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OF TWO STANDS OF VEGETATION IN THE
SONORAN DESERT.

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AN EVALUATION OF THE HOMOGENEITY
OF TWO STANDS OF VEGETATION IN THE
SONORAN DESERT

by

Robert Anderson Wright

A Dissertation Submitted to the Faculty of the

DEPARTMENT OF BOTANY

In partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY

In the Graduate College

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1965

THE UNIVERSITY OF ARIZONA
GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my
direction by Robert Anderson Wright
entitled An Evaluation of the Homogeneity of Two Stands
of Vegetation in the Sonoran Desert
be accepted as fulfilling the dissertation requirement of the
degree of Doctor of Philosophy

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TABLE OF CONTENTS

	PAGE
LIST OF TABLES	v
LIST OF FIGURES	viii
ABSTRACT	ix
INTRODUCTION	1
REVIEW OF LITERATURE	6
STUDY AREA	11
METHODS OF INQUIRY	17
RESULTS	24
DISCUSSION	45
LITERATURE CITED	53
APPENDIX	58

LIST OF TABLES

TABLE	PAGE
1. Analysis of variance for the contiguous quadrat analysis of 256 units	21
2. Analysis of variance for <u>Larrea tridentata</u> , percentage cover transformed to inverse sine (radians)	25
3. Analysis of variance for <u>Franseria deltoidea</u> , percentage cover transformed to inverse sine (radians)	25
4. Summary of variance ratio test for <u>Larrea-Franseria</u> stand	26
5. Analysis of variance for <u>Cercidium microphyllum</u> , percentage cover transformed to inverse sine (radians)	28
6. Analysis of variance for <u>Opuntia acanthocarpa</u> , percentage cover transformed to inverse sine (radians)	28
7. Analysis of variance for <u>Opuntia fulgida</u> percentage cover transformed to inverse sine (radians) .	29
8. Analysis of variance for <u>Opuntia engelmannii</u> , percentage cover transformed to inverse sine (radians)	29
9. Analysis of variance for <u>Opuntia macrocentra</u> , percentage cover transformed to inverse sine (radians)	30
10. Analysis of variance for <u>Acacia constricta</u> , percentage cover transformed to inverse sine (radians)	30
11. Analysis of variance for <u>Calliandra eriophylla</u> , percentage cover transformed to inverse sine (radians)	31
12. Analysis of variance for <u>Janusia gracilis</u> , percentage cover transformed to inverse sine (degrees)	31

LIST OF TABLES (continued)

TABLE	PAGE
13. Analysis of variance for <u>Olneya tesota</u> , percentage cover transformed to inverse sine (radians)	32
14. Analysis of variance for <u>Euphorbia capitellata</u> , percentage cover transformed to inverse sine (radians)	32
15. Analysis of variance for <u>Muhlenbergia porteri</u> , percentage cover transformed to inverse sine (radians)	33
16. Analysis of variance for <u>Hymenoclea monogyra</u> , percentage cover transformed to inverse sine (radians)	33
17. Analysis of variance for <u>Aplopappus spinulosus</u> , percentage cover transformed to inverse sine (radians)	34
18. Analysis of variance for <u>Hilaria belangeri</u> , percentage cover transformed to inverse sine (radians)	34
19. Summary of variance ratio test for <u>Cercidium-</u> <u>Carnegiea</u> stand	35
20. Analysis of variance of differences between 1,024 successive transect units for <u>Larrea</u> <u>tridentata</u> , percentage cover transformed to inverse sine (radians)	38
21. Analysis of variance of differences between 1,024 successive transect units for <u>Franseria</u> <u>deltoidea</u> , percentage cover transformed to inverse sine (radians)	38
22. Analysis of variance of differences between 1,024 successive transect units for <u>Cercidium</u> <u>microphyllum</u> , percentage cover transformed to inverse sine (radians)	38
23. Analysis of variance of differences between 736 successive transect units for <u>Opuntia acantho-</u> <u>carpa</u> , percentage cover transformed to inverse sine (radians)	39

LIST OF TABLES (continued)

TABLE	PAGE
24. Analysis of variance of differences between 512 successive transect units for <u>Opuntia fulgida</u> , percentage cover transformed to inverse sine (radians)	39
25. Analysis of variance of differences between 256 successive transect units for <u>Opuntia engelmannii</u> , percentage cover transformed to inverse sine (radians)	39
26. Analysis of variance of differences between 208 successive transect units for <u>Opuntia macro-centra</u> , percentage cover transformed to inverse sine (radians)	40
27. Analysis of variance of differences between 320 successive transect units for <u>Acacia constricta</u> , percentage cover transformed to inverse sine (radians)	40
28. Analysis of variance of differences between 496 successive transect units for <u>Olneya tesota</u> , percentage cover transformed to inverse sine (radians)	40
29. Analysis of variance of differences between 256 successive transect units for <u>Muhlenbergia porteri</u> , percentage cover transformed to inverse sine (radians)	41
30. Analysis of variance of differences between 192 successive transect units for <u>Hymenoclea monogyra</u> , percentage cover transformed to inverse sine (radians)	41
31. Analysis of variance of differences between 176 successive transect units for <u>Aplopappus spinulosus</u> , percentage cover transformed to inverse sine (radians)	41

LIST OF FIGURES

FIGURE	PAGE
1. Map of study area	13

ABSTRACT

Homogeneity of vegetation in the Sonoran Desert was evaluated by statistical techniques. The area studied is west of Tucson, Arizona-- the western slope of the Tucson Mountains and the adjoining Avra Valley. The vegetation consists of the species-poor, shrub dominated Larrea-Franseria association and the more diverse and complex tree dominated Cercidium-Carnegiea association.

Cover of all perennial plant species along a 12,000 meter transect was measured in contiguous 5 meter units using the line intercept method. These units were the basic units of analysis. Alternate units were analyzed to avoid trivial association between adjacent records.

Individual species populations were first analyzed for homogeneity of distribution within the confines of the stand. The data were converted to inverse sine and an analysis of variance performed using an IBM 7072 computer. The data from successive units were combined into blocks; these blocks being essentially larger sized units. The variance attributable to each block size allowed detection of a scale of heterogeneity for a particular sample size. Significance of variances was determined by the F test by comparing a variance with that for the next smaller block size. The criterion of homogeneity was constancy of variance for all species for block sizes above that block size representing minimal area.

In the Larrea-Franseria stand only two species--Larrea tridentata and Franseria deltoidea--had sufficient data to be analyzed. Larrea had a constancy of variance for all block sizes. Franseria had one possible significant variance, which occurred at a small block size. These results suggested a minimal area for the smallest block size of constant variance and homogeneity above this block size.

Of fourteen species analyzed in the Cercidium-Carnegieia association, six had no significant variances; five had one such variance; and three had two. Those species having no significant variances were considered to be homogeneously distributed. All significant variances occurred either at a small block size, which suggested a minimal area, or at a large block size, which represented the limits of the species distribution in the stand. The vegetation was then considered as homogeneous within the limits set by the two groups of variances.

In addition to testing for homogeneity within the stand, species populations extending throughout the range of the species in the area were analyzed to evaluate relative homogeneity; that is, stand homogeneity and ecotone heterogeneity. The differences in percentage cover between successive transect units were subjected to an analysis of variance. Relative homogeneity was indicated by the variance between transects being greater than that within transects. This test indicated that the species of the Larrea-Franseria

stand are homogeneously distributed within the stand and heterogeneous in the transition zone. Of the ten species analyzed in the Cercidium-CarNEGIEA stand, the distribution of only two species showed relative homogeneity. Since the other eight species were found to have homogeneous distributions by the first analysis, the lack of significance in the relative homogeneity test was taken to indicate that they were homogeneous in distribution in the ecotone as well as in the stand.

The results were discussed in relation to those concepts which have been associated with vegetational homogeneity: the stand and its boundary, the continuum concept, and the individualistic concept of the plant community. It was concluded that (1) the vegetation of the study area has two centers of homogeneity but no fundamental difference in structure between the stand and the ecotone and (2) the data present no direct evidence for evaluating the applicability of the continuum concept or the individualistic concept to vegetation of the Sonoran Desert.

