CALIFORNIA STATE UNIVERSITY, NORTHRIDGE

LOCAL PATTERNS OF VARIATION IN THE CALIFORNIA SCRUB OAK, *QUERCUS DUMOSA* NUTT. (FAGACEAE)

A theses submitted in partial satisfaction of the requirements for the degree of Master of Science in

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by

John Michael Flynn

August, 1977

The thesis of John Michael Flynn is approved:

California State University, Northridge

August, 1977

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LOCAL PATTERNS OF VARIATION IN THE
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Four vegetative characters of leaves (length, width, petiole length and a number of teeth) and two reproductive characters (acorn length and acorn width) were measured in 58 individual plants located in Wildwood Park, a natural area in Thousand Oaks, California, U.S.A. The 58 plants were grouped into seven units, or subpopulations, separated from each other by at least 100 meters. The data was analyzed statistically to determine if these seven subpopulations are distinct interbreeding units.

Hypotheses proposed to account for the variation were: genetic drift and founder effect, natural selection, hybridization, nonuniform dispersal of genotypes and environmental factors.

The results of univariate and multivariate analysis suggested a pattern of relationships among the individuals and subpopulations related to their distribution. The results suggested that there are not seven units, but three. Each of these units is composed of two adjacent subpopulations.

Evidence points to restriction of gene flow as a possible cause of the variation pattern. Other factors, such as environmental fluctuations, could not be excluded. Hybridization with other oak species, however, was rejected. The total variation among these plants was judged to be great, but within limits described by plant taxonomists.

CHAPTER ONE

INTRODUCTION

The objective of this study is a quantitative description of the phenotypic variation in a local population of the California Scrub Oak, Quercus dumosa Nutt. (Fagaceae). This species has been described previously as highly variable by several authors, including McMinn (1939), Tucker (1952) and Forde and Faris (1962). This study is based on the analysis of variation in six characters, utilizing univariate and multivariate techniques. Comparisons among samples at seven sites within the study area permits a test of microspatial differentiation. Phenotypic differences among spatially separated groups within a population, if genetically determined, may be interpreted as evidence of genetic drift, natural selection, hybridization or nonuniform dispersal of genotypes.

Ehrlich and Raven (1969) have challenged the notion of the significance of the species as the functional unit in evolution. They submit that the local breeding unit, not the species, is the unit of evolutionary change. Since Q. dumosa is recognized as being highly variable, this species may be a logical choice for a detailed study of

local population variability and may provide information to respond to the questions posed by Ehrlich and Raven.

CHAPTER TWO

LITERATURE REVIEW

The genus Quercus is a large and diverse one, comprising sixteen species in California (Munz, 1968). It contains evergreen and deciduous trees and shrubs. Members of this genus are found in many different communities in California (Munz, 1968). Q. dumosa is found primarily in the chaparral community, which is characterized by average rainfall of 14 to 25 inches, with hot dry summers and cool but not cold winters. (See Munz, 1968, p. 17.)

Hanes (1971) describes Q. dumosa as a common shrub of the Southern California chaparral. It is found both in the coastal mountains and the desert mountains, but more commonly in the interior. He considered it one of the climax plants of the desert chaparral environment. Tucker (1953 a,b) lists Q. dumosa as a common element of the more mesic chaparral in the semi-arid, interior mountains of Southern California.

In their study of the growth habits of several chaparral plants, Watkins and DeForest (1941) found Q. dumosa to be the slowest growing shrub species. During the study period, growth occurred only during the spring (between March 15 and May 15). Stem increases were typically from

2 to 3 centimeters during that period and were unevenly distributed. Leaf numbers increased threefold during the same time interval, but after May 15, leaf number increased only twenty percent through the remainder of the summer.

Taxonomic and morphological characters of Q. dumosa have been described by several authors. Jepson (1925) describes the leaves as oblong to elliptic or roundish. Leaf margins may be entire but more typically they are spinose-serrate. Leaves range from three-fourths of an inch to one inch in length, according to Jepson, and are highly variable in texture and outline. McMinn (1939) notes that the leaf blade is highly variable, ranging from one-fourth to one inch long and one-fourth to three-fourths of an inch wide. The petiole is about one-eighth of an inch long. Tucker (1953 a) describes the morphological characters as follows: upper leaf surface green and shiny, leaf margin mucronate-dentate to entire, twigs of current season pubescent to glabrate and brownish, acorn cups thick, with the scales strongly tuberculate, acorn cups hemispheric to about two-thirds spherical with the margins tapering inward. Munz (1968) described the leaf blade as:

> '"..oblong to elliptic or roundish, mostly mucronate-dentate to entire or subspinose, coriaceous, 1.5 - 2.5/cm long.."' (p. 905).

He also mentions that Q. dumosa apparently hybridizes freely with other species of oaks, notably Q. durata Jeps., Q. turbinella Greene, Q. Engelmannii Greene, and Q. Garryana

Dougl., with much introgression occurring. He also notes an apparent hybrid between Q. dumosa and Q. lobata found near Santa Barbara, referred to as Q. dumosa var. Kinselae C. H. Mull. and one found near Pasadena, supposedly a hybrid with Q. lobata Nee', referred to as Q. X Townei Palmer. He also mentions that small trees of Q. agrifolia may show introgression with Q. dumosa, but crossing between these two species has yet to be established.

Tucker (1952, 1953 a) describes Q. dumosa as integrating freely with many species, most notably, Q. turbinella, Q. durata, Q. Engelmannii and Q. Macdonaldii Greene. He explored the relationship between Q. undulata and Q. turbinella (1961) and showed that Q. undulata is a hybrid complex involving Q. gambeii Nutt. and several other species. In all studies, Tucker used morphological characters as the variables and intermediacy of characters was utilized as the test for hybridity. Forde and Faris (1962) described a population which combined characters of Q. dumosa and Q. durata in Northern California.

Muller (1952) expressed doubt that the variability observed in oaks was due to hybridization:

> "The species of oaks are notoriously variable in trivial characters. This variability has given rise to the belief that oaks hybridize freely. It is quite evident that the bulk of claims of hybridity are based upon trivial variations of the sort one may encounter in a relatively pure population of a single species.." (p. 148).

CHAPTER THREE

METHODS AND MATERIALS

The location for this study is in Wildwood Park, a natural area in the city of Thousand Oaks, California. It was chosen for its accessibility and the relatively undisturbed nature of the environment. This area has been set aside as a natural area and maintained by the Department of Parks and Recreation of the city of Thousand Oaks; there have been no studies of a scientific nature in this area.

The park consists of an east-west running canyon with a stream flowing intermittently through it. The park is approximately 2.5 kilometers long and 1.2 kilometers wide. The flora of the park consists of many mature stands of Quercus agrifolia, Yucca Whipplei Torr., Prunus ilicifolia Nutt., Ceanothus spp., and Adenostoma fasciculatum H & A. Seven sites could be identified within the study area, where oak trees were located. These groups or subpopulations were distributed along the course of the stream (Plate I). With the exception of subpopulation 1, all of the plants included in this study were found near the bottom of the canyon, that is, within fifteen meters of the stream. The members of subpopulation 1 were found at the top of the canyon, approximately 100 meters above the

stream. The seven subpopulations were separated from each other by at least 100 meters. The largest distance between two subpopulations (5 and 6) was about 1,200 meters. The park is surrounded at the top of the canyon by the Wildwood housing development, which contains approximately 300 homes. As a result, there is considerable recreational use of the park.

Collection of samples was made in November, 1976. Ten plants were sampled whenever the subpopulation size permitted. All members of subpopulations 2, 5 and 6, which consisted of less than ten plants, were sampled. Subpopulations 1, 3, 4 and 7 were large groups, consisting of as many as 100 individuals. The ten-plant sample was chosen to include individuals from throughout the area of the subpopulations, which were generally distributed in an east-west direction. A total of 58 plants was included in the study. Ten leaves and up to ten acorns were collected from each plant. All leaves were collected at eye level, beginning at the east side of the tree and continuing around to the west side of the tree. Each plant sampled was identified by number with a metal tag (see Appendix). Only mature, sclerotized leaves were collected. The collection of acorns was done similarly to the leaves.

