

CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

CLIMATIC FACTORS OF GEOGRAPHIC VARIATION IN

YUCCA WHIPPLEI TORREY

A thesis submitted in partial satisfaction of the  
requirements for the degree of Master of Arts in

Geography

by

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The opportunity provided by California State University, Northridge, to explore new avenues of understanding is a privilege open to anyone assiduously seeking knowledge. This generous freedom must be appreciated, supported, and protected, for without determined public backing such opportunities will be lost to future generations. Geography and natural history should not be separated by too narrow a view of the nature of geography and of its clear benefits for knowing human and material distributions. Geographers must take leading roles not only in learning and teaching about the relationships of energy and living organisms to the history and development of world ecosystems; they should lead also in preserving the geographic foundations of these ecosystems before so many are destroyed that man himself cannot prosper. Universities as custodians of human knowledge, by taking initiative in locating, studying, and preserving natural areas, will provide data, materials, and lasting natural beauty through which ecosystem research can be maintained, applied, and treasured for generations to come.

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ABSTRACT

CLIMATIC FACTORS OF GEOGRAPHIC VARIATION

IN YUCCA WHIPPLEI TORREY

by

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Master of Arts in Geography

Cursory comparisons of geographic distributions fail to reveal any obvious causes for the differences of morphology found in various parts of the California range of Yucca whipplei Torrey. The purpose of this study therefore is to determine from statistical, experimental, evolutionary, and spatial relationships the most probable connections between climatological factors and development of three major contrasting morphological lines or Series of Y. whipplei. Geographically, Series 1 represents large parts of Ssps. typica and intermedia; Series 2A is in western portions of Ssps. percursa and Parishii; Series 2B corresponds with Ssp. caespitosa and eastern portions of Ssp. percursa. Apparent hybrids between Series 1 and 2A, i.e., Series 3A, or between Series 2A and 2B, i.e., Series 3B, account for large remaining populations.

Several numerical and statistical methods were used to establish

the most likely genealogical relationships among these Series, using the sample data means of 285 field studies and of an additional 1,000 potgrown seedlings transplanted to a uniform garden for comparisons. Computer studies utilizing plotted morphology diagrams, numerical taxonomy, and statistical analyses were employed to establish the most consistent ordination, or morphological ranking of types, as an hypothetical genealogy of leaf rosette morphology in Y. whipplei. Size of fruiting panicle was directly correlated with size of leaf rosette, but leaf area and volume of the largest rosette of a plant were inversely related to annual effective sunlight energy available in wet growing seasons, and were positively related to rainfall. The same factors that influenced seedling success and different growth habits determined size and duration of leaf rosettes in an independent way. Plant size in turn determined inversely the rate and positively the amount of reproduction sufficient to maintain populations in each of three fundamental types of climate: (1) Relatively Optimal climates having longest and most favorable growing seasons and maximal effective insolation; (2) Adverse climates having shortest favorable growing seasons with minimal effective insolation and most deleterious non-growing seasons often with maximal irradiation; (3) Intermediate climates with moderately long, humid or mesic growing seasons, but with variable seasonal temperatures and limitation of effective insolation due to persistent light screens such as snow, fog, cloud cover, and shade.

In Optimal climates primitive pre-series and Series 1 yuccas with thin, narrow leaves of varying length predominated while in Adverse climates only Series 2B or 3B occurred, having leaves of maximal

thickness, moderate or large width, respectively, and varying length. Thin- but wide-leaved Series 3A and 2A occurred mostly in Intermediate climates, but in some areas of Intermediate climate, populations of other Series were located instead. Series 3A, 2A, and 3B were in comparatively mesic regions. Rainfall in areas of Series 1, pre-series, and especially Series 2B was sparse, air humidity being crucial to existence of the first two.

Twenty-four climatic factors were analyzed with respect to successive genealogical or phenotypical stages of morphological development in Series, i.e., MORPHs. Positive and negative graded climate variances of Series MORPHs from the intermediate climatic factor means of presumably primitive pre-series samples clearly demonstrated clinal relationships in Y. whipplei that paralleled factor gradients. The most precisely correlated climatic index related to the morphological variants found in different geographic populations of Y. whipplei was the complex variable: Degree-days of the  $-2.2^{\circ}\text{C}$  ( $28^{\circ}\text{F}$ ) Growing-Season having 13 mm (0.5 inch) or more of monthly precipitation. The relations between morphological development and climatic factor gradients supported the numerically derived genealogy of morphological Series within Y. whipplei. These relationships also provided a consistent and fundamental rationale based on energy availability by which to explain some evolutionary adaptive patterns found in these geographically unique plants.

CLIMATIC FACTORS OF GEOGRAPHIC VARIATION  
IN YUCCA WHIPPLEI TORREY

I. INTRODUCTION AND STATEMENT OF THE PROBLEM

The purpose of this thesis is to investigate by various quantitative measurements and statistical methods the relationships between morphologically varying populations of Yucca whipplei Torrey and the local climatic factors of their environments. Yucca is a genus of the Agavaceae family, named for the agave or century plant, and is native predominantly to the sunny, warm, southern regions of North America. Approximately forty Yucca species include Adam's needle (Y. filamentosa Linnaeus) and Joshua tree (Y. brevifolia Engelm.). Yucca whipplei Torr. is found only in the southern half of California, northern half of Baja California, and northwestern Arizona.

First, the published subspecies and their variation are discussed and a revised gradational grouping based on three major morphological clines or Series is proposed with evolutionary considerations. Then the geographic distribution of the various populations is described, and finally both the distribution and evolution of the clines are explained on the bases of geography, climate, and seasonal energy resources.

Yucca whipplei has long attracted the attention of botanists and

entomologists because of its pollinators, variability, and longlived monocarpic habit, i.e., plants with a habit of flowering only once in a lifetime. The huge inflorescences and long vegetative period as an acaulescent, i.e., trunkless, herbaceous plant, and its three varieties of exclusively symbiotic pollinating moths, signified an ancient and singular evolutionary history for Y. whipplei in the California region, but taxonomy in the species has proved to be difficult.

#### A. Taxonomic Review of Yucca whipplei Torr.

Geographic variations in plant morphology and in growth form or habit in Y. whipplei have been studied in efforts to clarify the taxonomy of this complex species (Trelease, 1902; Haines, 1941; McKelvey, 1947; Webber, 1953; Epling and Haines, 1957; Hoover, 1973). Five subspecies were recognized by Haines (1941) on the bases of predominant growth form and the sizes of leaf rosettes and fruiting stalks in large geographically distinct populations (Fig. 1, 2). Populations of predominantly rhizomatous habit from Santa Barbara County to the northern limits of the species in the Santa Lucia Mountains he named Subspecies percursa. Cespitose populations of the Greenhorn, Piute, Tehachapi, Ridge Basin and San Emigdio mountains, and of the western Mojave Desert margins, he called Subspecies caespitosa (Jones). Haines based Subspecies intermedia on plants having the habit of several leaf rosettes with only one flower stalk formed in a season, found in the Santa Monica and Santa Susana mountains. Haines (1941) and McKelvey (1947) considered this habit to be intermediate between cespitose habit in which numerous leaf rosettes form a dense, long-lived clump producing several flowering stalks in a season and monocar-

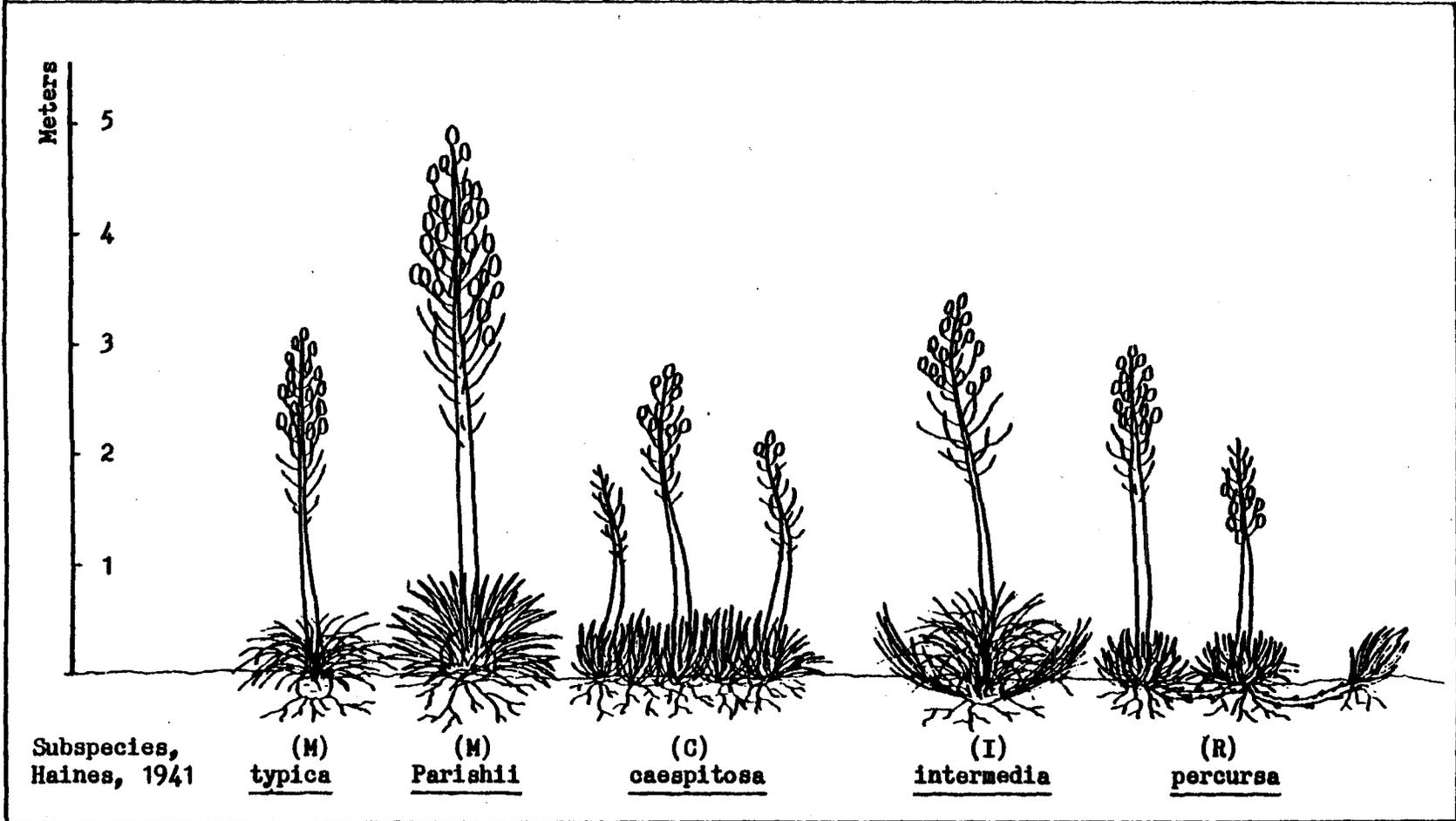


Figure 1. Types of Habit in Haines's Subspecies of Yucca whipplei Torr.

Habit Symbols: (M) = Monocarpic, (C) = Caespitose, (I) = Intermediate, (R) = Rhizomatous

Table 1. Distribution of Growth-Form or Habit in Haines's Subspecies of Yucca whipplei and Series.

a. Distribution of Habit.					
Subspecies, Haines, 1941	<u>typica</u>	<u>Parishii</u>	<u>caespitosa</u>	<u>intermedia</u>	<u>percursa</u>
Typical Habit	Monocarpic	Monocarpic	Cespitose	Intermediate	Rhizomatous
Percentages of Typical Habit in Population Samples	50-100	12-100	50-100	0-50	25-100
Other Habits* Found, Mean Percentages in Population Samples	C = 0-25 R = 0-23 I = 0-50	C = 0-68 R = 0-10 I = 0-30	R = 0-50 M = 0-20 I = 0-17	C = 15-100 R = 0-55 M = 0-32	C = 0-33 M = 0-65 I = 0-47
Sub-Populations Differentiated By Series Morphology	Pre-Series, Series 1, 2A, 3A, 3B	Series 2A, 2B, 3A, 3B	Series 2B, 3A, 3B, 2A	Pre-Series, Series 1, 3A,	Pre-Series, Series 2A, 3A, 2B
b. Distribution of Haines's Subspecies in Morphological Series.					
Morphological Series	Ssp. <u>typica</u>	Ssp. <u>Parishii</u>	Ssp. <u>caespitosa</u>	Ssp. <u>intermedia</u>	Ssp. <u>percursa</u>
Pre-Series	x			x	x
Series 1	x			x	
Series 2A	x	x		x	x
Series 2B		x	x		x
Series 3A	x	x	x	x	x
Series 3B	x	x	x		

\* Symbols for habit are as in Figure 1. Data is from D. Hoover, 1973, Appendix iii.

pic or solitary rosette habit in which the whole plant dies after the first seed production.

Monocarpic yucca populations in the San Gabriel and San Bernardino mountains were called Subspecies Parishii (Jones) by Haines (1941), who distinguished them by their great average size and bluegreen glaucous foliage from widespread monocarpic populations with smaller rosettes of flexible yellowish greygreen leaves. The latter monocarpic group Haines called Subspecies typica, the geographic range of which included the Santa Ana Mountains and most of the Peninsular Ranges south of Riverside extending into northern Baja California. The geographic distribution of Haines's subspecies is shown in Figure 2 with additional ranges of Y. whipplei discovered by subsequent workers. Characteristics of habit and morphology found in population studies of Haines's subspecies (Hoover, 1973) are set forth in Table 1 and Figures 1 and 3.

McKelvey (1947) and Webber (1953) thought Spps. Parishii and typica should be combined because both populations consisted predominantly of monocarpic plants and because their ranges of size and geography partially overlapped. Epling and Haines (1957) agreed and designated the combination as Y. whipplei Subspecies whipplei. However the two monocarpic subspecies again were separated by Munz and Keck (1959, pp. 1361-1362) who located Ssp. Parishii in only the front ranges of the San Gabriel and San Bernardino mountains. The range of the smaller monocarps, called Ssp. whipplei, extended from Orange and Riverside counties south into Baja California.

Disjunct monocarpic yucca populations occurring in Arizona along the southeast bank of the Colorado River and Lake Mead had leaf dimen-

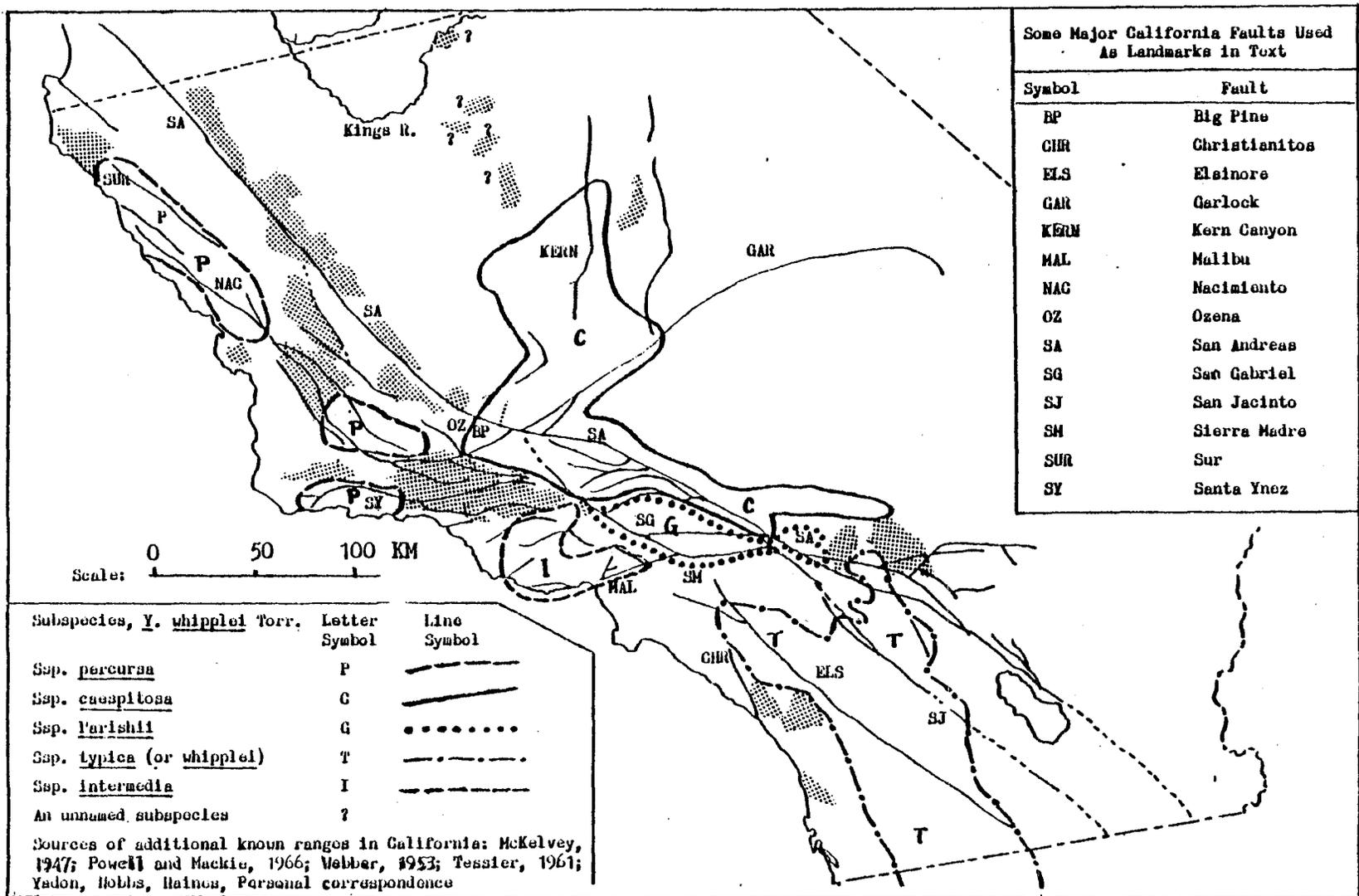


Figure 2. The Geographical Distribution of Haines's (1941) Subspecies of *Y. whipplei* with Subsequently Added Locations. Based on Geological Map of California in Oakeshott, 1971.

sions like Subspecies caespitosa (Webber, 1953). The Arizona plants, named Yucca Newberryi by McKelvey (1947), were relegated to Subspecies newberryi (McKelvey) of Y. whipplei by Webber (1953). A caespitose population in the Vizcaino Desert of Baja California was named Yucca peninsularis by McKelvey (1947). A new caespitose subspecies of Yucca whipplei from the same region was described as Subspecies eremica by Epling and Haines (1957) without mention of McKelvey's Y. peninsularis. From descriptions given, Y. peninsularis and Ssp. eremica appeared synonymous, and Shreve and Wiggins (1964) designated both as Subspecies eremica of Yucca whipplei.

That plant habit is subordinate to morphology in differentiating large geographic populations of Y. whipplei was shown by Hoover (1973). Habit mixtures often occur within a single local population sample regardless of general morphology (Table 1). Large contiguous geographic subspecies populations also exist with different predominant habits but with nearly identical leaf and rosette morphology. The term morphology in this thesis, as in Hoover (1973), is restricted explicitly to leaf counts and dimensions of largest leaves and the largest leaf rosette of a yucca plant, and also dimensions of largest fruit stalk of the same plant. Growth form or habit as used here, similar to Raunkiaer's (1934) use of life form and to Haines's (1941) use of growth form, refers to manner and degree of vegetative branching and number of flower stalks formed in a season on a single plant. No better terms were found in botanical usage for this type of distinction in the description of plants.

Because all populations of Y. whipplei are predominantly acaulescent, i.e., trunkless (Munz and Keck, 1959, p. 1361), manner of vegeta-

tive branching is restricted to rhizomatous, caespitose, intermediate, and monocarpic, the last having solitary or non-branching rosettes. In caespitose and rhizomatous plants more than one flower stalk per plant are formed in a season. In monocarpic and intermediate habits a single flower stalk forms in a season, but of the two only the intermediate plant, which has several leaf rosettes by the time of flowering, survives to produce flowers another year (Haines, 1941; Webber, 1953; Hoover, 1973).

Three major morphologically differentiated lineages in Yucca whipplei called Series 1, Series 2A, and Series 2B (Fig. 3) were recognized by Hoover (1973). Yucca Series were distinguished by their contrasting directions of morphological development or evolution. In sample means of Series 1, leaf length was maximal but leaf width and thickness were about minimal compared with sample means of other Series (Appendix A). Series 2A samples had maximal leaf widths, up to two or three times that of Series 1, but showed comparatively little difference from Series 1 in leaf thicknesses and lengths. Series 2B samples had maximal mean leaf thicknesses but minimal to average leaf widths and lengths. Leaf thickness in sample means of Series 2B was from one and a half to twice that in Series 1 or 2A (Appendix A) but individual plants showed yet more extreme differences between Series.

Series 3A populations were presumed hybrid because of intermediate dimensions between the means of Series 2A and 1 (Appendix A) and often because of high percentages of sterile stalks or aborted pods or both (Hoover, 1973, pp. 54-59). Series 3B showed similar indications of hybridity and were either hyperstatic or intermediate in mean dimensions between Series 2A and 2B as in Figure 3 (Hoover, 1973). Pre-

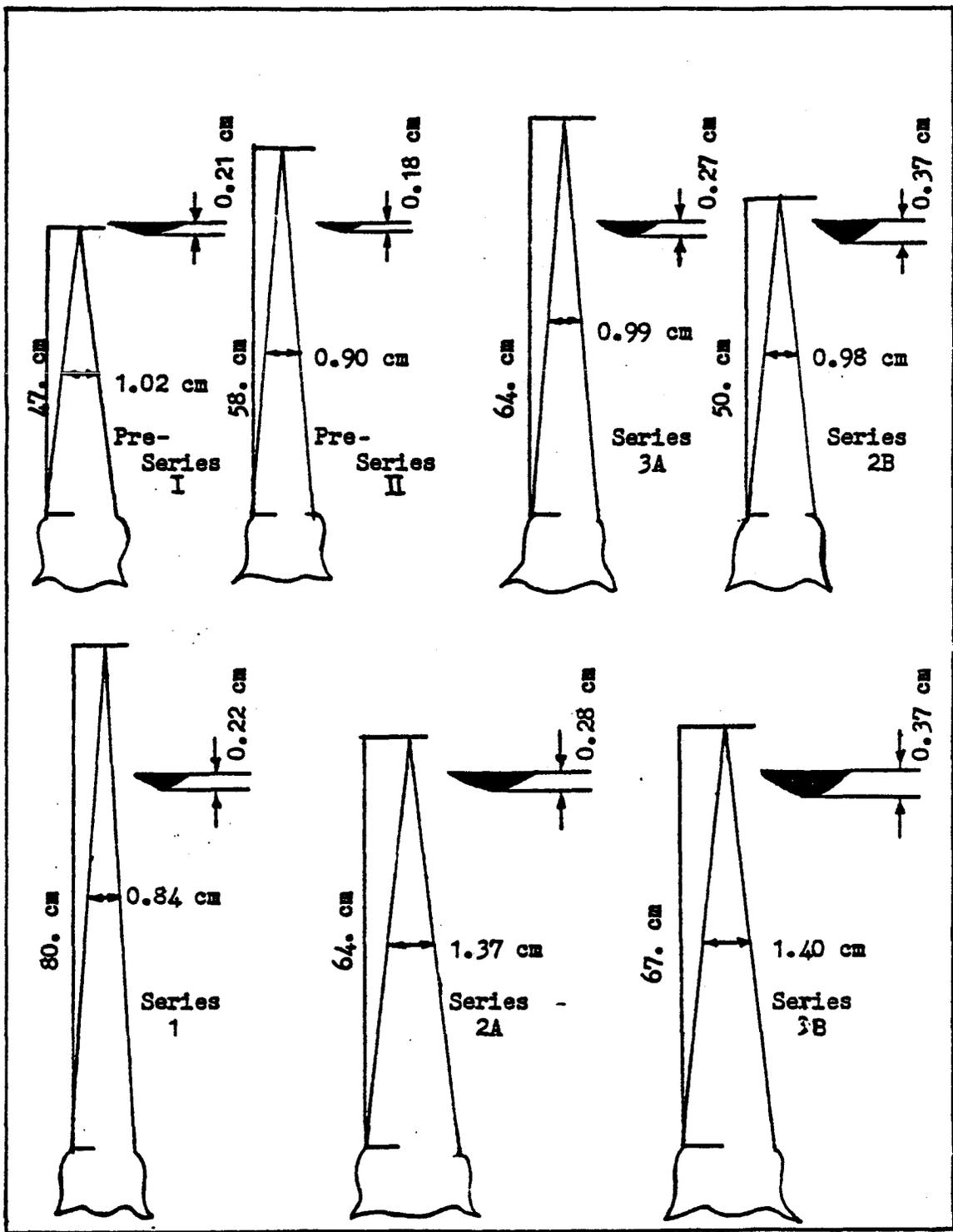


Figure 3. Leaf Morphology in Two Pre-Series Groups and Five Series of *Yucca whipplei*. Data from Table 7, Appendix A. Scale of Leaf Dimensions: Cross section at midpoint of leaf blade (  ) = 1:1; Leaf Length = 1:10; Leaf Width at midpoint (  ) = 1:2.

series samples represented the smallest forms of Y. whipplei found, one group (II) of which had mean leaf proportions resembling Series 1, the other (I) resembling Series 2A in leaf form.

These lineages were called Series because in each there were two or more distinct geographical sub-populations distinguished by habit dominance (Table 1). In Series 1 were monocarpic populations in the Peninsular Ranges, i.e., Ssp. typica, and mixed-habit populations in the Santa Monica Mountains, i.e., Ssp. intermedia. In Series 2A were mixed-habit and monocarpic populations of Ssp. Parishii and rhizomatous populations called Ssp. percursa. Series 2B encompassed large cespitose populations in the desert margins, northern Transverse Ranges, the Tehachapi and southern Sierra Nevada, as well as rhizomatous populations in the Temblor-Diablo ranges and San Emigdio Mountains.

Populations in the range of Ssp. Parishii (Haines, 1941) were subdivided morphologically as Series 2A and as hybrids like the central Sierra Nevada yuccas called Series 3B (Hoover, 1973). Series 3B = Series 2B X Series 2A. Subspecies typica (Haines, 1941) consisted of two large morphologically distinguished populations: (a) Series 1 in the Santa Ana Mountains and (b) hybrids or transitional populations called Series 3A, west and northwest of the San Jacinto Mountains. Series 3A = Series 1 X Series 2A. Therefore, although both Subspecies Parishii and typica were defined by habit as monocarpic in large parts of their ranges, each consisted of different morphologically defined genetic lineages (Appendix A; Fig. 1, 2, 3), (Hoover, 1973). Consequently, Ssps. typica (or whipplei) and Parishii should be retained as distinct subspecies of Y. whipplei, but the range of Ssp. typica as here understood is limited to the part of its region west of Elsinore

Fault (Fig. 2). Other parts of the range designated by Haines (1941) as Ssp. typica are occupied by monocarpic populations of Series 3A, or else 2A and 3B in the easternmost Peninsular Ranges, as in Haines's range of Ssp. Parishii.

Haines's Ssp. percursa consists of Series 2A in the northern Santa Lucia Mountains; Series 2A and or pre-series in the Santa Ynez and Sierra Madre-San Raphael ranges; Series 2B in the Diablo-Temblor ranges; and Series 3A in the southern Santa Lucias near San Luis Obispo and in Ventura County. (Morphological differences between yuccas of the coastal and interior Coast Ranges also were recognized independently by Vernon Yadon of the Pacific Grove Museum of Natural History, personal communication, September 26, 1970.) It can be seen therefore that each existing taxonomic subspecies is a comparatively artificial compendium of various morphologically distinct races united by similar growth habit and by contiguous geographic ranges into a single taxon. Taxonomic revisions will be published separately. Evolution of Series morphology and their distribution are major topics in this report and discussion of pre-series yuccas as a group is reserved for Chapter II.

#### B. Geographic or Physiographic Limits of Yucca Migration

Observers in the field (Haines, 1941; McKelvey, 1947; Webber, 1953; Hoover, 1973) agreed that Y. whipplei is virtually restricted to well-drained ridges and slopes of usually porous granular soils or rapidly drained sloping flood plains or ephemeral torrent beds. Yucca whipplei is never successful in marshy meadows nor in river valleys where the water table may rise to the surface for several hours at a

time in winter. Standing water after storms around the plant knolls in the Encino transplant garden frequently killed plants at the lower edge of the knolls but those growing only a foot or so above the water level usually survived. Standing water table therefore accounts, more than any other factor observed, for the absence of Y. whipplei in most valley bottoms or on gently rolling grasslands where soil can become oversaturated. Yuccas that do occur on gentle knolls are nearly always restricted to outcrops of bedrock in aerated gravelly soil of fissures and rapidly drained ledges. The fact that larvae of the obligate pollinator moth (Tegeticula maculata (Riley)) overwinter in the soil of a yucca colony (Powell and Mackie, 1966) also restricts yuccas from migration across wide river valleys where an annually rising water table would drown the larvae.

The evident requirement for maximum winter insolation (Ch. IV) as well as for well-drained soil tends to limit Y. whipplei colonies to predominantly south-facing slopes or bluffs in many areas (Haines, 1941; Hoover, 1973). However, in the hottest, driest, southern parts of its range Y. whipplei frequently extends around to north-facing slopes of low hills. These exceptional cases may be attributable to longer retention of optimal soil moisture on somewhat shaded slopes and also to adequate sunlight because of the relatively high angle of solar incidence in lower latitudes and to an increased proportion of diffused radiation available in humid air near the coast.

Although large areas of southern California long have been subject to agriculture and urban development, there is frequent evidence as to whether or not Y. whipplei formerly occurred in such regions. Yuccas still are to be found on bluffs, empty lots, steep parklands, and road-

sides in urban areas where they once were plentiful. Elsewhere their present absence from all undeveloped and suitable habitats, such as ridges, bluffs, and dry stream gullies around agricultural acreage or on isolated mountainous ridges across from other yucca-populated mountains now surrounded by urban development, is a reasonably dependable indicator that they did not occur there prior to settlement. Geological maps show that very few areas known to have been submerged in the Pleistocene by eustatic sealevel rises or by local subsidence of marine basins have any existing yucca colonies. Yet, along the Malibu coast, Y. whipplei covers the cliffs down literally to the edge of the strand. The sharp boundaries between yucca populations of contrasting morphology frequently coincide with river valleys and the borders of ranges of all Series excepting Series 3B often are defined still by Pliocene-Pleistocene shorelines (Ch. III).

#### C. Some Evidence of Great Geological Age of Y. whipplei

Without recognizable well-dated fossils it is impossible to assign a definite age to ancestral Y. whipplei. However, some geographical and biological indications support Axelrod's conclusion (1958, pp. 439, 460-461) that Y. whipplei was among very ancient members of the Madro-Tertiary geoflora, based on distribution, isolation, and floristic association. Paleogeography throughout the Cretaceous limited local ancestors of this flora to the western Cordillera south of the more ubiquitous Arcto-Tertiary geoflora but north of the South America coast where only Yucca elephantipes Regel is known, usually associated with human settlements. A Gondwanaland distribution of

several Agavaceous genera other than Yucca and Agave indicates a possible early differentiation of Yucca from common ancestors after the breakup of Pangea (140,000,000 y.b.p.) to account for Yucca's Laurasian distribution.

No other examples among the forty species of Yucca are found with the unique flower structure and multiple varieties of obligate pollinator moths known in Y. whipplei (Powell and Mackie, 1966), which plants Trelease (1902) assigned to a separate genus, now subgenus, Hesperoyucca. Most Yucca species have only Tegeticula yuccasella (Riley) as pollinators, but yuccas now occurring within the boundaries of the Cretaceous Cordillera have been associated with a number of other obligate pollinator Tegeticula species (pp. 15-17). The Joshua tree, Yucca brevifolia Englemann, has T. paradoxa (Riley) as its sole pollinator. Another moth, Tegeticula mexicana Bastida-Urrida, is associated with Yucca filifera McKelvey (1947) from San Luis Potosi, according to Powell and Mackie (1966). Yucca schidigera and Yucca baccata, both of which frequently are sympatric with Y. whipplei and or Y. brevifolia in California, are pollinated by T. yuccasella as are most yuccas (Powell and Mackie, 1966). This southwestern and once coastal distribution indicates a possible center of moth and yucca coevolution located originally near the once southern tip of the Cretaceous Cordillera in the region formerly existing southeast of Yuma, Arizona. Due to lack of space, detailed discussion of geological and paleogeographical relationships in Agavaceae must be reserved for later publication.

D. Life-Cycle and Variation of the Pollinator Moths,  
Tegeticula maculata (Riley)

Tegeticula maculata (Riley)--0.75 to 1.00 cm long--is closely related to but much smaller than nocturnal Tegeticula yuccasella (Riley)--1.25 to 1.50 cm long. Diurnal activity of T. maculata was affirmed from extensive observations (Powell and Mackie, 1966), and recent photographic studies seem conclusive (Aker and Udovic, 1981). As in T. yuccasella, the female moth is the exclusive pollinator and usually appears simultaneously with the yucca flowers in spring. She gathers a number of waxy pollinia, carefully packing them together in a rather large mass carried close to the thorax by specialized maxillae (Powell and Mackie, 1966). Aker and Udovic (1981) have confirmed that the moth immediately flies some distance to another part of the yucca population, an act that effectively precludes inbreeding of the yuccas. The moth carefully selects an ovary in a recently opened flower, apparently avoiding flowers that already have been pollinated, and after much tapping and searching inserts an egg into a septal groove of the ovary. Immediately afterward she diligently strokes the sticky hairy surface of the stigma with the pollen, and then she may lay one or several eggs elsewhere in this or other flowers. Pollinating movements were not repeated after subsequent egg insertions according to Aker and Udovic (1981), but Powell and Mackie (1966) reported otherwise. I have never been able to observe this process in spite of frequent attempts.

It is not known how long the adult moth lives nor how many eggs she is capable of producing, but it is virtually certain that only one season is spent as adult and one summer as feeding larva. The eggs

hatch after a pause of several weeks and larvae begin to eat the milky endosperm of ripening yucca seeds. By the end of summer each larva is found in a silk-lined case consisting of a series of 4 to 12 hollowed-out seeds and with a circular window cut through to the outer epidermis of the seed pod, the epidermis sealing the larval case. After a stimulus such as severe shaking of the seed pods, or presumably after a fall rainstorm (Powell and Mackie, 1966), the larvae quickly squeeze through their windows and drop to earth. They crawl rapidly away and finally bury themselves a few centimeters deep in loose, preferably damp, not wet, soil where they form a second cocoon. The succeeding diapause lasts through the winter, but they remain as potentially active larvae until a few weeks prior to flowering when they pupate prior to emergence as adults (Powell and Mackie, 1966). What stimulates pupation is not known. In my own experiments the larvae remained active and capable of reburying themselves for more than a year. It is believed that under natural conditions some larvae may not emerge as adults the first year but may survive as potential pollinators to the second or third season (Powell and Mackie, 1966).

The three varieties of T. maculata are separated geographically: the southern blackwinged var. extranea (Hy. Edwards) being found in the San Bernardino and Peninsular ranges, and var. apicella (Dyer) with white wings having black-spotted apices occurring in mountains around the Los Angeles Basin and northward in the Coast Ranges. The variety T. m. maculata (Riley) occurs in the northern Tehachapis and Sierra Nevada as well as in the northwestern margins of the Mojave Desert, and has white wings speckled with black (Powell and Mackie, 1966). Oddly the color variants do not coincide with any particular

morphological or habitual variations in Y. whipplei, all three moth varieties being known from primarily monocarpic yucca populations of different Series as well as in populations of other habits. The dark-winged T. m. extranea appears to coincide with yuccas having frequently purplish or dark-edged flowers, a plant attribute that also does not coincide with Yucca habit nor morphology, but is common to the southern half of its range. North of Cajon Pass nearly all Y. whipplei flowers are of various shades of white to cream or greenish.

Because of the obligate nature of the plant-moth symbiosis, it is believed that some of the climatic factors that limit or affect the success of Yucca whipplei may act indirectly through the moth instead (Schaffer and Schaffer, 1979). Cespitose habit in Y. whipplei is known to predominate in areas where pod-set is low and moths are infrequent, both of which cases may occur where climatic conditions are harsh, or infertility due to hybridity in the yuccas is high, or both (Powell and Mackie, 1966; Webber, 1963; Hoover, 1973; Udovic and Aker, 1981).

#### E. Correlation of Climate with Growth Habit of Y. whipplei

Many climatic and geologic attributes of location are cited as causes of geographic distribution patterns and evolution of species variation. Evolutionary theory is inextricably combined with concepts of ecological variation and natural selection of the most effectively reproducing variants in a species. Nevertheless comparatively few studies of the geographic factors responsible for particular directions of plant development within a species or among related species have ever been made (Stebbins, 1950; Turesson, 1922; Clausen et al., 1941; Gregor and Watson, 1961; Babcock, 1947). Careful test garden compari-

sons of scions of variant geographic races of plants in different climatic regions were initiated by such biologists as Turesson (1922, 1925) and Gregor (Gregor and Watson, 1961). Similar tests of California native plants were carried out by the Carnegie Institution of Washington at Stanford University (Clausen, 1951; Clausen et al., 1940, 1941, 1945; Clausen and Hiesey, 1958; Hiesey et al., 1971). Quantitative associations between measurable climatic factors and the growth or development of plants have been made by plant physiologists who compared growth results in phytotrons or under specific isolated physiologic conditions of nutrients, temperature, light, and moisture (Billings et al., 1973; Mooney and Billings, 1961; Evans, 1973; Slatyer, 1973; Whitehead, 1973). Additional ecological and genetic insights have come from testing the agricultural success of growth and reproduction in cultivars under various climatic conditions in the field (Bierhuizen, 1973; Chang, 1968; Aitken, 1974).

The work undertaken here was intended as part of a broad attack on the question of evolution of geographic variation in the species complex, Yucca whipplei of California. Field measurements for a master of science thesis in biology revealed two independent patterns of geographic variation in this species: (1) differences in incidence of four distinct growth forms or habits of branching; (2) differences in mean morphological dimensions of leaves, rosettes, and fruiting panicles (Hoover, 1973). Predominant habit was found to correlate with degree of climatic favorability to rapid and successful reproduction via seedlings. The climates most favorable to seedling success have highly monocarpic populations, i.e., single rosette plants that flower only once before death. Climates least favorable to seedlings

or to seed production have cespitose populations, i.e., plants with multiple short branches at ground level. Predominantly rhizomatous populations, with plants spreading by extended underground branches, are associated with maritime coastal conditions in which fog or vegetation cover reduces effective insolation, and soil desiccation may limit survival of young seedlings but not of rhizomatous juvenile shoots (Hoover, 1973). A paleohistory of frequent fluctuations in sealevel (Birkeland, 1972) also may have selected for rapid vegetative spread by rhizomatous populations along the coast (Hoover, 1973).

All populations of Y. whipplei show some intermixture of other habits in addition to their predominant habit. Populations of Yucca whipplei just inland from the coastal rhizomatous Ssp. percursa populations, i.e., Ssp. intermedia and also Ssp. Parishii, often consist of nearly equal percentages of all four habits (Fig. 1, 4; Table 1). The habits are rhizomatous, monocarpic, intermediate, and cespitose, but the populations are termed intermediate because intermediate habit seldom occurs in such great abundance elsewhere, i.e., up to 50 % (Hoover, 1973; Haines, 1941). These mixed populations indicate that different habits or growth forms could be selected from reseeded seedling progeny of heterozygous migrating populations having dominance in characters of rhizomatous habit (Fig. 4), (Hoover, 1973).

Morphological attributes such as leaf rosette size and panicle size do not necessarily coincide with a given vegetative habit. Instead, populations of similar morphology could be divided into large geographic sub-populations of different predominant habits. Similarly the taxonomic subspecies that were based mainly on habit differences (Haines, 1941) could be either subdivided or united into large geo-

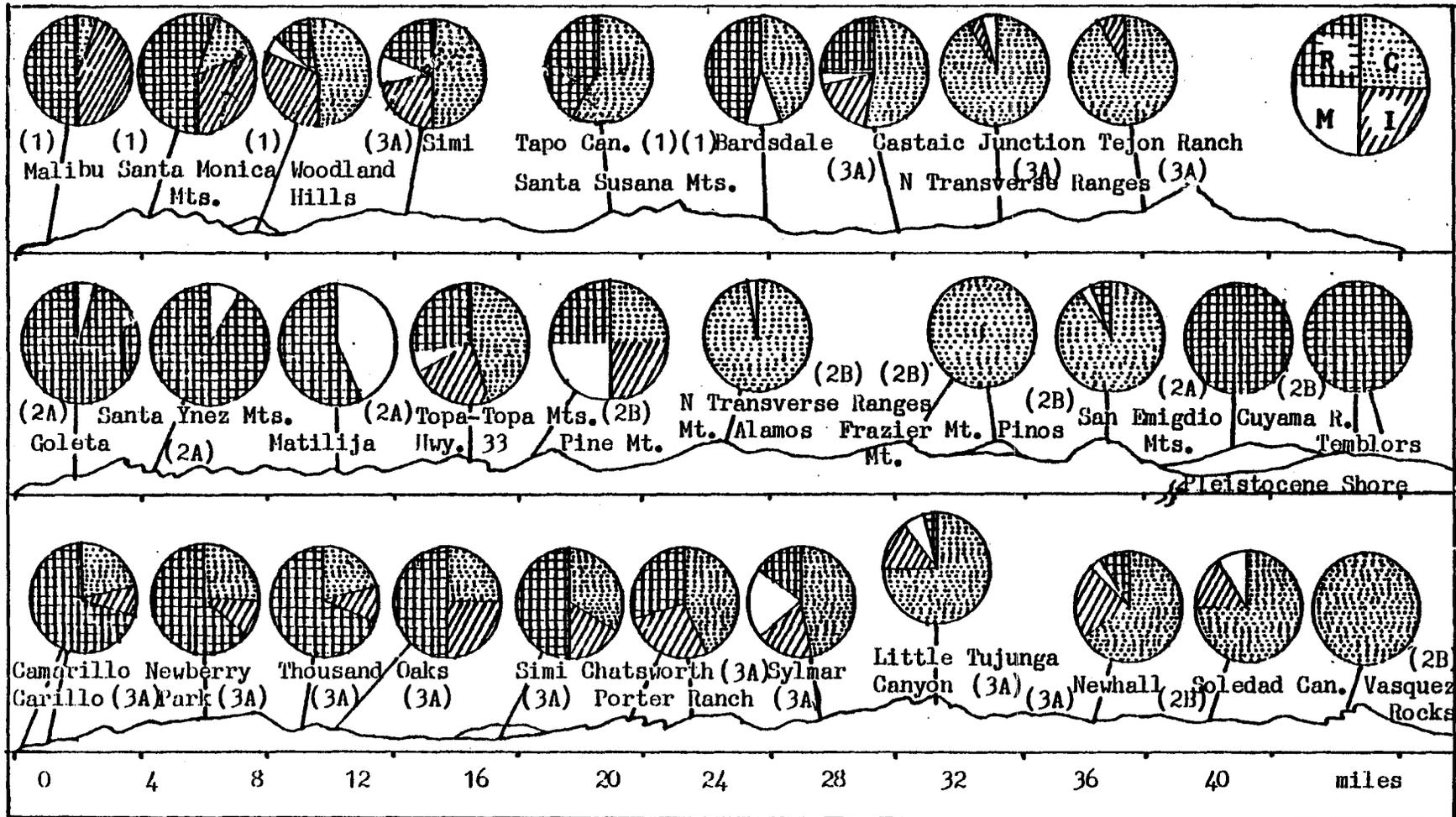


Figure 4. Percentage Incidence of Habit in *Y. whipplei* Samples Along Transects from Coast to Interior.

Habit Key: R = Rhizomatous; I = Intermediate; C = Gespitose; M = Monocarpic  
 Data from D. Hoover (1973). Scale approximate; Vertical exaggerated.

graphic races of differing morphology (Table 1, Fig. 4), (Hoover, 1973). For taxonomic purposes as well as for an understanding of evolutionary patterns and processes it was clearly necessary to study the geographic distribution of, and ecological conditions responsible for, morphological variation in Y. whipplei.

The plan for this thesis, therefore, is to determine from numerical taxonomy and statistical analysis of field measurements (1) the distribution of the morphological variants, (2) the most probable genealogical relationships among morphologically varying geographic races of Y. whipplei, and (3) the corresponding ecological factors most significantly associated with each of the morphologically distinct types. From such relationships as these can be found an understanding of the ecology of evolutionary phylogeny, and of taxonomic differences, in the Y. whipplei complex that provides an explanation of its geographic patterns of diversity.

#### F. The Conceptual Approach

Strategy for solving the question of causal relationships between patterns of geographic distribution of morphological differentiation in Y. whipplei and of varying ecological attributes of locations throughout its range was approached from the concept of biological variation known as clines (Endler, 1977; Heiser, 1973; Heslop-Harrison, 1967). Well recognized morphological clines in wild populations consist of gradationally differentiated populations generally corresponding with geographic gradients of a definable ecological factor or combination of factors. Thus clines may be recognized in a species where a morpholog-

ical trend becomes most pronounced at one end of a scale and least pronounced at the other end in conjunction with a corresponding increase or decrease in such ecological factors as groundwater saturation, exposure to light, soil acidity, or frequency of frost (Endler, 1977; Heiser, 1973).

Intermediate or transitional populations usually are separated from each other by small differences, but phenotypes at distal ends of a cline may be so well differentiated morphologically and genetically that often they can be separated justifiably as species. However, existence of transitional populations intergrading between the extremes makes taxonomic distinction difficult and these problems usually are resolved by differentiating distinguishable geographic sub-populations only to the subspecies level (Heslop-Harrison, 1967). Yucca whipplei has had such treatment because of intergrading populations, but little has been done previously to associate these morphological clines with any corresponding ecological or geographical gradients.

Two preliminary steps are necessary to accomplish the association of morphological trends in a cline with their presumably causal ecological gradients: (1) All natural populations from scattered locations must be analyzed objectively for their phenotypic differences and then ordinated numerically in a phenotypic gradient, i.e., arranged by gradational degrees of increasing phenotypic differentiation, preferably as a monodirectional series (Sokal and Sneath, 1973, pp. 3, 201, 245-253, 367-368). (2) All locations must be analyzed independently according to various ecological factors so that the locations themselves can be ordinated according to each separate factor into continuous gradients for comparison with the corresponding phenotypic ordi-

nations. These steps are complicated by the nature of multiple variation in biological species, and by the multi-factorial ecologies of their locations. One feature of the plants may vary positively with distance along a given factorial gradient, while another attribute may vary negatively or illogically. Pleiotropic, i.e., complex multiple, or combined, effects may be caused by combined multiple factors, or by complex multigenic effects stimulated by a single factor (Stebbins, 1974, pp. 102-103). In Y. whipplei and in many other wild plants, monodirectional ordination in a single gradient is difficult to conceive because of recognized variations along three or more separate lines of differentiation. This conceptual difficulty can be overcome by visualizing two or more separate clines, each evolving independently from different chronological or geographical points of origin.

Other ways to approach the question of causal relationships are by statistical analyses formulating correlation coefficients, and by methods of numerical taxonomy (Sokal and Sneath, 1973). In numerical taxonomy variant sample populations are compared individually with each other and are arranged numerically by their differences into branching series that link all similar samples into like groups separated from unlike groups in ranked phenotypic or hierarchic order. Several of these types of analysis were tried, each of which helped to corroborate or to indicate discrepancies in other findings.

In addition to field studies, various experimental germinations and plantings of seedlings from different geographic races of Yucca whipplei were compared as to effects of some ecological variables on growth and development. The transplanted seedlings provided indisputable evidence that the same morphological and habit differences

observed in wild samples of Y. whipplei remained strikingly characteristic of their parent populations when seedlings were grown together in a single uniform environment. This evidence demonstrated a genetic basis for plant differences like that revealed for geographic races in a broad group of native California plants by the work of Hiesey et al. (1971), Clausen et al. (1940, 1941, 1945), and others. The combined results of all these observations and analyses, it is hoped, represent the most plausible and least idiosyncratic interpretation of geographical evolution in Y. whipplei possible at this time.

## II. ORDINATION OF GEOGRAPHIC POPULATIONS OF Y. WHIPPLEI

Multivariate morphologies and ecologies that distinguished or accompanied the various geographical races of Y. whipplei were ordered quantitatively for two purposes: (1) to make possible needed phenotypic and ecological comparisons and (2) to reveal geneological relationships. Ordination of samples, as used here, means the measurement of degree of mean overall morphological development of samples, allowing the arrangement of the samples in an ordered or ranked array, as along the ordinate of a graph. Ordination differs from ordinal ranking in having real numbers derived from actual measurements as the criteria for ordering. Such objectively ranked gradients of plant morphology can be regressed against geographic gradients, such as distributions of annual temperature or rainfall means, or total climatic favorability to general plant growth. Factors of selective processes by which environment influenced the evolution of plant taxa and growth forms then could be recognized. Populations morphologically similar in the most ways were assumed to be genetically more closely related to each other than to groups with fewer similarities (Sneath and Sokal, 1973, pp. 5, 106-113, especially No. 7, p. 113). Ordination, i.e., ordering, placed together the most similar entities of a variable group and showed the most probable genetic and early geographic relationships among the different plant types as indicated by the characters measured. Evolutionary convergence or parallelism was assumed for variation in plant habit within the main three diverging morphological lines of Yucca

whipplei. Without knowing the chronology of evolutionary stages in specific populations sampled, morphological convergence could not be identified except in evidently hybrid populations.

#### A. Sources of Data on Plant Variation in Yucca whipplei

In previous research on population variation in Y. whipplei (Hoover, 1973), comparisons of 168 samples in wild populations revealed that this complex species consisted of three major branches called Series 1, 2A, 2B, and their apparent hybrids, Series 3A and 3B. Since 1973, additional field samples obtained for the present study increased the statistical resolution of plant variability in some neglected areas to bring a total of about 300 samples, or more than 3,000 measured plants (Fig. 3, 5, Appendix A). Field data consisted of six measurements of the largest leaf, leaf rosette base, and fruiting stalk of each plant and enumerations of leaves per rosette, rosettes and stalks per plant (Appendix A). Sample sizes varied from two to thirty plants, averaging about ten. Habits, ecological factors, vegetation, and other quantitative variables were noted in each of several, small, wild sample areas of large yucca populations. Field data in each sample were reduced to means and percentages and sums of squared differences from the means by standard statistical methods for subsequent statistical analysis. Both individual and summarized data were analyzed simultaneously by t-test, F-ratio, and ANOVA at different grouping levels by standard statistical methods. Other details of statistical approaches are presented in the text with summaries of particular analyses.

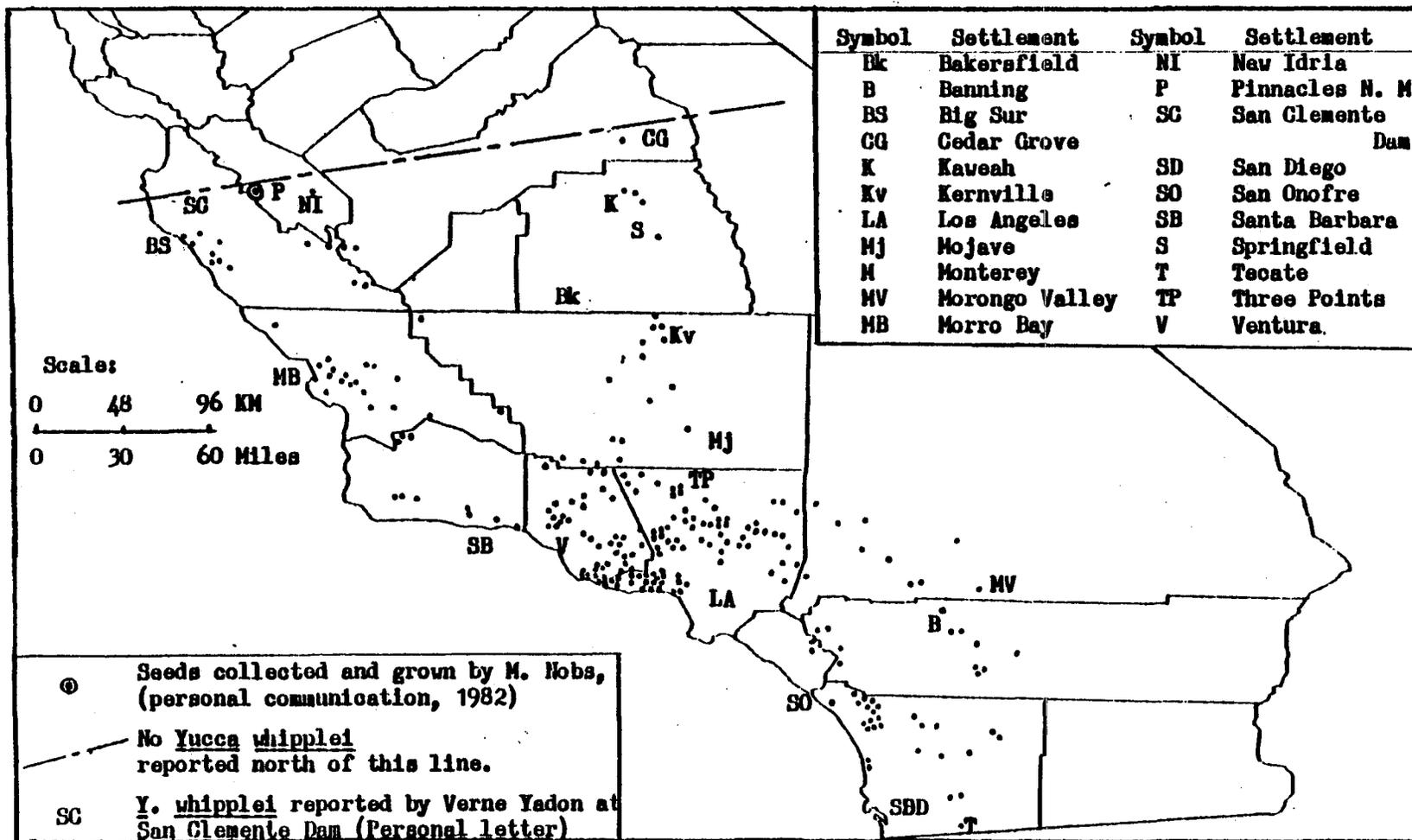


Figure 5. Station Locations of Field Samples of Yucca whipplei Populations in California

Additional data were obtained for experimental purposes from yucca seedlings germinated in pots in the University greenhouses and later transplanted to the relatively uniform environment of a test garden.

