
L:W 3–4:1	10	11	10	7	16	11	8	2	9	3	9	10
L:W >4:1	6	5	13	4	8	1	7	1	8	1	3	7
Shape obovate	20	16	13	11	19	16	21	14	24	11	19	21
Shape elliptic	48	32	48	52	32	42	42	56	47	61	38	41
Shape ovate	31	52	40	38	50	42	37	30	30	29	43	38

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Prescott Airport	Half Moon Bay	Crown King	Frederick	Kitt Peak	Powers	Troutdale	Port Orford	Arendts-ville	North Bend	Jemez Springs	Bandon
Lobed	7	18	10	23	0	17	17	15	25	19	17	9
No teeth	38	38	40	33	54	26	20	36	22	35	40	37
Teeth regular	39	40	32	55	27	50	56	48	64	45	25	50
Teeth close	45	42	27	39	28	46	57	38	59	44	33	42
Teeth round	33	36	30	26	37	38	42	39	26	39	53	32
Teeth acute	30	26	30	42	9	36	38	26	52	27	7	32
Teeth compound	15	28	14	21	15	32	37	31	33	33	17	33
Leptophyll 1	10	5	5	0	9	1	2	2	1	0	15	4
Leptophyll 2	27	13	17	5	24	10	5	9	5	10	25	10
Microphyll 1	31	25	29	14	35	21	18	17	19	19	28	11
Microphyll 2	22	31	34	28	25	33	34	31	35	23	21	35
Microphyll 3	7	17	10	31	7	17	27	21	27	27	8	26
Mesophyll 1	3	7	4	19	0	13	8	16	11	17	3	11
Mesophyll 2	0	2	2	3	0	6	6	4	3	5	0	3
Apex emarginate	30	24	20	0	22	24	10	13	6	4	8	4
Apex round	67	72	57	48	67	55	53	47	28	51	76	44
Apex acute	28	22	35	39	28	35	32	40	55	35	22	36
Apex attenuate	5	6	7	14	4	11	15	13	17	14	3	20
Base cordate	20	20	8	23	22	28	23	23	23	28	19	24
Base round	55	56	64	45	70	57	53	60	56	49	42	59
Base acute	25	24	28	32	9	15	23	18	20	22	40	17
L:W <1:1	5	8	4	13	4	11	10	10	8	12	12	7
L:W 1–2:1	58	48	54	57	58	51	52	40	70	47	42	54
L:W 2–3:1	25	25	27	30	33	28	29	37	21	29	26	26
L:W 3–4:1	3	11	7	0	3	7	6	9	1	12	8	9
L:W >4:1	9	7	7	0	1	4	3	4	0	1	13	4
Shape obovate	25	12	23	16	11	13	20	14	19	21	23	13
Shape elliptic	37	46	35	60	37	43	47	46	50	46	46	48
Shape ovate	38	42	43	24	52	45	33	41	31	33	31	39

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Hood River	Cape Blanco	Blue Canyon	Hasayampa	Three Lynx	Strouds-burg	Bowman Dam	Los Alamos	Wind River	Lake Spaulding	Tunk-hannock	Parkdale
Lobed	25	14	26	14	18	22	19	19	23	26	27	21
No teeth	16	40	37	27	18	33	40	27	20	40	17	23
Teeth regular	55	48	48	48	57	53	39	40	58	47	66	60
Teeth close	57	43	38	42	56	48	36	48	57	45	59	59
Teeth round	39	30	31	39	35	15	28	48	37	27	25	33
Teeth acute	45	30	32	34	47	53	32	25	43	33	58	44
Teeth compound	41	34	22	16	42	35	21	23	43	26	45	43
Leptophyll 1	0	4	3	4	4	3	3	12	2	13	1	1
Leptophyll 2	7	8	18	12	8	7	23	16	4	20	3	10
Microphyll 1	19	19	32	28	21	17	33	31	18	28	17	17
Microphyll 2	34	30	26	38	36	29	25	28	31	23	34	32
Microphyll 3	24	23	11	18	18	31	10	10	26	10	26	25
Mesophyll 1	14	14	7	1	11	9	4	3	11	4	15	13
Mesophyll 2	1	2	2	0	3	3	1	0	7	2	4	2
Apex emarginate	13	8	22	9	13	10	31	12	13	23	3	9
Apex round	47	39	71	60	54	33	73	59	41	66	28	54
Apex acute	41	49	24	26	37	45	20	34	41	27	55	34
Apex attenuate	13	13	6	15	9	22	8	7	18	7	17	11
Base cordate	32	26	17	11	27	30	19	15	30	16	34	36
Base round	51	54	70	65	52	45	55	59	49	63	45	49
Base acute	18	20	13	24	22	25	26	26	22	21	20	16
L:W <1:1	13	7	7	11	13	17	11	10	17	16	17	16
L:W 1–2:1	71	51	54	49	53	63	50	47	53	49	67	62
L:W 2–3:1	10	37	31	26	24	20	26	32	24	26	13	15
L:W 3–4:1	4	3	3	6	8	0	10	7	4	5	2	5
L:W >4:1	2	2	6	8	3	0	4	5	2	4	2	2
Shape obovate	8	18	19	19	16	8	31	19	19	25	15	14
Shape elliptic	51	46	45	38	43	51	42	44	43	46	48	33
Shape ovate	41	36	36	43	41	41	27	37	38	30	37	53

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Sierraville	Ketchikan	Cheesman Reservoir	Red Fleet	Mt. Pocono	Rimrock Lake	Lake Maloya	River Falls	Laurel Mountain	Tierra Amarilla	Danne-mora	Estes Park
Lobed	25	18	26	13	22	18	23	30	17	24	13	28
No teeth	32	24	17	42	17	18	28	16	23	26	13	22
Teeth regular	58	52	54	41	72	66	50	57	52	49	70	53
Teeth close	49	53	54	37	62	66	48	52	54	45	70	58
Teeth round	38	42	52	39	24	32	48	30	40	55	30	43
Teeth acute	30	34	32	18	59	50	23	55	38	19	57	35
Teeth compound	20	32	28	15	41	58	13	39	38	14	50	30
Leptophyll 1	8	20	10	20	3	1	4	0	7	17	1	7
Leptophyll 2	27	18	23	21	10	11	23	6	14	22	8	24
Microphyll 1	26	20	36	30	33	28	38	17	30	25	20	31
Microphyll 2	22	16	23	19	31	38	29	33	28	23	35	28
Microphyll 3	13	11	6	10	15	14	7	30	12	11	26	9
Mesophyll 1	3	7	3	1	8	5	0	12	7	2	8	1
Mesophyll 2	2	8	0	0	1	2	0	3	1	0	2	0
Apex emarginate	13	4	0	8	0	12	15	0	4	5	7	7
Apex round	71	57	50	63	24	59	54	17	52	64	20	61
Apex acute	21	25	46	30	46	33	39	49	42	31	65	27
Apex attenuate	9	17	4	7	30	9	7	33	6	5	15	11
Base cordate	19	24	24	8	28	26	18	34	25	17	37	27
Base round	56	64	48	50	56	54	60	43	52	48	58	52
Base acute	24	12	28	42	17	20	22	23	23	36	5	20
L:W <1:1	20	12	20	15	17	13	13	21	15	12	12	22
L:W 1–2:1	44	38	40	29	50	61	47	52	46	46	73	46
L:W 2–3:1	23	32	21	24	20	19	14	18	31	12	13	22
L:W 3–4:1	6	12	10	17	11	2	14	7	8	12	1	7
L:W >4:1	8	6	8	14	3	4	11	2	1	17	1	3
Shape obovate	31	18	14	30	6	15	14	9	15	23	5	19
Shape elliptic	46	36	47	38	52	39	54	55	44	42	45	41
Shape ovate	24	46	40	32	43	45	33	36	42	35	50	39

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Republic	Donner Lake	Government Camp	Nederland	Wanakena	Bumping Lake	Allens Park	Lake Placid	Soda Springs	Seward	Red River	Wolf Creek
Lobed	30	34	24	25	13	14	28	23	30	27	22	13
No teeth	20	34	21	21	23	21	37	10	28	23	26	30
Teeth regular	62	55	55	67	67	54	50	71	50	57	57	58
Teeth close	63	48	54	62	65	54	46	68	49	55	59	50
Teeth round	38	36	29	40	20	42	39	25	46	36	43	44
Teeth acute	41	30	50	39	57	37	24	65	26	41	31	27
Teeth compound	45	32	43	33	50	27	32	58	28	39	28	18
Leptophyll 1	0	11	8	10	1	10	6	7	7	10	9	6
Leptophyll 2	10	19	15	24	12	21	19	10	24	12	23	14
Microphyll 1	25	30	20	25	26	27	25	25	36	16	34	34
Microphyll 2	40	24	31	29	44	26	33	30	20	24	25	36
Microphyll 3	19	10	15	12	9	12	13	21	7	20	7	9
Mesophyll 1	4	5	8	0	5	3	3	5	4	8	2	2
Mesophyll 2	1	1	3	0	3	2	1	3	2	10	0	0
Apex emarginate	4	7	3	8	0	12	7	0	12	5	0	0
Apex round	41	67	47	49	20	50	59	18	71	43	64	46
Apex acute	41	24	38	41	58	44	31	45	24	39	29	41
Apex attenuate	18	9	16	10	22	6	10	37	5	18	7	13
Base cordate	30	38	22	25	25	14	32	40	29	36	17	20
Base round	57	45	52	54	65	65	46	34	59	43	52	58
Base acute	13	18	26	21	10	21	22	26	11	21	31	23
L:W <1:1	27	27	16	21	17	8	17	15	30	23	21	13
L:W 1–2:1	51	42	47	44	57	56	44	62	38	33	40	39
L:W 2–3:1	17	19	33	26	19	27	28	20	18	30	23	28
L:W 3–4:1	4	6	5	7	6	2	7	3	10	9	7	15
L:W >4:1	1	7	0	2	2	8	4	1	4	5	10	5
Shape obovate	7	24	17	23	7	15	25	14	21	20	19	19
Shape elliptic	41	40	39	40	51	42	32	51	43	42	43	43
Shape ovate	52	36	44	37	42	44	43	35	35	38	38	38

Table 2. Character-state percentages for CLAMP database—Continued.
[Sample locations described in text; listed in order of decreasing annual temperature]

	Tahosa Creek	Homer	Alyeska	Lake Granby	Dillon	Grand Lake	Kenai	Talkeetna	Eklutna Lake	Sheep Mountain
Lobed	10	10	19	11	29	16	14	15	13	8
No teeth	30	27	19	39	33	34	23	25	33	29
Teeth regular	48	49	50	44	50	55	48	48	47	42
Teeth close	44	48	48	44	50	52	52	52	45	44
Teeth round	43	42	45	39	48	43	46	43	44	44
Teeth acute	28	31	36	22	19	23	32	32	23	27
Teeth compound	30	35	31	22	19	25	36	32	28	29
Leptophyll 1	10	18	12	24	15	9	16	16	13	16
Leptophyll 2	29	20	10	31	29	19	17	15	18	15
Microphyll 1	28	17	21	24	29	25	17	17	22	26
Microphyll 2	21	20	25	15	21	31	22	25	21	24
Microphyll 3	9	12	19	4	4	14	18	14	15	12
Mesophyll 1	3	6	10	2	2	1	10	6	8	4
Mesophyll 2	0	7	4	0	1	0	1	8	3	3
Apex emarginate	0	4	5	13	8	4	5	11	7	17
Apex round	57	44	38	61	68	51	47	44	51	54
Apex acute	37	38	41	35	28	40	41	37	37	37
Apex attenuate	7	19	21	4	5	8	13	19	12	10
Base cordate	10	29	29	11	29	18	30	23	30	27
Base round	65	58	55	57	48	59	64	54	55	58
Base acute	25	13	17	33	23	23	7	23	15	15
L:W <1:1	17	13	14	11	21	18	19	20	18	14
L:W 1–2:1	34	40	50	30	39	35	41	36	36	43
L:W 2–3:1	31	30	33	25	24	23	22	24	32	26
L:W 3–4:1	14	12	2	17	7	11	12	16	11	11
L:W >4:1	4	6	2	17	9	13	6	4	4	7
Shape obovate	22	20	17	27	25	23	10	20	19	19
Shape elliptic	42	38	41	40	50	41	51	42	44	42
Shape ovate	37	42	43	32	25	37	40	38	36	40

is generally considered to be an improvement. In Correspondence Analysis, the database is constructed from plant community samples along environmental gradients; each species in each sample is scored for factors such as abundance of individuals or cover, and such scores are the variables. Correspondence Analysis constructs a covariance matrix of variables and produces sets of scores for variables and for samples on two or more axes. Although the principal components in Principal Components Analysis are assumed to be uncorrelated, in fact the principal components may be correlated to varying degrees; Correspondence Analysis attempts a more rigorous, noncorrelated separation of the linearized components. Further, high percentages of a particular variable relative to other variables in a given sample can, in Principal Components Analysis, produce outlier sample scores; this effect is minimized in Correspondence Analysis.

Detrended Correspondence Analysis is, as the name implies, a modification of Correspondence Analysis and was also developed for discerning distributional trends of species as they may relate to environmental gradients (Hill and Gauch, 1980). This modification does resolve some problems that can surface from standard Correspondence Analysis, but the modification involves the assumption that the abundance of a plant species along an environmental gradient probably can be represented by "normal" distribution, an assumption that should not be applied to the distribution of physiognomic character states.

In early stages of development of CLAMP, I subjected the database to Principal Components Analysis, Correspondence Analysis, and Detrended Correspondence Analysis. Of these various multivariate methods commonly used in the life sciences, Correspondence Analysis produced the most valid (accurate) estimates of climatic parameters; that is, this method ordinates the samples in a manner that best mirrors certain climatic parameters.

To be sure, Correspondence Analysis is generally regarded as an exploratory rather than a predictive method. However, biological, including paleontological, data sets tend to be "noisy" and may have some data missing and (or) skewed; such data sets can seriously affect results of, for example, Multiple Regression Analysis but have minimal effect on Correspondence Analysis. If biological, especially physiognomic, adaptations had 1:1 correlations with various environmental parameter and if the character states were not distributionally skewed, more rigorous statistical methods such as Multiple Regression Analysis would be merited, but the very nature of environmental selection and possible genetic linkage creates a data set that is inherently "noisy."

APPLICATION TO LEAF PHYSIOGNOMY DATABASE

The leaf physiognomy database (table 3) was subjected to Correspondence Analysis using the version in the computer program, MVSP Plus v.2.0, designed for personal computers by Warren L. Kovach.[1] In this program, each column represents a sample and each row represents a species, for which character state scores are substituted (see table 2). The program allows for adjustment of scores, for example, by weighting common species or rare species, but for leaf physiognomy no adjustment should be made. The results (tables 3, 4) of the initial run show that axis 1 accounts for almost one-half the total variance and axis 2 for more than one-fifth.

A plot (plate 2) of the resulting sample scores shows that axis 1 relates to temperature; all megathermal and most mesothermal samples receive positive scores, and microthermal samples generally receive negative scores. Axis 2, on the other hand, relates to water stress; Sonoran Desert samples receive the highest scores, and megathermal and mesothermal rain forest samples receive the lowest scores. The physiognomic character states are portrayed as vectors extended from the intersection of the two principal axes to the score of each character state.

One major and one minor anomaly are apparent in the sample plots. The major anomaly is formed by 19 of the 20 subalpine samples; those 19 samples define a contiguous, inlying area in the cool, dry (lower right) quadrant, plotting above, however, samples of warmer climate. One dry subalpine sample groups with an outlier of three other samples that represent dry, microthermal juniper woodland and these four form the minor anomaly. Three samples of dry, microthermal coniferous forest from Colorado, moreover, plot below the subalpine samples and have similar minor axis scores; these three samples will be considered with the subalpine samples. These inlier and outlier samples will be discussed later (see p. 56–59).

If the inlier and outlier samples are removed from the database and the remaining 80 samples subjected to Correspondence Analysis, the percent of total variance of the two principal axes rises from approximately 68 to 70 percent (tables 5, 6). The plot (plate 3) from this second run is the basis for the derivation of both temperature and precipitation estimates made in the following sections, except the section on the inlier and outlier samples.

The robustness of CLAMP can be inferred from experiments that involve deleting groups of character

---

[1] This program is available for purchase from Warren L. Kovach, 85 Nant-y-felin, Pentraeth, Anglesey, Wales LL75 8UY, United Kingdom.

Table 3. Character-state scores from Correspondence Analysis of all samples.
[Eigenvalues and percent total variance for each axis are as follows: axis 1, 0.106, 47.63 percent; axis 2, 0.045, 20.31 percent; axis 3, 0.018, 8.23 percent; axis 4, 0.011, 4.85 percent; axis 5, 0.009, 4.14 percent; axis 6, 0.006, 2.53 percent]

Character state	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Lobed	-1.33	0.46	–0.38	-1.73	1.27	-2.37
No teeth	1.61	–0.54	0.22	0.60	–0.15	–0.04
Teeth regular	-1.31	0.34	0.16	–0.19	0.31	0.21
Teeth close	-1.26	0.60	0.05	–0.12	0.23	0.15
Teeth round	–0.29	0.51	–0.25	-1.60	-1.58	–0.34
Teeth acute	-1.71	0.03	0.31	1.08	1.79	0.81
Teeth compound	-1.88	0.47	–0.05	1.38	0.91	–0.62
Leptophyll 1	2.38	4.06	4.28	2.96	0.81	–0.58
Leptophyll 2	0.52	1.93	–0.47	-1.10	–0.17	0.13
Microphyll 1	0.10	0.56	-1.10	-1.18	–0.17	1.04
Microphyll 2	–0.30	–0.81	–0.79	–0.28	–0.23	1.33
Microphyll 3	–0.39	-2.25	0.12	0.44	–0.18	–0.60
Mesophyll 1	–0.31	-3.26	1.27	0.77	–0.78	-2.98
Mesophyll 2	0.18	-3.82	1.89	1.51	-1.29	–6.73
Apex emarginate	2.21	–0.98	-3.15	0.96	2.19	–0.43
Apex round	0.83	0.57	–0.76	–0.10	–0.25	–0.91
Apex acute	–0.68	4.5E–0003	0.50	-3.5E–0003	0.42	1.42
Apex attenuate	–0.51	-2.91	2.69	0.34	-1.14	0.95
Base cordate	–0.83	0.29	1.9E–0003	0.78	0.22	-1.90
Base round	0.10	0.17	–0.53	0.65	-1.54	0.36
Base acute	1.10	–0.73	1.34	-1.85	2.25	0.88
L:W <1:1	-1.46	0.95	0.01	-1.35	0.22	-2.83
L:W 1–2:1	0.11	–0.02	–0.76	1.23	0.28	0.64
L:W 2–3:1	0.52	–0.99	0.92	–0.59	–0.52	–0.15
L:W 3–4:1	0.89	0.25	1.69	-2.04	-1.08	0.39
L:W >4:1	1.08	2.02	0.95	-2.15	-1.32	0.87
Shape obovate	0.99	0.16	0.19	–0.94	1.16	–0.86
Shape elliptic	0.07	–0.45	0.12	–0.29	0.21	0.24
Shape ovate	–0.13	0.29	-5.8E–0003	0.85	-1.36	0.43

states from the analysis (table 7). When different groups of character states are removed, the two principal axes continue to account for approximately 70 percent of total variance, except that removal of characters of the margin reduces total variance of the two principal axes to about 60 percent. Although removal of some character groups produces increases in eigenvalues and total variance on the first two axes, these removals result in more inaccurate estimates of meteorological parameters than obtained from the analyses of the full suite of 29 character states.

Similarly, restriction of the database to samples from a particular environment typically gives poor results in estimating meteorological parameters. Experiments that decrease the database to include, for example, only humid and mesic samples (those that have negative axis 2 scores in table 4) result in total variance on the first two axes of 75 percent, but positioning (as explained in the following paragraphs) of the samples relative to observed meteorological parameters is not as accurate as produced by the database of 80 samples.

The values for each collection site of a given meteorological parameter can be treated as if the parameter were a physiognomic character state. By this method, the relation of a given parameter to the sample scores can be derived. Each parameter can be separately entered into the database and then subjected to Correspondence Analysis. The character-state and sample scores (tables 5, 6) are little affected by this procedure, which, of course, implies that the major patterns are indeed correlated with the meteorological parameters. For example, using the total database of 106 samples, percent no teeth and Guanica have axis 1 scores of 1.61 and 2.06, respectively, and axis 2 scores of –0.54 and –0.80, respectively (tables, 3, 4); when mean annual temperature is run in the database, the axis 1 scores alter to 1.58 and 2.05 and the axis 2 scores alter to –0.45 and –0.73. Note that the score for Guanica shifts the Guanica plot to the right on plate 2 but the plot for the percent no teeth vector also shifts to the right. That is, the relations of sample plots to one another and to character-state plots remain almost unchanged. Meteorological parameter scores are given in table 8 and are plotted in plate 3.