Measurements of three dimensions of each leaf were subsequently taken as well as a count of the number of teeth present on the margin of the leaf. The dimensions

were leaf length (maximum), leaf width (maximum) and petiole length. Maximum acorn length and width were also measured. Measurements were estimated to the nearest tenth of a millimeter using calipers.

Herbarium specimens of each of the 58 plants in this study have been deposited at the University Herbarium, California State University, Northridge.

A mean for each plant was calculated for each of the six characters and used for all further computations and analysis. Computations were carried out on a CDC 3170 computer at California State University, Northridge. The types of analysis completed and library programs utilized are as follows: descriptive statistics from the MINT program (Swanson, 1976); Bartlett's test for homogeneity of variance (Sokal and Rohlf, 1969); Duncan's multiple range test from BMD07V (Dixon, 1974); Clustering by SAHN procedures from MINT (Swanson, 1976); discriminant analysis from SPSS (Nie et al, 1975) and principal component analysis from an unpublished program written by Dr. John Swanson, Department of Biology, California State University, Northridge.

PLATE I

A portion of the Newbury Park quadrangle; California-Ventura County; 7.5 minute series (topographic) from the U. S. Geological Survey. Longitude - 118° 54' 27" west, latitude - 34° 13' 1" north. This plate shows the study area, Wildwood Park, and the location of the seven populations. Scale, seven inches equals one mile.

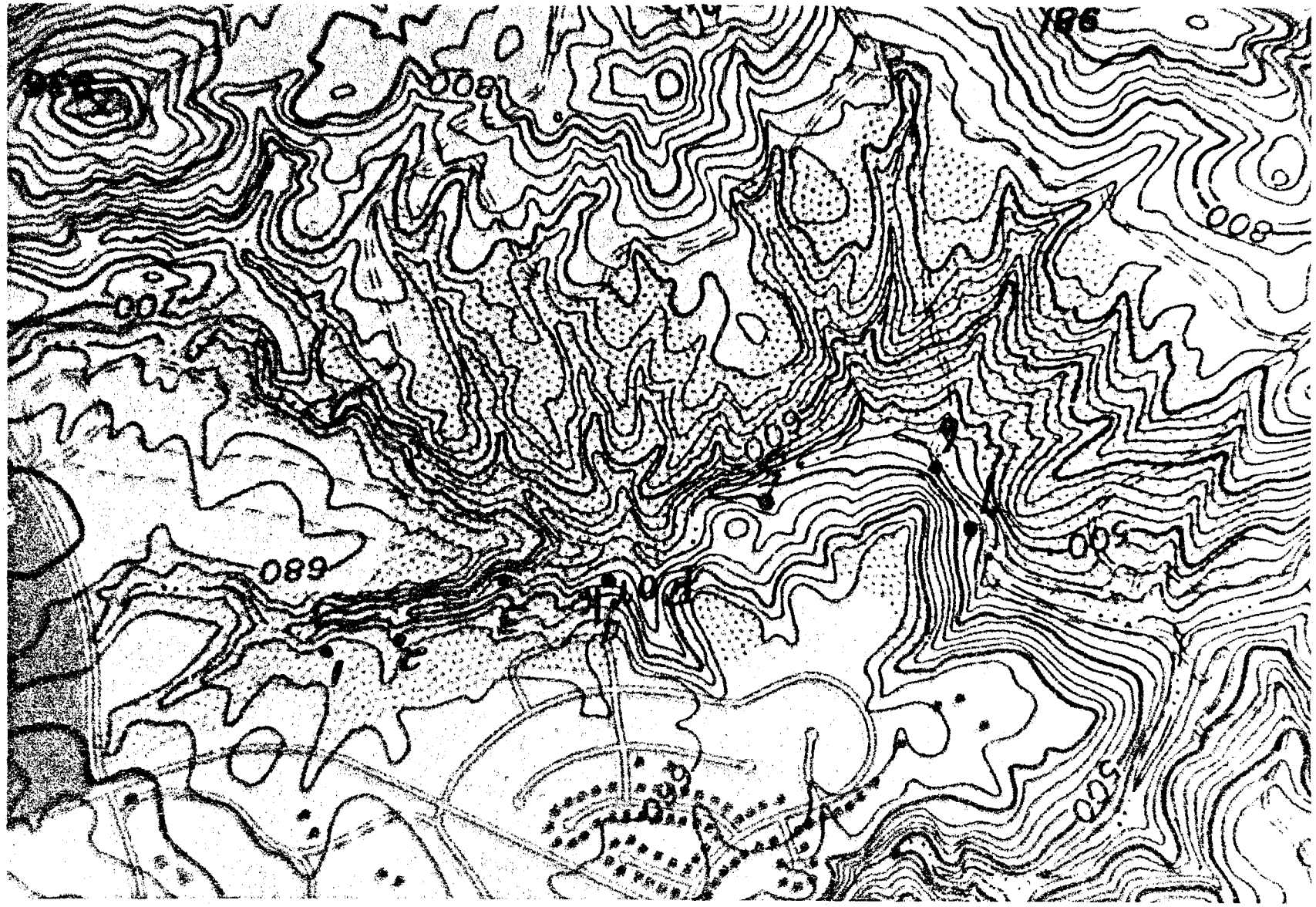

680
700
800

PLATE II

View of Wildwood Canyon from near the location of population 1, facing west.

PLATE III

View of Wildwood Canyon from near population 3, facing west.

CHAPTER FOUR

RESULTS OF UNIVARIATE ANALYSIS

4.1 Descriptive Statistics. The results of computations of descriptive statistics for the four vegetative characters are given in Table I and for the two reproductive characters in Table II.

4.2 Coefficient of Variation. Coefficients of variation are presented in Table III. The range of these values for the individual subpopulations extends from 54.2% for number of teeth in subpopulation 3 to 0.25% for acorn length in subpopulation 2. Fifteen of the 40 coefficients fall within the 20.00 to 29.99% range, while 19 fall below this interval and six lie above it. The mean coefficients indicate that the variation is higher for the vegetative characters than for the reproductive ones. In fact, the highest value for the reproductive characters (13.07%) is nearly half of the lowest value for the vegetative characters (25.57%). It should also be noted that the coefficients for number of teeth are among the higher values, particularly subpopulations 1, 2 and 3.

4.3 Homogeneity of Variance. The results of the test for homogeneity of variance are presented in Table IV. All of the adjusted chi-square values are lower than the

SUBPOPULATION NUMBER	SAMPLE SIZE	LEAF LENGTH (mm)	LEAF WIDTH (mm)	PETIOLE LENGTH (mm)	TEETH NUMBER
1	10	18.65 ± 1.28	11.73 ± 0.80	2.93 ± 0.24	8.77 ± 1.25
2	6	17.68 ± 0.56	11.42 ± 0.82	2.62 ± 0.32	11.32 ± 1.69
3	9	19.59 ± 1.33	13.04 ± 1.34	3.00 ± 0.27	11.97 ± 2.16
4	10	14.37 ± 0.59	10.17 ± 0.66	2.02 ± 0.15	10.35 ± 0.74
5	9	13.08 ± 0.87	8.07 ± 0.82	2.12 ± 0.26	8.32 ± 0.67
6	4	19.97 ± 2.47	11.62 ± 1.42	2.95 ± 0.34	8.27 ± 0.70
7	10	22.59 ± 1.24	14.79 ± 0.80	3.46 ± 0.21	9.79 ± 0.74

TABLE I

Mean and standard error ($\bar{Y}$ ± s.e.) for each of the vegetative characters in the seven subpopulations.