B. Morphological Gradients as Arbitrary Scales of Evolution  
in Yucca whipplei

Taxonomists and other biologists in general have disagreed on the possibility of establishing the true genealogical relationships of any modern groups of species without relatively complete fossil and genetic records. Very few, if any, plant groups have qualified for genealogical interpretation with such rarely obtained prerequisites (Hughes, 1976, pp. 14-31). Nevertheless repeated attempts have been made to find the natural phylogenetic organization of living organisms. Numerical taxonomists have actively pursued such goals using the fundamental assumptions described by Sokal and Sneath (1963).

Biological evolution generally is assumed to occur in relatively small stepwise changes (Stebbins, 1950, pp. 85-152, 551-556). Therefore, according to numerical taxonomists, the greater the number and degree of changes, the longer and greater was the differentiation process separating two races from a common ancestor and from each other. However, if there is relatively little phenotypic differentiation because of bradytely or parallel evolution or lack of divergent selective pressure, only the age of fossils can show how old the genealogical relationship actually may be. Two organisms that maintain a very close similarity do not necessarily have a relatively short history of differentiation from a common ancestor. Some

present-day sporebearing plants and "living fossil" animals match exceedingly early fossils, as shown by Smith and Rand (1975), Galston (1978), Ferris et al. (1976). Nevertheless, phenotypically similar races within a species usually are more closely related than are the phenotypically dissimilar races (Sokal and Sneath, 1963) and probably were differentiated more recently than races with obviously greater genetic dissimilarity. Without any better guidelines, likely genealogies are formed by the least number of genetic steps required to join all the variant races into a relatively continuous, parsimonious, and logical developmental sequence (Sneath and Sokal, 1973, pp. 31-35).

Based on these principles, a genealogy of the developmental variation in Y. whipplei has been devised:

Races of Y. whipplei with smallest mature leaf rosettes and thinnest, shortest, and narrowest leaves appear to be more primitive than races having largest rosettes and widest, longest, or thickest leaves, or than races of intermediate dimensions.

Four non-statistical lines of evidence supported this view:

(1) By starting with the smallest and gradually increasing the theoretical minimal number of "active genes" necessary to affect the different leaf dimensions, the most parsimonious genealogy resulted; that is, fewer genetic steps or mutations were required to attain all the discovered kinds of Y. whipplei leaves than if one started with the maximum-sized leaf type and worked backwards. Also more steps were required to attain all the discovered kinds of Y. whipplei by starting in the middle and proceeding both ways toward the various leaf extremes than by starting with the smallest (Sneath and Sokal, 1973,

pp. 44-45, offer an example of this method).

(2) The fewer the structural genetic units expressed morphologically, probably the less physical energy was required and the more "economical" was the evolutionary phase in terms of plant expenditure of energy. Small leaf rosettes were most frequent in Y. whipplei where external conditions supplied abundant energy for rapid photosynthesis. In regions where minimal amounts of energy were available annually, but water was abundant, plants with the largest and most long-lived rosettes were found (Ch. V), (Stebbins, 1974, pp. 332-333). Samples with greatest leaf thickness occurred in regions of greatest temperature variability combined with greatest seasonal drought and extremely high insolation. The largest phenotypic leaf adaptations involved the greatest degrees of genetic expression and therefore the greatest output of metabolic energy. Only in environments where survival favored plants in which this capacity for increased production and utilization of energy was pre-adaptive would such uneconomical energy-requiring differences become dominantly frequent.

(3) A third line of evidence for a developmental genealogy of Y. whipplei from small to large leaf rosettes was based on historical biogeography and paleoclimatology. That maximum leaf and rosette development evolved latest in geologic time was supported by (a) the environments of present-day distributions of Y. whipplei morphologies and (b) paleoclimatic evidence of the onset of adverse climatic conditions during the Pleistocene glacial phases. Mild, subhumid climates now in areas of least-developed yucca morphologies were grossly comparable with late Cretaceous and early Tertiary climates, but largest, thickest leaves predominated at high elevations and other regions of

severe climatic changes comparable to the Pleistocene.

(4) Hybridity probably was responsible for the character of the most highly developed morphological type and for the frequency of abortive seedpods and relatively sterile panicles of these Series 3B yuccas (Hoover, 1973). Series 3B yuccas evidently were derived through the geographic overlap of Series 2B and 2A, both of which were culminations of separate selective trends (Ch. IV). The combination of genes for maximum leaf width and length (Series 2A) and leaf thickness (Series 2B) was expressed as hyperstasis, i.e., hybrid vigor, in Series 3B which often achieved maximum size in all dimensions (Fig. 6, 7).

Several methods of ordering were devised to improve resolution of this theoretical sequence of small to large plants, and to achieve the best and most consistent ordination of population samples in Yucca whipplei. Results varied in quality and dependability but each method contributed to the understanding of others and therefore is discussed.

#### B-1. Developmental Rank Index (DRI)

A simple taxonomic key based on leaf width, length, and thickness did not result in a monodirectional scale of yucca leaf morphology. Consequently various weighting devices were studied to find a combination using leaf dimensions that would prevent quantitative magnitude in one dimension--length--from obscuring contributions of the other two. In previous studies, leaf thickness was a more significant source of differentiation than leaf width, and leaf width was more significant than leaf length (Hoover, 1973).

A numerical quantity that reflected the relative importance of

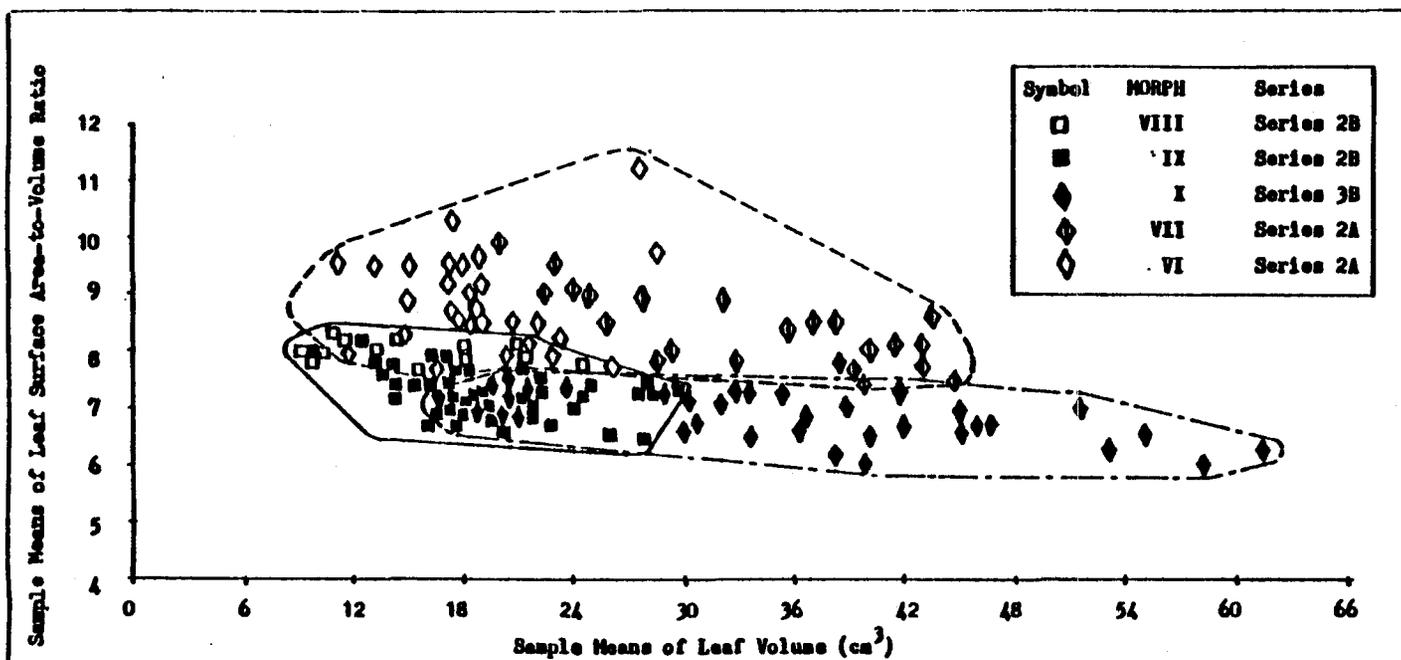


Figure 6. Morphological Relationships of Hybrid Series 3B and Its Putative Parental Races, Series 2A and Series 2B, *Yucca whipplei*, Leaf Volume vs. Leaf Surface-Area-to-Volume Ratio.

\* Methods of Calculating Leaf Volume and Leaf Surface-Area-to-Volume Ratio: Mean Sample Volume =  $V = LWT$ . Mean Surface-Area of Sample =  $A = 2L(W + T)$ . Leaf Surface-Area-to-Volume Ratio =  $A/V = 2(W + T)/WT$ . L = Mean Longest Leaf Length of Largest Rosette of a Plant. W = Width at Midpoint of Longest Leaf of Plant. T = Thickness at Midpoint of Longest Leaf of Plant.

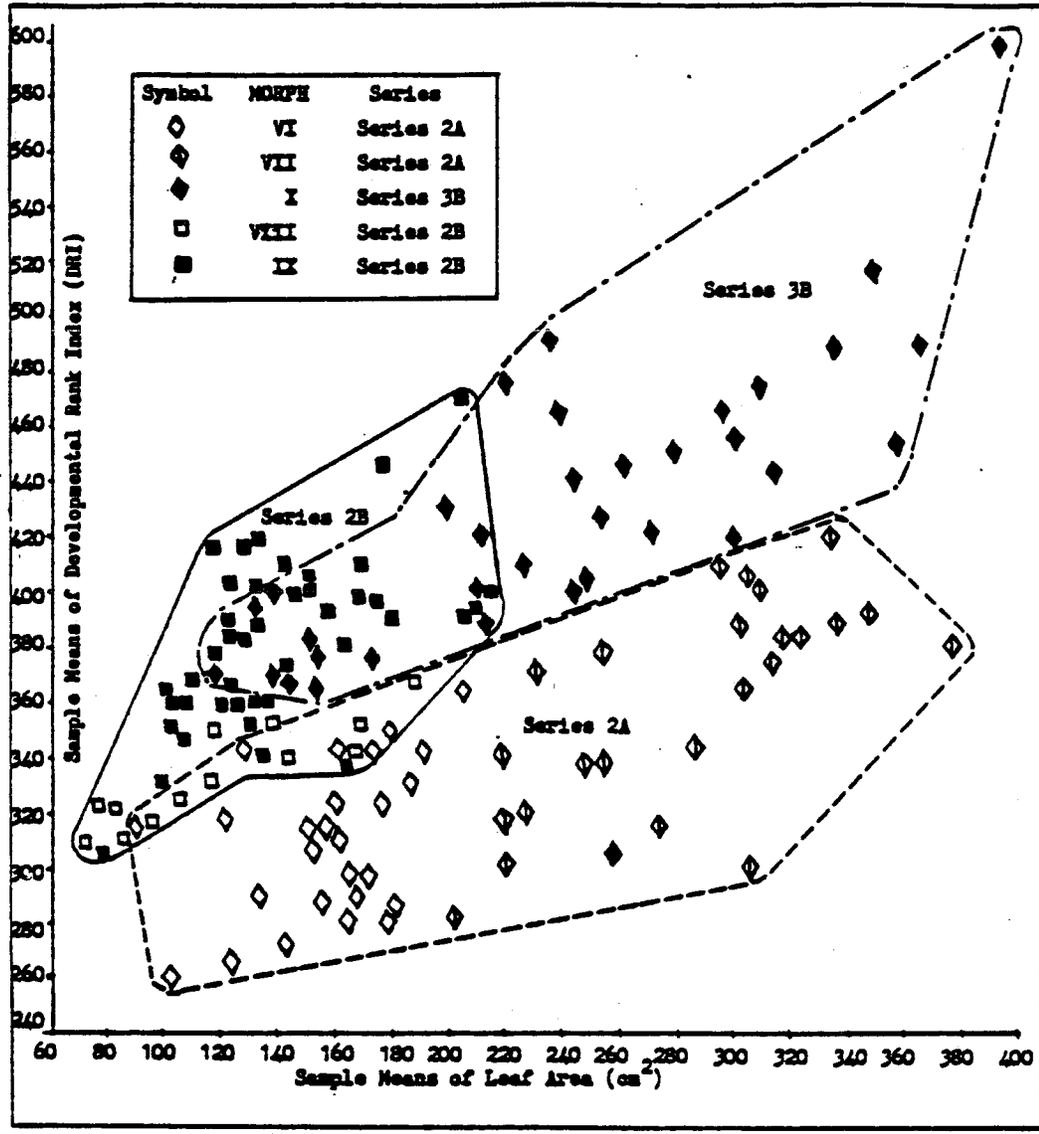


Figure 7. Morphological Relationships of Hybrid Series 3B and Its Putative Parental Races, Series 2A and Series 2B, *Y. whipplei*, Developmental Rank Index (DRI) vs. Leaf Area

three leaf dimensions was Developmental Rank Index (DRI), the sum of three mean weighted--i.e., standardized--leaf dimensions for each sample. DRI varied from less than 100 to more than 500 in a monodirectional sequence that indicated or paralleled the relative degree of genetic activity devoted to morphological development of leaf rosettes in different geographic races (Table 2, Appendix A). The following examples of Developmental Rank Index show the kinds of results found in differentiating major Series of Y. whipplei.

#### B-2. Calculation of Developmental Rank Index (DRI)

Method:  $DRI = 1000 (T - 0.16) + 10 + 100 W + L$

or:  $DRI = 1000 T + 100 W + L - 150$

The above equation provided an effective balancing of leaf dimensions having differences in scale of one to three orders of magnitude. Minimal leaf thickness that originally was set at 0.16 cm was first subtracted from the sample mean thickness (T) and the difference was multiplied by 1000. Later 10 had to be added in the equation to avoid zero and negative numbers for T when samples subsequently were found with T less than 0.16 cm. Leaf width (W) was multiplied by 100 but leaf length (L) was left unaltered. All measurements are in centimeters.

Examples. The following examples represent each of the major morphological types in Y. whipplei.

Series 1 Sample: Leaf Length = 100; Leaf Width = 0.75; Leaf Thickness = 0.22.

$$DRI = 1000 (0.22 - 0.16) + 10 + (100 \times 0.75) + 100 = 245$$

Series 2A Sample: L = 75, W = 1.54, T = 0.27

$$\text{DRI} = 1000 (0.27 - 0.16) + 10 + (100 \times 1.54) + 75 = 349$$

$$\text{Series 2B Sample: } L = 45, W = 0.89, T = 0.35$$

$$\text{DRI} = 1000 (0.35 - 0.16) + 10 + (100 \times 0.89) + 45 = 334$$

$$\text{Pre-Series Sample: } L = 45, W = 0.75, T = 0.19$$

$$\text{DRI} = 1000 (0.19 - 0.16) + 10 + (100 \times 0.75) + 45 = 160$$

$$\text{Series 3B Sample: } L = 95, W = 1.35, T = 0.39$$

$$\text{DRI} = 1000 (0.39 - 0.16) + 10 + (100 \times 1.35) + 95 = 470$$

$$\text{Series 3A Sample: } L = 65, W = 1.20, T = 0.30$$

$$\text{DRI} = 1000 (0.30 - 0.16) + 10 + (100 \times 1.20) + 65 = 335$$

B-3. A Geographic Ordination of Y. whipplei by DRI and Limitations of DRI as a Phenotypic Gradient

Developmental Rank Index (DRI) differentiated large populations of Y. whipplei and provided a ranking of geographic populations. The geographic distribution of mean DRI is indicated for regional groups of samples in Figure 8. In Table 2 these same regions are ranked by their increasing means of DRI to indicate possible genealogical relationships of their yucca populations.

Geographic directions of gradients of DRI usually did parallel the expected directions of differentiation that would result from environmental selection. Yucca populations east of the San Andreas Fault System in general were subjected to increasingly variable continental climates going inland and upward in altitude (Barbour and Major, 1977), which fact would result in natural selection of high developmental ranks in Y. whipplei. Climate also became cool, damp, and least favorable to yucca going from south to north on the coastal side of the San Andreas Fault System, a trend which corresponded with

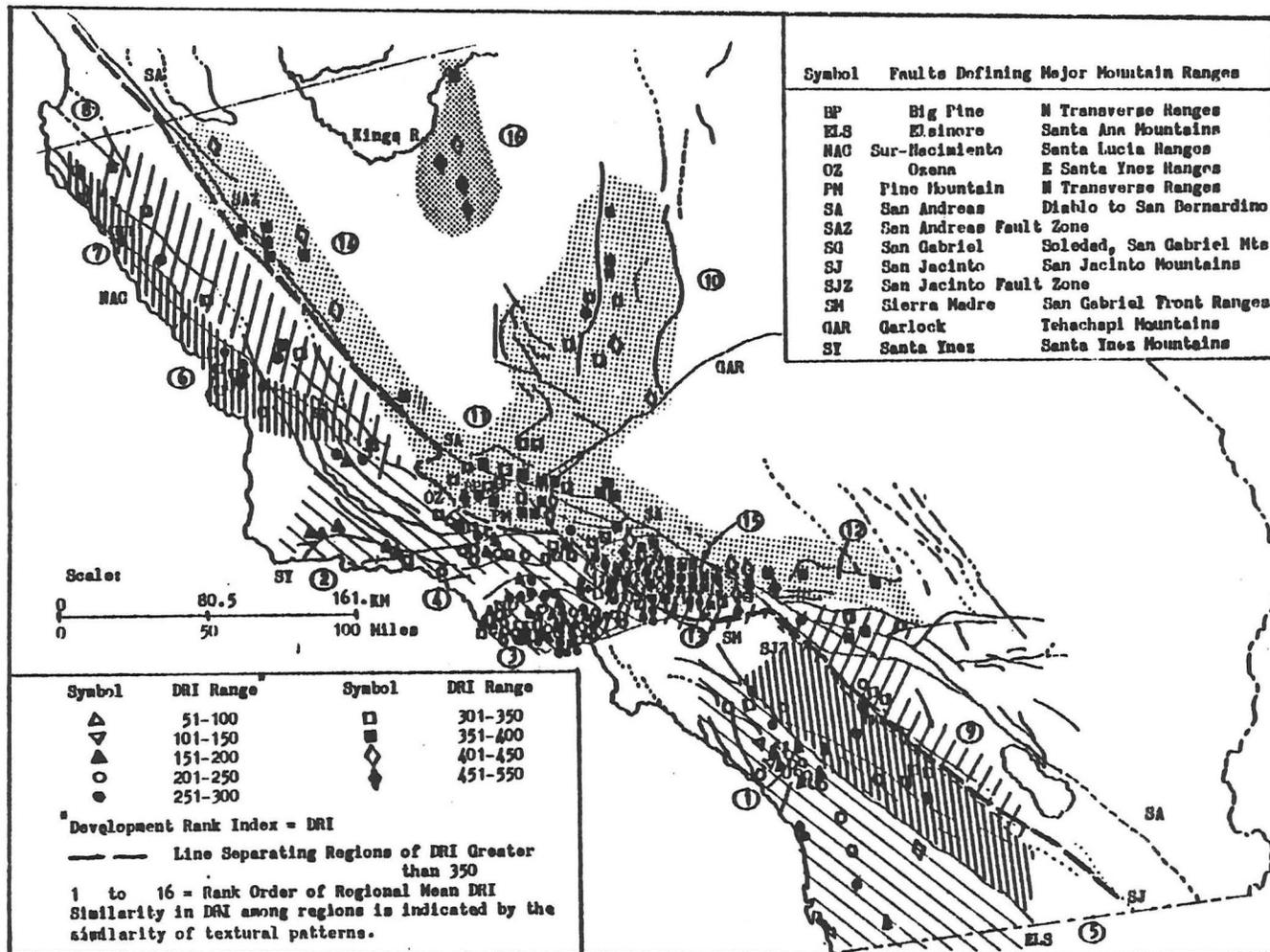


Figure 8. Geographical Distribution of Developmental Rank Index (DRI) in *Y. whipplei* of California

a similarly increasing gradient of DRI going northward in the coastal ranges. Nevertheless, these trends had important exceptions, for example the insignificant differences between DRI of the Santa Lucia Mountains at the north end of the geographic range of Y. whipplei and DRI in the San Jacinto Mountains toward the south end of its California range (Table 3, G, H). Yuccas of these widely separated areas were approximately equal in mean DRI (Table 2) in spite of differences in latitude between  $32^{\circ}15'N$  and  $36^{\circ}50'N$  and in spite of different distances of the areas from the coast (Fig. 8). This case may be an example of the correlation in severity of climate with increase in latitude and increased distance from the ocean (Major, 1977).

Predominance in a single dimension such as leaf width or thickness in one population frequently was offset quantitatively by predominance in the alternative dimension in another entirely different population, resulting in similar DRI between many populations in Series 2A and 2B. Additive combinations of genes in hybrids resulted in significant differences in DRI between hybrid populations such as Series 3B and some Series 2A or 2B "parental races" (Fig. 6, 7). Thus such closely related populations of comparatively recent derivation showed greater numerical deviation in DRI from putative parents than existed between these parents, the much older climax products of diverse evolutionary lines (Series 2A and 2B). This result was contrary to the suppositions (p. 25) of cluster analysis and numerical taxonomy (Sokal and Sneath, 1963; Sneath and Sokol, 1973, pp. 5, 106-113). On the other hand, great quantitative differences in DRI were indicated between populations of pre-series and either Series 2A-3A or 2B yuccas (Table 3, 4, 5, 6; Appendix A). However, there were only marginally

Table 2. Use of Mean Developmental Rank Index (DRI) of Y. whipplei  
For Ordination of Populations in Mountains of Occurrence

Rank of Mean DRI	Mountain Range or Fault Block	Number Samples Per Range	Mean DRI of Region	Standard Deviation	Series of Samples in Range
1	<sup>+</sup> W of Elsinore Fault S of Santa Ana River	29	213.8	48.1	1, 3A pre- #
2	W Ozena Fault, Cuyama to Santa Clara rivers	23	230.0	49.1	pre- 2A, 3A
3	Santa Monica Mts. <sup>*</sup> E of Leo Carillo Beach	35	260.2	38.6	1
4	Santa Susana Mts. E to Placerita Park	43	262.1	49.4	pre-, 3A, 2A
5	Elsinore Fault to San Jacinto Fault	6	272.2	63.9	3A
6	W Sur-Nacimiento Fault, San Luis Obispo County	11	294.9	24.7	3A
7	W Sur-Nacimiento Fault, Monterey County	5	313.8	15.6	2A, 3A
8	Sur-Nacimiento Fault to San Andreas Fault	8	334.4	40.7	2A, 3A
9	San Jacinto Fault to San Andreas Fault	7	335.1	59.6	2A, 3A
10	Kern River Basin to Mojave Desert	10	355.4	38.3	2B, 3A
11	San Andreas to Ozena, Pine Mountain faults	16	360.2	55.7	2B, 3B
12	E of San Andreas Fault, S of Garlock Fault	16	362.8	54.5	2B, 3A
13	Sierra Madre-Verdugo, to San Gabriel faults	26	377.6	45.3	2A
14	E San Andreas Fault to San Joaquin Valley	9	380.7	22.8	2B
15	San Gabriel Fault to San Andreas Fault	35	398.5	50.0	3B, 2B, 2A
16	Sierra Nevada N of Johnsondale	5	477.4	75.6	3B

\* Mts. = Mountains. <sup>+</sup>N, S, E, W = cardinal compass points

#pre- = Pre-series Yuccas

significant differences in DRI between yuccas of the Sierra Nevada (Series 3B) and of the Temblor-Diablo ranges (Table 3D, E; 4, 6), or between the Santa Lucia yuccas and those of the Greenhorn, Piute, Tehachapi, and Ridge Basin areas. Therefore regional differences in DRI alone were not dependable for showing quantitatively the significant effects of local ecological factors on morphology, for DRI could not always differentiate between some morphologies that qualitatively differed significantly.

#### B-4. Morphological Types of Y. whipplei (MORPH)

The purpose of ordination was to place each sample objectively in its proper evolutionary or phenotypic relationship to the other samples so that morphological differences could be studied without the subjective influence of sample location or of pre-existing taxonomy. Data from aberrant samples could be swamped too easily in the statistical variation around their regional mean. Existing taxonomic differentiation in Y. whipplei was based on much coarser population distinctions than the dimensions of leaves and rosette bases, and resulted in large artificial combinations of diverse morphological types (Fig. 1, Table 1). Diagrammatic models long have been used as taxonomic aids in sorting complex multivariate phenotypes (Anderson, 1949; Haines, 1941), and were an effective and objective method of ordering morphologically definable races of Y. whipplei independently of the previously defined geographic subspecies. The use of qualitative distinctions in diagrams as well as quantitative differences avoided the imprecision of additive differentiations employed in DRI.

To differentiate leaf characters qualitatively as well as quanti-

Table 3. Tests of Mean Developmental Rank Index (DRI) Between Yuccas of Different California Regions<sup>#</sup>  
(t-Tests)

Source of Regional Means Compared by t-test		Average DRI X <sub>1</sub>	Number Samples X <sub>1</sub>	Average DRI X <sub>2</sub>	Number Samples X <sub>2</sub>	t-ratio	Critical t-ratio <sup>*</sup>	
Group X <sub>1</sub>	Group X <sub>2</sub>						2-tailed	1-tailed
A. Combined population, Samples SW of San Andreas-to-San Jacinto Fault Line Series 1, 2A, 3A, pre-	Combined population, Samples NE of San Andreas-to-San Jacinto Fault Line Series 2A, 2B, 3B	250.7	83	371.2	75	13.99	1.96	1.64
B. SW of Cuyama-Lockwood Valleys, Santa Ynez to Topa-Topas Pre-series, Series 2A	NW Transverse Ranges (Tejon Region) Series 2B, 3B	232.2	14	336.0	15	5.45	2.05	1.70
C. S Sierra Nevada, Kern River Region Series 2B	Diablo-Temblor Ranges Series 2B	355.4	10	380.7	9	1.72	2.11	1.74
D. Central Sierra Nevada, N of Johnson-Series 3B	Diablo-Temblor Ranges Series 2B	477.4	5	380.7	9	3.64	2.18	1.78
E. Central Sierra Nevada, N of Johnson-dale and Kern R. Series 3B	Santa Lucia Range, Monterey County Series 2A-3A	477.4	5	334.4	8	4.48	2.20	1.80
F. Monterey County, Santa Lucia Mts. Series 2A, 3A	Diablo-Temblor Ranges Series 2B	310.9	15	380.7	9	5.89	2.07	1.72
G. Coastal Santa Lucias of Monterey County Series 2A, 3A	San Jacinto Mountains Series 2A, 3A	313.8	5	335.1	7	0.77	2.23	1.81
H. Interior Santa Lucia Mts. Monterey Co. Series 2A, 3A	San Jacinto Mountains Series 2A, 3A	334.4	8	335.1	7	0.03	2.16	1.77

<sup>#</sup>Data derived from Appendices D, E, F. <sup>\*</sup>Probability level, p = 0.95

Table 4. Tests Between DRI of Regional Pairs Northeast of San Andreas Fault Line, Y. whipplei (t-test)

Fault Block Mountain Range	Sierra Madre Blk. N=26	San Gabriel S. Andreas Blk. N=35	S. Jacinto S. Andreas Blk. N=7	E S. Andreas to Tumbler Diablo. N=9	E S. Andreas S Garlock Flt. N=16	Ridge, Tejon Basin, E of Ozona. N=16	Kern R. Nojave N=10	Sierra Nevada N=5
Sierra Madre Fault Block $\bar{X}=377.6$		t=1.6797 DF=59 ±20.9	t=2.0612 DF=31 -42.5	t=0.1954 DF=33 + 3.1	t=0.9514 DF=40 ±14.8	t=1.1070 DF=40 ±17.4	t=1.3687 DF=34 ±22.2	t=4.0399 DF=29 +99.8
San Gabriel: San Andreas Blk. $\bar{X}=398.5$	t.o.= 0.8398 +		t=2.9715 DF=40 -63.4	t=1.0342 DF=42 ±17.8	t=2.3020 DF=49 ±35.7	t=2.4506 DF=49 ±38.3	t=2.5162 DF=43 ±43.1	t=3.5206 DF=38 +78.9
San Jacinto San Andreas Blk. $\bar{X}=335.1$	t.o.= 1.0094 -	t.o.= * 1.4703 -		t=2.1202 DF=14 +45.6	t=1.0918 DF=21 +27.7	t=0.9745 DF=21 +25.1	t=0.8498 DF=15 +20.3	t=3.6567 DF=10 +142.3
E San Andreas, Tumbler Diablo $\bar{X}=380.1$	t.o.= 0.0960 +	t.o.= 0.5120 ±	t.o.= 0.9884 +		t=0.9338 DF=23 -17.9	t=1.0479 DF=23 -20.5	t=1.7208 DF=17 ±25.3	t=3.6382 DF=12 +96.7
E San Andreas, S Garlock Flt. $\bar{X}=362.8$	t.o.= 0.4708 ±	t.o.= * 1.1453 ±7	t.o.= 0.5249 +	t.o.= 0.4513 -		t=0.1335 DF=30 -2.6	t=0.3743 DF=24 ± 7.4	t=3.7569 DF=19 +114.6
Ridge, Tejon Basin, E Ozona Flt. $\bar{X}=360.2$	t.o.= 0.5478 ±	t.o.= * 1.2192 ±	t.o.= 0.4685 +	t.o.= 0.5065 -	t.o.= 0.0654 -		t=0.2386 DF=24 ± 4.8	t=3.7857 DF=19 +117.2
Kern, Nojave, Tehachapi $\bar{X}=355.4$	t.o.= 0.6726 ±	t.o.= * 1.2456 ±	t.o.= 0.3988 +	t.o.= 0.8156 ±	t.o.= 0.1814 ±	t.o.= 0.1156 ±		t=4.2281 DF=13 +122.0
Sierra Nevada H Johnsondale $\bar{X}=477.4$	t.o.= * 1.9784 +	t.o.= * 1.7383 +	t.o.= * 1.6412 +	t.o.= * 1.6697 +	t.o.= * 1.7950 +	t.o.= * 1.8087 +	t.o.= * 1.9574 +	

N = Number of samples; t = Student's t-ratio; DF = Degrees of freedom; ±Y = Difference from mean.  
 t.o. = t-order = t/Critical t at p = .95 (See Method of Calculating t-order on pp. 61-65.  
 2-tailed t-test: p = .95; 1-tailed t-test: p = .975. \* t-order = 1.1 = Significant Difference, p = .95.

Table 5. Tests Between DRI of Regional Pairs Southwest of San Andreas Fault Line, *Y. whipplei* (t-test)

Fault Block Mountain Range and Mean DRI	S. Monica Mountains N=35	S. Susana Mountains N=43	W Elsinore Flt. S Santa Ana R. N=29	Elsinore Flt. to S. Jacinto Flt. N=6	W Sur-Nacimiento Flt. S. L. O. Co. N=11	W Sur-Nacimiento Flt. Monterey Co. N=5	Sur-Nacimiento to S. A. Flt. N=8	S. Ynez SW Ozena Flt. Oak Ridge N=23
Santa Monica Mountains $\bar{X}=260.2$		t=0.0978 DF=76 + 1.9	t=4.2835 DF=62 46.4	t=0.6362 DF=39 +12.0	t=2.7952 DF=44 +34.7	t=3.0412 DF=38 +53.6	t=4.8592 DF=41 +74.2	t=2.6155 DF=56 +30.2
Santa Susana Mountains $\bar{X}=262.1$	t.o.= 0.0492 +		t=4.1704 DF=70 48.3	t=1.0397 DF=47 +10.1	t=2.1235 DF=52 +32.8	t=2.1744 DF=46 +51.7	t=3.8904 DF=49 +72.3	t=2.5208 DF=64 +32.1
W Elsinore Flt. S Santa Ana R. $\bar{X}=213.8$	t.o.= * 2.1418	t.o.= * 2.0904		t=2.5640 DF=33 +58.4	t=5.3053 DF=38 +81.1	t=4.5585 DF=32 +100.0	t=6.4684 DF=35 +120.6	t=1.1961 DF=50 +16.2
Elsinore Flt. S. Jacinto Flt. $\bar{X}=272.2$	t.o.= 0.3148 +	t.o.= 0.5173 +	t.o.= * 1.2593 +		t=1.0638 DF=15 +22.7	t=1.4097 DF=9 +41.6	t=2.2307 DF=12 +62.2	t=2.1486 DF=27 +42.2
W Sur-Nacim. Flt. S. L. O. Co. $\bar{X}=294.9$	t.o.= * 1.3838 +	t.o.= 1.0565 +	t.o.= * 2.6186 +	t.o.= 0.4992 +		t=1.6128 DF=14 +18.9	t=2.6350 DF=17 +39.5	t=4.1208 DF=32 64.9
W Sur-Nacim. Flt. Monterey Co. $\bar{X}=313.8$	t.o.= * 1.5033 +	t.o.= 1.0791 +	t.o.= * 2.2390 +	t.o.= 0.6232 +	t.o.= 0.7519 +		t=1.6128 DF=11 +20.6	t=3.7292 DF=26 83.8
E Sur-Nacim. S. Andreas Flt. $\bar{X}=334.4$	t.o.= * 2.4055 +	t.o.= * 1.9355 +	t.o.= * 3.1864 +	t.o.= 1.0237 +	t.o.= * 1.2488 +	t.o.= 0.4860 +		t=5.3918 DF=29 104.4
Ozena-S. Ynez -Oak Ridge Flt. $\bar{X}=230.0$	t.o.= * 1.2980	t.o.= * 1.2636	t.o.= 0.5951 +	t.o.= 1.0471	t.o.= * 1.8138	t.o.= * 2.0236	t.o.= * 2.6366	

t.o.= t-order ratio; N=number of samples; t=Students' t-ratio; DF=degrees freedom; +Y = Difference Mean.  
\* t-order = 1.1 = Significant Difference, 2-tailed; p = 0.95; 1-tailed, p = 0.975. See pp. 6-65.

Table 6. Tests Between DRI of Regions from Opposite Sides of the San Andreas Fault Line, Y. whipplei (t-Tests)

Fault Block Hln. Range.	Sierra Madre Mtk.	San Gabriel- San Andreas	San Jacinto- San Andreas	E. S. Andreas Diablo Tow- blor	E. S. Andreas S Garlock	Ridge, Tejon Insignis E	Kern R., Ozema	Sierra Nevada
Mean DRI Santa Monica Mts. $\bar{X}=260.2$	$\bar{X}=377.6$ $t=10.900$ DF=59 * +117.4 (5.4500)	$\bar{X}=398.5$ $t=12.958$ DF=68 * +138.3 (6.5116)	$\bar{X}=335.1$ $t=4.2641$ DF=40 * +74.9 (2.1099)	$\bar{X}=380.7$ $t=8.9221$ DF=42 * +120.5 (4.4169)	$\bar{X}=362.8$ $t=7.7174$ DF=49 * +102.6 (3.8380)	$\bar{X}=360.2$ $t=7.7402$ DF=49 * +100.0 (3.7016)	$\bar{X}=355.4$ $t=6.8872$ DF=43 * +95.2 (3.4095)	$\bar{X}=477.4$ $t=10.3287$ DF=38 * +1217.2 (5.182)
Santa Susana Mts. $\bar{X}=262.1$	$t=9.6996$ DF=67 * +115.5 (4.8742)	$t=12.064$ DF=76 * +136.4 (6.0623)	$t=3.5614$ DF=48 * +73.0 (1.7718)	$t=7.0026$ DF=50 * +118.6 (3.4839)	$t=6.7689$ DF=57 * +100.7 (3.3849)	$t=6.5502$ DF=57 * +98.1 (3.2751)	$t=5.5772$ DF=51 * +93.3 (2.7747)	$t=8.7268$ DF=46 * +1215.3 (4.3309)
W Flainore Flt. S Santa Ana R. $\bar{X}=213.8$	$t=12.9596$ DF=53 * +163.8 (6.4476)	$t=14.9741$ DF=62 * +184.7 (7.4870)	$t=6.5025$ DF=34 * +121.3 (3.2032)	$t=9.9997$ DF=36 * +166.9 (4.9260)	$t=9.4940$ DF=43 * +149.0 (4.7000)	$t=9.2431$ DF=43 * +146.4 (4.5758)	$t=7.1869$ DF=27 * +141.6 (3.5024)	$t=11.9311$ DF=32 * +263.6 (5.8406)
Flainore Flt. San Jacinto Flt. $\bar{X}=272.2$	$t=4.7578$ DF=30 * +105.4 (2.3300)	$t=5.5010$ DF=39 * +126.3 (2.7219)	$t=1.8356$ DF=11 +62.9 (0.8341)	$t=4.7343$ DF=13 * +108.5 (2.1918)	$t=3.3222$ DF=20 * +90.6 (1.5926)	$t=3.1777$ DF=20 * +88.0 (1.5234)	$t=2.8031$ DF=14 * +83.2 (1.3068)	$t=7.8883$ DF=9 * +205.2 (2.1610)
W Sur-Nacim- lento, SLO Co. $\bar{X}=294.9$	$t=5.6737$ DF=35 * +82.7 (2.7949)	$t=6.5903$ DF=44 * +103.6 (3.2706)	$t=2.0080$ DF=16 +40.2 (0.9472)	$t=7.9851$ DF=18 * +85.8 (3.8006)	$t=3.8529$ DF=25 * +167.9 (1.8703)	$t=3.6335$ DF=25 * +65.3 (1.7638)	$t=4.3397$ DF=19 * +60.5 (2.0734)	$t=7.4398$ DF=14 * +182.5 (3.4184)
U Sur-Nacim- lento, Hon- loray Co. $\bar{X}=313.8$	$t=3.0754$ DF=29 * +63.8 (1.5039)	$t=3.8238$ DF=38 * +84.7 (1.6920)	$t=0.7704$ DF=10 +20.3 (0.3458)	$t=5.7919$ DF=12 * +166.9 (2.6580)	$t=1.7241$ DF=19 +49.0 (0.8238)	$t=1.8114$ DF=19 +46.4 (0.8655)	$t=2.2979$ DF=13 +41.6 (1.0638)	$t=4.7408$ DF=8 * +163.6 (2.0558)
Sur-Nacim- lento-San Andreas Flt. $\bar{X}=334.4$	$t=2.4091$ DF=32 * +43.2 (1.1809)	$t=3.3720$ DF=41 * +64.1 (1.6293)	$t=0.0269$ DF=13 +0.7 (0.0124)	$t=2.9397$ DF=15 * +46.3 (1.3795)	$t=1.2990$ DF=22 +28.4 (0.6263)	$t=1.1594$ DF=22 +25.8 (0.5590)	$t=1.1242$ DF=16 +21.0 (0.5303)	$t=7.2835$ DF=11 * +143.0 (2.0370)
Ozema-S. Ynez To Oak Ridge Flt. $\bar{X}=230.0$	$t=10.9947$ DF=47 * +147.6 (5.4451)	$t=12.6526$ DF=56 * +168.5 (6.3105)	$t=2.1486$ DF=27 +105.1 (1.0471)	$t=8.9239$ DF=30 * +150.7 (4.3702)	$t=7.9486$ DF=37 * +132.8 (3.9233)	$t=7.7134$ DF=37 * +130.2 (3.8072)	$t=7.1649$ DF=31 * +125.4 (3.5088)	$t=9.4563$ DF=26 * +247.4 (4.5924)

\* (t-order) = 1.1 and therefore significantly different, 2-tailed at  $p = .95$ . Calculation of t-order p. 61-65.

tatively, and to determine the simplest, most parsimonious, developmental sequence of yucca leaf forms, a triangular graphic leaf model was chosen (Fig. 9, Appendix B). The positive x-axis represented leaf length (L); the negative x-axis leaf width (W); the positive y-axis leaf thickness (T). Each 3-unit axis was scaled to the maximum mean sample values so that the three maximum dimensions formed an isosceles triangle 3 units in altitude with a 6-unit base (Reduced in Appendix B). Because leaf proportions as well as dimensions were important diagnostic characters (Hoover, 1973), the two slopes of the triangle also were visually useful. After visual comparisons of twelve sets of these superimposed triangular plots, non-matching triangles (samples) were moved to more similar sets and re-plotted until the best sorting of samples was achieved. Plotting was done by computer so that only data cards had to be moved to re-sort and re-plot the samples (Appendix B). Artificial sub-classes were created to find intermediate stages that could not be differentiated in the field.

By objectively comparing dimensions graphically, the resulting twelve triangle classes were placed in a sequential arrangement of increasing leaf development that was based on field sample data means and that took into account simultaneously the gradual differences in all three leaf dimensions (Fig. 9). The final numbering of the main morphological types (MORPHs) from I to X represented approximately the order of increasing leaf development in the phenotypically derived evolutionary sequence, although there was some ambiguity due to branching of different directions of development at one or two points. MORPH I and II were artificially segregated as pre-series types to indicate which samples of the smallest plants had least leaf thickness.

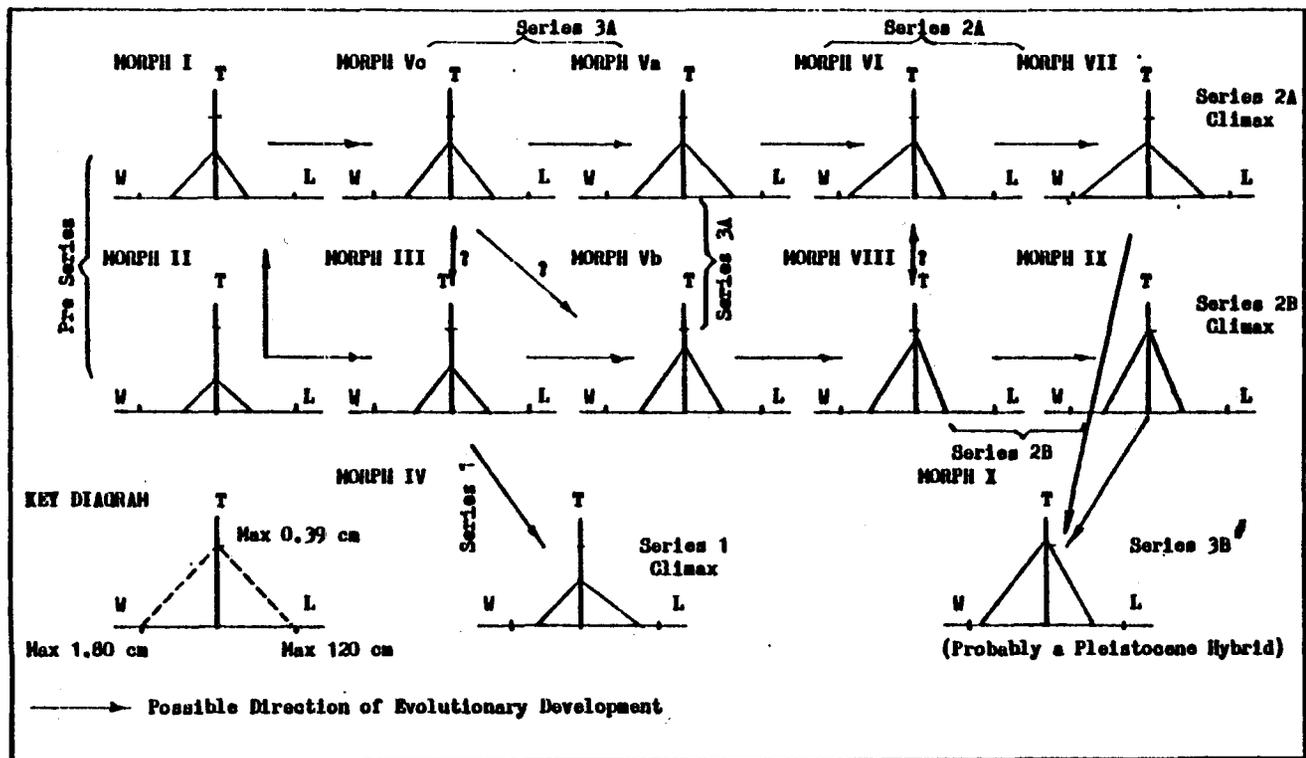


Figure 9. The Ordination of Morphological Types (MORPH) in *Y. whipplei* by Diagrams of Mean Leaf Dimensions

\* Data based on mean values of samples of each MORPH, i.e., Table 7. In each case measurements were made of longest leaf of largest rosette of a plant. L = Leaf Length from tip to base; W = Leaf Width at midpoint of blade; T = Leaf Thickness at midpoint of blade.

# Data of latest samples extended the mean dimensions beyond the previous maximum.

Samples with thinnest leaves were assigned to MORPH II, and MORPH I had only moderately thin leaves. MORPHs represent artificial quantitative grades within their respective Series populations, but they also form natural boundaries between the Series by their qualitative differences in direction, or dimensions emphasized, of morphological development. Statistical means of some morphological attributes in each MORPH, arranged by Series, are listed in Table 7. Note:

(1) In MORPH VII leaf length is about twice the length in MORPH VI but VII has only slightly greater leaf width and approximately equal leaf thickness compared to VI.

(2) In MORPH VIII and IX leaf length and width are about equal but leaf thickness in VIII ranges from .335 to .345 cm while that in IX ranges from .346 to .422 cm.

(3) In MORPH IV mean leaf length ranges from 80 to 120 cm while in MORPH III length ranges from 50 to 80 cm, and leaf width and thickness are largely overlapping in each.

(4) Interestingly MORPH Va is more similar to MORPH VII, the climax of Series 2A development than it is to VI, the supposed intermediate stage of Series 2A. MORPH Vc is more similar in proportion to Vb and Series 2B than to Va and Series 2A.

The geographical distribution of MORPHs, when plotted on a map of southern California to show geographic relationships of the different Series (Fig. 10), revealed some interesting features. The artificially segregated MORPH II was almost the sole type found on the southern coastal slopes of the Santa Ynez Mountains and was the only pre-series type found in the Santa Ana Mountains together with Series 1. MORPH I, on the other hand, was found predominantly north and east of the Santa

Table 7. The Ordination of Morphological Types (MORPH) of Yucca whipplei

Group Means of Dimensions $\pm$ Standard Deviation of Sample Means from Group Mean									
Series	MORPH	N #	Leaf Length (cm) <sup>†</sup>	Leaf Width (cm)	Thickness of Leaf (cm)	Mean DRI	SVRAT	Leaf Volume (cm <sup>3</sup> )	Leaf Area (cm <sup>2</sup> )
Pre-Series *	I	13	46.6 $\pm$ 13.0	1.02 $\pm$ .15	0.21 $\pm$ .01	209.2 $\pm$ 25.5	11.4 $\pm$ 0.6	10.2 $\pm$ 3.8	115.1 $\pm$ 40.0
	II	18	58.1 $\pm$ 10.2	0.90 $\pm$ .19	0.18 $\pm$ .01	174.3 $\pm$ 24.3	14.2 $\pm$ 2.8	9.3 $\pm$ 2.6	130.1 $\pm$ 38.9
Series 1	III	28	66.6 $\pm$ 6.8	0.82 $\pm$ .09	0.22 $\pm$ .02	222.2 $\pm$ 18.2	11.5 $\pm$ 0.6	13.2 $\pm$ 5.6	139.3 $\pm$ 18.5
	IV	27	94.2 $\pm$ 12.8	0.87 $\pm$ .09	0.23 $\pm$ .02	260.7 $\pm$ 29.0	11.2 $\pm$ 0.9	18.8 $\pm$ 3.9	206.9 $\pm$ 32.6
Series 3A *	VA	10	75.6 $\pm$ 6.1	1.15 $\pm$ .04	0.25 $\pm$ .03	289.5 $\pm$ 28.4	9.9 $\pm$ 1.0	21.6 $\pm$ 2.4	211.2 $\pm$ 17.3
	VB	9	57.1 $\pm$ 7.0	0.97 $\pm$ .11	0.32 $\pm$ .01	311.7 $\pm$ 30.6	8.4 $\pm$ 0.2	17.6 $\pm$ 3.1	147.2 $\pm$ 24.2
	VC	37	62.0 $\pm$ 10.1	0.95 $\pm$ .08	0.27 $\pm$ .03	280.7 $\pm$ 32.6	9.5 $\pm$ 0.8	16.2 $\pm$ 4.0	151.9 $\pm$ 30.5
Series 2A	VI	26	51.6 $\pm$ 8.2	1.24 $\pm$ .14	0.28 $\pm$ .03	309.4 $\pm$ 28.0	8.7 $\pm$ 0.7	18.1 $\pm$ 3.6	156.9 $\pm$ 27.2
	VII	24	78.0 $\pm$ 10.9	1.51 $\pm$ .18	0.28 $\pm$ .03	356.3 $\pm$ 38.8	8.6 $\pm$ 0.9	32.8 $\pm$ 7.6	279.1 $\pm$ 50.6
Series 2B	VIII	13	46.2 $\pm$ 14.0	0.96 $\pm$ .09	0.34 $\pm$ .01	333.6 $\pm$ 17.9	8.0 $\pm$ 0.2	15.2 $\pm$ 5.0	120.4 $\pm$ 39.0
	IX	41	51.4 $\pm$ 9.8	0.98 $\pm$ .12	0.38 $\pm$ .02	388.2 $\pm$ 33.3	7.3 $\pm$ 0.4	19.5 $\pm$ 4.9	140.8 $\pm$ 32.8
Series 3B	X	34	66.6 $\pm$ 17.4	1.40 $\pm$ .15	0.37 $\pm$ .03	421.8 $\pm$ 46.0	7.0 $\pm$ 0.5	34.2 $\pm$ 11.0	235.4 $\pm$ 68.8

\* MORPHs within these two Series are interchangeable in order. MORPH II is probably closest to the origin as shown by regression with DRI (See p. 64). MORPH VA represents the branchpoint of Series 2A; VB that of Series 2B; VC the main line of developmental evolution leading to Series 2A and 2B from Pre-Series or (?) MORPH III.

† SVRAT = Leaf Surface Area-to-Volume Ratio; DRI = Developmental Rank Index. Means and Standard Deviations by SCATTERGRAM program of SPSS, HOOVER24, 2/07/79. 1 cm = centimeters. # N = Number of Samples.

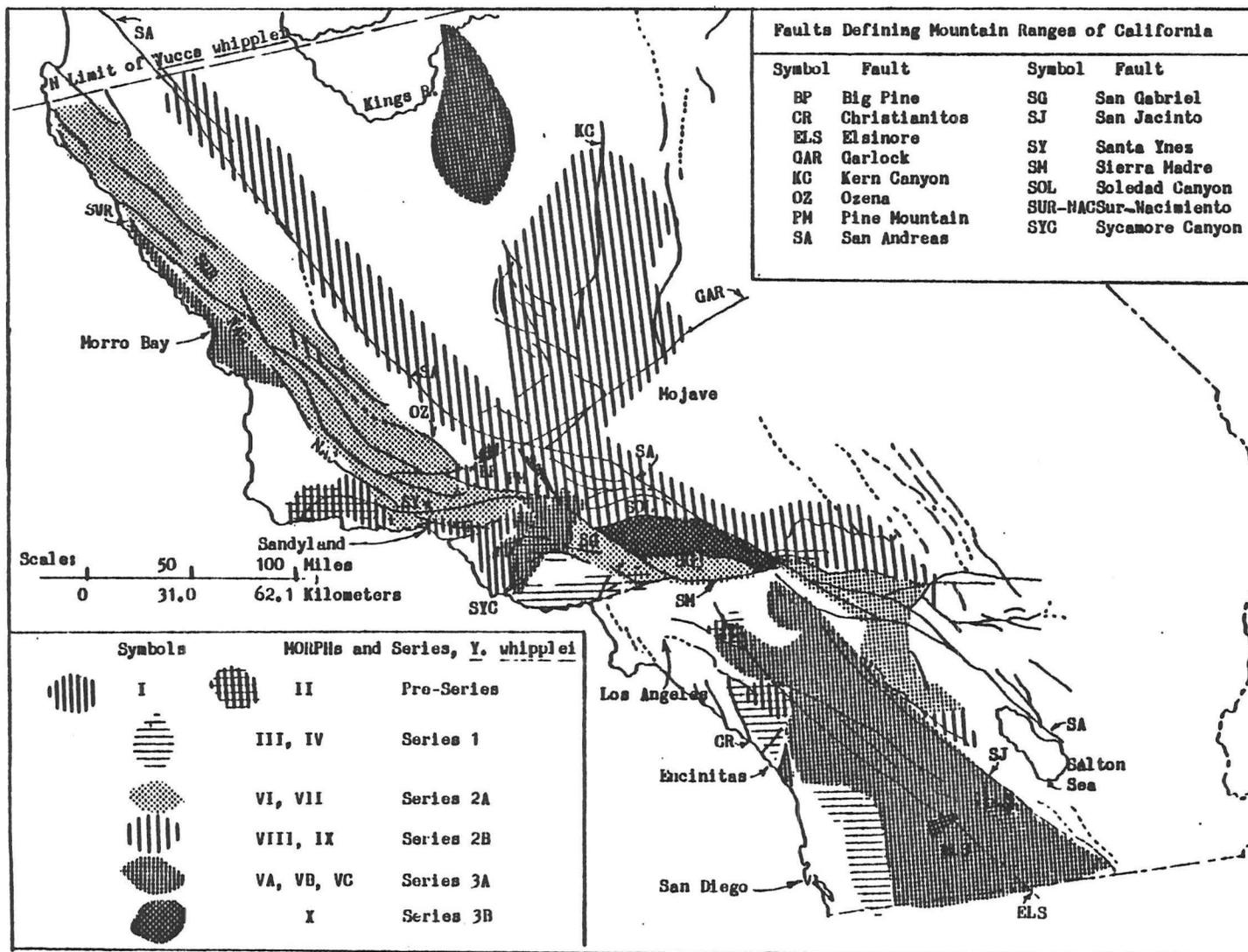


Figure 10. Geographical Distribution of Morphological Series of *Yucca whipplei*, Southern California

Ynez Range and in the Conejo Hills just west of the Santa Monica Mountains and in the Simi-Santa Susana ranges, but seldom elsewhere. MORPH II therefore seemed closest to Series 1 both phenotypically and geographically. MORPH I, having comparatively wide leaves, was differentiated along the lines of Series 2A-3A (Fig. 3) with which it was associated also geographically (Fig. 10). MORPH V and VI were separated from each other artificially on the bases of leaf width and length (Fig. 9, Appendix A), but they generally were geographically intermixed (Fig. 10). However, yuccas in the hills surrounding San Luis Obispo were predominantly of MORPH V while those of the Santa Lucia Ranges in Monterey County were usually of MORPH VI (Fig. 10). Sub-types of MORPH V were differentiated artificially as refinements on the bases of leaf thickness and width to distinguish possible branch points leading from Series 3A to Series 2A and 2B (MORPH Va, Vb, Vc, of Table 7 and Fig. 9, Appendix A). MORPH Vc consisted of the most generalized V samples having neither marked leaf thickness nor width dimensions.

