# GENETICS OF NATURAL POPULATIONS. VI. MICROGEOGRAPHIC RACES IN LINANTHUS PARRYAE 

CARL EPLING and TH. DOBZHANSKY<br>University of California ai Los Angeles, Los Angeles, California, and Columbia University, New York City

Received November 3, 1941

## INTRODUCTION

THE differentiation of a species into geographic races is a familiar phenomenon. Such races, usually referred to as subspecies by the systematist, consist of populations which exhibit a characteristic facies throughout a given geographic area. Although the populations may themselves be disjunct, the area which they occupy is essentially continuous. Such races are usually not homogeneous, unless greatly restricted, but present minor variants of at least two sorts. Some reflect an adaptive response of the species to the local environment; they tend to recur wherever the proper environment is found within the distribution area of the species; they are known as ecotypes (Turesson 1922). Other local variants display no apparent relation to a particular environment; for such variants the noncommittal term "microgeographic races" has been proposed (Dовzhansky 1937). Microgeographic races are of interest both to genetics and to systematics because they may represent one of the first steps in the process of spatial diversification of species. Investigation of this phenomenon may therefore shed light on the structure and the dynamics of natural populations. The present paper describes the results of an exploratory study of microgeographic races in Linanthus Parryae. The races studied differ in the relative frequencies of white and blue flowered plants.

The writers wish to express their appreciation to Mr. Harold Lint, Mr. Donald Rappoport, and Mr. Seymour Singer for their help in collecting the data and to Professor Sewall Wright for advice regarding statistical procedure.

## MATERIAL

Linanthus Parryae (Gray) Greene, a representative of the Polemoniaceae, is a diminutive annual of the Mojave Desert, California. Its stem is commonly the diameter of a pencil lead and sometimes as much as 10 cm tall, but usually less and often scarcely 1 cm .; it may become intricately branched. The flowers are large relative to the vegetative parts of the plant. The corolla is commonly r-I. 5 cm . long, with a spread of petals of as much as 2 cm . The number of flowers may vary from one to as many as 243 per plant, the usual number being $5^{-10}$. Several flowers may be open at the
same time on a given plant, and most of the plants within a given population flower simultaneously. The period of flowering varies usually from two to three weeks and occurs in April or May. The plant is inconspicuous tefore flowering, and several hundred may lie underfoot but be scarcely observed against the desert gravel. In flower and en masse they are conspicuous and showy, as attested by the name "desert snow."

Two types of flower color occur in Linanthus Parryae: white and blue. In the former, the prevailing white is relieved by a band of purple in the throat. The blue is constant neither in shade nor in intensity, but varies from violet to a more reddish purple. Nevertheless, the difference between white and blue is always discernible to a practiced eye whether the corolla is living or withered: In one instance a blue flowered plant was found on which the two flowers upon one branch were white.

## DISTRIBUTION AND HABITAT

Linanthus Parryae occurs around the southern and western margins of the Mojave Desert. The area described in this paper, the population of which has been studied in detail (maps in fig. I and 2), lies to the north of San Gabriel and San Bernardino Mountains in Los Angeles and San Bernardino Counties, California. This area is a gently rolling piedmont, sloping northward from an elevation of approximately 3,000 feet to approximately 2500 . It is terminated on the south by the mountain ranges mentioned above, and on the north by the more alkaline valley floor. The piedmont is homogeneous but not uniform in aspect, structure, and soils. It is trisected from south to north by the stream bed of the Mojave river (at stations 192 to 195 and at Victorville; see fig. 2) and by Big Rock Creek (northwest of Llano) and Little Rock Creek (east of Palmdale, fig. i) which rise in the San Bernardino and San Gabriel Ranges. All are intermittent, at least in the lower part of the slope. Their courses, like those of many desert streams, are inconstant. In addition to these streams a wet year produces smaller ephemeral ones which may flood the piedmont in their courses, depositing coarse gravel or rock, or silt, or carving a shallow and erratic channel.