INTRODUCTION

The community-unit theory of phytosociology concerns the relation of properties of natural communities to the conceptual units of classification (Whittaker, 1962). One aspect of this relationship concerns natural communities; that is, the stands of vegetation as they occur in the field. The first criterion of the stand as a unit for classification is homogeneity of its vegetation (Goodall, 1952). Few studies have objectively evaluated the validity of accepting the idea that homogeneous areas of vegetation actually exist. The purpose of the present study is to present the problem of homogeneity as a hypothesis and to test this hypothesis.

The community-unit theory proposes that natural units exist in vegetation and that the classification of these units is natural rather than arbitrary (Whittaker, 1962). Homogeneity is part of this general problem and it should be evaluated and discussed within this general context.

The idea that natural units exist in vegetation was developed mainly in Europe during the 1800's (for a historical perspective see Moss, 1910; Clements, 1916; Du Rietz, 1921; Whittaker, 1962). Except for some early dissenters such as Gleason (1926) and Shreve (1915), the community-unit theory was accepted by most classifiers of vegetation. Recently a rigorously supported denial of the validity of the

community-unit theory has been made, as exemplified by the investigations of Whittaker (especially 1951, 1953, 1957) and the Wisconsin school (particularly Curtis and McIntosh, 1951; Curtis 1955). (See Whittaker, 1962 for other references, particularly foreign ones). These workers believe that vegetation classification is arbitrary rather than natural.

The community-unit theory is therefore shown to be controversial. To aid in settling one aspect of this controversy, the validity of accepting homogeneous natural units of vegetation should be tested. The methods of inquiry employed should be quantitative and as free as possible from personal bias. An appropriate tool for such an inquiry would appear to be a statistical analysis of measured quantities. Homogeneity of vegetation was therefore tested by statistical analysis in order to help evaluate the relation of natural communities to the conceptual units of classification.

The statistical technique used was the analysis of variance. Homogeneity of species distribution was first sought within the confines of two distinct stands of vegetation in the Sonoran Desert using the contiguous quadrat analysis of variance (which will be further discussed in the literature review and methods sections). The contiguous quadrat analysis allows one to determine at what sample size a particular heterogeneity occurs and is especially valuable in detecting heterogeneity due to mosaic patterns. It is a

more powerful tool than the random quadrat method, which does not allow detection of various sizes of heterogeneity (Thompson, 1958).

In this analysis, data of individual species from adjacent quadrats or transects are combined into blocks of increasing sizes. The size of a particular block gives the number of quadrats or transects included; for example, block-size 1 is composed of single adjacent units, block-size 2 is composed of two adjacent units, etc. The sum of squares and the variances can be calculated for each block size. A significantly high variance for a particular block size will indicate some type of heterogeneity, perhaps due to a mosaic pattern.

Since significantly large variances represent a scale of heterogeneity, individual species populations are considered to be homogeneously distributed when the variance is constant for all block sizes. The vegetation would be considered homogeneous if its component species are homogeneously distributed. Significant variances could occur at one of the smaller block sizes for each species. It is the constancy of variance above this lower limit which would indicate homogeneity. A significantly high variance at a small block size with constancy of variance at larger block sizes would indicate a minimal area¹ for that species at the

1. Since the measurements in this study are linear, it would be more acceptable to refer to minimal intercept rather than minimal area, but the more commonly used term will be used here.

smallest block size of constant variance. If most of the species showed the same pattern, then the minimal area for the vegetation would be indicated.

If, on the other hand, there is no uniform block size beyond which variance is constant for all species, then there is no minimal area. Also, if there are significant variances at yet larger block sizes, the species would be heterogeneously distributed and accordingly the vegetation would be considered heterogeneous.

In addition to testing for homogeneity within the confines of the stand, relative homogeneity was evaluated for the entire distribution of species in the area by an analysis of variance. Relative homogeneity refers to homogeneous distribution of species within the stand and heterogeneous distribution in the ecotone between the stands. The existence of such distribution can be tested by a statistical procedure which will be termed the successive unit analysis of variance. Goodall (1954b) used such an analysis to compare the variance between replicate or successive quadrats within the stand to that in the transition zone. In the present study Goodall's procedure was followed, and for all those analyzable species whose distribution extended into the ecotone, the differences in percentage cover between successive transect units were subjected to an analysis of variance. If the stands are homogeneous and the ecotone heterogeneous, then the difference between a pair of units

should be more like the next pair than like a pair in the ecotone. In terms of the analysis of variance, if the variance accounted for between transects is significantly greater than the variance accounted for within transects, then the hypothesis of stand homogeneity and ecotone heterogeneity is accepted.

REVIEW OF LITERATURE

In the present study the vegetation is considered homogeneous when the component species are homogeneously distributed. This consideration is based on Goodall's (1952) statement that homogeneous vegetation is composed of homogeneously distributed species. Dahl and Hedac (1949) considered homogeneously distributed plant species as those in which the probability of obtaining an individual in an area of a given size is the same in all parts of that area. Goodall (1961) noted that this definition does not account for mosaic patterns in the vegetation. That homogeneity depends on the scale of observation when mosaic patterns are present had been noted earlier by Romell (1926). As stated by Goodall (1952), based on Romell's ideas, there is a small-scale heterogeneity when the size of the sample areas is smaller than the size of the individual plant, each plant being a discrete element. When these plants are distributed in clumps, there may be a larger scale heterogeneity. Homogeneity can be obtained in the case when these clumps are regularly or randomly distributed themselves if the sample size is large compared to the size of the clumps. To account for mosaic patterns, Goodall (1961) proposed as a working hypothesis: "the distribution of a species in an area of vegetation is homogeneous if there exists some sample size

for which the variation between replicate samples is independent of the distance between them."

Goodall (1954a, 1954b, 1961) tested the homogeneity of plant species based on his working definition. Using the contiguous quadrat analysis of variance to test the relation of variance to spacing of quadrats, Goodall (1954a) found that in the Salt Marshes at Rhyll in Phillips Island, S. E. Australia the vegetation showed no minimal area, thus no homogeneity.

In a later paper Goodall (1954b) evaluated homogeneity more extensively. He used three criteria to determine homogeneity: (1) random distribution of individuals of each species as tested by agreement with a Poisson series; (2) independence of variance from spacing of quadrats; i.e., constancy of variance with increasing quadrat spacing; and (3) lack of correlation between the quantities of species in a sample area. Finding that his data indicated no strictly homogeneous areas of vegetation, he suggested that there might be a greater degree of homogeneity within a stand than within a transition zone. By comparing the variance between replicate samples across the entire species distribution in his study areas, he concluded that the variances in adjacent areas did not agree better than variances in areas separated by a gap; thus no relative homogeneity was found.

Grieg-Smith (1957) commented that Goodall's (1954b) samples appeared to have been taken from what would more

than likely be considered as a single community and suggested that the approach be tried in areas of more diverse vegetation. Poore (1962) agreed with Grieg-Smith's comment and suggested an extensive analysis for homogeneity be made in a region where distinct claims have been made for phytosociological methods.

In 1961 Goodall reported that further testing with the contiguous quadrat analysis, in areas previously studied and in some additional areas, again showed no homogeneity of vegetation. He reported the results of testing an alternative hypothesis which he proposed in the earlier papers-- that variance is a continuous function of spacing, the function being a linear relationship between the logarithms of variance and mean distance between sample areas. A linear regression between the logarithms of these variables fitted the data in many cases; in others he found a quadratic or higher-order regression. His general conclusion was that the replacement of one vegetation type by another may well be a continuous, gradual phenomenon with no distinct homogeneous stands or transitional zones.

The contiguous quadrat method was first used by Goodall (1954a) and independently by Grieg-Smith (1952a). As mentioned above, Goodall used it on several populations of plants in Australia to relate variance with spacing. Grieg-Smith used it as a test for pattern within a community. Grieg-Smith's method was derived empirically from experiments

of artificial populations of known pattern. Later Thompson (1955, 1958) reviewed Grieg-Smith's method based on expected variances calculated for various models. Several further studies or discussions of the method have been made, especially in relation to pattern of distribution within a community (Grieg-Smith, 1952b, 1957, 1961a, 1961b, 1961c; Grieg-Smith and Kershaw, 1958; Grieg-Smith, Kershaw, and Anderson, 1963; Goodall, 1954b, 1961; Phillips, 1954; Kershaw, 1957, 1958, 1959, 1960, 1963; Kershaw and Tallis, 1958; Chadwick, 1960; Cooper, 1960, 1961; Agnew, 1961; Anderson, 1961a, 1961b; McDonough, 1961).