Either Series 1 (MORPH III, IV) or Series 3A (MORPH Va, Vb, Vc) were found on most coastal ranges from the Santa Monica Mountains to the Mexican border, in addition to the concentration of Series 3A (MORPH V) in coastal hills around San Luis Obispo. Series 2A (MORPHs VI, VII) mainly were distributed inland in the southern part of the range of Y. whipplei, but were parallel to the more coastal Series 1 and 3A, between them and the most interior range of Series 2B. In Monterey County Series 2A ranged from the coast itself only to the ranges west of Carmel Valley, but extended eastward and southward disjunctly into the La Panza and San Raphael-Sierra Madre ranges. Series

## B-5. Cluster Analysis

Cluster analysis is a numerical method by which the combined phenotypic differences between numerous multivariate samples or specimens can be estimated and by which the semi-automatic sorting or classifying of samples can be accomplished, based on these quantitative differences. Cluster analysis theoretically should be superior to the plotted triangular diagrams for sorting and ranking types in that it takes account of many more differentiating characters than can be done with a simple diagram. Computer programs for cluster analysis are relatively objective or mechanical sorting systems. A theoretical benefit of cluster analysis, as seen by Sneath and Sokal (1973, pp. 106-108, 112-113), is that by using a maximum number of quantitative characters available, investigative bias and errors are outweighed by the natural bias inherent in evolutionary selection of many attributes of different biotypes.

Twenty-one vegetative plant characters of Y. whipplei (Table 8) were examined with the cluster analysis program NT11 of NTPAK (Beverino and Swanson, 1976). A minimum of sixty characters was recommended by Sokal and Sneath (1963) for effective cluster analysis, but time did not allow the posting of additional data. Several different combinations of the optional methods available in NTPAK were tried to arrive at an optimal system for handling the yucca data in the form of sample means and percentages. Derived ratios of dimensions in various plant organs are common and highly acceptable taxonomic characters in both normal and numerical taxonomy, and are used as any other quantitative character in calculating taxonomic distance. Such character ratios expressing proportional dimensions frequently provide the

Table 8. Twenty-one Quantitative Vegetative Characters Used in Cluster Analysis of Means from Field Samples of Y. whipplei

1.	Development Rank Index	$L + 100W + 1000T - 150$	DRI
2.	Number of Leaf Rosettes per Plant		R
3.	Length (cm) of Longest Leaf Blade of Largest Rosette per Plant	L	L
4.	Width (cm) at Midpoint of " " " " " " " "	W	W
5.	Thickness (cm) " " " " " " " "	T	T
6.	Number of Leaves per Largest Rosette of Plant		N
7.	Stalk Diameter (cm) at 1 Meter Above Stalk Base		S
8.	Enlarged Rosette Base Diameter (cm)		D
9.	" " " Height (cm)		H
10.	Percentage in Sample of Plants with Enlarged Rosette Bases		P
11.	Area of Largest Leaf of Largest Rosette Per Plant ( $\text{cm}^2$ )		A
		$A = 2L (W + T)$	
12.	Volume of Largest Leaf of Largest Rosette Per Plant ( $\text{cm}^3$ )		V
		$V = LWT$	
13.	Ratio of Surface Area-to-Volume of Largest Leaf Per Plant		A/V
		$A/V = 2 (W + T) / WT$	
14.	Total Leaf Area Per Rosette ( $\text{cm}^2$ ) Based on Largest Leaf Only		NA
15.	Total Leaf Volume Per Rosette ( $\text{cm}^3$ ) Based on Largest Rosette Only and Largest Leaf		NV
16.	Total Leaf Area Per Plant Based on Largest Leaf and Largest Rosette Only	$NRA/100.$	NRA
17.	Total Leaf Volume Per Plant Based on Largest Leaf and Largest Rosette Only	$NRV/1000.$	NRV
18.	Ratio of Leaf Length to Width		L/W
19.	Ratio of Leaf Length to Thickness		L/T
20.	Ratio of Leaf Width to Thickness		W/T
21.	Ratio of Leaf Length-to-Width-by-Thickness Product		L/WT

strongest taxonomic distinctions available (Hoover, 1973), (Ch. IV, Discussion).

The most effective of the clustering systems tested used "Taxonomic Distance" as a measure of the morphological separation between plant samples. This measure was based on the sum of squared character differences in each sample pair (Sneath and Sokal, 1973, p. 124). To be accommodated in memory storage of the computer program, raw data were standardized by range of values in a variable. The sorting method chosen was called "unweighted pair group arithmetic average clustering" (Sneath and Sokal, 1973, pp. 230-234).

Cluster analysis is an iterative computerized method by which the totals of quantified phenetic differences between pairs of entities are repeatedly reviewed so that pairs joined by the smallest differences will be linked sequentially to other entities and groups with the smallest remaining differences. The process is repeated until all clusters are linked to one another. The hoped-for result in a case where a mixture of several distinct types of multivariate entities is sorted by cluster analysis is that likes will be joined to likes in clusters that are separated distinctly from other unlike clusters of internally similar entities. These results usually are shown in the form of a phenogram (e.g., Table 9). For better understanding the methods and ideas used in numerical taxonomy, of which cluster analysis is but a part, and in particular for theories and techniques used in NT11, Sokal and Sneath (1963) and Sneath and Sokal (1973) should be consulted.

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3A usually occupied regions intermediate between Series 1 and Series 2A, but also extended from the northernmost latitude of  $36^{\circ}30'N$  to the Mexican border. Series 3B occurred sporadically in some samples located between or near populations of Series 2A and 2B, but the northernmost range of Series 3B in the Sierra Nevada apparently entirely replaced its putative Series 2A parent from the Tule River northward. Series 3B, i.e., MORPH X, in the northern San Gabriel Mountains seems to have largely replaced the Series 2B parent (See Mill Creek Summit, Appendix A), but Series 2A samples in the eastern range, i.e., Crystal Lake and Highway 39 (Appendix A), may be relics of the former Series 2A parental population.

Various types of neighboring yucca populations associated with MORPH V (Series 3A) and VI (Series 2A) constituted other interesting possible cases of remnant paleobiogeography. Series 2B (MORPH VIII, IX) predominated in the Diablo-Temblor ranges and southernmost Sierra Nevada, including the Tehachapi Mountains, but occasional samples of MORPH V (Series 3A) were among them. Evidence of hybridity in the southern Sierra populations (pp. 31-33 and Ch. V) indicated that original colonies of Series 2A-3A later were supplanted in the Sierra and western Tehachapi by Series 2B from east of the Kern Canyon, and from the Ridge Basin.

In western San Diego County, Series 1 yuccas represented by MORPH III and IV are the nearest neighbors to MORPH V and VI of Series 3A-2A, and often V samples looked so similar to III and IV in the field that only the measurement averages revealed the distinction. Series 1 yuccas on the whole are located in warmer areas than MORPH V that frequently occupy higher elevations than MORPH III, IV; but the region

between the Santa Ana and San Jacinto mountains carries exclusively Series 3A-2A yuccas in an apparently reversed climate relationship to 3A-2A yuccas near the coast in Ventura and San Diego counties. Yuccas of intermediate morphology (Series 3A) in Orange, Riverside, and San Diego counties were highly productive of fertile seed, and therefore in this region MORPH V, instead of hybrid derivation, perhaps was a legitimate transitional stage in the original morphological clines (pp. 21-23) leading from Series 1 to 2A via their common pre-series origin (Fig. 9). Pre-series samples of MORPH II also were frequent in the same region. These locally geographically mixed MORPHs may indicate a possible center of origin for Y. whipplei where long-persistent favorable conditions have allowed a high degree of polymorphism in response to environmental tolerance of genetic mutations and recombinants, and or locally divergent selective environments.

Although both DRI and MORPH are useful methods for numerically ordering the supposed evolutionary stages of Y. whipplei to show increasing genetic development along a gradient, MORPH numbers are only relative rankings. One cannot quantitatively differentiate, for instance, between MORPH ranks of two closely related samples from the same location that are separated arbitrarily by minor differences into MORPH VI and V, and samples of other consecutive MORPHs VII and VIII that represent two separate and contrasting lines of genetic development. Obviously the genetic distance between samples of MORPHs VII and VIII of separately evolved populations is much greater than the genetic difference between samples of MORPHs V and VI obtained from a single location.

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13.	Ratio of Surface Area-to-Volume of Largest Leaf Per Plant		A/V
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14.	Total Leaf Area Per Rosette (cm <sup>2</sup> ) Based on Largest Leaf Only		NA
15.	Total Leaf Volume Per Rosette (cm <sup>3</sup> ) Based on Largest Rosette Only and Largest Leaf		NV
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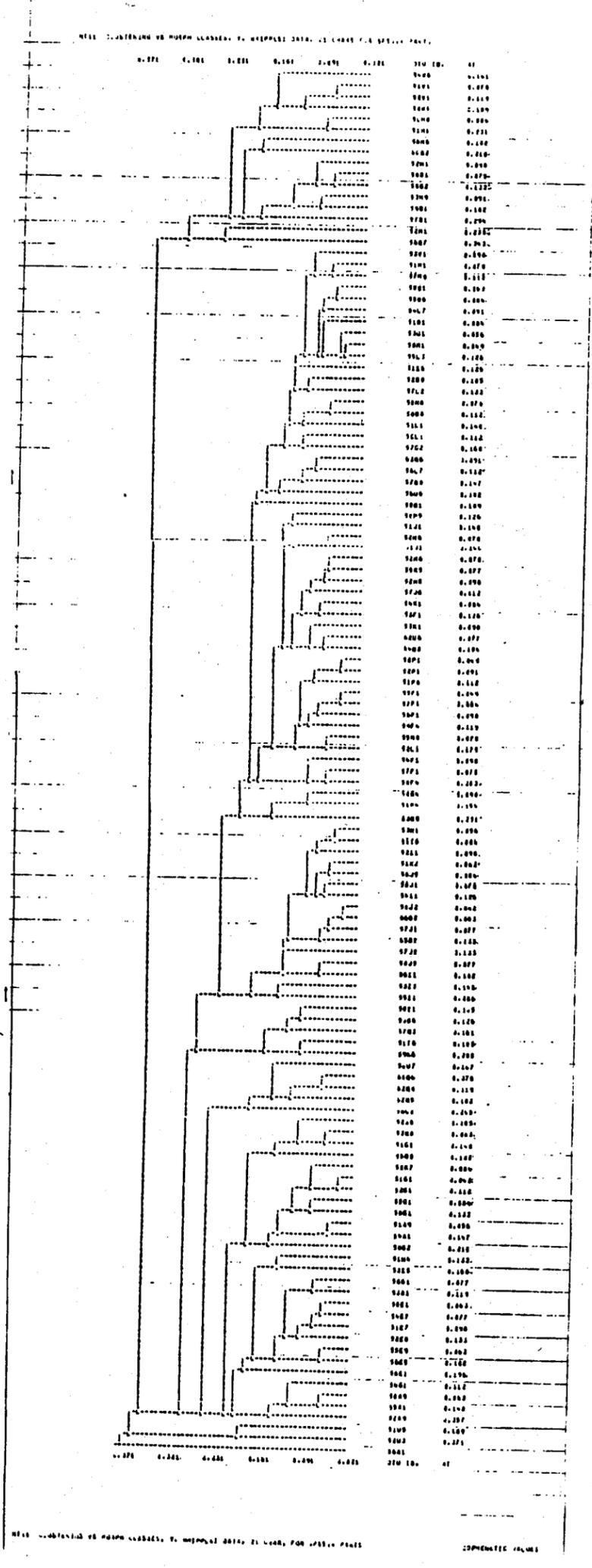
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Because only a maximum of 121 entities, or samples, was accommodated by the NT11 cluster analysis program, several runs were necessary

Table 9. A Phenogram from Cluster Analysis of 121 Field Samples of Y. whipplei



to classify all of the 284 samples adequately. To make these repeated runs as comparable as possible, large geographic groups of samples were broken randomly into sample sets commensurate with the smaller geographic groups to balance representation. The small groups were run each time with different subgroups of the large geographic groups of samples, an inefficient and time-consuming process.

An interesting result of cluster analysis using the available yucca data was that, instead of distinct clusters corresponding, for instance, to the morphological types sorted by diagrams (MORPH), (Appendix A, B), the clusters were joined in groups representing entire developmental Series. In these superclusters, plant samples of smallest developmental rank were linked by a mixed series of steps to samples representing the climax of differentiation, i.e., most extreme phenotypic stage, in one of the three major lines of evolution that were recognized previously, i.e., Series 1, 2A, 2B (Hoover, 1973), Table 7). Therefore cluster analysis, using 21 characters and 121 samples, did not differentiate always between MORPH I and II, or between MORPH V and VI, or between VIII and IX. However the three Series climaxes (MORPH IV, VII, IX) were nearly always well differentiated from each other (Table 9). Linking of the endpoints of several differentiating lines of phenetic development to their common origin may have been disappointing as a mechanical sorting of perceived types, but was rewarding in providing evolutionary insights supportive of the genealogical pathway also arrived at by other methods (pp. 25-50).

The phenograms illustrated some of the large geographic distances between yucca populations of California that were very similar morpho-

logically, as shown by their clustering relationships. Table 10 was excerpted from a phenogram produced from 121 samples of Y. whipplei that were selected to represent all geographic areas about equally. In this excerpt most of the samples grouped together were from MORPH V, but also a few similar samples from MORPH III and VI were found in these clusters, which was understandable considering their nearness in the morphological type gradient (Fig. 9). As seen in the chart, samples of MORPH V from much of the full geographic range of Y. whipplei in California were clustered together by their morphological similarities, though separated by hundreds of miles and presumably some climatic differences (Table 10). Table 11 was copied from another phenogram cluster to show the wide variety of geographic sources that were clustered from similarly representative samples of Series 2B. Closely clustered Series 2B samples came from distantly separated mountain ranges representing a presumably varied group of climates in California, and expressed in different predominant habits, e.g., rhizomatous, mixed, caespitose, and monocarpic (Fig. 1, Table 1a, b). The present local ecology therefore may be less important to distribution of a given morphology of Y. whipplei than other--perhaps paleohistoric--factors.

One of the weaknesses of the cluster analysis program was illustrated by the lower Series 2B cluster of Table 11. Here relatively large taxonomic distances linked MORPHs V, VI, and IX in bracketed sample pairs because these pairs were introduced fairly late in the clustering process. Reversing the order of sample introduction into the program caused different pairs to form in the initial stages, altering the final clustering relationships of individual samples. Taxonomic distances in pairs from the upper half of the phenogram

Table 10. Some Clustering Relationships of *Y. whipplei* Samples from Different Mountain Ranges, Series 3A

Cluster Relationships (Bracketed Pairs)*	Sample Identity	MORPH	Taxonomic Distance Between Samples In Sequence	Location of Sample Area	Mountain Range of Sample Area	
<u>Cluster A</u>						
	78A6	III	0.040	Kanan Rd. S Agoura	Santa Monica Mountains	
	79A6	III	0.112	Kanan Rd. N Agoura	Santa Monica Mountains	
	83A7	V	0.160	Lake Sherwood #2	Santa Monica Mountains	
	82A8	III	0.072	La Tuna Rd., Highway 1	Santa Monica Mountains	
	80E7	V	0.104	Elsinore, Summit Highway 74	Santa Ana Mountains	
	55F13	V	0.064	Rigetti Ranch	E San Luis Obispo	
	52L11	V	0.088	Ponderosa Camp	N Santa Lucia Mountains	
	55M8	V	0.120	Big Morongo Creek	E San Bernardino Mts.	
	52S5	V	0.152	N Idyllwild Junction	San Jacinto Mountains	
	58G22	III	0.176	Newberry Park #1	Conejo Hills	
	77G8	V	0.088	Flintridge	San Raphael Hills	
	84G6	VI	0.072	Fillmore #2, Sespe Creek	Topa-Topa Mountains	
	85G7	V	0.192	Porter Ranch #2	Santa Susana Mountains	
	<u>Cluster B</u>					
		52F10	V	0.096	Huasna Rd. NE Arroyo Grande	S Santa Lucia Mountains
50P17		V	0.048	Highway 58	NW La Panza Mountains	
52P10		V	0.080	Highway 58	NE La Panza Mountains	
51P6		VI	0.112	E Huasna Area	W La Panza Mountains	
59F4		V	0.168	Cuesta Botanical Area #2	San Luis Obispo Hills	
50F10		VI	0.072	El Toro Creek, Morro Bay	S Santa Lucia Mountains	
53F16		V	0.136	Atascadero Rd. E Morro Bay	S Santa Lucia Mountains	
51F13		V		Cuesta Botanical Area #1	San Luis Obispo Hills	

\* Brackets indicate the order of pairing of the two samples joined by the ends of each bracket. Order of linkage is from right to left. Clusters of most similar samples are those groups that are tied by the most brackets and have the lowest taxonomic distances separating units. Actual relationships must be visualized as a 3-dimensional network or "tree" with freely rotating linkages or branches represented by brackets.

therefore were more typical of true relationships in the "real" clusters than were later ones. The last link in the phenogram of this program was always the largest taxonomic distance depicted and it linked the two most different phenotypes remaining after all other clustering was complete. Which samples remained for this final linkage depended greatly on the order of sample introduction in the matrix and had little interpretive significance, as was shown by several runs of the same computer cards rearranged in the data deck.

The technical explanation for these problems is that taxonomic distance is calculated by computer between each possible pair of samples and set up in a matrix of 121 samples prior to the clustering procedure. The computer then must make repeated passes through the whole matrix to join pairs with the smallest taxonomic differences. As pairs from the first passes become linked to other samples in later passes, the taxonomic distances between remaining ones are of larger dimensions than those already linked. Consequently each successive pass joins samples of larger taxonomic differences. However, because the whole matrix must be read--and entities linked--before returning to the beginning, certain pairs at the end of the matrix are linked by larger taxonomic distances than those still remaining unlinked at the beginning of the matrix with smaller differences that cannot be read until the next pass. The arbitrary order of appearance of samples in the matrix therefore affects the order of particular pairings of samples to prior-existing clusters and can importantly alter some clustering relationships.

The frequent and annoying break-up into separate clusters of groups of samples that were known to be very similar was largely a

Table 11. Some Clustering Relationships of Y. whipplei Samples from Different Mountain Ranges, Series 2B

Cluster Relationships (Bracketed Pairs)*	Sample Identity	MORPH	Taxonomic Distance Between Samples	Location of Sample Area	Mountain Range of Sample Area
Cluster A	{ 84A27	V	0.080	Lake Sherwood # 1	Santa Monica
	{ 52K7	VIII	0.104	Vineyard Canyon	Diablo
	{ 56I12	VIII	0.080	East of Caliente	Piute
	{ 58J5	IX	0.136	3 Points, L. Hughes Rd. # 1	N Liebre
	{ 65D23	IX	0.072	NE Cuddy Valley	San Emigdio
	{ 66D25	IX	0.040	Hungry Valley, Tejon Region	N Transverse
	{ 50J27	IX	0.064	Devil's Punch Bowl	SW Mojave Desert
	{ 57J14	IX	0.104	3 Points, L. Hughes Rd. # 2	N Liebre
	{ 51I6	IX	0.056	N of Kernville # 1	S Sierra Nevada
	{ 53M12	IX	0.080	Cushenbury Grade	N San Bernardino
	{ 52I13	IX	0.144	N of Kernville # 2	S Sierra Nevada
	{ 54I10	IX	0.080	N Walker Basin	Piute
	{ 56J5	IX	0.104	Green Rd., S Highway 138	SE Mojave Desert
	{ 57J24	IX	0.120	N Agua Dulce, Mint Canyon	Soledad Basin
	{ 55I13	IX	0.176	NW of Mojave, 6 miles	SE Piute
Cluster B	{ 64D23	IX	0.080	Gold Camp, Piru Creek	N Transverse
	{ 53K11	IX	0.096	N of New Idria, 6 miles	Diablo
	{ 55J5	IX	0.048	N Acton, Red Rover Mine Road	Soledad Basin
	{ 50K5	IX	0.088	NE Parkfield-Coalinga Road	Diablo
	{ 54K11	VIII	0.128	E County Line, Highway 198	Diablo
	{ 51J13	IX	0.112	Cajon Pass Railroad Crossing	W San Bernardino
	{ 57J6	IX	0.072	3 Points Lake Hughes Rd. # 3	N Liebre
	{ 52N6	IX	0.096	E of Summit	San Bernardino
	{ 50P5	IX		Highway 58 # 2	NW La Panza
	{ 54F18	V	0.096	Cal Poly University	San Luis Obispo
Cluster C	{ 58F4	VI	0.128	Atascadero Road, Morro Bay	S Santa Lucia
	{ 55K8	IX	0.160	Coalinga Hot Springs Rd.	Diablo
	{ 59K6	IX	0.104	W Priest Valley	Diablo
	{ 51T6	IX	0.152	Orchard Peak	N Temblor
	{ 57Q3	V	0.120	Highway 33, Pine Mt. Rd.	NW Transverse
	{ 50T11	IX	0.240	Crocker Springs Rd.	Temblor
	{ 53I3	VIII		Wofford Heights, L. Isabella	Greenhorn

\* See Table 10 for explanation of pairing by brackets. # Sequence number of sample at a given location.

result of the position effect in the matrix also (Table 9). The arbitrariness of cluster breaks made impossible any definite conclusions about the morphological relationships based on clustering alone. One had to interpret these clusters "subjectively" on the basis of other known facts, such as the existence of similar samples on the same mountain range. Such judgments might have been allowable for most taxonomic purposes, but for geographic studies such as this one, where it was important for population differences to be assessed as objectively as possible, cluster analysis, as represented by these programs, left much to be desired. Nevertheless, cluster analysis is a widely used and accepted technique and cannot be overlooked as a taxonomic tool. Its chief utility in the present study is to demonstrate the degree of phenotypic similarity between widely dispersed yucca populations and, conversely, the phenotypic differentiation between other neighboring yucca populations.

#### B-6. PRIM Networks

Besides a phenotypic dendrogram, the cluster analysis computer program (NT11) provided a minimal linkage graph in which the most similar entities, based on the same matrix of indices or of taxonomic distances as used in the cluster analysis, were linked pairwise using a slightly different logic from that of cluster analysis. In this "PRIM" method, repeated passes were made through the matrix to connect samples of the smallest taxonomic differences only to samples that already were joined to the single initial network, not to other unlinked samples or to scattered sample pairs as in cluster analysis (Prim, 1957; Sneath and Sokal, 1973, p. 255; Beverino and Swanson,

1976). Sequentially increasing differences joined samples pairwise to the network so as to form expanding branches with no closed loops. PRIM networks of yucca samples were sketched by hand from the numerically listed sample pairs in the computer printout, and several runs of 121 samples each, arranged in the matrix alphabetically by location, were made to compare all 284 samples adequately. Similar PRIM networks resulted, showing a linkage pattern (Fig. 11) that was more revealing than the dendrograms for cluster analysis.

PRIM networks displayed a radiating or fanwise evolution of the main three Series of yuccas from a common pre-series set of yucca samples--MORPH I and II (Fig. 11 a, b). Nearly the same branching pattern was obtained by PRIM networks using 21 characters as was devised initially after sorting of leaf triangle diagrams of all samples using only five of these characters (Fig. 9). However, the PRIM network diagram revealed a tendency to link or branch directly from pre-series I and II to MORPH V instead of through MORPH III to V. Samples of MORPH III joined samples of MORPH IV to MORPH V instead of to samples of MORPH II (Fig. 11). This relation indicated an evolutionary reversal of direction, but may have been due only to the mechanistic similarity to their parental races of samples that were derived by hybridity in MORPH V of Series 3A (pp. 8-11, 45-50).

The PRIM network arrangement agreed with results of other ordinations in skipping MORPH III to reach MORPH V, but seemed incorrect in linking MORPH III to V in order to reach MORPH IV. The path, according to later-discovered climatic factor relationships (Ch. IV), should have linked III and IV directly to MORPH II, but V directly to MORPH I. In climatic factors studied, MORPH III was allied to MORPH II and IV in

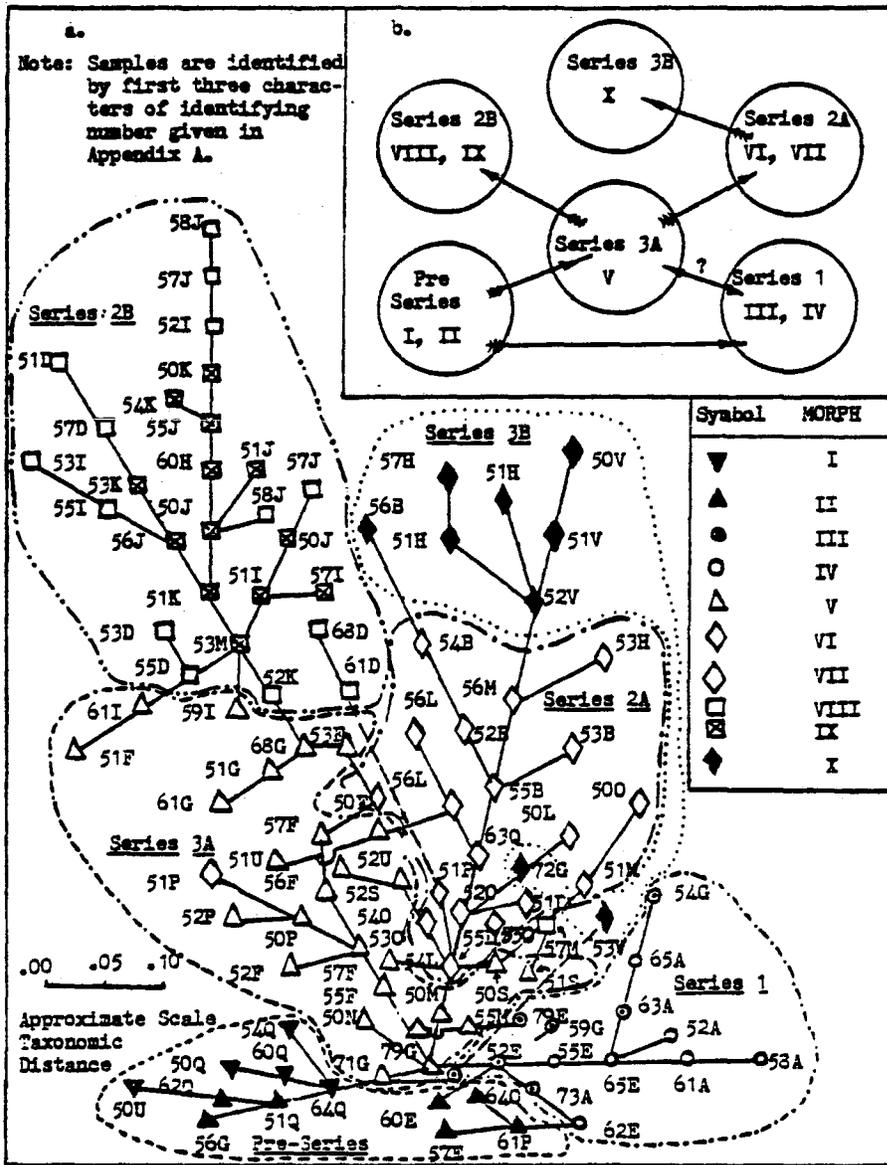


Figure 11. Relationships of MORPHs Found in PRIM Networks

a. Example of PRIM Network

b. Diagram of Series Relationships

gradients that usually were opposite in trend to MORPH V, VI, and VII (Ch. IV). But for some factors in climatic relations MORPH V was allied instead with MORPH II, III, and IV. The geographic intermixture of pre-series samples, MORPH II, with MORPH III and IV (Series 1) in the coastal Peninsular Ranges also included nearby samples of MORPH V (pp. 45-50; Fig. 10). Similar mixtures of I, V, and III samples occurred near the Big Sycamore Canyon in the western Santa Monica Range and in the Simi-Santa Susana mountains. These geographic mixtures did not resolve the question of ordination as to whether (1) MORPH III was transitional between pre-series MORPHs I, II, and MORPH V and also IV, or (2) whether V was intermediate between II and III as well as between I and VI. The former (1) seemed the safer assumption based on phenotypes because generally MORPH III was lower in total gene expression as shown by DRI than MORPH V. Fewer genetic changes were required in the evolutionary pathway (1) from III either to IV or V than if III were only reached from II through I and V and then had to be reduced from V as a first stage of Series 1 connecting IV to V (Fig. 3, 9, 11; Table 7). Possibly some MORPH V samples resulted from cross-pollination between nearby MORPHs I and III or IV.

In PRIM networks the order of introduction of data in the matrix strongly affects results. This fact weakens the confidence that can be placed in any proposed gene logical relationships based only on these programs of cluster analysis. Similar criticisms have been made of other methods of numerical taxonomy (Sneath and Sokal, 1973, pp. 202-288).

#### B-7. Ratios of Relative Significance, t-Order and F-Order

Student's t-test and Snedecor's F-ratio, used in early studies as measures of phenotypic differences in Y. whipplei (Hoover, 1973), were calculated for the present studies in a computer program employing methods of Taylor (1977), Sokal and Rohlf (1969), and Arkin and Colton (1972). The t and F-ratios could not be averaged for samples of  $n < 30$ , nor could they be compared easily across multiple sets of samples unless all of the sample sizes were the same because the "critical ratios" of t or F used to designate significant differences varied with sample size. Field data samples, due to time limits and working conditions at different locations, were of varying sizes, usually much less than 30. Furthermore, when field samples were grouped according to different criteria, such as exposure, or climate, or particular morphology, the groups consisted of varying numbers of sample means. A solution for this difficulty, to eliminate sample size and number from consideration and to make across-the-board comparisons of t or F possible, was a concept referred to herein as the relative significance of differences. Multifactorial analysis of variance (a form of ANOVA) was not a feasible method of analysis because multiple factors required prohibitively high numbers of samples (degrees of freedom). Furthermore, multiway analysis of variance required lengthy and complicated subsequent tests to determine which of the sources of variance were most effective. Therefore a more direct means of comparison seemed desirable, one employing familiar statistics and less circuitous reasoning than have many of the more complex statistical methods found in the literature.

By the concept of relative significance of differences a useful

form of "Taxonomic Distance" was calculated based on the comparative significance of t-tests (or  $F$  in ANOVA) between samples in each diagnostic character and then combined by averaging  $t/t^*$  of all characters,  $t^*$  being the appropriate critical ratio for each t-test made. Because taxonomic diagnostics depend on the number of characters that are significantly different in two populations as well as on their relative measurements, the averaging of comparative significance of t-tests in a selected number of characters provides a composite index combining number as well as degree of significant differences between two samples or sample groups. By averaging again the results for any number of pairs of samples composing a particular group or population and also for all intergroup pairs of such samples, intra- and intergroup taxonomic "distances" can be compared by their relative significance of differences.

The statistical analysis of differences between sample means by t-test or ANOVA consists in testing an hypothesis that both samples are in fact members of one population of like entities. If they are statistically the same, then in 95 % or more of such tests in the same population the difference between two means will be equal to or less than  $t^*$  times the standard deviation of the mean difference. The probability that any other samples from the same population will have differences greater than  $t^*$  standard deviations from the mean difference therefore is 5 % or less as they approach 3 standard deviations ( $n \geq 30$ ). If  $\bar{t}$  is much greater than  $t^*$  therefore, the hypothesis that both samples are of the same population is rejected at the 95 % level of probability, at which level the probability  $p$  of making an erroneous judgment is less than 5 %. Outside the limits of means set by  $t^*$

standard deviations, the probability that two plant samples actually come from the same population decreases quite rapidly from 5 % to 0 %. However, when means fall far outside the limits of a normal distribution curve of either sample ( $n \geq 30$ )--or t-distribution of samples with fewer than 30 individuals--there is no meaning to  $p$  as a measure of separation or of significance of the differences. Beyond three standard deviations the probability that means are significantly different is said to approach 100 %, no more. Yet, it is the experience of every statistician that  $t$  does continue to increase as the difference between sample means increases, from three standard deviations--the practical limits of a "normal" distribution curve--to 15 or 100 times the standard deviation of the sample differences or more. Why not use this empirical fact as a taxonomic measure and designate the relative significance of the differences between sample populations thereby?

One mentally compares the calculated  $t$  with the critical  $t^*$  every time one makes a t-test,  $t$  being either greater than or equal or less than critical  $t^*$ , which is obtained from t-distribution tables according to the degrees of freedom (dependent on size and number) of the samples compared. By actually dividing the calculated  $t$  by  $t^*$  one obtains a simple mathematical expression of the comparison that otherwise is made mentally. Likewise the relative significance of  $F$  by ANOVA also can be determined from an F-ratio simply by dividing it by the critical ratio given in the F-distribution tables for the appropriate sample sizes and numbers at the 0.95 probability level. F-order and t-order ratios then are quantities representing the number of times greater or less than the corresponding critical values are the calcu-

lated  $\underline{F}$  or  $t$ -ratios. Order-ratios eliminate further use of the critical ratios that are dependent on sample size to interpret the relative significance of differences among samples or among sample groups; and they therefore eliminate further consideration of sample size and number.

One can read the relative significance of differences directly from the  $t$ -order or  $F$ -order ratio. Any  $\underline{t}$  or  $F$ -order ratio less than or equal to 1.000 shows no significant difference at the 0.95 probability level in a given sample pair. Order-ratios between 1.000 and 1.500, or any other arbitrary small limit chosen, are considered as marginally significant differences, and order-ratios equalling or greater than 2.000 are of increasing orders of significance. (Critical ratios of  $\underline{t}$  or  $\underline{F}$  expressed to four significant figures were sufficient to differentiate between variant samples of Y. whipplei.)

Presumably closely related groups of samples will occur in very similar clusters of distributions with overlapping critical areas, i.e., regions under the distribution curves between  $\pm \underline{t}^*$ . More distantly related populations will have correspondingly greater differences between means of certain diagnostic characters; and the separation between their distribution means may lie several times the distance of critical  $\underline{t}^*$  from its central mean. Ideally, similar clusters will be distributed within the circle scribed by the 0.95  $p$ , or  $\underline{t}^*$ , of their common mean and will be separated from other unlike clusters by differences greater than three times the standard deviation of the means. However, in reality there can exist significant differences within a cluster of similar samples, and also some "unlike" clusters may include samples that are not significantly different from all

samples of another cluster. But if the cluster means can be shown to be significantly different by comparison of t-order ratios indicating large differences of "relative significance" between clusters as compared with t-order ratios of pairs within clusters, we will have a much better tool for judging the effectiveness of cluster analysis than has been available until now.

Some relationships of  $F$  obtained from ANOVA using yucca data are indicated with the corresponding critical ratios for a 0.95 probability level of significance in figures (Ch. III, pp. 108-114). As their name implies, orders of significance are especially useful for comparing relative efficacy of independent factors when a number of factors are capable of producing significant differences in the dependent parameters (Fig. 20, 21). Normally, t-tests and F-ratios are used to determine whether a statistically significant difference exists in a relatively marginal situation. However, it also is important to know how much greater significance should be attached to one or the other of two or more undoubtedly significant factors. These two or three figures (pp. 108-114) illustrate why relative significance can be used in place of multifactorial analysis of variance to show the comparative importance of different selective criteria in producing variances among samples or sample groups of yucca field data in a number of phenotypic characters. The visual comparison of F-ratios obtained for various classificatory factors, e.g., Fig. 20, 21, helps to put into perspective the relative degree of differentiation of sample groups by several accepted significant factors and does so without introducing the complex strategies or artificial manipulations of data and consequent relationships imposed by some forms of higher statistical analy-

sis. Also they illustrate how the averaged effects on different kinds of phenotypic characters exhibit considerable variation according to the type of independent factor used to sort the data. The t-order or F-order ratios, like any other measure of taxonomic distance or difference, can be averaged for several plant characters to provide a composite summary of the significance of variation found among samples grouped by different criteria. The relative degree of significance is directly readable for any sample pair or cluster pair from the combined averages of t-order or F-order values.

One advantage of order-ratios, not easily estimated for other taxonomic distances, is the direct comparability of significance at the 0.95 probability level. Because t-order and F-order ratios are direct expressions of the degree of significance at the 0.95 p level, the ideal justification for a cluster analysis can result, with 0.95<sup>+</sup> p for significant similarity of samples within cluster groups and 0.95<sup>+</sup> p for significant differences between and among clusters. Order-ratios also could be calculated for higher levels of probability by dividing the calculated t or F-ratio by the appropriate critical ratio. Tables 4, 5, 6 include examples of t-order ratios between mean DRI of yuccas in California regions.

#### B-8. Graphic Ordination of MORPHs by t-Order Ratios

The averaged t-order ratios for eleven characters were used in place of standard "taxonomic distances" to compare the MORPHs of Yucca whipplei. MORPHs were groups of samples classified by visual comparisons of graphic diagrams or models of leaf dimensions to obtain a continuous gradient of phenotypes following evolutionary or developmental

paths leading to different extremes of differentiation (Fig. 9). In Table 12 averaged t-orders of eleven characters determined for each possible MORPH pair were shown as "taxonomic distances" between MORPHs. The t-orders between MORPHs were combined by averaging the t-order ratios of all possible sample pairs between two different MORPHs. These were compared with all possible averaged sample pairs within each MORPH for each of the recognized morphological Series, i.e., evolutionary lines or clines, of Y. whipplei. They were averaged again for each inter-Series pair of MORPHs to show comparative size (significance) of differences among the morphologically defined Series, of which MORPHs constitute subsets.

The t-order results among MORPHs included within each major Series were small (0.96-4.53) as compared with nearly all of the t-orders of MORPH pairs from separate Series (3.14-8.29). All t-orders between pre-series MORPH I and all other MORPHs constituted the highest t-orders found (12.66-16.42), but the same comparisons made between pre-series MORPH II and all other MORPHs were relatively moderate (2.38-8.26) like the range of inter-Series comparisons. For Series 1, however, the mean t-order difference from MORPH II of 2.38 was well within the internal range of variation between MORPHs of Series 1, i.e., pre-series MORPH II could be considered as part of Series 1; but Series 1 was not at all "similar" to pre-series MORPH I. Very small or moderate differences between Series 3A (MORPH V) and all other Series (1.64-4.84) reflected its intermediate or transitional character. These t-order ratios--excepting the order-ratios differentiating MORPH I from all other groups--expressed clearly the intra-Series similarities and inter-Series differences that had been discovered by

Table 12. Order-Ratios Between Series and MORPHs of Y. whipplei, by t-Tests

Series and MORPHs Compared	Pre-Series		Series 1		Series 3A	Series 2A		Series 3B	Series 2B	
	MORPH I	II	III	IV	V	VI	VII	X	VIII	IX
Pre-Series I		15.42	16.42	12.66	13.12	14.27	16.22	14.58	11.41	15.00
II			2.40	2.38	4.84	5.32	7.18	7.21	5.88	8.26
Series 1 III				2.37	4.77	7.13	7.30	6.97	5.88	8.29
IV					3.86	5.19	6.01	5.65	4.39	6.42
Series 3A V						3.29	4.41	3.74	1.64	2.42
Series 2A VI							3.46	2.92	3.14	4.70
VII								2.65	5.12	7.13
Series 3B X									3.73	4.53
Series 2B VIII										0.96
IX										
Pre-series I		15.42	14.83	13.12	14.54	14.58	13.69			
Pre-series II	15.42		2.39	4.84	5.78	7.21	5.78			
Series 1				4.49	6.41	6.31	6.24			
Series 3A	13.12	4.84	4.49		3.85	3.74	2.60			
Series 2A	14.54	5.78	6.41	3.85		2.78	5.02			
Series 3B	14.58	7.21	6.61	3.74	2.78		4.13			
Series 2B	13.69	7.12	6.24	2.60	5.02	4.13				

other more direct methods. The extreme differences between MORPH I and others are difficult to explain and may indicate a previously unsuspected uniqueness in this group. Perhaps the uniqueness of MORPH I represents an original primitive condition from which major genetic changes led on the one hand to Series 1 via MORPH II and on the other to Series 2A and 2B via MORPH V (Diagrams a, b, c of Figure 12).

By using  $t$ -order ratio as a taxonomic distance, a taxonomic hierarchy of morphological categories was confirmed within the Y. whipplei species complex, in which three Series and their inter-Series hybrids formed major subdivisions. Within each Series were one to three subdivisions, defined as morphological grades called MORPHs. When these MORPHs were ordered according to their inter-MORPH similarities and differences by  $t$ -order ratios, a similar genealogical relationship was exhibited to that formed by PRIM (Fig. 11). Three distinct Series were united to the intermediate MORPH V with Series 1 derived directly from MORPH II. MORPH V--from which Series 2A and 2B were derived--was related in some way to MORPH I (Fig. 11, 12).

Because of the unfamiliarity of this proposed use of  $t$  or  $F$  to form order-ratios of relative significance and its consequent controversial aspects, some hours were spent in consultation with Dr. Ernest Scheuer and Dr. Elizabeth Trybus of the CSUN departments of Mathematics and of Management Systems. In testing order-ratios by the usual conditions that must be fulfilled for a variable to serve as a useful measure of distance, it was found that order-ratios fulfilled all but the triangular inequality test, and did meet the latter more often than not. These qualifications for distance measures are as follows:

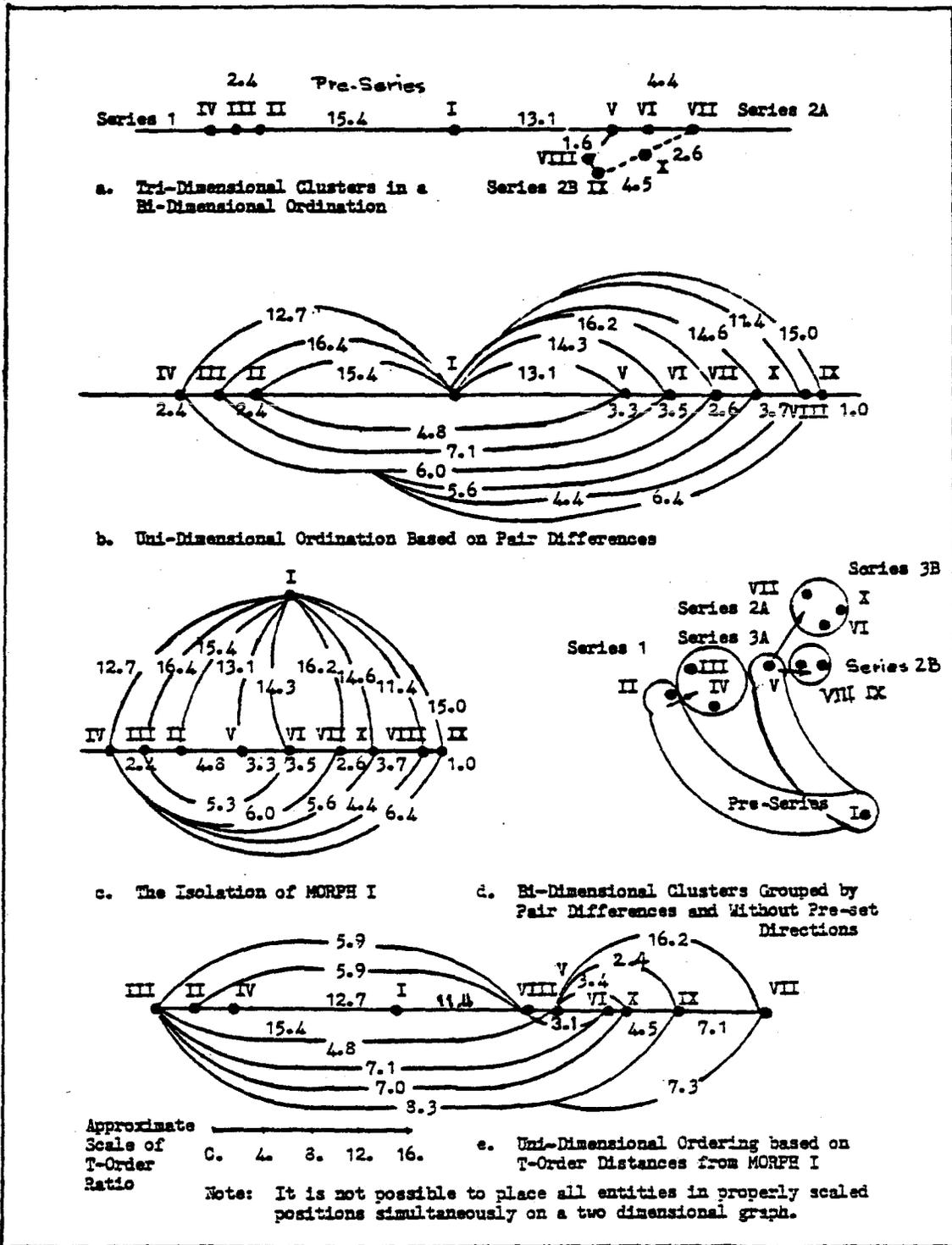


Figure 12. Some Attempts to Ordinate MORPH Graphically Using T-Order Ratios as Taxonomic Distances.

$$d(A,B) = d(B,A). \quad d(B,C) = d(C,B). \quad d(C,A) = d(A,C).$$

$$d(A,B) \geq 0. \quad d(B,C) \geq 0. \quad d(C,A) \geq 0.$$

Triangular Inequality Test:

$$d(A,B) \leq d(B,C) + d(C,A). \quad d(B,C) \leq d(C,A) + d(A,B).$$

$$d(C,A) \leq d(A,B) + d(B,C).$$

Although results of testing by the triangular inequality test usually were positive, in some specific conditions the test could not be met. These conditions usually existed when the largest distance measured was between samples of two different yucca Series and one of the other distances was between closely related samples within a Series. These were predictable relationships entirely suitable to the expected conditions. It was also discovered that actual taxonomic distances taken from cluster analysis matrices likewise failed the triangle inequality test in similar situations. Furthermore, consideration of numerous nearest neighbor distances, as between the shores of different-sized islands or between borders of large and small cities, whether expressed in miles, kilometers, or hours of travel--all highly acceptable as distance measures--also failed the triangle inequality test in many situations. The triangle inequality therefore simply is not appropriate consistently as a test of measurements unless the "points" between which distances are measured do in fact form the three points of a real triangle.

As a result of our discussion, it was finally agreed that for the purposes of this research, t-order and F-order ratios of relative significance were acceptable as indices to represent the multivariate differences between the yucca samples and sample groups. Further applications of this method to problems of cluster analysis would be

most welcome to test its utility under a broad range of conditions in nature.

### C. Chapter Summary

In the foregoing sections geographical patterns and possible phenotypical relationships between variant populations of Y. whipplei were explored. Several methods were used to find a phenotypic gradient that would indicate the most probable order of plant differentiation in Y. whipplei: (1) Developmental Rank Index (DRI) reflecting total genetic contribution to different leaf dimensions in yucca populations; (2) Morphological Types (MORPH), objectively classified by sorting scaled leaf diagrams representing qualitative and quantitative similarities in dimensions; (3) Cluster Analysis and PRIM Networks from multivariate sorting by computer of leaf and rosette dimensions and functions thereof; (4) Order-ratios of relative significance of t-ratios between sample means of all characters measured.

Each method was only partially effective for ordering of these multivariate phenotypes that have branched in three evolutionary directions. The most useful multivariate ordination seemed to be that indicated by MORPH, as shown in Figure 9, or as modified in Figures 11, 12, i.e., PRIM and t-order ratio. Combined, these different ordering methods resulted in considerable realization of the most likely evolutionary relationships and pathways leading to the various morphological types of Y. whipplei. In the next chapters, relations between climate and morphology in Y. whipplei are explored to find whether climatic differences can explain the geographical patterns of morphological differentiation.

### III. GEOGRAPHIC VARIATION IN Y. WHIPPLEI AND HOLISTIC CLIMATE GRADIENTS

Classification of plant habitats in terms of physical, chemical, and climatic traits is very complex. The microclimatic effects of slope and aspect in natural habitats cannot readily be evaluated quantitatively because of the inseparable effects of cloudy days, prevailing wind patterns, relative humidity, rainfall, latitude, and altitude. Each factor of habitat is complexly involved with several others, not only as to origin but also as to influence on plant growth, creating what may be called a holistic environment. Differences in seasonality exist for the most important climatic factors, such as precipitation and air temperature suitable to plant growth and hours of sunlight for photosynthesis. The direct positive effects of insolation on productive photosynthesis may not be separable from a simultaneously negative wilting effect due to increased evapotranspiration which also results from insolation. High insolation along the southern California coast raises air temperature and results in a relatively high absolute humidity in air, but in dry interior regions high insolation causes a decrease in absolute air humidity by expansion of warm air in the absence of large water bodies or dense vegetation (Seeman et al., 1979, pp. 6-16; Neiburger et al., 1971, pp. 65-67, 83, 92-93; Press and Siever, 1974, pp. 56-59; Strahler, 1969, pp. 131-132, 170, 182-184, 159-160). The potential effect of temperature on radiation absorption by air in these two regions therefore may differ considerably, affect-

ing wavelengths of incident light on plants and long-wave energy loss through the atmosphere (Neiburger et al., 1973, pp. 56-65; Chang, 1968, pp. 4-15; Seeman et al., 1979).

Plants differ in ability to survive changing conditions of habitat. Quite different patterns of seasonal variability of climate together with other attributes of location may result in habitats that are equally suitable to the range of tolerances of a certain kind of plant. Genetic flexibility allows adaptation of populations to fluctuating climates so that some endemic plants or cultivated crops can succeed under conditions much different from their native climates (Clausen et al., 1959; Aitken, 1974; Kimball and Gilbert, 1967 a). Slightly changed cultivation practices or sowing season can ensure success of crops in climates differing from those where a crop was developed (Aitken, 1974; Chang, 1968; Slatyer, 1973; Kimball and Gilbert, 1967 a; Geiger, 1973). Some wild plants are adapted genetically to a specific narrow range of stable factors and may not be adaptable to new conditions, and so become isolated as paleoendemics in localized relict stations (Raven and Axelrod, 1978; Stebbins and Major, 1965).

Observations of varying effects of conflicting climatic factors in plant differentiation have resulted in general agreement that evolution and adaptation of wild populations is through selection by the totality of environmental factors acting in a given place to affect the success of living things occurring there. This holistic multivariate environment was called a biogeocenosis by Walter (1973, pp. 12-16). A biospace or ecospace represents a similar concept of the multivariate geographic environment of a certain adapted biologi-

cal ecotype, or the combined environments of a related group of ecotypes (Dobzhansky et al., 1977, pp. 247-249). No single controlling factor can be identified because all factors act concertedly in a holistic environment where some organisms succeed while others do not (Clausen and Hiesey, 1958, pp. 110-123). The factor of shading by competitive vegetation is dependent on local temperatures, precipitation, soil depth, and such. Duration of snow cover--another factor in certain yucca habitats--depends on shading, air temperature, slope, compass aspect, altitude, latitude, and distance from the ocean. Both of these so-called independent factors seem important to the selection of plant types in Y. whipplei.

Because of considerations such as these, therefore, an ordination--i.e., a monodirectional ordering as a gradient--of general climates was sought by which climatic regions of southern California could be compared holistically as to their general favorability to growth of plants. Two practical systems of ordination of local climate regions were tried as gradients of condition for plant survival and productivity: (1) Plant Climate Areas, (2) Wild Vegetation Associations. By regressions of morphological traits against such climatic gradients, and by analyses of variance, correlations with different trends in yucca plant morphology were obtained.

#### A. Plant Climate Areas

The requirement of a map of monotonically ranked climate types was first filled for present purposes by the map of Plant Climate Areas developed for agricultural climate classification by Marston H. Kimball, former Chief Bioclimatologist of the University of California

Extension Service (Kimball and Gilbert, 1967 a, b). Although the state plant climate area map remains in an unfinished condition, published county segments are available through U. C. Extension (1963-1970). In this classification, local precipitation and soil type were disregarded in part because in agriculturally usable areas water could be supplied by irrigation, and soils could be improved by leaching and additions of fertilizer. Kimball's maps were constructed using climatic data from the U. S. Weather Bureau for each county, but were based primarily on the personal and practical experience by Extension farm advisors of crop success or failure in the counties (Kimball and Gilbert, 1967 a, pp. 69-71).

Kimball and his associates classified farmable areas by climate suitability for various crops in sets of climatic attributes decreasingly favorable to subtropical crop plants. The mildest, most equable, coastal marine belt was too cool and foggy for ripening citrus, but in the south was most suitable on account of equability, mildness, and humidity for tropical and subtropical horticulture. Just inland from the fog belt was the citrus-avocado thermal zone--still mild and equable due to maritime influence, or to moderate elevation, but warm and sunny. Next in climatic severity was the non-citrus portion of the overlapping citrus and Bermuda grass-rice zones (Kimball, personal communication, 1978) followed at higher altitudes, or in more continentally controlled inland areas, by a deciduous fruit zone. Beyond that was the conifer--or lumbering and recreation--zone, not much differentiated from pasture grass zones in which little or no agriculture besides grazing or forestry was recommended (Kimball and Gilbert, 1967 a, b).

Limitations of this system for the study of variation in yucca morphology are three-fold: (1) Yuccas are dependent on local rainfall, not irrigation, for survival, and (2) usually grow in the higher altitudes, rough topography, and rocky soils where agriculture is marginal and where, consequently, local climate data seldom are obtainable. (3) The plant climate areas are divided into sets of subzones that can not easily be numerically ordered by their qualitatively described attributes.

In an adaptation of Kimball's map by Sunset Magazine and Sunset Books (1976), twenty-four subzones were defined in terms of horticultural success, and all regions were classified in a numerically ranked sequence by their increasing favorability for tropical plants. Numerous botanists, commercial growers, and state climatologists collaborated in this revision of the Kimball Plant Climate Area map. This classification of California climate areas was chosen for this study to describe climate gradients (Appendix C, D).

Values for two climate variables were obtained for each yucca sample from its location on the Sunset plant climate area maps (Appendix C): the rank number of the local climate area in which the sample grew, and the rank number of the most severe locally adjacent climate area likely to affect negatively the success of yuccas. In the mildest warmest climates influenced by marine air, very little difference in rank number existed for these two variables, both being nearly optimal for growth of subtropical plants. But in the more interior continental climate areas, the existence of high mountains frequently resulted in closely neighboring climates with greatly contrasting ranks and consequently highly changeable weather conditions.