Table 4. Sample scores from Correspondence Analysis of all samples.
[For eigenvalues and percent total variance see table 3]

Sample	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Barro Colorado Island	1.09	−3.55	3.40	−1.11	−0.51	−1.94
Guanica	2.06	−0.80	−2.80	0.94	1.94	−0.59
Cabo Rojo	1.86	−0.42	−1.83	1.22	0.84	−0.69
Borinquen	1.86	−0.60	−3.06	1.24	0.83	0.18
Cambalache	1.46	−2.03	0.11	0.90	−0.89	0.42
Susua Alta	1.79	−0.49	−1.74	1.04	0.77	−0.22
Guajataca	1.08	−2.50	1.13	0.74	−1.76	−1.67
Avon Park	1.40	−1.26	0.30	−1.59	3.04	1.82
Orlando	1.25	−0.98	0.26	−1.71	1.42	0.60
Buena Vista	1.67	−1.29	−1.15	−0.43	1.24	0.53
Canyon Lake	2.23	1.97	2.68	1.87	1.13	−0.10
Maricao	1.48	−2.04	−1.63	1.64	−1.35	−1.24
Lake George	0.70	−1.64	0.97	−1.97	−0.27	0.40
Bartlett Reservoir	2.15	1.51	0.84	2.01	1.01	−0.22
Castle Creek	2.20	1.60	1.61	0.98	0.80	−0.28
Superior	1.88	1.80	2.18	0.52	0.54	0.24
Saguaro Lake	1.78	1.72	1.22	1.43	0.18	−0.71
Roosevelt Lake	1.91	1.68	1.99	1.37	0.60	0.48
Brunswick	1.01	−1.33	0.66	−1.84	1.96	1.09
Monte Guilarte	1.00	−1.73	−0.07	0.66	−2.27	−0.30
Beaufort	0.14	−1.54	0.72	−0.92	0.56	−1.34
Punkin Center	1.46	1.36	1.22	−0.11	−0.03	0.49
Yakushima	0.31	−2.55	2.16	−0.64	−2.34	0.10
Childs	1.32	1.08	1.23	0.66	0.33	−1.13
Simmonsville	0.97	−1.02	−0.16	−1.84	3.22	−1.11
Toro Negro	0.85	−1.91	0.34	0.09	−0.58	0.74
Kure Beach	0.77	−1.26	−0.31	−2.34	1.71	1.49
Santa Rita	0.97	0.91	0.10	0.95	−1.22	−0.20
Miami	1.13	0.86	−0.39	0.16	−0.69	1.01
Camp Pardee	0.76	0.22	−1.06	−0.71	−1.35	1.09
Auburn	0.55	−0.15	−1.94	0.02	−1.39	−0.78
Sierra Ancha	0.67	0.31	−0.01	0.44	−1.88	0.88
Yava	1.18	1.55	1.04	0.95	−0.53	0.81
Colfax	0.42	−0.46	−1.07	−0.71	−0.27	−1.36
Zozu-san	−0.21	−1.87	0.89	0.32	−0.42	0.47
Jerome	0.86	0.83	−0.16	0.05	0.34	0.20
Jasper Ridge	0.33	0.10	−1.53	−0.37	−0.67	0.24
Natural Bridge	0.22	−9.2E−0003	−0.31	0.05	−1.06	1.07
Lakeport	0.29	0.03	−0.93	−0.64	−0.89	−0.08
Kiyosumi	−0.21	−1.41	1.44	−0.09	−0.96	2.52
Canelo	0.64	0.69	0.37	−0.05	−1.11	0.56
Santa Cruz	−0.06	−0.16	−0.87	0.18	−1.59	−0.03
Nevada City	8.7E−0003	−0.52	−0.86	0.45	−0.27	−0.93
S.I.E.R.C.	−0.85	−1.14	0.57	0.64	0.24	0.56
Placerville	0.09	0.06	−1.14	−1.00	−1.75	0.26
Battle Creek	−0.93	−1.04	0.78	−0.22	−0.29	0.91
Junipine	−0.35	−0.20	0.02	0.03	−0.04	1.07
Payson	0.49	0.57	−0.51	−0.11	−1.38	0.50
Prescott Airport	0.20	0.65	−1.15	0.16	0.50	0.96
Crown King	0.17	0.06	−0.83	−0.05	−0.22	1.85
Half Moon Bay	−0.12	0.09	−0.94	−0.02	−0.14	−0.34
Frederick	−0.80	−0.94	0.42	0.15	0.94	−0.68
Kitt Peak	0.44	0.54	−1.52	1.02	−1.98	1.26
Powers	−0.61	−0.31	−0.77	0.65	−0.15	−0.84
Troutdale	−0.85	−0.39	−0.10	0.20	0.20	−0.48
Port Orford	−0.51	−0.55	0.01	0.21	−0.84	−0.56

Table 4. Sample scores from Correspondence Analysis of all samples—Continued.
[For eigenvalues and percent total variance see table 3]

Sample	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
Arendtsville	–1.20	–0.52	2.0E–0003	1.00	1.17	1.02
North Bend	–0.65	–0.58	0.26	–0.15	–0.35	–1.58
Jemez Springs	0.39	0.97	8.0E–0003	–2.02	–0.41	–0.62
Bandon	–0.65	–0.53	0.38	1.00	–0.78	0.55
Hood River	–1.16	–0.20	–0.69	0.92	0.65	–0.18
Cape Blanco	–0.62	–0.52	0.20	0.78	0.01	0.28
Blue Canyon	–0.21	0.23	–1.33	0.08	–0.17	–0.38
Hasayampa	–0.38	0.13	–0.47	–0.52	–0.75	1.54
Three Lynx	–0.94	2.1E–0003	–0.33	0.56	0.69	–0.20
Stroudsburg	–1.06	–0.64	0.22	1.52	1.42	0.25
Bowman Dam	0.11	0.22	–1.31	–0.56	1.01	–0.42
Los Alamos	–0.25	0.60	–0.30	–0.74	–0.31	0.62
Wind River	–1.08	–0.45	0.02	0.60	0.75	–1.13
Lake Spaulding	–0.16	0.55	–0.66	0.08	0.85	–0.80
Tunkhannock	–1.50	–0.41	0.22	1.19	1.48	–0.17
Parkdale	–1.12	–0.02	–0.49	1.11	0.33	–0.92
Sierraville	–0.32	0.68	–0.46	–1.21	0.47	–1.24
Ketchikan	–0.56	0.63	0.92	0.54	–1.10	–1.51
Cheesman Reservoir	–0.81	1.10	0.08	–1.61	0.01	0.24
Red Fleet	0.32	1.00	0.84	–1.92	0.04	0.54
Mt. Pocono	–1.45	–0.10	0.64	0.55	0.42	1.47
Rimrock Lake	–1.15	0.33	–0.84	0.89	0.94	0.34
Lake Maloya	–0.33	0.76	–0.86	–1.71	–0.51	1.16
River Falls	–1.52	–0.75	0.91	0.38	0.88	–0.02
Laurel Mountain	–0.83	0.43	–0.06	–0.11	0.16	0.21
Tierra Amarilla	–0.12	1.19	0.28	–1.91	–0.24	0.14
Dannemora	–1.63	–0.07	–0.32	2.15	0.50	1.54
Estes Park	–0.78	0.83	–0.47	–0.85	0.18	–0.65
Republic	–1.39	0.17	–0.41	0.26	–0.07	–0.23
Donner Lake	–0.65	0.87	–0.24	–0.68	0.49	–2.41
Government Camp	–1.01	0.11	0.44	0.45	0.77	–0.13
Nederland	–0.89	0.80	–0.10	–0.54	0.65	5.4E–0003
Wanakena	–1.50	–2.3E–0003	0.17	1.34	0.31	2.17
Bumping Lake	–0.57	0.64	–0.40	0.18	–0.17	1.39
Allens Park	–0.55	0.47	–0.28	–0.66	0.05	–1.05
Lake Placid	–1.64	–0.22	1.07	1.15	1.88	0.75
Soda Springs	–0.59	1.01	–0.89	–1.14	–0.35	–2.38
Seward	–1.00	0.02	0.91	–0.01	0.47	–2.41
Red River	–0.62	1.01	5.7E–0004	–1.49	0.01	0.08
Wolf Creek	–0.57	0.41	0.22	–1.25	–0.89	1.61
Tahosa Creek	–0.39	0.85	0.28	–1.09	–0.79	0.73
Homer	–0.58	0.48	1.06	0.63	–0.93	–0.76
Alyeska	–0.86	–0.04	0.62	0.59	–0.40	–0.49
Lake Granby	0.25	1.40	0.73	–1.20	–0.02	0.59
Dillon	–0.26	1.20	–0.14	–1.65	0.10	–1.61
Grand Lake	–0.47	0.75	0.13	–1.22	–0.62	0.61
Kenai	–0.79	0.59	0.49	0.57	–1.04	–0.67
Talkeetna	–0.57	0.25	0.91	–0.04	–0.21	–1.06
Eklutna Lake	–0.46	0.40	0.45	–0.17	–0.82	–1.11
Sheep Mountain	–0.28	0.60	–6.4E–0003	0.33	–0.56	–0.18

Table 5. Character-state scores from Correspondence Analysis of samples, excluding inlier and outlier samples.
[Eigenvalues and percent total variance for the axes are as follows: axis 1, 0.126, 50.81 percent; axis 2, 0.047, 19.08 percent; axis 3, 0.021, 8.63 percent; axis 4, 0.011, 4.45 percent; axis 5, 0.009, 3.69 percent]

Character state	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Lobed	-1.41	0.46	-0.19	1.48	1.90
No teeth	1.35	-0.58	0.19	-0.27	-0.83
Teeth regular	-1.39	0.47	0.24	0.28	0.06
Teeth close	-1.32	0.77	0.10	0.23	0.13
Teeth round	-0.18	0.27	-0.52	-1.18	2.26
Teeth acute	-1.85	0.51	0.60	1.48	-1.03
Teeth compound	-2.07	0.93	0.09	0.70	-1.96
Leptophyll 1	2.95	4.30	4.69	-0.16	-1.74
Leptophyll 2	0.92	1.72	-0.72	0.28	0.63
Microphyll 1	0.16	0.45	-1.15	0.20	1.20
Microphyll 2	-0.42	-0.65	-0.75	-0.21	0.54
Microphyll 3	-0.61	-1.87	0.14	-0.30	-0.49
Mesophyll 1	-0.57	-2.79	1.12	-0.85	-1.15
Mesophyll 2	0.01	-3.85	1.09	-1.09	-3.01
Apex emarginate	1.63	-0.69	-2.59	2.08	-1.34
Apex round	0.86	0.44	-0.84	-0.12	-0.10
Apex acute	-0.70	0.19	0.64	0.40	0.59
Apex attenuate	-0.70	-2.75	2.48	-1.48	-0.47
Base cordate	-0.80	0.52	0.15	0.02	-0.60
Base round	0.10	0.23	-0.65	-1.58	-0.33
Base acute	0.94	-1.02	1.35	2.33	1.16
L:W <1:1	-1.52	0.81	0.03	0.49	0.63
L:W 1-2:1	0.02	0.28	-0.58	0.01	-1.01
L:W 2-3:1	0.48	-1.21	0.75	-0.35	0.46
L:W 3-4:1	0.99	-0.23	1.40	-0.55	2.95
L:W >4:1	1.32	1.63	0.71	-1.05	2.62
Shape obovate	1.00	-0.12	0.10	1.43	0.41
Shape elliptic	7.8E-0003	-0.47	0.15	0.29	0.16
Shape ovate	-0.09	0.44	-0.04	-1.64	-0.26

MEAN ANNUAL TEMPERATURE

Axis 1 does not itself represent mean annual temperature. The positioning of the cool megathermal Sonoran desert samples higher on axis 1 than the warm megathermal samples from Panama and Puerto Rico suggests that a vector rep resenting mean annual temperature would be inclined to the left of the positive part of axis 1. When mean annual temperature for the samples is treated as a physiognomic character state, indeed the score for mean annual temperature determines a vector in such a position.

If the sample scores are projected orthogonally to the mean annual temperature vector, the relative positioning of the projected samples approximates mean annual temperature. This positioning could form the basis for moderately accurate estimates of mean annual temperature, but inspection of the positioning indicates that the drier samples generally have lower relative positions than the wetter samples of approximately the same mean annual temperature. Thus, a vector that is a compromise between the orientations of the mean annual temperature vector and axis 1 might rank the samples more accurately.

The vector defined by the percent no teeth character state, in fact, represents such a compromise. When the

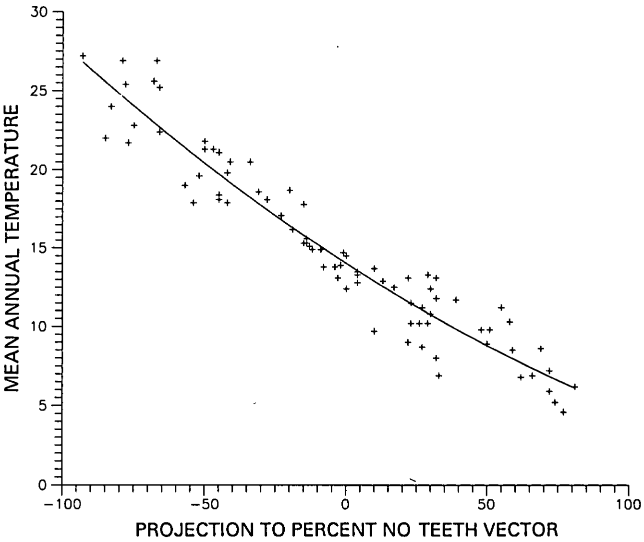

Figure 11. Polynomial regression of mean annual temperature (in °C) for all samples. The plot for each sample (plate 3) is orthogonally projected to the vector derived from the score for percent no teeth. The horizontal axis represents the relative spacing of the projections on this vector. Percent of residuals about mean explained is 93 and residual mean square is 2.36. Standard error for mean annual temperature is 1.2°C (standard deviation=0.95).

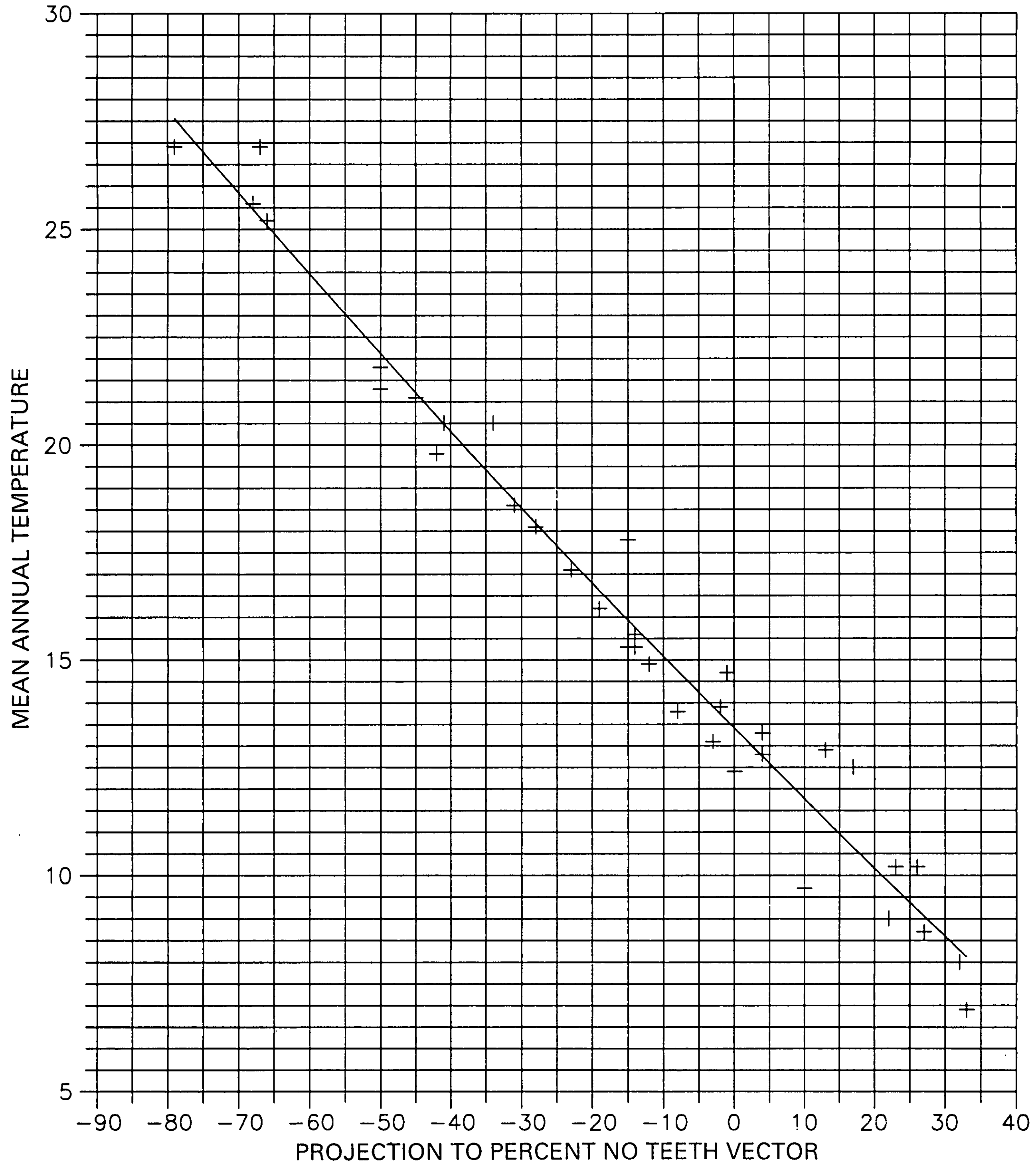

Figure 12. Polynomial regression of mean annual temperature (in °C) for dry samples. These samples plot on plate 3 to the right of the percent no teeth vector. The plot for each sample is orthogon-ally projected to the vector derived from the score for percent no teeth. The horizontal axis represents the relative spacing of the projections on this vector. Percent of residuals about mean explained is 97 and residual mean square is 0.84. Standard error for mean annual temperature is 0.7°C (standard deviation=0.6).

sample scores are projected orthogonally to this vector, the relative ranking of the samples produces rather accurate estimates of mean annual temperature with a linear best-fit and especially with a polynomial best-fit (fig. 11). The numbers on the horizontal (x) axis have only relative meaning and were derived from the scales on plate 4.

If the projected rankings on the percent no teeth vector are divided into two groups, those to the left of the

Table 6. Sample scores from Correspondence Analysis of samples, excluding inlier and outlier samples.
[Eigenvalues and percent total variance for the axes are as follows: axis 1, 0.126, 50.81 percent; axis 2, 0.047, 19.08 percent; axis 3, 0.021, 8.63 percent; axis 4, 0.011, 4.45 percent; axis 5, 0.009, 3.69 percent]

Sample	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Barro Colorado Island	0.70	-3.47	2.76	–0.37	-7.6E–0003
Guanica	1.59	–0.70	-2.36	1.82	-1.97
Cabo Rojo	1.47	–0.32	-1.53	0.70	-1.81
Borinquen	1.43	–0.47	-2.63	0.77	-1.93
Cambalache	1.05	-1.86	0.02	–0.97	-1.50
Susua Alta	1.41	–0.39	-1.48	0.69	-1.47
Guajataca	0.72	-2.32	0.75	-1.66	-1.52
Avon Park	1.02	-1.23	0.40	2.92	0.91
Orlando	0.92	–0.99	0.27	1.58	1.58
Buena Vista	1.25	-1.24	-1.00	1.31	–0.34
Canyon Lake	2.06	1.89	2.70	0.40	–0.99
Maricao	1.04	-1.80	-1.55	-1.34	-2.18
Lake George	0.43	-1.59	0.73	0.04	1.95
Bartlett Reservoir	1.92	1.48	0.96	0.44	-1.83
Castle Creek	1.73	1.39	1.43	–0.04	–0.04
Superior	1.73	1.65	2.08	0.19	0.16
Saguaro Lake	1.65	1.63	1.08	–0.06	–0.85
Roosevelt Lake	1.74	1.63	1.96	0.08	–0.64
Brunswick	0.69	-1.30	0.64	2.02	1.45
Monte Guilarte	0.69	-1.55	–0.26	-2.14	–0.76
Beaufort	–0.11	-1.32	0.64	0.59	0.66
Punkin Center	1.31	1.26	1.15	–0.09	0.85
Yakushima	0.05	-2.34	1.70	-2.18	0.85
Childs	1.17	1.06	1.17	0.13	–0.41
Simmonsville	0.65	–0.99	–0.04	3.29	1.10
Toro Negro	0.53	-1.73	0.20	–0.53	–0.50
Kure Beach	0.46	-1.22	–0.24	1.97	2.18
Santa Rita	0.81	1.00	0.18	-1.33	0.19
Miami	0.95	0.90	–0.31	–0.61	0.56
Camp Pardee	0.58	0.28	-1.01	–0.98	1.54
Auburn	0.34	5.3E–0003	-1.78	-1.06	0.31
Sierra Ancha	0.53	0.41	–0.11	-1.71	0.30
Yava	1.07	1.56	1.00	–0.74	–0.05
Colfax	0.19	–0.30	–0.92	–0.02	1.06
Zozu-san	–0.44	-1.48	0.86	–0.61	–0.25
Jerome	0.70	0.90	–0.03	0.27	0.64
Jasper Ridge	0.15	0.27	-1.37	–0.40	0.83
Natural Bridge	0.07	0.18	–0.29	–0.98	0.51
Lakeport	0.13	0.18	–0.84	–0.62	1.32
Kiyosumi	–0.39	-1.11	1.25	-1.05	0.26

vector and those to the right, the two regression analyses have somewhat different curvatures (figs. 12, 13) and both analyses have better fit statistics than the first, combined analysis. These polynomial regressions produce excellent statistical fits and indicate that mean annual temperature estimates derived from this method have a standard error of less than 1°C and, combined with the standard deviations, produce estimates with an accuracy of 1.7°C.