SUBPOPULATION NUMBER	SAMPLE SIZE	ACORN LENGTH (mm)	ACORN WIDTH (mm)
1	4	26.40 ± 1.48	10.70 ± 0.74
2	2	28.05 ± 0.05	11.15 ± 0.25
3	2	25.50 ± 0.36	12.57 ± 0.59
4	10	22.82 ± 0.86	11.67 ± 0.31
5	9	24.00 ± 1.30	11.13 ± 0.58
6	4	24.97 ± 1.25	11.57 ± 0.88

TABLE II

Mean and standard error ($\bar{Y}$ ± s.e.) for each of the reproductive characters in the seven subpopulations.

SUBPOPULATION NUMBER	LEAF LENGTH	LEAF WIDTH	PETIOLE LENGTH	TOOTH NUMBER	ACORN LENGTH	ACORN WIDTH
1	21.72	21.54	25.49	44.96	11.23	13.76
2	7.70	17.59	29.74	36.70	0.25	3.17
3	20.34	30.86	26.98	54.20	2.45	8.13
4	12.89	20.43	24.23	22.49	11.88	8.41
5	20.00	30.65	37.46	24.07	16.21	15.70
6	24.71	24.49	23.24	16.81	10.04	15.23
7	17.36	17.08	28.89	23.87	---	---
1-7	25.57	28.64	31.04	37.87	13.07	12.05

TABLE III

Coefficients of variation for the six characters, given for the seven subpopulations and the mean for all seven.

CHARACTER	DF	ADJUSTED CHI-SQUARE	CRITICAL CHI-SQUARE
Leaf length	6	18.62	12.59
Leaf width	6	7.75	12.59
Petiole length	6	2.69	12.59
Tooth number	6	15.86	12.59
Acorn length	5	1.87	11.07
Acorn width	5	1.73	11.07

TABLE IV

The results of the Bartlett's test for homogeneity of variance. Given are the degrees of freedom (DF); the adjusted chi-square value; and the critical chi-square value at the 5% level (Rohlf and Sokal, 1969).

critical chi-square values except for leaf length and number of teeth.

Upon examination of the data (see Appendix), it is apparent that a few members of some of the subpopulations are quite different from the remainder of the subpopulations. This could account for the heterogeneity for leaf length and number of teeth. For example, plant 306 has a mean leaf length of 28.5 mm. All the other members of subpopulation 3 have mean lengths ranging from 17.1 mm to 22.3 mm. Bartlett's test is very sensitive to departures from normality; a significant chi-square value may indeed indicate nonnormality and not heterogeneity (Sokal and Rohlf, 1969). In the case of these two variables, a test of skewness may indicate that a data transformation may be appropriate, thereby removing part or all of the heterogeneity of variance.

4.4 Character Correlations. The results of the character correlation are presented in Table V. Data for acorns was not used because it was incomplete. There is a positive correlation between leaf length and petiole length (0.809) and a negative correlation between leaf length and number of teeth (-0.815) and between petiole length and number of teeth (-0.823). There is a smaller negative correlation between leaf width and number of teeth (-0.373). A test for the significance of these correlations shows that, for 56 degrees of freedom, a

	LEAF LENGTH	LEAF WIDTH	PETIOLE LENGTH	NUMBER OF TEETH
Leaf Length	1.000			
Leaf Width	-0.165	1.000		
Petiole Length	0.809	-0.119	1.000	
Number of Teeth	-0.815	-0.373	-0.823	1.000

TABLE V

Correlation coefficients for each character.

significant value should exceed 0.324 (Rohlf and Sokal, 1969). The correlation values mentioned all exceed the significant value, therefore, they are significant.

4.5 Duncan's Multiple Range Test. The results of this procedure are presented in Table VI. The means for leaf length for subpopulations 2, 1, 3 and 6 are not sufficiently different to consider them as separate groups. Subpopulations 3, 6 and 7 are members of the same group. In all the tests, subpopulations 1, 2 and 6 are part of the same group. Subpopulations 2, 4 and 5 tend to be grouped on the left side of the table for all characters except acorn width, and subpopulations 6 and 7 tend to be grouped on the right for the vegetative characters. There is considerable change in the ranked order of the means for number of teeth, and acorn dimensions. In addition, all of the subpopulations fall in the same group when number of teeth, acorn length and acorn width are used as the variable. The maximum distinction among subpopulations was found to apply for leaf length, where 13 out of 21 paired comparisons were significant. These results suggest that, at least for one variable, leaf length, these seven subpopulations fall into two or three phenotypically distinguishable groups.

4.6 Summary of Univariate Analysis. The univariate analysis supports the conclusion that one or more of the subpopulations within this local population are

	SUBPOPULATIONS						
Leaf length	5	4	2	1	3	6	7
Leaf width	5	4	2	6	1	3	7
Petiole length	4	5	2	1	6	3	7
Tooth number	6	5	1	7	4	2	3
Acorn length	4	5	6	3	1	2	
Acorn width	1	5	2	6	4	3	

TABLE VI

Ranked means for the seven subpopulations (1-7). Results of Duncan's multiple range test. Lines under subpopulation numbers represent homogeneous subsets.

phenotypically distinguishable. There is no evidence that there is a gradient in expression which is associated with distance. The multiple range test indicated that some subpopulations are statistically similar and, therefore, could be considered as a single group (except for leaf length). It also indicated that subpopulations 3, 6 and 7 are indistinguishable.

The coefficients of variation (Table III) give some indication of the amount of variability of each character for the various subpopulations as well as the total. The number of teeth is the most variable of the six characters. The range of the coefficients for number of teeth is comparatively large, extending from 54.2% to 16.81%. The values for four vegetative characters in subpopulation 7 extend from 17.08% to 23.87%. The relatively narrow range indicates expression of these four characters in subpopulation 7 is comparatively uniform.

There is a significant correlation among leaf length, petiole length, number of teeth, and leaf width, although it is positive in one case and negative in the others.

CHAPTER FIVE

RESULTS OF MULTIVARIATE ANALYSIS

5.1 Clustering by SAHN Procedures. Application of SAHN procedures (sequential, agglomerative, hierarchic, nonoverlapping, Sneath and Sokal, 1973) produces a grouping or clustering of the individual plants in the study. A taxonomic distance between OTUs (plants) was computed for the raw data matrix. Two phenograms (Figures I and II) were constructed using the unweighted pair group method using arithmetic averages (UPGMA) and the weighted pair group method (WPGMA). The plant numbers which appear at the end of the stems on the phenograms and in the scattergrams for principal component analysis and their membership in each of the subpopulations is found in Appendix B.

UPGMA. The phenogram showed four distinct cluster levels (Figure I). The clustering within the various levels suggests certain similarities among the plants. For example, in the upper level, 19 plants were clustered, including eight from subpopulation 7 (49-58) and five from subpopulation 1 (1-10). In the second level, 21 plants were clustered, among which are included seven members of subpopulation 4 (26-35). In the third level, one finds four members of subpopulation 5 (36-44) and three from