These two general climates therefore were characterized as mild and severe, respectively, and were found to be highly correlated with yucca leaf and rosette morphology. Regression of sample means of many of the twenty-two plant characters measured, and nine proportion ratios of measurements, against these two climate variables gave much insight as to effects of climate severity on the types of yucca that succeeded best in different parts of its range. In Y. whipplei, as in many other plants, leaf surface-area was greatest where there was moderate seasonal variability of climate and relatively good water relations. Ratio of leaf surface-area to volume decreased as the rank of climate area decreased, indicating that severity of climate and also drought affected leaf thickness directly. Yet all such regressions included relatively large numbers of samples that fell far from the general curve, causing questions as to fundamental effectiveness of present climates on selective plant variation in Y. whipplei.

Because of lack of space, many regression graphs and discussion of them are omitted from this thesis, but the most important relationships shown in them are covered by charts that combine a number of factors or attributes, e.g., Figures 6, 7, 13, 14, 20-22, 28-31. Geographic distribution of plant climate areas with respect to distribution of morphological Series of Y. whipplei was examined closely to learn the extent of climatic toleration by morphological variants. Of the twenty-four climates described for the western United States (Sunset, 1976) Y. whipplei occurred in only seventeen.

To provide a quantitative basis for comparison of the Sunset (1976) plant climate subzones--previously described qualitatively--the ranges and means of some important climate factors for areas critical

to yucca distribution in California are displayed in Appendix D. The subzones in parts of which Y. whipplei occurs are indicated by an asterisk, but in Appendix D data for these areas may come mostly from weather stations outside of the actual yucca range. Thus the amounts of snow registered for a mountainous climate zone, e.g., (3) or (1), usually are recorded at snow sport stations, many of which are located at elevations away from the nearest yucca colonies. Therefore subzone means are not necessarily typical of yucca locations but represent the limited data sources from a subzone. In Appendix E the climatic data were selected and averaged to indicate as well as possible the conditions at locations where Y. whipplei grew, but sources of these data were scarce.

The elongate ribbonlike subzones following elevation contours in northwest-to-southeast extending mountain ranges of California (Appendix C) were divided arbitrarily at the northern latitudinal limit of the range of Y. whipplei, i.e., subzones (7), (8), (9), (15), (16), (17) in Appendix D. Conditions in the northern and southern halves therefore could be compared with the subzone mean for the whole, and also related to the occurrence or absence of Y. whipplei.

In Appendix D the number N refers to number of data sources or items on which the corresponding average is based. However this number should not be viewed as a statistical sample of locations in the subzone. Figures from different time periods for a given station, of different kinds of published material (map isolines, tables) were included in the means of subzone stations. In Appendix E the number N represents a similar mixture of data sources, not only the number of stations averaged in different yucca areas.

Compared to quite small differences among the subzone means as a whole, there are much greater differences between the means of northern and southern halves of a given elongate subzone representing the ranges in which Y. whipplei do or do not exist. In reference to presence or absence of yuccas, parallel subzones tend to differ in adequacy of rainfall, but northern and southern segments of subzones differ mainly in mean temperatures. In the northern half of its range Y. whipplei occurs predominantly in Subzone (7), or toward the coast in Subzones (15) or (16), but is not found in parallel Subzones (8) and (9) because of too little precipitation, presumably.

#### B. Adverse, Optimal, and Intermediate General Climates

Very coarse divisions of climate--each consisting of a group of consecutive similar ranks of plant climate areas--were found effective as determinants of plant type. In these coarse climate divisions, seven of the seventeen subzones in which Y. whipplei occurred were classified as Adverse, five as Optimal, and five as Intermediate, according to their general favorability for active growth of subtropical plants throughout the year in each plant climate area subzone. Classification of the general climates is shown below and in Figure 13. The mapped distribution of study samples and their morphology with respect to general plant climate areas (Sunset, 1976) are illustrated in Appendix C.

Consecutively ranked climate areas were placed into general groups based on the descriptions of plant climate areas (Kimball and Gilbert, 1967 a; Sunset, 1976). Severe climates from (1) to (11) were

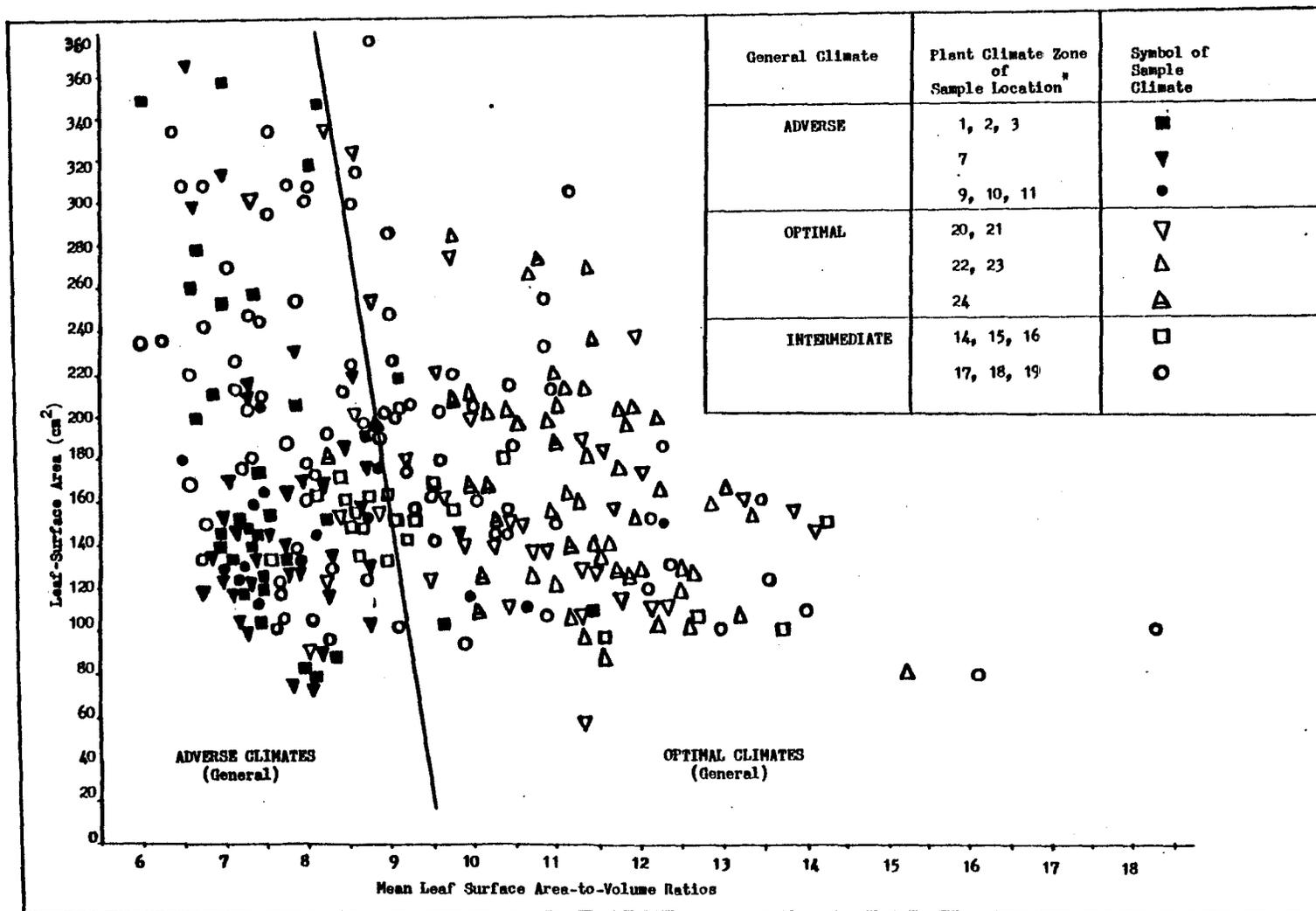


Figure 13. Discernment of Naturally Selective Climates by the Morphological Attributes of *Y. whipplei*. Leaf Surface Area =  $2L(W + T)$ . Leaf Volume =  $LWT$ . Leaf Surface Area to Volume Ratio =  $2(W + T)/WT$ .

termed adverse because of short growing seasons limited by severe temperatures in winter and some also by severe drought in summer. In these climates plant growth ceased yearly for several months. Climates from (20) to (24) were termed optimal because, except for summer drought, their favorable growing seasons lasted virtually all year. The climates from (14) to (19) were termed intermediate because moderately long fall and spring and summer growing seasons were broken by short severe periods of winter weather with weak sunlight, and by distinct but short hot, or foggy but dry, summer drought (Appendix D, E).

To exhibit the relations between climate severity and plant attributes included in leaf surface-area and ratio of leaf surface-area to volume, a scatter diagram (Fig. 13) was constructed with these two variables as axes. Each sample point was given a symbol representing climate rank where the sample grew. Most of the samples from mild favorable climates occurred to the right on the graph among the samples with largest ratios of surface-area to volume. Samples from intermediate climate zones occurred throughout the entire range of morphological combinations, but adverse climate samples fell on the left side.

A straight line in Figure 13 minimizes overlap of yucca samples in adverse and optimal climates to 5 and 6 %. The number of points representing each of the three general groups of climate types was counted for the adverse and optimal sides of the scattergram, a total of 142 on the adverse side and 139 on the optimal side (Fig. 13, Table 13 a). However, samples from actual adverse climates were just 55 % of the samples on the adverse side of the diagram, while actual optimal climate samples were only 59 % of the samples on the optimal

Table 13. Holistic Climates and Morphology in Y. whipplei

13 a. Distribution of Climate Types According to Morphology						
General Climate Type Where Field Samples Grew	ADVERSE Side Scattergram ( $A/V \leq 9$ )		OPTIMAL Side Scattergram ( $A/V \geq 9$ )		Total Samples	
	Number of Samples	Percentage of Samples	Number of Samples	Percentage of Samples	Number of Samples	Percentage Of Samples
ADVERSE 1-11	78	54.9	7	5.0	85	30.0
OPTIMAL 20-24	9	6.3	82	59.0	91	32.4
INTERMEDIATE 14-19	55	38.7	50	36.0	105	37.4
Total	142	50.5	139	49.5	281	100.0

13 b. Distribution of INTERMEDIATE Climate Samples According to Leaf Area							
Area Classes	Climate	ADVERSE Side Scattergram		OPTIMAL Side Scattergram		Total Samples	
		Number of Samples	Percentage of Samples	Number of Samples	Percentage of Samples	Number of Samples	Percentage of Samples
Low Leaf Area 70-180 cm	Severe, Int. 14, 15, 16	11	20.0	10	20.0	21	20.0
	Mild, Int. 18, 19	17	30.9	20	40.0	37	35.2
High Leaf Area 181-400 cm <sup>2</sup>	Severe, Int. 14, 15, 16	0	0.0	0	0.0	0	0.0
	Mild Int. 18, 19	27	49.1	20	40.0	47	44.8
All Leaf Areas	Total Int.	55	52.4	50	47.6	105	100.0

Leaf-Surface Area-to-Volume Ratio = AREA/VOLUME = A/V. See pp. 81-85 of text for explanation.

<sup>2</sup>Int. = INTERMEDIATE

side as divided by the line. One might conclude from these distributions that 41 to 45 % of the samples were not growing in the general climates most correlated with their types of morphology, for they were either in intermediate climates or in climates of the opposite extremes. The adverse side of Figure 13 consisted of yucca samples with low ratios of leaf surface-area to volume, and on the optimal side were samples with high ratios of mean leaf surface-area to volume. Samples from intermediate climates constituted 39 % of the low surface-area-to-volume-ratio samples to the left of the line and 36 % of the high-ratio samples to the right (Table 13 a). Of 91 samples in optimal climates, 82 (91 %) had ratios of leaf surface-area to volume greater than 9, the mean at the dividing line. Of 85 samples in adverse climates 78, or 93 %, had ratios lower than or equal to 9.

Because nearly equal percentages (52 and 48 %) of intermediate climate samples occurred in the adverse and optimal sides of the diagram respectively, samples from intermediate plant climate areas were examined more closely with respect to mean leaf area of samples and relative severity or mildness of the intermediate plant climates (Table 13 b, Fig. 13). In samples of small leaf area (70 to 180 cm<sup>2</sup>), mild intermediate climates, i.e., subzones (18), (19), prevailed in 31 and 40 % of the plants on the adverse and optimal sides of the graph (Fig. 13). Twenty percent of the plants of small leaf area were in severe intermediate climates on both sides of the diagram, i.e., subzones (14), (15), (16). In samples with large mean leaf area (181 to 400 cm<sup>2</sup>) no samples from severe intermediate climates were found on either side of the line, but mild intermediate climates (18) and (19) were associated with large leaf area in 40 and 49 % of such

samples on both sides of the graph. Clearly average warmth and mildness of climate favor Y. whipplei regardless of leaf area, but moderate severity of climate strictly limits large thin-leaved plants, and not so strictly the small thin-leaved plants. Whether or not leaves were large or small evidently also was determined by other factors besides temperature, e.g., humidity and light exposure. Although in severest intermediate climates, large leaves were not tolerated, in adverse climates 22 out of 53 samples, or 43 % had leaf area over 180 cm<sup>2</sup>. These large leaf area samples from adverse climates, however, also had very low surface-to-volume ratios due to maximal leaf thickness, as in MORPH X of the Sierra Nevada and San Gabriel Mountains.

Because almost all portions of the scattergram included samples from mild intermediate climates, I conclude that intermediate climate areas allow ample refuge for morphologically specialized plants originating from either the adverse or optimal climatic extremes. Apparently this toleration of various climates by several different MORPHS accounts for much of the variance exhibited in regressions and would be sufficient to allow numerous yucca populations to survive gradual climate changes. Considerable climatic adaptability of yuccas without morphological change therefore exists, especially in the coastal mountains with relatively mild climates.

### C. General Climate and the Morphological Evolution of Y. whipplei

Another graphic approach was made to find relationships between general climate favorability and leaf morphology in Y. whipplei. Ordination of Developmental Rank Index (DRI) on the x-axis and of Morphological Type (MORPH) on the y-axis in Figure 14 allowed creation

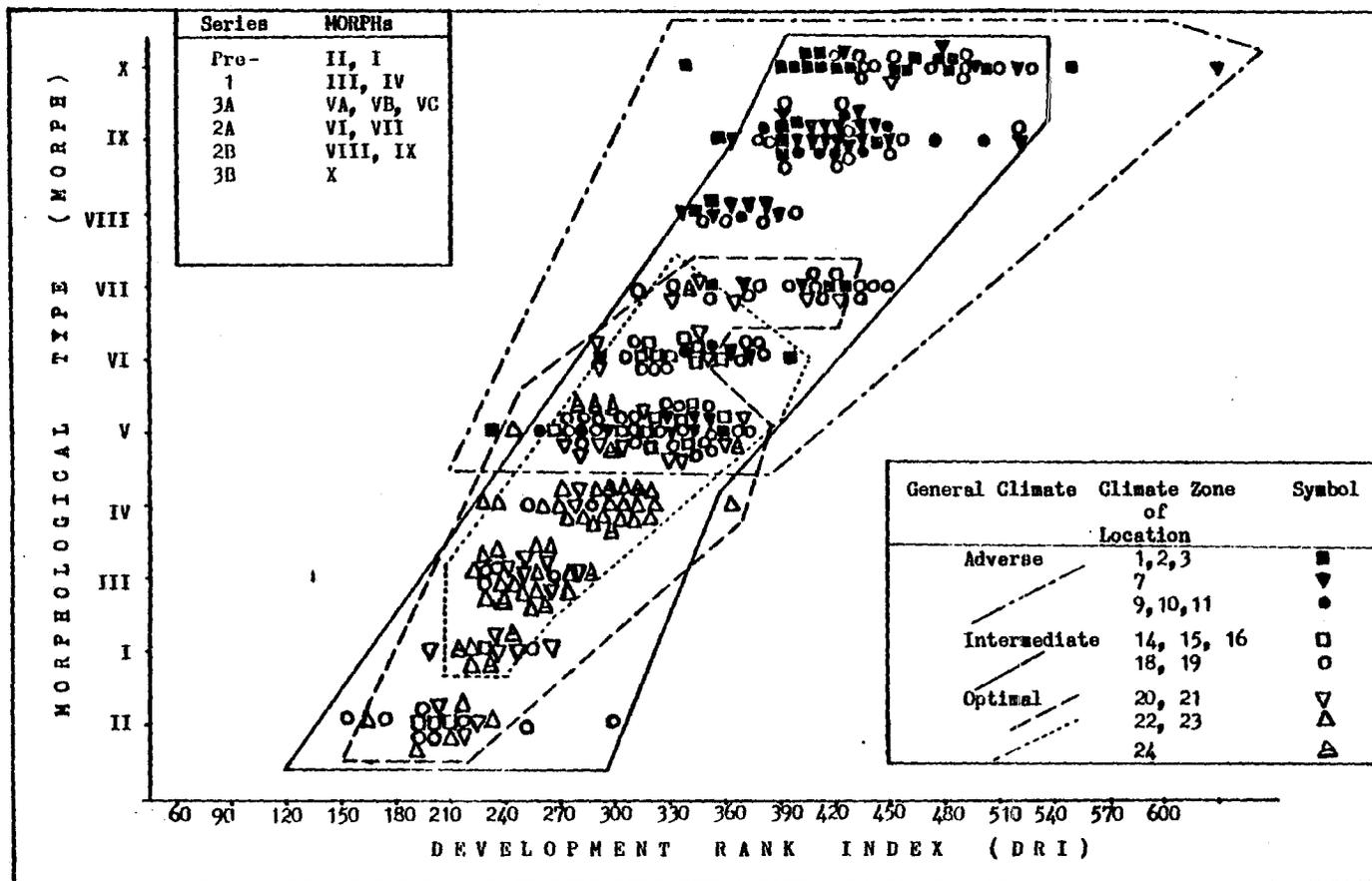


Figure 14. General Climates and Morphology in Y. whipplei

of a scattergram of all sample means that was based on the assumed best sequence of MORPHs in an evolutionary gradient (Ch. II). These samples were grouped by pre-series and Series 1, 3A-2A, and 2B-3B, the sequence which produced the best and straightest regression against DRI, an independently obtained scale of increasing leaf development in the yucca field samples (pp. 31-39; Fig. 14). This "fit" between DRI and order of MORPH helped to support the idea that leaf morphology in Y. whipplei commenced with the smallest leaf rosettes with least numbers of expressed productive genetic components, and gradually increased in size with evolution.

To indicate visually the climatic associations of samples within this sequence, each glyph on the scattergram (Fig. 14) was coded according to the climate subzone rank (Sunset, 1976) of the sample's location. They were further combined by line symbol to indicate the morphological range of three general climate types: adverse, optimal, and intermediate, using the same climatic groupings of "plant climate areas" (Appendix C) as in Figure 13. Pre-series and Series 1 samples occurred most consistently in the mildest, warmest, most equable, optimal climates. Series 2B-3B samples predominantly were in adverse climates characterized by longest, coldest winters and, in Series 2B, the hottest dry summers. A majority of intermediate climate samples were in Series 2A-3A but some also occurred in pre-series.

There were numerous exceptions to these generalities. In fact, the frequency distribution of general climate types under each MORPH of a Series followed a distinct pattern according to Series. These climate distributions found in Figure 14 were summarized by MORPH and by Series in Table 14. Some samples in each MORPH were located in an

Table 14. Distribution of General Climate at Sample Locations in the Series of Y. whipplei

Series	MORPH	Number of Samples	ADVERSE Climates		INTERMEDIATE Climates		OPTIMAL Climates	
			Number	Percent	Number	Percent	Number	Percent
2B-3B	X	34	21	61.8	12	35.3	1	2.9
	IX	41	31	75.6	10	24.4	0	0.0
	VIII	<u>13</u>	<u>9</u>	<u>69.2</u>	<u>4</u>	<u>30.8</u>	<u>0</u>	<u>0.0</u>
		88	61	69.3	26	29.6	1	1.1
2A-3A	VII	25	5	20.0	13	52.0	7	28.0
	VI	27	6	22.2	16	59.3	5	18.5
	V	<u>57</u>	<u>11</u>	<u>19.3</u>	<u>31</u>	<u>54.4</u>	<u>15</u>	<u>26.3</u>
		109	22	20.2	60	55.0	27	24.7
1	IV	27	0	0.0	2	7.4	25	92.6
	III	28	1	3.6	3	10.7	24	85.7
		55	1	1.8	5	9.1	49	89.1
Pre-Series	I	13	0	0.0	3	23.2	10	76.9
	II	<u>19</u>	<u>0</u>	<u>0.0</u>	<u>11</u>	<u>57.9</u>	<u>8</u>	<u>42.1</u>
		32	0	0.0	14	43.8	18	56.2

apparently inappropriate climate type. In general, however, the three Series of Y. whipplei seem to correspond with the three general types of climate.

Percentages of samples in each of the three most general climate categories--adverse, optimal, and intermediate--were plotted for each Series Group (Fig. 15). The resulting Series curves showed the strong selective tendencies associating each of the main climate categories with each of the six main yucca groups according to general favorability to plant growth: adverse climates with Series 2B-3B, optimal climates with Series 1 and pre-series, intermediate climates with Series 2A-3A. The terms adverse, optimal, and intermediate were not chosen with respect to the special requirements of Y. whipplei, but represent general classifications of climate with respect to common growth requirements of subtropical, warmth-requiring autotrophs.

One might attribute anomalous cases to particular aspects of climate that are not necessarily associated with the severity of growing conditions indicated by ranking of plant climate areas (Sunset, 1976). Factors such as hours of sunlight in the growing season, or summer precipitation, may be more critical to survival of particular morphologies than is general severity of the temperature regime. Often a regional climate classified as adverse or intermediate includes areas with different microclimates very favorable to yuccas within the same geographic range. Such favorable microclimates may occur regularly within the more general climatic regimes and so account for the regularity of appearance of seemingly anomalous sample climates in each MORPH (Table 14). Little is known of the effects of climates on the survival of the obligate pollinating moths (pp. 12-17) although moths

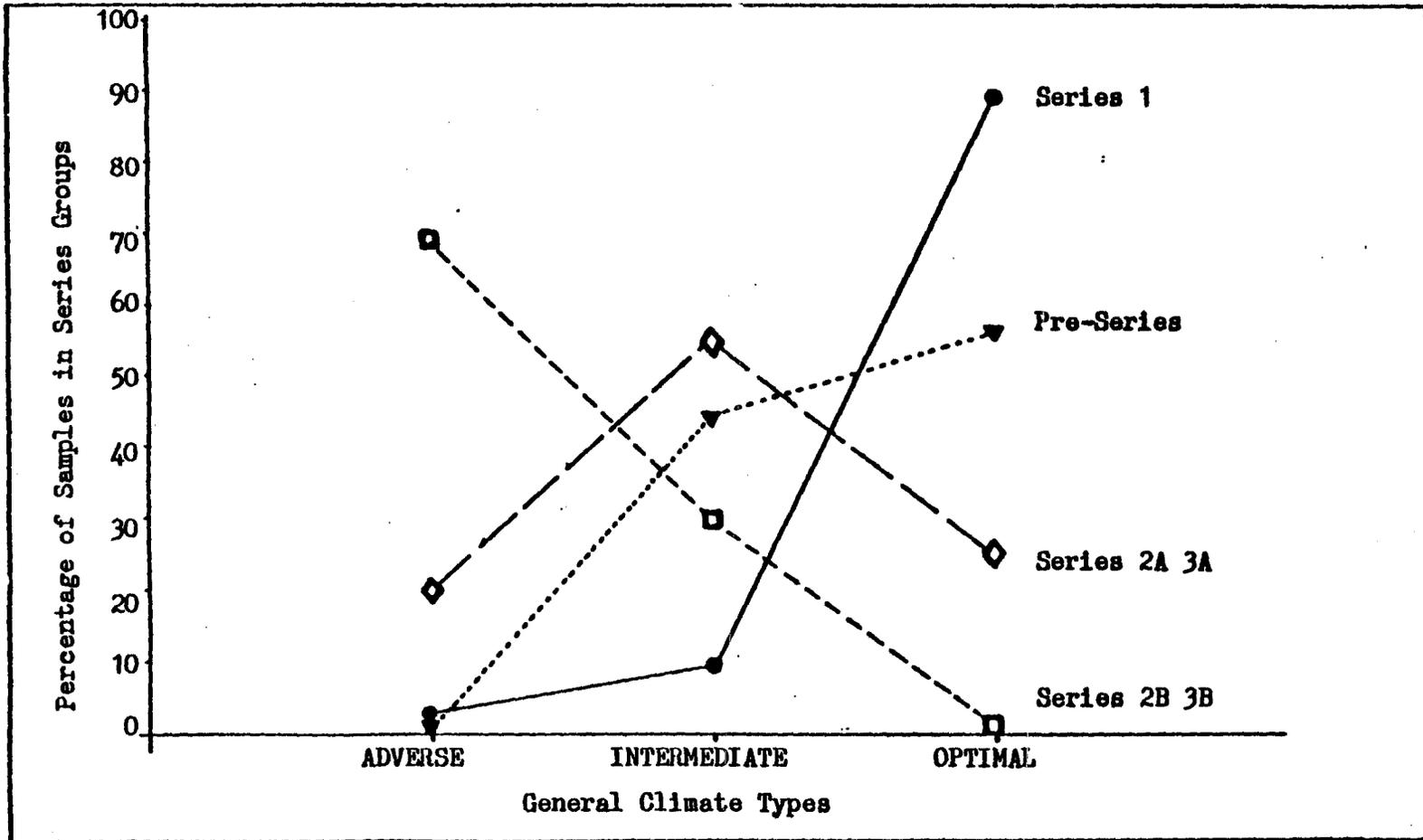


Figure 15. Distribution of Samples in Series of Y. whipplei and the General Climate of Locations. (For Data see Table 14.)

evidently were scarce in regions of severe climatic conditions (Powell and Mackie, 1966).

Another explanation for anomalous occurrences might be the relative time that the yucca populations sampled have existed under their present climate regimes. Certain regions emerged from Pleistocene seas only a few thousand years ago, but in other areas having similar climates today, yuccas apparently have existed several millions of years under climates quite different from the present (Fig. 16, pp. 13-14). During the Pliocene, for instance, large land areas emerged in what is now the offshore continental shelf of southern California (Corey, 1953). Therefore some of the present coasts formerly were many miles from the sea, or in the reverse case, present inland areas formerly were coastal. In general the present boundaries of most modern Y. whipplei populations correspond strikingly to late Pliocene shorelines (Fig. 16) and because of unfavorable edaphic conditions (pp. 11-12) these colonies are slow to invade lowlying coastal plains that were inundated in the Pleistocene. The Channel Islands, remnants of former large islands and or peninsulas, were nearly submerged during the eustatic high sea levels of the Pleistocene-Holocene (Birkeland, 1972). Yuccas now are not native to the islands, but may have been prior to inundation. Knowledge of past paleogeographic conditions is essential to understanding the evolution of modern populations of native plants and their present distributions.

To combine information about associated climates with the evolutionary pattern proposed for MORPHs of Y. whipplei, the same data found in Table 14 were arranged in a diagram of squares representing each MORPH (Fig. 17), and the squares were arranged so as to conform

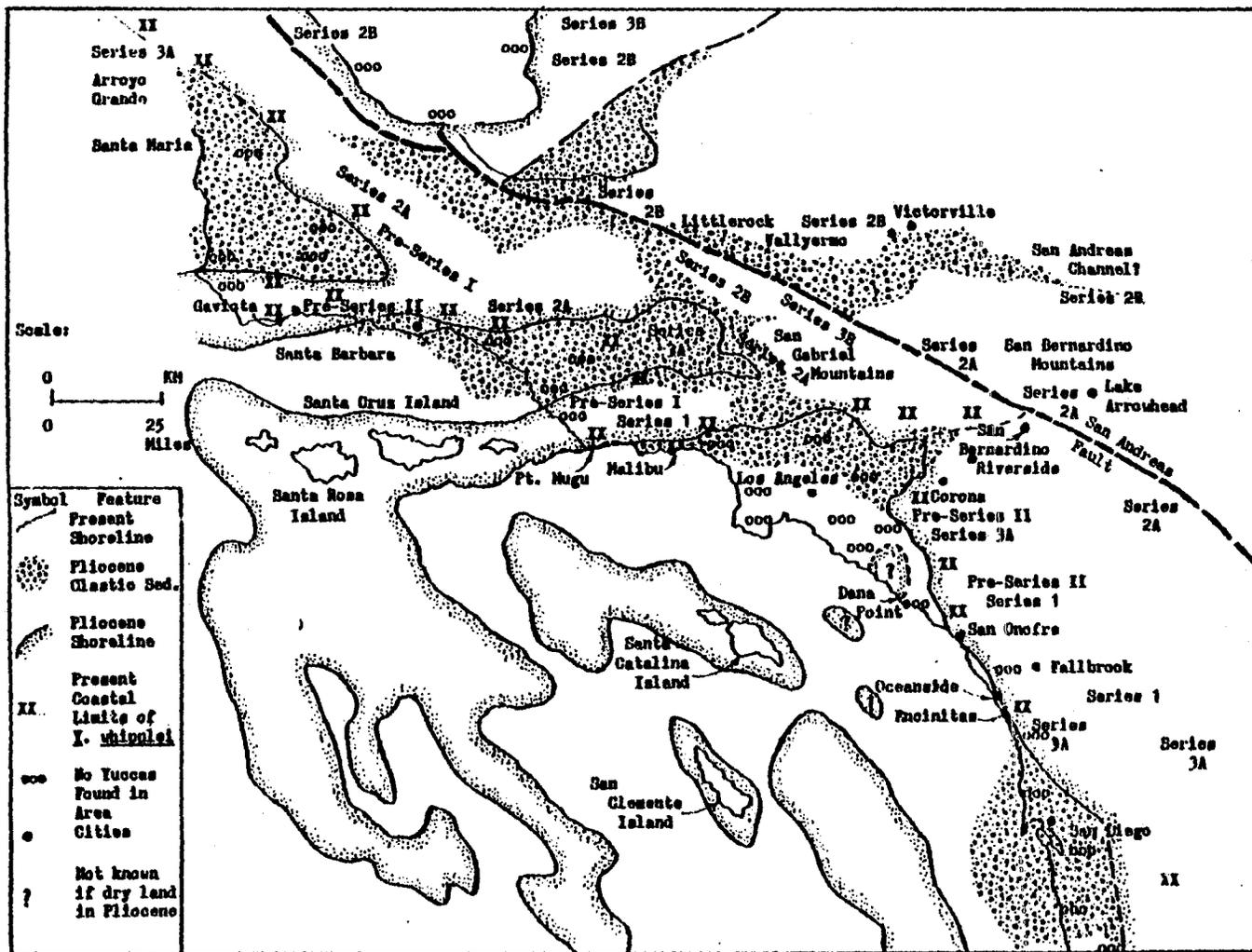


Figure 16. Pliocene Paleogeography and the Modern Distribution of *Y. whipplei* Series  
 Adapted from W. H. Corey, 1953, including a 25-mile offset along San Andreas Fault.

with the evolutionary pathway dictated by the most economical increases of mean leaf dimensions from MORPH to MORPH as in Figure 9. Climatic notes for each morphological type based on local climate from Table 14 were included to show how the distribution of different patterns of climate paralleled each of the divergent morphological trends (also Ch. IV). Increase of mean leaf thickness most definitely paralleled increased severity and variability of climate, as shown by a high percentage of yucca samples from adverse climates in mesic situations as well as in desert areas. Leaf length was great in favorable moderate to warm humid environments having a relatively long growing season, and possibly a corresponding competition for light with other vegetation that was favored also by generally good growing conditions (Ch. V).

Greatest leaf width occurred in numerous yucca samples growing near the coast or at medial elevations on the coastal side of mountain ranges. These areas usually had moderate climates where total annual solar incidence was limited generally, as by fog, cloudy weather, or by other universal sunscreens such as a winter blanket of snow or shading by vegetation (Ch. IV, V). Widened leaf in Series 3A-2A multiplied the minimal surface area and presumably resulted in more efficient use of sunlight by plants during relatively short periods of full exposure. Improved photosynthetic efficiency in wide leaves may have resulted in part from the increased amount of vascular tissue per unit length of leaf (Ch. IV, V). Light incidence was indirectly related to climate in that xeric or severe climate often removed shading by competing vegetation. A paucity of sunlight in regions of high precipitation best explained the existence of yucca plants with the

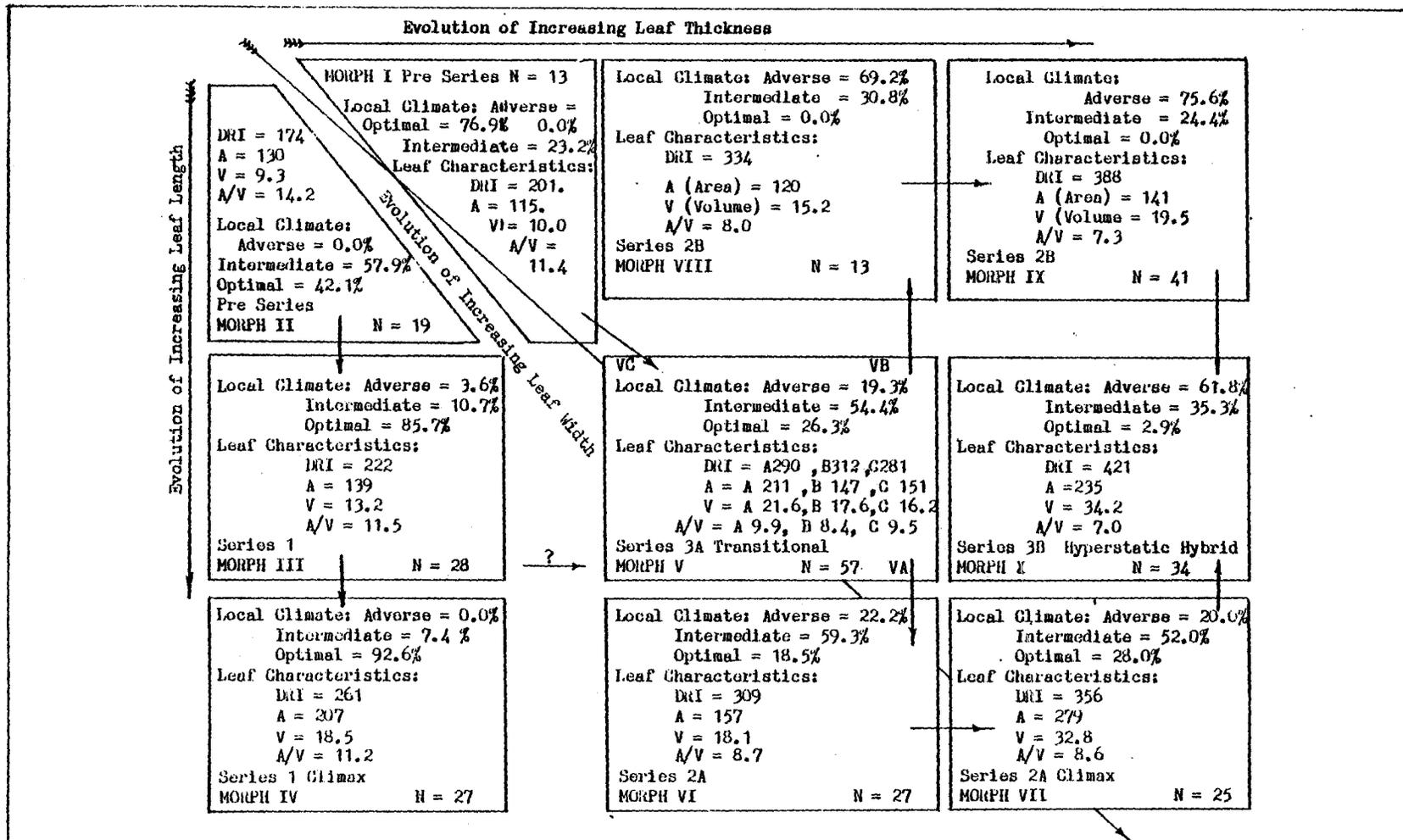


Figure 17. The Relation of Local Climate to Morphological Development of Leaves in Populations of Y. whipplei  
 Climate Data from Table 14; Dimensions in centimeters, centimeters squared, centimeters cubed.  
 Phylogenetic pathway is hypothetical.

largest leaf surface-areas. In spite of statistically important exceptions, the distributions illustrated in Figures 14, 15, 17 explained well some general relationships between climate and morphological specialization in Y. whipplei. Further evidence of climatic factor trends with MORPH are described in following chapters.

D. Native Vegetation as Holistic Climate Indicator  
in the Distribution of Variants, Y. whipplei

Vegetation classes have long been used as keys to climate zones, e.g., Köppen (James, 1966; Court, 1967; Strahler, 1969, Plate 2; Espenshade and Morrison, 1975; Daubenmire, 1978, pp. 2-3). Therefore, in a second attempt to obtain a defined and graded series of climate types--one that should reflect local precipitation--yucca samples were grouped and compared according to types of wild vegetation of which they were a part.

D-1. State and U. S. Forestry Maps of Vegetation

The incomplete series of vegetation maps published by the California State Division of Forestry and the U. S. Forest Service (1932-1940) used a numerically graded series of vegetation types which corresponded recognizably with a climatic gradient accountable for success of the various vegetation belts (Munz and Keck, 1959; Major, 1977). Due to the detailed and intricate vegetation patterns mapped and relative obsolescence of these maps, it was difficult to decide exact locations of yucca samples with respect to the mapped vegetation. Field notes as to locally "dominant" wild plant species at yucca sample locations were helpful, but usually were repetitive of all the

commonest members of coastal sage scrub or chaparral, with occasional plants of a higher dominance level, i.e., higher storey. According to Munz and Keck (1959, pp. 1361-1362) all subspecies of Y. whipplei occur in chaparral and coastal sage scrub, but Ssp. caespitosa is also listed in Joshua tree and piñon-juniper woodlands, and Ssp. Parishii is located also in yellow pine forest. To enhance differentiation of vegetation types wherever possible, I chose highest storey plants to represent vegetation types on the theory that they indicated formerly abundant vegetation in the area where present vegetation was either a seral stage of development or a remnant (Barbour and Major, 1977). Seres are chronological sequences or successions of characteristic natural vegetation communities adapted to consequential environmental changes either, in secondary seres, following catastrophic destruction of the former climax vegetation, e.g., by major weather changes, flooding, landslide, fire, agriculture, or lumbering--or else, in primary seres, on newly created ground area due to such cataclysms as volcanism, glacial retreat, or coastal emergence.

Until a few years prior to my sample studies there, many areas of coastal sage scrub, or of chamisal, had consisted of Ceanothus or manzanita chaparral, or of mixed conifer or oak-conifer woodland, judging by burned stumps and snags still present and by the living vegetation in neighboring areas. In these cases, former "climax" dominants provided a basis for classifying the vegetation, for the yuccas with scorched leaves and boles clearly were survivors of the same fire and not newcomers in a seral plant community. Yucca samples for convenience were measured usually in openings characterized by coastal sage scrub, but these openings were considered to be only

"temporary", being on the border of, or surrounded by, impenetrable high chaparral or by woodland where yucca plants of the same types, or Series, also were found to be a significant part of the vegetation. Similarities of these yuccas were checked in manmade openings such as along fuel breaks and roads through the heavy brush (sun vs. shade studies, Ch. IV). Virtually identical vegetation types were described for many yucca samples of different Series.

In the desert margins, attempts to classify samples as to associated types of vegetation also were difficult. Desert chaparral containing yuccas interdigitated and overlapped with Joshua tree woodland, which in turn overlapped with juniper or piñon woodland including identical yuccas. The vegetation type for each yucca sample was named arbitrarily on the basis of the highest storey species noted in the immediate vicinity, with a listing of other common species within 1 to 15 meters in a relatively uniformly distributed vegetation. Identifications of vegetation containing yucca agreed with the classifications of yucca vegetation as described in Barbour and Major (1977) more than with those of Munz and Keck (1959). Nevertheless, the various local "desert" or xeric montane vegetation communities exhibited no corresponding differences in the regional types of yucca associated with them.

A partial explanation for comparatively insignificant correlation found between vegetation type and morphology of Y. whipplei in these maps and my own records is that time lags in the development of seral stages of vegetation dependent on rainfall patterns or fire cycles, or both together, apparently removed local vegetation patterns from strict conformity to general climate patterns (Johnson, 1975). Adap-

tive phenotypical variation in Y. whipplei clearly was much more stable geographically than was the local vegetation pattern. As an example, in wild vegetation associations studied by Johnson (1975) in a 2.5 mile square of Wilson Canyon in the western San Gabriel Mountains, 197 of the 319 stands, or 62 %, included Y. whipplei, and it was named in 15 of his 19 vegetation associations, i.e., 79 %. In this small area all yuccas were of essentially the same morphology, consisting of hybrids in Series 3A-3B. Associations including Yucca whipplei of this morphology therefore ranged in type from bare ground and annual grasses through coastal sage scrub, Adenostoma chaparral, Ceanothus chaparral, to Pseudotsuga macrocarpa and Pinus coulteri associations. Similarly varied lists of vegetation types could be made for other morphological Series of Y. whipplei, a fact illustrating how unlikely morphological specialization in the yucca is based on shortterm conditions that determine the presence of one local plant community in place of another.

D-2. The Kùchler Vegetation Map and Distribution of Variation in  
Y. whipplei

The map of California vegetation formations (scale, 1:1,000,000) by A. W. Kùchler (1977) is generalized to the extent that regional differences exist within the geographic range of Y. whipplei. Kùchler used not only the U. S. and California vegetation maps of others, that were seldom defined as to particular species and subspecies of plants, but also had the collaboration of numerous botanists, especially those whose work also was included in Barbour and Major (1977). Map generalization does not deny the existence of various microclimates and of

interdigitating vegetational habitats within the regions that may be crucial to successful establishment of Y. whipplei. The recognition of general plant formations typical on a broad scale in different parts of the range of Y. whipplei, however, may show relationships with particular types of Y. whipplei, either due to gross climatic characteristics of a region or to paleofloristic connections or both.

The frequencies of samples of Y. whipplei MORPHS that, according to their map locations, were found in different Kuchler vegetation formations were plotted in Figure 18 and summarized in Figure 19. By far, the most frequent associates of Y. whipplei were the chaparral formation and, surprisingly, the southern oak forest (Quercus agrifolia). Less than half as many samples were located in each of: mixed hardwood Arbutus-Quercus, blue oak-digger pine forest, or the coastal sage brush. Few yucca samples occurred in juniper-piñon woodland. In my opinion the latter group ought to have been combined logically with Joshua tree scrub and Mojave creosote bush because these formations usually were inseparable geographically in regions where Y. whipplei also occurred. Combined, the incidence of Yucca whipplei in these "desert" formations equalled those in mixed hardwood or blue oak-digger pine forest, or in coastal sage brush. An historic significance was recognized in the association of these six major vegetation combinations with Y. whipplei. Not only were the relatively recently differentiated chaparral and coastal sage scrub formations--associated with Mediterranean climate that developed since the Pliocene (Barbour and Major, 1977; Raven and Axelrod, 1978, pp. 26-27)--important in the distribution of Y. whipplei. Also segregates of much older woodland associations known from the early

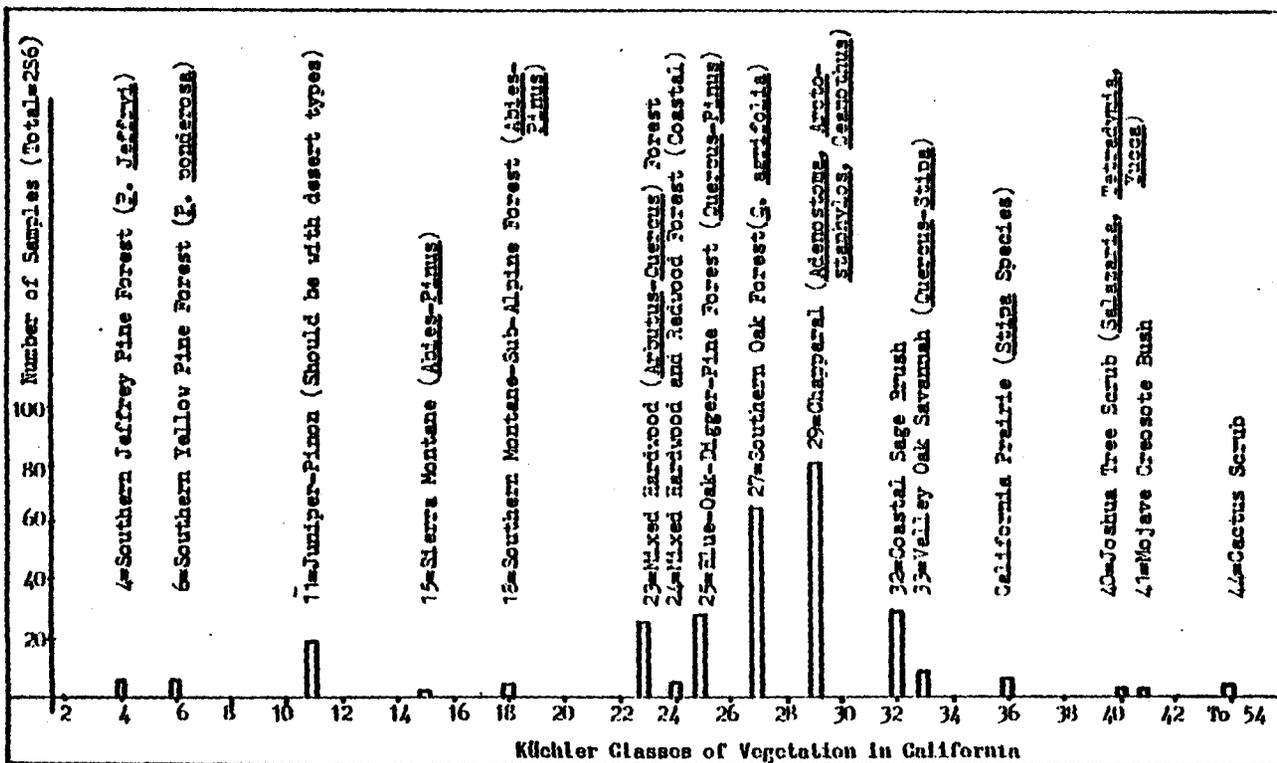


Figure 18. Distribution of *Y. whipplei* in Major Vegetation Formations of the Küchler Vegetation Map of California (1977)

Tertiary (Axelrod, 1958, 1973, 1975) were still correlated geographically with the modern distribution of Y. whipplei.

To further analyze the distribution of yucca types within each kind of vegetation, the Kuchler vegetation formations in which Yucca whipplei samples were located were plotted as histograms of sample incidence in Figure 19. Each column was divided as percentages of samples of various MORPHs of Y. whipplei occurring in the same vegetation type. Some conclusions drawn from this breakdown had a bearing on the historical interpretation of Y. whipplei colonization in California. The breakdown also explained the relatively low variance ratios found by ANOVA comparing morphology of groups of Y. whipplei located in different formations of the Kuchler classification of vegetation, discussed later.

Nearly equal percentages of samples were found for all Series and pre-series groups of yuccas in the column representing chaparral (Fig. 19). MORPH VIII of Series 2B was not represented in chaparral but MORPH IX was. More than one possible interpretation of this varied MORPH distribution in chaparral existed: (1) Either there were several climatic subdivisions of the Kuchler chaparral formation (Raven and Axelrod, 1978), or (2) chaparral representing a specific climatic zone has developed recently compared to the other forest and woodland associations and has drawn its members from whatever localized plant forms existed previously as a result of early evolution in geographically distinct regions (Hanes, 1977). Relatively late climatic selection of chaparral vegetation as in (2) resulted in superficially alike communities consisting of similar but previously differentiated representatives of variable taxa. I think both explanations largely

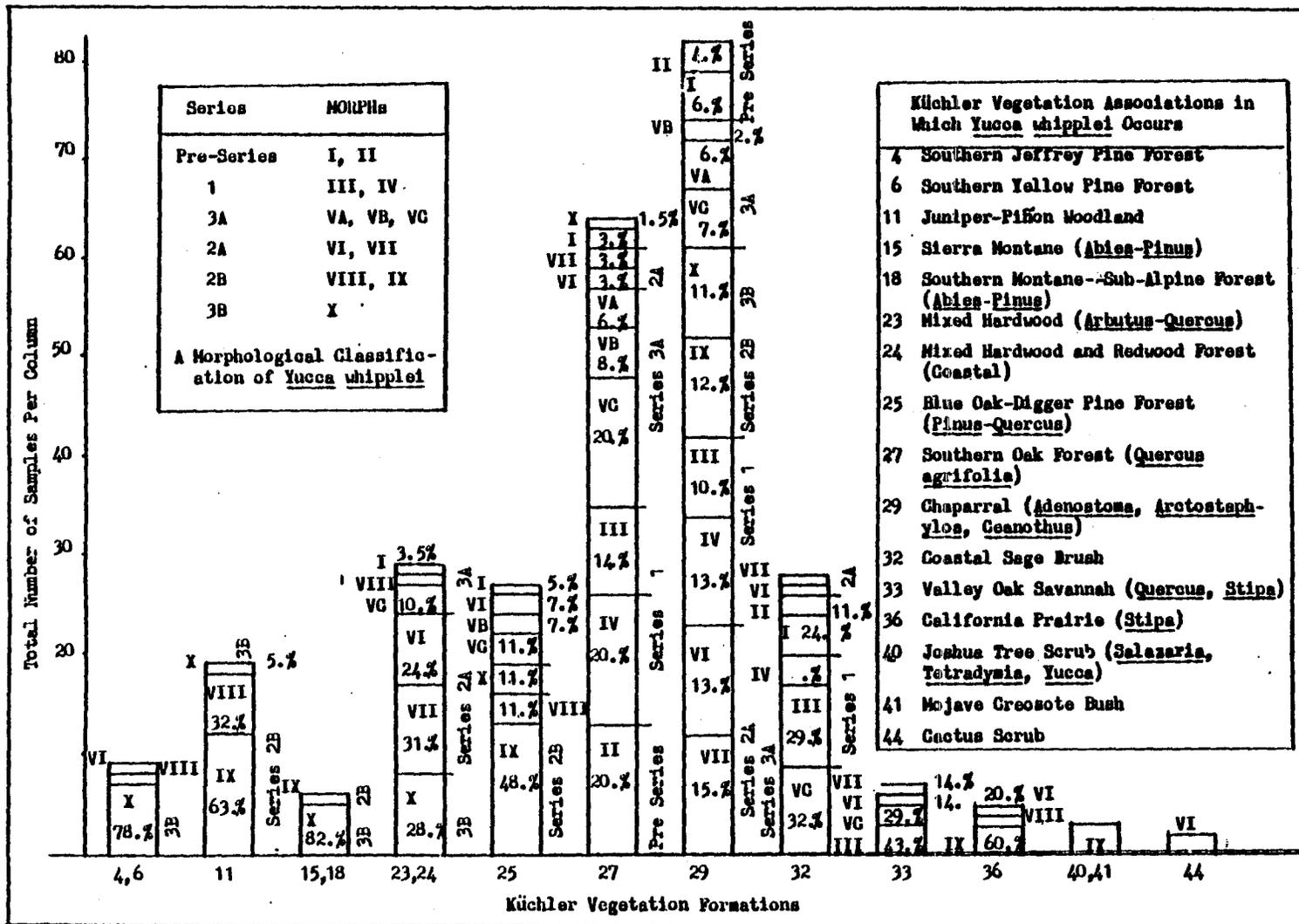


Figure 19. Distribution of MORPHs of *Yucca whipplei* in Vegetation Formations of the Küchler Map (1977).

are true, based on the kinds of yucca MORPHs found in Tertiary types of woodland vegetation (Fig. 18, 19).

Of samples in southern oak forest, yuccas of Series 1 and pre-series represented 57 % and intermediate Series 3A yuccas constituted an additional 34 %. The remaining 9 % included Series 2A (VI and VII) and Series 3B (X) but no Series 2B occurred at all. The preponderance of low developmental rank indices (DRI) represented by this selection of yucca morphologies indicated (pp. 28-39) a possibly early historic or evolutionary connection between Y. whipplei of Series 1 and 3A and the southern oak forest, nearly all of which was mapped on the coastal side of the San Andreas Fault System (Küchler map, 1977). Coastal sage scrub included a similar selection of MORPHs having low DRI.

In the mixed hardwood forests of central and southern California no yuccas of Series 1 and only minimal percentages of pre-series and Series 2B were found, but 65 % of the samples consisted of Series 2A-3A and another 28 % were of Series 3B, all with high DRI. In blue oak-digger pine forest about 77 % of the samples were in Series 2B and 3B while 13 % were of Series 3A and pre-series. In juniper-piñon woodland, Series 2B yuccas accounted for 95 %, as also in Joshua tree scrub, Mojave creosote bush scrub, and California prairie. Yuccas of Series 3B occurred predominantly in the yellow pine and Jeffrey pine forests as well as in high mountain pine-fir forests.

It appeared likely therefore that the three major yucca Series evolved in regions where one of three major types of Tertiary vegetation also developed: pre-series and Series 1 in coastal regions of southern oak forest, Series 2A in northerly regions of mixed hardwood forest, Series 2B either in blue oak-

digger pine regions or in desertic vegetation of rain-shadowed areas. Series 3B probably evolved latest in conjunction with Pleistocene expansion of boreal forests (pp. 29-31).

E. Comparison of Climatic and Geographic Factors by One-Way Analysis of Variance of Yucca whipplei Samples

One-way analysis of variance, i.e., ANOVA, determines the significance of variation between or among related groups of samples from the ratio,  $F$ , of intergroup variance of samples to the infragroup variance. In groups that differ significantly from each other, the intergroup variance will be greater than the variance within these groups, i.e.,  $F \geq 1.00$ . A variance ratio of Among/Within groups equal to or less than 1.00 indicates no significant difference between groups. Depending on size and number of samples and sample groups, the critical ratio  $F^*$  may be greater than 1.00 and statistical significance then will be determined relative to the critical  $F^*$  for the particular case. Effective factors of evolutionary selection may be tested by comparing the F-ratios for groups divided according to the different factors in question, e.g., rainfall, mean temperature, length of growing season. Those factors resulting in the highest F-ratios as compared to the respective critical  $F^*$  and with a known standard set are deemed to be the most effectively selective environmental factors with regard to the variable attributes of the biota compared. This series of ANOVA tests of five different measures of environmental differentiation included three climatic and two vegetative criteria as compared with the result of maximal morphological differentiation and of strictly geographic

divisions (mountain ranges). This series of analyses would be comparable to a series of Model I ANOVA tests of a number of new drugs as measured by the results of comparable dosages on several different symptoms of the disease to be treated, and as compared with the results of a known drug. Presumably the most effective new drug would be that producing the highest F-ratio mean, i.e., the greatest reduction of symptoms with respect to dosage and with respect to corresponding dosages of the known drug (Sokal and Rohlf, 1969, Ch. 8, also 9.6). I have not seen this particular graphic approach used in connection with environmental settings of biogeographic populations although similar applications to ecological problems may exist.