The polynomial regression for the wetter samples, however, shows that samples from the southeastern North American area of anomalous vegetation (see Wolfe, 1979) tend to have high errors (table 9). The exceptions are samples from less than 1 km from the Atlantic Ocean (Brunswick, Simmonsville, and Kure Beach), where the vegetation is predominantly broad-leaved evergreen. These

Table 7. Results from removal of groups of character states.
[Analyses are based on database of 106 samples]

	Axis 1		Axis 2		
	Eigen-values	Percent variance	Eigen-value	Percent variance	Total variance
All characters	0.106	47.63	0.045	20.31	67.94
Less margin	0.074	38.25	0.043	22.18	60.43
Less size	0.114	58.95	0.024	12.26	71.51
Less apex	0.105	49.07	0.045	21.07	70.14
Less base	0.116	48.56	0.052	21.72	70.28
Less L:W	0.116	49.59	0.049	20.85	70.43
Less shape	0.120	48.10	0.052	20.93	69.03

Table 6. Sample scores from Correspondence Analysis of samples, excluding inlier and outlier samples—Continued.

[Eigenvalues and percent total variance for the axes are as follows: axis 1, 0.126, 50.81 percent; axis 2, 0.047, 19.08 percent; axis 3, 0.021, 8.63 percent; axis 4, 0.011, 4.45 percent; axis 5, 0.009, 3.69 percent]

Sample	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
Canelo	0.52	0.75	0.32	−1.01	0.95
Santa Cruz	−0.20	0.08	−0.83	−1.38	0.48
Nevada City	−0.19	−0.18	−0.65	−0.32	−3.9E−0003
S.I.E.R.C.	−0.99	−0.65	0.65	−0.05	−0.45
Placerville	−0.03	0.19	−1.15	−1.24	1.80
Battle Creek	−1.04	−0.62	0.76	−0.33	0.59
Junipine	−0.47	0.11	0.09	−0.11	0.44
Payson	0.37	0.66	−0.52	−1.12	0.79
Prescott Airport	0.07	0.86	−0.92	0.49	0.09
Crown King	0.02	0.27	−0.71	−0.14	0.51
Half Moon Bay	−0.26	0.35	−0.78	−0.07	0.30
Frederick	−0.93	−0.50	0.53	0.72	−0.26
Kitt Peak	0.31	0.73	−1.39	−1.81	−0.36
Powers	−0.74	0.10	−0.58	−0.21	−0.39
Troutdale	−0.95	9.4E−0003	1.7E−0003	0.12	−0.05
Port Orford	−0.64	−0.20	0.03	−0.78	0.14
Arendtsville	−1.29	0.05	0.27	0.74	−0.69
North Bend	−0.76	−0.25	0.23	−0.26	0.27
Bandon	−0.76	−0.10	0.40	−0.96	−0.63
Hood River	−1.24	0.36	−0.37	0.34	−0.53
Cape Blanco	−0.74	−0.10	0.30	−0.18	−0.53
Blue Canyon	−0.34	0.49	−1.13	−0.05	0.13
Hasayampa	−0.47	0.37	−0.41	−0.62	1.13
Three Lynx	−1.02	0.45	−0.11	0.48	−0.31
Stroudsburg	−1.18	−0.05	0.50	0.80	−1.54
Bowman Dam	−0.06	0.40	−1.10	1.16	0.40
Los Alamos	−0.31	0.51	−0.44	−0.11	0.91
Wind River	−1.18	0.04	0.19	0.49	−0.54
Lake Spaulding	−0.28	0.80	−0.44	0.80	−0.04
Tunkhannock	−1.57	0.22	0.51	0.94	−1.00
Parkdale	−1.19	0.50	−0.24	0.02	−0.85
Sierraville	−0.39	0.82	−0.39	0.72	1.21
Mt. Pocono	−1.48	0.42	0.78	0.11	−0.07
Rimrock Lake	−1.22	0.82	−0.54	0.65	−0.84
Lake Maloya	−0.39	0.89	−0.77	−0.07	2.59
River Falls	−1.58	−0.18	1.05	0.49	−0.08
Dannemora	−1.67	0.64	0.04	−0.08	−1.53
Republic	−1.43	0.65	−0.20	−0.21	0.21
Wanakena	−1.53	0.58	0.38	−0.07	−0.93
Lake Placid	−1.67	0.40	1.29	1.22	−1.10

Table 8. Meteorological parameter scores from Correspondence Analysis.

Parameter	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Percent variance 1	Percent variance 2
None						50.94	18.99
Temperature							
Annual	1.08	−0.77	0.19	0.12	0.57	51.66	18.82
Warm month	0.98	−0.68	0.19	0.07	−0.51	51.45	18.92
Cold month	0.83	−0.77	−0.19	−0.17	−0.57	51.64	18.87
Precipitation							
Annual	−0.15	−2.09	0.34	−0.33	−0.60	50.06	19.64
Growing season	0.82	−3.67	1.11	−1.00	−0.94	49.58	20.75
Monthly growing season	0.18	−2.88	1.10	−0.59	−0.76	50.03	20.14
Three consecutive driest months	−0.77	−2.91	2.23	0.27	−1.87	48.73	20.44
Driest month	−0.72	−3.28	2.93	0.57	1.69	50.10	19.39

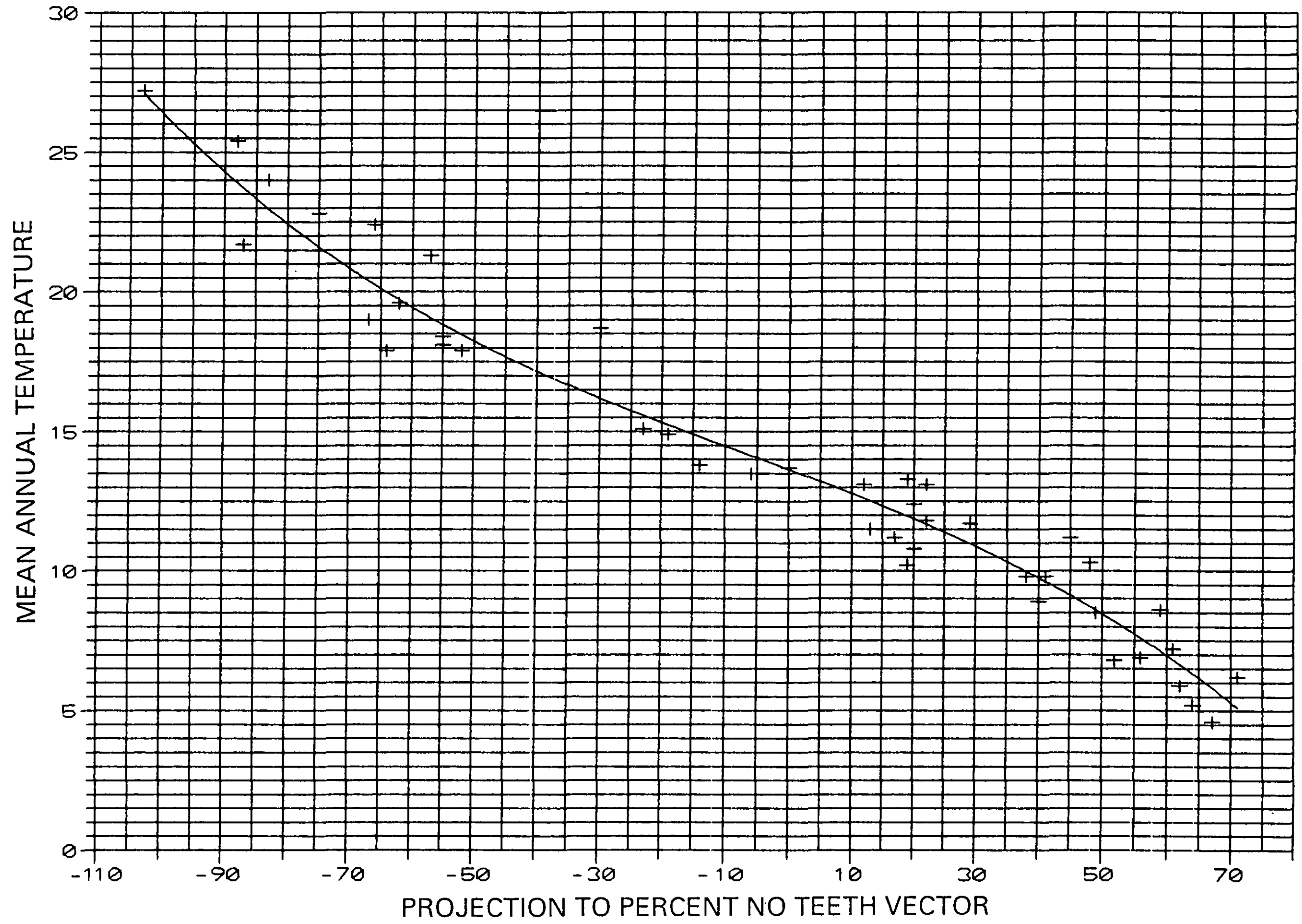

Figure 13. Polynomial regression of mean annual temperature (in °C) for wet samples. These samples mostly plot on plate 3 to the left of the percent no teeth vector. The plot for each sample is orthogonally projected to the vector derived from the score for percent no teeth. The horizontal axis represents the relative spacing of the projections on this vector. Percent of residuals about mean explained is 96 and residual mean square is 1.44. Standard error for mean annual temperature is 1.0°C (standard deviation=0.7).

coastal samples are concordant with the three Japanese samples from mesothermal, broad-leaved evergreen vegetation. A polynomial regression that excludes the four interior samples is shown in figure 14.

The samples from east-central Pennsylvania, New York, and Wisconsin plot consistently with samples of similar mean annual temperature from the Pacific Northwest. The eastern samples all come from areas in which the cold-month mean temperature is less than –2°C, and thus large-leaved, broad-leaved evergreens would be excluded, as in eastern Asia (Wolfe, 1979). That is, the vegetation is consistent with vegetation in other areas of similar major temperature parameters and is broad-leaved deciduous and (or) coniferous.

COLD-MONTH MEAN TEMPERATURE

Either cold-month mean temperature or warm-month mean temperature could be analyzed; at a given mean annual temperature, cold-month and warm-month mean temperatures must be approximately the same value of departure but in opposite directions from mean annual temperature. Although orthogonally projecting sample scores to the mean cold-month vector shows that a general relation exists between sample positions and the cold-month mean temperature (fig. 15), the standard error is greater than 3°C. Inspection of the relative ranking of the samples on the vector indicates that the driest samples, the wettest samples, and the intermediate samples might form different groups that would produce a smaller standard error. Subjecting each group separately to a polynomial regression analysis indeed reduces the standard error to 1.5°C for the dry samples, 1.7°C for the mesic samples, and 2°C for the humid samples (figs. 16–19).

Most microthermal samples in the mesic sample set represent coniferous forests, and all microthermal samples in the humid sample set represent broad-leaved forests. I suggest that, in fact, the broad-leaved microthermal samples in the mesic sample set would be better placed in the humid sample set, and coniferous-forest samples should be analyzed only in

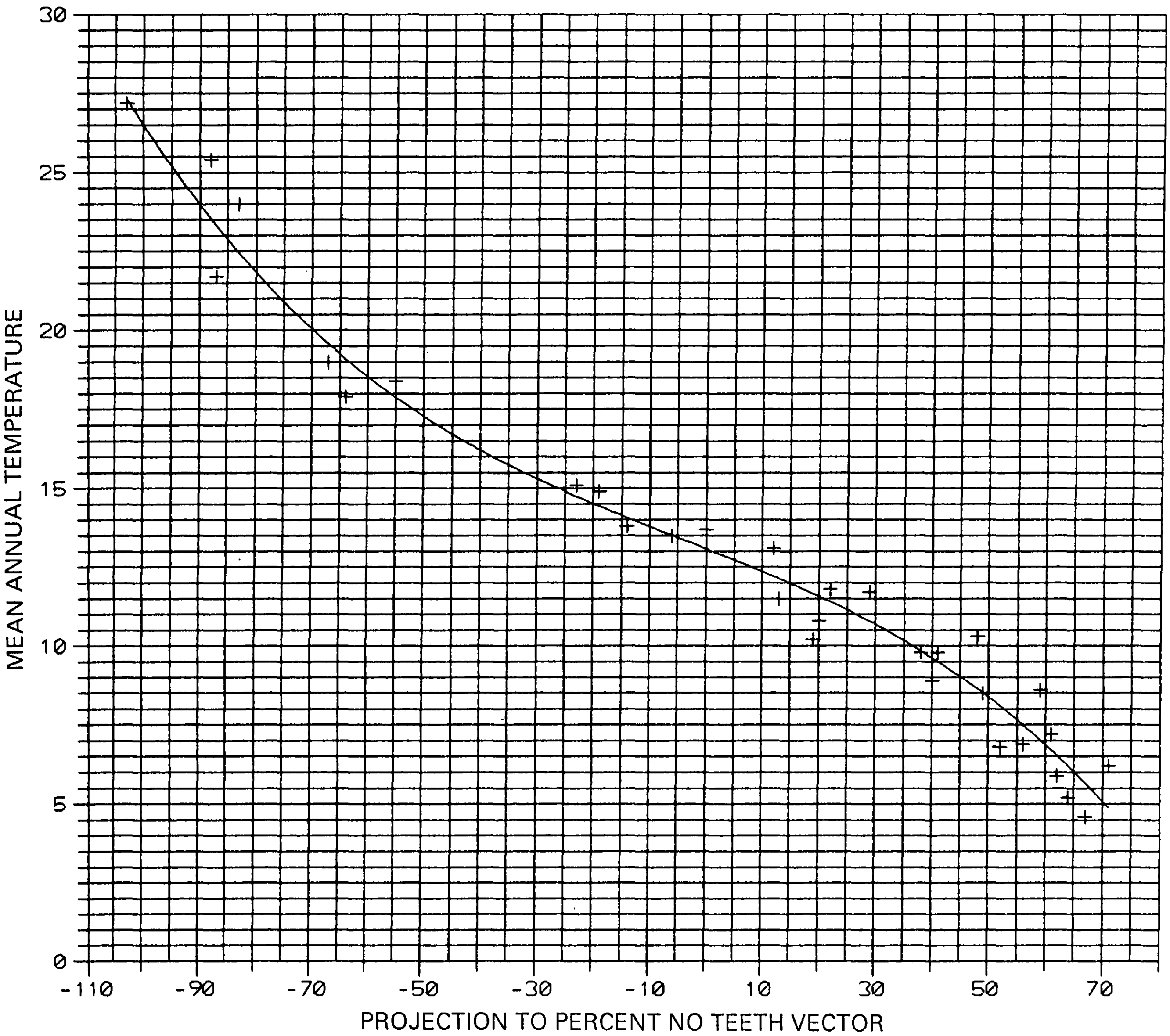

Figure 14. Polynomial regression of mean annual temperature (in °C) for wet samples excluding some from the Eastern United States. The samples excluded are from the anomalously deciduous vegetation of the southeastern United States and the Middle Atlantic states. The plot for each sample is orthogonally projected to the vector derived from the score for percent no teeth. The horizontal axis represents the relative spacing of the projections on this vector. Percent of residuals about mean explained is 98 and residual mean square is 0.88. Standard error for mean annual temperature is 0.8°C (standard deviation=0.5).

the mesic data set. More samples, especially from the very humid coniferous forests of eastern Asia, would clarify this suggested relation.

Mean annual range of temperature does not produce a statistically significant ranking of the samples. However, if both mean annual and mean cold-month temperatures can be estimated from CLAMP, then a simple arithmetic calculation can produce an estimate of both mean warm-month temperature and mean annual range of temperature because the mean of the warm-month departs from mean annual temperature by approximately the same numerical value as does the mean of the cold month. Thus, a sample from which mean annual temperature is estimated at 10°C and the cold-month mean is estimated at 2°C will have come from an area where the warm-month mean temperature is approximately 18°C and mean annual range of temperature is approximately 16°C.

MEAN ANNUAL PRECIPITATION

The score for mean annual precipitation is strongly negative on axis 2. Because the vector defined by the

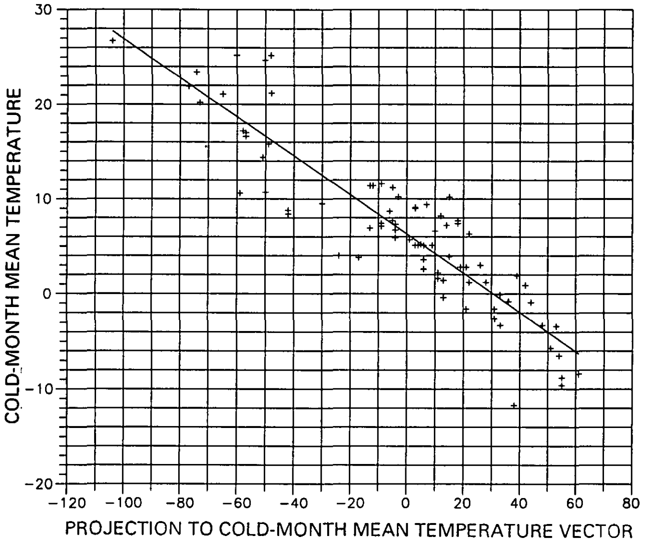

Figure 15. Relation of sample plots to cold-month mean temperature (in °C) for all samples. The plot for each sample is orthogonally projected to the vector derived from the score for mean temperature of the cold month. The horizontal axis represents the relative spacing of the projections on this vector. Some relation is apparent, but the accuracy is low; dividing the samples into three groups (fig. 16) produces more accurate results (figs. 17–19).

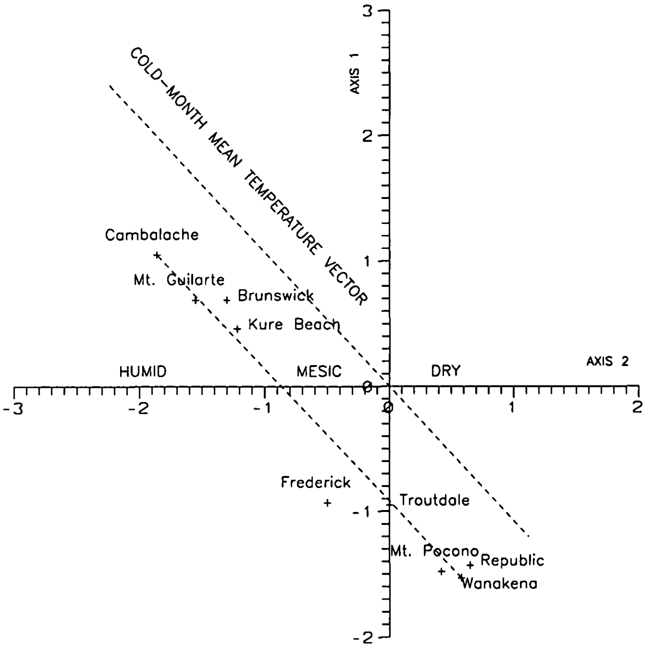

Figure 16. Division of samples into three groups for purposes of analysis of cold-month mean temperature. Dry sample set plots to the right of the percent no teeth vector. Humid sample set plots to the left of a line parallel with and left of the percent no teeth vector. Mesic sample set plots between these other two sample sets.

Table 9. Errors in estimates of mean annual temperature (MAT) for some samples from the Eastern United States.
[Samples are arranged from north to south. MAT values in °C]

Sample	MAT actual	MAT CLAMP	MAT error	Geographic position
Arendtsville	11.2	9.1	2.1	Interior
Frederick	12.4	11.9	0.5	Interior
S.I.E.R.C.	13.3	12.0	1.3	Interior
Battle Creek	13.1	11.7	1.4	Near coastal
Kure Beach	17.9	18.5	0.6	Coastal
Simmonsville	18.1	18.8	0.7	Coastal
Beaufort	18.7	16.2	2.5	Interior (part)
Brunswick	19.6	19.7	0.1	Coastal
Lake George	21.3	19.0	2.3	Interior
Orlando	22.4	20.2	2.2	Interior
Avon Park	22.8	21.5	1.3	Interior

score for mean annual precipitation is virtually coincidental with axis 2, the sample scores on axis 2 can be used for ranking. The relative ranking generally approximates precipitation but with a high standard error (fig. 20). The scatter of the samples is moderate for megathermal samples but particularly high for microthermal samples. In microthermal environments in which the length of the growing season is a major variable, mean annual precipitation is not particularly significant to the vegetation. That is, abundant precipitation that occurs outside the growing season should be generally irrelevant to plants that are not growing when the precipitation occurs.

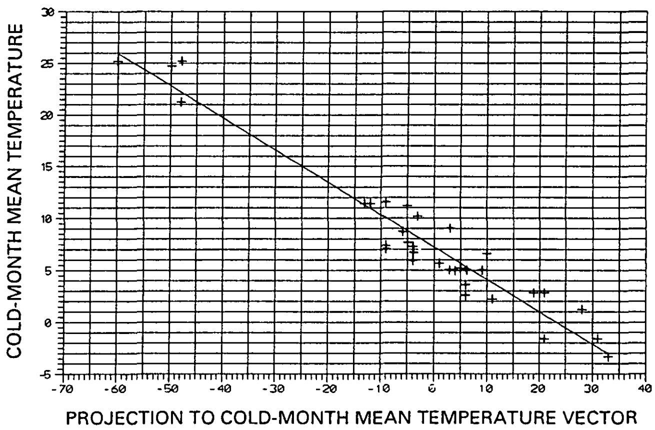

Figure 17. Polynomial regression of cold-month mean temperature (in °C) for dry samples. The plot for each sample is orthogonally projected to the vector derived from the score for mean temperature of the cold month. The horizontal axis represents the relative spacing of the projections on this vector. Percent of residuals about mean explained is 93, and residual mean square is 3.17. Standard error of cold-month mean temperature is 1.5°C (standard deviation=0.9).