Exclusive of the stream beds, in the detritus of which Linanthus Parryae does not occur, the principal soils of the area are as follows: Adelanto sand, Adelanto loamy sand, Adelanto sandy loam, Hesperia loamy sand, and Hesperia loamy fine sand. Only the areas in the vicinity of Palmdale and Victorville have been soil surveyed, however. Because the short hair-like roots of Linanthus would probably be but little affected by the nature of the subsoil during their short course of life, the actual variation in soils with reference to this species is less than appears from the above list, and the soils of the whole area can be taken as relatively uniform. They are similar
in their alluvial origin from granitic rocks. We are indebted to Professor M. R. Huberty for the above interpretation.

The vegetation of the piedmont is also homogeneous. It falls chiefly within the Larrea-Franseria association, the characteristic cover of the Mojave and Colorado deserts. The most widespread perennial is Larrea divaricata. Associated with it are such species as Eriogonum polifolium, Ephedra californica, Dalea Schottii, Haplopappus linearifolius, Hymenoclea Salsola, and in some areas the grasses Oryzopsis hymenoides, Stipa speciosa, and Hilaria rigida. Yucca brevifolia is scattered throughout most of the area. Juniperus californica enters from the mountain slopes at the southern margin, and Atriplex communities are usually found in the valley floor at the foot of the piedmont. The spacing of these shrubs is wide, and it is doubtful if they cover as much as 60 percent of the ground. Around the base of most of the bushes, the soil has accumulated so as to form a slight mound. Linanthus Parryae occupies the ground between these mounds, forming a widespread recticulum which is interrupted only by the stream beds or depositions alluded to above. The species ordinarily ranges upward as far as the Juniper belt and terminates at the lower margin of the piedmont where the soil becomes very sandy or alkaline (the approximate limits of its occurrence are shown in figures 1 and 2 by a broken line). As far as can be judged from the nature of the soils and the vegetation which they support, there is nothing to suggest any selection differential in the habitat nor any physical barrier to a free interchange of genes from one end of the area to the other, except for the stream beds. Of such barriers, if any, the arroyo of the Mojave River would appear to be the principal one.

The incidence and amount of rainfall upon the desert varies greatly from year to year. The abundance of Linanthus Parryae varies accordingly. In unfavorable years the species may be found only in sparse concentration or abundant only locally; in favorable years it may form an almost continuous sheen of white amongst the bushes where it grows, almost to the exclusion of other annuals. The flowering season of 1941 was exceptional in the amount of rainfall in the area described. As a result, an abundant and practically continuous population of Linanthus Parryae was developed from the vicinity of Palmdale to Lucerne Valley (fig. r, 2). This population was largely, if not wholly, cut off from other similar populations in other parts of the desert by the conformation of the terrain and soils and hence can be treated as a unit.

## POLLINATION

The pollination mechanism is as yet unknown but it is presumed from the flower structure that the species is normally insect pollinated. The petals are spread during the day, loosely closed at night. Nevertheless, al-

Figure 1.-Collecting stations in the western portion of the region in which Linanthus Parryae has been examined. Solid lines, the roads traveled; broken line, approximate limit of the occurrence of Linanthus Parryae; dotted line, approximate limit of the "variable areas."

though thousands of plants in full flower were seen on several successive days, from dawn until sundown, no conspicuous insects were observed upon them. However, in collecting seed at a later date, the following facts were brought to light. The set of seed on a plant varied greatly. Some plants matured no seed whatever, others only occasional capsules, still others most of the capsules. If a capsule matured at all, as a rule most of the potential seeds developed. The capsules which did develop were not necessarily the earliest nor the latest but occurred in any position on the plant. These facts suggest insect pollination and, by inference, crosspollination. The failure of many capsules to mature suggests the possibility that the insects responsible for pollination were too few in number to cope with the extraordinary abundance of the species in the spring of 1941.