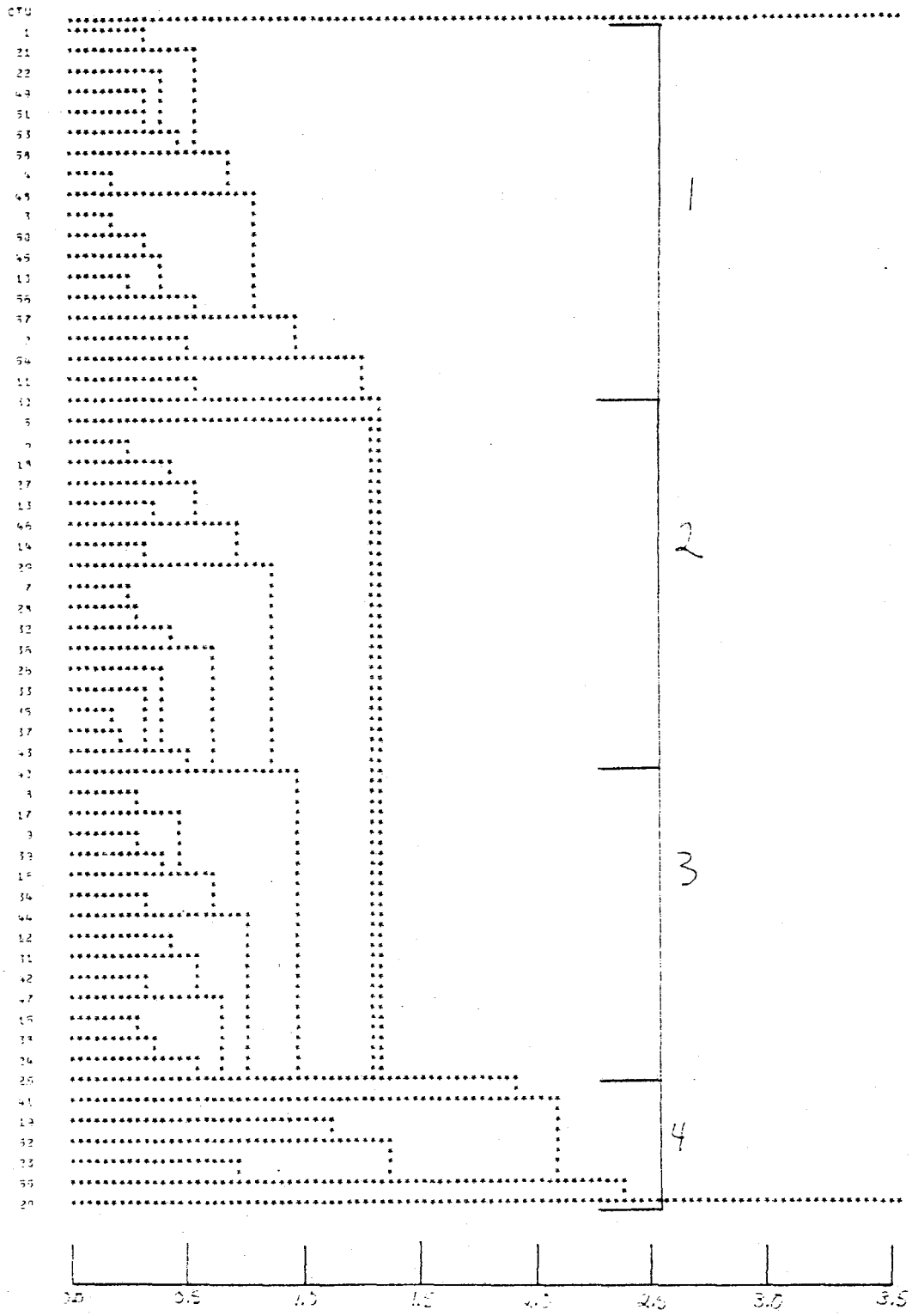
FIGURE I

Phenogram produced using unweighted pair group method using arithmetic averages. Four characters were used; leaf length, leaf width, petiole length, and number of teeth.

Abscissa = OTU (operational taxonomic unit) or individual plant.

Ordinate = cophenetic values.

Cophenetic correlation = 0.78


CTU
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57
9
54
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27
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18
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42
47
16
33
24
25
41
13
32
33
55
20
1
2
3
4
2.0
2.5
3.0
3.5

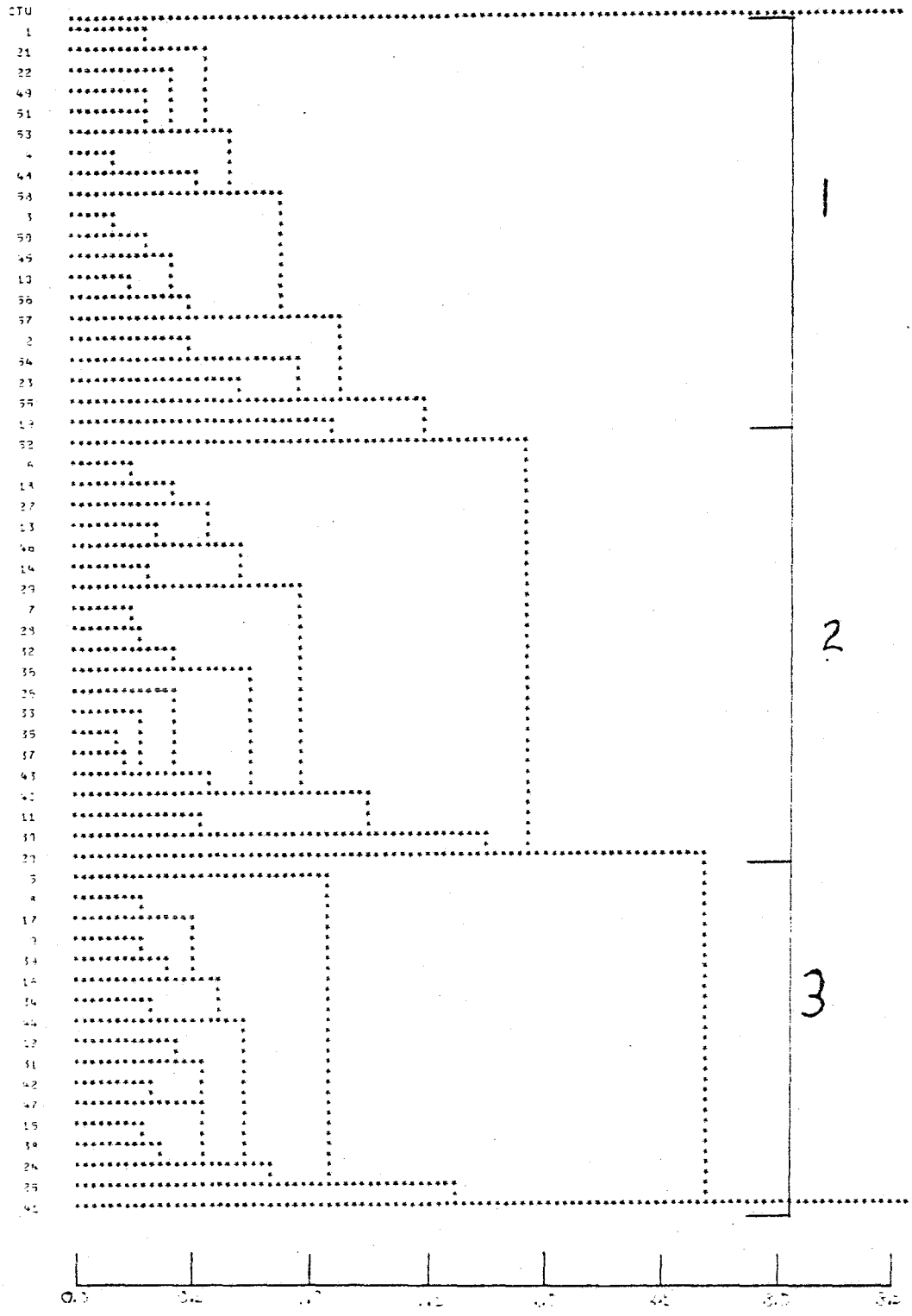
FIGURE II

Phenogram produced using weighted pair group method using arithmetic averages. Four characters were used; leaf length, leaf width, petiole length, and number of teeth.

Abscissa = OTU (operational taxonomic unit) or individual plant.

Ordinate = cophenetic values.

Cophenetic correlation = 0.33


CTU
1
21
22
49
51
53
4
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24
26
41
1
2
3

subpopulation 2 (11-16) among the 15 plants clustered there. Three members of subpopulation 3 (17-25), two from subpopulation 7 are found in the lower level. A summary of the cluster levels is found in Table VII.