Claims to homogeneity of distribution can be noted in some of the following investigations on species distribution in the Sonoran Desert. Shreve (1951) mentions that in the Arizona Upland (the sub-division of the Sonoran Desert in which the study area is situated) the vegetation is relatively homogeneous. He also mentions that there is no suggestion of the mosaic type of distribution in the Sonoran Desert.

Turner(1962), investigating the distribution of Larrea divaricata (=tridentata) and Franseria dumosa as dominants in a desert area near Phoenix, Arizona, concluded that both species are distributed homogeneously; Franseria being dispersed strikingly uniformly.

McDonough (1963) obtained density data for nine species in the Tucson Mountains using quadrat radii of 10, 20, and 30 feet. From the ratio of variance to the mean, he

found indications of aggregation at the larger quadrat sizes in particular stands and believed this to be due to the presence of localized sites favorable to the establishment and growth of the species. He concluded that in the Sonoran Desert in general, with the limited exceptions of Larrea tridentata, Fouquieria splendens, and Opuntia spp., the stands show a low degree of heterogeneity, with little tendency toward the organization or maintenance of particular grouping of species. He considered that the outstanding feature of the habitat is its uniformity with respect to occupancy by individuals of the species he investigated.

Bingham (1963) considered that the vegetation in the lower San Pedro Basin of the Sonoran Desert existed as a vegetational continuum following a gradient of soil moisture.

Lowe (1959, 1964), apparently considering vegetation on a large scale, regards the North American Desert as embodying both the continuum and the mosaic as ecologic configurations. Considering mosaics, he states that there is often "abrupt repetition of climax biotic associations in the emerging form of a huge and irregular environmental chessboard on which the plants and animals are the pawns of the paired controls of the topography and soil under the same climate."

THE STUDY AREA

The study area is located on the western slope of the Tucson Mountains and the adjacent Avra (or Altar) Valley. This area was selected because it met the following requirements:

(1). The site should include what would subjectively be called more than one community. As noted in the literature review, Grieg-Smith (1957) and Poore (1962) criticized a study by Goodall (1954b), which motivated my study, for including only a single community. The present study included two stands to satisfy the desire for a study of homogeneity of diverse vegetation.

(2). There should be a gradual change in the gradient of the slope. In the Sonoran Desert, one of the two communities studied (the Cercidium-Carnegiea community) occurs mainly on slopes, while the other (the Larrea-Franseria community) occurs mainly on more nearly level topography. A gradual change in the gradient of the slope prevents a rapid transition from one stand to the other due to rapidly changing environmental factors.

(3). There should be no irregular topographic features. Homogeneity depends on uniform variation in species distribution over an area. Sharp changes in topography

might well cause a change in the variation and prevent the detection of homogeneity.

(4). There should be no large unnatural discontinuities in the vegetation cover. Such discontinuities would not allow species distributions to be continuously followed.

Yang (1957) studied vegetational, edaphic, and faunal correlations along a transect in this area. For the convenience of using an established transect with permanent markers, the present transect was established coincident with that of Yang.

The transect starts at a point about one-half mile downslope from Wasson Peak. It extends from there approximately 12,000 meters to a point delimited by Sandaria Road, about 0.8 mile south of Twin Peaks Road (Figure 1). The highest point of the transect is at 3,500 feet; the lowest at 2,075 feet (Yang, 1957).

The area is in the northeastern part of the Sonoran Desert and is part of the Basin and Range physiographic Province (Fenneman, 1931). The climate of this area is semi-arid, the outstanding characteristic of which is precipitation with low mean values and high variability (McDonald, 1956). The principal sources of precipitation are the moist, Polar Pacific air during the winter and the moist, warm Tropical Gulf air during the summer (Dorroh, 1946). The greater percentage of annual precipitation occurs during July, August, and September. The spring and fall months are

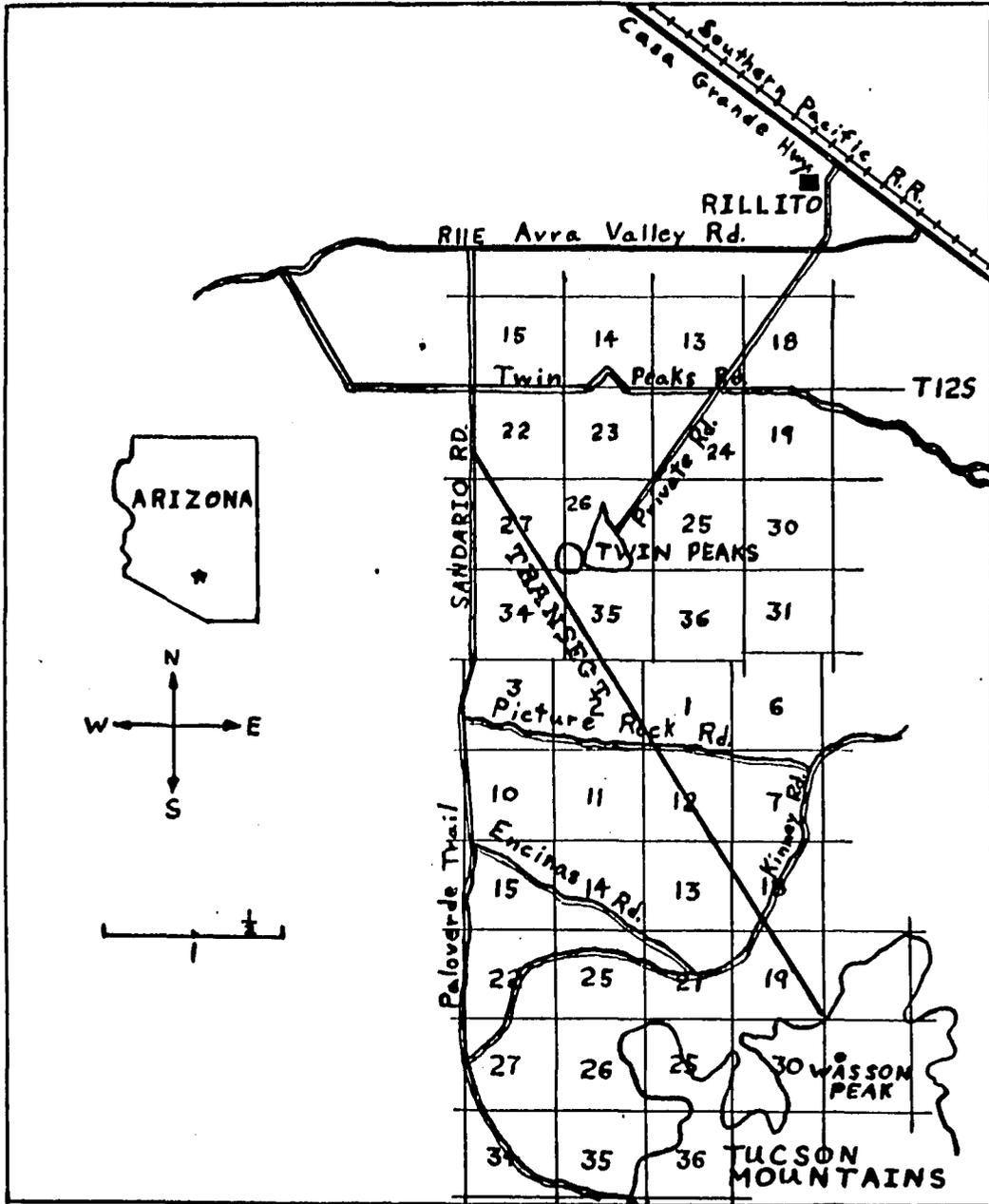


Figure 1. Map of the study area

transitory periods of relatively little precipitation. Daily temperatures fluctuate widely. Smith (1956) gives a yearly evaporation figure for Tucson of 85.15 inches. Using an annual precipitation value of 10.36 inches, the ratio of precipitation to potential evaporation is 1:8.2.