## METHOD OF COLLECTING THE DATA

Approximately 200 miles of roadway within the population area were traversed by a party in two automobiles. As can be seen from figures i and 2 , these roads form a rough grid. A stop was made at each half-mile by the speedometer, and each station, thus determined, was numbered. At each station a transect was run at approximately right angles to the road; within this transect were established four sampling points, two on either side of the road at distances of approximately 20 and 70 paces. Allowing ten paces for the width of the road cut, the four samples were therefore spaced approximately 50 paces from each other (approximately 250 feet apart). The distance between the most remote sampling points at each station was 150 paces or 750 feet.

At each sampling point, a count of white and blue flowered plants was made until a hundred plants were counted within a radius which obviously varied with the density. If the area around the sampling point was entirely white or blue, simple inspection was sufficient to determine this fact. If mixed, a count was made. The total number of sampling stations was 427 ; the total number of samples 1261; the total number of plants recorded 126,100 . The reason why the number of the samples is less than four times that of the stations is that at some of the sampling stations and sampling points no Linanthus Parryae was found. The absence of the plants at these points was due either to occasional cultivated areas, as near Little Rock, the stream courses alluded to, or for some reason not discernible.

In the vicinity of the station No. 24 (fig. 1) a transect was run, along which 30 samples of 100 plants each were taken at intervals of five paces (approximately 25 feet). These 3000 plants are not included in the above total of 126,100 , but will be referred to later.

At alternate stations from Lucerne Valley westward to Palmdale, de-
terminations of the density were made by counting the numbers of plants enclosed by a rigid wire which had been bent into a frame approximately one square foot. This frame was tossed onto the ground at one of the points of the transect where a sample was taken.

## THE DATA

A condensed summary of the data is given in table 1 , which is constructed in the following manner. The numbers of the blue flowered plants found in the four samples at each station are indicated consecutively from left to right. Thus, the numbers $39,58,57$, and 52 at station No. 14 mean that 39 blue flowered plants were found in the sample which was taken 70 paces on the left of the road, 58 in that 20 paces on the left, 57 in that 20 paces on the right, and 52 in that 70 paces on the right of the road. The corresponding numbers of the white flowered plants found, but not cited, were hence, $61,42,43$, and 48 . Zero means that no blue flowered plants were found in a given sample; the sign - means that no plants at all were encountered. At many stations the entire population consisted of white flowered plants. Wherever two or more such stations occur consecutively this fact is indicated in table a by the words "all white." This method of presentation has been adopted for saving space, although it conceals the fact that at some of the stations or substations in the "all white" regions the plants were entirely absent.

The thirty samples on the special transect at station No. 24 (see above) are not included in table 1 . The numbers of blues in these samples were as follows: $1,6,2,6,3,3,5,5,9,3,6,9,9,13,22,24,33,24,26,10,27,73$, $35,70,82,82,89,94,94,89$. This transect, which was made in a singularly homogeneous site, illustrates the nature of the gradient from a "blue" to a "white" area.

The white flowered form was definitely more abundant than the blue flowered form in the region studied. A total of 1 I 3,955 whites and I2,145 blues were recorded. However, examination of the data in table in in conjunction with the maps in figures 1 and 2 shows that the distribution of the white and of the blue was by no means uniform. The blue flowered plants occurred almost entirely in three disjunct areas, which are indicated by dotted lines in figures 1 and 2. They will be referred to hereafter as the "variable areas." The largest occupies the western extremity of the region around the town of Palmdale and the hamlet of Llano (fig. r); another lies between Victorville and Lucerne Valley; the third and smallest lies southwest of Victorville (fig. 2). The samples of the variable areas consisted neither entirely nor, with few exceptions, even predominantly of blue flowered plants, and infrequent and often solitary blues occurred outside these areas. However, among the 12,145 blues recorded, only 108 were