WPGMA. The phenogram produced three cluster levels (Figure II). The clustering of the various plants is quite similar to the UPGMA phenogram. In the upper level, all ten members of subpopulation 7 (plants 49-58) are found with five members of subpopulation 1 (plants 1-10). The middle level contains eight individuals from subpopulation 4 (26-35) and four from subpopulation 5 (36-44). In the lower level, there are five from subpopulation 5 (36-44) and four from subpopulation 3 (17-25). See Table VII.

The cophenetic correlation coefficient is a measure of the degree of correspondence between the relationships among the individual plants in the distance matrix and the relationships between the plants as expressed in the phenogram. The coefficient for the UPGMA phenogram is 0.78. For the WPGMA procedure it is 0.33, indicating that it is a less satisfactory representation of the distance matrix.

In summary, it appears that members of subpopulations 4 and 5 are phenotypically similar, owing to the fact that they tend to cluster together. Subpopulation 7 (49-58) appears to be very distinct, because 80-100% of the members tend to cluster in the upper level when either procedure is used. Subpopulation 6 (45-48) shows somewhat less

TABLE VII

Arrangement of the four cluster levels for the different phenograms; WPGMA and UPGMA. The number of members of each subpopulation within the several cluster levels is depicted.

UPGMA		WPGMA		UPGMA		WPGMA	
NO. OF PLANTS	SUB-POP. NO.	NO. OF PLANTS	SUB-POP. NO.	NO. OF PLANTS	SUB-POP. NO.	NO. OF PLANTS	SUB-POP. NO.
8	7	10	7	0	7	0	7
2	6	1	6	1	6	1	6
0	5	0	5	4	5	5	5
1	4	0	4	2	4	2	4
2	3	4	3	3	3	4	3
1	2	0	2	3	2	3	2
5	1	5	1	1	1	3	1
	Level one				Level three		
0	7	1	7	2	7	-	-
2	6	1	6	0	6	-	-
4	5	4	5	1	5	-	-
7	4	8	4	0	4	-	-
2	3	2	3	3	3	-	-
3	2	2	2	0	2	-	-
4	1	2	1	0	1	-	-
	Level two				Level four		

distinctness, although its members tend to cluster in the upper two levels. Subpopulation 3 (17-25) appears to be the least distinct, because its members are found in all cluster levels. Subpopulation 2 (11-16) tends to cluster in the second and third levels. Subpopulation 1 is found in the upper three levels.

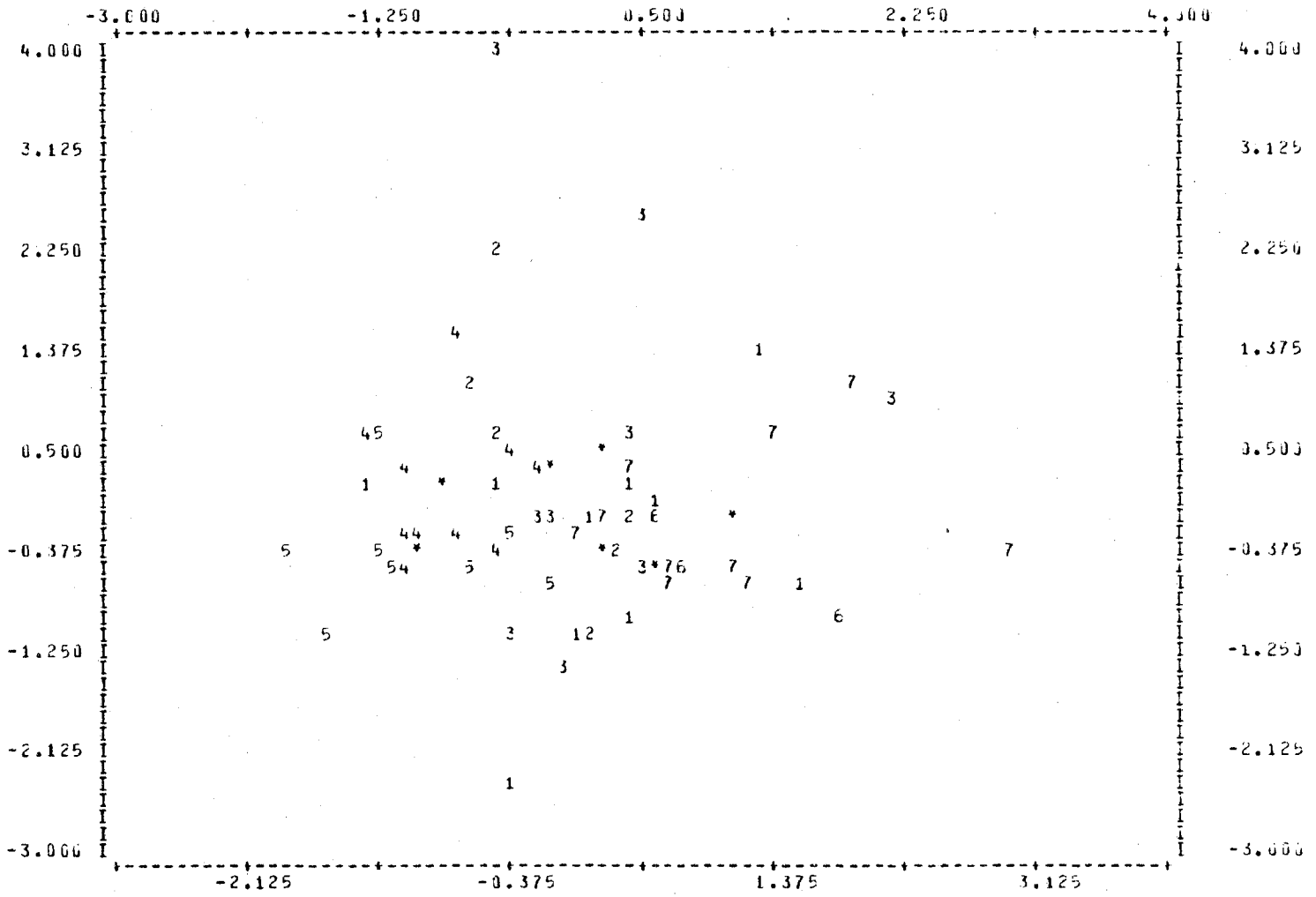
5.2 Discriminant Analysis. In discriminant analysis, the groups are pre-defined, the characters most useful in discriminating these groups are selected, and each individual is subsequently classified into the group for which it has the highest probability of membership. A scattergram may be constructed illustrating the placement of each plant relative to all the other plants and to the centroid of the group to which it belongs. A scattergram for the discriminant analysis is shown in Figure III.

Table VIII gives the relationships between the actual groups and the predicted groups. The analysis selected leaf length and number of teeth as the characters to be used for discrimination. It should be noted that the relative discrimination for leaf length is 88.84% and 11.16% of number of teeth. Leaf length accounts for almost all of the discrimination among the various plants, while number of teeth contributes relatively little. In addition, petiole length is approximately equal to the number of teeth in discriminating ability.

FIGURE III

Plot of discriminant score 1 (horizontal) versus discriminant score 2 (vertical). * indicates a group centroid.

Four characters were discriminated, leaf length, leaf width, petiole length and number of teeth. Analysis chose leaf length and number of teeth as the discriminating characters.


-3.000
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0.500
2.250
4.000
4.000
3.125
2.250
1.375
0.500
-0.375
-1.250
-2.125
-3.000
-2.125
-0.375
1.375
3.125

TABLE VIII

Prediction results from Discriminant Analysis, using four characters (leaf length, leaf width, petiole length, and teeth number). Analysis determined that characters one and four were best at discriminating populations.