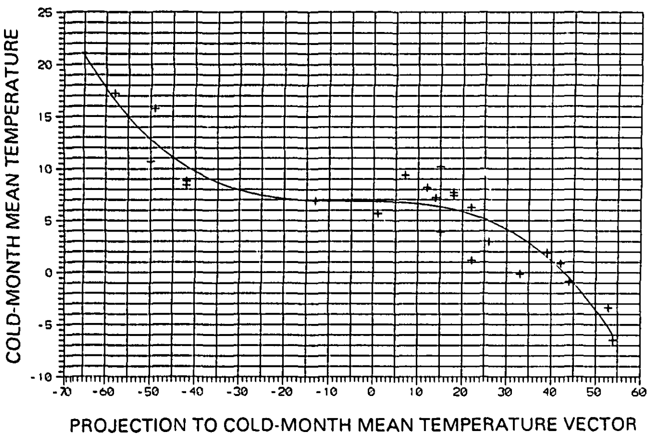

Figure 18. Polynomial regression of cold-month mean temperature (in °C) for mesic samples. The plot for each sample is orthogonally projected to the vector derived from the score for mean temperature of the cold month. The horizontal axis represents the relative spacing of the projections on this vector. Percent of residuals about mean explained is 89, and residual mean square is 4.14. Standard error of cold-month mean temperature is 1.6°C (standard deviation=1.3).

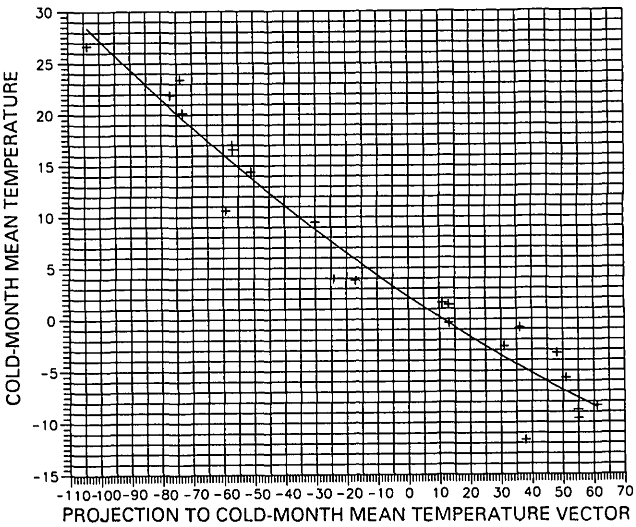

Figure 19. Polynomial regression of cold-month mean temperature (in °C) for humid samples. The plot for each sample is orthogonally projected to the vector derived from the score for mean temperature of the cold month. The horizontal axis represents the relative spacing of the projections on this vector. Percent of residuals about mean explained is 95, and residual mean square is 6.84. Standard error of cold-month mean temperature is 2.0°C (standard deviation=1.7).

Among megathermal samples included are two samples (Buena Vista and Susua Alta) that represent serpentine soil, a type of soil that is generally deficient in nutrients. In both instances, but particularly in the instance of Buena Vista, the foliar physiognomy is that of a much drier climate. The overall physiognomy (small and scattered rather than closed-canopy trees) is similarly more indicative of a drier environment than of one of 267-cm mean annual precipitation. A similar, but less pronounced, relation exists for samples from coastal areas that have very sandy soil (especially Kure Beach and Simmonsville).

MEAN GROWING SEASON PRECIPITATION

As defined here, the growing season comprises those months in which the monthly mean temperature is 10°C or above. This value was selected because a warm-month mean of approximately 10°C delineates forested from treeless, tundra or tundralike vegetation (Wolfe, 1979); that is, a mean warm-month temperature of at least 10°C is necessary to promote the growth of trees.

In climates of high winter warmth where most plants do not enter dormancy, the growing season precipitation is, of course, the same as mean annual precipitation. The score of mean growing season precipitation is by far the highest of any of the precipitation parameters. Ranking of the samples, when orthogonally projected to the vector defined by the score for mean growing season precipitation, shows some relation to this parameter when plotted against mean growing season precipitation (fig. 21). The rankings can be allocated to two subsets: megathermal and mesothermal samples that generally have positive scores on axis 1 and microthermal samples that generally have negative scores on axis 1.

The megathermal-mesothermal plot against mean growing season precipitation (fig. 22) has considerable scatter for samples from sites that have more than 145 cm of growing season precipitation. For the samples from sites that have less than 145 cm of growing season precipitation, however, this parameter can be estimated to an accuracy of about 12 cm. This suggests that megathermal or mesothermal areas that receive at least 140–150 cm of precipitation during the growing season will produce leaf physiognomy that indicates little or no water stress. Increases in precipitation above that amount will not be mirrored in leaf physiognomy; that is, 140–150 cm of precipitation is sufficient to meet the photosynthetic and transpirational needs of the plants. Decreases in precipitation below that amount, however, show marked and gradational effects in water stress.

Surprisingly, microthermal leaf physiognomy shows no marked response to varying amounts of growing season precipitation (fig. 23). The samples that represent the broad-leaved deciduous forests of northeastern and north-central United States, which receive abundant growing season precipitation, plot on plate 3 to the left of samples from areas of lesser summer rainfall, but this relation is not marked and is only evident in a general manner in figure 23.

The lack of an apparently marked response to growing season precipitation in microthermal environments may relate to the warm-month mean temperatures of the samples analyzed. The Pacific Northwest samples that plot close to the northeastern United States samples are all from areas in which the warm-month mean temperature is generally 16°C–19°C, whereas the Middle Atlantic and northeastern samples are mostly from areas in which the warm-month mean temperature is generally greater than 20°C. Thus, the lower summer temperatures in the Northwest could at least partially compensate for the lesser summer rainfall by reducing water stress. However, the Republic, Wash., sample (July mean temperature of 17.4°C) plots close to the Wanakena, N.Y., sample (July mean temperature of 18.4°C) and to the Lake Placid, N.Y., sample (July mean temperature 17.8°C).

Growing season precipitation can also be evaluated by mean monthly precipitation. Although considerable scatter is present in figure 24, a general relation is apparent. This relation is again mostly in the megathermal and mesothermal subset (fig. 25) rather than in the microthermal subset (fig. 26). Megathermal and mesothermal samples segregate into two groups: a wet group, in which mean monthly growing season precipitation is at least 10 cm, and a dry group, in which mean monthly growing season precipitation is from 3 to 6 cm.

SEASONAL DROUGHT

One measure of drought during the growing season is to consider the mean precipitation of the consecutive three driest months. This parameter has a reasonably high score on axis 2. Projecting the sample score of the vector defined by the score for mean precipitation of the three driest months does not appear to produce a significant relative ranking of the samples (fig. 27). However, if megathermal and mesothermal samples are considered alone, all samples from areas in which the three driest months have precipitation that totals less than 6 cm plot to the right in figure 28.

The megathermal and mesothermal samples that plot to the right in figure 28 include ones from areas in which the three driest months coincide with the three warmest months (that is, areas of summer drought such as California) and areas in which the three driest months are early in the growing season and the warmest months receive at least moderate rainfall (areas such as Arizona that receive at least moderate rain in July and August). The timing of the drought period relative to the warmest months does not appear to be significant.

In microthermal samples, the signal of seasonal drought is not apparent. The California samples and most Pacific Northwest samples have marked summer drought but project to the same position on the mean three driest months precipitation vector as samples from the northeastern United States where the growing season has no drought (fig. 29).

FACTORS THAT MIGHT INFLUENCE CLAMP SCORES

FLUVIATILE ELEMENT

The major factor in introducing error into the estimates for the various precipitation parameters probably is the relative proportions of fluviatile species in the various samples. This is particularly valid relative to samples from areas of some drought during the growing season. Examination of the axis 2 scores for the California mesothermal samples, for example, indicates that the samples that have the higher percentages of fluviatile species tend to have the lower (wetter) axis 2 scores (table 10). A similar relation between percentages of fluviatile species and axis 2 scores also is apparent for Arizona mesothermal vegetation (table 11).

Microthermal samples from California and the Southern Rocky Mountains, however, display no apparent relation between percentages of fluviatile species and axis 2 scores (tables 12, 13). In the microthermal vegetation sampled, many taxa that in warmer vegetation are restricted to streamside habitats typically also occur in the slope forests; species of *Populus*, *Salix*, and *Betula* are notable examples. Far less floristic and physiognomic differentiation occurs between fluviatile and slope vegetation in moist to slightly subhumid microthermal vegetation than in subhumid mesothermal vegetation.

Although relative representation of the fluviatile element in a given sample introduces error into estimates of precipitation parameters, no significant error appears to be introduced into estimates of thermal parameters. This point is well illustrated by the Kitt Peak sample, which was collected from a mountain top that has no streams, either perennial or ephemeral. The Kitt Peak sample plots drier than expected from the moderately high growing season precipitation, but the estimates of mean annual temperature and cold-month mean temperature have only small errors. That relative representation of the fluvial element has no significant effect on thermal estimates should be expected: plants living along margins of streams are adapted to the same temperatures as plants living on adjacent lower slopes.

SAMPLE SIZE

The samples included in the CLAMP database range in size from 20 to 139 species; the median is 28 species. The error of estimate of mean annual temperature is not

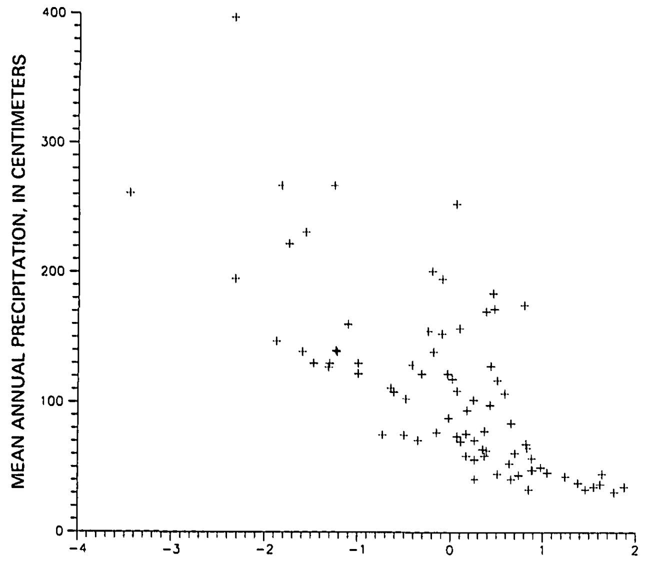

Figure 20. Relation of sample plots to mean annual precipitation. Because the vector derived from the score for mean annual precipitation is almost coincidental with axis 2, the samples are plotted according to their axis 2 scores. Only a very general relation is apparent between mean annual precipitation and the sample scores.

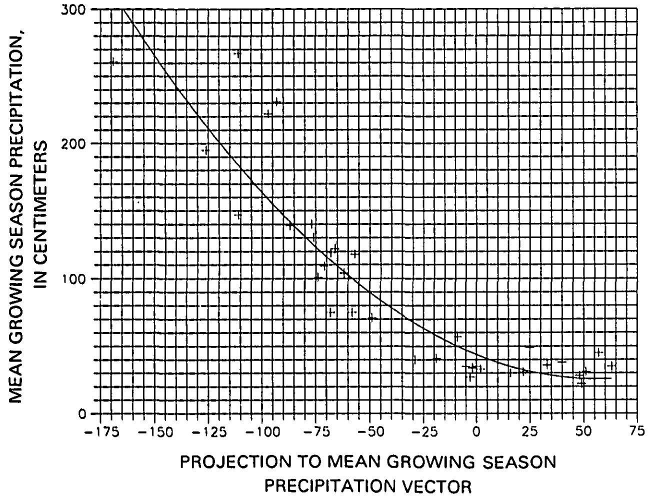

Figure 21. Relation of sample plots to mean growing season precipitation. The plot for each sample is orthogonally projected to the vector derived from the score for mean growing season precipitation. The growing season is defined as all months that have a mean temperature of at least 10°C. A general relation is apparent between mean growing season precipitation and the sample scores. Percent of residuals about mean explained is 85, and residual mean square is 482.

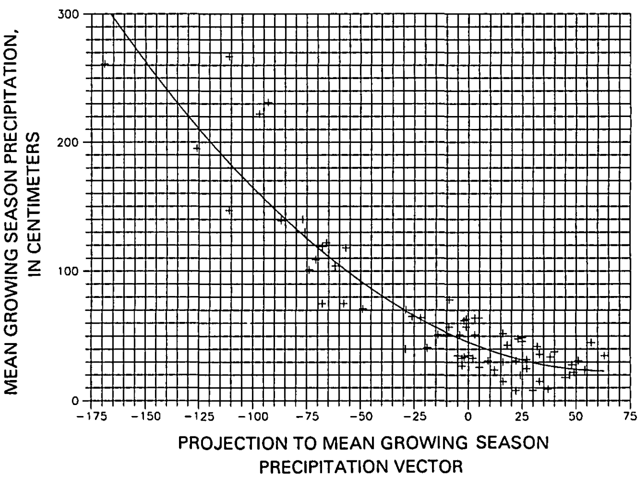

Figure 22. Polynomial regression of mean growing season precipitation for megathermal and mesothermal samples. Samples from soils derived from serpentine are omitted. The plot for each sample is orthogonally projected to the vector derived from the score for mean growing season precipitation. The growing season is defined as all months that have a mean temperature of at least 10°C. Percent of residuals about mean explained is 84, and residual mean square is 778. The samples that plot above 80 on the horizontal axis have mean growing season precipitation less than 145 cm and show less scatter than the samples that plot below 80, which all have mean growing season precipitation of more than 145 cm. For the samples that plot above 80, the standard error for mean growing season precipitation is 12 cm (standard deviation=8).

significantly greater for samples containing 20–24 species than for samples containing more than 24 species (table 14). Thus, application of CLAMP to fossil samples of at least 20 species should yield estimates of mean annual temperature that have standard errors of approximately 0.7°C–1.0°C.

What is the accuracy for mean annual temperature estimates of samples of less than 20 species? To answer this question, I took all samples of at least 30 species and reduced the sample size to 15 and to 10 species. This reduction was made by tabulating character states for (1) every other species until a total of 15 species was tabulated and (2) for every third species until a total of 10 species

Table 10. Comparison of percent fluviatile element and axis 2 score for mesothermal samples from California.

Sample	Percent fluviatile	Axis 2 score
Lake Cachuma	3	1.01
Santa Cruz	20	0.08
Half Moon Bay	20	0.35
Camp Pardee	22	0.28
Jasper Ridge	22	0.27
Placerville	29	0.19
Auburn	31	5.3E–0003
Colfax	37	–0.30
Nevada City	38	–0.18

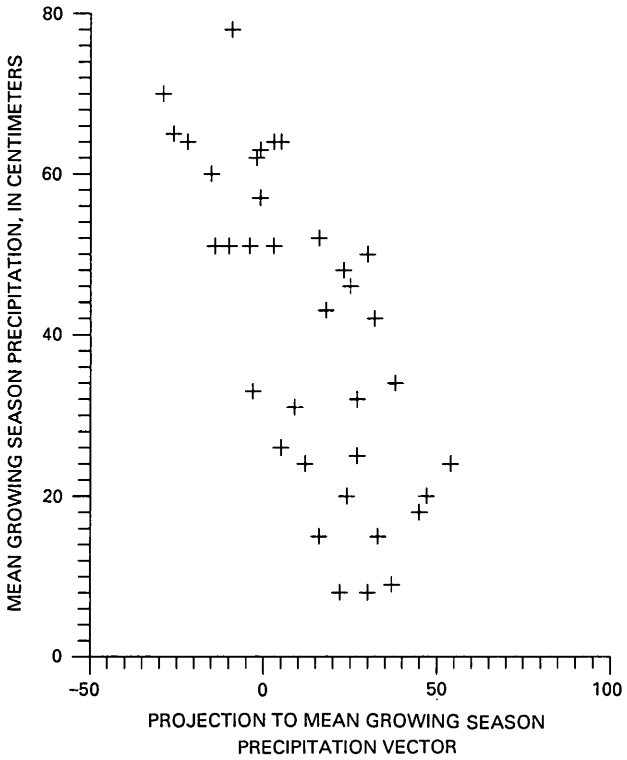

Figure 23. Relation of microthermal sample plots to mean growing season precipitation. The plot for each sample is orthogonally projected to the vector derived from the score for mean growing season precipitation. Only a very general relation is apparent to mean growing season precipitation.

was tabulated; the 10-species sample thus shares only half its species with the 15-species sample. For the samples in this analysis, the full sample size of at least 30 species yields an accuracy of mean annual temperature estimate of 0.9°C (s.d.=0.7°C), with departures from meteorological data of 2.4°C, 2.1°C, and 1.4°C; the samples analyzed include most of the anomalous vegetation of eastern North America that tend to have the highest errors. The analysis of the reduced sample size indicates that for samples of 15 species, mean annual temperature is accurate to about 1.6°C (s.d.=1.1°C), with departures from meteorological data of 3.5°C, 3.4°C, and 3.2°C. For samples of 10 species, the level of accuracy is about 2.2°C (s.d.=1.3°C), with departures of 5.5°C, 4.1°C, and 3.8°C. Thus, as sample size is reduced below 20 species, accuracy is also reduced.

Relative to precipitation estimates, sample size is even more critical, as might be expected from the lower amount of physiognomic variation explained on axis 2. The samples that yield the least accurate estimates of precipitation parameters are generally those of less than 25 species. Particularly notable are the samples from Nevada City and Lake Maloya, although the samples from Miami, Lakeport, River Falls, Saguaro Lake, and Bartlett Reservoir provide as accurate estimates as samples of 30 or

Table 11. Comparison of percent fluviatile element and axis 2 score for mesothermal samples from Arizona.

Sample	Percent fluviatile	Axis 2 score
Yava	25	1.56
Prescott Airport	27	0.86
Childs	29	1.06
Miami	29	0.90
Santa Rita	29	1.00
Payson	29	0.66
Sierra Ancha	30	0.41
Jerome	31	0.90
Canelo	32	0.75
Crown King	36	0.27
Junipine	37	0.11
Natural Bridge	39	0.18

Table 12. Comparison of percent fluviatile element and axis 2 score for microthermal samples from California.

Sample	Percent fluviatile	Axis 2 score
Sierraville	40	0.82
Blue Canyon	35	0.49
Bowman Dam	29	0.40
Lake Spaulding	19	0.80

Table 13. Comparison of percent fluviatile element and axis 2 score for microthermal samples from the Southern Rocky Mountains.

Sample	Percent fluviatile	Axis 2 score
Cheesman	48	1.10
Los Alamos	46	0.60
Hasayampa	44	0.13
Nederland	42	0.80
Lake Maloya	42	0.76
Estes Park	33	0.83

Table 14. Comparison of errors of mean annual temperature estimates relative to sample size for samples that have 20 or more species.

Number of species	Number of samples	Standard error	Cumulative error
20	2	1.0	1.0
21	3	0.4	0.7
22	2	0.8	0.7
23	3	0.5	0.7
24	5	0.6	0.6
25	5	0.7	0.6
26	4	0.6	0.6
27	7	0.6	0.6
28	24	0.8	0.7

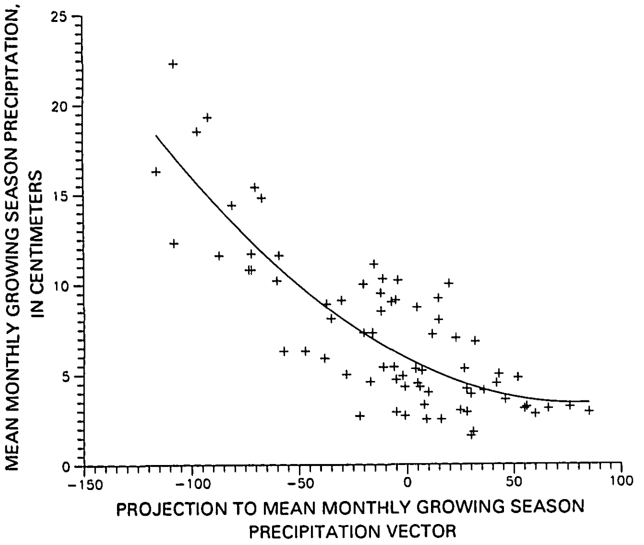

Figure 24. Relation of sample plots to mean monthly growing season precipitation. The plot for each sample is orthogonally projected to the vector derived from the score for mean monthly growing season precipitation. The growing season is defined as all months that have a mean temperature of at least 10°C. A general elation is apparent to mean monthly growing season precipitation.