## Table i

Numbers of blue flowered plants in samples of 100 individuals. The stations at which no plants were found are omitted in this table; large regions in which only white flowered plants were found are marked "all white"; o-indicates that a given sample consisted of white flowered plants only; the sign - indicates that no plants were found at that point. Further explanation in text.

| STATION NUMBER |  | NUMB BL | $\begin{aligned} & \text { ERS } \\ & \text { UES } \end{aligned}$ |  | STATION NUMBER | NUMBERS OF blues |  |  |  | Station NUMBER | NUMBERS OFBLUES |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 1 | - | I | $\bigcirc$ | - | 147 | 4 | 15 | 20 |  | 291 | 62 | 47 | 25 | 49 |
| 3 | 10 | - | I | - | 148 | - | - | $\bigcirc$ | $\bigcirc$ | 292 | - | - | 15 | II |
| 4 | - | $\bigcirc$ | - | - | 149 | 3 | 14 | 10 |  | 293-340 |  | all w | hite |  |
| 6 | - | - | - | 100 | 152 |  | - | 46 |  | 341 | $\bigcirc$ | 0 | 5 | $\bigcirc$ |
| 8 | 55 | 91 | - | - | 153 | - | $\bigcirc$ | - | $\bigcirc$ | 342-352 |  | all w | hite |  |
| I 1 | 33 | 60 | 77 | 45 | 154 |  | 36 |  | $\bigcirc$ | 353 | - | I | - | - |
| 12 | 74 | 8 | 10 | 6 | 156-168 |  | all w | hite |  | 354 | 19 | 47 | 26 | 15 |
| 13 | 32 | - | 47 | 65 | 170 | - | - | - | 3 | 355-366 |  | all w | hite |  |
| 14 | 39 | 58 | 57 |  | 171 | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | - | 367 | 3 | - | 3 | I |
| 19 | - | - | - | $\bigcirc$ | 172 |  | 10 | $\bigcirc$ | $\bigcirc$ | 368 | $\bigcirc$ | $\bigcirc$ | - | $\bigcirc$ |
| 20 | - | 86 | 72 | 4 | 173-174 |  | all w | hite |  | 369 | 100 | 99 | 100 |  |
| 21 | I | - | - | 20 | 175 | 0 | - | 4 | 2 | 371 | $\bigcirc$ | - | 100 |  |
| 22 | I | 2 | $\bigcirc$ | 0 | 176 | - | - | - | 6 | 372 | $\bigcirc$ | I | 1 | - |
| 23 | - | I | 4 | 10 | 177 | - | $\bigcirc$ | $\bigcirc$ | - | 373 | 3 | I | $\bigcirc$ | $\bigcirc$ |
| 24 | $\bigcirc$ | $\bigcirc$ | - | $\bigcirc$ | 178 | - | 17 | 21 | 33 | 374-375 |  | all w | hite |  |
| 25 | 100 | 98 | 96 | 100 | 179 | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | - | 376 | - | - | 2 | $\bigcirc$ |
| 26 | 60 | 85 | 79 | 85 | 180 | 88 | 92 | 57 | 53 | 377 | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ |
| 27 | $\bigcirc$ | 991 | 100 | - | 181 | 69 | 100 | 100 | 00 | 378 | - | - | $\bigcirc$ | 4 |
| 28 | 100 | 100 | - | - | 182 | - |  | 98 | 92 | 379 | - | - | $\bigcirc$ | - |
| 29-35 |  | all wh | hite |  | 183 | 94 | 100 | 100 | 00 | 380 | - | 2 | $\bigcirc$ | $\bigcirc$ |
| 36 | - | I | - | $\bigcirc$ | 184 | 38 | - | - | - | 383 | - | - | $\bigcirc$ | $\bigcirc$ |