The transect extends over two distinct physiographic elements, the Altar alluvial embankment and the Altar pediment, to near the base of a third, the western escarpment of the Tucson Mountains (Brown, 1939). According to Brown, the Tucson Mountains are a tilted, lava-capped range consisting of a series of folded and thrust-faulted Paleozoic and Mesozoic sedimentary rocks. After thrusting and intrusion, there was a period of erosion resulting in peneplanation and almost complete removal of the sheet of Paleozoic sedimentary rocks. Tertiary volcanics accumulated on the erosion surface and then the entire area was broken by high angle faults; blocks were tilted to the northeast and later eroded. Erosion caused a retreat of the western escarpment and developed a wide pediment. The rock-floored pediment slopes westward to the Altar embankment which is covered with alluvium of unknown depths.

Yang (1957) studied specific edaphic characteristics of the area in relation to spatial distribution of the vegetation. A mantle of debris, or alluvium, which is the unconsolidated substrate of a desert climate covers the pediment. This alluvium is known as fanglomerate and

characterizes the soil of the general area. There is an edaphic gradient from the coarser textured soils at the base of the escarpment, across the Altar pediment, to the finer textured soils of the Altar alluvial embankment. Yang found that the coarser textured soils have a smaller amount of capillary water, as measured by moisture equivalent methods, but have more water available to the plants as indicated by wilting coefficient values. The finer textured soils, on the other hand, have a greater amount of capillary water but a relatively smaller portion of it is available to the plants.

Yang (1957) emphasizes that there are two and only two major plant communities occurring in the entire study area. One is the Larrea-Franseria association (Lowe, 1959); a shrub dominated community which occurs on the finer textured soils. The other is the Cercidium-Carnegiea association (Lowe, 1959); a tree dominated community which occurs on the coarser textured soils. Between these distinct communities there occurs an ecotone in which the dominants of each commingle. The extent of the stands in relation to the ecotone are indicated by Yang's (1957) division of the transect. Based on quadrats at fourteen stations along the transect he determined, by noting the dominant species within each quadrat, that 33.1% of the transect was Larrea dominated, 47.5% was Larrea-Cercidium co-dominated, and 19.5% was Cercidium dominated. Yang and Lowe (1956) consider these associations as climax vegetation types existing under the

same macroclimate but each underlain by specifically different soil types.

METHODS OF INQUIRY

Field Methods

The analytic characteristic chosen for describing the vegetation was cover. The difficulty of determining the extent of a single individual of Larrea tridentata,² (the individuals of which often occur clumped together in a mound) and the difficulty of comparing individuals of varying sizes within and between species argues against using density or frequency for this purpose. In addition, canopy coverage may be the most important single obtainable parameter of a species in its community relations (Lindsey, 1956) and is an approximation of the area upon which a plant influences the other components of the ecosystem (Daubenmire, 1959).

A line intercept method was used to determine cover. This method has two advantages especially valuable in a study of this type: actual measurements are made rather than estimates, and these can be made quickly. A possible disadvantage of the method may be an introduction of bias in measuring columnar plants, especially Carnegiea gigantea. A distance of only a few centimeters is critical in either intercepting or not such a plant. The investigator may be biased in including or excluding certain plants and can only

2. Plant nomenclature in this paper follows that of Kearney and Peebles (1960).

hope that the probable error is compensatory rather than cumulative. Also since the columnar plants have no canopy but yet may be quite tall, intercept values alone undoubtedly give an underestimate of biomass relative to other plants.

As indicated above, the present transect was made coincident with that of Yang (1957). The twenty-four equally spaced galvanized iron pipes which were established by Yang were used for orientation in the present study. Poles, about 15 feet long with flags attached, were used for recognition of these points. Additional poles were placed between the others so that two poles were in the line of sight at all times. In particularly dense vegetation a sighting was taken with a Bunton-type surveying compass.

A stout cord was used as the line and was laid between the poles over the tops of shrubs, stretched taut and anchored by steel stakes. When necessary, the string was lowered to measure the lower growing strata. Distance along the transect was measured with a 15-meter steel tape placed immediately beneath the line. The foliage of all perennial plants intercepting the line was measured to the nearest whole centimeter using a metal hand tape. The boundaries of plants were determined by the polygon method of Daubenmire (1959) as modified for a line transect by Rickard (1963). The canopy margins of each plant are defined by visualizing the intercept of a vertically projected polygon drawn about its extremities. Measurements were made in contiguous

5-meter units along the entire length of the transect. Since cover data are not normally distributed, the percentage cover of each species was transformed to inverse sine as suggested by Grieg-Smith (1961b) when tests of significance are required.

Statistical Methods

As mentioned in the introduction, two types of analysis of variance procedures were used to evaluate homogeneity. The procedure used to test for relative homogeneity, in which the between and within variance of pairs of transect units is analyzed, is a straight-forward analysis of variance and needs no further comment. The contiguous quadrat method was used to evaluate homogeneity of species population within a single stand. Since this method is an unusual application of the analysis of variance, it needs to be discussed further.

That the scale of heterogeneity detected depends on the sample size was noted above. The contiguous quadrat analysis allows one to determine at what sample size a particular heterogeneity occurs, and is especially valuable in detecting heterogeneity due to mosaic patterns. Adjacent units (quadrats or transect units) are grouped into blocks; these blocks being essentially larger sized units. The variance attributable to each block size will then allow detection of a scale of heterogeneity for a particular sample size. The data from the basic units are grouped into blocks of 2,

4, 8, etc. samples and the sum of squares for each block size are obtained. The following formula for obtaining the series of sum of squares (using for purposes of example 256 units) is modified from Thompson (1958):

$$S_k = \frac{1}{k} \sum_{i=1}^{256/k} B_{k(i)}^2$$

Where S_k is the sum of squares for the k th unit and $B_k(i)$ is the total cover of plants in the i th block of k units ($i = 1, 2, 3, \dots, 256/k$)

The variance for each block size is then obtained by dividing the difference of two adjacent sum of squares by the appropriate degrees of freedom. This procedure, for 256 units, is shown in Table 1.

The testing of variances for significance presents a problem. Thompson (1958) states that the association of plants into clumps will cause non-independence and non-normality, and significant results can thus be obtained when none exist. The basic unit used in the present study was five meters long; larger than the most obvious clumping, that of Larrea tridentata individuals. Hopefully this reduced somewhat the source of error resulting from the association of these plants into clumps.

Kershaw (1957, from information given by M. S. Bartlett in personal communication) stated that once non-randomness is found, the variance ratio test no longer applies, but that it allows the sampling irregularities to be

TABLE 1. Analysis of variance for the contiguous quadrat analysis of 256 units (after Thompson, 1958).

<u>Block Size (k)</u>	<u>Degrees of Freedom (nk)</u>	<u>Mean Square (Vk)</u>
1	128	$(S_1 - S_2)/128$
2	64	$(S_2 - S_4)/64$
4	32	$(S_4 - S_8)/32$
8	16	$(S_8 - S_{16})/16$
16	8	$(S_{16} - S_{32})/8$
32	4	$(S_{32} - S_{64})/4$
64	2	$(S_{64} - S_{128})/2$
128	1	$(S_{128} - S_{256})$

separated out as non-significant fluctuations. Kershaw believes that the test can be applied to give at least an indication of the true level of significance if used with caution. Since non-normality results in the required significance level being higher than that given in the table of F values, the variances presented here which seem to be significant at $P = 0.01 - 0.05$ must be interpreted with caution. Variances found to be significant at $P = 0.005 - 0.01$ and at $P > 0.005$ may be actually significant at a lower level.

Goodall (1961) uses the F test by testing a particular variance against that for the next smaller spacing and when finding non-significance at $P = 0.05$, pools the variances to test against the next variance. M. D. Finkner (personal communication) suggests that a more conservative approach would reduce the probability of committing a Type II error by not pooling at all or only after finding non-significance at about $P = 0.20$. In the present study, a particular variance was tested against that for the next smaller block size. Variances were not pooled.