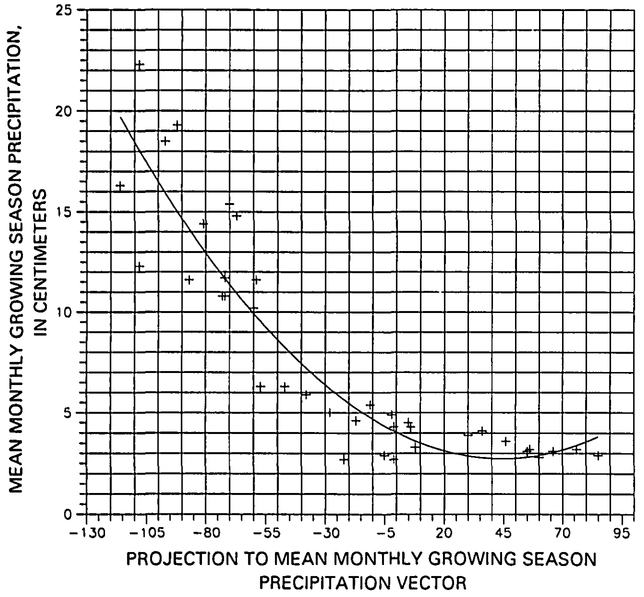

Figure 25. Polynomial regression of mean monthly growing season precipitation for megathermal and mesothermal samples. Samples from soils derived from serpentine are omitted. The plot for each sample is orthogonally projected to the vector derived from the score for mean monthly growing season precipitation. The growing season is defined as all months that have a mean temperature of at least 10°C. Percent of residuals about mean explained is 83, and residual mean square is 5.17. The samples that plot above 120 on the horizontal axis have mean monthly growing season precipitation between 3 and 6 cm; the samples that plot below 120 have mean monthly growing season precipitation of at least 10 cm.

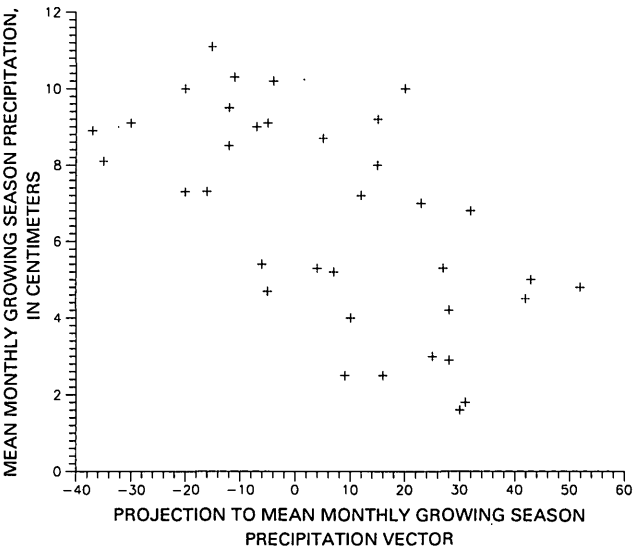

Figure 26. Relation of microthermal sample plots to mean monthly growing season precipitation. The plot for each sample is orthogonally projected to the vector derived from the score for mean monthly growing season precipitation. The growing season is defined as all months that have a mean temperature of at least 10°C. Only a very general relation is apparent.

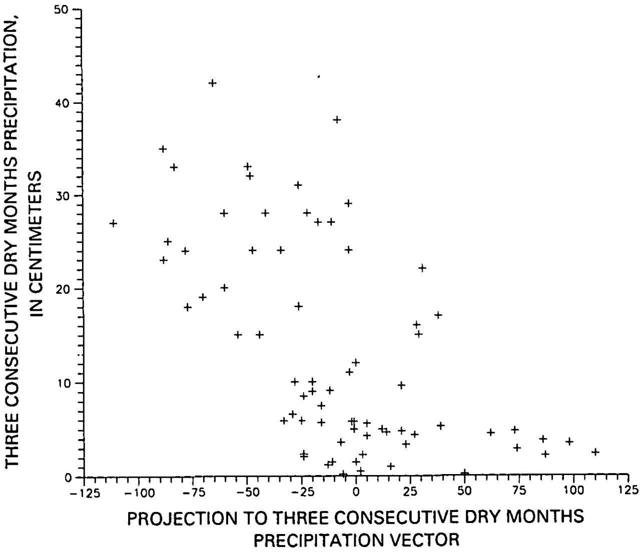

Figure 27. Relation of sample plots to seasonal drought. Seasonal drought is measured by the total precipitation of the consecutive three driest months during the growing season. The plot for each sample is orthogonally projected to the vector derived from the score for three consecutive dry months. The growing season is defined as all months that have a mean temperature of at least 10°C. Only a very general relation is apparent.

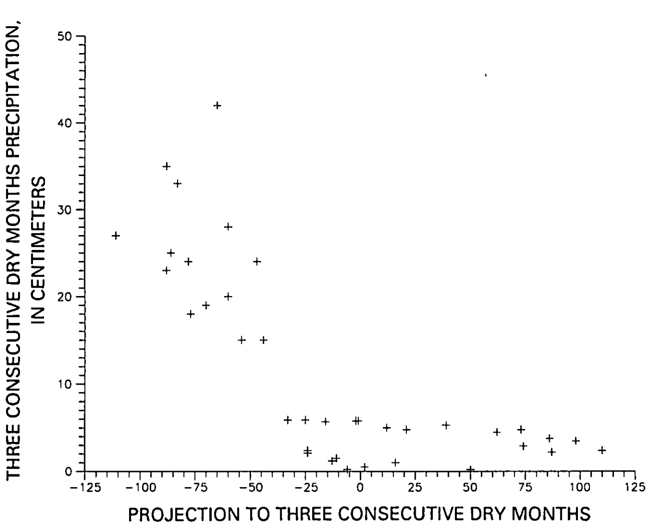

Figure 28. Relation of megathermal and mesothermal sample plots to seasonal drought. Samples from soils derived from serpentine are omitted. Seasonal drought is measured by the total precipitation of the consecutive three driest months during the growing season. The plot for each sample is orthogonally projected to the vector derived from the score for three consecutive dry months. The growing season is defined as all months that have a mean temperature of at least 10°C. Samples that plot above 120 on the horizontal axis have total precipitation during the three consecutive driest months of the growing season of less than 6 cm; samples that plot below 120 have total precipitation during the three consecutive driest months of the growing season of at least 15 cm.

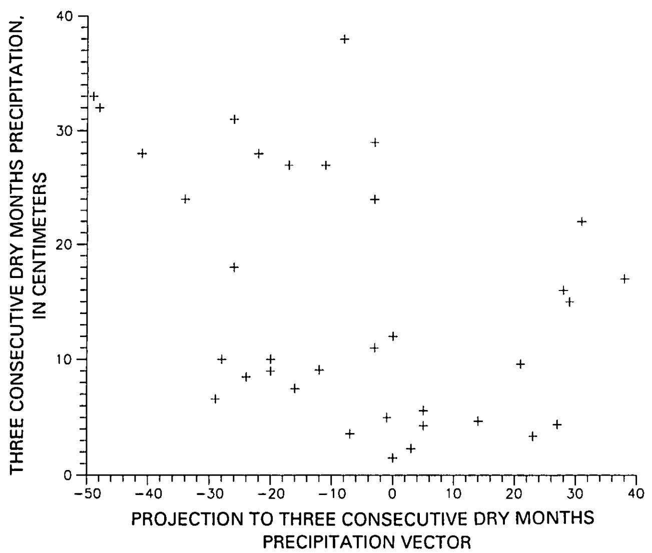

Figure 29. Relation of microthermal sample plots to seasonal drought. Seasonal drought is measured by the total precipitation of the consecutive three driest months during the growing season. The plot for each sample is orthogonally projected to the vector derived from the score for three consecutive dry months. The growing season is defined as all months that have a mean temperature of at least 10°C. Little relation is apparent.

more species. The sample scores of the samples of arbitrarily reduced size just discussed, however, typically greatly enlarge the errors of estimates of precipitation parameters. Except for general inferences (for example, subhumid versus mesic or humid), most small (<25 species and especially <20 species) samples yield inaccurate precipitation estimates.

SUCCESSIONAL STAGE

Does the foliar physiognomy of different successional stages differ markedly from one another? To be sure, the earliest successional stage will not have species that typically prefer understory conditions. Leaves of shady environments will be absent in an extensive area that has been subjected to, for example, fire. In such an area, the leaves will be exposed to full sun and would thus be under the same selective pressures as canopy leaves in "climax" vegetation. If the "climax" vegetation is open-canopy, no difference should be apparent between successional and "climax" samples. However, if the "climax" vegetation is closed-canopy forest, some differences might appear. Mitigating such possible differences is that closed-canopy forest grows in areas of moderate to high rainfall, a climatic regime that would not favor extensive forest fires; a sample from a partially burned area would probably include leaves from both successional and "climax" vegetation. Also emphasized here is that the validity of "climax" vegetation is a widely debated issue in plant ecology, although some form of approximate equilibrium with respect to environment must be achieved.

The various samples collected for the CLAMP database include, as noted in the descriptions of the collection sites, vegetation in varying degrees of disturbance. Most samples, moreover, include some species that, although uncommon in the vegetation of the area sampled, may be important successional species. That certain climatic parameters can be estimated with moderate to high accuracy from these samples strongly indicates that successional stage has a minimal influence on foliar physiognomy.

LIGHT REGIME

The abundance of large leaves in fossil-leaf assemblages from arctic and subarctic regions has been commented on previously (for example, Wolfe, 1985). This abundance has generally been attributed to the low angle of incidence of sunlight. R.A. Spicer (oral commun., 1983) also noted that the variation in leaf size for a given species in arctic leaf assemblages tends to be highly variable, perhaps the result of variation in positioning to the sun on the plant. A leaf of a high-latitude woody plant is exposed to almost the same angle of sunlight throughout the growing season, and shading (or lack thereof) by other leaves could cause significant differences in leaf sizes on the same plant.

Table 15. Variation in, and occurrence of, large leaf sizes in samples from Alaska.

[Samples are arranged from highest to lowest latitude. Variation is measured by the percent of species that fall into four or more size classes. Columns designated "1" are the percent of species that have some leaves in the size class and columns designated "2" are the tabulated percent scores for the size class]

Sample	Variation	Microphyll 3		Mesophyll 1 and 2	
		1	2	1	2
Talkeetna	36	43	14	29	14
Sheep Mountain	46	38	12	17	7
Elkutna Lake	53	50	15	30	11
Alyeska	48	62	19	48	14
Kenai	36	64	18	36	11
Seward	36	64	20	36	18
Homer	42	42	12	29	13
Ketchikan	40	40	11	28	15

The Alaskan CLAMP samples strongly support the concept that subarctic vegetation can have an abundance of large leaf sizes (table 15). Equally strongly supported is the high variability of leaf size in a given species. This variability is in species that fall into the leptophyll sizes as well as the species that fall into the mesophyll sizes. None of the CLAMP samples from lower latitudes shows such a consistently high degree of variability in size.

When the Alaskan CLAMP samples are compared to samples of comparable temperature and (or) precipitation regimes from lower latitudes, the differences in leaf-size variability and in percent of large-leaved species are apparent (table 16). Although decrease in the percent large leaves in samples such as Bumping Lake and Soda Springs might be attributed to the summer drought that occurs in these lower latitude sites, this cannot explain the lower leaf sizes for the collections from Allens Park, Tahosa Creek, and other samples from the Southern Rocky Mountains. Although the typically three-month growing season has low precipitation in June, the still-melting snowpack provides abundant soil moisture and July and August are characterized by abundant rainfall.

Comparison of samples from the Pacific Northwest (lat 45° N., or higher) with samples from farther south (lat 38° N. or lower) shows no significant difference in variability of leaf size (table 17). This comparison, however, does indicate that the percentages of species that have large leaf sizes are higher in the northern samples than in the southern samples. This point is emphasized by the comparison of the Pacific Northwest samples, which are from areas of marked summer drought, with the samples from Arizona, Colorado, and New Mexico, which are from areas of at least moderate rainfall that occurs from July through early September.

Despite the greater leaf size in samples from high latitudes in comparison to samples from mid-latitude, high-altitude environments, all these samples still plot in the subalpine nest; other aspects of leaf physiognomy must compensate in the analysis for the increased leaf size in some species. Part of this compensation may be the moderately high incidence in the Alaskan CLAMP samples of leptophyll species. These species, which are typically evergreen and low growing (about 10 cm high or less), persist through the winter under a cover of snow. Although some of these species (or physiognomically similar taxa) are present in mid-latitude, high-altitude environments, these species tend to be much less common and thus less frequently encountered in the lower latitude samples than in the higher latitude samples.

The larger leaf size in the Pacific Northwest samples relative to lower latitude samples may, however, result in the divergent plots of these sample sets on plates 2 and 3. That is, the overall larger size in the Pacific Northwest samples of especially the microphyll 3 category results in more strongly negative scores on axis 1 than the lower latitude microthermal samples.

BROAD-LEAVED EVERGREENS

The occurrence of broad-leaved evergreens of microphyll 2 or larger size is also a phenomenon that is

Table 16. Comparison of leaf size between samples from Alaska and mid-latitude subalpine samples.

[Samples are grouped by similarities in mean annual and mean annual range of temperature. Variation is measured by the percent of species that fall into four or more size classes. Columns designated "1" are the percent of species that have some leaves in the size class and columns designated "2" are the tabulated percent scores for the size class

Alaskan sample	Variation	Microphyll 3		Mesophyll 1 and 2		Mid-latitude sample	Variation	Microphyll 3		Mesophyll 1 and 2	
		1	2	1	2			1	2	1	2
Ketchikan	40	40	11	28	15	Laurel Mountain	8	38	12	21	8
						Government Camp	7	40	18	21	11
Seward	36	64	20	36	18	Bumping Lake	15	27	12	8	5
						Allens Park	11	37	13	11	4
						Soda Springs	11	19	7	11	6
Homer	42	42	12	29	13	Tahosa Creek	5	25	9	10	3
Alyeska	48	62	19	48	14	Red River	3	17	7	7	2
Kenai	36	64	18	36	11	Wolf Creek	0	25	9	5	2
						Dillon	8	15	4	8	3
						Grand Lake	4	36	14	4	1

Table 17. Comparison of large leaf size and leaf-size variation between samples from the Pacific Northwest and samples from the Sierra Nevada and the Southern Rocky Mountains.

[Samples are grouped by similarities in mean annual and mean annual range of temperature. Variation is measured by the percent of species that fall into four or more size classes. Columns designated "1" are the percent of species that have some leaves in the size class and the columns designated "2" are the tabulated percent scores for the size class]

Northwest sample	Variation	Microphyll 3		Mesophyll 1 and 2		Southern sample	Variation	Microphyll 3		Mesophyll 1 and 2	
		1	2	1	2			1	2	1	2
Wind River	7	67	26	30	18	Blue Canyon	4	30	11	17	9
Three Lynx	13	50	18	30	14	Bowman Dam	3	26	10	13	5
						Lake Spaulding	7	29	10	10	6
Hood River	13	66	24	22	15	Hasayampa	5	41	18	5	1
Rimrock Lake	4	36	14	16	7	Cheesman	7	15	6	7	3
						Lake Maloya	5	15	7	0	0
Republic	4	50	19	11	5	Tierra Amarilla	5	24	11	5	2
Bumping Lake	15	27	12	8	5	Allens Park	11	37	13	11	4

probably related to light regime (Wolfe, 1980). In the Pacific Northwest, the CLAMP samples show a marked decline in the abundance of broad-leaved evergreens between lat 43° and 45° N. This decline is probably not related to temperature because coastal areas of Oregon north of North Bend have higher cold-month mean temperatures than the area from which the Powers sample was collected. Even more conclusive is comparison of Pacific Northwest samples with California samples that have comparable temperature and precipitation regimes (table 18). The only significant environmental difference between the two sets of samples is light regime.

The scarcity of broad-leaved evergreens in the Northwest versus the California samples (and, as well, in microthermal samples from Arizona and New Mexico) is another factor (see preceding section) that probably results in the lower axis 1 scores for the Northwest samples relative to the Southwest samples. Givnish's (1979) observation that broad-leaved evergreens tend to have more untoothed margins relative to broad-leaved deciduous plants is certainly supported by the CLAMP samples, and the microthermal Southwest samples tend to have higher percent no teeth totals than the Northwest samples. In turn, character states that tend to give samples negative axis 1 scores (for example, any of the toothed character states) will have an effect on the scores for samples from areas that exclude broad-leaved evergreens because of factors such as light. On the other hand, CLAMP gives the Northwest samples more negative axis 2 scores than the Southwest samples and thus associates the summer-dry Northwest samples with the mesic Northeast samples. That CLAMP can give only general estimates of precipitation parameters for microthermal samples may be related to exclusion of broad-leaved evergreens in some regions of microthermal climate.

Table 18. Comparison of the broad-leaved evergreen element between samples from the Pacific Northwest and samples from California.

Sample	Latitude (degrees north)	Cold-month temperature (°C)	Percent broad-leaved evergreen
Port Orford, Oreg.	43	8.2	32
Jasper Ridge, Calif.	37	9.1	41
Powers, Oreg.	43	6.3	21
Colfax, Calif.	38	6.9	26
Lakeport, Calif.	38	5.7	35
Placerville, Calif.	38	5.1	29
Laurel Mountain, Oreg.	45	2.5	17
Three Lynx, Oreg.	45	1.9	10
Bowman Dam, Calif.	38	2.2	23
Blue Canyon, Calif.	38	2.8	17
Lake Spaulding, Calif.	38	1.2	26

Broad-leaved evergreens are also absent (or almost so) in the CLAMP samples from Maryland and southern Pennsylvania. In forests in eastern Asia that have the same mean annual and mean annual ranges of temperature as the Maryland-Pennsylvania region, the vegetation has a diverse, if not dominant, broad-leaved evergreen element. Similarly CLAMP samples from the Sierra Nevada that have cold-month mean temperatures approximately the same as the Maryland and Pennsylvania samples (see pl. 1) also have a diverse broad-leaved evergreen element. The Maryland-Pennsylvania samples associate on plates 2 and 3 more closely to the Pacific Northwest samples than to the samples that have a diverse broad-leaved evergreen element. Scarcity of broad-leaved evergreens in the Northwest samples probably results from light regime whereas scarcity in the Maryland and Pennsylvania samples results from extreme minimal temperatures.

INLIER AND OUTLIER SAMPLES

SUBALPINE SAMPLES

By "subalpine" I mean those environments in which the mean of the warmest month is less than 16°C and the mean of the coldest month is less than 3°C. The vegetation in this climatic area includes the High Coastal Mixed

Coniferous forest and parts of the Low Coastal Mixed Coniferous forest and Taiga of Wolfe (1979, 1985). In some areas (for example, parts of Alaska), the vegetation can be dominated by broad-leaved trees such as *Betula*.

Early in sampling for CLAMP, the first subalpine samples plotted anomalously in relation to other samples. The subalpine samples gave warmer and drier inferences than meteorological data would indicate. As more subalpine samples were added to the database, they also plotted too warm and too dry, but almost all these samples nested in a contiguous area of the sample plot resulting from Correspondence Analysis; this area includes only subalpine samples.

That the subalpine samples appear, from the standpoint of foliar physiognomy, to be drier and warmer than they actually are was recognized by Bailey and Sinnott (1916). These authors suggested that areas at high altitude and (or) high latitude are physiologically arid, especially because of winter cold. However, how can physiological aridity of winter cold produce adaptations of organs that are functioning only during the growing season? Although, as pointed out elsewhere in this report, some small-leaved evergreen dicotyledons persist through winters under snow cover, the bulk of subalpine woody plants are deciduous; leaves are not produced during the winter cold, and I cannot accept that such leaves are adapted to winter cold.

The subalpine environment produces moderate abundances of some of the same physiognomic character states as in dry, warm microthermal environments. These particular character states are an untoothed margin; teeth, if present, tend to be irregularly and distantly spaced and rounded; small leaves, especially the leptophyll 2 and microphyll categories; rounded apices and bases; and length to width ratios of 1–2:1 or higher. The moderate abundances of these character states in subalpine environments may relate to the few species that have the mesic, microthermal syndrome of character states (see p. 61). In dry, warm microthermal environments, the mesic microthermal syndrome would be nonadaptive; little precipitation occurs during the growing season and, even in the understory, woody plants must prevent excessive transpiration.

In subalpine environments growing season precipitation can be very high (for example, as at Ketchikan), as is soil moisture. If the mesic microthermal syndrome of characters is to function well, however, then water must be given off into the atmosphere. In mesic subalpine environments, the air, even during the warmest days of the growing season is cool, and cool air can hold much less actual moisture than can warm air at the same relative humidity. That is, the inability of the air in mesic sub-alpine environments to hold much moisture makes the mesic microthermal syndrome also nonadaptive for these environments as well as for dry microthermal environments.

The great majority of the subalpine samples have different axis 3 scores than other samples immediately adjoining the contiguous area. The samples in the lower left part of the subalpine nest, for example, have moderate to high axis 3 scores in contrast to the negative axis 3 scores of samples adjoining the nest (fig. 30). Samples in the upper part of the subalpine nest also typically have positive axis 3 scores in contrast to the negative axis 3 scores of adjoining samples.

The significance of the separation on axis 3 of the subalpine samples from adjoining samples can be gleaned from table 3. Samples that have high axis 3 scores have (1) moderate representation of both leptophyll 1 and mesophyll sizes, (2) moderate representation of attenuate apices, and (3) moderate representation of length to width ratios of both 3–4:1 and >4:1. In contrast, samples that have low axis 3 scores are especially characterized by moderate to high representation of emarginate apices and low representations of the character states just listed.

As discussed later, the emarginate apex probably results from brief periods of drought during leaf expansion that causes the apical meristem of the leaf to cease growth. Brief, periodic drought resulting from increasing irregularity of spring rains characterizes areas such as the Sierra Nevada, New Mexico, and Arizona, from where the samples that adjoin the upper part of the subalpine nest were collected. In the subalpine environment, the major period of leaf growth occurs while abundant soil moisture is still available from the melting snowpack, and thus emarginate apices are uncommon. Higher daytime temperatures in nonsubalpine environments relative to subalpine environments might also be a factor in increasing water stress and producing emarginate apices.