| 37 | $\bigcirc$ | I | - | $\bigcirc$ | 185 | 11 | 15 | 50 | - | 384 | $\bigcirc$ | 6 | $\bigcirc$ | $\bigcirc$ |
| $3^{8-40}$ |  | all wh | hite |  | 186-208 |  | all w | hite |  | 385-386 |  | all w | hite |  |
| 4 I | - | $\bigcirc$ | 3 | - | 209 | - | 7 | $\bigcirc$ | $\bigcirc$ | 387 | 54 | 47 | 55 | 79 |
| 42-44 |  | all wh | hite |  | 210 | - | - | 9 | - | 388 | 43 | 60 | 64 | 30 |
| 45 | $\bigcirc$ | $\bigcirc$ | - | 3 | 2 I | - | - | - | - | 389 | 65 | 82 | 89 | 57 |
| 46 | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | 212 | - | - | - | 2 | 390 | 44 | 38 | 60 | 67 |
| 47 | 6 | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | 213 | - | $\bigcirc$ | 5 | 1 | 392 | - | - | - | - |
| 48-102 |  | all wh | hite |  | 214 | - | $\bigcirc$ | - | $\bigcirc$ | 394 | - | 90 | 66 | 98 |
| 103 | $\bigcirc$ | 5 | $\bigcirc$ | $\bigcirc$ | 215 | - | - |  | 16 | 395 | 54 | 65 | 52 | 59 |
| 104-108 |  | all wh | hite |  | 216 | 7 | $\bigcirc$ | 5 | 8 | 396 | 37 | 40 | 26 | 50 |
| 109 | - | I | - | - | 217 | $\bigcirc$ | $\bigcirc$ | - | $\bigcirc$ | 397 | 55 | 40 | 28 | 20 |
| 110-130 |  | all wh | hite |  | 218 | 11 | 60 | 62 | 79 | 398 | 36 | 50 | 50 | 62 |
| 131 | - | $\bigcirc$ | 0 | 9 | 219-230 |  | all wh | hite |  | 399 | 22 | 24 | 18 | 13 |
| 132-134 |  | all wh | hite |  | 23 I | $\bigcirc$ | $\bigcirc$ | I | 16 | 400 | 26 | 26 | 50 | - |
| 135 | 11 | 15 | 35 | 27 | 232 | $\bigcirc$ | - | $\bigcirc$ | 12 | 401 | 50 | 50 | 52 | 72 |
| 136 | - | $\bigcirc$ | $\bigcirc$ | $\bigcirc$ | 233-26I |  | all wh | hite |  | 402 | 42 | 72 | 54 | 50 |
| 137 | - |  |  | $\bigcirc$ | 262 | 5 | - | $\bigcirc$ | $\bigcirc$ | 403 | 14 | - | 54 | 56 |
| 138-139 |  | all wh | hite |  | 263 | - | - | $\bigcirc$ | - | 404 | 69 | 46 | 50 | 63 |
| 140 | 0 | 1 | - | 8 | 264 | - | $\bigcirc$ | I | $\bigcirc$ | 405 | 35 | 21 | 46 | 59 |
| 141 | 4 | - | $\bigcirc$ | - | 266-276 |  | all wh | hite |  | 406 | 47 | 50 | 42 | 79 |
| 142 | - | 17 | - | 16 | 277 | 1 | $\bigcirc$ | - | $\bigcirc$ | 407 | 40 | 60 | 66 | 64 |
| 144 | 38 | - | $\bigcirc$ | 7 | 278-288 |  | all wh | hite |  | 408 | - | 32 | - | - |
| 145 | 14 | 4 | - | - | 289 | - | - | 1 | $\bigcirc$ | 409 | - | 16 | 991 | 100 |
| 146 | 4 | 4 | 6 | 36 | 290 | $\bigcirc$ | - | $\bigcirc$ | $\bigcirc$ | 410 | 28 | 96 | - | - |

Table i-Continued

found outside these areas. Among the above ro8, as many as 29 were found at two adjacent stations, Nos. 23I and 232 (fig. 2), perhaps indicating the existence there of a very small fourth variable area. The remaining 79 blue flowered plants were found scattered sporadically in the predominantly white area, mostly as single plants or as groups of fewer than ten plants.