Since the present study uses transect units rather than quadrats, the procedure will be referred to as the contiguous unit analysis. The 5-meter transect units were longer than the intercept of the average size of any individual species and longer than the average clump diameter of Larrea tridentata, thus this small-scale heterogeneity was not evaluated. D. W. Goodall (personal communication) suggested that to avoid the most trivial type of association

between adjacent records the individuals units should be separated by at least a diameter of the largest individual present. Each unit was therefore separated by five meters.

The contiguous unit analysis was performed on all species with sufficient data within the confines of the two stand. The confines of the stand were determined in accordance with Yang's (1957) division of the transect in which 33.1% was considered as Larrea dominated, 47.5% as Larrea-Cercidium co-dominated, and 19.5% as Cercidium dominated.

All statistical analyses, except the contiguous unit analysis of Janusia gracilis, were performed on an I B M - 7072 computer at the Numerical Analysis Laboratory of the University of Arizona.

RESULTS

The results of the contiguous unit analysis for the Larrea dominated stand are presented for each species in Tables 2 and 3. A summary of the variance ratio test for both species is given in Table 4. The lack of significant values in Table 2 indicates a constancy of variance for all block sizes for Larrea tridentata. This species is therefore considered to be homogeneously distributed within the confines of the stand. The data for Franseria deltoidea, Table 3, shows a variance for block size 8 which may be significantly higher than that for the next smaller block size. The significant variance at block size 8 may suggest a mosaic pattern with the average linear dimension of one phase of that mosaic being 80 meters. The lack of other significantly large variances at larger block sizes suggests that this species is homogeneously distributed from a minimum sample size of 160 meters, represented by block size 16, which is the lowest block size for which the variance is constant.

Homogeneity of the vegetation of the Larrea dominated stand is determined by the distribution of its component species. Table 4 presents a summary of the variance ratio tests for the component species. These data indicate a minimal area for a sample size of 160 meters, beyond which the vegetation is homogeneous.

TABLE 2. Analysis of variance for Larrea tridentata, percentage cover transformed to inverse sine (radians).^a

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.1006	--
2	64	0.1028	1.02
4	32	0.1125	1.09
8	16	0.1835	1.63
16	8	0.1881	1.03
32	4	0.1298	< 1.00
64	2	0.0612	< 1.00
128	1	0.2617	4.28

TABLE 3. Analysis of variance for Franseria deltoidea, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0178	--
2	64	0.0220	1.24
4	32	0.0176	< 1.00
8	16	0.0436	2.48*
16	8	0.0446	1.02
32	4	0.0935	2.10
64	2	0.1590	1.70
128	1	0.1108	< 1.00

* P = 0.01--0.05

a. The sum of squares for each analysis are listed in the Appendix.

TABLE 4. Summary of variance ratio test for Larrea-Franseria stand.

Species	k							
	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>16</u>	<u>32</u>	<u>64</u>	<u>128</u>
Larrea tridentata								
Franseria deltoidea				*				

* P = 0.01--0.05

The results of the contiguous unit analysis for each of the analyzable species of the Cercidium dominated stand are presented in Tables 5-18. The results of the variance ratio tests for all species are presented in Table 19. These results are not as clear as are the results from the first stand. Constancy of variance for all block sizes is indicated for Cercidium microphyllum (Table 5), Opuntia acanthocarpa (Table 6), O. fulgida (Table 7), O. engelmannii (Table 8), Acacia constricta (Table 10), and Muhlenbergia porteri (Table 15). Opuntia macrocentra (Table 9), Olneya tesota (Table 13), Euphorbia capitellata (Table 14), Hymenoclea monogyra (Table 16), and Aplopappus spinulosus (Table 17) each show variances at a particular block size which are significantly higher than those for the next smaller block size, and variance is constant for all other block sizes, Calliandra eriophylla (Table 11), Janusia gracilis (Table 12), and Hilaria belangeri (Table 18) each show significantly high variances at more than one block size.

The interpretation of these results is best made with reference to Table 19. The six species having no significantly different variances are considered to be homogeneous throughout their distribution within the stand. The significantly high variances at the lower block sizes may represent mosaic patterns, one phase of which has the average linear dimension of 20 meters for Calliandra eriophylla and Olneya tesota and of 40 meters for Janusia gracilis, Euphorbia

TABLE 5. Analysis of variance for Cercidium microphyllum, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.1418	--
2	64	0.1301	< 1.00
4	32	0.0974	< 1.00
8	16	0.1028	1.06
16	8	0.1721	1.67
32	4	0.1554	< 1.00
64	2	0.0438	< 1.00
128	1	0.7613	17.38

TABLE 6. Analysis of variance for Opuntia acanthocarpa, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0177	--
2	64	0.0159	< 1.00
4	32	0.0171	1.08
8	16	0.0236	1.38
16	8	0.0211	< 1.00
32	4	0.0509	2.41
64	2	0.0265	< 1.00
128	1	0.0086	< 1.00

TABLE 7. Analysis of variance for Opuntia fulgida, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0055	--
2	64	0.0042	<1.00
4	32	0.0047	1.12
8	16	0.0071	1.51
16	8	0.0059	<1.00
32	4	0.0087	1.48
64	2	0.0115	1.32
128	1	0.0061	<1.00

TABLE 8. Analysis of variance for Opuntia engelmannii, percentage cover transformed to inverse sine, (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0059	--
2	64	0.0079	1.34
4	32	0.0063	<1.00
8	16	0.0095	1.51
16	8	0.0063	<1.00
32	4	0.0042	<1.00
64	2	0.0104	2.48
128	1	0.0140	1.35

TABLE 9. Analysis of variance for Opuntia macrocentra, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0040	--
2	64	0.0045	1.13
4	32	0.0036	< 1.00
8	16	0.0039	1.08
16	8	0.0049	1.26
32	4	0.0012	< 1.00
64	2	0.0087	7.25*
128	1	0.0102	1.17

* P = 0.01--0.05

TABLE 10. Analysis of variance for Acacia constricta, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0233	--
2	64	0.0285	1.22
4	32	0.0200	< 1.00
8	16	0.0278	1.39
16	8	0.0184	< 1.00
32	4	0.0151	< 1.00
64	2	0.0517	3.42
128	1	0.0008	< 1.00

TABLE 11. Analysis of variance for Calliandra eriophylla, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0036	--
2	64	0.0056	1.56*
4	32	0.0041	< 1.00
8	16	0.0078	1.90
16	8	0.0148	1.90
32	4	0.0003	< 1.00
64	2	0.0055	18.33**
128	1	0.0902	16.40

* P = 0.01--0.05; ** P = 0.005--0.01

TABLE 12. Analysis of variance for Janusia gracilis, percentage cover transformed to inverse sine (degrees).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	16.4657	--
2	64	13.3916	< 1.00
4	32	26.3507	1.97*
8	16	15.7472	< 1.00
16	8	13.2631	< 1.00
32	4	3.2711	< 1.00
64	2	27.2317	8.32*
128	1	221.4888	8.13

* P = 0.01--0.05

TABLE 13. Analysis of variance for Olneya tesota, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0122	--
2	64	0.0297	2.43***
4	32	0.0293	<1.00
8	16	0.0291	<1.00
16	8	0.0092	<1.00
32	4	0.0062	<1.00
64	2	0.0380	6.13
128	1	0.1621	4.27

*** P > 0.005

TABLE 14. Analysis of variance for Euphorbia capitellata, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0010	--
2	64	0.0005	<1.00
4	32	0.0013	2.60***
8	16	0.0009	<1.00
16	8	0.0014	1.56
32	4	0.0036	2.57
64	2	0.0075	2.08
128	1	0.0212	2.83

*** P > 0.005

TABLE 15. Analysis of variance for Muhlenbergia porteri, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0010	--
2	64	0.0011	1.10
4	32	0.0007	< 1.00
8	16	0.0008	1.14
16	8	0.0012	1.50
32	4	0.0011	< 1.00
64	2	0.0017	1.55
128	1	0.0024	1.41

TABLE 16. Analysis of variance for Hymenoclea monogyra, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0234	--
2	64	0.0233	< 1.00
4	32	0.0646	2.77***
8	16	0.0818	1.27
16	8	0.1613	1.97
32	4	0.0648	< 1.00
64	2	0.0307	< 1.00
128	1	1.6441	5.36

*** P > 0.005

TABLE 17. Analysis of variance for Aplopappus spinulosus, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0014	--
2	64	0.0017	1.21
4	32	0.0017	1.00
8	16	0.0001	< 1.00
16	8	0.0032	32.00***
32	4	0.0015	< 1.00
64	2	0.0024	1.60
128	1	0.0019	< 1.00

*** P > 0.005

TABLE 18. Analysis of variance for Hilaria belangeri, percentage cover transformed to inverse sine (radians).