Along the lower left margin of the subalpine nest, sample separation on axis 3 may involve attenuated apices and leaf sizes. The three subalpine samples (Alyeska, Seward, and Government Camp) are from areas that have moderate to abundant growing season precipitation and moderate representations of attenuated apices, whereas the adjoining samples are from areas that experience extended summer drought. Further, the three subalpine samples tend to have sizes distributed across the leaf-size spectrum, whereas the adjoining samples tend to have high abundances in the microphyll 1 and 2 categories and low representation in the leptophyll 1 and (or) mesophyll categories. These adjoining nonsubalpine samples are from areas in which the dryness of the climate is accompanied by only moderate summer temperatures, an environment which will not create the water stress that selects for the smallest leaf sizes, and the dryness and moderate temperatures do not select for large leaves. The adjoining subalpine samples, in contrast, are from areas of almost continuous winter snow cover, which allows the persistence of low-growing, small-leaved, broad-leaved evergreens, and areas that have

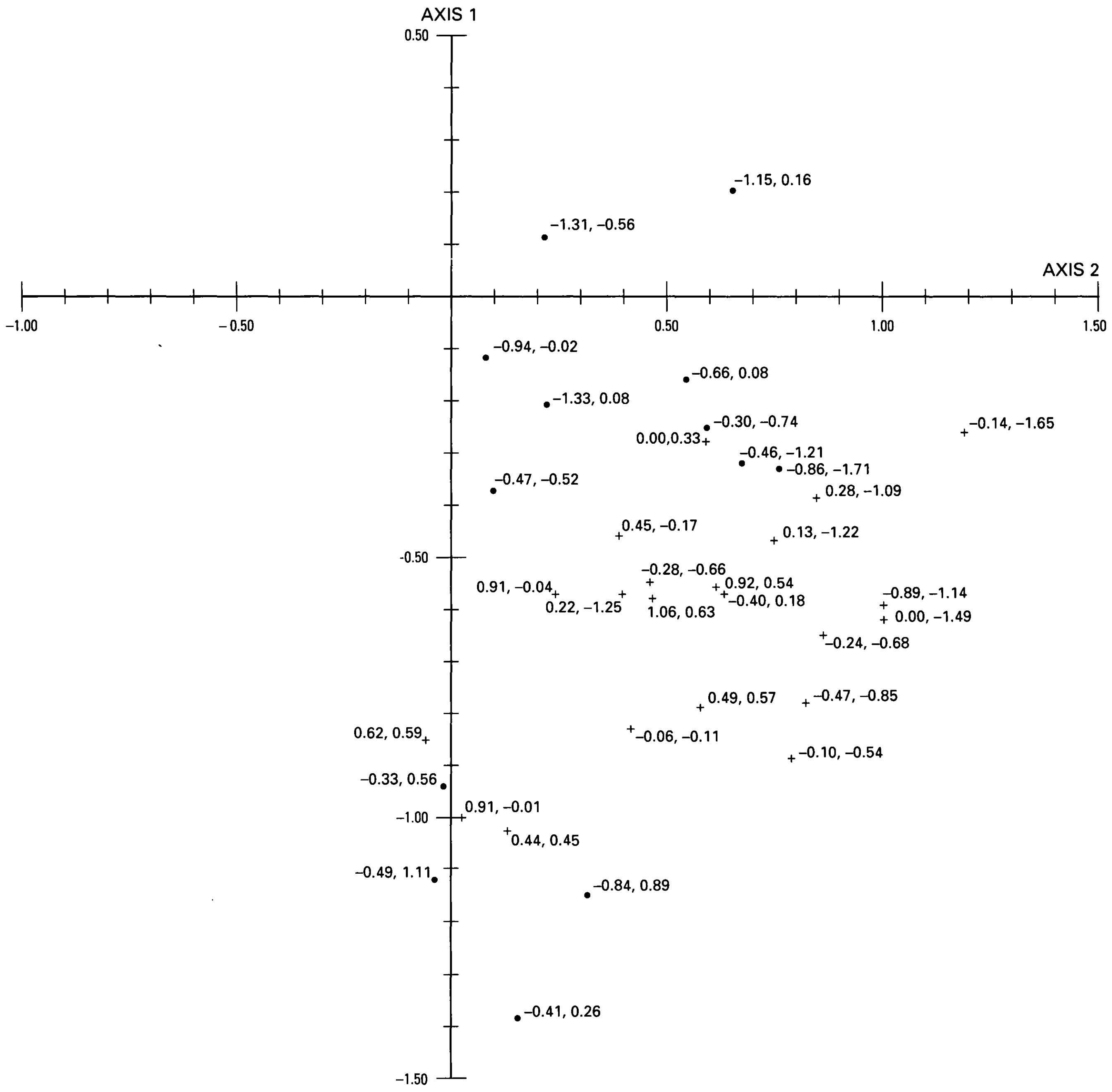

Figure 30. Plot of axis 3 and axis 4 scores for subalpine (+) and adjacent (*) samples.

abundant growing season precipitation, which allows the growth of some large-leaved shrubs.

Within the subalpine nest (fig. 30), vertical positioning of the samples is reversed relative to mean annual temperature: when orthogonally projected to the percent no teeth vector, the warmer samples generally plot lower than the cooler samples (fig. 31). The vector of decreasing mean annual temperature, which has a consistent, almost linear, relation to the other samples, can be visualized as wrapping around the subalpine nest and reversing course.

Considering that many of the subalpine samples are not of high diversity and that a limited range of mean annual temperature (<10°C) is represented, the standard error of 1.3°C is surprisingly low (fig. 31). Of the two most anomalous samples, Kenai has only 22 species, and Ketchikan (25 species) has a large element of small-leaved bog plants that probably give the Ketchikan sample its anomalously high score (even for the subalpine sample set) in CLAMP. Mean temperature of the warmest month

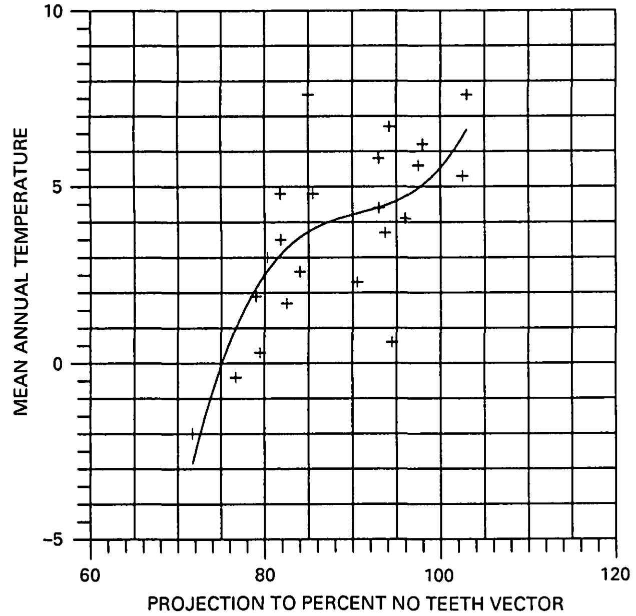

Figure 31. Polynomial regression of mean annual temperature (in °C) for subalpine samples. The plot for each sample is orthogonally projected to the vector derived from the score for percent no teeth; unlike other analyses, mean annual temperature has an inverse relation to percent no teeth. Percent of residuals about mean explained is 57, and residual mean square is 2.74. Standard error is 1.3°C.

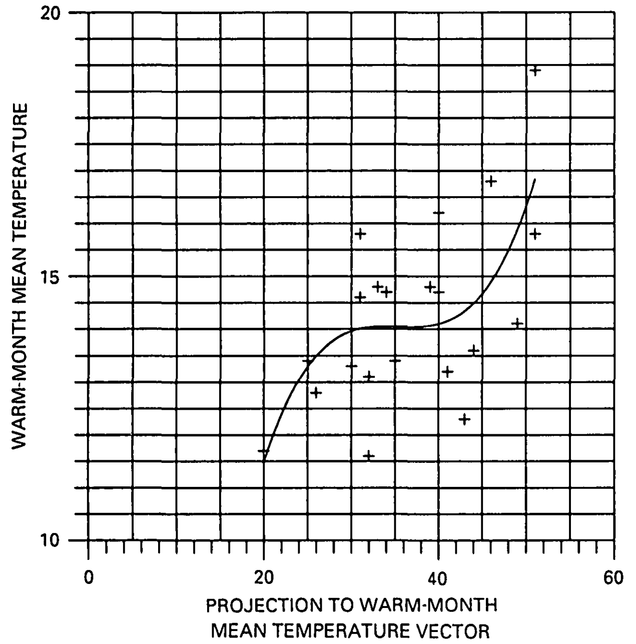

Figure 32. Polynomial regression of warm-month mean temperature (in °C) for subalpine samples. The plot for each sample is orthogonally projected to the vector derived from the score for warm month mean temperature. Percent of residuals about mean explained is 42 and residual mean square is 1.65. Standard error is 1.3°C.

can also be approximately estimated for the subalpine sample set (fig. 32).

Also plotted in figures 30, 31, and 32, are the samples of High Montane Mixed Coniferous forest (Wolfe, 1979) from Colorado. These are the samples that on plate 2 plot below the subalpine nest and share with the adjoining subalpine samples axis 4 scores. Although the area of Colorado from which these samples were collected generally receives moderate precipitation in July and August from monsoonal circulation, in some years the monsoons are weak and do not reach this area of Colorado. That is, the foliar physiognomy is probably adapted to the dry summers that are only occasional but persistent.

Another factor that may produce similarities in foliar physiognomy between these Colorado samples and the subalpine samples is that the montane regions of Colorado can receive freezing temperatures during almost any month of the growing season. In any case, these Colorado samples appear to respond physiognomically to environment in a manner similar to the subalpine samples.

On the other hand, samples from areas of cool summers but where winters are moderately warm do not plot in the subalpine nest. The mean temperature of the warm month at Cape Blanco, Oreg., for example is 12.3°C, but this sample plots with other samples that have warm-month means above 16°C. At some as yet indetermined cold-month mean temperature, leaf physiognomy is changed from the normal to the subalpine. This indetermined temperature must lie between 7.4°C (Bandon, Oreg.) and 2.5°C (Laurel Mountain, Oreg., which plots with the subalpine samples). Samples from coastal points of Washington and Vancouver Island would be very informative.

DRY MICROTHERMAL SAMPLES

Three microthermal samples plot dry but anomalously warm on plate 2 (see p. 38); these samples are Jemez Springs, Tierra Amarilla, and Red Fleet, the only three samples of juniper woodland in the database. These samples also have the three lowest axis 4 scores (table 3) and plot together as outliers. All three samples produce estimates of mean annual temperature that are approximately 2°C higher than actual values. Many more samples of juniper woodland vegetation are needed to determine conclusively if a separate calibration is required for these dry outliers, but that all three samples show the same overestimate of mean annual temperature suggests that a separate calibration is necessary.

SAMPLES FROM THE SOUTH PACIFIC

CLAMP is an outgrowth of data initially gathered from samples collected in Fiji, New Caledonia, and New South Wales. The standards for collection of these samples were considerably less rigorous than those adopted for the collection of later samples; emphasis was placed almost exclusively on untoothed versus toothed and on obtaining the larger leaf sizes rather than on obtaining the full range of all character states. Further, collections in New South Wales were almost exclusively of the rain forest vegetation generally confined to valleys of deep soils rather than enlarging a given sample to include the sclerophyll vegetation of adjacent slopes. Finally, most samples were not collected proximal to meteorological stations, and meteorological data for the samples are based on estimates of varying quality.

Because of these qualifications regarding sampling strategy, the South Pacific samples are not included in the database. However, the Fiji and New Caledonia samples plot reasonably consistently with the Caribbean samples when a slight adjustment is made for the emphasis made during collecting on large leaf sizes. Streamside species in humid to mesic megathermal environments typically are also distributed away from streams, and thus whether streamside vegetation is included in a sample is not a significant factor.

The Australian samples, even when adjustment is made for leaf size, mostly plot higher (warmer) on axis 1 than the humid to mesic, warm mesothermal samples included in the CLAMP database. Two samples (Kiola and Lyons Creek), both unfortunately of small size (25 and 17 species), plot consistently with the other CLAMP samples. These two samples, unlike the other four New South Wales samples, include all species encountered, including both putative rain forest remnants and sclerophyll (eucalypt) forest. Some neobotanists (for example, see various papers in Beadle, 1981) maintain that, until burning by early aboriginal man, all the eastern slope of Australia was covered by rain forest of the type now restricted to some alluvial valleys and that the sclerophyll forest is a successional stage, held in that stage by continuing human disturbance.

To varying extents, successional taxa occupy small, disturbed areas in normal "climax" vegetation. Thus, even if the original vegetation of the eastern slope of Australia had been rain forest, it would have included in local habitats the species that now form sclerophyll forest. The foliar physiognomy of an Australian sample should include all taxa in the area, not just those taxa conjectured to be in the original vegetation. Moreover, if many rain forest taxa once occupied slope habitats but no longer do, the total variation of foliar physiognomy in these taxa (a requisite for CLAMP sampling) will not be represented in a sample that only includes the same taxa now restricted to moist bottom land. While I admit the possibility that Australian vegetation operates on a somewhat different physiognomic scale than the vegetation included in the samples now included in the CLAMP database, I also suggest that eastern Australian samples that indicate anomalously high temperatures do so because the samples included species from a limited habitat.

SOME INTERPRETATIONS OF FOLIAR ADAPTATIONS

That various climatic parameters can be derived from the CLAMP database implies that the CLAMP samples provide information on the distributions of various physiognomic characters states relative to climate. In turn, the CLAMP samples should provide some insight into the adaptive significance of particular character states. Much of the following discussion is conjectural but is offered in the hope that at least some of the suggestions will form the basis for further research.

Some of the character states, however, may be forced by the environment during a brief period, rather than genetically controlled (that is, adaptations). As suggested in the following subsections of this discussion, the emarginate apex and certain overall growth patterns, possibly reflected in the shape and base character states, may result from direct environmental influences during the period of active leaf expansion.

LOBING

Lobing can be viewed as a reduction in effective laminar area on a single leaf while still maintaining most of the laminar area. The individual lobes will not overheat to the same extent that would occur if the same total laminar area were unlobed. The most deeply lobed leaves are generally found on canopy trees in microthermal forests; conspicuous lobing typically is in canopy trees of *Quercus* and *Acer*. Notable is that subcanopy species of *Acer*, for example *A. spicatum* and *A. pennsylvanicum*, are shallowly lobed. However, in open-canopy microthermal vegetation, whether early successional in mesic environments or "climax" in subhumid environments, lobing is also common, for example in *Rubus* and *Ribes*. The CLAMP score for lobing clearly indicates that lobing is most characteristic of microthermal environments.

In mesothermal and especially megathermal vegetation, lobing is increasingly uncommon. If, as suggested here, a particular clade can adapt to the canopy by lobing, more lobing might be expected in mesothermal and megathermal environments. I suggest that the scarcity of lobing in warmer climates is related to the genetic makeup of the microthermal flora versus the mesothermal flora and the megathermal flora. As discussed in the next section, the palmately veined leaf provides an optimal base for the evolution of a leaf type best adapted to the subcanopy of microthermal forests. Added to this suggestion is that, compared especially with megathermal climates, relatively few woody clades have been able to adapt to microthermal climates. A clade that possessed the developmental flexibility to adapt to both canopy and subcanopy habit should be successful in microthermal vegetation.

In mesothermal and megathermal climates, in contrast, the general diversity is much higher than in microthermal climates. Further, except for the palmate dilleniids (and derivative groups such as Urticales; see Wolfe, 1989), palmately veined groups are uncommon. Reduction in leaf size for adaptation to the canopy could be accomplished by lobing in the palmate dilleniids, as occurs in some Sterculiaceae, but most mesothermal and megathermal clades are pinnately veined; most lobing is associated with palmate, rather than pinnate, venation.

MARGIN CHARACTERS

The untoothed versus the toothed margin is putatively a reflection of temperature, and the similarities in scores for mean annual temperature and percent untoothed margin support this interpretation. That a marked correlation exists between untoothed margin and mean annual temperature cannot be denied. The physiological significance of the toothed versus the untoothed margin has, however, been widely debated.

In one view, the toothed margin is simply a default state associated with a deciduous habit, whereas the untoothed margin, which is typically associated with an evergreen habit, is adaptive to prevent water loss. I suggest, on the other hand, that the untoothed margin is equally adaptive when viewed in the context of associated character states.

Most paleobotanists and neobotanists involved in foliar physiognomy have uncritically accepted Richards' (1952) observation on the type of leaf prevalent among Tropical Rain forest lianas. Indeed, Richards' observation that many lianas have broad, cordate-based, and palmately veined leaves is valid, but his implication is that this physiognomy is restricted to Tropical Rain forest lianas. CLAMP strongly indicates otherwise. The character states of a length to width ratio of less than 1:1 and a cordate base are characteristic of samples from humid to mesic microthermal environments. Although venation characters are not scored in CLAMP, the particular microthermal taxa that have these two character states also have palmately veined leaves (for example, *Acer, Oplopanax, Tilia,* and *Ribes*), and all are erect plants rather than lianas. Other taxa, for example *Betula*, *Corylus*, and *Viburnum*, are pinnately veined but tend to have secondary veins that splay outward from near the base, and their leaves are cordate based and broad. These predominantly microthermal taxa also typically have numerous, sharp teeth, many of which are compound, and the scores for acute, regular, close, and compound teeth are very similar to the scores for length to width ratio less than 1:1 and for cordate base.

The similarities in scores for all these physiognomic character states strongly suggest that the character states are part of the same syndrome that is highly adaptive to humid to mesic, microthermal environments. These are environments in which growing season temperatures are moderate and moisture is no serious problem. These leaves also tend to belong to subcanopy trees and shrubs, and thus the leaves typically are in the larger size categories. I suggest that this type of leaf is the most economical for deciduous plants in subcanopy, moist, microthermal environments.

The leaves should be large to intercept as much sunlight as possible; they will not overheat because they are subcanopy. To conserve food, they should be produced with as little tissue as necessary; they can thus use water turgidity rather than thick veins for structural support. To most efficiently transport water through the leaves, the major veins should originate from the top of the petiole, which selects for palmately veined (or nearly so) leaves and cordate bases. Numerous teeth are selected for because the teeth are basically functioning as pumps, to allow large amounts of water to pass continually through the lamina. Major veins are typically craspedodromous for the most efficient water transport to the margin.

That teeth can give off fluids has been demonstrated for leaves that have glandular hydathodes. However, observations made during the chemical clearing of leaves supports this function for almost all teeth. The final stages of the clearing process involve removing leaves from a solution of 100 percent alcohol and placing them in pure toluene in a petri dish. Replacement of the alcohol by the toluene is a rapid process and generates kinetic energy in the leaf. Leaves that have no teeth vibrate rapidly during the replacement but otherwise move little. Leaves that have teeth (especially numerous teeth) move rapidly around the petri dish, pushed by jets of fluid emanating from the ends of the teeth.

Combining the observations from leaf clearing with the inferences from CLAMP suggests that teeth are critical in maintaining a rapid flow of water through leaves. An additional benefit of rapid water flow is that nutrients are also being transported into, and concentrated in, the leaf. Many teeth along the margin may also tend to create turbulence in air flow and further increase the evaporation of water from the tips of teeth.

A further basis for inferring that teeth are selected for is that many broad-leaved evergreens also have teeth; that is, the vegetation may be overwhelmingly broad-leaved evergreen, but, if mean annual temperature is only mesothermal, many of the broad-leaved evergreens have teeth. For example, even in the cool megathermal, totally evergreen forests of New Caledonia a higher proportion of the taxa have teeth than in the warm megathermal, totally

Table 19. Occurrence of margin character states in samples from the South Pacific.
[Samples are arranged from highest to lowest mean annual temperature. All figures are percentages]

Sample	No teeth	Teeth regular	Teeth close	Teeth round	Teeth acute	Teeth compound
Keka, Fiji	87	5	4	8	5	0
Natua, Fiji	79	15	9	18	4	2
Magenta, New Caledonia	71	5	3	25	4	0
Seqaqa, Fiji	61	16	11	67	2	9
Riviere Bleue, New Caledonia	59	11	10	32	9	4
Koghis, New Caledonia	71	15	11	25	5	3
Bundagen, New South Wales	66	15	5	26	3	3
Woolgoolga, New South Wales	57	23	10	26	8	5
Kioloa, New South Wales	44	30	22	37	15	4
Mobong, New South Wales	52	34	18	34	5	5

evergreen forests of Fiji, and the percentage of toothed species increases into the almost entirely evergreen mesothermal rain forests of New South Wales (table 19).

Summer drought has a marked effect on leaf-margin type. With increasing need to retain water, as in dry microthermal environments, not only are fewer species with teeth present but teeth are less pointed and tend to be adpressed (many with glands) or markedly rounded. Teeth also become more irregularly and widely spaced. These changes in character scores are most marked in deciduous plants.

As temperature and the need for water conservation increase, leaves show a similar reduction in teeth. Broad-leaved evergreen plants may also become a more significant element, and these, even if toothed, typically have fewer and more rounded and (or) adpressed teeth than deciduous plants. Some evergreen plants develop spinose margins, but spinose teeth, which are formed by an extension of a fimbrial vein, cannot function relative to assisting in water transport; thus, spinose teeth are treated in the scoring for CLAMP as nonexistent. Spinose teeth, moreover, are typically found on the same branch with leaves that have perfectly entire margins; if the primary function of spinose leaves is to prevent browsing (see p. 21), then only some leaves in the typically dense clusters need to be furnished with spines.