The question may be raised whether or not the delimitation of the variable areas is an arbitrary procedure. To a certain extent it is admittedly arbitrary; indeed, some of the stations within the variable areas yielded only whites, and some blues were found outside these areas. Nevertheless, there is no doubt that the whites and the blues were not distributed at random throughout the entire region studied. Casual inspection of the region en route by automobile was sufficient to suggest this, and anyone who will take the trouble to compare the data in table I with the maps in figures I and 2 will be convinced not only that the distinction between the variable and the predominantly white areas is a real one, but also that the limits of these areas were approximately as they are indicated on these maps. To illustrate this point, the frequencies of blue and white flowered plants recorded at stations in the eastern part of the Palmdale variable area are shown in sector diagrams in figure 3 . There was only a weak tendency for the blues to occur more frequently in the central parts of the variable areas than they did at the margins of these areas. Thus, only whites were recorded at station No. 392 (fig. 3), which is surrounded by stations at which 50 percent or more of the plants were blue. On the other hand, at station No. 28 all the plants were blue, although to the east of it there lies a large area in which only whites were recorded. The boundary of the variable area was drawn between stations 28 and 29, 352 and 353, and 373 and 374. Perhaps one would be equally justified in drawing this boundary west of station No. $37^{2}$ and between stations 353 and 354 (fig. 3). However, the location of the boundary is fixed within these limits.

## FREQUENCY OF SAMPLES WITH DIFFERENT PROPORTIONS OF WHITE AND BLUE FLOWERED PLANTS

Some of the samples in our material contained exclusively white, other samples only blue, and still others were mixtures of white and blue flowered

plants. In the variable areas outlined above, 349 samples ( 34,900 individuals, not counting the 3000 individuals recorded on the transect near station No. 24) were taken. Figure 4 shows the frequencies of the samples with different proportions of blue flowered plants. The horizontal axis of the histogram indicates the percentages of the blue in the samples; the lefthand column includes those entirely white and the righthand column those entirely blue. On the vertical axis the percentage frequency of each class of samples is shown. Thus, 98 samples, or 28 . I percent, contain only white; 33 samples, or 9.5 percent, contain one to four percent blue, etc. Disregarding the probably non-significant hump in the middle (lying between 45 and 60 percent), the histogram in figure 4 shows a skewed U shaped curve. Wright has shown (1931, fig. 7-10; $\mathbf{1 9 3 7}$, fig. 1, 4, 7; 1940, fig. 4) that curves of this type characterize the distribution of gene frequencies in populations of small genetically effective size.
The shape of the curve in figure 4 is evidently due to the zero class (all white) and the one hundred class (all blue) being more frequent than the intermediate classes. One would expect such a distribution to arise if the blues were concentrated in one part of the region studied, the whites in another part, and the mixed populations in a transition zone. However, this is not the situation which is found in our material. As stated above, pure white and pure blue populations were encountered in the middle as well as on the margins of the variable areas (cf. fig. 3 and table if for illustrations). Examination of correlations (see below) shows that in the variable areas the composition of a population at a given point is independent of that of populations residing 1.5 mile or more away. Under these circumstances, a U-shaped distribution curve probably indicates a restriction of the genetically effective population size in Linanthus Parryae.
Among the 912 samples from the predominantly white areas, 887 samples were pure white, 23 samples had from one to ten percent blue, and two samples (stations 231 and 232) 16 and 12 percent blue, respectively. Inclusion of these samples would change the histogram in figure 4 by rendering the curve much more skewed toward the left, without, however, altering the type of the curve. Since four samples were obtained at each station, a histogram was constructed for the average frequencies of blues in populations of whole stations. Such a histogram resembled that in figure 4, but the distribution curve was not clearly $U$-shaped, owing to the fact that pure blue populations of whole stations were less frequent than in substation samples.