Grouped cases correctly classified = 41.38%

PREDICTED GROUP MEMBERSHIP

ACTUAL GROUP	NO. OF CASES	1	2	3	4	5	6	7
1	10	3 30.0%	0 0.0%	1 10.0%	2 20.0%	0 0.0%	2 20.0%	2 20.0%
2	6	3 50.0%	2 33.3%	0 0.0%	1 16.7%	0 0.0%	0 0.0%	0 0.0%
3	9	2 22.2%	2 22.2%	3 33.3%	0 0.0%	0 0.0%	1 11.1%	1 11.1%
4	10	0 0.0%	2 20.0%	0 0.0%	4 40.0%	4 40.0%	0 0.0%	0 0.0%
5	9	1 11.1%	1 11.1%	0 0.0%	2 22.2%	5 55.6%	0 0.0%	0 0.0%
6	4	0 0.0%	0 0.0%	0 0.0%	0 0.0%	1 25.0%	2 50.0%	1 25.0%
7	10	2 20.0%	0 0.0%	1 10.0%	0 0.0%	0 0.0%	2 20.0%	5 50.0%

An analysis of Figure III illustrates a number of important relationships. Members of subpopulation 7 are, for the most part, located in the lower right quadrant of the scattergram. Members of subpopulation 4 and 5 tend to cluster to the left while those of subpopulation 1 are scattered throughout the figure. Individuals of subpopulations 2 and 3 are located centrally and those of subpopulation 6 cluster to the right-center.

Table VIII lists the results of the classification procedure. It places 70% of the plants in subpopulation 7 in groups 6 and 7; all members of subpopulation 6 are classified in groups 5, 6 and 7. This suggests a certain similarity between the members of these subpopulations. The classification procedure places 77.8% of subpopulation 5 and 80% of subpopulation 4 in groups 4 and 5. 77.7% of subpopulation 3 are clustered in groups 1, 2 and 3, while 83.3% of subpopulation 2 are clustered in groups 1 and 2. Subpopulation 1 is not clearly defined and its members are distributed among several of the pre-defined groups.

In summary, classification procedures from discriminant analysis suggest that three major sub-groups may be recognized within the seven subpopulations. One group consists of members of subpopulations 6 and 7; another made up of subpopulations 4 and 5; and one composed of plants in subpopulations 2 and 3. Subpopulation 1 is morphologically diverse and its members do not fit in any one group. This

is also reflected in the positions of the members of subpopulation 1 in the phenograms (Figures I and II).

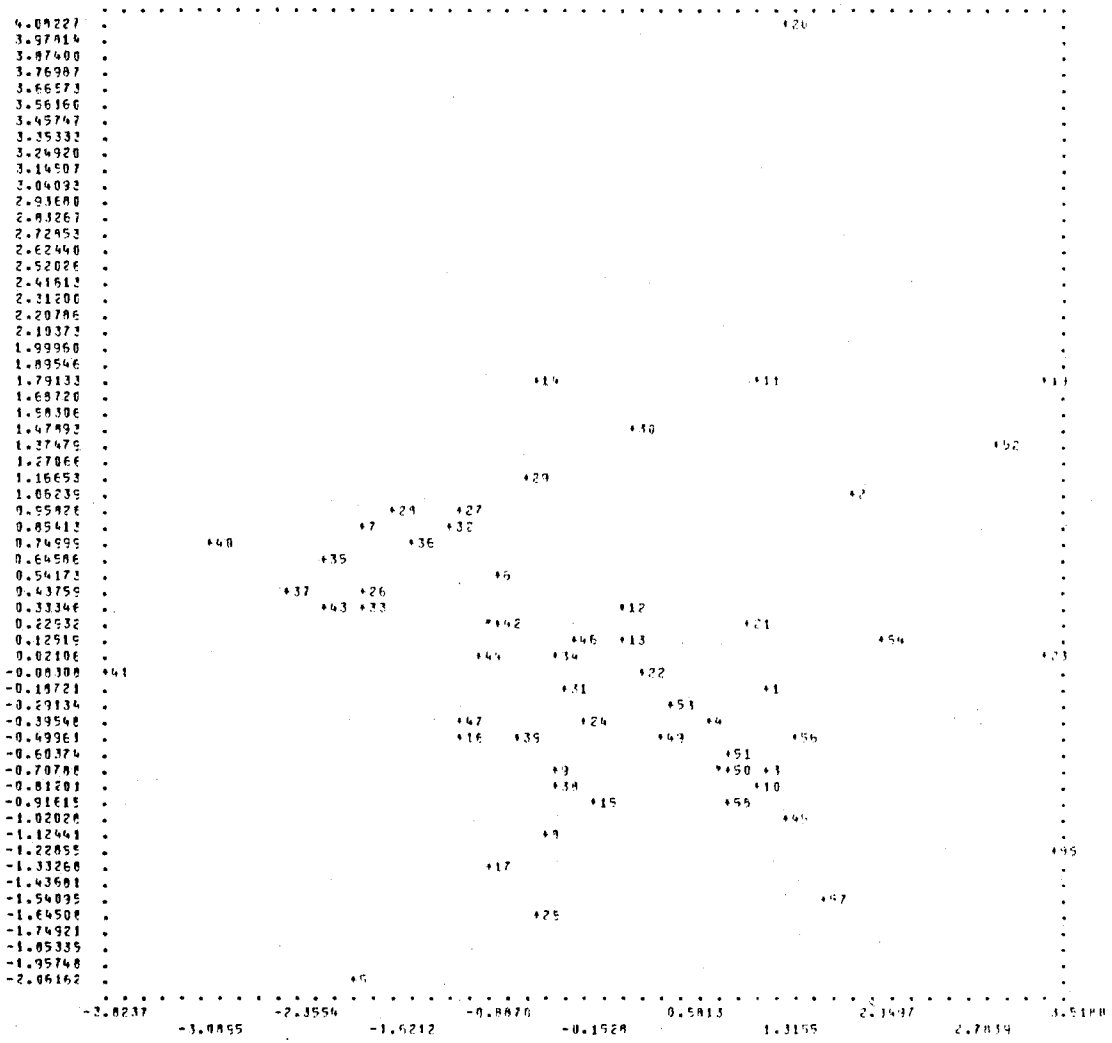
5.3 Principal Component Analysis. A principal component analysis of the 58 OTU-X-OTU correlation matrix is illustrated in Figure IV. Principal component analysis is a multivariate ordination procedure which is most useful in examining broad relationships existing within a set of plants (Sneath and Sokal, 1973). The 58 plants in this study do not separate out into clear-cut subsets in all cases. Nevertheless, the pattern of relationships which emerges is related to that produced by the phenograms (Figures I and II) based on taxonomic distance. It should also be noted that the individual plants tend to cluster in groups more or less corresponding to the clustering of the plants in discriminant analysis (Figure III). For example, the plants of subpopulation 7 (49-58) are found in the lower right quadrant of the scattergram. The members of subpopulations 4 (26-35) and 5 (36-44) are clustered to the left center. This clustering further suggests relationships between subpopulations 4 (26-35) and 5 (36-44). Subpopulations 1 (1-10), 2 (11-16), 3 (17-25) and 6 (45-48) are more widely spread out and don't seem to form any distinct units. This lack of clustering is reflected in both of the clustering procedures.

The more distinct subpopulations (4, 5 and 7) tend to cluster in clear-cut areas on the scattergram, while those

FIGURE IV

Scattergram from principal component analysis.

Horizontal eigenvector = 1; vertical eigenvector = 2. Numbers represent OTUs 1-58.