To return to Richards' (1952) typical liana type of leaf in the Tropical Rain forest, Richards perhaps exaggerated the occurrence of this type of leaf among Tropical Rain forest lianas; leaves of lianas of Annonaceae, Apocynaceae, and Asclepiadaceae, for example, do not conform to the "typical" pattern. This "typical" leaf, however, does share a number of characters with leaves in the subcanopy of humid to mesic, microthermal forests. The selection for these characters in some tropical lianas may also, as in microthermal trees and shrubs, be related to a need to transport water. Tropical lianas certainly need to transport water to some height, and they typically have a limited number of leaves to act as pumps. Although teeth are absent on leaves of some lianas, especially Menispermaceae (presumably water in this instance is given off exclusively by stomates), other tropical lianas that have the "typical" leaf also have conspicuous teeth (for example, Vitidaceae). Lianas of Phytocreneae appear not to have teeth but, in fact, the leaves typically have craspedodromous veins ending in conspicuous marginal glands. This syndrome of characters is fundamentally the same as in the subcanopy leaves of plants in humid to mesic, microthermal forests but is much more prevalent in these forests than in tropical lianas.

LEAF SIZE

The relations between environment and leaf size are perhaps the best understood. The occurrence of larger leaves is related to availability of nutrients and water for the production of large leaves. An additional requirement is general warmth, which is probably related to productivity. CLAMP samples that have the highest tabulated totals in the mesophyll sizes are megathermal and humid. Leaf size decreases with (1) decreasing mean annual temperature, (2) decreasing length of the growing season, (3) decreasing growing season precipitation, or (4) nutrient-poor soils such as sandy or serpentine soils. The first three factors are typically linked; that is, as mean annual temperature decreases, the growing season may be shorter and the total growing season precipitation less. However, even if the growing season is year long and the precipitation high, as in the instances of the cool megathermal Maricao and warm mesothermal Monte Guilarte and Toro Negro samples, totals in the mesophyll categories are less than in the warm megathermal rain forest samples such as Barro Colorado Island and Guajataca (table 3). Richards (1952) and Dolph and Dilcher (1980) also emphasized decrease in leaf size with decreasing temperature in other tropical areas.

Mesothermal samples, even if they are from areas that receive abundant precipitation during the growing season and have high growing season temperature, do not have high mesophyll totals, especially in the mesophyll 2 category (table 20). Some microthermal samples, such as Ketchikan, are from areas of high rainfall but cool summers; such samples have moderately high totals in the mesophyll sizes, but this phenomenon is probably primarily related to light regime (see p. 54).

Indeed, the largest leaves in mesothermal and megathermal rain forests typically belong to subcanopy trees and shrubs (Richards, 1952), which, like the large-leaved microthermal species, also live under low-light regimes. Thus, as the canopy in vegetation is opened, whether because of nutrient-poor soils or decreased precipitation, totals in the large-leaf categories decrease. In order to have very large leaves, the leaves typically must be protected from overheating in sunlight. At the same time, large leaves are economical in a low-light regime because they provide large areas for the reception of available light for photosynthesis.

At the other end of the leaf-size spectrum, the highest totals of the smallest leaves (leptophyll categories, especially leptophyll 1) are in samples from megathermal deserts. Indeed, some desert plants have almost or totally eliminated leaves, presumably because of the overheating problem concomitant with the need to conserve water. In some desert plants (*Simmondsia*, jojoba) that have relatively large leaves compared to other desert plants, the leaves are positioned upright; during the hottest part of the day the leaves receive a minimal amount of direct sunlight and probably have less heating than if the leaves were at right angles to sunlight. Other relatively large leaved desert plants (*Chilopsis*, desert willow) have high length to width ratios (that is, they are very narrow), again an adaptation to prevent overheating (see below); as well, leaves of *Chilopsis* hang almost vertically. The largest leaves in the desert samples were collected from streamside plants, but even these have a significant size reduction compared to the same species in mesothermal chaparral streamside vegetation. That the score for the smallest leaf size, leptophyll 1, indicates hot and dry environments is consistent with the necessity for plants to reduce leaf size in desert environments.

The scores for the leptophyll 2 and microphyll 1 character states are the only leaf sizes that indicate low temperature, although both also indicate, especially in the instance of leptophyll 2, low precipitation. The leptophyll 2 category reaches levels of 25–30 percent in desert samples and in dry microthermal, including subalpine, samples. The microphyll 1 category reaches levels of 25 to almost 40 percent in subhumid megathermal and dry mesothermal and microthermal samples.

The microphyll 2 and especially the microphyll 3 (approximately Webb's 1959 notophyll size-class) categories both indicate moderate temperature and humid to mesic conditions. Mesic (as opposed to humid) megathermal samples have a preponderance of these two categories combined, as does mesic to humid mesothermal and warm microthermal vegetation.

Table 20. Comparison of leaf sizes in samples from humid environments.
[All figures are percentages]

Sample	Leaf size Microphyll 3	 Mesophyll 1	 Mesophyll 2
Megathermal			
Barro Colorado Island	26	33	16
Guajataca	27	21	15
Maricao	29	15	10
Mesothermal			
Monte Guilarte	27	14	6
Yakushima	33	16	8
Toro Negro	23	13	6
Zozu-san	33	12	4
Kiyosumi	22	10	2
Microthermal			
Port Orford	21	16	4
North Bend	27	17	5
Bandon	26	11	3
Aberdeen	21	21	5
Cape Blanco	23	14	2
Ketchikan	11	7	8

APEX

The CLAMP score for an attenuated apex clearly indicates that this character state associates with high rainfall, as suggested previously (for example, Richards, 1952). Attenuated apices are found on leaves of deciduous or evergreen plants, although the classic drip-tip has generally been attributed to evergreen plants. The suggestion appears reasonable that attenuated apices are an adaptation to drain a leaf rapidly, primarily to prevent fungal growth in humid climates.

As the growing season becomes drier in microthermal climates, the apex becomes sharp but not attenuated and finally rounded. In megathermal and mesothermal climates, however, few leaves have truly acute apices; at least in part, this may result from a coriaceous, typically evergreen leaf always having a somewhat rounded apex, even when attenuated. Thus in mesothermal and megathermal vegetation, a nonattenuated apex is rounded. Thus acute apices are found typically in wet, microthermal climates, whereas rounded apices predominate in dry megathermal to microthermal climates.

A special state of the apex is emarginate. Some, but few, taxa invariably have emarginate apices. More typical is a species that generally has a rounded or even attenuate apex but some emarginate apices. This character state is particularly common in megathermal, subhumid climates. The samples from the south coast of Puerto Rico have a high percentage of species that have some emarginate apices. Apparently this character state develops in climates that encourage development of moderate-sized leaves (particularly microphyll 2 and 3 categories), which, during their expansion, encounter some brief drought of a few days. The apical meristem of the leaf is developmentally retarded, with a resulting emarginate apex. In the smallest desert leaves, emarginate apices are rare but tend to develop in desert taxa that typically reach the microphyll state.

BASE

The cordate base was discussed previously relative to margin characters and is most characteristic of microthermal forests. The cordate base scores less negative on axis 1 than the margin characters suggested to be associated, partly because some warm microthermal and cool mesothermal taxa have narrowly but not broadly cordate bases.

Acute bases are particularly characteristic of megathermal and warm mesothermal vegetation in humid to mesic environments. An acute base may result from rapid growth of the leaf, as might be expected in such climates; many of these acute bases are actually attenuated along the midrib-petiole axis, suggesting that growth from the apical meristem is very rapid with minimal concomitant lateral growth.

The low score received by rounded bases, which can total 70–80 percent in some samples, indicates that this character state is not adaptive to any particular climate.

LENGTH:WIDTH

The strong association of a length to width ratio of less than 1:1 with the microthermal syndrome of margin characters was discussed previously. Scoring the highest of all the length to width ratio character states, however, is the stenophyllous condition, in which length:width is greater than 4:1. Stenophylls are more common in dry mesothermal to megathermal climates than in any other climate. The adaptive significance of stenophylls is clear: a leaf can have a large (at least relative to other plants in dry climates) area but, because no part of the lamina is far from the margin, will not readily overheat (Parkhurst and Loucks, 1972).

Stenophylls, however, have also been suggested to be characteristic of streamside environments in many climatic regimes, and the elongation of the leaves has been suggested to be adaptive to water and (or) wind currents (Richards, 1952). Stenophylls in megathermal and warm mesothermal, dry vegetation are present both in plants that live along streams (*Salix, Baccharis*) and in plants that live on interfluves (*Chilopsis, Dodonaea*) in totally open vegetation. In the instance of the interfluve plants, the adaptive significance of stenophylly is almost certainly to prevent overheating. An argument could be made for the same relation for the streamside plants because these are typically shrubs that live along (or in) ephemeral streams and are, compared to other desert plants, large leaved. In microthermal dry vegetation, a similar dual distribution of stenophylls occurs. Streamside vegetation has stenophyllous species of *Salix* (and some *Populus* as well), but interfluve vegetation has various stenophyllous shrubs to subshrubs, which are primarily members of Compositae. What I define as true stenophylly, where length is more than four times width, is most likely to be adaptive to prevent overheating. In closed-canopy forested environments, stenophylly is notable along streams because the streamside habitat receives full sunlight and overheating of leaves can be a problem.

A length to width ratio of between 2:1 and 3:1 is most characteristic of leaves in humid to mesic, megathermal to warm mesothermal forests. Many species that have this ratio also produce many leaves that extend into the 3:1 to 4:1 ratio, ratios which also occur in species whose leaves are predominantly stenophylls. Thus, the score for the 3:1 to 4:1 character state reflects, in part, a mean between the 2:1 to 3:1 ratio and the greater than 4:1 ratio. Samples that have the highest totals of the 3:1 to 4:1 ratio tend to occur in megathermal climates that have only moderate (120–140 cm) precipitation and that support a mixture of open- to closed-canopy vegetation. True stenophylly may not be selected for, but a moderate elongation of the lamina to prevent overheating is.

A length to width ratio of 1:1 to 2:1 is common in many environments, and many species score exclusively in this ratio. This ratio thus can be thought of as unspecialized relative to climate.

SHAPE

Like the length to width ratio category of 1:1 to 2:1, an ovate shape has low scores on both axes 1 and 2 and is considered to be generalized and adapted for almost any climate. An elliptic shape has a somewhat more significant score on axis 2 and tends to occur in humid to mesic, megathermal to warm mesothermal climates in association with a length to width ratio of 2:1 to 3:1.

An obovate shape, however, has a moderately high score on axis 1 and has a vector that approximates axis 1. Further, an obovate shape tends to associate most closely with an acute base, a length to width ratio of 3:1 to 4:1, and an emarginate apex. This syndrome of character states may indicate that laminar expansion occurred under moderate to high temperatures to induce rapid growth but that after initial expansion under abundant moisture growth was slowed by declining moisture supply.

APPLICATION TO FOSSIL LEAF ASSEMBLAGES

The primary reason for initiating the collection and analysis of samples that now comprise CLAMP was to obtain accurate (valid) and precise (repeatable) estimates of paleoclimate. The preceding analyses and discussions show that, relative to the collections of present-day vegetation, the estimates of various climatic parameters are certainly precise and, to varying degrees, accurate. However, various historical and other factors might conceivably introduce error in the application of CLAMP to fossil assemblages.

SCORING CHARACTERS

Ideally, an assemblage of fossil leaves should be scored from actual collections rather than from illustrations. Few, if any, published fossil floras illustrate or fully describe the full range of physiognomic variation of each species. Unillustrated fragments may represent character states not present in illustrated museum-quality specimens. This is particularly critical in scoring for size because large leaves may have been fragmented during transport to the depositional site; in such instances, estimates of sizes of fragmentary leaves should be made. Similarly, apices may be partially absent on many fossil specimens, but, for example, a change in marginal curvature can indicate that the mostly missing apex was attenuate.

In tabulating totals and converting them to percentages for CLAMP analyses, the percentage should be based on the number of species that have the particular set of character states preserved. For example, the base or apex of some species may not be preserved; thus the total number of species from which the base or apex percentage is calculated will be less than the total number of species in the fossil assemblage.

SOME EXAMPLES

Three examples are here used to illustrate how CLAMP can be applied to fossil leaf assemblages. The first is the La Porte flora, an earliest Oligocene, radiometrically dated assemblage from the Sierra Nevada of northern California (Potbury, 1935; see also Wolfe, 1992b). Potbury illustrated 35 dicotyledonous leaf species, although 2 of these include divergent elements, which means that the dicotyledonous leaf flora comprises 37 species. The percentages for each physiognomic character state, given in the same order as in text figure 10, were entered into Kovach's MVSP Plus 2.0 computer program as a new column added to the CLAMP database used for plate 3 (that is, the database that excludes inliers and outliers). When this database was subjected to Correspondence Analysis, the La Porte assemblage received a score of 0.58 on axis 1 and –2.41 on axis 2. This score was then plotted on plate 4. To estimate mean annual temperature, a line was projected to the vector for percent no teeth so that the line and the vector are orthogonal to one another. The intersection of that line and the vector is at a position of –70 on the vector; on the regression given in text figure 13, a score of –70 on the x-axis corresponds on the y-axis to a mean annual temperature of 22.3°C. Other estimates of climatic parameters can be similarly obtained for the La Porte.

A second example is the Creede assemblage, a radiometrically dated late Oligocene flora from southern Colorado. Although Axelrod's (1987) taxonomic treatment of the Creede recognized 53 dicotyledonous species, a later treatment (Wolfe and Schorn, 1990) recognized only 25. Despite this major divergence in taxonomic treatment, the percentages for each character state using either treatment are very similar and result in Correspondence Analysis scores that are also very similar. Using the more recent treatment, the Correspondence Analysis score for the Creede is –0.60 on axis 1 and 0.85 on axis 2; this score is obtained from the entire database used for plate 2. In the instance of the Creede, the entire database was used because one interpretation (Wolfe and Scorn, 1988) suggested that the Creede represented subalpine vegetation. Indeed, the Creede score places the assemblage within the inlier subalpine nest on plate 2, and the positive axis 3 score (0.42) is consistent with subalpine vegetation. Plotting the Creede score on plate 5 and projecting a line from the score to the percent no teeth vector gives a position of 40; using figure 31, this position on the x-axis indicates a mean annual temperature for the Creede of 4.2°C.

A third example is presented for comparison with the Creede. The Yaquina assemblage is in a delta that interfingers with late Oligocene marine rocks in western Oregon (McClammer, 1979). As illustrated by McClammer, the Yaquina flora contains 36 dicotyledonous species. Perusal of the Yaquina assemblage indicates that it represents a humid to mesic rain forest, so the database for plate 3 is used, which results in a score for the Yaquina of –0.37 on axis 1 and –1.48 on axis 2. The projection of the Yaquina to the percent no teeth vector gives a position of –0.9, and reference to text figure 13 indicates a mean annual temperature of 15.5°C. Thus, the difference of more than 11°C in mean annual temperature between the Creede leaf assemblage in southern Colorado and the approximately isochronous lowland Yaquina assemblage at a paleolatitude 4°–5° north of Creede strongly indicates a paleoaltitudinal difference of more than 2 km.

TAXONOMY

A problem encountered in scoring fossil samples is assigning all leaves encountered to the various species.

Some paleobotanists, especially in the 19th and early part of the 20th century, were "splitters" relative to current concepts in leaf architecture. Leaves of what would now be regarded as a single species were assigned in some instances to several different species (and even genera). This could introduce error into CLAMP. My experience, however, indicates that such splitting typically involved all species in a fossil assemblage; tabulations based on some assemblages as published and on my own interpretations of the taxonomy suggest that splitting has little effect on the percentage of a given character state.

SAMPLE SIZE

Accuracy of, for example, mean annual temperature is dependent on sample size, with samples of 20 or more species yielding the most accurate results (see p. 50). For the most accurate estimates of precipitation parameters, samples of at least 25 species should be analyzed (see p. 52). Note that, although some of the Cretaceous-Tertiary boundary assemblages that I (Wolfe, 1990a) analyzed using an early version of CLAMP had 10 species or less, even such small assemblages would not affect the conclusions that involve major increases in both mean annual temperature and precipitation shortly after the boundary. My conclusions, however, were also based on some assemblages of more than 30 species, and the analyses of both small and large collections produced a consistent pattern. If a detailed analysis of paleoclimate in a particular area is the goal, then a number of assemblages of moderate (20 species) to large (30 species) size should be analyzed.

EVOLUTIONARY FACTORS

Does floristic evolution affect CLAMP analyses? No certain answer can be provided, but that highly advanced groups of angiosperms occupy the same habitats and have the same basic foliar physiognomy as less advanced groups in the same habitats suggests that floristic evolution should have minimal impact. A prime example of convergent foliar evolution is *Baccharis glutinosa*, a member of the advanced family Compositae, which first enters the fossil record near the Oligocene-Miocene boundary; leaves of this species have strong physiognomic similarities to species of *Salix*, a member of Salicaceae that first enters the fossil record near the Paleocene-Eocene boundary. Both *Salix* and *B. glutinosa* grow side by side along ephemeral streams in the Sonoran Desert.

Indeed, that species in the CLAMP samples are members of more than 150 angiosperm families strongly argues that foliar physiognomy is an environmentally adaptive feature that crosses phylogenetic boundaries. Included in the CLAMP samples are members of Magnoliidae, putatively the most primitive subclass of angiosperms, as well as Asteridae, putatively the most advanced subclass of angiosperms. Genetic imprints on foliar physiognomy are everywhere apparent; leaves of Tiliaceae, even in tropical climates, tend to have toothed margins and cordate bases, and leaves of Lauraceae and Annonaceae, even in microthermal climates, have untoothed margins. If this genetic imprint were not present, possibly the percent variance accounted for on axes 1 and 2 would closely approach 100. Even with the genetic imprint on foliar physiognomy, the relation between foliar physiognomy and environmental adaptation appears clear.

From at least the Cenomanian, arctic leaf assemblages are dominated by broad, cordate-based, strongly toothed leaves (Spicer, 1986); that is, these assemblages have many species that have the humid to mesic, microthermal syndrome of character states. These species also have the wide variation in leaf size that now characterizes high-latitude woody plants. The untoothed margin percentages for individual assemblages, moreover, show a marked latitudinal gradient during all intervals within the Late Cretaceous (Wolfe and Upchurch, 1987). Unless strongly contradictive evidence is forthcoming, I see no reason that CLAMP cannot be reliably applied to leaf assemblages of the last 90–100 million years.

CATASTROPHIC EVENTS

Catastrophic extinctions accompanied by major climatic change, such as inferred at the Cretaceous-Tertiary boundary (Wolfe and Upchurch, 1986; Wolfe, 1990a), could conceivably increase the error of CLAMP estimates. Despite, however, the apparent extinction of many broadleaved evergreen, untoothed-margin taxa at the Cretaceous-Tertiary boundary in the Western Interior of North America, CLAMP indicates that mean annual temperature significantly increased within a brief interval after the bolide impact (Wolfe, 1990a). Even should one or several character states be altered by extinction, the large number of character states in CLAMP appears to overcome such alterations to produce reasonably accurate estimates of climatic parameters.

ANOMALOUS CLIMATIC CONDITIONS

Anomalies caused by unusual climatic conditions can make CLAMP estimates somewhat inaccurate. The extremely low winter temperatures in eastern North America resulting from Arctic cold-air masses are, in the present-day world, more typical of cold-month means and mean annual temperatures lower than those that actually occur in eastern North America. However, the CLAMP estimates for the samples from these eastern American anomalous areas are accurate to within approximately 2°C. Further, the anomalously low winter temperatures in eastern North America are not inferred from the fossil record to have occurred until approximately 13 million years ago (Wolfe, 1985); at that time, most broad-leaved evergreens disappeared from the fossil record in the Middle Atlantic States. Before that time, this anomaly can probably be ignored for application of CLAMP to the fossil record in eastern North America or any area subject to regular outbreaks of frigid Arctic air masses.

Until more modern samples from eastern Asia are included in the database, I suggest that estimates of mean annual temperature for humid to mesic fossil assemblages should be based on figure 16. When more modern samples from nonanomalous vegetation are included in the database, however, a polynomial curve such as that in figure 17 may provide the most accurate estimate of mean annual temperature.

SOIL

The CLAMP samples are from areas of a wide variety of soils. Type of soil introduces no significant error into temperature estimates. However, CLAMP estimates of precipitation factors can depend on soils: very sandy or serpentine soils can indicate considerably drier conditions than actually prevail. Investigation of the lithologic context of a given fossil leaf assemblage should be able to take this factor into account. The influence of sandy soil should be looked for especially in relation to fossil assemblages from coastal areas.

TIME

Although some fossil-leaf assemblages represent catastrophic events, such as an assemblage preserved by a volcanic eruption, most assemblages represent collections made from a few to several meters of sediment. As such, the assemblage represents vegetation that grew over a few to many years. I suggest that CLAMP estimates will be most accurate if based on an assemblage from a very limited stratigraphic interval. Estimates based on an assemblage collected from many meters of section will probably produce an estimate that is a mean for the duration of the sedimentation during that stratigraphic interval. Particularly if the goal is a detailed analysis of climatic change through an interval of thousands of years, then assemblages should be as stratigraphically restricted as possible. The limiting factor will, of course, be obtaining a sufficient number of species in each assemblage for accurate paleoclimatic estimates.