F-ratios resulting from ANOVA were compared graphically (Fig. 20, 21, 22) to determine whether factors most accountable for the geographical distribution of consistent morphological differences among samples of Y. whipplei were climatic or paleogeographic. Grouping of samples by geographically defined mountain ranges tested the importance of historical geology or paleogeography in determining distribution of yucca types. Different climatic criteria used for dividing samples into groups were the rank numbers of the local subzone climates of samples (Sunset, 1976), and of the most severe adjacent climate--both separately and combined--the Kuchler vegetation formations, and California and U. S. Forest Service vegetation classifications. All results were compared against a standard set of F-ratios provided by ANOVA in ten different plant characters with groups defined by MORPH.

In every statistical experiment a separate ANOVA was computed for each of ten quantitative morphological characters at three different

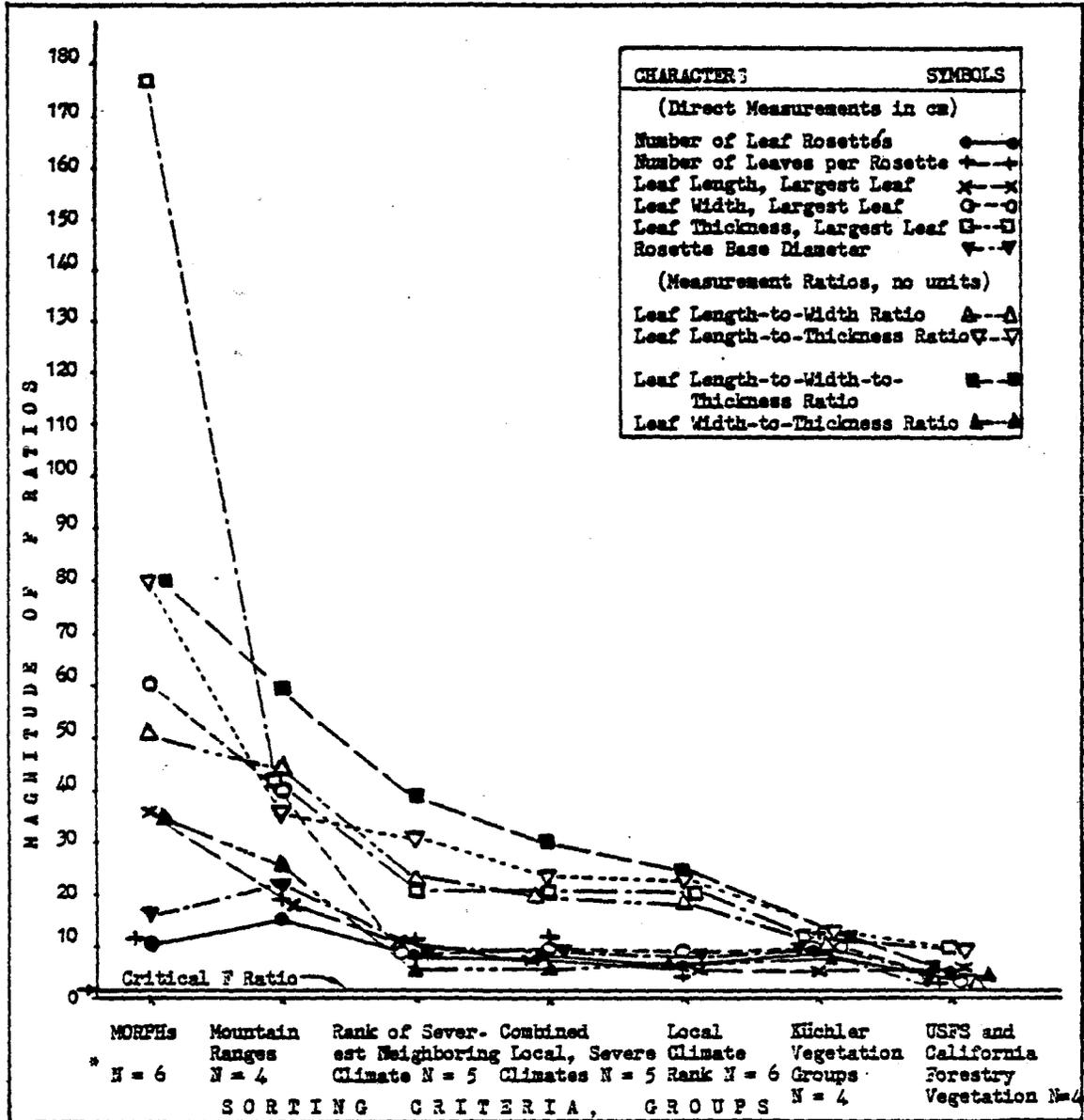


Figure 20. Analysis of Variance Ratios of Ten Characters in Groups of Sample Means Sorted by Seven Criteria, *Y. whipplei*

\* N = Number of Computer Runs Using Varied Sample Groupings, Averaged

levels of comparison. Because of storage limitations of the computer program, ten groups of up to twenty-five samples each were the maximum capacity for any ANOVA run. This program was designed for simultaneous analyses of (1) ten groups of individuals combined from a number of 25 samples or less, (2) ten groups of up to 25 sample means each, and (3) up to 250 unsorted samples of individuals. Capacity limits of the program made necessary several repeated runs for each sorting criterion using different sample selections to compare all the data. The F-ratio results of repeated comparisons were averaged and graphed (Fig. 20, 21, 22). Separate F-ratio polygons for each of ten plant characters analyzed showed differences in character response to the sorting factors. Corresponding points on each of the polygons represented averages of F-ratios for a given character from several computer runs using different sample selections. Points were connected by symbolic lines to facilitate comparison of results using different group-selecting factors. Selective factors deliberately were arranged on the graphs according to their consistently diminishing mean results in ANOVA to emphasize visually the comparative results, but without affecting them. The point polygons were preferable to histograms for clarity of presentation and because these complex graphs were not of frequency distributions but of averaged rational or real numbers.

The ten morphological types compared by ANOVA were determined arbitrarily by matching triangular scaled graphic models of the mean leaf dimensions of each yucca sample (MORPH, Ch. II). Ten geographically defined classes compared by ANOVA consisted of combinations of mountain ranges bearing similar yuccas (Fig. 8, Table 2). ANOVA F-ratios also were found for (a) ten classes of grouped sequential

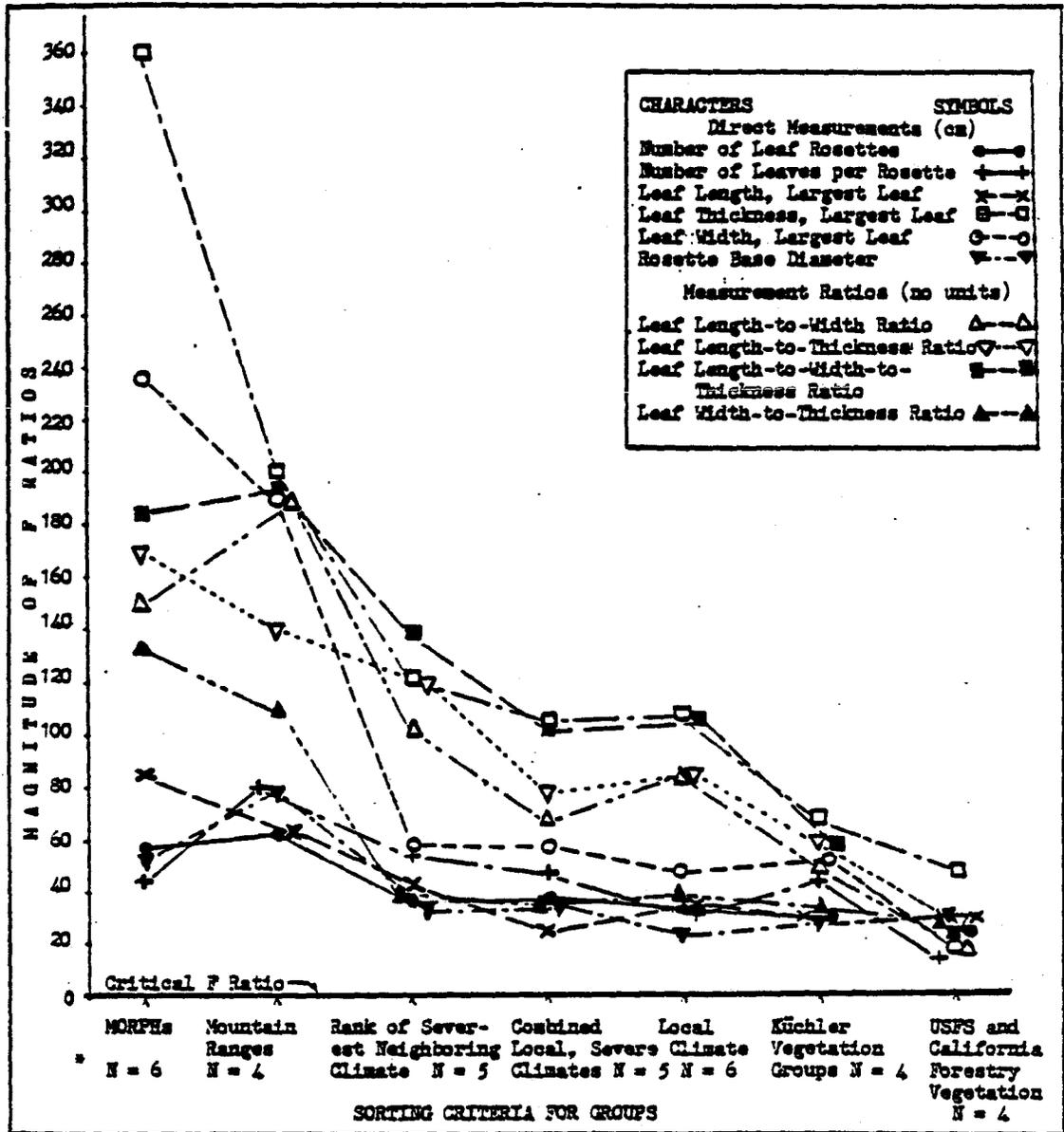


Figure 21. F-Ratios of Ten Characters from Analyses of Variance Among Yucca Groups of Individuals Sorted by Seven Criteria

ranks of climate, i.e., for the climate of the sample location (Sunset, 1976), and (b) for the most severe neighboring climate (Ch. III). Additional runs grouping samples according to combined minimal and local climate rankings were made to compare effects of total climate variability. The final analyses of variance were made for ten groups of closely related or sequential ranks of vegetation types. The vegetation types were classified according to the California State Division of Forestry maps in one set of sample runs and by the Kuchler (1977) classification of vegetation in California (Barbour and Major, 1977, Appendix map) for another. In different runs of all these tests, various combinations of samples were tried to provide "best" and "worst" cases in addition to random or "ordinary" cases. F-ratio results therefore varied greatly in each set of runs, but did not change significantly the differentiation among mean results of different sorting criteria.

In all these one-way ANOVA studies the sorting criteria resulted in F-ratios much greater than 1, showing highly significant differences among the groups as compared with the variation within them (Fig. 20, 21, 22). However, the differences in magnitude of this significance indicated much about the relative importance of the general sorting factors in determining most precisely the geographic ranges of different yucca morphologies (relative significance, Ch. II).

As expected, greatest F-ratios were obtained in most characters for the ten visually sorted groups of MORPH because MORPHs deliberately were sorted by their internal similarities and their external differences in leaf dimensions. The next largest F-ratios were

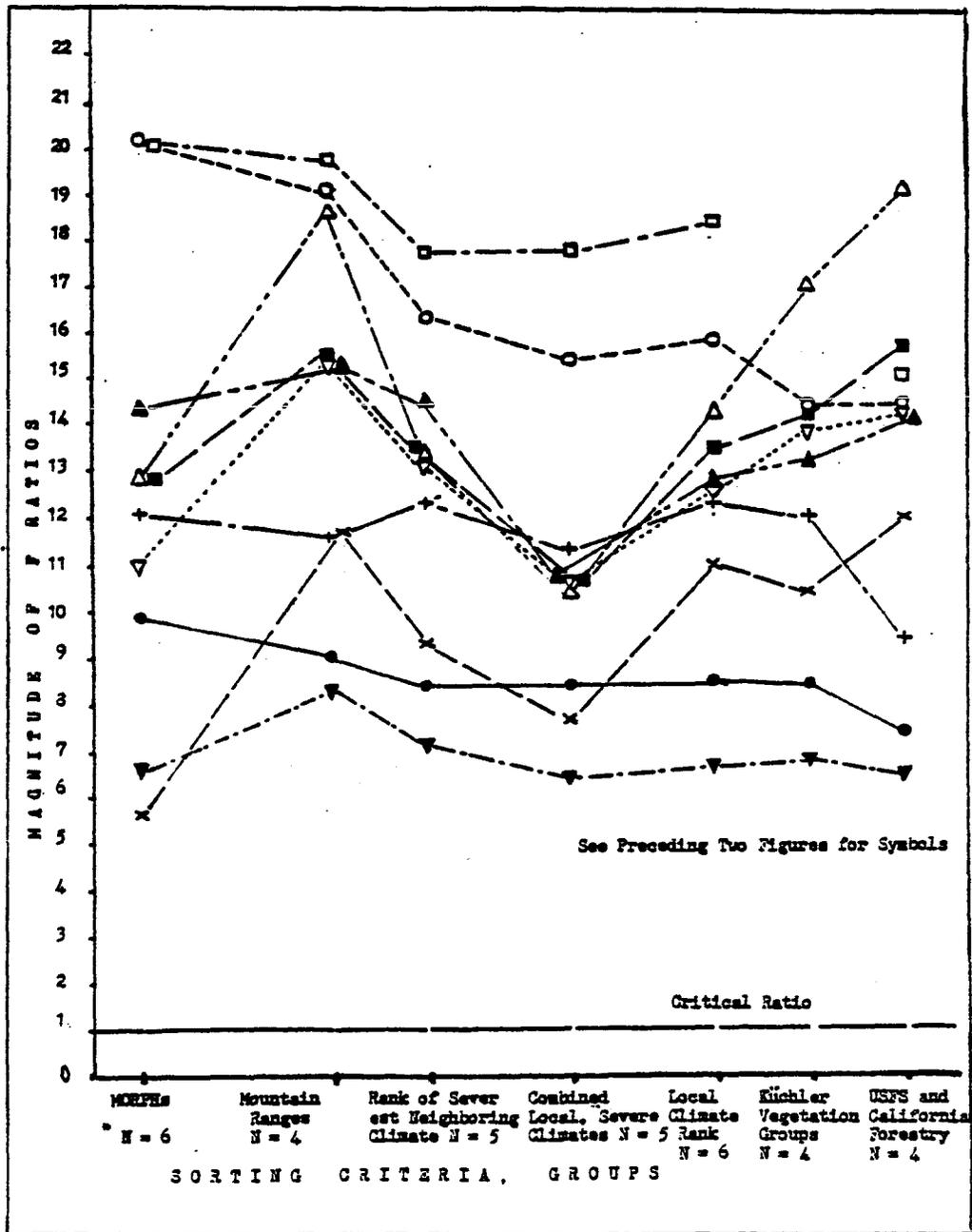


Figure 22. Analysis of Variance Ratios Among All *Y. whipplei* Samples of Individuals, Unsorted  
 \* N = Number of Computer Runs Using Varied Sample Groupings, Averaged

obtained from the objective and geographically arbitrary groupings of samples on different mountain ranges. Mountain ranges, or rather the yuccas on them, were divided into groups based on their geographic locations within the physical bounds of specific mountains ranges. Some ranges in which yuccas were most similar were combined, even though separated by great distances, to keep the number of groups at 10, the maximum usable. The F-ratios obtained from the objective and geographically arbitrary groupings of samples on different mountain ranges were only slightly less than F-ratios from direct artificial selection of similar leaf diagrams, and in a few plant characters F-ratios actually were higher in the mountain ranges than in MORPH. Smaller but highly significant F-ratios were obtained for groups based on severest neighboring climate, and only slightly less significant ratios than these resulted from grouping by normal local climates.

Grouping samples by their combinations of local climate and worst neighboring climate ranks summed the influences of local seasonal variability and mean warmth of climate; but F-ratios, instead of being larger than for worst or local climate alone, i.e., additive, were somewhat intermediate between them. No mean F-ratios among habitat factors equalled or exceeded the corresponding F-ratios for mountain ranges. The least but still significant F-ratios were obtained from grouping by local vegetation, the Kuchler divisions being slightly greater than California Forestry divisions in significance of ANOVA results (Fig. 20, 21, 22).

In each grouping of samples F-ratios were similar in repeated runs using different sample selections by the same factor, but ANOVA among and within all the unsorted samples showed apparently random

variations in F-ratio between runs, regardless of the simultaneously analyzed sorting factors (Fig. 22). F-ratios of variation among unsorted samples compared to within-sample variation were highly significant, although random, being always four to six times higher than the critical ratio. No conclusions could be drawn logically from such "statistical significance" other than the fact that variation within samples was very close to the sample means and there was considerable, albeit aimless, variation among unsorted sample means.

#### F. Chapter Summary and Conclusions

In analyses of the association of types of Y. whipplei with Kùchler vegetation classes, a great amount of internal variability was contributed by the presence of all major MORPHs in samples from the most representative single wild vegetation formation--geologically recent chaparral (Axelrod, 1975). This variability was sufficient to reduce drastically the statistical variance ratio obtained by ANOVA in vegetational groupings of Y. whipplei samples. Infra-group variation in other older types of vegetation was comparatively small and inter-group variation of Y. whipplei among them was high, a fact obscured in ANOVA results by the internal variation of Y. whipplei in chaparral. Yucca Series developed in isolation in Tertiary woodlands were evidently combined under the influence of Mediterranean climate as local representatives of chaparral communities since the Pliocene (Raven and Axelrod, 1978; Axelrod, 1970, 1977, 1975, 1978, 1973), (Fig. 18, 19).

Morphological and geographical differentiation of yucca Series found together with segregated remnants of Tertiary woodland forma-

tions (Fig. 18, 19) indicated a coevolution that preceded the Pleistocene development of chaparral and coastal sage scrub as widespread distinctive vegetation formations in California (Raven and Axelrod, 1978, pp. 26-27; Axelrod, 1978). These two latest formations with which Y. whipplei often has been associated (Munz and Keck, 1959) diverged from former Tertiary woodland, sclerophyll, and savannah vegetation in the Pliocene and Pleistocene as summer rainfall decreased (Axelrod, 1971, 1973, 1975, 1977, 1978; Raven and Axelrod, 1978). However, these two distinct "new" vegetation types were created in response to Mediterranean style climate changes without changing or rendering uniform the morphology of locally distributed variant populations of Y. whipplei (Fig. 18, 19), or probably, of other constituent shrubs that formerly had constituted local elements of sclerophyll and thorn-forest vegetation in the California region (Axelrod, 1973; Raven and Axelrod, 1978; Searcy, 1969). Associated Kuchler vegetation types provided evidence, therefore, that ancient biogeographical conditions were most responsible for the morphological differentiation of Series in Y. whipplei, rather than were more recent climatic changes that were responsible for the new Mediterranean vegetation formations since the Pleistocene. With the latter there was only a partial correlation of yucca morphology confined chiefly to "recent" hybrids in Series 3A and 3B.

Comparisons of F-ratio results in ANOVA between various groupings of yucca samples indicated that historic associations of specific morphologies with certain mountain ranges produced much more distinct differentiation of yucca morphology than did any combination of climatic evidence tested (Fig. 20, 21). Such results may be explained by

the isolation of mountain ranges as ecological islands (Stebbins and Major, 1965; Raven and Axelrod, 1974; Cody, 1975) and also by the actual island history of many such mountain ranges of California during the Tertiary (Corey, 1953; Oakeshott, 1971)

The above results indicated that historical geography of mountain ranges occupied by different morphological populations of Y. whipplei, as a whole, most precisely defined the natural distribution of the different MORPHs, regardless of climate changes or differences within and among the mountains. Evidently there was plenty of latitude for tolerance within a morphological type of Y. whipplei for a considerable range of climate change; or else enough climate variation within mountain ranges existed to accommodate an historically associated yucca population regardless of its particular morphology. The geographic limits of morphological types, that evidently resulted from the historical geography of mountain ranges more than from present local climate variation, often were expressed within very narrowly defined geographic boundaries (Fig. 10).

#### IV. VARIATION OF Y. WHIPPLEI IN RELATION TO SOME CLIMATE VARIABLES

Climates vary in two major components: (1) temperature range, mean, and monthly distribution; and (2) precipitation range, mean, and monthly distribution. Although causally related to each of the other major climate factors, insolation also has its own specific effects on the geography of vegetation through evapotranspiration and as the photosynthetic energy resource of growth and development in plants and constitutes a most important third factor of distribution.

##### A. Relations of Temperature to Plants

As variables affecting plant survival and reproductive success, it is commonly recognized that diurnal differences in temperatures (Chang, 1968) and the differences between mean daily minimum temperature of coldest month and mean daily maximum temperature of hottest month and their magnitudes are more important than the annual mean temperature (Walter, 1973, pp. 16-17; MacArthur, 1975; Kimball and Gilbert, 1967 a; Major, 1977, p. 13; U. C. Extension, 1967-1970). Although this difference generally is not calculated for standard published weather data, these monthly mean maximum and minimum temperatures were regularly included in the published climate data for California counties (U. C. Extension, 1967-1970). The annual mean differences for hottest and coldest months therefore were calculated

here as a measure of continentality (variability and severity) of regional climates and of yucca locations. For lack of a better name it can be called DMAMMMT for Difference of Mean Annual Monthly Maximum and Mean Annual Monthly Minimum of Temperature.

The importance of temperature to plants also consists in the amounts of daily heat and light energy, within usable limits imposed by plant physiology, that exist at the time of year during which plant growth is feasible. Temperature regimes determine how long optimal usable energy is available for plant growth (Bierhuizen, 1973). Equable, moderately warm temperature conditions--depending on their timing and time-spans and on the simultaneous availability of other essentials such as water and light--select plant features suited to rapidity and ease of plant growth and reproductivity. This process can be called optimal selection--similar in positive effect to, but not the same as so-called r-selection when reproductive rate  $r$  is maximal and without much competition (MacArthur, 1972, pp. 226-230; Hoover, 1973, pp. 87-92). Optimal selection by favorable growing conditions is quite a different process from the frequently assumed process of selection by adverse conditions.

Periods of temperature extremes impose time limits in which plant growth is not possible and also select surviving types of plants "best suited" to a region. Extreme and drying heat or cold, or their wet extremes, can cut short the growing period and continue to exert great stress on least-suited biotypes in a population throughout the non-growing season. This process is adverse selection, similar in negative effect to, but not the same as, K-selection from competition (MacArthur, 1972, pp. 226-230; Hoover, 1973). Therefore different

possible directions of plant evolution are imposed by different aspects of only one primary factor in the environment--air temperature. In areas of dense vegetation air temperature is either increased by the release of energy from heated leaves, or else can be moderated through evapotranspiration of moisture from leaves. But Y. whipplei seldom occurs in such density as to greatly affect air temperature compared to other vegetation or compared to the bare rocky soil where it occurs. Therefore, because only air temperature is known from the weather bureau records, we consider it as the effective variable. The relative lengths of time during a year in which favorable temperatures occur, compared with the time during which severely unfavorable temperatures exist, create a whole spectrum of possible selective patterns, and may result in various unexpected adaptive combinations of plant reproductive cycles, dispersal, overwintering, or oversummering mechanisms. Does this single factor of temperature then account by itself for the three different directions of leaf and stalk evolution in Y. whipplei? Or do other climate factors play an equal or more crucial role? Does the geographical distribution of different yucca morphologies coincide with the geographical pattern of different temperature regimes? As seen in Appendix C, they do coincide in part, but with important exceptions (Fig. 8, 14).

#### B. Relations of Precipitation to Plants

Precipitation regimes, like temperature regimes, can influence morphological development in plant populations by natural selection in several contrasting ways. Replacement of ground water by precipitation is as fundamental to natural selection of suitable wild plant

types as is temperature. Water provides one of two major building blocks of all living tissue; it is a known limiting factor and is clearly important for determining not only general distribution of different types of vegetation but also for selecting the particular ecotypes within a species that are representative in different climate zones. Precipitation and soil-water storage capacity and availability are major determinants of length, quality, and time of onset or termination of the growing season for most native plants of California (Clausen et al., 1940; Clausen and Hiesey, 1958; Major, 1977). Also the non-growing season, due to lack or excess of water, selects for different survival and reproductive systems in different kinds of plants (Clausen and Hiesey, 1958).

Carbon dioxide is the other major building block of living plant tissue. Virtually no data exist on availability of carbon dioxide in the atmosphere of California wilderness areas, and in spite of its importance, carbon dioxide customarily is ignored as a limiting factor in wild vegetation but for a few exceptions, e.g., Woodwell et al., (1978); McLean (1978 a, b); Hiesey et al., (1977, pp. 124-148). According to Arnold Court (personal communication, 1983) carbon dioxide becomes so rapidly mixed in the atmosphere that strong concentration gradients rarely persist except in industrial and perhaps in active volcanic environments.

In most of California where Y. whipplei is found, the so-called Mediterranean climate prevails in which the summer warm season is dry and the winter cool or cold season is wet. In such areas the growing seasons of wild plants may be restricted to short but comparatively warm and moist fall and spring periods (Clausen et al., 1945; Clausen

and Hiesey, 1958). Degree of winter chill, summer heat, and total precipitation vary considerably throughout the California Mediterranean climate region (Major, 1977).

Yucca whipplei and the other agavaceous plants of California such as Y. brevifolia, Y. schidigera, Y. baccata, Nolina parryi, Nolina bigellovii, N. interrata, and Agave deserti occur also in "desert climates" (Hutchinson, 1959; McKelvey and Sax, 1933; McKelvey, 1947; Webber, 1953; Haines, 1941; Hoover, 1973). But in truth most of these species are found on sub-desertic margins at fairly high altitudes in a relatively equable, warm, sub-humid, climate zone where sparse winter rains usually are supplemented by scattered summer and fall thunder-showers (Thrower and Bradbury, 1977, Plate XIV; Harris, 1959). Some of these xeric subtropical plants also must tolerate quite a lot of freezing weather in winter, for Joshua trees and Yucca whipplei and Yucca schidigera frequently are covered by snow on the desert margins and on mountains 900 to 2300 meters in elevation. Nolina parryi is found with Y. whipplei on the rim of the Kern Plateau (Twisselmann, 1967, p. 205), and in some other unexpected places such as in coastal sage scrub of San Diego, Orange, Riverside, and Ventura counties (Munz and Keck, 1959, p. 1362). Apparently agavaceous plants once were more widespread than now, but presently are limited to scattered locations where local conditions allow their continued survival (Axelrod, 1958, 1972).

### C. Some Differential Phenotypic Effects of Insolation in Y. whipplei

A primary factor in all green plant growth and survival, particularly in the case of Y. whipplei, is the amount of sunshine available for photosynthesis and plant development. Insolation, in fact, has a

most direct effect on yucca plant morphology, as can be seen readily from morphology differences of seedlings from identical collections of seed germinated in sun or shade (Table 15). No direct comparisons of soil moisture content, nor of temperature, were made in these sun vs. shade germination experiments. However, efforts were made to keep the soil from becoming critically hot or dry during germination. The morphology changes should indicate mainly responses to light availability together with the side effects of heating and drying about as they would exist in nature under relatively favorable conditions.

In virtually all cases the mean lengths of longest leaves of yucca seedlings were shortest in full sun and longest in shade or partial shade. Leaf proportions in these young seedlings were much more plastic than in sun vs. shade comparisons of mature plants. In full sun, leaf length-to-width ratios of young seedlings in Series 1 had values typical of mature plants in pre-series or in Series 2A-3B. In shade-grown seedlings of Series 2A, leaf length-to-width ratios were those typical of Series 1 or 3A. Leaves sometimes were wider in sun-grown than in shaded seedlings of Series 1, Series 3A, and 2B, 2A, and 3B (Table 15). Comparison of these results with those of published growth studies in selected or controlled environments of other monocots important in agriculture, i.e., maize, barley, rye, grass, etc., indicated that similar changes occurred perhaps universally in monocots as responses to light intensity. According to published studies, the leaves of the monocots listed above became shorter, wider, and thicker when grown in full sunlight than when in shade (Evans, 1973, pp. 23-24; Chang, 1968, pp. 68-69; Slatyer, 1973).

Paradoxically in older plants possibly two different adaptive

Table 15. Summary of Leaf Dimensions of Y. whipplei Seedlings Germinated in Sun and Shade\*

Series and Subspecies of <u>Y. whipplei</u> Seed Sources	S U N					S H A D E				
	Number Samples N	Number Seedlings n	Mean Leaf Length (cm)	Mean Leaf Width (cm)	Mean Leaf Length to Width Ratio	Number Samples N	Number Seedlings n	Mean Leaf Length (cm)	Mean Leaf Width (cm)	Mean Leaf Length to Width Ratio
Pre-Series <u>Ssp. percursa</u> Sandyland	2	7	11.8	0.45	27.0	4	51	29.0	0.55	54.9
Series 1 <u>Ssp. typica</u>	4	40	22.0	0.49	45.0	4	16	32.8	0.52	69.1
Series 1 <u>Ssp. intermedia</u>	2	20	20.0	0.73	28.2	2	14	30.7	0.69	47.1
Series 3A <u>Ssp. percursa</u> San Luis Obispo	5	7	17.5	0.45	38.7	5	7	28.2	0.38	74.4
Series 2A <u>Ssp. Parishii</u>	3	15	11.2	0.41	32.5	3	37	23.9	0.31	83.0
Series 3B <u>Ssp. Parishii</u> Transverse Ranges	2	20	15.6	0.74	21.3	2	8	19.7	0.60	24.1
Series 3B Sierra Nevada	1	5	24.6	0.48	52.0	1	2	27.7	0.44	64.0

\* Growth conditions of sun and shade pairs were comparable, having identical seed samples and similar cultural treatment excepting light incidence. However the various subspecies were grown at different times and were measured at different ages; therefore vertical comparisons were only usable as to trends, not directly as to sizes. N = Number of Samples. n = Number of Seedlings Measured, usually 5 or 10 per sample.

responses to shade were exhibited in Y. whipplei, each involving different leaf dimensions. In nature, shading of yucca stands arose from competitive vegetation, compass aspect, steep topography, and frequent clouds or fog. In Series 1--MORPH III and IV--only leaf length was increased in situations that were least exposed to sunlight, as was shown by field measurements in wild populations and in transplants to the experimental garden (Tables 16, 17). But in some samples of Series 2A, and in some 3B also--MORPH VI, VII, X--shaded plants had wider leaves than plants in sun. Mean leaf lengths also were longer for Series 2A-3B in shade than in sun but usually without much change in the generally low leaf length-to-width ratio (Table 16, 17). Both morphological responses effectively could improve incidence of sunlight energy on the leaf for photosynthesis when there was shade (Whitehead, 1973).

#### C-1. Leaf Measurements of Y. whipplei Seedlings in a Test Garden

A summary of statistical analyses (t-tests) of leaf measurements in Ssp. typica (Series 1) and Ssp. Parishii (Series 2A) seedlings after about a year of growth on north- and south-facing and horizontal surfaces in the transplant garden at Sepulveda Garden Center, Encino, California, appears in Table 16 (Calculations by A. A. Hoover at UCSC, 1976, from my data). The planted mounds were about 6.5 meters across and slopes varied from about 60 to 90 cm in 3 meters, i.e., approximately 20 to 30 %. Difference in exposure to sun on the north and south slopes was considerable, as judged by the rapidity with which soil dried out, the comparative growth of grass in winter, and by frequent loss of yuccas on the north slope to heart rot caused by

Table 16. Differential Response of Leaf Morphology to Shade Stress, *Y. whipplei*

Table 16a. Leaf Measurements of Seedlings on Different Slope Aspects 1.5 to 3.5 Years after Transplantation									
Subspecies, Seed Source	Mean Leaf Length (cm)			Mean Leaf Width (cm)			Mean Leaf Length-to-Width Ratio		
	South Slope	Top Slope	North Slope	South Slope	Top Slope	North Slope	South Slope	Top Slope	North Slope
Sep. <i>lyrica</i> Purple Rainbow	66.8 ± 15.6 n = 28	64.0 ± 7.5 n = 8	71.5 ± 17.5 n = 52	0.75 ± 0.15 n = 28	0.80 ± 0.17 n = 8	0.77 ± 0.13 n = 52	90.3 ± 19.0 n = 28	82.2 ± 15.7 n = 8	119.4 ± 43.1 n = 52
Sep. <i>lyrica</i> Via Loma	68.3 ± 15.6 n = 32	66.6 ± 8.1 n = 16	80.2 ± 17.6 n = 28	0.72 ± 0.11 n = 32	0.67 ± 0.13 n = 16	0.71 ± 0.13 n = 28	98.5 ± 13.0 n = 32	100.6 ± 3.9 n = 16	119.0 ± 43.0 n = 28
Sep. <i>lyrica</i> Rancho Santa Ana	40.9 ± 11.3 n = 15	50.7 ± 14.8 n = 15	47.5 ± 10.6 n = 8	0.64 ± 0.14 n = 15	0.58 ± 0.08 n = 15	0.56 ± 0.15 n = 8	64.6 ± 14.9 n = 15	103.6 ± 15.2 n = 15	87.4 ± 23.0 n = 8
Sep. <i>Parishii</i> , Rancho Santa Ana	16.0 ± 4.5 n = 11	15.8 ± 3.4 n = 7	18.1 ± 5.4 n = 23	0.80 ± 0.12 n = 11	0.88 ± 0.12 n = 7	0.96 ± 0.20 n = 23	20.6 ± 6.7 n = 11	18.2 ± 4.2 n = 7	19.0 ± 4.5 n = 23
When Transplanted	mean = 33.9 ± 4.4			mean = 0.82 ± 0.11			mean = 42.2 ± 9.0		

Table 16b. Results of T-tests Between Leaf Measurements on Different Slope Aspects							
Subspecies, Seed Source	Exposure Conditions T-test Comparison	Leaf Length (cm)		Leaf Width (cm)		Leaf Length-to-Width Ratio	
		Greater Value	Significance Level	Greater Value	Significance Level	Greater Value	Significance Level
Series 1 Sep. <i>lyrica</i> , Purple Rainbow	Top vs. South Top vs. North South vs. North					North North	.01 .01
Series 1 Sep. <i>lyrica</i> , Via Loma	Top vs. South Top vs. North South vs. North	North North	.01 .01	South	.10	North North	.05 .05
Series 1 Sep. <i>lyrica</i> , Rancho Santa Ana	South vs. North North vs. Lathhouse South vs. Lathhouse	North Lathhouse Lathhouse	.10 .10 .01	South	.10	North Lathhouse Lathhouse	.01 .05 .01
Series 2A Sep. <i>Parishii</i> , Rancho Santa Ana	South vs. North Top vs. South Top vs. North North vs. Lathhouse South vs. Lathhouse Top vs. Lathhouse			North Top North	.05 .10 .05	Lathhouse Lathhouse Lathhouse	.01 .01 .01

\*Lathhouse was shadier than outdoors, but drought stress also affected plants after transplanting outdoors. Average dimensions of Sep. *Parishii* at time of transplantation represent Lathhouse means. See text for further explanation of results.

#Slopes = 15 to 30 %

excessive dampness. Maximal effective differences in insolation on the north and south slopes existed during the fall and spring seasons of most active growth when sun angle was relatively low (Geiger, 1973, pp. 388-393, 422-424).

Significantly greater leaf widths without significant increase of leaf length were found in Ssp. Parishii plants on north-facing slopes compared to plants on south slopes. Significant increase of leaf length and length-to-width ratio without other significant changes were found in Ssp. typica transplants on the north slopes of the mounds compared to plants on south slopes. Leaf width in Ssp. typica was increased significantly sometimes in plants growing on sunniest slopes. These different responses to sun and shade in two different Series or subspecies of Y. whipplei were not conclusive without more experimentation, but they tied in with observations of differentiation in pre-series yuccas below. Loss of outer leaves of rosettes due to water stress soon after transplantation may have been responsible for some wider leaf dimensions in that the central, often widest, leaves became the largest remaining leaves to be measured.

#### C-2. Field Measurements in Wild Populations

In pre-series populations, all leaf dimensions were virtually minimal (Fig. 9), but two different morphological trends similar to the differences between Series 1 and Series 2A were distinguished (Appendix A). Some pre-series samples (MORPH II) tended toward Series 1 with relatively great leaf lengths within the pre-series dimensions, but minimal widths and thicknesses. Pre-series in MORPH I had relatively great leaf widths but small leaf lengths and normal thicknesses.

Apparently two alternative genetic mechanisms for increasing leaf area were present in pre-series populations of Y. whipplei (Appendix A, Fig. 3, 9). What factor determined selection between these alternative types of areal enlargement in yucca leaves if shading were the common stimulus to both? To better understand the effects of sunlight and shade on morphology of wild populations, wild plants of different subspecies of Y. whipplei growing in shade or partial shade were compared to others in the same locale growing in full sun. Could shading in different Series of Y. whipplei change leaf morphology of mature yucca populations to resemble those of Series 1? Was there enough phenotypic plasticity in wild yucca plants growing in shade to affect the sample means significantly and thereby to confuse proper identification of Series?

The averaged results for different Series and subspecies (Table 17) showed that the most significant differences caused by shading in wild populations was in Series 1 itself, in which leaf length increase was the only significant change. Shading therefore made Series 1 more distinct from other Series in the wild, but it did not create much similarity to Series 1 plants in other Series and subspecies populations. General morphology was found to be consistent with the local Series in both sun and shade, and in some shaded samples differential results in leaf width were found for wild Ssp. Parishii similar to the results found in the cultivated Parishii seedlings (Tables 15, 16, 17).

Due to prolonged juvenile growth in Y. whipplei, conditions at the time of germination may differ from those at the time of leaf measurement and could cause early selection or phenotypic compensation that results in seemingly inappropriate morphology years later. Wild

Table 17. Mean Leaf Dimensions in Samples of Wild Populations of *Y. whipplei* Growing in Sun or Shade

Series and Location of <i>Yucca</i> Samples	SUN SAMPLES					SHADE SAMPLES				
	Number of Samples (N) Plants (n)	Mean Leaf Dimensions (cm)			Length-to-Width Ratio	Number of Samples (N) Plants (n)	Mean Leaf Dimensions (cm)			Length-to-Width Ratio
		Length	Width	Thickness			Length	Width	Thickness	
Series 1 <i>Ssp. typica</i> , San Diego Co.	N = 5 n = 51	65.	0.75	0.21	90.	N = 5 n = 58	88.	0.83	0.21	107.
Series 1 <i>Ssp. inter-</i> <i>media</i> , Santa Monica Mtns.	N = 6 n = 87	79.	0.87	0.24	91.	N = 6 n = 44	114.	0.85	0.24	135.
Average Series 1	N = 11 n = 138	79.	0.81	0.23	91.	N = 11 n = 102	102.	0.85	0.23	122.
Series 2A-3B <i>Ssp. Parishii</i> , San Gabriel Mountains	N = 11 n = 157	69.	1.52	0.32	46.	N = 11 n = 121	73.	1.49	0.32	49.
Series 2B <i>Ssp. caespit-</i> <i>osa</i> ; Mojave, Ridge Basin, Kern River	N = 4 n = 29	47.	0.95	0.36	50.	N = 4 n = 28	50.	1.01	0.36	49.

\* N = Number of Samples.    † n = Total Number of Plants in N.    # cm = Centimeters

yucca seedlings often germinate and become established initially in the shade of nurse plants such as Artemesia. As a yucca develops it outgrows the shortlived protecting shrub, which dies, leaving the mature yucca in full sun. Reversed conditions also were observed commonly in ecotone situations where Y. whipplei is an important lower storey member marginal to riparian vegetation. Seedlings that had germinated in full sun were overgrown in a few years, shaded by expanding upper storey growth. Seeds responsible for some "anomalous" samples in steep-sided canyons of the San Gabriel Mountains apparently fell or were washed down from dry sunny slopes into moist shady canyons; their morphologies then differed from that expected for plants adapted to shaded conditions. However, some other cases may have been examples of differential adaptation by Ssp. Parishii--increased width in shade--as found in the transplant garden (Table 16) and in wild Ssp. caespitosa (Table 17).

Hybridity in wild populations of Y. whipplei emphasized in some samples the apparent effects of insolation. In the San Gabriel Mountains, especially along the San Gabriel Fault, variable hybrid populations have as putative parental races yuccas of Series 2A in the Front Range and Series 2B in the interior ranges (Fig. 6, 7, 10). Series 2B has the characters of a xeric, sun-adapted subspecies, and Series 2A appears to be adapted to mesic, partially shaded conditions.

From field studies of hybrid swarms of oaks on sunny and shady sides of ridges in the Ridge Basin of the northern Transverse Ranges, Benson et al. (1967) found that local habitat favored selectively the hybrid intermediates morphologically most similar to the parental species best adapted to the habitat. This effect also appeared evident

in sun- and shade-grown portions of hybrid yuccas near the San Gabriel Fault, for sunny banks had yuccas quite similar to Series 2B, whereas in most shaded humid locations local yucca morphology was like Series 2A (Appendix A).

Some doubt may exist as to the importance of regional vs. microclimatic environments in evolution of the three major Series of Yucca whipplei. Microclimate and insolation differences due to topography and competing vegetation may follow different general trends in different mountain ranges because of large-scale geographical and climatological factors. These modern regional differences probably have affected selection of overall average morphology of Y. whipplei to a degree. But it cannot be said that a preponderance of one type of habitat studied in a given mountain range favors one type of yucca morphology and another predominant yucca habitat studied in another range favors a significantly different morphology. The majority of all field samples, by far, were taken from south-facing--SW, S, SE--slopes in nearly full sun, and therefore average plant phenologies for all mountain ranges were set by the predominantly sun-grown plants. Consequently they should reflect regional climate differences more than differences due to microclimates.

In the Santa Monica Mountains, shade-grown yucca samples in chaparral tended toward the most extreme characters of Series 1, i.e., length of leaves was greatest; therefore shade enhanced the Series 1 means in this area (Table 17). In the San Gabriel Mountains northeast of the San Gabriel Fault, shade-grown Series 2B-3B samples definitely were within the normal morphological range of characters typical of Series 2B-3B. South of the San Gabriel Fault the means of shaded

samples tended to enhance, if anything, the most characteristic measurements of Series 2A sun-grown plants, sometimes with an increased average leaf width like that found in the experimental garden in shaded plants of Ssp. Parishii (Table 16, 17; Appendix A). As described above, local conditions along the San Gabriel Fault often exaggerated selection in the direction of either Series 2A or 2B, thus actually reducing the expected tendency of hybrids to blur morphological boundaries between their neighboring, putative, parental races (Stebbins, 1950, pp. 250-297).

D. Solar Radiation and the Range Limits of *Y. whipplei*

No clear physical causes of limits that coincided with the known total range of *Y. whipplei* were found on general climate maps. Regions having the same means of winter low temperatures as in areas where *Y. whipplei* was found extended much farther north than did the yuccas. The same could be said for precipitation patterns and vegetation patterns shown on general maps (Küchler, 1977; Walter Lieth, 1960-1964; James, 1966; Landsberg, 1973; Unesco Cartographia, 1979; CDWR, 1981; Cohen, 1973; Bartholomew and Herbertson, 1899; Espenshade and Morrison, 1975, pp. 10-16, 80-82; and from various sources in Court, 1973). Most isolines for different climatic factors lie parallel to the Pacific Coast and so extend far north and south of the range of *Y. whipplei*. General maps that coincided best with distribution limits indicated an original sub-tropical climatic affinity and a localized or isolated persistence of the yucca colonies rather than adaptive conformation with any general set of modern climatic factors (in Raven and Axelrod, 1978; Stebbins and Major, 1965). In maps of percentage of possible

sunshine or insolation between December and April (Court, 1973; Bartholomew and Herbertson, 1899; Espenshade and Morrison, 1975, p. 81) areas of greater than 50 % sunny days followed east-west isolines enclosing the total range of Y. whipplei, the northern yucca limit lying about midway between 50 and 60 % sunny days in winter (Chang, 1977, Fig. 3, 6; Court, 1973). These sunshine maps were based on fewer than ten data stations in southern California (Court, personal communication, 1983). The sketchy evidence prompted an investigation as to whether or not maximum availability of sunlight in winter actually restricted Y. whipplei to suitable habitats below  $36^{\circ}50' N$  latitude.

In a search for California climate data to explain the apparent latitudinal limit of natural northward occurrence of Y. whipplei (Fig. 5, 10, 23), a useful source of information reflecting the distribution of solar radiation in California was found (California Department of Water Resources, 1975, i.e., CDWR). Tables of Potential Evapotranspiration (PET), Pan Evaporation (E), and Solar Radiation were summarized by monthly means according to eleven regions having different "evaporative demand". These regions of California were divided according to their uniformity of water requirements in terms of specific crop irrigation needs (Fig. 23). Variables applicable to Y. whipplei were obtained from tables of data for irrigated pasture grass. Plots were made of the monthly mean values of PET, E, and Solar Radiation for each region of evaporative demand (Fig. 24, 25, 26), and these plots brought out some interesting relationships between solar energy availability and effective length of growing season of Y. whipplei. Although Y. whipplei usually does not occupy the same microhabitat as irrigated pasture grass, general regions in which yucca

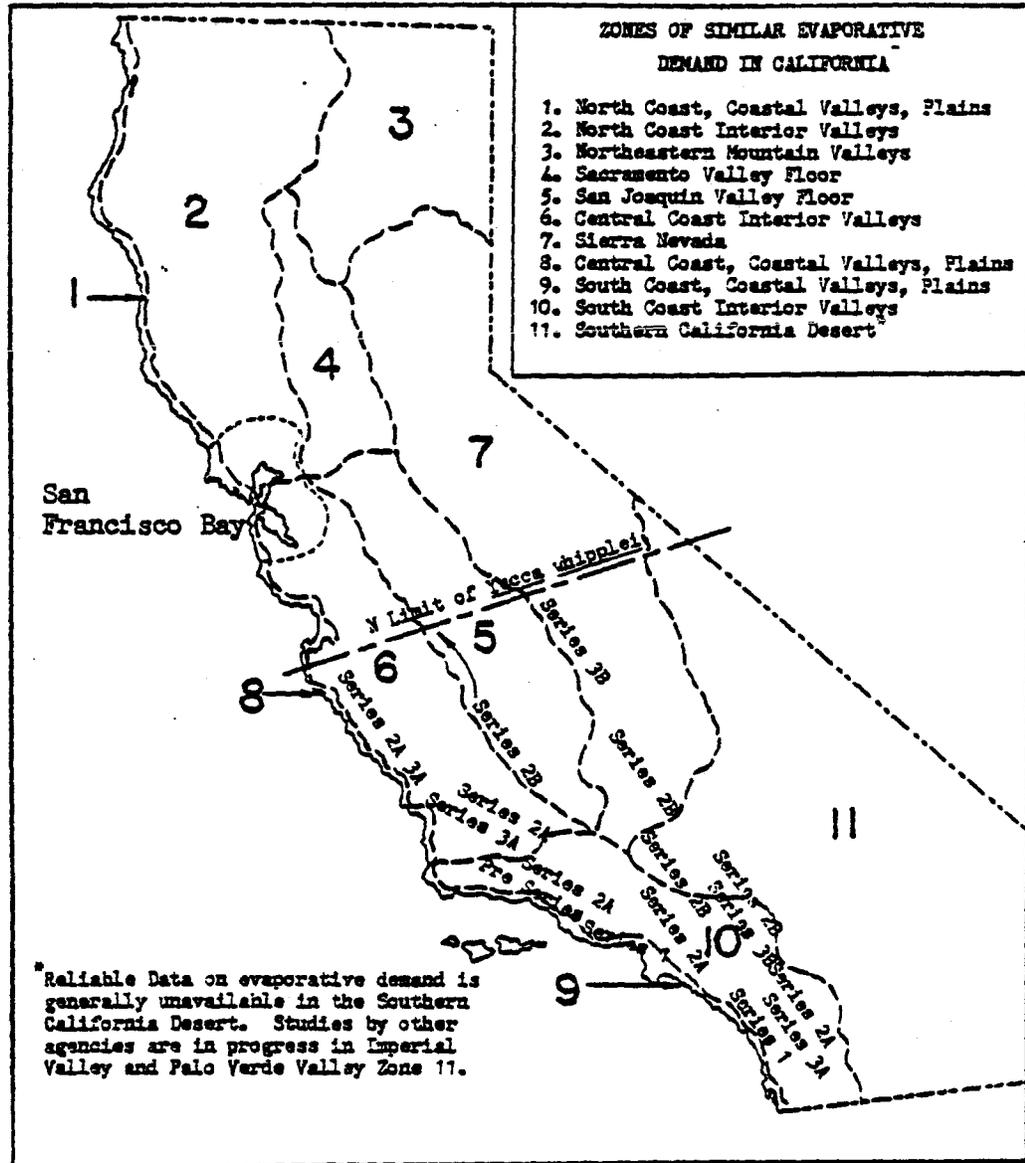


Figure 23. Zones of Similar Evaporative Demand in California<sup>#</sup>

<sup>#</sup>Adapted from Figure on page 275 of California Department of Water Resources, 1975.

does or does not occur can be characterized and compared according to regional evaporation parameters of this single crop, as identified by areas of different evaporative demand, a factor combining regional characteristics of sunlight incidence, humidity, and rainfall deficiency.

Standard climatic data must be handled differently from its use in agriculture to be profitable for study of most long-lived wild plants because the growing seasons of irrigated crops do not often coincide with those of native plants in a Mediterranean climate. Totals of evapotranspiration, pan evaporation, and solar radiation during the fall-winter-spring growing season of most wild plants in California were calculated in the different regions of known evaporative demand for periods of November or October through March, April, or May from tables in CDWR (1975). Data given for southern California and the desert were said by the authors to be largely educated guesswork, but because no more reliable sources of information existed at the time, these published data had to be accepted. No data at all were given for the Sierra Nevada but the available data were adequate for making some general regional comparisons.

Expressed as millimeters of evaporation, the plotted diagrams indicated monthly and regional distributions of energy values that evidently were critical to upper latitudinal limits of Y. whipplei (Fig. 24, 25, 26; Table 18); mathematical relations of evaporation to radiation are given by Chang (1977, Ch. 13-18). Striking regional differences were found (Fig. 24) in the annual distribution of monthly mean Potential Evaporation (PET) in the ten regions out of eleven for which data were available (CDWR, 1975, Table 6). The lowest PET in all

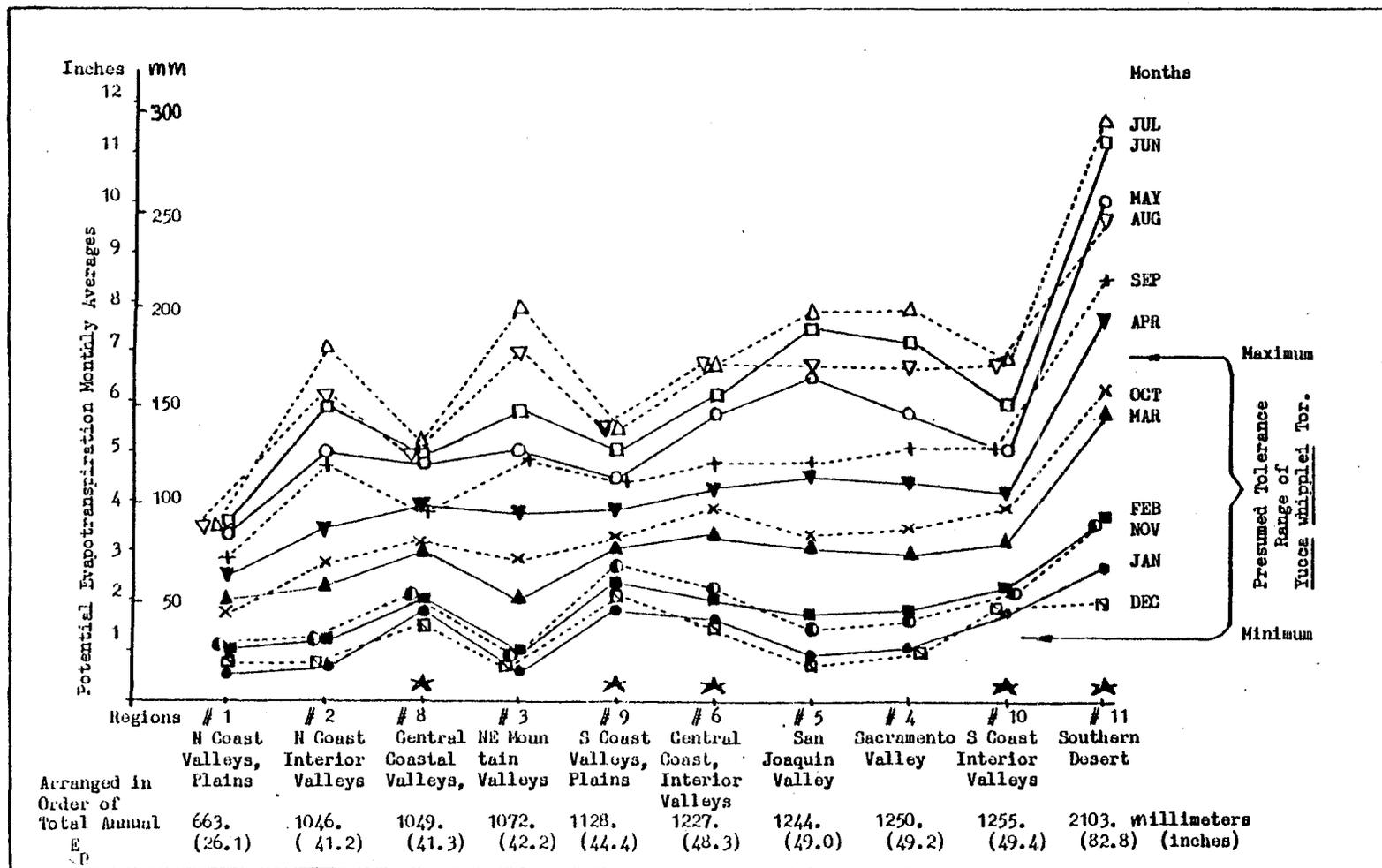


Figure 24. Mean Monthly Potential Evapotranspiration in Ten Regions of Evaporative Demand, California, and Presumed Tolerance Limits of *Y. whipplei*

\* Data from California Department of Water Resources (1975, Table 6)

months occurred in the northwestern coastal corner of the state, in region #1 (Fig. 24). As was to be expected, the highest amounts were found consistently in the southern California desert, region #11. In all areas falling between these two extremes, just two other distinct annual distribution patterns of PET were discerned easily from the graph (Fig. 24). One had great variation in monthly PET values between coldest and warmest months, representing a continental climate. Coldest months had lowest values like those of the northwest coastal corner region #1, but warmest months had values like that of April in the southern desert, excepting that in region #2 they were less than April in the desert. In the alternate more tropical pattern, all values for coldest months were about equivalent to December in the southern California desert, but none of the warmest monthly values were as high as April in the desert. In other words, the latter, more equable, non-desert pattern had higher average PET (1351 mm), but much less variation than the former continental type of non-desert pattern (1054 mm), (Table 18).