4.09227
3.97814
3.87400
3.76987
3.66573
3.56160
3.45747
3.35333
3.24920
3.14507
3.04093
2.93680
2.83267
2.72853
2.62440
2.52026
2.41613
2.31200
2.20786
2.10373
1.99960
1.89546
1.79133
1.68720
1.58306
1.47893
1.37479
1.27066
1.16653
1.06239
0.95826
0.85413
0.74999
0.64586
0.54173
0.43759
0.33346
0.22932
0.12519
0.02106
-0.08308
-0.18721
-0.29134
-0.39548
-0.49961
-0.60374
-0.70788
-0.81201
-0.91615
-1.02028
-1.12441
-1.22855
-1.33268
-1.43681
-1.54095
-1.64508
-1.74921
-1.85335
-1.95748
-2.06162
-3.8237
-3.0895
-2.3554
-1.6212
-0.8870
-0.1528
0.5813
1.3155
2.0497
2.7839
3.5181

which are more heterogeneous tend to be more spread out. When compared with the discriminant analysis (Figure III), the groupings are less distinct. This result is expected because principal component analysis does not select the characters to be used in the analysis and weight them unequally in order to maximally separate the groups, which would result in more definitive clustering of the plants.

CHAPTER SIX

DISCUSSION

The seven subpopulations were selected on the basis of their relative positions with respect to the east entrance to the park and the distance between them. Subpopulation 1 was the closest to the entrance of the park and subpopulation 7 was the furthest away. Subpopulation 1 is a very large one, consisting of nearly 100 individuals. It is subjected to the greatest amount of human impact, owing to its proximity to a playground. The plants in this group range from 1-4 meters in height.

Subpopulation 2 is located alongside the main trail leading down into the canyon. It consists of six individuals of similar size and age. All members of this group were sampled. Subpopulation 3 is a uniform stand of approximately 50 individuals, spread out along a slope above the main trail. Subpopulation 4 is a dense grouping of plants, located in a cluster between two roads. All the members (about 20) appear to be the same height and age. Subpopulation 5 is a group of 9 oaks, growing in a row near the main trail. All members were sampled. Subpopulation 6 is a group of 4 plants, all of which were sampled, growing within seven meters of the stream. Subpopulation 7 is a

very old, dense stand of oaks, containing over 100 members, growing in an area reasonably free of human impact, as it is about 1.6 km from the main entrance.

The notion that there are seven distinct subpopulations is not supported by the data. There are significant differences, however, between some of the groups. Walraven (1970) has used the multiple range test in an attempt to subdivide the genus Rhynchosia (Leguminosae). He found, based on several characters, three major sub-groupings. The multiple range test in this study suggests some grouping of the subpopulations. Using all characters, members of subpopulations 3, 6 and 7 are phenotypically close and may be considered as a single group. Leaf width and petiole length produce results which link subpopulations 4 and 5 together.

Overall, subpopulations 1, 2, 3 and 6 tend to group together; subpopulations 4 and 5 form a single group; and subpopulations 3, 6 and 7 tend to group together.

SAHN clustering procedures have been used extensively for analyzing phenotypic relationships between OTUs (Walraven, 1970; Makurath and Anderson, 1973; Parker, 1976; Jensen and Eshbaugh, 1976 ab; Crovello, 1970; and Jackson and Crovello, 1971). Phenograms, a component of SAHN procedures, are directed graphs that reflect phenotypic relationships (Crovello, 1970). The phenograms in this study (Figures I and II) show a relationship among the

subpopulations which combines the various characters. Subpopulations 6 and 7 show a phenotypic similarity between them, since the individuals of these groups (plants 45-58) are clustered together. Subpopulations 4 and 5 (plants 26-44) are clustered together in levels two and three. Subpopulations 2 and 3 (plants 11-25) are also clustered in levels two and three. (See Table VII.)

Discriminant analysis has also been used as a technique for interpreting variability in nature (Ellis et al, 1971; Ledig et al, 1969; Jensen and Eshbaugh, 1976 ab; Rees, 1969 ab, 1970; and Crovello, 1970). The discriminant analysis in this study tends to support the relationships found in the phenograms (Table VIII, and Figure III). There appears to be, based on the discriminating characters, three major sub-groups of oaks in Wildwood Park. Group one consists of members of subpopulations 2 and 3; group two consisting of members of subpopulations 4 and 5; group three being plants in subpopulations 6 and 7.

Crovello (1970) cites several authors who have used principal component analysis. Principal component analysis shows, in this study, some of the same relationships among the seven subpopulations. It shows a close relationship between subpopulations 4 and 5, and that the members of subpopulation 7 are a distinct unit. Thus, it supports the SAHN procedures in this way and shows that subpopulations 1, 2, 3 and 6 are heterogeneous.

Among the hypotheses proposed to explain the causes of the similarities and differences among these oaks are genetic drift and founder effect, natural selection, hybridization, and nonuniform dispersal of genotypes. The possibility of hybridization implicates Q. agrifolia as a candidate for interspecific hybridization, since it is the only other species of Quercus in the general area. In describing the leaf character of Q. agrifolia, Munz (1968) wrote:

> "..oblong to oval or elliptic, 2-6 cm long, harsh, strongly convex above, glabrate or somewhat stellate-pubescent especially in vein axils on the underside.." (p. 904).

The vast majority of the leaves sampled in this study, however, do not resemble this description (see Appendix). With the exception of some members of subpopulations 1, 3, 6 and 7, all leaves were less than 20 mm in length. Q. agrifolia was present in the vicinity of subpopulation 7 only. Further, all leaves collected of Q. dumosa were highly pubescent and not convex, but flat. Munz (1968) further states that the petioles of Q. agrifolia have lengths of from 5 to 15 mm. No samples of Q. dumosa had petioles as long as 5 mm.

Watkins and DeForest (1941) reported that the growth of Q. dumosa occurs primarily in the spring, after the major rainfall period of the winter. It remains, in effect, dormant during the dry summer season, only to begin growth again when the rainy season returns. The amount of soil

moisture, therefore, would have little effect on the growth of the individual plants, in that the soil is saturated during the growing period, no matter where the plants are. The soil types present in the study site are similar, composed of clay and adobe with a small amount of humus and decomposed granite. Other plants found in the study site, for example, Y. Whipplei, P. ilicifolia, Ceanothus spp., and A. fasciculatum, were found consistently in association with the subpopulations of Q. dumosa. Since the major growth period is in the early spring, when the park is used little by humans, their effect may be minimal. Although several factors point in the direction of relative uniformity of the environment in the study area, it has not been possible to assess the sensitivity of leaf and acorn characters to fluctuations in the environment which undoubtedly occur.

Extensive evidence in recent years has indicated that genotypic differentiation in plants can take place over very short distances. Jain and Marshall (1967) describe variation in species of wild oats, Avena. They observed A. barbata Brot. was much more monomorphic and had greater genetic homogeneity within populations than A. fatua L. Because A. fatua grew primarily in disturbed areas, they hypothesized that it "needed" more variability to cope with this unstable environment.

McNeilly and Bradshaw (1968) studied Agnostis tenuis Sibth. growing around copper mines.

> "..There is evidence of gene flow into mine populations and also for genetic segregation within these populations. By contrast, there is little evidence of gene flow into nontolerant populations.." (p. 118).

They used the amount of copper in the soil that a plant could tolerate as the measure of gene flow. Sample plants, collected from areas where the soil copper content was high (near the mines), showed a high degree of copper tolerance. Yet some others collected from the same area were found to have no copper tolerance in the laboratory. Yet these plants grew very well among the copper tolerant ones. On the other hand, in populations growing where the copper content of the soil was low were found to have little copper tolerance. No copper tolerant plants were found in these areas. This suggests that the gene flow was in the direction of the copperladen soils, but not the other way.

If gene flow was the major cause of the variation pattern in the oaks, there should be some consistent pattern distinguishable among the subpopulations. One might expect the subpopulations that are in closest proximity to be the most similar. The order of the ranked means for subpopulations 1-7 (Table VI) is not consistent, however, with their spatial arrangement from east to west in the study area. Therefore, evidence seems to be lacking to

support the hypothesis that gene flow is the cause of the pattern of variability.