ATMOSPHERIC CARBON DIOXIDE

Some evidence from geochemical analyses suggests that levels of carbon dioxide in the atmosphere in the past probably exceeded present levels by as much as eight times (Arthur and others, 1991). Such higher levels conceivably could affect plant growth and, in turn, leaf physiognomy. In present-day closed-canopy forests, however, carbon dioxide concentrations from decaying humus (Bazzaz, 1990) can exceed the general atmospheric concentrations inferred for any interval of the past; the influence of high carbon dioxide concentrations on leaf physiognomy of subcanopy plants should thus be mirrored in the CLAMP samples.

The leaf physiognomy of canopy trees or trees and shrubs in open-canopy vegetation is inferred to be controlled primarily by intensity of solar radiation and the associated phenomenon of overheating. That is, even if atmospheric carbon dioxide substantially increased over present-day levels, character states such as leaf sizes and length to width ratios should still be mostly controlled by the necessity to prevent overheating. Although a wide variety of experimental data should be obtained on the effects of increased carbon dioxide on leaf physiognomy of woody dicotyledons, theoretical considerations suggest that CLAMP should be little affected by increased levels of general atmospheric carbon dioxide.

TAPHONOMY

Taphonomic factors introduced by transport could conceivably bias applications of CLAMP. The most obvious alteration would involve destruction of large leaves and the differential transport by wind of sun versus shade leaves (Spicer, 1981). Thus an assemblage might have misleading totals for leaf sizes, some of which receive the highest character-state scores. However, when scoring a fossil assemblage, I estimate leaf sizes from fragments of large leaves in order to mitigate these taphonomic factors.

Another alteration could involve the destruction of thinner, deciduous leaves, such that broad-leaved evergreens might be overrepresented in a fossil assemblage; this could significantly alter totals for margin character states, most of which receive moderately high scores. Again, scoring of fragmentary specimens will at least partially negate effects of this possible alteration.

Screening by vegetation immediately surrounding a depositional area might lead to underrepresentation of interfluve vegetation (Spicer, 1981, 1989). This is probably not a serious problem for three reasons. First, because CLAMP is based on species rather than numerical representation, an underrepresented species is just as significant as an overrepresented species. Second, streamside vegetation is typically not diverse; in order to attain the requisite

20–25 species for an accurate CLAMP analysis, some interfluve species will almost invariably be included. Third, relative representation of streamside versus interfluve species may introduce error into precipitation estimates but will not introduce error into temperature estimates (see p. 50).

In order to further examine taphonomic factors, I sampled three sites in Arizona, obtaining both CLAMP samples and taphonomy samples. Because all three sites represent open-canopy vegetation, screening was not operational. None of the taphonomy samples were collected from permanent ponds but instead represent leaves that had accumulated in ephemeral streambeds during two major rainstorms within two weeks prior to collection of the samples. All three samples represent high-energy runoff from these rains. Total volume of each sample is approximately 0.05 m^3, and a minimum of 600 leaves is present in each sample.

In northern Japan, I made no collections sufficiently large to include in the CLAMP database. One taphonomy sample, however, was collected from the Oirase River Valley in northern Honshu. Although this sample cannot be compared to a CLAMP sample, it can be analyzed in CLAMP for the validity of its climatic estimates.

Payson.—The taphonomy sample comprises a collection from two sites, one site at the topographically lowest part of the area sampled for CLAMP and a second site approximately 50 m downstream from the first site. Neither site had trees within 10 m or shrubs within about 5 m. Being early fall, many of the deciduous trees and shrubs had recently lost their leaves or were still in the process of leaf fall.

The combined taphonomy sample contains only 13 species of woody dicotyledons, as opposed to the CLAMP sample of 28 species. As might be expected, leaves of evergreen *Quercus* are the most abundant leaves in the sample; these leaves persist in the leaf litter on the adjacent slopes because of thick, coriaceous texture and resistance to biological degradation. Foliage of *Fraxinus* and of *Populus*, both small to large trees along the stream, are the next most common, followed by foliage of *Salix*.

Scoring and analysis of the taphonomy sample produces a score very close to that of the CLAMP sample for the area (fig. 33). The taphonomy sample contains a higher proportion of fluviatile taxa than does the CLAMP sample and thus produces a score indicating somewhat wetter conditions than the CLAMP sample (see p. 50). The estimate of mean annual temperature, however, is only 0.2°C greater for the taphonomy sample than for the CLAMP sample.

Santa Rita.—A single sample was collected in the ephemeral streambed where the stream is crossed by the road; the roadway forms a solid embankment that has a culvert about 10 cm above the lowest point in the streambed. The leaves had accumulated in this depressed area, presumably during the final period of runoff. The sampling site is near the topographically lowest part of the area sampled for CLAMP.

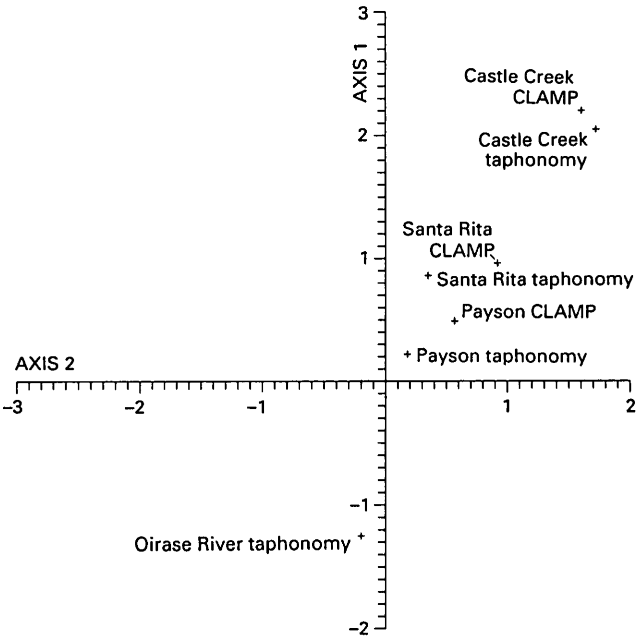

Figure 33. Correspondence Analysis plot of taphonomy samples. The taphonomy samples from Arizona plot close to the CLAMP samples obtained from the same area (see text). No CLAMP sample was collected from the Oirase River Valley in northern Honshu, but the taphonomy sample produces estimates of temperature and precipitation that are concordant with meteorological data from this area.

Only 11 species are represented in the taphonomy sample. Leaves of evergreen *Quercus* and the deciduous *Celtis*, which was in the process of shedding its leaves, are the most abundant leaves in the sample; *Quercus* is the most abundant tree in the woodland and overhangs the stream, whereas *Celtis* is the most abundant shrub within 10 m of the stream. Noteworthy is that the taphonomy sample includes some leaves of *Platanus*, the nearest trees of which are about 100 m upstream.

As in the instance of the Payson taphonomy sample, the species in the Santa Rita taphonomy sample are mostly streamside, and the taphonomy sample thus plots wetter than the CLAMP sample. The taphonomy sample, however, indicates a mean annual temperature only about 0.7°C cooler than the CLAMP sample.

Castle Creek.—The taphonomy sample was obtained by combining six accumulations of leaves that had gathered behind roots along the margins of two minor ephemeral streams tributary to Castle Creek, which is also an ephemeral stream. No leaves had accumulated from the rains on the bottom of the streambeds or in Castle Creek, presumably because of the steep gradients and (or) very high energy of the runoff. These streams drain into Castle Creek approximately 1 km downstream from the area sampled for CLAMP.

The combined taphonomy sample contains a total of 22 species, considerably more diverse than the other two taphonomy samples. The diversity is probably partly related to the high energy of the runoff and to the total diversity in the drainage area; five leaves of the chaparral shrub *Quercus*, which must have been derived from 250 to 300 m above the sampled area, were encountered in the taphonomy sample. The most abundant species in the taphonomy sample are Leguminosae (especially *Prosopis* and *Cercidium*) and *Simmondsia*; *Celtis*, a common shrub along the streams, is also represented by numerous leaves.

The Castle Creek taphonomy sample indicates as dry conditions as does the CLAMP sample, presumably because in this instance slope vegetation is well represented. The taphonomy sample yields a mean annual temperature estimate about 0.6°C less than the CLAMP sample.

Oirase River.—The sample was collected from a minor depression in an almost dry side channel of the Oirase River in early September, during the period of monsoonal rains. The high-statured, closed-canopy forest is dominated by *Cercidiphyllum*, *Betula*, and other broad-leaved deciduous trees and shrubs. The most abundant leaves in this sample are *Cercidiphyllum* and *Betula*; a total of 15 species are represented in the sample of about 500 leaves.

Scoring of the sample for CLAMP required some estimates of leaf size because the high-energy depositional environment had torn the larger leaves. The score produced by CLAMP for this sample places the sample in humid climate with an estimated mean annual temperature of about 9°C. This placement is consistent with meteorological data from this area of Honshu.

CONCLUSIONS

The Climate-Leaf Analysis Multivariate Program (CLAMP) provides a rigorous methodology for scoring and analyzing leaf assemblages and derives estimates of paleoclimatic parameters for leaf assemblages that are independent of the taxonomic placement of a given species. Application of CLAMP to fossil leaf assemblages thus circumvents the typically contentious problems of extinct taxa, changing tolerances of clades, and various assumptions relative to community stability through time. Because no identification of fossil-leaf species in terms of extant families or genera is required, CLAMP also can be applied to fossil-leaf assemblages much more rapidly than traditional, nonrigorous methods of floristic analysis. CLAMP represents a numeric analysis of the adaptive responses of leaves to environment and produces results readily interpreted in numeric terms.

Not all character states analyzed in CLAMP are adaptive in a strict sense. Some of the character states, especially basal configuration and general shape, may be determined directly by environmental conditions that prevail at the time of leaf growth. Both types of character states, however, are related to environment and thus their analysis produces estimates of the environment.

Mean annual temperature is the climatic parameter that is most accurately estimated by CLAMP; the estimates of this parameter have a standard error of 1°C or less. Estimates of cold-month mean temperature have a standard error of 1.5°C–2.0°C; estimates of this parameter for dry climates are the most accurate and progressively decrease in accuracy through mesic into humid climates. Estimates of mean annual range of temperature are dependent on estimates of cold-month mean temperature.

Precipitation parameters are strongly affected by the inclusion of the streamside element; a sample that has a proportionately large number of streamside species will indicate wetter conditions than a sample that has a small proportion of streamside species. As sample size increases, this increase typically results from the addition of more slope species, and thus precipitation estimates should become more accurate. However, if mean annual precipitation is approximately 145 cm or higher in megathermal and warm mesothermal environments, the amount of precipitation above that value appears not to be critical to leaf physiognomy and thus precipitation cannot be accurately estimated. Seasonal drought can also be generally estimated using CLAMP, but, if the driest three months have total precipitation of less than approximately 6 cm, the amount below this total cannot be estimated. Precipitation estimates can also be significantly altered by special soils; both serpentine-derived and sandy soils produce vegetation and leaf physiognomy that appears drier than vegetation and leaf physiognomy of other soil types.

In microthermal environments, CLAMP estimates of precipitation parameters are very approximate. Within microthermal climates, leaf physiognomy is apparently much less influenced by precipitation, even during the growing season, than by temperature.

The four taphonomy samples and their analyses indicate that taphonomic factors will not influence CLAMP temperature estimates; if a sample is large and thus has a large representation of slope vegetation, then precipitation estimates will probably also be unaffected. The problem of fragmentation of large leaves is not serious, probably because the species that have large leaves are typically found along streams, and the abundant shedding of large leaves into streams tends to compensate for large leaves that might be destroyed by current action. Although more data are desirable, especially from areas of closed-canopy forest, available evidence indicates that taphonomic factors will not introduce significant errors into CLAMP estimates of various climatic parameters.

Previously established physiognomic principles can and should be used with CLAMP. For example, if a leaf assemblage has several leaf species that are markedly coriaceous (and thus probably were evergreen) and have some leaves at least as large as the microphyll 3 category, then the cold-month mean temperature must have been greater than –2°C (Wolfe, 1979). Similarly, the warm-month mean temperature of 20°C approximates the division between diverse broad-leaved and diverse coniferous forests; if a fossil-leaf assemblage is from sediments that also produced a palynomorph assemblage dominated by diverse bisaccate, coniferous pollen, then the warm-month mean temperature was less than 20°C.

The overall physiognomy of vegetation—typically accompanied by major floristic changes—can change over short distances and result from critical levels of certain environmental parameters. Such changes occur, for example, (1) at the 20°C mean annual temperature isotherm, where multistratal, megathermal rain forests are replaced with lowering temperature by unstratified or poorly stratified mesothermal rain forests and (2) at the 30°C warm-month mean, where open desert (including large succulents) is replaced because of lower summer temperature by chaparral. CLAMP shows no such marked breaks in foliar physiognomy that are related to mean annual temperature; such breaks would be indicated by noticeable flattening of the curves in figures 12 and 13 at certain mean annual temperature values. That is, marked changes in leaf physiognomy, as mirrored in wide displacement along the horizontal axis, would occur in a limited temperature range. Warm-month mean temperatures are significant in producing a marked effect on overall physiognomy at certain critical values, but this is not obvious in CLAMP.

Leaf physiognomy does, however, appear to change rapidly in mesic vegetation (fig. 18) at a cold-month mean temperature of 8°C–11°C. However, in neither humid (fig. 19) nor subhumid (fig. 17) vegetation does this change in leaf physiognomy apparently occur; in subhumid vegetation, samples that have a cold-month mean between 11°C and 20°C are lacking, and thus the evidence for or against a break in subhumid vegetation is lacking.

Additional work remains to refine CLAMP. Compared to other vegetation types, few samples of humid megathermal to warm mesothermal forests are now included in the database; this lack may account for the less accurate resolution of CLAMP in humid climates than in dry megathermal climates; collections from areas such as Taiwan, mainland southeast Asia, Indonesia, and Mexico should add a significant body of data. More collections should also be added from the mesothermal to microthermal forests of Japan for comparison with samples from the anomalous mesothermal and microthermal region of eastern North America; these apparently anomalous samples will perhaps be eventually excluded from the CLAMP database. Samples from the cool-summer coastal areas of Washington and British Columbia should determine at what cold-month mean temperature leaf physiognomy switches from normal to subalpine. Mesothermal and microthermal samples from the Southern Hemisphere would resolve whether the CLAMP database of Northern Hemisphere samples can be applied to the Southern Hemisphere or whether a separate database is required. Nevertheless, CLAMP in its present stage offers the most accurate and precise method of obtaining estimates of nonmarine climates of the last 90–100 million years.

REFERENCES CITED

Afifi, A.A., and Clark, Virginia, 1990, Computer-aided multivariate analysis: New York, Van Nostrand Reinhold, 505 p.

Arthur, M.A., Allard, David, and Hinga, K.R., 1991, Cretaceous and Cenozoic atmospheric carbon dioxide variations and past global climate change: Geological Society of America, Abstracts with Programs, v. 23, no. 5, p. A178.

Bailey, I.W., and Sinnott, E.W., 1915, A botanical index of Cretaceous and Tertiary climates: Science, v. 41, p. 831–834.

———1916, The climatic distribution of certain types of Angiosperm leaves: American Journal of Botany, v. 3, p. 24–39.

Bazzaz, F.A., 1990, The response of natural ecosystems to rising CO_2 levels: Annual Review of Ecology and Systematics, v. 21, p. 167–196.

Beadle, N.C.W., ed., 1981, The vegetation of Australia: Stuttgart, Germany, Gustav Fischer Verlag, 690 p.

Benson, L., and Darrow, R.A., 1980, Trees and shrubs of the southwestern deserts: Tucson, University of Arizona Press, 416 p.

Chaney, R.W., 1924, Quantitative studies of the Bridge Creek flora: American Journal of Science, v. 8, p. 127–144.

Chaney, R.W., and Sanborn, E.I., 1933, The Goshen flora of west-central Oregon: Carnegie Institution Washington Publication 435, 103 p.

Dolph, G.E., 1979, Variation in leaf margin with respect to climate in Costa Rica: Bulletin of the Torrey Botanical Club, v. 106, p. 104–109.

Dolph, G.E., and Dilcher, D.L., 1979, Foliar physiognomy as an aid in determining paleoclimate: Palaeontographica, v. 170, pt. B, p. 151–172.

Dorf, Erling, 1942, Upper Cretaceous floras of the Rocky Mountain region: Carnegie Institution Washington Publication 508, 168 p.

Givnish, T.J., 1979, On the adaptive significance of leaf form, *in* Solbrig, O.T., Jain, S., Johnson, G.B., and Raven, P.H., eds., Topics in plant population biology: New York, Columbia University Press, p. 375–407.

———1986, On the economy of plant form and function: Cambridge, England, Cambridge University Press, 717 p.

Hill, M.O., 1973, Reciprocal Averaging—An eigenvector method of ordination: Journal of Ecology, v. 61, p. 237–249.

———1979, Correspondence Analysis— A neglected multivariate method: Applied Statistics, v. 23, p. 340–354.

Hill, M.O., and Gauch, H.D., 1980, Detrended Correspondence Analysis—An improved ordination technique: Vegetatio, v. 42, p. 47–58.

Kaji, Mikio, 1975, Studies on the ecological status of *Abies firma* forest in the Boso Peninsula (in Japanese): Tokyo University Forests Bulletin, no. 68, p. 1–23.

Leslle, L.D., 1989, Alaska climate summaries: University of Alaska, Alaska Climate Center Technical Note 5 (unpaginated).

MacGinitie, H.D., 1937, The flora of the Weaverville beds of Trinity County, California: Carnegie Institution Washington Publication 465, p. 83–151.

———1941, A middle Eocene flora from the central Sierra Nevada: Carnegie Institution Washington Publication 534, 178 p.

McClammer, J.U., 1978, Paleobotany and stratigraphy of the Yaquina flora (latest Oligocene–earliest Miocene) of western Oregon: University of Maryland, M.A. thesis, 224 p.

Parkhurst, D., and Loucks, O., 1972, Optimal leaf size in relation to environment: Journal of Ecology, v. 60, p. 505–537.

Potbury, S.S., 1935, The La Porte flora of Plumas County, California: Carnegie Institution Washington Publication 465, p. 29–82.

Raunkiaer, C., 1934, The life forms of plants and statistical plant geography: Oxford, England, Clarendon Press, 632 p.

Richards, P.W., 1952, The Tropical Rain Forest: Cambridge, England, Cambridge University Press, 450 p.

Sanborn, E.I. 1935. The Comstock flora of west central Oregon: Carnegie Institution Washington Publication 465, p. 1–28.

Sellers, W.D., and Hill, R.H., 1974, Arizona climate, 1931–1972: Tucson, University of Arizona Press, 616 p.

Spicer, R.A., 1981, The sorting and deposition of allochthonous plant material in a modern environment at Silwood Lake, Silwood Park, Berkshire, England: U.S. Geological Survey Professional Paper 1143, 77 p.

———1986, Comparative leaf architectural analysis of Cretaceous radiating angiosperms, *in* Spicer, R.A., and Thomas, B.A., eds., Systematic and taxonomic approaches in palaeobotany: Oxford, England, Oxford University Press, p. 221–232.

———1989, The formation and interpretation of plant megafossil assemblages: Advances in Botanical Research, v. 16, p. 95–191.

Webb, L.J., 1959, Physiognomic classification of Australian rain forests: Journal of Ecology, v. 47, p. 551–570.

Windsor, D.M., 1990, Climate and moisture variability in a tropical forest, long-term records from Barro Colorado Island, Panama: Smithsonian Contributions to the Earth Sciences 29, 145 p.

Wolfe, J.A., 1971, Tertiary climatic fluctuations and methods of analysis of Tertiary floras: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 9, p. 27–57.

———1972, An interpretation of Alaska Tertiary floras, *in* Graham, Alan, ed., Floristics and paleofloristics of Asia and eastern North America: Amsterdam, Elsevier, p. 201–233.

———1977, Paleogene floras from the Gulf of Alaska region: U.S. Geological Survey Professional Paper 997, 108 p.

———1979, Temperature parameters of humid to mesic forests of eastern Asia and their relation to forests of other areas of the Northern Hemisphere and Australasia: U.S. Geological Survey Professional Paper 1106, 27 p.

———1980, Tertiary climates and floristic relationships at high latitudes of the Northern Hemisphere: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 30, p. 313–323.

———1985, Distribution of major vegetational types during the Tertiary, *in* Sundquist, E.T., and Broecker, W.S., eds., The carbon cycle and atmospheric CO_2—Natural variations Archean to Present: American Geophysical Union Monograph 32, p. 357–376.

———1989, A leaf architectural analysis of the Hamamelididae, *in* Crane, P.R., and Blackmore, S., eds., Evolution, systematics, and fossil history of the Hamamelidae, v. 1—Introduction and "lower" Hamamelidae: Oxford, England, Clarendon Press, p. 75–104.

———1990a, Palaeobotanical evidence for a marked temperature increase following the Cretaceous-Tertiary boundary: Nature, v. 343, p. 153–156.

———1990b, Estimates of Pliocene precipitation and temperature based on multivariate analysis of leaf physiognomy, *in* Gosnell, L.B., and Poore, R.Z., eds., Pliocene climates—Scenario for global warming: U.S. Geological Survey Open-File Report 90–94, p. 39–42.

Wolfe, J.A., and Schorn, H.E., 1989, Paleoecologic, paleoclimatic, and evolutionary significiance of the Oligocene Creede flora, Colorado: Paleobiology, v. 15, p. 180–198.

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.

Published in the Central Region, Denver, Colorado
Manuscript approved for publication July 2, 1992
Graphic design by Patricia L. Wilber
Cartography by Springfield & Springfield
Photocomposition by Marie Melone
Tables prepared by Judith Stoeser
Edited by Judith Stoeser

☆U.S. GOVERNMENT PRINTING OFFICE: 1993-573-038/86003