In California, Y. whipplei grew only in regions with the sunnier more equable pattern of the two, and also on the western margins of the desert at moderately high elevations where similar conditions were to be expected. Taking the highest and lowest values in the equable regions, where yuccas were found, as the PET factor limits beyond which active growth of Y. whipplei colonies was unlikely provided a basis from which to calculate the total PET in each region for the months that occurred within this tolerance range (Table 18). In all areas where Y. whipplei grew, annual totals of "tolerable PET" were 1049 mm or more, and where they did not grow, annual totals of "tolerable PET"

Table 18. Some Measures of Available Annual Solar Energy During Possible Growing Seasons of Y. whipplei

Measure (mm Water)	Mean Annual Total and Range of Evaporation mm		Mean Annual Total and Range Within Maximum and Minimum Tolerances of <u>Y. whipplei</u> , mm		Tolerance Limits (Extreme Values within Regions of <u>Y. whipplei</u> ) mm		Ranges and Averages for Different Growing Seasons (mm)					
	Yuccas*	No Yucca	Yuccas	No Yucca	Maximum	Minimum	November to April		November to May		October to March	
Potential Evapotranspiration	1351 (1049-1255)	1054 (663-1250)	1351 (1049-2103)	795 (586-949)	180 (297 = desert)	38 (51 = desert)	460 (381-628) N = 5	252 (119-338) N = 5	614 (503-884) N = 5	383 (205-487) N = 5	442 (363-593) N = 5	233 (99-325) N = 5
Pan Evaporation	1526 (1377-1646)	1372 (858-1626)	1526 (1377-1646)	933 (744-1067)	224	53	447 (423-462) N = 4	305 (224-380) N = 5	610 (575-629) N = 4	472 (332-580) N = 5	433 (401-452) N = 4	279 (203-353) N = 5
Solar Radiation	2853 (2822-2873)	2678 (2530-2792)	2853 (2822-2873)	1874 (1417-2207)	340	127	1118 (1116-1155) N = 3	919 (875-947) N = 5	1445 (1411-1480) N = 3	1245 (1190-1280) N = 5	1033 (1010-1059) N = 3	837 (798-869) N = 5

\* Yuccas: Regions of Evaporative Demand (California Department of Water Resources, 1975) where Y. whipplei is native. No Yucca (None): Areas of Evaporative Demand where Y. whipplei is not native. Data from Figures 23, 24, 25, 26. N = Number of areas averaged.

were 949 mm or less. Other totals of PET were calculated for the number of months per year that had rainfall suited to yucca growth (Table 18).

Mean PET calculated on the basis of different rainy growing seasons was consistently higher for the areas where Yucca whipplei occurs than in areas where no yucca is native.

These two comparisons provided independent evidence that quantity of sunlight availability during periods of active growth is critical to the northward distribution of Y. whipplei.

Regional patterns of annual monthly distribution of average Pan Evaporation (E), (CDWR, 1975, Table 1) were very similar to patterns of Potential Evapotranspiration, with an extremely varying range of values for regions where yuccas were not native, and a much more equable distribution of values with a higher average in areas where Y. whipplei was found (Fig. 25). Annual regional means where yuccas grew averaged 1526 mm compared with an average annual pan evaporation of 1372 mm where no yuccas existed. When only the months within the tolerance limits of Y. whipplei were totaled in different regions, the contrast of course was greater, with yucca areas being "tolerable" twelve months of the year (E = 1526 mm) and non-yucca areas having averaged growing seasons of only 7.4 months within the tolerance limits and total pan evaporation for these months averaging 933 mm (Table 18). Mean pan evaporation during possible rainy growing seasons was consistently higher in areas where yuccas grew than in areas where they were absent.

A similar graph (Fig. 26) was prepared from the table of solar radiation values which had been converted by formula to inches of

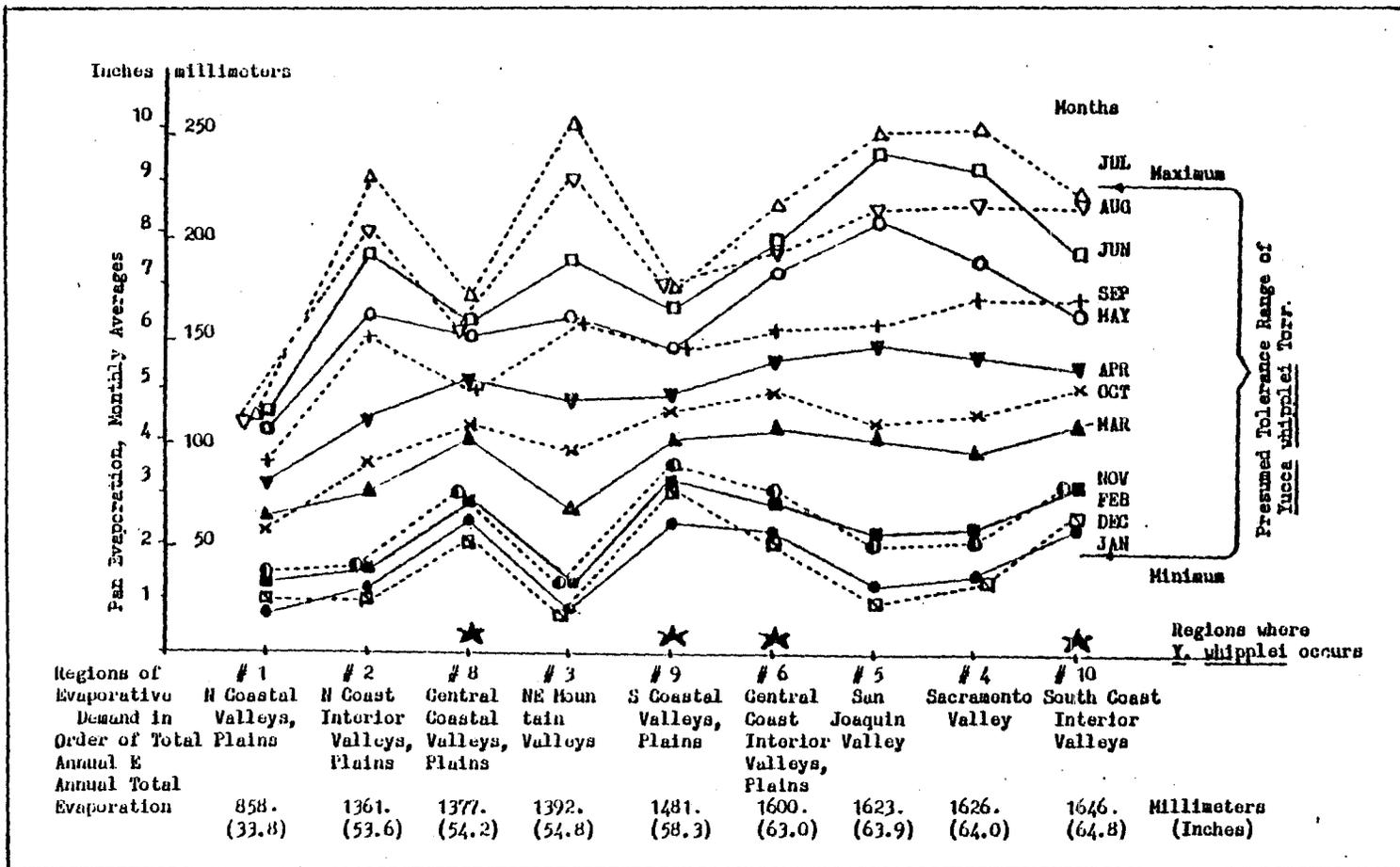


Figure 25. Mean Monthly Pan Evaporation in Nine Regions of Evaporative Demand, California, and Presumed Tolerance Limits of Y. whipplei

\* Data from California Department of Water Resources (1975, Table 3)

evaporation (CDWR, 1975, Table 3). As in the other graphs (Fig. 24, 25), the different regions were arranged in ranked sequence of increasing annual totals, but only in the solar radiation graph (Fig. 26) did this arrangement result in clear graphic separation of the areas into yucca regions and non-yucca regions. Data were available only for eight of the eleven regions. In all corresponding calculations the totals of solar radiation for yucca regions were consistently higher than in non-yucca regions (Table 18).

To conclude, analyses of three available types of solar radiation data, according to regions of different irrigation requirements due to regional rainfall and potential evapotranspiration averages, revealed two distinctive annual patterns of seasonal insolation in California, (a) a highly variable monthly distribution and (b) a much less variable monthly distribution with a higher mean value than in the more variable pattern. Eight of the ten regions of evaporative demand, for which data existed, exhibited one or the other of these two patterns, but Y. whipplei was native only to regions having the sunnier milder pattern of energy inflow, and also in the elevated margins of the southern desert as well as parts of the western Sierra Nevada for which data were not obtainable (Fig. 26). According to the three kinds of available data (CDWR, 1975), areas where Y. whipplei was native (#6, #7, #8, #9, #10, and southwest margins of #11) received higher and more equable annual and seasonal amounts of insolation than did areas with no native yuccas.

It appears therefore that the northern latitudinal limit of Yucca whipplei is truly a latitudinal limit, in that it clearly reflects the plants' need for high levels of insolation, especially during the wet

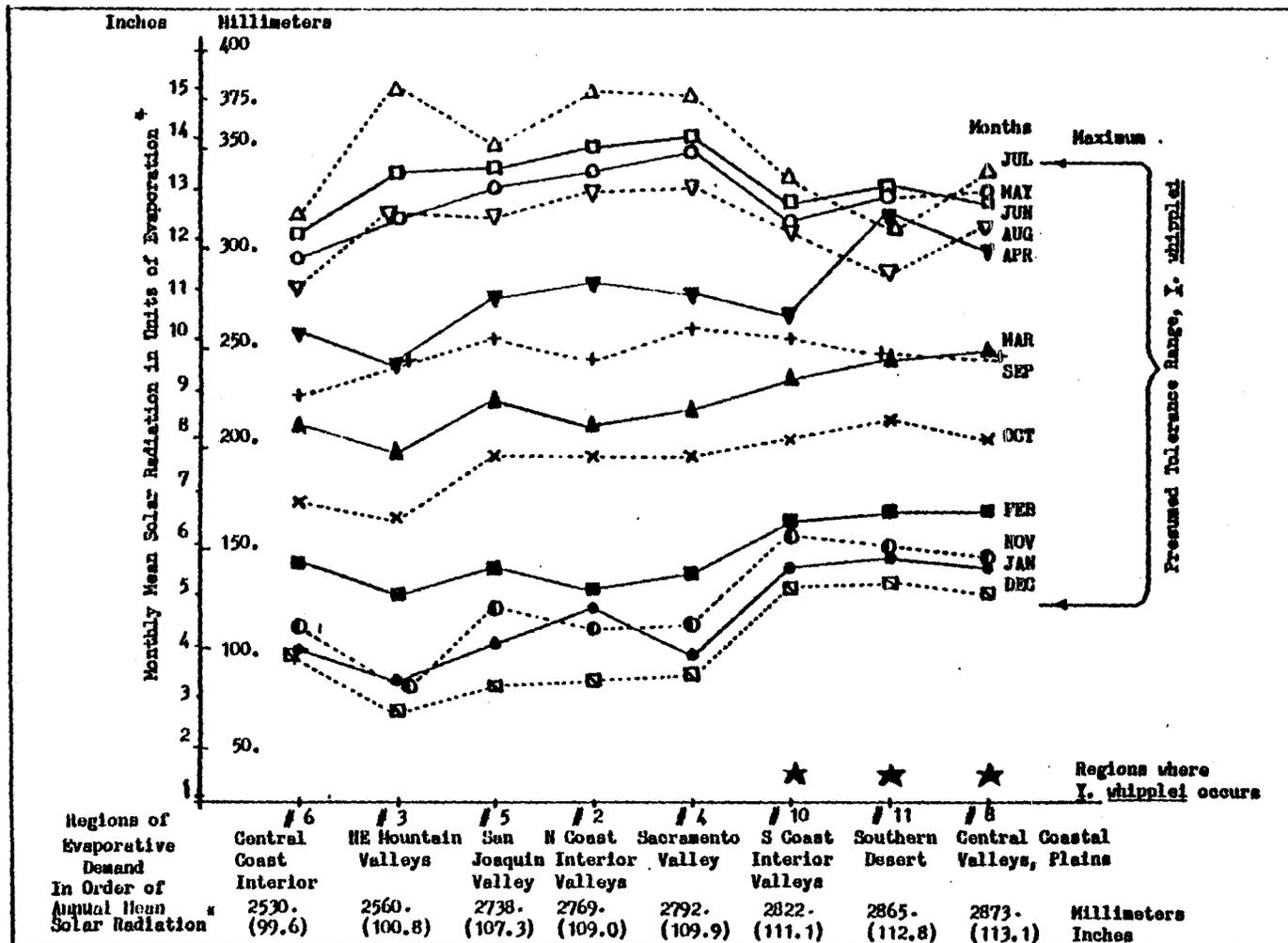


Figure 26. Mean Monthly Solar Radiation\* in Eight Regions of Evaporative Demand, California, and Presumed

\*Tolerance Limits of *Y. whipplei*

\*Expressed as equivalent inches of evaporation. 1486 langleys = 1 inch evaporation  
Data from California Department of Water Resources (1975, Table 3)

season of active growth. This insolation requirement adequately explains the existence of a cutoff zone at or below the latitude of  $36^{\circ}50'$  N for all northern populations of Y. whipplei in California (Fig. 5, 10, 23), and perhaps also explains similar northern limits for Yucca schidigera, Y. baccata, and Y. brevifolia in California. Isolated stands of Y. brevifolia, however, are reported in protected southslope canyons of the White Mountains near  $37^{\circ}30'$  N latitude (Beatley, 1976). The scattered distribution of Y. brevifolia in desert mountains east of the Sierra Nevada evidently is affected by water relations and by temperature extremes as well.

If insolation were only a relative factor in the case of Yucca whipplei, i.e., if excessive or insufficient rainfall were limiting in the north also, then other northern regions of highest or lowest rainfall might include colonies of Y. whipplei, but they do not. If world climates became warmer or colder than at present, the northern limit of Y. whipplei might change (Hays et al., 1976). Humidity of air near the coast may be responsible for the observed slight southward obliquity of the northern limit line toward the coast (Fig. 10, 11, 23) because of atmospheric absorption of critical wavelengths by dispersed water particles (Chang, 1977, pp. 4-11). Water strongly absorbs light at 2.4 to 3.6  $\mu\text{m}$  and 4.8 to 7.5  $\mu\text{m}$ , and the absorption spectrum of plant chlorophyll is strongest for light of 4.0 to 4.5  $\mu\text{m}$  (violet) and 6.0 to 6.8  $\mu\text{m}$  (red). Carotene absorbs at 4.0 to 4.8  $\mu\text{m}$  and other plant pigments at 5.2 to 6.5  $\mu\text{m}$  (Rost et al., 1979; Evans, 1973; Neiburger et al., 1973). Thus water in the atmosphere strongly affects the incidence of light used for photosynthesis (Evans, 1973).

Another more recent compilation of solar energy data for Califor-

nia (CDWR, 1978) measures incident (direct and global) radiation on horizontal surfaces using instruments such as pyranometers of different designs. Since 1970, an increased number of measuring stations in southern California provide much more detailed and reliable data for that area than existed for the evaporation data used above (Fig. 24, 25, 26; Table 18). These measurements are expressed in langley's per day, and are averaged by month and by year for each station. By sorting the stations according to location into comparable areas and averaging the stations within each area by month and totalling by month and by year, a similar graph of the annual march of insolation in langley's (ly) was made and sums for different seasons of the year were totaled as for the evapotranspiration data above. Eight such areas in California were averaged. There were no data for the extreme northwest coastal strip, nor for the Sierra Nevada as a whole. The remaining regions were divided in such a way that boundaries between southern and northern regions were fixed by the northern limiting boundary of Y. whipplei at  $36^{\circ}50'N$ . A separate coastal area surrounding the San Francisco Bay was created between San Jose and Santa Rosa and inland to Vacaville, Pittsburg, and Livermore (Fig. 23). The few San Joaquin Valley stations north of the  $36^{\circ}50'N$  limit were included in the Sacramento Valley data. Monthly daily averages were multiplied by the number of days in the month to give monthly totals, and these totals were added to obtain annual and seasonal totals for each area.

The resulting graph (Fig. 27) shows much less extreme variation from region to region than was exhibited by the evapotranspiration data (Fig. 24, 25, 26), and the regional yearly averages show gradual increase in a southerly direction rather than a higher mean in equable

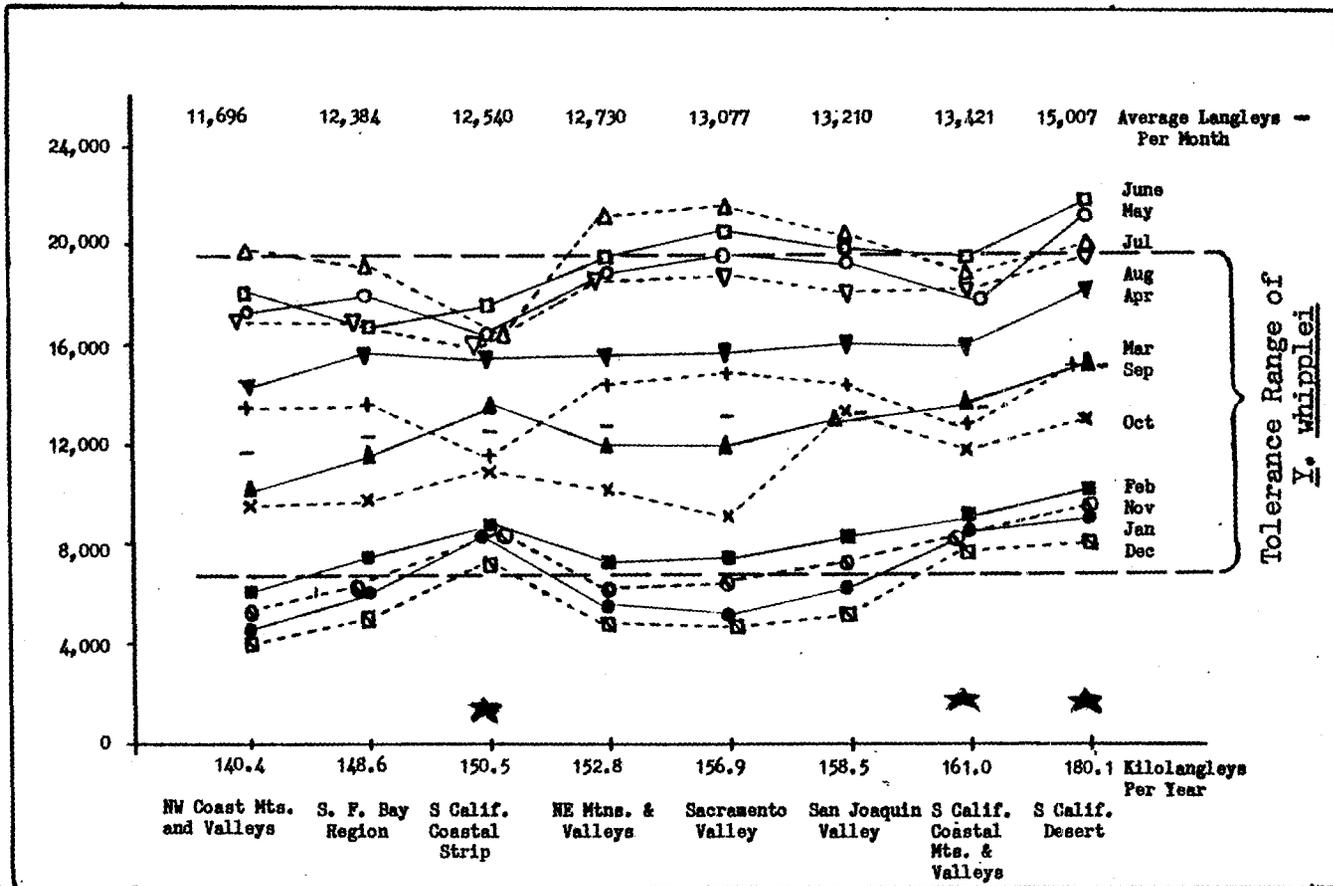


Figure 27. Solar Radiation by Pyranometer (Langley's per Month) in Eight California Regions With or Without Y. whipplei  
(Data from CDWR, 1978)

marine-influenced climates and lowered means in continental climate areas. The southern coastal strip in fact had a mean of only 220  $\lambda$ y per year greater than the San Francisco Bay region, which in turn was just 8300  $\lambda$ y higher than the northwest coastal mountain region, the lowest regional mean of all. Annual totals for the regions of the state were hardly significantly different except when combined as a southern and northern group.

It should be remembered that Y. whipplei generally grows on rather steeply angled south-facing slopes in most of its range, but in the southern parts may be more likely found on north-facing slopes at a small angle of incidence to the sun's rays in summer. Therefore the measurements taken at the earth's surface by pyranometer throughout the year may give misleading figures insofar as the sun's effect on Y. whipplei physiology in different regions is concerned. The northernmost colonies of Y. whipplei are limited to steep south-facing slopes to catch the largest possible angle, i.e.,  $90^{\circ}$ , to rays of winter sunshine. The comparatively steep angle of leaf position found in hottest areas (Series 2B) as compared to more globosely radiant leaf rosettes (Series 2A-3A-3B), or more horizontally spreading leaf rosettes in regions of less extreme or more diffused sunlight (Series 1, 3A) also must affect greatly the actual energy impact by sunlight on these plants. The incident angle of sunlight on erect leaves would be greater in winter than in summer, but on spreading leaves would be greater in summer than in winter. Although field data were collected for arrangement of leaves in rosettes of Y. whipplei, they were not summarized for this thesis. Warm summer nights in the San Joaquin and Sacramento valleys undoubtedly result in high losses of photosynthetic

energy through nightly respiration for many plants (Pease, 1982; Calder, 1973), contributing to loss of productive growth potential coincidentally with drought.

The degree of tolerance by Y. whipplei for extreme insolation during summer months in the desert is difficult to determine from the data of Figure 27. Three aspects of the distribution of Y. whipplei indicate that the mean maximum monthly insolation (21,500 h/y) of June in the desert is not intolerable to Y. whipplei: (a) Although these yuccas occur on high southwestern margins of the desert at 1070 to 1370 meters (3500 to 4500 feet), they receive about the same insolation in summer there as is available elsewhere in the desert. (b) The fact that Y. whipplei is found also in the desert along the Colorado River and Lake Mead in Arizona and at the Vizcaino Desert in Baja California indicates a rather high tolerance of extreme insolation, even though the plants are found on north slopes. (c) Late-flowering yuccas in the desert (May to July of coldest years) indicate that optimal growth conditions may occur in April through June in most years at the mean annual peak of insolation in the desert (CDWR, 1978), (Fig. 27). Water availability is the most critical limiting factor of yucca distribution in the desert.

To compare amounts of effective energy from sunlight available to plants in which excessive insolation is not a limiting factor, total kilolangleys was measured including the summer months higher than the "tolerable range" of Y. whipplei (Table 19 C), as well as for the months within its supposed insolation range (Table 19 B). The months of winter below the tolerated range were not included in these two sums. In all regions where Y. whipplei is not native the total usable energy

Table 19. Annual Solar Radiation (Kilolangleys) Measured by Pyranometer in Eight Regions of California.\*

Regions	A. Total Solar Radiation Per Year	B. Total in Tolerance Range of <u>Y. whipplei</u>	C. Interior Desert Limits of <u>Y. whipplei</u>
<u>With Yucca whipplei</u>			
Southern Desert	180.1	117.5	180.1
S California Coastal Mountains, Valleys	161.1	161.1	161.1
S California Coastal Strip	150.5	150.5	150.5
<u>Without Yucca whipplei</u>			
San Joaquin Valley	158.5	107.2	147.2
Sacramento Valley	156.9	99.0	140.7
San Francisco Bay Region	148.6	131.4	131.4
NE California Mountains, Valleys	152.8	115.6	136.5
NW Coastal Mountains, Valleys	140.4	100.5	120.3

\* Data from CDWR (1978) and Figure 27.

was less than that available throughout the year in yucca regions because of the subtracted months. One might argue that this subtraction is not reasonable because all energy reaching the plants in winter must contribute in some degree toward the survival of the plants and therefore ought to be included in all of the regional totals. This argument seems valid, but we must consider why the yuccas are supported in some regions but not in others. Evaporation data of Figures 24, 25, 26, and Table 18 show a clear distinction between amount of evapotranspiration--whether potential or actual--in yucca regions and non-yucca regions; but total langleyes found in three out of five non-yucca regions overlapped the amounts found in yucca-supporting regions and the remaining two regions had only 2 to 20 kilolangleyes fewer annually than did yucca areas (Table 19 A).

A possible explanation for the inadequacy of insolation despite similar energy totals in five of the eight regions is that the amount of photosynthesis occurring in coldest months is insufficient to compensate for the energy loss from respiration by the plants (Pease, 1982?). Another likely possibility is that nightly respiration is so greatly restricted by extremely low winter temperatures that starch formed during sunny days cannot be transferred and so results in severe damage to the chloroplasts with consequent temporary disuse of available daily sunlight for productive photosynthesis, as is known to occur in some tropical grasses (West, 1973).

Sunlight incidence is least in December, not January (Fig. 27) when usually mean temperatures are lowest in the desert (Mathias et al., 1968), and May and June (solstice) totals of energy incidence are higher than in July or August when the highest temperatures of the year

occur. June insolation also is greater than May, July, or August means in the two other southern California areas where Y. whipplei occurs, but July insolation is highest in all regions where the yucca does not occur, excepting the San Joaquin Valley where July is nearly equal to June (Fig. 27). No data is known of the upper and lower energy limits for growth in Y. whipplei, but it is likely that energy levels do exist below which physiological growth cannot take place and above which excessive insolation or heat also is damaging to plant productivity (Rost et al., 1979, p. 121). This spread or lag between highest and lowest energy levels of June and December and their corresponding temperature extremes of July and January can extend the periods of physiological damage or hindrance postulated for the inability of yucca colonies to succeed in certain regions. However, high incidence of irradiation in May and June, combined with runoff from the mountains, prior to the air temperature peaks of July and August that coincide with minimal precipitation in the desert may be most favorable to yucca success in the high desert areas where they occur. The real differences in energy availability between yucca regions and non-yucca regions, probably, is in the more even distribution throughout the year of non-excessive but sufficient levels of energy in yucca regions (Fig. 27). In non-yucca regions, just as in the graphs of evapotranspiration (Fig. 24, 25, 26), energy distribution shows more extreme peaks and lows during the year and may reduce the effective average in non-yucca regions.

Judging by the discrepancies between extremes of measured insolation (Fig. 27) and indirectly measured energy via evaporation data (Fig. 24, 25, 26) for similar areas, I assume that other factors of

evapotranspiration besides sunlight incidence--e.g., seasonal rainfall, groundwater retention, cloudy and foggy days, air humidity, or location of measuring apparatus in irrigated pasture--alter in different ways the effective incidence of solar radiation as measured by pyranometers. In other words, very slight-seeming differences in actual insolation as measured by pyranometer result in rather large differences in measured pan evaporation or evapotranspiration by plants, depending on rainfall patterns, distance from the ocean, and other factors.

In Table 20 only the insolation (in kilolangleys) for different possible winter rainy seasons is totaled for yucca-supporting regions as compared with non-yucca regions. No months are omitted from the winter rainy seasons because of inadequate sunshine, but summer months of inadequate precipitation are absent from totals. Insolation in the same season in non-yucca areas is consistently less than the totals for yucca areas. However different regions, e.g., interior mountains vs. coastal slopes may also differ in length of rainy growing season, and may therefore provide totals equivalent to those of regions that presently support yuccas elsewhere. Absence of yuccas from areas of equivalent energy incidence during appropriate growing seasons therefore must be due to the difficulty of migration exhibited by Yucca whipplei for various edaphic reasons (pp. 11 to 13). Such considerations also may explain the success of transplanted Yucca recurvata from southeastern coasts of the United States as far north as Juneau, Alaska, and also of transplanted Y. whipplei occasionally seen flourishing in gardens as far north as San Francisco and Sacramento.

Table 20. Ranges and Averages of Insolation (Kilolangleys)\* for Different Rainy Growing Seasons in Areas With or Without Y. whipplei

Seasons Regions	November to April	November to May	October to March	August to April
Yucca Areas				
S California Coastal Mts. & Valleys	63.1	80.9	78.8	125.4
S California Coastal Strip	61.6	78.0	57.1	100.0
Southern Desert	70.2	91.3	64.8	117.5
Averaged Yucca Areas	65.0	83.4	66.9	114.3
Areas Without <u>Y. whipplei</u>				
San Francisco Bay Region	52.1	70.2	46.2	92.6
N Coastal Mountains & Valleys	44.7	62.2	39.9	85.0
NE Mountains & Valleys	50.8	69.5	45.5	93.6
Sacramento Valley	51.2	70.8	42.6	95.6
San Joaquin Valley	55.7	75.0	51.0	99.3
Averaged Non-yucca Areas	50.9	69.5	45.0	93.2

\* Data from CDWR (1978), and Figure 27

E. Evolution of Geographic Variation in *Y. whipplei*

In Response to Some Climatic Factors

To find how different climatic factors may have affected the evolution of *Y. whipplei*, various published climatic data were collected for about 250 field samples. Most of these data consisted of averaged records for weather stations nearest to sample locations and were obtained from county publications of monthly and annual averages summarized from U. S. Weather Bureau and other U. C. Extension sources (University of California Extension, 1963, 1965, 1967, etc.). The county publications were far from uniform in their summaries and maps, and comparable data were not always available; nor was there always mutual agreement of data in cases of overlapping information. Extrapolation or averaging of data from different local stations often was necessary. In a few cases arbitrary selections had to be made from contradictory data, and this was done to carry out the most consistent agreement with other data of the same geographic area. Some counties have not published such agricultural data, including Los Angeles County, but information about yucca ranges frequently was obtainable from marginal territories on maps of bordering counties, or from more general statewide maps (USWB, Dept. of Commerce, 1959). For a number of areas annual data were averaged from the last ten years of Weather Bureau records (to 1971) to supply missing values or to compare with older summaries for these areas. Dr. Arnold Court has kindly provided additional temperature data covering 30 years from 1951-1980 as well as the above insolation data and numerous other helpful materials from

published and unpublished sources.

#### E-1. Method of Analysis

The available information on climate of a location was sorted according to the morphological type (MORPH) of each yucca sample and was summarized statistically according to MORPH and Series (Appendix E). Twenty-one climatic factors considered in this analysis were listed in Figures 28, 29, 30, and in Appendix E. At first, there seemed to be few differences between climatic factors in different MORPHs and Series that deserved notice in the data as a whole. However, by comparing the differences of data means of the MORPHs from mean climatic data of MORPH II--the supposedly primitive, pre-series "origin" of Y. whipplei (Ch. II, III)--interesting and consistent relationships were revealed between climatic factors and the development of Series morphology. Magnitude and direction of the differences between climate factor means of pre-series MORPH II samples and those for each MORPH of the other Series for 21 climatic factors were summarized in Figures 28, 29, 30. MORPH was arranged in the figures according to the logical evolutionary order shown in Figures 9, 11, and 12 a, d, except that the hybrid Series 3B, MORPH X, was placed between its putative parental MORPHs--VI, VII, and VIII, IX--because of its variable but often intermediate character. Positive and negative differences found between MORPH II means and means of other MORPHs were illustrated as columnar graphs above or below the baselines of MORPH II means. Three forms of a complex factor called Growing-Season Degree-Days are illustrated in Figure 31.

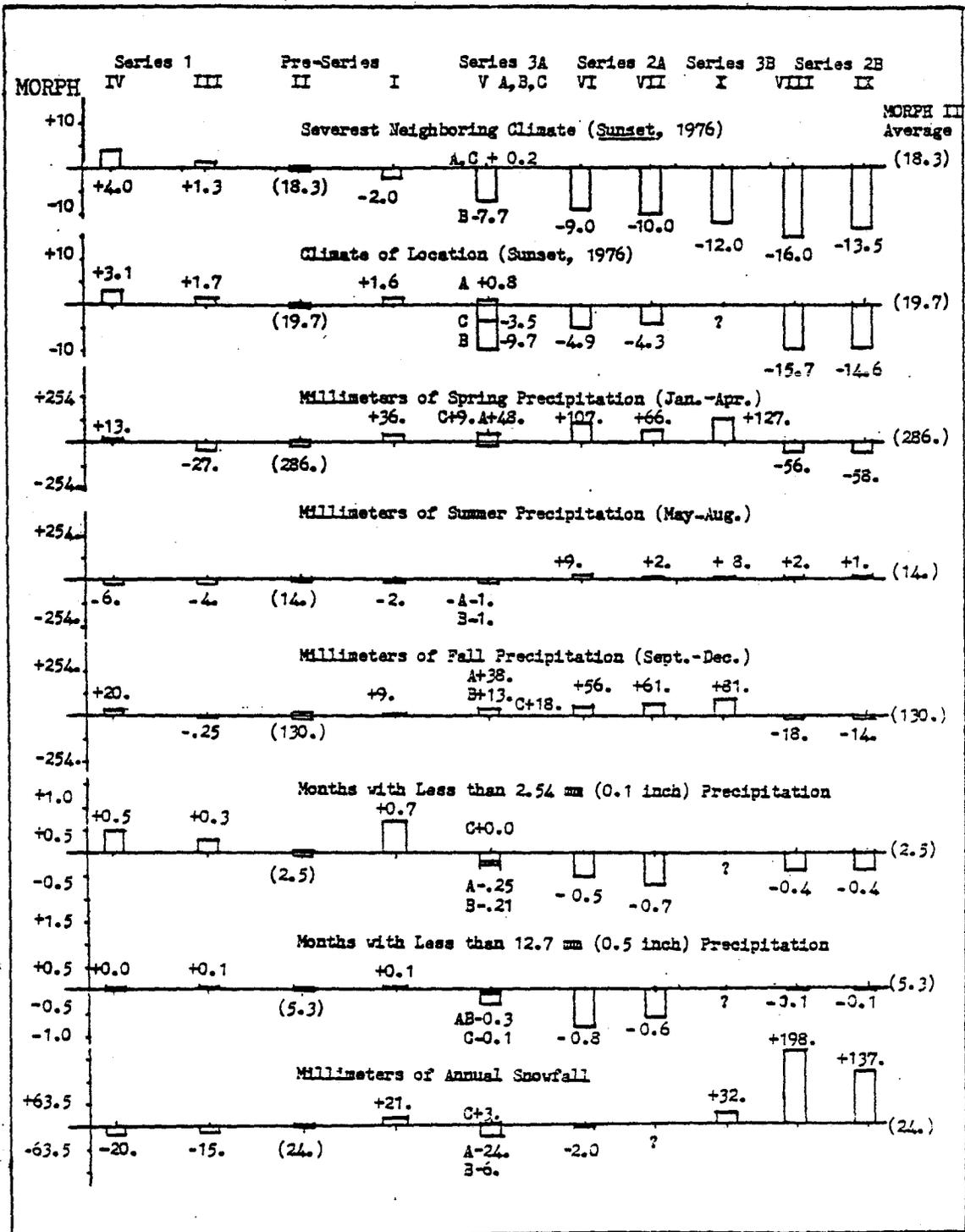


Figure 28. Differences Between Averages of Climatic Factors in "Primitive" MORPH II and Averages of Other Morphological Types (MORPHs) of Y. whipplei

## E-2. Twenty-one Climate Variables.

Series 1 grew where there was very little difference between the climate of location and of severest neighboring climate, both variables being, in Series 1 populations, of the most nearly optimal climates existing in California for subtropical plants. Series 1 locations had the least likelihood of snowfall, and rainfall about the same or slightly less than for pre-series populations during spring, summer, and fall. Correspondingly, the number of summer months with less than 2.5 mm (0.1 inch) or 13 mm (0.5 inch) rainfall was greatest in the relatively coastal Series 1 and pre-series yuccas, for apparently the montane Series 2A and "desert" 2B relied on the minimal summer showers or early fall rains where they grew.

In actual evapotranspiration, that of Series 1 areas as well as of Series 3A was greater than that of areas with pre-series yuccas while Series 2A, 2B, and 3B locations exhibited much lower actual evapotranspiration. The low figures in Series 2A and 3B locations probably were caused by relatively high humidity or cloudiness, but in Series 2B probably were due to low precipitation and plant reaction to stress from aridity. In evaporative demand (CDWR, 1974, pp. 170-176) the relationship was reversed, quantitatively speaking, but values for Series 3A coincided with those of Series 2A, 2B, and 3B instead of with those of Series 1 and pre-series yuccas. Because evaporative demand represents amount of irrigation water that must be supplied to a crop, in this case pasture grass, in regions of different potential and actual evapotranspiration and rainfall averages, it is a general measure of water deficiency for plants in natural areas of a region.

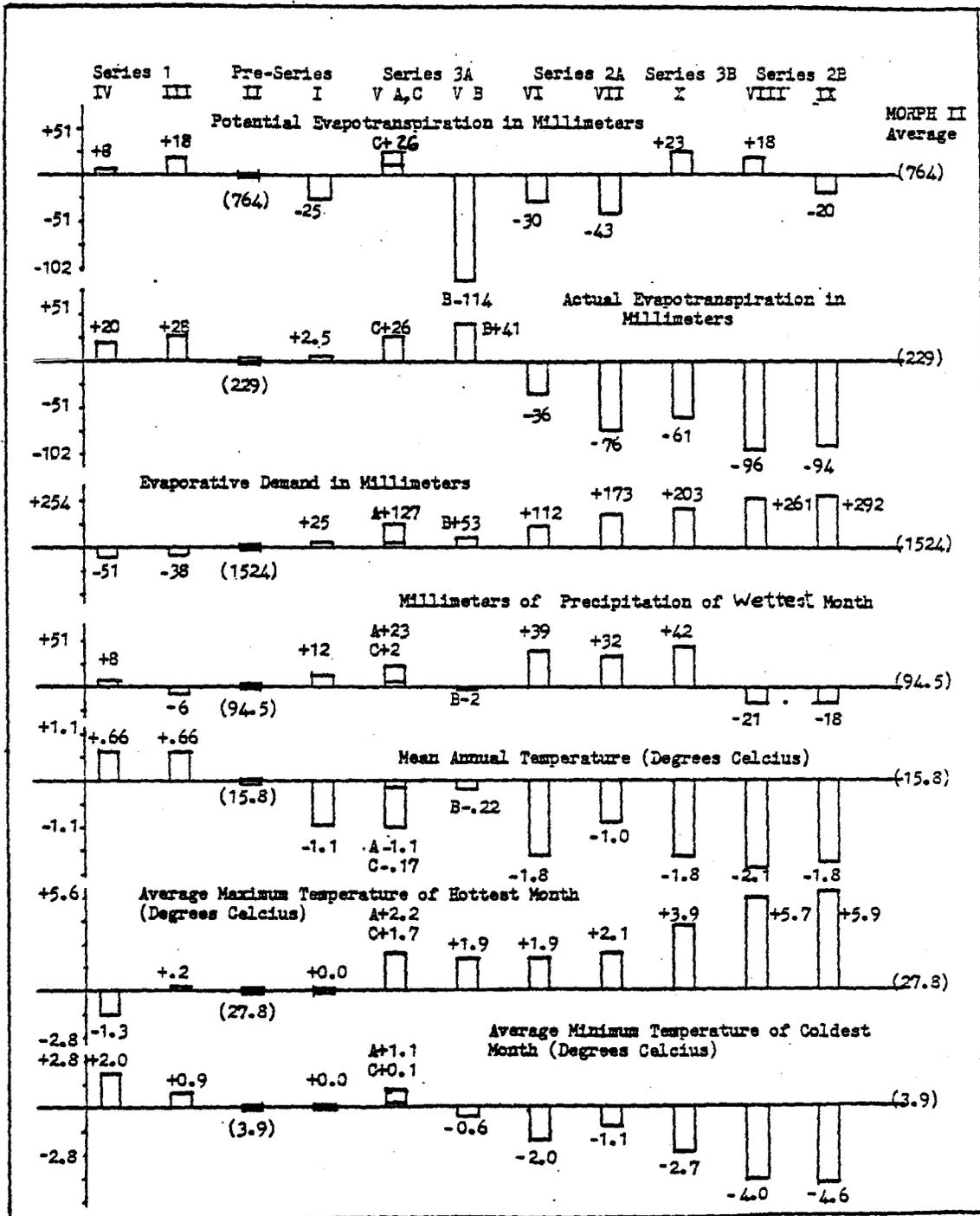


Figure 29. Differences Between Averages of Climatic Factors in Various MORPHs from MORPH II Averages, Continued.

Series 2B locations had very low maximum monthly precipitation, similar to amounts for pre-series locations (89 to 114 mm) while locations of Series 2A-3B had much heavier precipitation in months of maximum rainfall. Locations of Series 2B were still lower than those of Series 1 in maximum monthly rainfall. It is quite probable from their maritime and summit sites on coastal mountains that pre-series and some Series 3A yuccas receive additional unrecorded precipitation as condensation from fog (Chang, 1968, pp. 230-231; Geiger, 1973, pp. 348-349, 441-442; Vogl, 1973; Major, 1977). The similarly low rainfall figures for thin-leaved Series 1 and thick-leaved Series 2B are surprising in that Series 1 tends to have high seedling production and Series 2B usually shows minimal seedling success (Hoover, 1973). The difference in seedling success and of leaf thickness both can be attributed to mild temperatures and humidity of air in the coastal Series 1 locations and to long, comparatively warm, wet, winter growing seasons there also.

In mean annual temperature, Series 1 locations were distinctly higher by  $0.7^{\circ}\text{C}$  than pre-series locations, but annual temperature means were much lower in Series 3A, 2A, and 2B locations than the MORPH II average value of  $15.8^{\circ}\text{C}$ --usually  $1.0^{\circ}$  to  $2.0^{\circ}\text{C}$  lower. Maximum temperature averages of hottest month in Series 2A-3A locations were about  $2^{\circ}\text{C}$  higher, and Series 2B-3B locations were  $4^{\circ}$  to  $6^{\circ}\text{C}$  higher than the pre-series average, while Series 1 maximums were equal to or a degree less than pre-series. Contrarily too, average minimum temperature in the coldest month was, respectively for Series 1 and Series 3A,  $3^{\circ}$  to  $1^{\circ}\text{C}$  higher than, or else nearly the same as the MORPH II average ( $3.9^{\circ}\text{C}$ ), but was  $1^{\circ}$  to  $4.6^{\circ}\text{C}$  lower than  $3.9^{\circ}\text{C}$  in Series 2A,

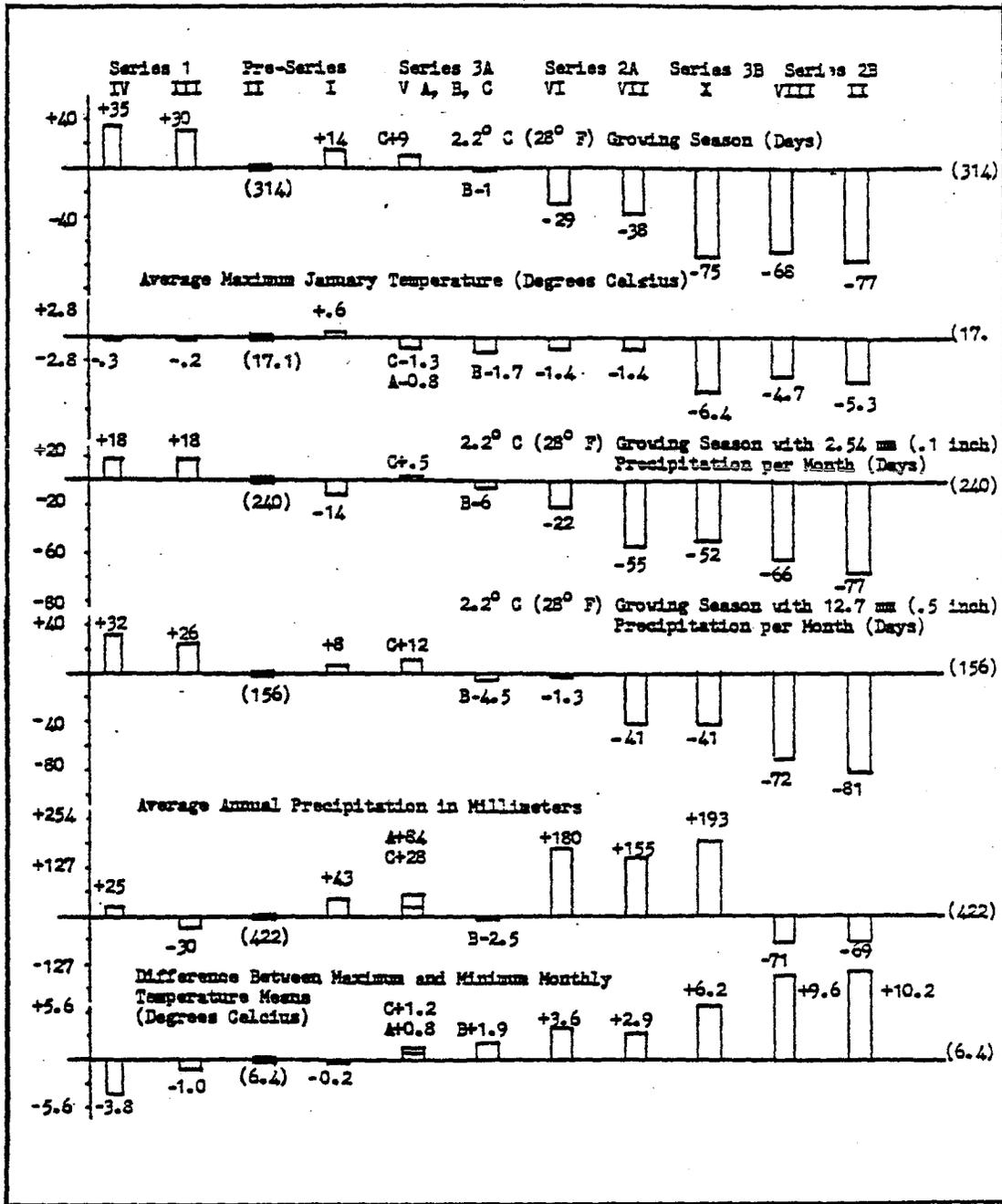


Figure 30. Differences Between Averages of Climatic Factors in Various MORPHs from MORPH II Averages, Continued

2B, and 3B.

In other words, both Series 2A and 2B, and their hybrid, Series 3B, occurred in regions of relatively severe variation between seasonal temperature extremes, while Series 1 was exposed to the least extreme, or mildest, annual climate changes, even compared with pre-series averages of which many samples were from maritime locations. In every respect Series 1 had the longest growing seasons of all Y. whipplei, not only in terms of temperatures above freezing, but also in terms of seasonal precipitation during favorably warm seasons.

In only six climatic factors of the twenty-four used in this study did Series 2B-3B and Series 2A-3A diverge to follow opposite trends. All six were basically differences in water availability. Spring and fall precipitation were lowest in Series 2B compared to pre-series but higher than that of MORPH II in 3A, 2A, and 3B. There were fewer months without 2.54 or 12.7 mm (0.1 or 0.5 inches) of precipitation in Series 2A-3A than in Series 2B. Average annual precipitation in Series 2A-3B locations was about 150 to 180 mm higher than the pre-series average, but was about 70 mm lower than this average in Series 2B locations. The wettest month of precipitation for Series 2A was 30 to 42 mm higher than the average for MORPH II, but for 2B was about 20 mm lower than for MORPH II.

Snowfall was much higher in Series 2B locations than in locations of most other Series known, for in the others it was close to the pre-series average. Snowfall data for Series 3B was not always available; but in the moderately high elevations at which most Series 3B populations occurred, snowfall was close to the maximum for Series 2B or yet

higher.

To summarize, Series 2A-3B occurred where rainfall was greatest and therefore had longer favorable growing seasons than in Series 2B locations. Series 2B--and in some temperature factors 3B also--survived the most extreme temperature contrasts, least precipitation, longest droughts, and shortest, least energy-productive, effective growing seasons of all the Y. whipplei populations studied.

### E-3. Growing-Season Degree-Days (GSDD and PSDD)

Early scientific efforts to measure or predict the relations between plant growth or development and total energy resources available to the plant in its lifetime introduced a measure known as degree-days (Chang, 1968, pp. 77-78; Newman et al., 1967, pp. 127-129; Wickman, 1981). Growing Degree-days (GDD) are estimated as the sum of the daily differences in degrees between mean air temperature and an assumed minimum temperature suited for growth of the plant, or for the lifetime of the plant or the period of life-cycle being studied. However, because the critical physiological growth temperature required for Y. whipplei is unknown, a slightly different criterion, GSDD (Growing-Season Degree-Days) was based on the length of the  $-2.2^{\circ}\text{C}$  ( $28^{\circ}\text{F}$ ) annual growing season multiplied by the annual mean air temperature. Length of the  $-2.2^{\circ}\text{C}$  growing season is the average number of days between the last spring  $-2.2^{\circ}\text{C}$  freeze and the first  $-2.2^{\circ}\text{C}$  freeze in fall. This estimate of GSDD is based on the assumption that most growth in Yucca whipplei takes place after the period of subfreezing night temperature has passed. Energy available for metabolism therefore is roughly

proportional to annual mean air temperature and to length of the growing season in days.

$$\text{GSDD} = \text{GS}_{-2.2} \times \bar{T}_a$$

Because of quite different bases of calculations, GSDD is not directly comparable with Growing (or other) Degree-days, but does parallel them as measures of a location's energy availability to plant growth.

On the assumption that the length of a yucca's growing season is limited not only by minimal temperature, but also by the availability of water for use in photosynthetic and respiratory metabolism, two other more refined versions of Growing-Season Degree-days were calculated on the bases of length of  $-2.2^{\circ}\text{C}$  Growing Season having precipitation equal to or more than 2.5 mm (0.1 inch) and more than 13 mm (0.5 inch) per month. It was not known whether either one or both of these amounts of minimal precipitation were effective in determining the growing season of Y. whipplei. These Precipitation-Season Degree-Days (PSDD) then were calculated as follows:

(a)  $\text{PSDD} = \bar{T}_a (\text{GS}_{-2.2} - 30M_{2.5})$ , where  $M_{2.5}$  is the number of months with precipitation less than 2.5 mm.

(b)  $\text{PSDD} = \bar{T}_a (\text{GS}_{-2.2} - 30M_{13})$ , where  $M_{13}$  is the number of months with precipitation less than 13 mm.

These latter two estimates of Precipitation-Season Degree-Days representing total energy available to wild plants perhaps are more sensitive to the requirements of plant physiology than are standard estimates of degree-days in which no variation in length of growing-season due to precipitation is considered (Chang, 1968, pp. 77-78; Newman et al., 1967, pp. 127-129).

The results for different MORPHs and Series of Y. whipplei using

these three measures of Growing-Season or Precipitation-Season Degree-Days are summarized as means in Appendix E and as differences from MORPH II means in Figure 31 a, b, c, by columnar graphs above and below the baseline of MORPH II means for each method of calculation. In all three estimates of GSDD and PSDD for different MORPHs, relatively large increments of degree-days separated the MORPHs of different Series. The direction of change in solar energy available to a given MORPH during its growing season varies in parallel with the direction of change in morphology to a remarkable degree. To illustrate these parallels, three graph networks were constructed (Fig. 32 a, b, c) in which the MORPHs of Y. whipplei were located on the graph by the calculated differences in their energy environments (GSDD and PSDD) from that of MORPH II, rather than by their phenotypical differences. As can be seen in each graph network, their relationships virtually replicated the graph networks found phenotypically in PRIM (Fig. 11), providing evidence of a strong correlation between available solar energy during the comparatively wet growing season and development or occurrence of the three main contrasting lines of morphological differentiation represented by the Series of Y. whipplei.