<u>k</u>	<u>n_k</u>	<u>V_k</u>	<u>F</u>
1	128	0.0015	--
2	64	0.0015	1.00
4	32	0.0041	2.73***
8	16	0.0050	1.22
16	8	0.0011	< 1.00
32	4	0.0408	37.09***
64	2	0.1396	3.42
128	1	0.2028	1.45

*** P > 0.005

TABLE 19. Summary of variance ration test for Cercidium-Carnegiea stand.

Species	k							
	<u>1</u>	<u>2</u>	<u>4</u>	<u>8</u>	<u>16</u>	<u>32</u>	<u>64</u>	<u>128</u>
Cercidium microphyllum								
Opuntia acanthocarpa								
Opuntia fulgida								
Opuntia engelmannii								
Opuntia macrocentra							*	
Acacia constricta								
Calliandra eriophylla		*					**	
Janusia gracilia			*				*	
Olneya tesota		***						
Euphorbia capitellata			***					
Muhlenbergia porteri								
Hymenoclea monogyra			***					
Aplopappus spinulosus					***			
Hilaria belangeri			***			***		

* P = 0.01-0.05, ** P = 0.005-0.01, *** P > 0.005

capitellata, Hymenoclea monogyra, and Hilaria belangeri. An unequivocal demonstration of a minimal area would require that these significantly large variances occur at the same block size. Although this is not precisely the case, a minimal area of about 80 meters is suggested. However the significantly large variances at the larger block sizes must be satisfactorily explained if this indication is to be valid. As P. Grieg-Smith (personal communication) notes, high variance values will be obtained at a scale corresponding to the distributional limits of the species. In all cases these large variances seem to result from the limits of the species distribution essentially being reached on that portion of the transect occurring in this stand; in the case of Aplopappus spinulosus at 160 meters, of Hilaria belangeri at 320 meters, and of Opuntia macrocentra, Calliandra eriophylla, and Janusia gracilis at 640 meters.

Assuming these explanations to be correct, Olneya tesota and Hymenoclea monogyra can be considered homogeneously distributed for a minimum sample size of 40 and 80 meters respectively. Opuntia macrocentra and Aplopappus spinulosus can be considered homogeneously distributed up to 640 and 160 meters respectively, where the limits of their distribution are reached. Calliandra eriophylla, Janusia gracilis, and Hilaria belangeri can be considered homogeneously distributed beyond 40, 80, and 80 meters respectively, up to 640, 640, and 320 meters respectively.

The vegetation, being the whole comprised of the above species, can be considered as homogeneous within the limits set by the significant variances at the smaller block sizes, or minimal area, and the significant variances at the larger block sizes representing distributional limits.

Complementary to the idea of vegetational homogeneity within the boundaries of the stand is the idea of vegetational heterogeneity within the transition between stands. This relative homogeneity of the vegetation requires that the species themselves should be homogeneously distributed within the stand but heterogeneously distributed between the stands. The existence of such distribution was tested for by the successive unit analysis of variance.

The results of the analysis of variance of differences between successive transect units for the twelve analyzable species are presented in Tables 20-31. The variance ratio tests for Larrea tridentata (Table 20) and for Franseria deltoidea (Table 21) are both significant, and thus indicate that the difference between a pair of units is more like the difference between another pair within the stand than that between a pair in the ecotone. This test, in conjunction with the contiguous quadrat analysis, indicates that the vegetation of the Larrea dominated stand is homogeneous within the boundaries but heterogeneous, or significantly less homogeneous, in the transition zone.

TABLE 20. Analysis of variance of differences between 1,024 successive transect units for Larrea tridentata, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	255	2551.24	10.00**
Within transect lengths of 40 m.	<u>256</u>	<u>1498.16</u>	5.85
Total	511	4049.40	

** P = 0.01 - 0.005

TABLE 21. Analysis of variance of differences between 1,024 successive transect units for Franseria deltoidea, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	255	1157.22	4.54**
Within transect lengths of 40 m.	<u>256</u>	<u>744.45</u>	2.91
Total	511	1901.67	

** P = 0.01-0.005

TABLE 22. Analysis of variance of differences between 1,024 successive transect units for Cercidium microphyllum, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	255	2605.38	13.64n.s.
Within transect lengths of 40 m.	<u>256</u>	<u>2849.84</u>	14.84
Total	511	5455.22	

n.s. = non-significant for $P > 0.05$

TABLE 23. Analysis of variance of differences between 736 successive transect units for Opuntia acanthocarpa, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	183	401.72	2.20*
Within transect lengths of 40 m.	<u>184</u>	<u>299.13</u>	1.63
Total	367	700.85	

* P = 0.01 - 0.05

TABLE 24. Analysis of variance of differences between 512 successive transect units for Opuntia fulgida, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	127	103.06	0.81n.s.
Within transect lengths of 40 m.	<u>128</u>	<u>81.47</u>	0.64
Total	255	184.53	

n.s. = non-significant for $P > 0.05$

TABLE 25. Analysis of variance of differences between 256 successive transect units for Opuntia engelmannii, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	127	189.37	1.49n.s.
Within transect lengths of 40 m.	<u>128</u>	<u>156.47</u>	1.22
Total	255	345.84	

n.s. = non-significance for $P > 0.05$

TABLE 26. Analysis of variance of difference between 208 successive transect units for Opuntia macrocentra, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	103	100.22	0.97n.s.
Within transect lengths of 40 m.	<u>104</u>	<u>117.07</u>	1.13
Total	207	217.29	

n.s. = non-significance for $P > 0.05$

TABLE 27. Analysis of variance of difference between 320 successive transect units for Acacia constricta, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	159	537.30	3.38 n.s.
Within transect lengths of 40 m.	<u>160</u>	<u>500.60</u>	3.13
Total	319	1037.90	

n.s. = non-significance for $P > 0.05$

TABLE 28. Analysis of variance of difference between 496 successive transect units for Olneya tesota, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	247	821.48	3.33n.s.
Within transect lengths of 40 m.	<u>248</u>	<u>825.72</u>	3.33
Total	495	1647.20	

n.s. = non-significance for $P > 0.05$

TABLE 29. Analysis of variance of difference between 256 successive transect units for Muhlenbergia porteri, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	127	22.59	0.18n.s.
Within transect lengths of 40 m.	<u>128</u>	<u>26.25</u>	0.21
Total	255	48.84	

n.s. = non-significance for $P > 0.05$

TABLE 30. Analysis of variance of difference between 192 successive transect units for Hymenoclea monogyra, percentage cover transformed to inverse sine (radians).

<u>Source of variation</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	95	489.82	5.16**
Within transect lengths of 40 m.	<u>96</u>	<u>183.60</u>	1.91
Total	191	673.42	

** $P = 0.01.-0.005$

TABLE 31. Analysis of variance of difference between 176 successive transect units for Aplopappus spinulosus, percentage cover transformed to inverse sine (radians).