Since the subpopulations, as shown by the multiple range test (Table VI), SAHN clustering procedures (Figures I and II), and discriminant analysis (Table VIII) form phenotypically distinguishable groups; that is, subpopulations 2 with 3, subpopulations 4 with 5 and subpopulations 6 with 7, it would appear that the causal agent for the variability may be a restriction of gene flow to boundaries within each of the three groups. It may be that groups were initially established by a few pioneer individuals whose progeny were spread, perhaps by animals, and became established in the various locations where they are presently found. Therefore, the pattern of variability is consistent with the hypothesis that the variability of these oaks is due, primarily, to a restriction of gene flow and founder effect (Mayr, 1968).

The variability of Q. dumosa has been documented in this study. As described by Jepson (1925) and McMinn (1939) this local group of oaks is highly variable in leaf character. Yet the sizes of the leaves and petioles are reasonably close to the ranges mentioned by them and also by Munz (1968). On the basis of those criteris, this local group of scrub oaks is basically similar to other populations in Southern California.

The use of the species as a functional unit has been questioned by some authors (Ehrlich and Raven, 1969; Burger, 1975). They suggest that the local population is the important evolutionary unit, a point of view which is supported by this study. A strict adherence to the notion of a species, particularly one as widely diverse in environments as Q. dumosa, fails to take into account all of the variables which can effect the phenotypic variations of organisms. More extensive studies of this type, that is, of local groups of organisms, should be undertaken in order to document the patterns of variation and discover the factors responsible for these patterns.

CHAPTER SEVEN

CONCLUSIONS

The following statements summarize the conclusions reached in this study:

1) The variation in six morphological characters, four vegetative and two reproductive, in a local population of oaks has been found to be great, coefficients of variation ranging from 12.05% to 37.9%.

2) Differences in means among plants at seven sites within the study area were found to be significant for three of the six characters, leaf length, leaf width, and petiole length. No evidence was obtained suggesting that differences in means between subpopulations were associated with a geographic gradient.

3) Differences in variances among plants at seven sites within the study area were found to be significant for two vegetative characters, leaf length, and number of teeth.

4) The variation for each of the four vegetative characters was greater than that of either of the two reproductive characters, based on the coefficients of variation.

5) Associations between dimensions were found to be significant for leaf length and petiole length ($r = 0.809$), leaf length and number of teeth ($r = 0.815$), petiole length and number of teeth ($r = 0.823$), and leaf width and number of teeth ($r = 0.373$).

6) Cluster analysis arranged the individuals in four major groups.

7) Additional multivariate analyses, using three different procedures, resulted in the classification of individual plants into three major groups which were similar, but not identical in their membership in each case.

8) The possible role of interspecific hybridization as a potential source of the observed microspatial differentiation was rejected. Other mechanisms, including founder effect and genetic drift, gene flow, natural selection, and nonuniform dispersal of genotypes could not be fully assessed, particularly since the data did not permit an assessment of the relative contributions of genotype and environment to the observed phenotypic variation.

9) The founder effect and restriction of gene flow between the more widely separated subpopulations appears to be the most likely explanation for some of the differences.

10) Although the subpopulations have been distinguished phenotypically, it has not been within the scope of this study to determine to what extent they represent isolated reproductive units.

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APPENDIX A

MEAN VALUES FOR EACH CHARACTER OF THE 58 INDIVIDUAL PLANTS (OTUs).

PLANT NUMBER	OTU NUMBER	LEAF LENGTH	LEAF WIDTH	PETIOLE LENGTH	NUMBER OF TEETH	ACORN LENGTH	ACORN WIDTH
100	1	20.6	14.8	3.3	10.4	24.7	12.0
101	2	24.8	14.3	2.9	15.5	26.0	8.9
102	3	18.6	14.6	3.9	9.8	30.7	11.8
103	4	24.3	13.4	2.5	7.6	--	--
104	5	14.2	7.8	2.8	0.8	24.2	10.1
105	6	16.0	9.9	2.2	10.7	--	--
106	7	12.1	8.6	1.7	10.4	--	--
107	8	17.0	11.0	3.1	5.5	--	--
108	9	19.0	10.7	2.7	6.4	--	--
109	10	19.9	12.2	4.2	10.6	--	--
201	11	17.6	14.3	2.9	17.9	28.0	10.9
202	12	16.4	11.7	3.1	12.0	28.1	11.4
203	13	19.5	11.7	2.6	9.9	--	--
204	14	16.0	12.5	1.4	13.5	--	--
205	15	18.9	8.8	3.6	8.6	--	--
206	16	17.7	9.5	2.1	6.0	--	--
300	17	16.4	9.5	3.0	4.4	--	--
301	18	17.2	8.9	2.3	9.6	--	--
302	19	22.3	20.5	3.5	19.3	--	--
303	20	19.3	15.0	1.5	24.5	--	--
304	21	20.3	13.6	3.2	12.3	26.0	13.3
305	22	19.8	13.8	2.4	8.0	--	--
306	23	28.5	16.9	4.0	14.1	--	--
307	24	17.1	10.3	3.2	9.6	24.8	11.4
308	25	15.4	8.9	3.9	5.9	--	--
400	26	12.4	10.1	1.5	7.4	23.5	11.8
401	27	17.4	8.7	1.6	10.9	19.9	10.6
402	28	12.3	8.2	2.0	11.9	21.0	12.0
403	29	16.6	11.7	1.7	11.7	17.2	11.3
404	30	15.8	12.5	2.5	15.3	24.9	10.8
405	31	14.3	12.1	3.0	9.1	25.9	11.4
406	32	13.3	10.0	2.0	11.2	23.1	11.9
407	33	12.8	7.7	2.0	9.0	23.7	12.8
408	34	15.6	13.1	2.4	8.3	23.5	10.5
409	35	13.2	7.6	1.5	8.7	25.5	13.6
500	36	13.0	7.2	2.4	12.2	25.6	9.5

PLANT NUMBER	OTU NUMBER	LEAF LENGTH	LEAF WIDTH	PETIOLE LENGTH	NUMBER OF TEETH	ACORN LENGTH	ACORN WIDTH
501	37	12.3	7.4	1.4	7.4	24.3	12.4
502	38	16.1	8.8	3.6	8.7	20.1	9.2
503	39	16.6	10.6	2.6	7.1	23.0	10.8
504	40	9.3	6.7	1.2	8.2	32.1	14.6
505	41	9.5	2.9	1.3	5.1	27.4	11.5
506	42	14.3	9.6	2.7	10.3	20.7	12.3
507	43	11.9	8.2	1.7	8.0	20.8	10.0
508	44	14.7	11.2	2.2	7.9	22.0	9.9
600	45	21.0	14.6	3.9	8.3	23.4	12.5
601	46	20.4	9.5	2.4	9.9	27.8	10.0
602	47	13.3	8.9	3.0	8.4	22.4	10.2
603	48	25.2	13.5	2.5	6.5	26.3	13.6
700	49	20.5	12.8	2.9	8.0	--	--
701	50	19.0	13.3	3.8	9.6	--	--
702	51	20.5	14.9	3.1	7.8	--	--
703	52	27.4	20.6	2.3	14.4	--	--
704	53	18.1	13.7	3.1	9.0	--	--
705	54	24.5	15.0	3.5	12.8	--	--
706	55	30.6	17.8	4.1	9.0	--	--
707	56	20.2	13.5	4.0	11.5	--	--
708	57	22.4	13.4	4.5	8.3	--	--
709	58	22.7	12.9	3.3	7.5	--	--

APPENDIX B

OTU (PLANT) NUMBERS WHICH ARE FOUND IN EACH OF THE SUBPOPULATIONS

OTU NUMBERS	SUBPOPULATION NUMBER
1 - 10	1
11 - 16	2
17 - 25	3
26 - 35	4
36 - 44	5
45 - 48	6
49 - 58	7