Growing-Season Degree-Days in Series 1 locations were about 500 to 800 higher than in pre-series and Series 3A locations, as well as much higher than all the others (Fig. 31, 32). Series 2B-3B areas were about 1300 to 1600 degree-days below the pre-series and Series 3A averages of around 2400 to 4900, while Series 2A areas were 250 to 900 degree-days below the pre-series level of growing-season energy resources. The quite regular stepwise distribution of energy resources exhibited among the Series indicated that sunlight energy

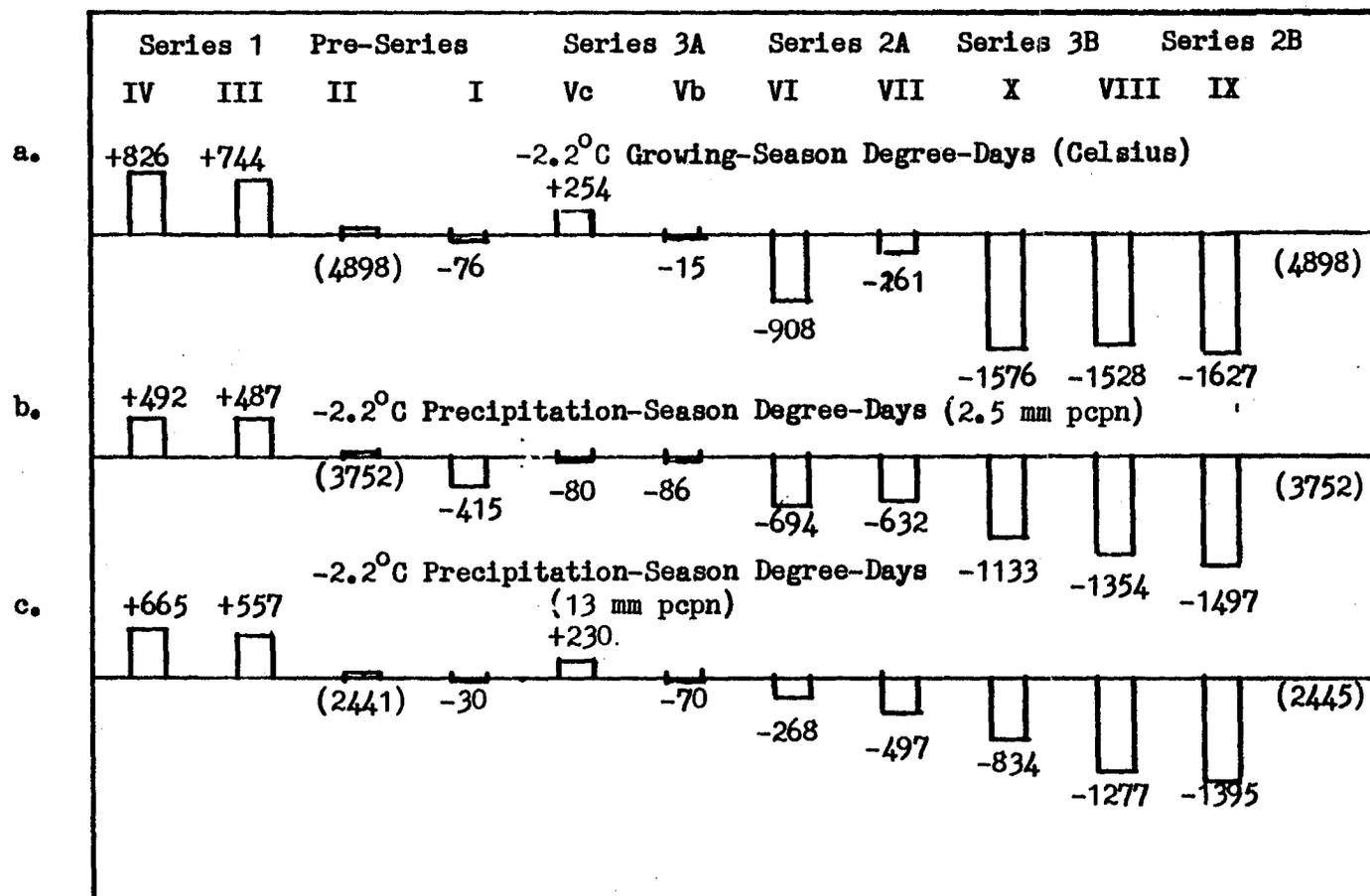


Figure 31. Differences Between Averages of -2.2°C Growing-Season or Precipitation-Season Degree-Days of Pre-Series MORPH II and other MORPHs of Y. whipplei

- a. Precipitation not included. b. For months with precipitation = 2.2 mm (0.1 inch).  
 c. For months with precipitation = 13 mm (0.5 inch). pcpn = precipitation.

availability had an important selective significance in determining the morphological steps in the Series. The consistently large and regular gaps between values of GSDD or PSDD in different MORPHs perhaps signified that annual incremental energy values of much less than 250 to 500 degree-days (Celsius) were insufficient to implement a selected adaptive change in yucca morphology. Possibly some triggering mechanism or physiological threshold value exists, associated with 250 to 500 degree-day increments, to selectively determine the proportions of leaves, and thus to result in different Series. However, the existence of additional critical requirements other than adequate precipitation, sufficiently warm temperatures, and high insolation may account for such gaps.

Calculation of Growing-Season Degree-Days seemed arbitrary and crude, but for Yucca morphology resulted in the most precisely correlated climate variables of any that were studied. In Figure 32 a, b, MORPHs VI and VII are in reversed order to their presumed direction of increased development, but in Figure 32 c, this reversal is corrected by inclusion of the factor of months with precipitation equal to or greater than 13 mm in the calculation of length of growing season. There are smaller and more regular increments of GSDD among MORPHs in Figure 32 c than in a or b, and in c is the greatest coordination of degree-days with Series morphology. Note also that the positions of presumed hybrid Series 3A and 3B are almost exactly halfway between the PSDD levels for their postulated parental Series in accordance with expectations from their intermediate genetic positions. Because of these quite precise relationships, I conclude that the calculation of PSDD limited to months with 13 mm (0.5 inch) precipitation or more

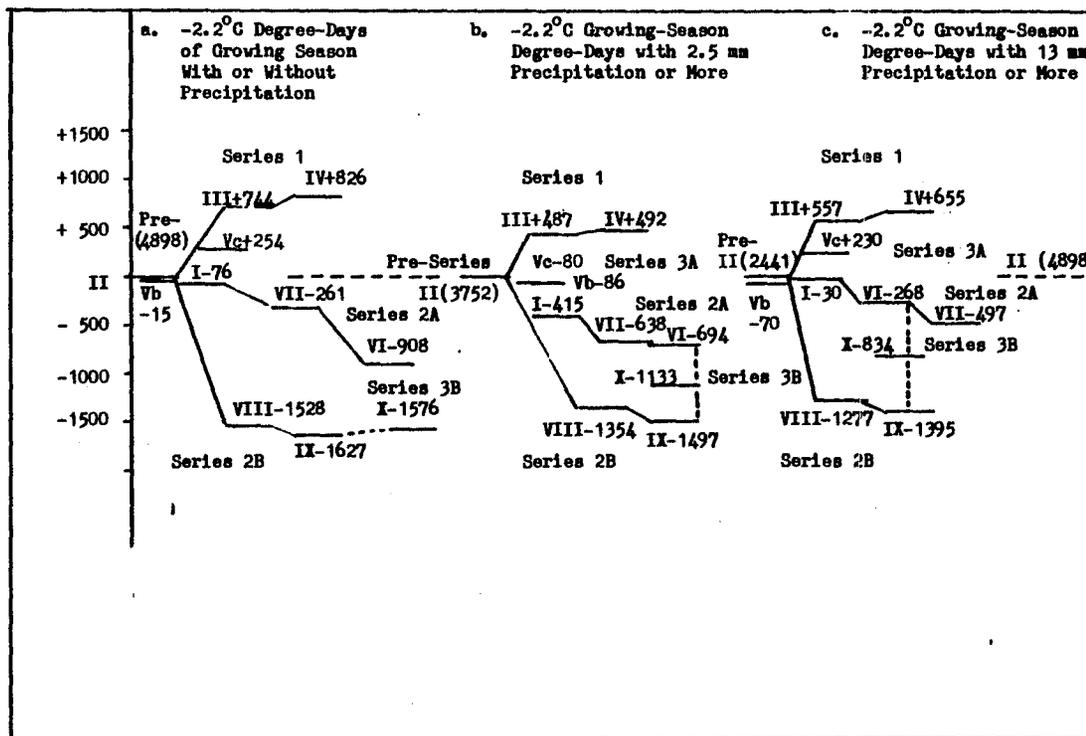


Figure 32. Relationships Between Series and MORPHs of *Y. whipplei* with Levels of -2.2°C Growing-Season Degree-Days

is by far the best of the three composite estimates of selective climate factors for Y. whipplei.

The exceedingly low GSDD and PSDD energy factors for Series 2B yuccas (Fig. 31) seemed surprising according to commonly accepted views about their habitats in the California deserts as high solar energy environments (Fig. 24). Usable energy available to wild plants must be regarded therefore as being limited by the periods of soil-water availability, particularly in xeric regions of low humidity. On the coast relatively high humidity evidently compensated for generally low precipitation and prevented high evapotranspiration and seasonally damaging light energy levels that possibly were limiting to plant success in desert areas, thus allowing the persistence of pre-series, Series 1, and 3A yuccas in dry coastal areas.

#### E-4. Discussion

Parallels between trends of various climatic factors and the morphological trends of Series probably indicated some original causal relations between climatic factors and the paleohistorical evolution of leaf and stalk morphology in Y. whipplei. Directions and degrees of climatic differences shown between pre-series MORPH II and MORPHs of the three major Series of Y. whipplei supported the evolutionary pattern that had been indicated by morphological comparisons alone and by PRIM networks and t-order differences (Ch. II). These comparisons of climatic means also reflected nearly the same relationships between climate and evolution that were expected from careful consideration of the general locations of Series on the map of California and from the relationships shown by holistic climate gradients (Ch. III).

MORPH II apparently did represent the simplest origin from which Series 1 developed. In accordance with climatic relations, Series 2A and 2B evidently originated from MORPH I and V without involving MORPH III directly. MORPH III consistently followed the trend of IV in Series 1 while MORPHs I and V usually were similar to Series 2A in climate trends and often were also similar to Series 2B and 3B. The most consistent general observation made from the charts in Figures 28, 29, 30, 31 was that--when mean climate factors of pre-series yuccas were taken as being intermediate or average for the species as a whole--factor means for Series 1 either were close to the pre-series average or else were opposite in trend to those of the other Series. In other words, Series 1, in regard to any climate factor, was rarely on the same side of the MORPH II average with Series 2A, 2B, or 3B; but sometimes it was very close in climate association to Series 3A.

The above results constituted evidence for correlation of morphological differences with various climatic factors that separated Series 1 as a distinct evolutionary branch compared with Y. whipplei of either Series 3A-2A or Series 2B-3B. Series 1 also was distinct from pre-series populations in mean values of several climate factors. The climate patterns of the three yucca Series with highest Developmental Rank Indices (DRI) resembled each other in trend, but Series 2B-3B usually were found in the most extreme, adverse climatic conditions and Series 3A-2A were in intermediate but variable temperatures and quite mesic situations. In most factors studied, the values followed clear gradients of differentiation from Series 1 through pre-series, Series 3A and 2A, to finally Series 3B and 2B, in that order (Fig. 28, 29, 30, and 31).

The close tracking exhibited between climatic factor averages and the developmental rank of MORPHs constituting supposedly artificial subgroups of the different Series was impressive. In several climatic factors, values increased or decreased in definitely stepwise changes from one MORPH to the next, whereas values in other factors changed along a relatively smooth continuum. Stepped values of climatic factors were found in: length of  $-2.2^{\circ}\text{C}$  ( $28^{\circ}\text{F}$ ) growing season, average daily maximum January temperature, difference between average daily mean maximum and daily mean minimum temperatures of hottest and coldest months, mean annual temperature, and growing-season degree-days. The factor GSDD was found by multiplying stepwise values of two of these environmental factors, mean annual temperature and length of  $-2.2^{\circ}\text{C}$  growing season (days), (pp. 162-163), a fact that partially accounted for reenforcement of quantum or stepped incremental values of this attribute in connection with morphological differentiation of Y. whipplei. If stepped values of climatic factors--attributable to energy quanta--were required for evolution of different morphological Series in Y. whipplei due to certain threshold or unit physiological demands, this fact perhaps accounted for the relatively large climatic "tolerances" exhibited by MORPHs (Fig. 14, 15; Table 14), especially in intermediate climate zones.

#### E-5. Geographical Genetic Patterns

In comparisons of the mapped distribution of morphological trends, an abrupt discontinuity was observed in the distribution of eco-morphological relationships that concerned evolution in Yucca whipplei (Fig. 33). The geographic distribution of morphology was not

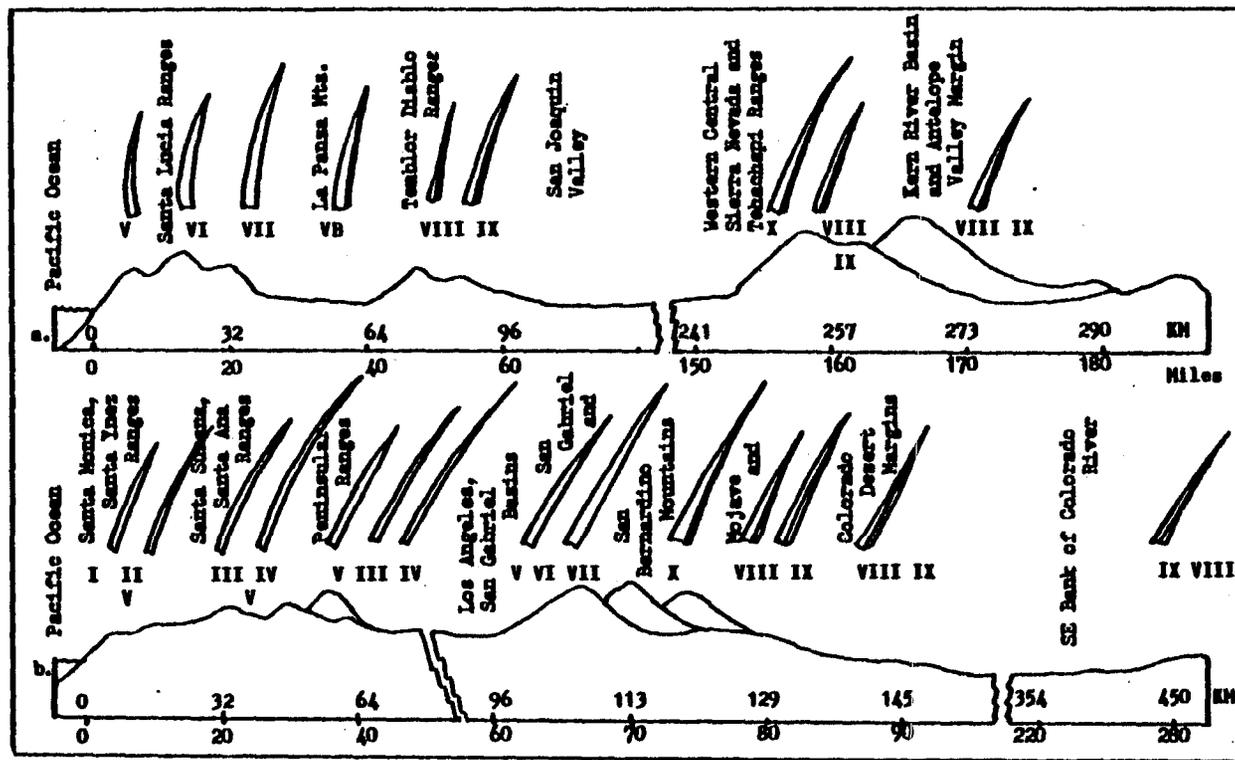


Figure 33. Combined Cross-Sections of California Showing Relative General Distribution of MORPHs of *Yuca whipplei*\*

- a. Southern Central California from Big Sur and San Simeon to Kern, Isabella, and Tehachapi
- b. Southern California from Carpenteria and San Onofre to Colorado River, Lake Mead

\* Not drawn to scale, but leaves indicate comparable proportions among MORPHs; relative distances from the coast are approximate but comparable, with breaks in scaled distances indicated.

entirely clinal in the sense that a single morphological trait--such as mean leaf length or width--continued increasing or decreasing in one direction as the associated climate variable changed in value. Instead there was an abrupt switch or reversal in trend in the yuccas along a west-to-east transect from cool, humid, mild coastal regions to dry, warm interior, to mesic, variable, coast-facing, middle altitudes, then to highest, wettest, coldest peaks, and finally down into the hot and cold, dry contrasts of the desert margin.

The morphological trend following this coast-to-interior gradient in a southern transect (Fig. 33 b) was (1) increasing leaf length from pre-series to Series 1, followed or accompanied by (2) increasing leaf width in Series 2A and 3A, followed by (3) increasing leaf thickness in Series 3B; then a sudden change to (4) the original short, narrow leaves, but with maximal leaf thickness in Series 2B (Fig. 3, 9, 10). In a northern transect (Fig. 33 a), the first two stages were omitted and the last stage appeared twice, separated by the range of Series 3B.

While the first three or four stages (Fig. 33 b) conceivably could have proceeded sequentially by evolution in response to distance from the ocean and increase in altitude, the yuccas of Series 2B in the last most interior stage apparently evolved in isolation from the "cline" of the preceding stages. Therefore two or three clines must have been responsible for evolutionary patterns in *Y. whipplei*, two coastal and the other interior. In the interior cline, morphology differentiated from pre-series only in the variable of leaf thickness--on which depended leaf volume and  $A/V$ --but in the coastal clines variation occurred mainly in leaf area, first by increase in leaf length, then by increase of leaf width above the minimal sizes of

pre-series biotypes. Some increase of leaf width also occurred independently of leaf length in pre-series yuccas near the coast, resulting in MORPH I (Fig. 3, 9, 10). Geographically the development of Series 1 may be said to follow a N-to-S cline; Series 2A a S-to-N cline; and Series 2B a south coast-to-north interior cline, all radiating from a pre-series, central, subxeric and approximately coastal origin.

Initially my taxonomic differentiation of Series 1 from Series 2A and 2B was based on leaf length-to-width ratio (L/W), (Hoover, 1973). Series 1 had leaf L/W ratios about twice those in Series 2, but the low L/W ratios in Series 2A were achieved differently in the phenotypic sense from those in Series 2B. In Series 2B samples, leaves tended to be short and narrow, as in the pre-series yuccas, but very thick. Therefore pre-series and Series 2B yuccas both had small L/W ratios. Series 2B leaf dimensions were not selected by climate favoring small L/W ratios, but encouraging minimal surface areas, i.e., photosynthetic and or evapotranspiration surface. Better stated, least area-to-volume ratio was selected in Series 2B-3B, and least leaf area was selected in pre-series and Series 2B yuccas. In Series 2A (MORPH VI, VII) both leaf length and width have increased proportionately from pre-series levels, maintaining the original small L/W ratio, but with double or quadruple the minimal leaf areas of pre-series yuccas. Some pre-series phenotypes have doubled the minimal leaf width without increasing leaf length beyond the minimal, i.e., MORPH I. In MORPH I leaf area was increased by one-half to twice the minimal average area of pre-series II, but L/W ratios were lowest of all. Therefore, in Series 3A-2A an increase of leaf area was the selected

trait, and L/W was only incidental, although it provided an important diagnostic character and a high DRI for differentiating Series, being determined by two independent phenotypic variables.

Lengthening of leaves probably was the simpler and more primitive of the two most fundamental methods of areal increase in yuccas because it involved no numerical addition of vascular primordia. The same elongation process responsible for leaf growth in pre-series plants, if allowed to continue unchecked for a longer time, would result in Series 1 phenotypes. Such a simple adaptation could have been achieved probably by a single gene operator-inhibitor mechanism in an environmentally controlled phenological adaptation of individual plants (Maniatis and Ptashne, 1976; Aitken, 1974; Rost et al., 1979, Ch. 2, 8). The environmental control of shading may have caused a slowdown in production of an inhibitor substance, which slowdown in turn allowed the continuation of leaf elongation. Shade-caused elongation of parts is of course a commonly occurring phenomenon in plants. Certain wavelengths of light are known to stimulate stem and leaf elongation in many crop species (Chang, 1968; Evans, 1973). Such genetic controls could become permanently fixed in a population by natural selection when predominant conditions in the environment make least-inhibited, or most-inhibited plants the fastest and most successful reproducers in a population.

Series 1 was probably the oldest specialized group beyond the pre-series minimal stages of development. Its polymorphic populations also could have given rise to MORPH V through natural selection of a preponderance of pre-series MORPH I biotypes in an environment that favored increased leaf area requiring greatest leaf widths and

lengths. Such selection might have been facilitated by cross-pollinations between the long-leaved Series 1 biotypes and relatively broad-leaved MORPH I biotypes in adjacent populations. But how was MORPH I adaptation first accomplished by leaf widening in pre-series II populations? Leaf widening involved a multiplication of the number of parallel, lateral, vascular bundles as well as of parenchyma tissue, and this numerical increase could have required duplication of the activity of a number of particular genes needed to produce a narrow leaf. What advantage might this presumably more costly method of areal increase--in terms of plant expenditure of energy--have provided over that of simple leaf elongation in the usual, humid, coastal regions where MORPH I and II occurred (Fig. 10)?

Observations of cultivated seedlings of Y. whipplei and of wild yucca plants indicated that frequent soil-water shortages in a humid or foggy climate probably were responsible for evolution of leaf widening in pre-series MORPH I. In the test garden, yucca plants that suffered drought damage usually lost the outermost, often longest leaves but survived drought by means of the younger, shorter, and frequently wider, inner leaves of the rosette. In a coastal region of shallow, dry, rocky soil where infrequent exposure of plants to sun is intense due to lack of competing vegetation, the most effective increase of photosynthetic area would be one allowing quickest, most efficient translocation of water by additional vascular tissue.

In coastal regions fog-drip is a major source of ephemeral soil moisture (Vogl, 1973; Hoover, 1970; Major, 1977), especially at low altitudes where rainfall is less than on the heights. Humidity of air near the ocean prevents excessive water loss by evapotranspiration.

Short thin leaves therefore likely are sufficient if additional leaf width provides enough photosynthetic area to take advantage fully of abbreviated periods of full sunlight and longer periods of light filtered through clouds, and if the proportionate addition of vascular tissue allows full use in photosynthesis of slight but frequent condensation from fog on leaves and soil. Low ground-hugging habits are common to many coastal plants evidently as a result of and as a protection from wind (Chang, 1968, pp. 233-238); also probably for the advantage of extra heat and light energy reflected close to the ground (Geiger, 1973, pp. 417-419, 446-449). Low availability of soil water on exposed rocky bluffs also must play a part in keeping growth minimal (Barbour and Major, 1977, Ch. 13).

Samples of high Developmental Rank Index in Series 2A (MORPH VI, VII) seem to have been brought about by further multiplication of active chromosome sections involved with producing new vascular bundles and width in leaf primordia, as in other plants (Clausen, 1951; Clausen and Hiesey, 1958). The likelihood of segmental chromatin replication being responsible for Series 2A specialization was indicated by relatively great and regular gaps in width between sample means of phenotypes found in Series 2A and 3B (Fig. 34, 35). Leaf dimensions of Series 2A and 3B from different sample areas often varied by large increments rather than by the small increments commonly exhibited between sample means in Series 1, 2B, and pre-series, as seen in any scattergram where leaf width was figured (Fig. 6, 7, 34, 35). However, hybridity with Series 2B may account for frequent small phenotypic gaps in Series 3B, about one-fourth to half the breadth of the largest gaps in Series 2A.

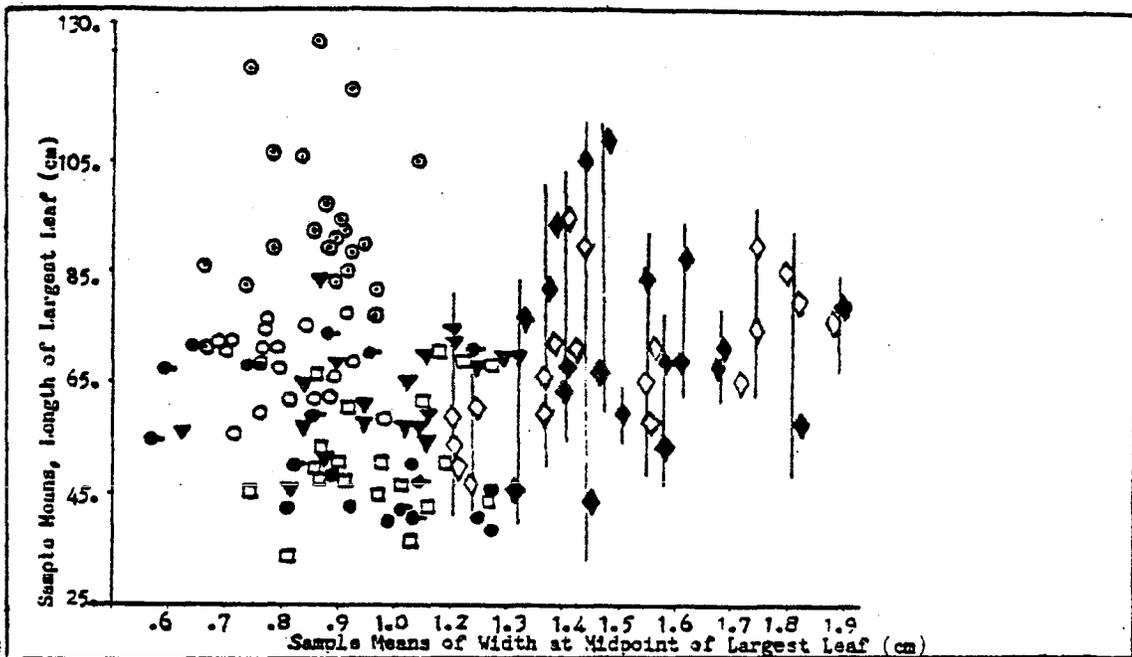


Figure 34. Twenty Randomly Chosen Samples from Each Series or MORPH in Scattergram of Leaf Length vs. Leaf Width, Yucca whipplei

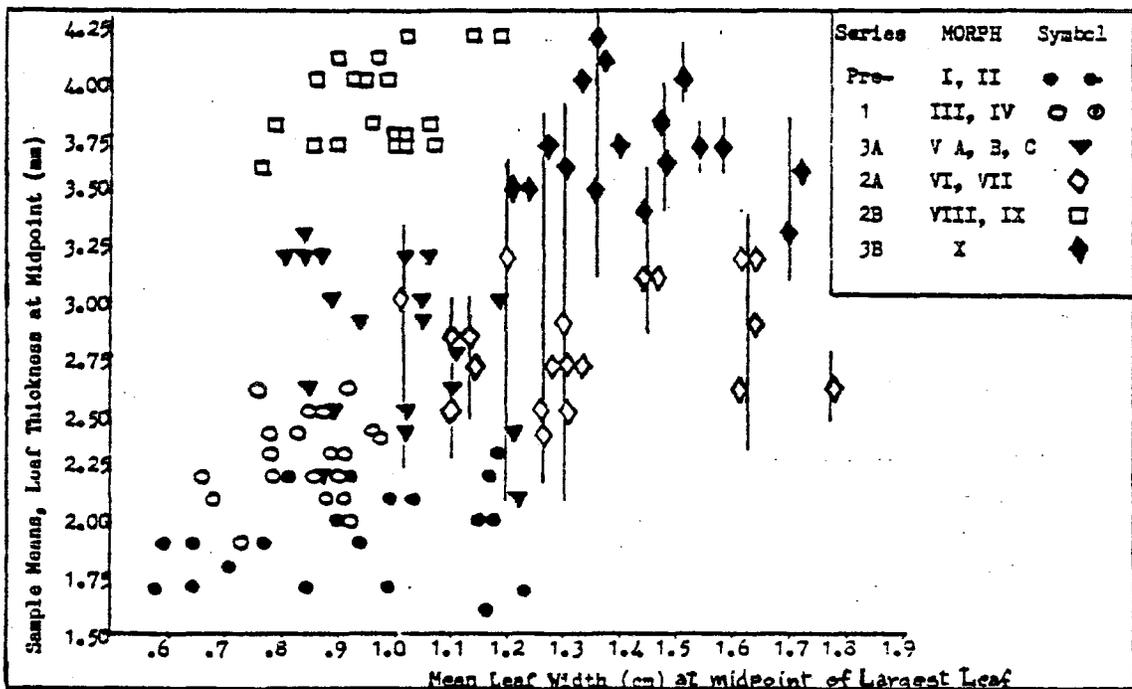


Figure 35. Twenty Randomly Chosen Samples from Each MORPH in a Scattergram of Leaf Thickness vs. Leaf Width, Y. whipplei

In Series 2A MORPHs, leaf length increase kept pace with width, possibly as a result of ancient introgression or biotype selection from Series 1, and or by gene linkage of leaf length and width in chromosomes of Series 2A (Clausen, 1951; Clausen and Hiesey, 1958). Consequently Series 2A retained low L/W ratios as in pre-series yuccas. But in numerous samples of Series 3B, mean leaf length was increased proportionately more than width, and resulted in leaf ratios significantly higher than in Series 2A or 2B (Appendix A). The selected hyperstatic increase of leaf length in Series 3B also resulted in the largest Y. whipplei plants known. These giants predominate at 600 to 1900 meters of elevation in the central Sierra Nevada and in the San Gabriel Mountains, but are scattered also in the northern Transverse and interior Peninsular ranges (Fig. 10, p. 49).

In the Kern River drainage, which geographically divides the two main Series 3B yucca populations, Y. whipplei Ssp. caespitosa of Series 2B hardly was distinguishable visually from the Ssp. caespitosa populations of the Ridge Basin and margins of the Mojave Desert. Differences in leaf dimensions were not great, as shown by blending of these populations in MORPH IX (Fig. 9; Table 9, 11; Appendix A) and by relationships in PRIM networks (pp. 61-64). However these Kern River yuccas had moderately high leaf L/W ratios like those of 3A-3B instead of low ratios as in pre-series or in other Series 2B samples. Intermediate leaf ratios and frequent occurrence of abortive seedpods in the Greenhorn Mountains of the Kern River region indicated a probable history of introgression with Series 3A or 3B back to the putative Series 2B parent to form intermediate populations combining these two morphologies slightly (Anderson, 1949; Heiser, 1973).

V. SOME EFFECTS OF GROWING SEASON ON MORPHOLOGY AND  
REPRODUCTION IN Y. WHIPPLEI

It is one thing to find a statistical correlation between the geographic occurrences of particular climatic features and certain attributes or characteristics of plant morphology and habit, but quite another to explain physiological or evolutionary connections between the correlated features. Frequently such explanations are little more than plausible guesses, particularly when only one plant feature and one correlative environmental factor are studied at a time. A much stronger argument can be supported when several plant features are found to be interrelated and when each correlation for several features contributes logically to an entire system of adaptive evolution under the contrasting circumstances found in nature. Different adaptive systems or "strategies" encountered in the major Series of Y. whipplei are seen to represent alternative reactions to contrastive circumstances, and each adaptive system is found to operate through the most fundamental functions that, combined, determine survival and success of plants in any population.

A. Growing Season and Maturation

For most yuccas in the southern coastal mountains of California, spring flowering is preceded by vegetative growth during late fall, winter, and early spring--a result, in part, of mild winters with

abundant sunshine concurrent with peak precipitation. Occasionally Series 1 seedlings from San Diego County have flowered at the experimental garden in Encino, California, by February. In late February of wet years following years of drought, a few San Diego County yuccas were seen flowering in the wild, but most plants flowered from March to May (Powell and Mackie, 1966; my field notes, 1968-1982). In Series 1 yuccas, abundant seedpods were dried and split several weeks before the first fall rains; therefore, inhibition of pollination or of seed maturation seldom resulted from too short or late a growing season. Series 1 yuccas had, as a rule, small leaf-rosette bases, usually less than ten centimeters in diameter, and flowering panicles often were shorter and more compact than in other Series (Fig. 1, Appendix A), (Haines, 1941, Fig. 3, 4).

In the experimental garden some Series 1 plants flowered at the age of 5 years, only 3 years after being transplanted, but plants of Series 2A and 3A, of high DRI (Ch. II), delayed flowering by some additional years at ages of 7 to 12 or more years (my notes, 1970-1980), (Table 21). Habit was independent of age of flowering to a degree in the test garden, for intermediate and cespitose plants of Ssp. intermedia flowered as early as the monocarpic plants of both Ssps. intermedia and typica (Series 1). Monocarpic individuals of Ssp. intermedia were the earliest to complete maturation as a group in that population of seedlings, however.

How could a comparatively short season for seed production affect the size and leaf proportions of vegetative rosettes in the huge plants of Series 2A and 3B yuccas of the Sierra Nevada, San Gabriel, and other interior mountains where severe winters restricted the

Table 21. Age at Flowering of Different Series and Habits, Yucca whipplei, in a Transplant Garden

Series	Sample Source	Date of Collection	Date of Sowing	Date of Transplanting	Date of First Flowering	Earliest Age at Maturation	Predominant Habit in Sample
1	Via Loma, Fallbrook		2/18/68	8/12 13/71	1/28/74	6 years	Monocarpic
1	(Purple) Rainbow		3/2/68	8/4 5/71	6/4/73	5½ "	Monocarpic
1	Abargo, Woodland Hills		12/8/67	8/20/71	5/4/73, 10/2/73	5½ "	Mixed Habits
1	Rancho Santa Ana		1971?	7/5 6/73	5/12/76	5 "	Monocarpic
2A*	Big Tujunga Can.		1/12/68		6/5/78	10½ "	Monocarpic
2A	Nacimiento Rd.	1-2 yr. transplant		8/13/71	/ /77	7 8 "	Monocarpic
2A*	Rancho Santa Ana		1971?	7/5/73	None*	d. heart rot, 5 left, 1982	Monocarpic
2A*	Altadena		9/30/71		None*	d. heart rot, 0 left, 1982	Monocarpic
3A	Reservoir Can. San Luis Obispo		9/25/69	8/20/71	7/?/77	8 years	Rhizomatous
3A	Roscoe Blvd. Burbank		10/22/67	5/8/68	4/18/74	7½ "	Mixed Habits
Pre-I	Sandyland	9/6/69	10/16/69	8/20/71	4/26/78	8½ "	Rhizomatous
Pre-I	Cuyama Gorge	9/6/71	9/15/71	1/27/77	died (only 1)	too much shade?	Rhizomatous
3B	Kaweah River	7/3/71	9/28/71	1/10/79	None in 10½ yr.		Monocarpic
2B	Devil's Punch Bowl		12/8/67	7/10/73	5/?/82	15 years	Caespitose
2B	Cuddy Valley		3/2/68	7/1 9/71	None in 14 yr.		Caespitose

\* Because of nearby overhead sprinkling in the park, Ssp. Parishii plants suffered virtually 100 % Mortality during 10 years, including replacements from Rancho Santa Ana. Plants became suddenly susceptible to heartrot after a spurt of growth and enlargement of rosette base on approaching maturity, or even earlier.

annual season of plant growth prior to flowering? To promote earliest possible flowering commensurate with rising spring temperatures, coming latest in regions where a mild winter growing season is unlikely, the plant must store up sufficient photosynthate products to last through winter. The surplus then supplies an abundance of energy for bolting the large flowering panicle as soon as air and leaf temperatures make rapid growth possible. This interpretation was indicated by the late May-June-July flowering season and by the morphology of these Series 2A and 3B yuccas. Not only did they have the greatest numbers and largest leaves in a rosette, but also the thickest rosette base--a huge, pithy, bulbous trunk to which the leaves were attached in spiral ranks (Appendix A), a typical compensation of shade plants to low light intensity (Whitehead, 1973).

These trunks and fleshy leaf bases stored nearly all the nutrient energy needed for production of the gigantic flower stalks produced by Series 2A-3B yuccas. Early in May following the Big Tujunga fire of 1975 and a winter of abundant precipitation in the San Gabriel Mountains, hundreds of scorched yuccas, nearly leafless since the previous November, put on a spectacular display of normally developed flowering panicles (R. A. Minnich, personal communication, 1976; my field notes, 1968-1980). Stalk and flower primordia had been protected within the growth bud buried in the heart of the rosette base, insulated from heat and freezing weather by layers of fleshy leaf bases. Along margins of the burn, many of the yuccas were pollinated by surviving Tegeticula moths to produce fertile pods the next fall. A rainstorm in early November, 1975, before the fire, may have stimulated many moth larvae to bury themselves (Powell and Mackie, 1966) and so survive the fire.

To store large quantities of photosynthate, equivalent to the energy needed for plants to produce panicles 3 to 6 meters high, weighing 2 to 9 kilograms, would require excessive amounts of starch. Many leaves were needed to produce such a reserve; but the production of numerous large leaves and the big storage base supporting them also required many more hours of photosynthesis, apparently, than could be had in a few summers. In the experimental garden, large-based Series 2A-3A plants (Ssp. Parishii and Ssp. percursa) bloomed 2 to 3 years later in their life cycles than did the small-based rosettes of Series 1 (Ssps. intermedia and typica), (Table 21; Fig. 1,3). In studies of crop monocots Aitken (1974) found that the larger the normal vegetative portion of a plant, the longer was the developmental period prior to flowering, and often the greater was the total seed production per plant (also Evans, 1973, and Whitehead, 1973). Size of flowering rosette and percentage of flowers resulting in seed production were correlated positively also in Y. whipplei as observed by Schaffer and Schaffer (1979) and myself.

In Y. whipplei with maximum-sized leaves and thick-based rosettes, i.e., Series 2A and 3B populations, environmental conditions were typical of coast-facing slopes at middle elevations of the highest interior ranges of mountains in central and southern California. Runoff from snow and rain at high elevations in the spring, and also late summer thunderstorms, make the spring-summer growing season relatively mesic in these mountains, with warm daytime temperatures conducive to rapid vegetative growth (Fig. 28, 29, 30). Fairly large diurnal changes in temperature during the growing season also may have favored growth rate (Endler, 1977; Chang, 1968; Hiesey et al., 1971).

However, plant growth in winter, early spring, and late fall would have been inhibited greatly in the canyons by drainage of cold air from higher peaks causing a shortened effective growing season even below the snow line (Geiger, 1973, pp. 393-418). In certain tropical grasses cold night temperatures inhibit the nightly respiration and translocation of starch produced during daylight, and this fact results in damage to the chloroplasts by accumulated starch in the leaves (West, 1973). Yucca whipplei, as a sub-tropical plant, may be similarly damaged in diurnally variable climates. Occasional snow at 1220 meters (4,000 feet) or below and frequent cloud cover in the mountains also reduce total photosynthetic energy available for effective growing period. In many sites, these Series 2A-3B yuccas compete for light with high chaparral on the slopes, or in riparian broadleaf and conifer ecotones of steep canyons, or in relatively open pine and pine-fir forests of the southern ranges, resulting in restricted light energy for photosynthesis.

Shortness of effective growing season also figured importantly in Series 2B yuccas (MORPH VIII, IX), but in quite different ways from Series 2A-3B. Series 2B locations usually had not only a severe winter season, during which little vegetative growth was possible, but also the handicap of a very hot, dry, and relatively long summer. As observed in the test garden, most growth in Ssp. caespitosa occurred during the short wet seasons of spring and fall. During the coldest weeks of January, February, or March when snow might cover the high desert, and when cold night air flowed from the bordering mountains, rate of metabolism on which growth depended would have been diminished (Bierhuizen, 1973; Geiger, 1973, pp. 453-461; West, 1973). In recent

years snow on the high desert sometimes lasted a week at a time, and evidence of water frozen in the ground nightly also was seen in *Ssp. caespitosa* ranges, e.g., near Gorman, Mt. Piños, Mt. Frazier, western Antelope Valley. In mountainous areas infrequent snow occurred as late as April of coldest years, and flowering was delayed until May, June, or mid-July even in the desert, e.g., Cajon Pass or Ridge Basin (Webber, 1953; Powell and Mackie, 1966; my field notes, 1968-1980.)

Studies of many other kinds of plants by physiologists have indicated results that were parallel to relations observed between xeric climates and morphology of Series 2B yuccas and their frequently caespitose habit, composed of numerous stiffly erect, few-leaved rosettes. Erect-standing leaves were less liable to be overheated by the sun than horizontally spreading leaves (Shaver, 1973; Evans, 1973). Decrease in water loss by evapotranspiration was correlated with narrow thick leaves of very low leaf surface-area-to-volume ratio (Rost et al., 1979, pp. 102-103, 174-175). Maximum rate of photosynthesis increased linearly with leaf thickness, and the thick-leaved sun species studied invariably had higher saturation levels, i.e., greater tolerance for intense light, than had shade species with thin leaves (Chang, 1977). Sunken stomates and thickened cuticle further cut down on water loss and are common attributes in xeric plants, including yuccas (Rost et al., 1979, Fig. 5.7, p. 102). High insolation often results in a proliferation of vegetative branching in monocots (Evans, 1973, p. 24), and so accounts for caespitose habit in numerous alpine and desert plants.

The dense caespitose mounds of yucca rosettes effectively shade a

relatively large ground area and protect it from drying rapidly. Also, numerous densely growing rosettes reduce risk of a catastrophic loss of potential flowering branches due to accident, dessication, grazing, and freezing. Usually in plants of Ssp. caespitosa (Series 2B) several rosettes bloom in a single season over a number of weeks (Haines, 1941; Webber, 1953). Normally at least one of these stalks coincides with moth emergence and produces some fertile seedpods, but frequently no fertile pods form on any of the panicles (Webber, 1953; Powell and Mackie, 1966; Hoover, 1973). Flower stalks and rosette bases of Ssp. caespitosa generally are not very large compared with other Y. whipplei subspecies (Appendix A), (Haines, 1941, Fig. 3, 4).

The long dry summers in the desert and in dry, but foggy, southwestern coastal areas provide adequate time for seeds to ripen, however late the plants may have bloomed, but conditions for seedling survival in most years are poor (Hoover, 1973). Rhizomatous or caespitose habits and leaf morphology of low surface-to-volume ratio in Series 2B provide features for survival of maturing plants and for a continued flowering potential. They allow reproductive populations to persist between the relatively few years in hot or cold desert or foggy, dry, coastal areas when successful flower and seed production in spring is followed by good germination and seedling-survival conditions in the next growing season or two. Caespitose Series 2B yucca plants in the experimental garden did not flower until the fourteenth year after they were sown, but individuals of each other surviving Series, habit, and subspecies tested already had bloomed previously. Rhizomatous Ssp. percursa plants of pre-series and Series 2A from Santa Barbara and Series 3A from San Luis Obispo first flowered at ages between

eight and ten years (Table 21).

B. Correlation of Stalk Size with Size of Leaf Rosette  
in Yucca whipplei

Correlation between fruiting stalk size and leaf area or volume was high, but it was unknown whether nutrition necessary for rapid bolting of a large flower stalk came only from a single leaf rosette basal to the stalk or if additional nutrition was supplied by the other non-flowering rosettes of a multibranch habit (Nobel, 1977). Stalk diameter generally was proportional to panicle size. Pearson's product-moment correlation coefficients ( $\underline{r}$ ) were computed between climate rank, stalk diameter, area and volume of single largest leaf, total leaf area and volume of single largest rosette, and total leaf volume or area of the whole plant (Table 22).

High coefficients of correlation existed between stalk diameter and total leaf volume of a single rosette (0.81) and total leaf area of a single rosette (0.77). These two coefficients showed that size of a single rosette, not of the whole plant (Total area:  $\underline{r} = 0.03$ ; total volume:  $\underline{r} = 0.03$ ) was best correlated by far with flower stalk size in Y. whipplei. Nutrition for stalk production apparently was not contributed by the connected rosette branches to improve stalk size, for stalk diameter was negatively correlated with number of rosettes per plant ( $\underline{r} = -0.28$ ).

Correlation of some plant variables with stalk diameter increased in the following order: number of rosettes per plant, total plant leaf volume, total plant leaf area, single leaf area, percentage of plants

Table 22. Correlations of Stalk Diameter with Morphological Traits and Climate in Series of Y. whipplei

Compared Variables	All Series Combined			Series 1			Series 2A-3A			Series 2B		
	r	Rank	p	r	Rank	p	r	Rank	p	r	Rank	p
MORPH	0.52	7	0.00	-0.23	7	0.03	0.46	7	0.00	0.15	11	0.07
Climate Location	-0.49	10	0.00	-0.19	9	0.07	-0.45	9	-0.00	0.18	9	0.04
Minimum Climate	-0.51	8	0.00	-0.43	5	0.00	-0.63	5	-0.00	0.30	6	0.00
Area/Volume of Leaf	-0.50	9	0.00	-0.01	14	0.47	-0.45	10	-0.00	0.22	8	0.02
DRI	0.55	6	0.00	-0.11	12	0.19	0.55	6	0.00	0.22	7	0.02
Rosette Number	-0.28	13	0.00	-0.21	8	0.05	-0.27	13	-0.00	0.16	10	0.06
Base Diameter	0.86	1	0.00	0.73	1	0.00	0.81	1	0.00	0.64	1	0.00
% Bases = 10 cm	0.47	11	0.00	0.33	6	0.00	0.42	12	0.00	0.39	5	0.00
% Bases X Base Diam.	0.74	4	0.00	0.51	2	0.00	0.67	4	0.00	0.48	4	0.00
Leaf Surface Area	0.42	12	0.00	-0.16	11	0.10	0.45	11	0.00	0.02	15	0.41
Leaf Volume	0.58	5	0.00	-0.17	10	0.10	0.54	8	0.00	0.11	12	0.14
Rosette Area	0.77	3	0.00	0.46	4	0.00	0.76	3	0.00	0.60	3	0.00
Rosette Volume	0.81	2	0.00	0.47	3	0.00	0.78	2	0.00	0.61	2	0.00
Total Area Plant	0.03	14	?	-0.01	15	0.48	0.02	15	0.43	0.05	14	0.32
Total Volume Plant	0.03	15	?	-0.01	13	0.46	0.06	14	0.27	0.07	13	0.25

Number of Samples, N = 281.  $2 \leq$  Sample Size  $\leq$  30; Average Size = 10. r = Pearson's Correlation Coefficient, of Sample mean values. p = probability level of significance.

MORPH = Morphological Type of Y. whipplei sample. Stalk Diameter measured 1 m from the top of base. Climate of Location of Sample and Minimum Climate of Sample are ranked climate subzones (Sunset, 1976) increasing in order of favorability to tropical kinds of plants. Minimum Climate is the severest climate zone neighboring the sample location. Area/Volume = Ratio of largest leaf of largest rosette. Base Diameter of Rosette. Rosette Area = Leaf Area X Leaf Number per Rosette. Rosette Volume = Leaf Volume X Leaf Number per Rosette. Total Area of a Plant = Rosette Area X Rosette Number per Plant. Total Volume of Plant = Rosette Volume X Number of Rosettes per Plant.

with enlarged rosette bases, leaf area/volume ratio, developmental rank index (DRI), and single leaf volume. Highest correlation with stalk diameter was with the index of combined percentage and diameter of enlarged rosette bases, total leaf area of a rosette, total leaf volume of a rosette, and diameter of a rosette base, increasing in that order (Table 22). Coefficients of correlation also were tabulated for three Series separately (Table 22).

A theory based on the energetics of pollinator relationships to size of panicles in Y. whipplei (Tegeticula moths) and in other agavaceous species (bees and flies) has been advanced by Schaffer and Schaffer (1979). Although pollinator preference--or rather acuity of recognition and minimal energy expenditure by pollinators--for largest flowering panicles indubitably was a driving force in evolution of maximal reproductive expenditure in various large semelparous (monocarpic) plants, it did not account for the significant differences in size between monocarpic populations of Ssp. Parishii and Ssp. typica. The Schaffers' studies of pollinator relationships in Y. whipplei did not consider that Y. whipplei plants with multiple rosette branches and comparatively large panicles flowered repeatedly, not just one time before dying--contrary to the stated theoretical assumptions (Schaffer and Schaffer, 1979).

### C. Chapter Summary

Probably the various sizes of leaves and leaf rosettes in Yucca whipplei evolved according to length and timing of the effective growing season and of seed-productive periods available in locations where

yuccas survived. Amount and rate of successful reproduction by means of seedlings determined inversely the length of life cycle and also the growth form as expressed by number of potentially flowering rosettes per plant. Number of rosettes per yucca in turn often affected rosette size inversely (Table 22), (Hoover, 1973). Differing length and onset of annual growing season and relative favorability of environments for reproduction by seed corresponded with several distinct patterns of morphology and habit in populations of Y. whipplei.

(1) Where a Mediterranean climate with mild winter temperatures and sunlight with associated periods of adequate rainfall provided annually a long pre-flowering growing season, flowering was early in spring and early in the plant's life cycle. This rapidity of flowering under benevolent growth conditions resulted in a relatively short life span because the total plant or flowering rosette died soon after fruiting. Abundant photosynthesis prior to early flowering provided energy directly usable for reproduction in areas of mild winter temperatures because of small net losses to respiration in short non-growing seasons. With early plant maturation and seed production and an environment conducive to successful germination and survival of seedlings, comparatively small fruiting panicles and small energy-storage organs were sufficient to maintain a sexually reproductive population. Thus single-rosette plants of small to moderate size were typical in some pre-series and many Series 1 and 3A populations.

(2) But if inadequate sunshine with freezing winter temperatures limited growth in winter and shortened the flowering and seed-ripening period, energy storage became necessary, even though mesic spring and summer conditions were favorable to annual growth and survival of new

seedlings (Raunkiaer, 1934). Energy storage required more and larger leaves, larger food storage organs, and consequently a longer juvenile vegetative stage than in short-cycle plants. Loss of stored energy to respiration in non-growing seasons delayed accumulation of sufficient energy for flowering. In compensation for delay of several years before flowering and as a result of large amounts of stored energy, the predominantly monocarpic yucca plants produced seedstalks much larger than the average. Correspondingly high numbers of fertile seedpods possibly resulted from pollinators' reluctance to travel needlessly, or higher visual or odorous detectability by pollinators, as observed by Schaffer and Schaffer (1977). Features of large size were most advanced in Series 2A and 3B regardless of growth form in individual plants, and that (habit) often was mixed within a single population sample.

(3) In areas with great extremes in seasonal temperatures, and a short period of available soil moisture attributable to long dry summers and low winter precipitation, the need for efficiency in photosynthesis, for conservation of moisture, and for repeated flowering in a climate hazardous to seedling survival, resulted in greatest expenditure of energy for adaptive specialization of yucca plants. In Series 2B increased leaf thickness and erectness resulted in maximum efficiency of photosynthesis and least water loss by evapotranspiration in xeric climates. The photosynthetic adequacy of a few thick erect leaves per rosette was due to more efficient photosynthesis and reduction of overheating and chlorosis by strong sunlight. In cespitose habit, size of rosette usually was reduced in favor of increased number as was true of rhizomatous habit, either of which was

common in Series 2B populations; size of flower stalk usually also was somewhat reduced. In some Series 3A or 3B populations however, commonly at moderately high elevations with relatively high seasonal precipitation, great leaf size was combined with moderate or high numbers of leaf rosettes and huge flower stalks in iteroparous caespitose plants, e.g., Hasley Canyon, Frenchman's Flat, Live Oak Flat, Charlton Flat (Appendix A). On the other hand, in xeric regions of fairly severe climatic extremes with nevertheless sufficient summer rainfall to main young seedlings, populations of Series 2B occurred with monocarpic habit predominant--e.g., *Ssp. newberryi* along the Colorado River canyon and so-called *Ssp. typica* in the eastern Santa Rosa Mountains--or with habit mixtures like those of *Ssp. intermedia* (e.g., Mill Creek).

(4) A long, mild, winter growing season in regions along the coast with fairly high atmospheric humidity but moderately low winter rainfall and arid soil in summer seemed in some areas to reduce effective seed production or germination and survival of seedlings, i.e., in *Ssp. percursa* (Hoover, 1973). Vegetative survival and reproduction by rhizomes predominated over seedling production for several years at a time in these populations. The vegetative period eventually was followed by seasons of high seedling production due to cyclic climate changes. Longterm climate changes accompanying seaward retreat of the shoreline and coastal uplift during the Tertiary and Quaternary apparently favored regeneration by seedlings in old rhizomatous populations (Fig. 4), (Hoover, 1973).

(5) The population differences of leaf and stalk morphology found in *Ssp. percursa*, i.e., populations of predominantly rhizomatous *Yucca*

whipplei, can be attributed to localized environmental conditions that varied in coastal situations according to the three alternative selective environments responsible for evolution of Series 1, Series 2A-3A, and Series 2B as described above. Coastal pre-series MORPH II represented the original Series 1 type and MORPH I represented the original Series 3A and 2A types. MORPH Va, Vb, and Vc apparently resulted from continued selection in the direction of either Series 2A or 2B, as existed in the more challenging interior or northern coastal areas while MORPH III and IV developed in the warm southern interior coastal areas that were most favorable to rapid growth and reproduction by sexual means.

## VI. SUMMARY AND CONCLUSIONS

The experimental and field work of this study were undertaken to clarify the causes of geographic relations between trends in various environmental factors and marked differences and similarities among large definable populations of Yucca whipplei. Differentiating characteristics among geographic populations of Y. whipplei existed in plant morphology, habit, and pattern of reproductive cycles. The objectives of this geographical study were to show (1) the geographical distribution of morphological variation in Y. whipplei and (2) the most likely causal relationships between gradients of different climatological factors and specific morphological trends or clines within the species. The geographic patterns of adaptation found in Yucca whipplei not only revealed some probable causes of geographical relationships but in so doing also illuminated possible evolutionary processes responsible for variation patterns in this complex species.

### A. Summary

To achieve objectivity in the ordination and classification of yucca morphology and of associated local climates, multivariate quantitative approaches were used. Several different methods of ordination and classification of Y. whipplei populations based on their chief distinguishing morphological characters were employed.

(1) Developmental Rank Index (DRI). This numerical index was

based on three dimensions of the largest leaf of the largest rosette of a yucca plant: the sum of standardized length and width and thickness at the midpoint. Ordination of DRI paralleled the sum of constructive genetic activity contributing morphologically to leaf development.

(2) Morphological Types (MORPH). These types of Y. whipplei were sorted visually by comparing scaled triangular diagrams of the sample means of three leaf dimensions in which two dimension ratios also were represented by slopes. Visual sorting resulted in differentiation of ten major groups of samples. These MORPHs were arranged in ascending order of a developmental sequence that corresponded to the simplest, most economical pathway by which the three major genetic lines of Yucca whipplei (Series 1, 2A, 2B) could have differentiated. MORPHs represented subdivisions of increasing developmental rank within each of the Series and their hybrids, Series 3A and 3B, and provided the most effective ordination of geographic populations according to their leaf morphology.

(3) Cluster Analysis and PRIM Networks. Computer programs for multivariate sorting were applied to 284 field samples of Y. whipplei based on mean measurements of 21 plant characters. Cluster analysis was employed to separate "natural" morphological groups objectively among the field samples from all California regions where Y. whipplei was native. Graph networks (PRIM) were produced by the same computer program used for cluster analysis. Cluster analysis and graph networks showed similar developmental patterns leading to the same three Series climaxes that were recognized previously. Cluster analysis tended to link together all the lower developmental stages with the

Series climaxes without differentiating well between the lowest evolutionary stages (MORPHs). Series climaxes were well differentiated, however.

(4) F-Order and t-Order Ratios. These ratios were a further development from Student's t-test and Snedecor's F-ratio and represented orders of significance (t or F divided by the appropriate critical ratio at the 0.95 probability level). Order-ratios were used as taxonomic distances to compare quantitatively the multiple phenotypic significant and insignificant differences between geographically or climatologically or morphologically defined populations. The use of t-order ratios between MORPHs provided an independent ordering of MORPHs in Y. whipplei and supported the same genealogy or phenotypic developmental pattern that other methods had revealed.