<u>Source of variance</u>	<u>df</u>	<u>SS</u>	<u>MS</u>
Between transect lengths of 40 m.	87	19.61	0.23n.s.
Within transect lengths of 40 m.	<u>88</u>	<u>22.45</u>	0.26
Total	175	42.06	

n.s. = non-significance for $P > 0.05$

The results of the two analyses for the species of the Cercidium stand do not show such coherence as for the Larrea stand. According to the successive unit analysis, Cercidium microphyllum (Table 22) does not show relative homogeneity. When Goodall (1954) found no significant differences in a similar analysis, he interpreted it to mean that the species were heterogeneously distributed, having previously found no homogeneity on other grounds. But if the species were homogeneous throughout its distribution, then one would not expect the difference between a pair of units to be any more like that of the adjacent pair than another pair more removed. Since Cercidium microphyllum appears to be homogeneously distributed by the first criterion, the results of Table 22 are interpreted to signify that it is also homogeneously distributed in the transition zone.

The results from the analysis on Opuntia acanthocarpa (Table 23) may indicate relative homogeneity, but the results for O. fulgida and O. engelmannii (Tables 24 and 25) present the same type of problem as did Cercidium and can be explained in the same way.

Analyzing O. macrocentra (Table 26) presents a seeming incongruity in that the results of the contiguous unit analysis indicate that the limits of its distribution were reached at 640 meters and yet it was subjected to the successive unit analysis which demands distribution into the ecotone. This is explained by a disjunction in its

distribution along the transect, being essentially absent beyond 640 meters and then appearing again in the ecotone. The results of Table 28 are interpreted to indicate that O. macrocentra does not show relative homogeneity.

For the remainder of the species, the analyses for Acacia constricta (Table 27) and for Muhlenbergia porteri (Table 29) are interpreted as for Cercidium. Olneya tesota (Table 28) seems to have a homogeneous distribution that extends from the lowest block size of constant variance, occurring at 40 meters, into the transition zone. Hymenoclea monogyra (Table 30) is indicated to be homogeneously distributed within the stand beyond 80 meters and heterogeneously distributed in the ecotone. Aplopappus spinulosus (Table 31) is similar in distribution to Opuntia macrocentra.

Considering the results in their entirety, it would be ideal to have either of two situations: (1) a definite homogeneity of vegetation within the stand with all significantly large variances at the same block size and thus a definite minimal area, and heterogeneity in the transition zone or (2) all species distributed heterogeneously throughout their extent with each species showing significantly large variances at several block sizes and no indication at all of a minimal area. Either of these results, although completely opposed to each other in their implications, would be relatively easy to interpret. The results reported here do not clearly fit into either category. The contiguous

unit analysis indicates the possibility of a minimal area and an even greater possibility for homogeneity. The results from the successive unit analysis of the Cercidium community are less conclusive in that they do not indicate the vegetation to be heterogeneous in the transition zone as well as homogeneous within the stand.

DISCUSSION

The results of this study suggest that in certain areas of the Sonoran Desert homogeneous vegetation may exist. These results will be considered first in relation to similar evaluations of vegetational homogeneity and second in the context of the general matter of fundamental units of vegetation and the classification of these units. The second consideration will involve conjecture since it includes inductive inferences from an incomplete study; incomplete as any one study on such a complex subject must be.

As to the first consideration, Goodall's studies (1954a, 1954b, 1961) are the only ones directly concerned with the same general problem as is the present study. Goodall (1954b) found that homogeneity of vegetation was not indicated in tests for random distribution of individuals of species; in tests relating variance between sample areas to their spacing; and in tests of correlations between quantities of species in sample areas. He also found no indication of relative homogeneity. This led Goodall (1961) to test an alternate hypothesis which he had proposed earlier (1954a, 1954b). He suggested that variance may be a continuous function of spacing. A linear regression between the logarithms of variance and mean distance between sample areas fitted most of the data. His general conclusion was that

vegetation may exist not as distinct homogeneous stands and distinct transition zones but rather as a continuous gradual replacement of vegetation types.

The results of my study do not agree with those of Goodall. This is especially true for the Larrea dominated stand. The results from Table 4 were interpreted to mean that this stand exists as a homogeneous unit. The component species are distributed heterogeneously in the transition zone thus indicating relative homogeneity (Tables 20 and 21). Admittedly, there is no convincing evidence for a minimal area for this stand. Although the data from the Cercidium dominated stand (Table 19) do not present such a clear-cut picture, they can better be interpreted as representing homogeneous rather than heterogeneous vegetation.

I found no indication of a continuous increase in variance with block size as did Goodall (1961). For sake of contrast, Tables 4 and 19 show no species with significantly high variances at more than two block sizes. Goodall (1961), on the other hand, found in the Rhyll Salt Marsh, for example, that of the six species tested, one had two significantly high variances, three species had three such variances, one had four, and one had five. While these latter results offer evidence for proposing the alternative hypothesis of variance being a continuous function of spacing, mine do not. To the contrary, my results are interpreted to mean that the two variables are independent within the boundaries set by the

significant variances at the smaller block sizes, or minimal area, and by the significant variances at the larger block sizes representing distributional limits.

The present study in conjunction with those of Goodall, presents the possibility that neither homogeneity nor heterogeneity is a universal property of vegetation. Generalizations stating that all vegetation must be one or the other may have been premature. The generality of vegetational homogeneity arrived at by early phytosociologists from deductive reasoning has been found to be invalid upon intensive investigation. Yet the generality of vegetational heterogeneity arrived at from inductive inferences of too few cases may also be invalid. This lack of universality for the applicability of one or the other of two alternatives is found for other ecological concepts. For example, Goodall (1963) presents several references (e.g., Whittaker, 1956; Martin, 1959; Poulton and Tisdale, 1961) showing that certain vegetational situations can best be described by classification but others by a continuum.

The problem of the homogeneous stand is one aspect of the community-unit theory which concerns the relations of properties of natural communities to the conceptual units of classification. As to the implications of the present study to this general problem, homogeneity of vegetation will be discussed in relation to those concepts which have been involved in discussions on the community-unit theory. These concepts concern (1) the stand and its boundary; (2) the

continuum hypothesis; and (3) the individualistic concept of the plant community.

A recent paper by Goodall (1963) considers the three problems listed in the preceding paragraph and their relationships one to another, and thus should serve as a proper vehicle for transporting the results of studies on homogeneity to those other areas of concept in the ecologic terrain with which homogeneity has been associated. Goodall argues that the problems of homogeneity and distinct stand boundaries, the view of the community as being highly integrated vs. the individualistic view, and the conflict between classification and continua are distinct from one another. There is no necessary relationship between these three problems, he contends, and any one of the three alternatives is not necessarily incompatible with the others.

The first of the three problems concerns the stand and its boundary. Goodall (1963) apparently considers homogeneity of the stand and the distinctness of the boundary of the stand to be two interdependent properties of a single phenomenon, of which two alternatives may exist: (1) homogeneous stands separated by relatively narrow transition zones or (2) heterogeneous vegetation without a definite transition zone. I think that they are not necessarily dependent on one another. That is, homogeneous units of vegetation may exist, but with or without definite boundaries separating them. There may be centers of homogeneity with

the gradual independent sifting out of individual species from these centers according to physiological tolerances of individuals as conditioned by the genetic attributes of the Mendelian population. In the present study such centers of homogeneity seem to exist, but there is no evidence of a coincidence of species distribution in which limits of tolerance are mutually exceeded. In addition, it should be noted that in Yang's (1957) division of the transect 47.5% was considered as ecotone. The picture which emerges, then, is that of a vegetational matrix with centers of homogeneity and wide ecotone areas where the limits of tolerance of the majority of the species are independently exceeded.

If the existence of homogeneous vegetation is accepted, does this mean that the concept of the continuum should be relegated to limbo? Goodall (1963) thinks not. One idea concerns vegetation as it occurs in the field and the other concerns the arrangement of stands into abstract classificatory units. That homogeneity and the continuum concept are compatible is indicated by the fact that Curtis and McIntosh (1951) in their continuum arrangement used stands which were determined to be homogeneous by the chi-square homogeneity statistic. The acceptance, then, of homogeneity of desert vegetation does not require a concomitant acceptance or rejection of the existence of a continuum of stands of desert vegetation. But the statement by Shreve (1915) that "It is nowhere possible to pick out a group of

plants which may be thought of as associates without being able to find other localities in which the association has been dissolved" would lead one to believe that the continuum concept is applicable.

Goodall (1963) also considers that there is no necessary connection between the ideas of the stand and its boundary and the individualistic vs. integrated concepts of the plant community. It is significant that Gleason (1917, 1926, 1939), while being the foremost proponent of the individualistic view, accepted homogeneity of vegetation. One can accept homogeneity without also accepting the integrated view. Homogeneous vegetation can be interpreted, to give the extreme views, as arising from mutual adaptations of plants which have evolved as an integrated whole (Dice, 1952) or as being due to a coincidental unity of species populations having arisen from the coincidence of historical events and the coincidence of overlapping tolerances (Mason, 1947). The present study offers no evidence in this case. But if Shreve's (1915) contention that the impact of the physical environment on desert plants greatly outweighs the biologic coaction among plants be taken with his statement quoted in the previous paragraph, then the evidence seems to favor an individualistic view of desert communities.

The remaining pair of alternatives to compare are those of the individualistic vs. integrated view and the continuum vs. classification view. Although this comparison

does not involve the stand and is therefore not of direct concern to this study, it is a part of the same general picture. Goodall (1963) contends that acceptance of any combination of these viewpoints presents no inconsistency. He claims that an individualistic interpretation is compatible with a natural classification if certain site types are more commonly found than ones intermediate between them. The converse would seem to be that an integrated interpretation could be combined with a continuum approach if the intermediate sites are common. This argument does not seem to properly take into account that there are two parts to either the individualistic or the integrated view. The pure integration view, for example, purports that (1) the joint evolution of communities results in obligate relations and (2) these obligate relations organize species into associations so that the species do not occur independently of these associations (Whittaker, 1962). This would prohibit diverse distribution of species, and it is such distributions that links the two concepts. The continuum as proposed by Curtis (e.g., 1959) depends on stand to stand variability within the community. The individualistic concept of Gleason (e.g., 1939) also emphasizes this same point. There does, then, seem to be a logical connection between the two sets of concepts.

In conclusion, the present study offers evidence in favor of homogeneity of vegetation in the Sonoran Desert.

The existence of a fundamental difference in community structure between the stand and the ecotone is not definitely demonstrated. As such, this perhaps ill-defined picture is not consistent with, not diametrically opposed to, Goodall's (1961) view of a continuous replacement of one vegetation type by another, without any distinct homogeneous stands or transitional zones. It is inconsistent with that view because of the homogeneity found, but not diametrically opposed to it because of the lack of distinctness between the stand and the ecotone. I suggest that these centers of homogeneity represent what is perhaps the closest approximation to the fundamental units of natural communities, and as such they may serve as stands in the classification of vegetation. However, this study offers no direct evidence for the relation of these units to the conceptual units of classification and thus gives little information about the arbitrariness of such a classification. This information properly comes from the study of many stands of vegetation and their relationships to one another.

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APPENDIX. Sums of squares of species data subjected to the contiguous unit analysis of variance, inverse sine transformation of percentage cover (radians)⁵

Larrea tridentata

$S_1 = 51.2693$

$S_2 = 38.3972$

$S_4 = 31.8161$

$S_8 = 28.2173$

$S_{16} = 25.2806$

$S_{32} = 23.7754$

$S_{64} = 23.2564$

$S_{128} = 23.1340$

$S_{256} = 22.8724$

Cercidium microphyllum

$S_1 = 43.5585$

$S_2 = 25.4087$

$S_4 = 17.0792$

$S_8 = 13.9620$

$S_{16} = 12.3179$

$S_{32} = 10.9412$

$S_{64} = 10.3197$

$S_{128} = 10.2321$

$S_{256} = 9.4707$

Franseria deltoidea

$S_1 = 7.2898$

$S_2 = 5.0119$

$S_4 = 3.6029$

$S_8 = 3.0384$

$S_{16} = 2.3412$

$S_{32} = 1.9843$

$S_{64} = 1.6103$

$S_{128} = 1.2922$

$S_{256} = 1.1814$

Opuntia acanthocarpa

$S_1 = 5.1790$

$S_2 = 2.9186$

$S_4 = 1.9041$

$S_8 = 1.3554$

$S_{16} = 0.9786$

$S_{32} = 0.8099$

$S_{64} = 0.6062$

$S_{128} = 0.5532$

$S_{256} = 0.5447$

5. Data for Janusia gracilis in degrees.

Opuntia fulgida

$S_1 = 1.3964$

$S_2 = 0.6982$

$S_4 = 0.4271$

$S_8 = 0.2780$

$S_{16} = 0.1636$

$S_{32} = 0.1167$

$S_{64} = 0.0818$

$S_{128} = 0.0588$

$S_{256} = 0.0527$

Acacia constricta

$S_1 = 7.1839$

$S_2 = 4.2060$

$S_4 = 2.3834$

$S_8 = 1.7424$

$S_{16} = 1.2970$

$S_{32} = 1.1501$

$S_{64} = 1.0898$

$S_{128} = 0.9865$

$S_{256} = 0.9857$

Opuntia engelmannii

$S_1 = 1.7605$

$S_2 = 1.0070$

$S_4 = 0.5035$

$S_8 = 0.3034$

$S_{16} = 0.1517$

$S_{32} = 0.1016$

$S_{64} = 0.0846$

$S_{128} = 0.0639$

$S_{256} = 0.0498$

Calliandra eriophylla

$S_1 = 1.3955$

$S_2 = 0.9324$

$S_4 = 0.5732$

$S_8 = 0.4412$

$S_{16} = 0.3158$

$S_{32} = 0.1975$

$S_{64} = 0.1962$

$S_{128} = 0.1852$

$S_{256} = 0.0950$

Opuntia macrocentra

S ₁	=	1.0965
S ₂	=	0.5838
S ₄	=	0.2974
S ₈	=	0.1818
S ₁₆	=	0.1200
S ₃₂	=	0.0806
S ₆₄	=	0.0758
S ₁₂₈	=	0.0583
S ₂₅₆	=	0.0481

Janusia gracilis

S ₁	=	4,786.0512
S ₂	=	2,678.4393
S ₄	=	1,821.3759
S ₈	=	978.1537
S ₁₆	=	726.1991
S ₃₂	=	620.0945
S ₆₄	=	607.0101
S ₁₂₈	=	552.5468
S ₂₅₆	=	331.0580

Olneya tesota

S ₁	=	5.3671
S ₂	=	3.8070
S ₄	=	1.9035
S ₈	=	0.9644
S ₁₆	=	0.4987
S ₃₂	=	0.4252
S ₆₄	=	0.4003
S ₁₂₈	=	0.3242
S ₂₅₆	=	0.1621

Hymenoclea monogyra

S ₁	=	12.7593
S ₂	=	9.7673
S ₄	=	8.2756
S ₈	=	6.2083
S ₁₆	=	4.8989
S ₃₂	=	3.6089
S ₆₄	=	3.3496
S ₁₂₈	=	3.2882
S ₂₅₆	=	1.6441

Euphorbia capitellata

S ₁	=	0.2941
S ₂	=	0.1719
S ₄	=	0.1380
S ₈	=	0.0974
S ₁₆	=	0.0831
S ₃₂	=	0.0718
S ₆₄	=	0.0574
S ₁₂₈	=	0.0423
S ₂₅₆	=	0.0212

Aplopappus spinulosus

S ₁	=	0.3945
S ₂	=	0.2157
S ₄	=	0.1079
S ₈	=	0.0539
S ₁₆	=	0.0518
S ₃₂	=	0.0259
S ₆₄	=	0.0198
S ₁₂₈	=	0.0149
S ₂₅₆	=	0.0130

Muhlenbergia porteri

S ₁	=	0.2678
S ₂	=	0.1437
S ₄	=	0.0719
S ₈	=	0.0496
S ₁₆	=	0.0372
S ₃₂	=	0.0280
S ₆₄	=	0.0238
S ₁₂₈	=	0.0204
S ₂₅₆	=	0.0181

Hilaria belangeri

S ₁	=	1.3507
S ₂	=	1.1636
S ₄	=	1.0666
S ₈	=	0.9357
S ₁₆	=	0.8564
S ₃₂	=	0.8479
S ₆₄	=	0.6847
S ₁₂₈	=	0.4056
S ₂₅₆	=	0.2028