The climate gradient used for ecological comparisons was numerically classified by Sunset (1976) from modifications of the U. C. Extension plant climate area maps devised by Marston H. Kimball, former California Chief Bioclimatologist. This holistic gradient, based on favorability of climate for increasingly tropical crop plants, served to compare climate of sample locations by regression with sample means in MORPHs of traits studied in Y. whipplei. Maximal variability or severity and aridity of climate with high insolation coincided with maximum leaf thickness in sample means. Mildness, i.e., equability and warmth, of climate with wet winters and moderate insolation due to humidity or shade coincided with increased length of thin leaves. Relatively mesic warm summer climates with moderate to extreme winter variability and severity combined with limited insolation were associated with maximal leaf width, length, and area. Other

holistic climatic gradients based on sequences of vegetation types were less effectively coordinated with morphological clines than were the plant climate areas and indicated instead a primary importance of paleogeographic floristic associations.

Published temperature, precipitation, frost, snow, and evapotranspiration data from weather stations nearest localities where the yucca field samples grew were averaged for each of the MORPHs and were compared for common differences and exceptional cases. MORPH II was considered the most primitive, or least developed, origin of the other morphological types or Series of Y. whipplei. The averaged climatic factor differences between each other MORPH and MORPH II formed definite yucca clines and climatic gradients associated with the selective evolution of each of the three different major Series of Y. whipplei radiating from pre-series MORPHs I and II.

Series 1 of Y. whipplei occurs in regions of mildest sunniest climates with long dry summers but longest, sunny, moist, fall-winter-spring growing seasons, and with probable partial shading due to air humidity and to plant competition. Series 2A occurs in regions of relatively extreme and variable seasonal temperatures, but with a warm and mesic, spring-summer-fall growing season and a distinct limitation of annual availability of sunshine. Series 2B occurs in desertlike regions with the greatest annual variation in mean temperatures, the most severe summer drought, the shortest, wet, growing seasons, and highest annual availability of intense sunlight. Series 2B experienced the least effective energy resources because of shortness of its active growing season, limited by both drought and winter cold to spring and fall.

Some experimental studies were undertaken in connection with this research. Seedlings from all three Series of Y. whipplei were raised under different germination and growth conditions; also comparative analyses of morphological differences in these yucca seedlings and wild field samples clarified the selective importance attributable to shade and sunlight. Availability of sunlight and length of effective growing season determined the northern latitudinal geographic limits of Y. whipplei between  $36^{\circ}30' N$  and  $36^{\circ}50' N$  latitudes.

Regressions and scattergrams between climatic factors and morphological traits and types of Y. whipplei elucidated some causal relationships between environmental conditions, differences in effective growing season, and morphological variation. Maximal leaf area of largest rosette increased the potential photosynthesis of a plant in areas where effective illumination was limited by universal sunscreens such as snow, fog, clouds, or shading by competitive vegetation. Increased leaf thickness reduced leaf area-to-volume ratio and resulted in diminished evapotranspiration in areas of extreme desiccation and also protected leaves from overheating and chlorophyll burnout in strong sunlight by allowing an erect posture. Minimal leaf thickness and width but varying leaf length in Series 1 corresponded with rosettes of relatively low leaf volume and total photosynthetic area in regions of optimal conditions for photosynthesis and of rapid reproduction by seedlings or rhizomes. Reduced size of rosette bases and of fruiting stalks correlated with reduced photosynthetic area and volume of leaf rosettes in Series 1 but were adequate for early reproduction because of long, favorable, winter, growing seasons.

Series 2A found in mesic moderate climates of variable seasons

exhibited maximal leaf area per flowering rosette to compensate for a photosynthetic energy shortage caused by a relatively short, effective, annual season for growth prior to flowering. Series 2A during a prolonged period of juvenile growth produced long-lived many-leaved rosettes with large nutrient storage bases and correspondingly huge fruiting panicles to compensate for delayed maturation. Monocarpic plants often predominated in Series 2A because of mesic summer conditions suitable to seedling growth and survival, but rhizomatous (*Ssp. percursa*) or mixed-habit Series 2A and 3A populations were also common.

Series 2B in California generally had the slowest maturation of all, with many small leaf rosettes and comparatively small but numerous fruiting panicles formed per plant in its usually cespitose or rhizomatous populations. Several small flower stalks formed on a plant in a season, compensating in part for maximal delay in plant maturation and for hazardous climates with extremely limited annual growing seasons, frequently unsuited for seedling production and survival. However, highly monocarpic Series 2B populations known in the San Gabriel and eastern Santa Rosa mountains and in northwestern Arizona (*Ssp. newberryi*) indicated that in arid regions of strong sunlight and limited seasons for winter growth, but with slight yet significant summer rainfall, Series 2B morphology was developed independently of a multiple-rosette habit.

## B. Conclusions

The evolution of morphological variation of Yucca whipplei and the geographic distribution of variant types was found to coincide predominantly with the comparative length of suitable annual growing seasons prior to flowering and with the degree of effective annual insolation or photosynthetic energy available to plants in each geographic area. Effective insolation was determined not only by factors directly interfering with sunlight incidence, but also by factors such as precipitation and freezing temperatures that controlled the onset and termination of growing periods for plants.

In general, the earlier and greater was the annual effective energy available per growing season, and the longer the following dry season for seed development, the more rapid was the sexual maturity of plants, and consequently the lower was the total amount of energy required for "reproductive effort" per plant, even if the total plant died after fruiting. The smaller was the annual effective energy available for photosynthesis by a plant, the longer was the delay in plant maturation, or flowering, and consequently the larger was the eventual compensatory expenditure of energy required for perennialism and for total reproductivity per plant to maintain a population.

In areas of somewhat limited effective energy but with sufficiently mesic summer conditions favoring reproduction and establishment of seedlings, maximal size of the seed-producing panicle was selected, and few (or one) such large flowering rosettes were required for adequate reproduction by a plant. In areas of comparatively low effective energy that also were unfavorable for seed production or

seedling establishment or both, perennialism compensated for few seedlings, as in caespitose or rhizomatous habits. High numbers of fruiting panicles per plant per season reduced the risk of seed loss caused by unseasonable weather during reproductive periods, and compensated for long delay in plant maturation. Minimal leaf surface-area-to-volume ratio in unfavorable regions provided maximal photosynthetic efficacy in compensation for shortness of effective growing season and for extremely high insolation.

Combined energy effects and conditions of seasonal climates therefore were responsible for selection of the reproductive systems or "strategies" in populations of Y. whipplei and for variation in their morphological attributes by virtue of growth-rate energetics and reproductive efficiency. Due to various seasonal climate patterns in different areas, these two results did not always coincide, and this fact accounted for a relatively independent occurrence of predominant habit and of leaf rosette and stalk size. The abrupt northern latitudinal range limit of Y. whipplei also indicated the importance of energetics of photosynthesis to reproduction in the evolution of Yucca whipplei.

Taxonomically the findings reported above apparently justify retention of both growth habit and morphology in the differentiation of subspecies of Y. whipplei because significantly definable combinations of these attributes characterize large geographic populations. However, the occurrence of various habits within populations of each morphologically defined Series indicates that plant habit is more variable and less conservative as a taxonomic character than is differentiation by leaf and rosette morphology. It is projected that taxonomic

treatment of Y. whipplei should designate within each of three or five Series--counting the transitional or hybrid Series--various geographically defined subspecies based on locally predominant growth forms. Whether the major Series finally should receive taxonomic status as separate species will depend on results of interbreeding experiments and other studies. Taxonomic treatment of the variation in Yucca whipplei Torr. will be published elsewhere.

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Appendix A. Mean Measurements of Field Samples of Yucca whipplei, Grouped by Morphological Similarities

MORPH- OLOGICAL TYPE	Location of Sample  Pre-Series	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identifi- cation *
		Length	Width	Thickness					
	Camarillo								
I	Summit E Hospital	49.21	0.90	0.20	189	2.6	146	7.8	80G7
I	W Camarillo Hospital #2	42.62	0.92	0.22	205	2.3			81G8
I	E Camarillo Hospital	51.60	0.86	0.20	188		168	13.9	82G16
I	W Camarillo Hospital #1	42.52	0.81	0.22	194		140	12.0	83G30
I	Fillmore, Sespe Cr. #1	50.73	1.03	0.21	204		160	12.2	84G26
I	Hwy. 33, Cherry Cr.	38.67	1.17	0.22	226	7.5	450	15.5	54Q3
I	Hwy. 150, Ojai Pass	30.33	0.77	0.21	167	3.1	203	10.0	55Q3
I	W Matilija Lake	41.58	1.15	0.20	207	5.0	362	12.7	60Q6
I	Hwy. 33, Sespe Gorge	39.10	1.18	0.23	237	3.9	344	10.8	61Q5
I	Summerland, Sta. Barb. Co.	46.44	1.17	0.20	213	5.5	349	16.8	53Q16
I	N Matilija Lake	47.57	1.13	0.21	221		299	10.3	64Q21
I	S Cuyama River Gorge	40.29	0.99	0.21	199	4.8	454	15.4	50U7
II	W Rainbow Glen #2	61.80	0.64	0.17	146	3.4	256	10.2	53E5
II	Pauma Valley	59.13	0.85	0.18	174	4.2	441	13.2	56E15
II	WNW Red Mt., San Diego Co.	56.92	0.57	0.17	134	3.3	216	10.5	57E12
II	San Onofre	74.43	0.88	0.19	202	4.3	203	12.0	60E7
II	Via Loma SUN, Fallbrook	55.00	0.77	0.19	162		173	10.0	81E15
II	De Luz-Murrieta Road	54.80	0.57	0.16	122	4.0	397	8.3	83E5
II	W Rainbow #1	60.58	0.71	0.18	162		200	12.0	85E6
II	W Lassen St. Chatsworth	50.42	0.82	0.19	172	2.2	172	9.7	50G12
II	N Zelzah Av., Northridge	57.20	1.73	0.17	190		166	13.4	56G25
II	Bardsdale #1, Ventura Co.	71.00	0.95	0.18	196	1.8	198	9.8	60G11
II	Steckel Park, Ventura Co.	67.45	0.99	0.17	186	2.2	134	10.0	64G11
II	N Simi Pass, Chatsworth	70.68	1.13	0.19	114		118	10.7	89G31

\* Identification Number = Acquisition Order, of Letter Region, Number of Plants in Sample.  
! Cr. = Creek. # = Number. Co. = County. W, E, N, S = Cardinal compass points.

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Pre-Series, Series 1	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification
		Length	Width	Thickness					
II	Dulzura-Barrett Road	72.50	0.84	0.17	176	3.9	170	14.0	51N4
II	San Marcos Pass #2, Goleta	47.38	1.04	0.19	191		277	12.0	51Q13
II	S Buellton, E Hwy. 101	41.00	1.03	0.17	164	3.8	301	11.2	56Q7
II	S Buellton, W Hwy. 101	46.90	0.94	0.19	181	3.5	316	12.1	62Q5
II	San Marcos Pass #1, Goleta	41.87	1.01	0.19	183	5.2	177	11.8	62Q8
II	E Nojoqui Park, Sta. Ynez	56.64	1.16	0.16	173		267	11.1	52Q11
III	Cold Cr., Maynard Dr.	62.92	0.81	0.21	204	2.3	148	9.2	53A13
III	Griffith Park, SUN	68.25	0.79	0.22	217		233	10.8	59A16
III	Liberty Canyon, Calabasas	62.44	0.85	0.20	197	1.6	232	9.7	63A16
III	Cold Cr., Canyon #2	78.11	0.91	0.21	229	1.9	158	10.0	72A7
III	Piuma Rd., Malibu #2	77.07	0.77	0.22	224	4.3	214	12.0	73A7
III	Mulholland Dr., Calabasas	72.07	0.68	0.21	200	2.8	216	12.3	77A7
III	Summit Topanga Can. Road	72.30	0.66	0.21	198	3.1	241	11.6	78A5
III	S Hwy. 101, Kanan Rd.	72.25	0.76	0.26	258	2.4	150	9.8	78A6
III	N Hwy. 101, Kanan Rd.	71.67	0.79	0.25	251	2.1	154	9.2	79A6
III	Hwy. 1, N La Tuna Canyon	66.00	0.87	0.25	253		217	16.1	82A8
III	Mulholland Pl., W Hwy. 5	76.35	0.77	0.24	243		190	11.0	82A17
III	Summit Scheuren Rd., Malibu	64.08	0.86	0.22	220		145	11.0	86A13
III	Mission Rd. #1 SUN Fallbr'k.	60.30	0.76	0.24	226	4.0	278	9.8	50E10
III	Mission Rd. #2 SUN Fallbr'k.	58.57	0.65	0.22	194	3.6	283	11.3	51E7
III	Mission Rd. #1 SHADE	76.25	0.84	0.23	240	2.8	258	11.0	52E8
III	SE Rainbow, San Diego Co.	59.19	0.79	0.21	198	3.7	350	9.5	54E7
III	E San Pasqual, San Diego Co.	69.44	0.92	0.21	221	6.6	309	13.0	55E9
III	SE Vail Lake, San Diego Co.	68.50	0.89	0.20	207	5.2	372	14.0	56E5
III	Red Mtn. Fire Sta., SUN	68.89	0.74	0.23	223		333	10.8	59E9
III	Santiago Can. N Modjeska	68.61	0.95	0.22	234	3.9	300	12.4	61E14
III	N Alberhill, Elsinore Lake	66.92	0.89	0.23	236	4.8	329	11.6	64E13

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 1	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification
		Length	Width	Thickness					
III	Valley Center, S. Diego Co.	55.86	0.76	0.23	212	4.8	373	10.6	79E7
III	Mission Rd., Hwy. 395 SUN	55.87	0.71	0.24	207		231	14.0	84E15
III	Newberry Park #2	64.08	0.84	0.24	238	2.7	196	11.3	58G13
III	Newberry Park #1	62.23	0.85	0.24	237			14.4	58G22
III	Pt. Mugu, L. Syc. Can. WNW	59.00	0.98	0.22	227	2.8	165	9.1	74G12
III	Pt. Mugu, L. Syc. Can. SSW	55.77	0.92	0.21	208	2.4	196	9.6	75G11
III	NE Moorpark, Ventura Co.	72.45	0.98	0.20	220	2.4	185	10.8	63G11
IV	N of St. Mary's College	95.22	0.90	0.22	291	3.3	171	11.8	50A9
IV	Mulholland W Westlake Blvd.	83.67	0.96	0.25	280	3.8	128		51A9
IV	Mulholland S Calneva	107.44	0.78	0.24	275	2.6	243	11.0	52A9
IV	Hwy. 1, Encinal Can.	84.45	0.97	0.26	291	4.2	208	11.9	54A11
IV	S Malibu Lake	90.00	0.78	0.23	248	2.6	176	10.7	55A12
IV	N Stunt Can., Mulholland	84.82	0.76	0.21	240		203	12.1	56A11
IV	Mulholland, Decker Can.	88.83	0.92	0.26	291	2.6	173	9.2	57A6
IV	Griffith Park SHADE	126.50	0.86	0.27	332		140		58A4
IV	Hwy. 1 W Topanga Can.	82.35	0.96	0.24	268		300	13.9	60A20
IV	Upper La Tuna Can. SHADE	119.17	0.92	0.22	281	4.2	193	13.7	61A6
IV	Will Rogers State Park #1	92.63	0.85	0.25	278	3.9	232	11.6	62A8
IV	Moraga Golf Range, Hwy. 5	97.40	0.87	0.23	264	3.9	236	10.6	63A10
IV	Broad Beach Rd., Trancas	83.86	0.89	0.23	253	3.0	209	9.4	64A11
IV	Will Rogers State Park #2	92.27	0.90	0.21	242	4.5	218	14.0	65A11
IV	Abargo St., Woodland Hills	86.23	0.66	0.22	222	2.5	139	8.3	66A11
IV	Cold Creek Canyon #1	91.60	0.89	0.23	261	3.2	146	10.5	74A5
IV	Kanan Rd, 1 mi. N Hwy. 1	85.75	0.91	0.23	257	2.8	237	11.5	77A6
IV	Forest Lawn, Griffith Park	122.30	0.74	0.23	276	2.6	107	10.0	80A15

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 1, 2A	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification*
		Length	Width	Thickness					
IV	NW Pepperdine Univ. SHADE	106.17	0.83	0.24	269	2.4	180	10.0	81A3
IV	Summit Scheuren Rd. SHADE	105.00	1.04	0.23	289		189	22.5	87A7
IV	Red Mtn. Fire Sta. SHADE	83.00	0.73	0.19	186		284	12.0	58E14
IV	W Via Loma #2 SUN	82.90	0.81	0.19	238	3.6	252	12.0	62E10
IV	W Via Loma #2 PART SHADE	90.00	0.88	0.21	204	4.3	336	11.7	63E10
IV	W Via Loma #2 DEEP SHADE	101.23	0.78	0.22	249		220		65E13
IV	W Via Loma #3 PART SHADE	88.92	0.92	0.20	231		230	10.0	82E13
IV	Ehrenberger, Santa Paula	93.64	1.05	0.20	249	2.1	179	9.4	54G11
IV	Tapo Can., N Simi Valley	77.70	0.96	0.24	264	2.1	178	9.5	59G10
Va	San Raphael Hills, L.A.	85.20	1.14	0.22	269		192	12.3	83G24
Va	Ganahl Ranch, Corona	74.75	1.10	0.26	295	4.6	230	14.0	60E14
Va	San Raphael Hills #3, L.A.	80.31	1.11	0.22	261	4.0	240	14.4	77G8
Va	Fillmore #2, Sespe Creek	70.83	1.12	0.21	243	2.8	179	10.4	84G6
Va	San Raphael Hills #2, L.A.	89.75	1.19	0.22	279		242	18.3	85G7
Va	Porter Ranch #2, L.A.	70.29	1.21	0.24	281	3.5	179	10.0	84G8
Va	Porter Ranch #1, T #2 1	77.25	1.16	0.23	273		185	15.6	87G24
Va	Newhall Circle K Ranch	70.95	1.19	0.30	340		143	13.5	91G21
Va	NW Valencia, W Hwy. 5	70.43	1.15	0.28	315		160	0.0	92G3
Va	E Castaic Lake	73.33	1.10	0.28	313	3.7	207	10.8	94G6
Va	Hilltop, S. Fernando A.P. <sup>+</sup>	77.60	1.17	0.25	295		200	10.0	96G3

<sup>1</sup> T = Thickness. <sup>+</sup>A.P. = Airport. #1, #2, #3 = Additional studies in same area. S. = San. L.A. = Los Angeles. Univ. = University. Mtn. = Mountain. Sta. = Station. Can. = Canyon. Hwy. = Highway. cm = centimeters. \* Sample Identification; See p.

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 3A	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification*
		Length	Width	Thickness					
Vb	Lake Sherwood #1, #2 T	65.44	0.84	0.33	330		133	12.1	84A27
Vb	Mt. Pleasants, S. Anas	49.20	1.00	0.32	319	4.1	268	10.0	66E5
Vb	E Arroyo Grande Creek	59.50	1.06	0.32	236	4.8	279	17.1	52F10
Vb	NW Cal Poly U., S.L.O.	63.00	1.05	0.31	328		324	15.4	54F18
Vb	Perfumo-See Can. Summit	57.77	0.84	0.32	312	4.2	243	14.3	56F13
Vb	Dunes N Pt. Mugu St. Park	65.00	1.09	0.31	334		204	9.8	94G5
Vb	Wagy Flat, Greenhorn Mts.	45.90	0.81	0.32	297	3.5	156	10.3	59I10
Vb	NE La Panza Mts., Hwy. 58	51.30	0.99	0.32	320		302	14.2	52P10
Vb	Idyllwild Rd.	56.62	1.02	0.32	329	5.6	452	13.6	50S13
Vc	Thousand Oaks, S Hwy. 101	67.27	0.89	0.27	276	2.6	212	10.1	62A15
Vc	Sherwood Lake #2	83.93	0.87	0.32	341	2.8	182	9.0	83A7
Vc	Manchester Dr., Encinitas	62.95	1.05	0.25	268	6.2	355	12.4	78E10
Vc	San Elijo Lag., Encinitas	65.66	1.02	0.25	268		341		79E11
Vc	Summit Elsinore Grade	64.71	1.00	0.25	265	4.8	279	11.7	80E7
Vc	Mt. Palomar Rd., S.D. Co.	50.43	0.86	0.22	206		323	15.0	90E7
Vc	Cuesta Ridge Bot. Area	62.77	0.99	0.26	272	3.7	112	13.3	51F13
Vc	Atascadero Rd. #1, S.L.O.	55.44	1.05	0.30	310		261	11.2	53F16
Vc	Rigetti Ranch, E S.L.O.	62.88	0.93	0.28	286	4.2	276	14.9	55F13
Vc	Reservoir Can. #1, S.L.O.	61.95	0.94	0.29	296	4.0	324	13.8	57F10
Vc	Reservoir Can. #2, S.L.O.	62.31	0.86	0.29	288		284	16.2	57F13
Vc	W Cuesta Ridge Bot. Area	67.75	0.89	0.30	307	4.1	215	13.3	59F4
Vc	N Gate Pt. Mugu St. Park	43.80	0.99	0.25	243	3.2	176	10.0	51G10
Vc	Wayside Honor Ranch	69.33	1.00	0.28	299	3.2	197	11.4	52G15
Vc	Circle K Ranch, Saugus #1	70.46	1.05	0.29	315	2.3	192	11.4	51G13
Vc	Leo Carillo Beach N Gate	56.36	0.85	0.26	251	2.5	154	10.0	55G11

S.L.O. = San Luis Obispo. #1, #2 = Repeated studies in same area. S. = Santa. U. = University. Lag. = Lagoon. Can. = Canyon. Pt. = Point. Hwy. = Highway. Rd. = Road. Mts. = Mountains. Bot = Botanical.

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 2A	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification
		Length	Width	Thickness					
VI	Old Ridge Route, Castaic	59.18	1.12	0.26	281	2.8	221	12.3	62G11
VI	Almetz, Leedy, Sylmar	61.50	1.14	0.27	296	3.4	272	11.4	70G11
VI	Hwy. 39 E S. Gabriel Flt.	48.82	1.34	0.31	343	10.7	560	23.0	61H11
VI	Crystal Lake, Hwy. 39	58.75	1.45	0.31	364	7.0	402	19.7	62H12
VI	Mt. Manuel Tr., Big Sur	52.89	1.48	0.28	331	6.5	326	15.7	51L18
VI	Nacimiento Rd. #2	53.50	1.10	0.30	314	6.0	413	14.0	55L3
VI	Hwy. 1, 6 mi. S Big Sur	45.50	1.48	0.28	324	8.0	363	16.2	56L5
VI	Nacimiento Rd. #1, #2 T	47.23	1.13	0.28	290	5.2	600	18.4	47L23
VI	Waterman Can., S. Berdo.	56.70	1.10	0.27	287	5.6	374	14.1	50M10
VI	Below Running Springs	59.00	1.20	0.32	349	8.1	466	17.2	51M10
VI	Alpine, San Diego Co.	52.33	1.10	0.26	272	4.4	358	11.0	50N6
VI	Culp Val., Borrego Spr.	56.62	1.27	0.29	323	4.2	478	17.0	52O8
VI	Inaja Picnic Area	58.33	1.34	0.30	342	5.3	333	15.0	51O12
VI	Pena Spr., Borrego Spr.	53.67	1.13	0.29	307	6.8	343	16.6	53O18
VI	E Anza, W S. Jacinto Flt.	58.92	1.13	0.32	342	5.8	415	15.0	55O6
VI	S La Panza, Cuyama River	38.75	1.34	0.32	343	6.4	457	13.2	51P4
VI	E Huasna Flt., S.L.O. Co.	52.00	1.22	0.29	314	5.5	267	16.5	51P6
VI	Hwy. 33, Rose Valley Jnct	44.50	1.12	0.26	266	3.2	232	10.3	53Q8
VI	Hwy. 33, S Cherry Creek	31.00	1.15	0.32	316	4.8	490	13.2	58Q4
VI	Cuyama Gorge S side	53.00	1.34	0.25	295		200	10.0	51U5
VI	Cuyama Gorge S side, seed	49.33	1.61	0.22	280	4.0	450	25.0	52U3
VII	Padua Hills	66.29	1.61	0.26	337	5.9	576	20.2	52B17
VII	San Gabriel Res., Hwy. 39	80.00	1.71	0.20	301	6.9	439	17.4	53B9
VII	Sturtevant Falls	76.70	1.78	0.27	375	9.0	626	22.5	54B10
VII	Loma Alta, Lake, Pasadena	81.59	1.44	0.24	316	6.9	482	18.4	55B11

Val. = Valley. Spr. = Spring. Flt. = Fault. Hwy. = Highway. S. = San. Rd. = Road. mi. = miles  
 Res. = Reservoir. S.L.O. Co. = San Luis Obispo County. S.D. Co. = San Diego County. L.A. = Los Angeles.  
 Tr. = Trail. S. Berdo. = San Bernardino. Jnct. = Junction.

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 2A, 2B	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification
		Length	Width	Thickness					
VII	Big Tujunga Wash #4	71.88	1.46	0.31	378	7.8	396	18.5	57B8
VII	Anderson Study, S. Anita	74.93	1.89	0.27	384		347	14.7	57B14
VII	Big Tujunga Wash #1	75.24	1.64	0.32	409		260	17.5	58B17
VII	Angeles Crest 3,000 ft.	74.52	1.73	0.30	388		285	16.0	58B29
VII	Big Tujunga Wash #2	85.40	1.64	0.32	419		260	21.7	59B10
VII	Big Tujunga Foothill Bl.	78.79	1.65	0.31	404		408	36.0	60B24
VII	San Fernando Airport	72.90	1.28	0.27	321		280	14.3	57G20
VII	Top Haskell, La Canada	88.10	1.61	0.29	389	4.5	356	13.3	69G10
VII	Hillard Av., La Canada	70.57	1.31	0.25	302	4.3	240	13.8	72G7
VII	Descanso Pk., La Canada	83.00	1.25	0.28	338	5.2	232	17.6	73G5
VII	Las Tunas SUN, Verdugo	89.82	1.33	0.27	343		198	10.8	85G11
VII	Las Tunas SHADE, Verdugo	102.07	1.58	0.27	380		231	17.6	86G14
VII	N Balboa Bl. 88G6 T	66.92	1.26	0.24	282		215	17.1	89G13
VII	Clear Cr. For. Sta. SHADE	91.44	1.44	0.30	385		352	20.0	53H9
VII	Switzer Falls SUN	90.00	1.64	0.29	394	11.2	518	24.0	55H10
VII	Switzer Falls SHADE	64.00	1.45	0.26	319		323	16.8	56H6
VII	Los Padres Dam, S. Lucia	66.08	1.44	0.31	370	5.6	288	19.9	50L12
VII	Arroyo Seco, S. Lucia	62.57	1.47	0.28	340	7.1	402	19.7	56L7
VII	S Mountain Home	95.33	1.30	0.29	365	8.4	453	21.8	56M6
VII	Rattlesnake Can., S. Bar.	63.42	1.30	0.27	313	6.3	523	18.0	63Q6
VIII	Apache Summit, S. Emigdio	27.00	1.02	0.33	309	5.3	480	13.8	50D6
VIII	Quatal Can., San Emigdio	26.67	1.05	0.34	322	5.2	415	11.3	51D6
VIII	NW Mt. Frazier	37.20	0.84	0.34	311	4.4	285	11.4	53D13
VIII	NE Mt. Pinos, S. Emigdio	32.96	0.90	0.35	323	3.6	213	12.8	54D13
VIII	Palmdale Rd., Quail Lake	39.70	0.86	0.34	316	3.2	269	10.8	55D10
VIII	S Quail L. Offramp Hwy. 5	41.33	0.94	0.34	325	3.3	316	11.4	56D12
VIII	Mill Cr. Summit, Hwy. N3	41.07	1.08	0.35	349	9.0	254	15.4	53H15
VIII	Ft. Tejon Nat. Monument	57.44	0.92	0.34	339	2.9	211	12.8	50I9

Bl. = Boulevard. S. Bar. = Santa Barbara. Ft. = Fort. Nat. = National. ft. = Feet. For. = Forest.

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 2B	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification
		Length	Width	Thickness					
VIII	Wofford Hts., Greenhorns	51.00	0.80	0.35	331	2.2	170	9.5	53I3
VIII	E Caliente, Piute Mts.	65.33	0.96	0.33	341	3.2	146	9.2	56I12
VIII	Vineyard Can., Diablo Mts.	64.57	0.98	0.34	353	3.3	213	12.6	52K7
VIII	Hwy. 198 E Fresno Co. Line	51.50	1.00	0.35	352	5.1	207	13.8	54K11
VIII	Creek NW Forest Home	65.33	1.11	0.34	366	6.8	423	15.8	57M9
IX	Pine Mtn. Club, S. Emigdio	40.43	1.07	0.38	377	4.5	274	16.6	52D7
IX	Mid-Lockwood Valley	40.80	0.95	0.36	346	5.8	468	13.7	57D10
IX	Ft. Tejon Rd., Pearblossom	50.67	0.90	0.41	401	3.7	240	10.8	60D3
IX	1 mi. E Ozena, Lockwood Rd.	43.25	1.18	0.39	491	7.1	580	16.5	61D4
IX	Thorne Mdw., Lockwood Road	36.92	1.03	0.37	360	6.1	370	10.0	62D6
IX	Gold Camp., Piru Creek	44.72	1.02	0.37	366		366	14.5	64D23
IX	NE Cuddy Val., Mt. Pinos T	33.85	0.81	0.36	325		229	13.0	65D23
IX	Hungry Val., Mt. Alamo Rd.	39.72	0.91	0.37	351		177	14.0	66D25
IX	Frenchman's Flat, Templin T	61.71	1.05	0.38	397		268	11.4	86G24
IX	Sandberg Forest Fire Sta.	52.62	1.02	0.42	425	3.8	242	13.0	52H8
IX	S Vincent, Hwy. N3	46.75	1.01	0.42	418	3.2	246	12.7	54H12
IX	Agua Dulce, Soledad Canyon	54.00	1.14	0.42	399	3.4	224	14.2	58H8
IX	Mt. Waterman, Hwy. 2	42.50	1.06	0.36	358		355	18.0	59H6
IX	SW Lebec	54.40	0.95	0.40	399	3.4	195	12.0	60H10
IX	Ruby Canyon Road	68.50	1.17	0.36	395	7.0	194	13.8	63H12
IX	Lazy R. Lodge, N Kernville	54.50	0.79	0.38	383	2.9	162	8.0	51I6
IX	Lazy R. Lodge, Slate, " "	45.62	0.74	0.39	360	2.4	135	9.0	52I13
IX	N Walker Basin, Piute Mtns.	61.00	0.99	0.40	410	3.8	262	9.3	54I10
IX	NW Mojave, Tehachapi Grade	52.08	0.98	0.41	410	3.4	183	8.7	55I13
IX	NE Point, Lake Isabella	44.10	0.77	0.36	331		166	4.0	57I10
IX	Kern R., S Salmon Creek E	67.00	0.86	0.37	373	3.8	195		58I8
IX	SE Gorman, Palmdale Road	54.08	0.86	0.37	360	3.7	263	12.2	63I6
IX	N Phelan, Mojave Desert	60.75	0.92	0.39	393	4.4	211	12.4	50J12

Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 2B, 3B	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification
		Length	Width	Thickness					
IX	Devil's Punch Bowl Phelan T	42.04	0.96	0.38	368		189	12.0	50J17
IX	Cajon Pass R.R. Crossing	71.23	1.08	0.36	469	5.6	274	13.9	51J13
IX	Red Rover Mine Rd., Acton	46.40	0.93	0.40	389	3.6	262	12.0	55J5
IX	Green Rd., Hwy. 138	49.90	0.86	0.43	416	3.7	260	10.0	56J5
IX	3 Points, L. Hughes Rd. #1	62.83	1.07	0.37	390	3.8	247	13.8	57J6
IX	3 Points, L. Hughes Rd. #2	47.93	0.91	0.37	359		135	12.7	57J14
IX	Agua Dulce N Vasquez Park	55.62	1.19	0.42	445		155	14.6	57J24
IX	3 Points, SHADE	69.40	1.12	0.36	391		135		58J5
IX	Parkfield-Coalinga Rd.	53.20	0.86	0.40	389	4.7	284	12.2	50K5
IX	Peachtree Val. S Hwy. 198	49.00	0.86	0.40	385	3.9	240	9.5	51K2
IX	6 mi. N New Idria	42.95	0.94	0.44	417	5.4	364	13.4	53K11
IX	Coalinga Hot Spr. Rd.	50.94	1.10	0.39	401	4.7	345	13.8	55K8
IX	Hwy. 198 W Priest Valley	51.50	1.01	0.37	373	4.8	340	13.2	59K6
IX	Cushenbury Grade S. Berdo.	53.79	0.87	0.36	351	3.2	207	10.9	53M12
IX	E summit, S. Berdo. Mts.	60.00	1.00	0.37	380	4.6	293	15.8	52M6
IX	Hwy. 58, NW La Panza #2	69.94	1.17	0.36	297	5.2	227	19.6	50P5
IX	Crocker Spr., Temblors	34.18	1.10	0.37	364	5.2	535	20.2	50T11
IX	Orchard Peak, Temblors	44.75	0.97	0.41	402	4.6	430	12.5	51T6
X	Summit Ozena-Lockwood Rd.	41.50	1.22	0.37	394	7.7	584	19.6	63D5
X	Big Tujunga?	80.75	1.54	0.37	455		293	16.0	51B12
X	S Lytle Creek	58.36	1.72	0.36	440	8.6	511	17.0	56B7
X	W Bear Div. Little Tujunga	69.18	1.44	0.34	403	4.7	247	14.8	72G11
X	Stough Pk., Verdugo Hills	84.25	1.44	0.34	418	4.6	306	13.3	76G6
X	Summit Circle K, Saugus #3	77.50	1.23	0.35	400	3.0	125	10.0	79G4
X	Templin Hwy., Oak Flat Sta.	82.50	1.27	0.37	420	5.4	272	16.4	85G5
X	Chlorite, Magic Mtn. Flt. Rd.	66.75	1.36	0.42	463	10.3	348	19.9	50H8
X	Anorthosite, " " " "	64.73	1.30	0.40	475	10.1	307	18.6	51H11

T = Thickness. R.R. = Railroad. Spr. = Spring. Div. = Divide. Sta. = Station. Flt. = Fault.

## Appendix A. (Continued)

MORPH TYPE	Location of Sample Series 3B	Leaf Dimensions (cm)			DRI	Stalk Diameter (cm)	Leaves Per Rosette	Rosette Diameter (cm)	Sample Identification
		Length	Width	Thickness					
X	Maple Can., Big Tujunga	80.75	1.54	0.37	455		293	16.4	52H12
X	Clear Cr. For. Sta. SUN	79.31	1.79	0.41	517	10.0	531	26.6	52H13
X	White Rock L. Soledad Can.	66.83	1.32	0.45	491	8.3	245	17.1	57H12
X	Switzer's Sta. SUN	71.57	1.58	0.37	450	10.0	415	20.8	62H14
X	.5 mi. Switzer's, SHADE	90.77	1.62	0.35	453	8.8	438	24.3	63H13
X	Chilao Camp entrance	46.32	1.21	0.35	367	10.6	471	19.3	65H11
X	Chilao Camp Flat & W Side	43.29	1.39	0.35	382	8.8	417	21.7	66H7
X	Charlton Flat, PART SHADE	59.50	1.40	0.37	420	12.7	600	27.5	67H2
X	Charlton Flat, Picnic Area	51.86	1.34	0.34	376	9.6	456	24.8	67H11
X	Angeles Crest, Gneiss	68.86	1.48	0.36	427	11.0	563	21.7	68H7
X	Chilao Camp, ESE Flat	42.50	1.25	0.38	398	8.7	551	20.3	69H11
X	Bear Divide, Chlorite T	87.67	1.51	0.40	489		296	14.4	70H15
X	Charlton Flat SW Slope SUN	59.50	1.26	0.35	369		472	23.3	70H33
X	E Kratka Ridge #2	44.00	1.35	0.35	379	13.0	584	31.2	72H7
X	E Kratka Ridge #1, #2 T	44.25	1.25	0.34	364		400	16.0	73H4
X	Magic Mtn. Flt. Rd. Gabbro	68.38	1.30	0.36	408	7.0	440	18.2	75H8
X	Mt. Baldy Ski Lift	67.50	1.56	0.38	444	10.6	502	22.6	76H5
X	Mt. Baldy Glacier Picnic	67.86	1.57	0.33	305	12.0	680	21.2	77H7
X	N Chilao Flat School, Seed	37.12	1.24	0.36	371	7.4	538	19.5	78H4
X	Garnet Mtn., Laguna Mtns.	53.90	1.47	0.38	431	7.5	443	19.0	50010
X	W Earthquake Valley	64.58	1.30	0.36	389	5.3	423	13.7	5606
X	Middle Fork Tule R. Sierra	105.50	1.33	0.40	489	8.4	395	23.1	50V12
X	N Fork Kaweah R., Sierra	88.50	1.27	0.40	465	6.9	391	19.6	51V12
X	S Gate Sequoia Park, "	94.50	1.29	0.37	443	8.1	335	17.4	52V11
X	King's Can., Yucca Point	64.50	1.28	0.35	393	7.2	354	13.1	53V10
X	Mineral King Rd.	109.87	1.37	0.41	597	8.6	207	19.2	54V6

Appendix D. Some Climate Variables for Plant Climate Area Subzones (Sunset, 1976) of Southern California

I. ADVERSE CLIMATES										
General Climate, Subzone	Mean Annual Temp. °C	Jan. Temperatures Mean °C		Temperature Range, °C, in 30 Years		July Temperatures Mean °C		Mean Max. Monthly Pcpn, mm	Mean Annual Precipitation, mm	Mean Annual Snowfall mm
		Minimum	Maximum	Lowest Observed	Highest Observed	Maximum	Minimum			
* (1)	10.6 N=14	-6.6 N=14	7.7 N=14	-37.0 to -11.7	29.4 to 41.1	28. N=14	9.8 N=14	171.0 N=38	864.0 N=38	4305 N=15
* (2)	Insufficient data to distinguish between (2) and (3), therefore combined in (3)#									
* (3)	12.7 N=61	0.2 N=74	11.3 N=38	--	--	30.8 N=74	--	136.0 N=36	604.5 N=89	300 N=26
(4), (5), (6)	(4), (5), (6) subzones not located in southern half of California.									
* (7)	15.0 N=14	0.2 N=21	11.9 N=21	-21.0 to -1.1	31.1 to 46.7	34.2 N=20	14.9 N=20	107.0 N=35	505.5 N=36	907 N=19
(8)	16.9 N=8	1.8 N=13	12.9 N=13	-11.7 to -2.8	42.8 to 48.3	37.2 N=13	16.4 N=13	43.0 N=12	216.2 N=12	≤ 2.5 N=7
(9)	17.0 N=17	2.2 N=25	13.1 N=25	-11.7 to -2.2	40.0 to 47.8	37.4 N=25	16.8 N=25	60.2 N=25	304.3 N=25	≤ 2.5 N=15
* (10)	(10) Not in California but in Arizona high desert; <u>Y. whipplei</u> Ssp. <u>Newberryi</u> is located in (10) along the south and east bank of the Colorado River Canyon, in northwest Arizona.									
* (11)	16.4 N=16	-0.5 N=46	14.2 N=44	-20.6 to -1.7	38.9 to 50.6	38.8 N=43	18.9 N=36	27.3 N=16	178.3 N=16	121 N=20
* (12)	Not located in southern half of California.									

\* Plant Climate Areas where Yucca whipplei occurs.

Appendix D. (Continued)

I. ADVERSE CLIMATES CONTINUED									
General Climate, Subzone	Growing Season, Days		Number of Months Without Precipitation Greater Than		Actual Evapotranspiration, mm		Potential Evapotranspiration, mm		Months With no Trace Snow
	0.0°C (32°F)	-2.2°C (28°F)	13 mm (.5 inch)	2.5 mm (.1 inch)	0.0°C (32GS)	Annual	0.0°C (32GS)	Annual	
	* (1)	111.0 N=14	166.0 N=11	2.4 N=36	0.8 N=37	119.4 N=14	304.8 N=14	388.6 N=14	
* (2)	Insufficient data to distinguish between (2) and (3), therefore combined in (3)#								
* (3)	--	223.0 N=40	4.4 N=27	1.2 N=27	132.0 N=24	--	--	520.7 N=24	--
(4), (5), (6)	(4), (5), (6) subzones not located in southern half of California.								
* (7)	217.4 N=14	261.0 N=11	4.5 N=34	2.5 N=35	177.3 N=13	289.0 N=13	721.4 N=13	823.0 N=13	6.5 N=16
(8)	249.4 N=8	301.6 N=7	5.8 N=12	3.3 N=12	152.4 N=8	208.3 N=8	841.8 N=8	905.5 N=8	10.1 N=7
(9)	252.5 N=17	302.5 N=13	5.0 N=25	2.9 N=25	165.1 N=17	228.1 N=17	833.6 N=17	901.7 N=17	9.9 N=15
* (10)	(10) Not in California but in Arizona high desert. <u>Yucca whipplei</u> Ssp. <u>Newberryi</u> is located in (10) along the south and east bank of the Colorado River Canyon, in northwest Arizona.								
* (11)	223.3 N=24	249.7 N=13	7.0 N=20	2.8 N=20	88.9 N=10	215.9 N=10	723.9 N=10	791.0 N=10	7.8 N=
(12)	(12) Not located in southern half of California.								

## Appendix D. (Continued) II. INTERMEDIATE CLIMATES

General Climate, Subzone	Mean Annual Temp. °C	Jan. Temperature		Range in 30 yrs.		July Temperature		Mean Max. Monthly Pcpn, mm	Mean Annual Precipitation, mm	Mean Annual Snowfall mm
		Mean Minimum °C	Mean Maximum °C	Lowest Observed T°C	Highest Observed T°C	Mean Maximum °C	Mean Minimum °C			
(13)	19.3 N = 7	3.8 N =	19.4 N =	-10.5 to -9.4	49.4 to 52.2	41.9 N =	24.2 N =	20.8 N =	105.9 N =	≤2.5 N =
(14)	14.3 N =	2.0 N =	14.6 N =	-10.0 to -4.4	42.8 to 45.0	28.9 N =	10.6 N =	87.4 N =	396.2 N =	≤2.5 N =
(15)a N of <u>Y. w.</u>	14.0 N=36	3.4 N=38	13.9 N=37	-8.9 to -5.6	38.9 to 43.3	27.9 N=42	11.7 N=14	167.1 N=23	698.5 N=48	29.0 N=36
*(15)b	14.3 N=13	4.2 N=18	16.6 N=19	-7.8 to -4.4	39.4 to 43.3	23.9 N=20	11.0 N=18	101.4 N=14	452.1 N=32	≤2.5 N=9
(16)a N of <u>Y. w.</u>	14.0 N=18	3.2 N=18	13.4 N=18	-7.8	38.9 to 39.4	27.1 N=18	--	139.4 N=13	640.1 N=28	39.6 N=18
*(16)b	14.3 N=6	3.7 N=8	16.8 N=8	-7.8 to -5.0	41.7 to 43.3	24.0 N=8	10.3 N=8	86.9 N=9	493.3 N=14	28.2 N=19
(17)a N of <u>Y. w.</u>	13.4 N=	4.1 N=	14.7 N=	-6.7 to -1.7	29.4 to 42.8	20.0 N=	10.8 N=	--	721.4 N=	≤0.25 N=
*(17)b	13.7 N=	5.6 N=	14.5 N=	-5.6 to -1.1	29.4 to 47.2	21.6 N=	10.3 N=	--	602.0 N=	≤0.25 N=
*(18)	14.3 N=11	-0.6 N=13	14.7 N=13	-11.7 to -7.8	42.2 to 44.4	34.0 N=13	12.0 N=13	101.6 N=10	447.0 N=10	141.5 N=11
*(19)	15.6 N=7	2.6 N=8	16.9 N=8	-8.3 to -6.1	41.1 to 45.6	33.6 N=8	13.6 N=8	88.4 N=7	436.9 N=7	28.7 N=7

a = Northern half of plant climate area. b = southern half of climate area. \* = Area in which Yucca whipplei occurs. T°C = Temperature degrees Celsius. mm = Millimeters. Y. w. = Y. whipplei

## Appendix D. (Continued) II. INTERMEDIATE CLIMATES--CONTINUED

General Climate, Subzone	Growing Season, Days		Number of Months Without Precipitation Greater Than		Actual Evapotranspiration, mm		Potential Evapotranspiration, mm		Months With No Trace Snow
	0.0°C (32°F)	-2.2°C (28°F)	13 mm (.5 inch)	2.5 mm (.1 inch)	0.0°C (32GS)	Annual	0.0°C (32GS)	Annual	
	(13)	251.4 N=7	318.4	9.7	2.3	38.1	78.7	924.6	
(14)	255.9	287.3	5.2	3.4	188.0	312.4	619.8	749.3	11.5
(15)a N of <u>Y.</u> <u>W.</u>	268.0 N=33	338.0 N=33	4.2 N=18	2.5 N=18	259.1 N=37	345.4 N=37	635.0 N=37	698.5 N=37	11.2 N=12
*(15)b	289.0 N=13	337.0 N=13	5.3 N=15	2.5 N=15	259.0 N=13	353.1 N=13	579.1 N=13	706.1 N=13	10.9 N=9
(16)a N of <u>Y.</u> <u>W.</u>	259.0 N=18	316.0 N=18	3.9 N=14	2.4 N=14	276.9 N=17	350.5 N=17	622.3 N=17	731.5 N=17	9.0 N=1
*(16)b	272.0 N=4	339.0 N=4	5.6 N=7	2.9 N=7	254.0 N=4	342.9 N=4	586.7 N=4	706.1 N=4	11.0 N=3
(17)a	287.0 N=	344.0	4.1	2.2	243.8	284.5	640.1	730.7	11.3
*(17)b	338.0 N=	353.0	5.0	3.2	309.9	365.8	639.8	672.3	11.4
*(18)	179.0 N=11	233.5 N=11	3.4 N=10	0.8 N=10	152.4 N=10	309.9 N=10	574.0 N=10	739.1 N=11	6.3 N=10
*(19)	215.0 N=7	284.0 N=7	4.6 N=7	1.4 N=7	205.7 N=7	335.3 N=7	647.7 N=7	789.9 N=7	8.2 N=6

Appendix D. (Continued) III. OPTIMAL CLIMATES

General Climate, Subzone	Mean Annual Temp. °C	Jan. Temperatures Mean °C		Temperature Range, °C, in 30 Years		July Temperatures Mean °C		Mean Max. Monthly Pcpn, mm	Mean Annual Precipitation, mm	Mean Annual Snowfall mm
		Minimum	Maximum	Lowest Observed	Highest Observed	Maximum	Minimum			
*(20)	Insufficient data to distinguish between (20)# and (21), therefore combined in (21).									
*(21)	16.6 N=4	2.2 N=6	18.3 N=6	-9.4 to -6.7	40.0 to 42.2	32.7 N=6	14.5 N=6	80.3 N=10	396.2 N=10	12.2 N=9
*(22)	16.8 N=1	4.0 N=2	18.8 N=2	-6.7 to -3.9	40.6 to 45.0	28.1 N=2	14.8 N=2	65.3 N=2	332.7 N=1	≤0.25
*(23)	16.6 N=9	5.0 N=11	18.7 N=11	-8.3 to -2.8	41.7 to 45.0	28.2 N=11	15.1 N=11	73.2 N=9	350.5 N=9	1.3 N=7
*(24)	15.9 N=14	6.8 N=17	17.3 N=17	-6.7 to 1.7	39.4 to 46.1	23.7 N=17	15.8 N=16	55.9 N=11	267.2 N=12	≤2.5 N=

# Coastal canyons in which cold night air drainage makes climate slightly more severely variable than on exposed coastal slopes and flats (Kimball and Gilbert, 1967 a; Sunset, 1976).

Appendix D. (Continued) III. OPTIMAL CLIMATES--CONTINUED

General Climate,	Growing Season, Days		Number of Months Without Precipitation Greater Than		Actual Evapotranspiration, mm		Potential Evapotranspiration, mm		Months Without Trace Snow
	0.0°C (32GS)	-2.2°C (28GS)	13 mm (.5 inch)	2.5 mm (.1 inch)	0.0°C (32AE)	Annual (AE)	0.0°C (32PET)	Annual (PET)	
* (20)	Insufficient data to distinguish between (20) and (21), therefore combined in (21)#								
* (21)	245.0 N=4	297.8 N=4	5.1 N=10	1.8 N=10	210.8 N=4	330.2 N=4	706.1 N=4	812.8 N=4	8.8 N=9
* (22)	258.0 N=1	314.0 N=1	5.0	2.0	218.4 N=1	348.0 N=1	721.4 N=1	825.5 N=1	11.0
* (23)	304.0 N=4	340.0 N=4	5.1 N=9	2.2 N=9	251.5 N=4	315.0 N=4	759.5 N=4	823.0 N=4	10.6 N=7
* (24)	356.0 N=11	365.0 N=11	7.3 N=7	3.0 N=11	287.0 N=10	289.6 N=10	777.2 N=11	787.4 N=11	11.0 N=10

Appendix E. Averaged Climate Variables for Morphological Types  
(MORPH) in Y. whipplei

MORPH, Series, Averaged	Severest Neighbor Climate	Local Climate Subzone	Precipitation, mm			Months ≤ 2.5 mm (0.1 inch)
			Spring Jan-Apr	Summer May-Aug	Winter Oct-Dec	
I	16.3	21.3	321	12	139	3.2
II	18.3	19.7	286	14	130	2.5
Pre- Series	17.4	20.4	301	13	134	2.8
III	19.6	21.4	259	11	130	2.8
IV	22.3	22.8	298	8	149	3.0
Series 1	21.0	22.1	279	9	139	2.9
Va	18.5	20.5	334	11	167	2.2
Vb	10.6	11.6	276	13	143	2.3
Vc	14.1	16.2	295	14	148	2.5
Series 3A	14.0	16.0	295	14	149	2.4
VI	9.2	14.8	391	34	185	2.0
VII	8.3	15.4	378	16	190	1.8
Series 2A	8.8	15.0	386	27	187	1.9
VIII	2.7	9.8	229	16	112	2.1
IX	4.8	10.7	228	16	116	2.1
Series 2B	4.2	10.5	228	16	115	2.1
X Series 3B	6.3		412	22	211	

## Appendix E. (Continued)

MORPH, Series, Averaged	Precipitation		Mean Annual	Temperature, Celsius	
	Months ≤ 13 mm (.5 inch)	Mean Annual mm		Average Minimum of Coldest Month	Mean Maximum of January
I	5.4	472	14.7	3.9	17.7
II	5.3	429	15.6	3.9	17.1
Pre- Series	5.3	447	15.3	3.8	17.3
III	5.4	399	16.4	4.8	17.3
IV	5.3	455	16.4	5.9	17.3
Series 1	5.3	427	16.4	5.6	17.3
Va	5.0	513	16.9	5.0	17.9
Vb	5.0	432	15.6	3.3	15.3
Vc	5.2	457	15.9	4.0	15.7
Series 3A	5.1	457	15.9	3.9	15.8
VI	4.5	610	14.0	1.9	15.6
VII	4.7	584	16.8	2.8	15.7
Series 2A	4.6	599	15.0	2.2	15.6
VIII	5.2	358	13.7	-0.4	12.3
IX	5.2	361	13.8	-0.7	11.7
Series 2B	5.2	358	13.8	-0.6	11.9
X Series 3B	4.3	627	13.9	1.2	10.6

## Appendix E. (Continued)

MORPH, Series, Averaged	Average Maxi- mum Tempera- ture, Hottest Month, ( $^{\circ}$ C)	Difference Between Maxi- mum-Minimum Mean Tempera- tures of Hot- test, Coldest Months ( $^{\circ}$ C)	Seasonal Snow mm	Month of Greatest Precipita- tion  mm	Evapora- tive Demand  mm
I	27.8	23.9	46	107	1549
II	27.8	23.9	24	94	1524
Pre- Series	27.8	24.0	34	100	1534
III	28.0	23.2	9	88	1486
IV	26.4	20.5	4	103	1458
Series 1	27.2	21.6	7	96	1473
Va	30.0	25.0	20	117	1702
Vb	29.7	25.4	19	93	1577
Vc	29.4	25.4	27	96	1590
Series 3A	29.5	25.6	22	98	1595
VI	29.7	27.8	39	134	1636
VII	29.9	27.1	71	126	1702
Series 2A	29.8	27.6	55	131	1656
VIII	33.4	33.8	222	73	1786
IX	33.7	34.4	162	76	1816
Series 2B	33.6	34.2	198	75	1808
X Series 3B	31.7	30.5	208	137	1725

## Appendix E. (Continued)

MORPH, Series, Averaged	Evapotranspiration mm		Growing Season, Days -2.2°C (28°F)		
	Potential	Actual	Mean Annual	With 2.5 <sup>+</sup> mm Precipitation (0.1 inch)	With 13 <sup>+</sup> mm Precipitation (0.5 inch)
I	739	231	328	227	164
II	764	229	314	240	156
Pre-Series	752	229	320	235	160
III	782	256	344	258	183
IV	772	249	349	259	189
Series 1	777	254	346	259	186
Va					
Vb	650	256	313	235	152
Vc	775	269	324	241	168
Series 3A	752	267	323	240	169
VI	734	196	285	218	155
VII	721	152	276	186	116
Series 2A	732	193	284	214	150
VIII	782	132	246	175	85
IX	744	135	237	164	76
Series 2B	754	135	239	167	79
X Series 3B	787	168	239	188	116

## Appendix E. (Continued)

MORPH, Series, Averaged	Growing-Season Degree-Days, $-2.2^{\circ}\text{C}$ ( $28^{\circ}\text{F}$ )		
	Annual	With = 2.5 mm (0.1 inch) Precipitation	With = 13 mm (0.5 inch) Precipitation
I	4822	3337	2411
II	4898	3752	2411
Pre-Series	4896	3592	2445
III	5642	4239	2998
IV	5724	4244	3096
Series 1	5674	4241	3042
Va			
Vb	4883	3666	2371
Vc	5152	3832	2671
Series 3A	5136 ?	3818 ?	2689 ?
VI	3990	3058	2173
VII	4637	3120	1944
Series 2A	4260	3208	2247
VIII	3370	2398	1164
IX	3271	2255	1046
Series 2B	3298	2303	1085
X Series 3B	3322	2619	1607