## VARIABILITY

Examination of table i shows that not only populations of adjacent stations but also samples from the same station may exhibit striking differ-


Figure 4.-Frequency of samples containing different proportions of blue flowered plants. Horizontal axis, percentage frequency of blues; vertical axis, percentage of samples.
ences in the frequencies of white and blue flowered plants. Thus, the three samples taken at station No. 27 contained 0,99 , and 100 blues, respectively; at station No. 409 samples with 16, 99, and 100 blues were recorded. It is accordingly desirable to know whether or not different samples from the same station resemble each other to a greater extent than do those of different stations. To answer this question, we may compare the intrastation with the interstation mean squares in our material (computed according to Snedecor 1934, 1937).

In the western variable area (fig. I) four samples were obtained at each of 39 stations (table I). Hence, the material consists of 156 samples or 15,600 plants. The mean squares are as follows:

Between Stations
Sum of Squares Degrees of Freedom Mean Square

$$
162,655 \cdot 2
$$

38
4280.4

Within Stations
II7
222.9

In the two eastern variable areas (fig. 2) four samples are available from each of 25 stations. The mean squares are thus:

|  | Sum of Squares | Degrees of Freedom | Mean Square |
| :--- | :---: | :---: | :---: |
| Between Stations | $84,959.9$ | 24 | 3540.0 |
| Within Stations | $9,232.5$ | 75 | $\mathbf{1 2 3 . 1}$ |

In all variable areas three samples were taken at each of 18 stations. Computation of mean squares shows:

Sum of Squares Degrees of Freedom Mean Square

| Between Stations | $50,124.5$ | 17 | 2948.5 |
| :--- | :--- | ---: | ---: |
| Within Stations | $\mathbf{1 5}, 714.0$ | 36 | 436.5 |

Finally, i5 stations in all varible areas yielded only two samples each. Mean squares in this material are:

Sum of Squares Degrees of Freedom Mean Square

| Between Stations | $48,172.2$ | 14 | 3440.9 |
| :--- | ---: | ---: | ---: |
| Within Stations | $4,373.0$ | 15 | 291.5 |

The $F$ values, that is, the ratios of the larger mean square to the smaller mean square, for the above four fractions of the data are 19.2, 28.8, 6.7, and im. 8 , respectively. These values show that the intra-station variances are very significantly smaller than the inter-station variances. It is certain therefore that population samples taken within a station are in general more similar than samples from different stations.

## SPATIAL DIFFERENTIATION

The conclusion just stated raises a more general question: to what extent is the similarity (or the difference) between populations of Linanthus Parryae a function of the distance between territories inhabited by these populations? To answer this question, a study was made of the correlation between the frequencies of blue flowered plants in populations found at different distances from each other. The following groups of data are useful for this purpose: 30 samples taken at approximately 25 foot intervals in the vicinity of station No. 24 (see p. 323); samples taken at about 250 feet intervals at most of the collecting stations (table i); and samples taken at different stations, the successive stations being approximately half a mile apart (table i). Only the data for the variable areas have been included in these correlation tables.

To find how strongly the frequencies of blue flowered plants are correlated in populations found 25 feet apart, pairs of figures which represent the successive samples on the transect near the station No. 24 have been arranged in a correlation table. Similarly, the correlation between populations living half a mile apart has been computed by tabulating pairs of
adjacent samples from successive stations (if the order of the stations be represented as abcde, the pairs $a b, b c, c d$, de were entered); for distances of one mile, pairs of alternate samples were entered (ac, bd, ce). It is fully realized that the validity of the correlation coefficients in our material may be questioned because the frequency distribution of the different classes of samples shows a striking departure from normality (fig. 3). The justification of using the correlations in this material for our purpose lies in this: that ( I ) all the correlation coefficients to be compared were derived from distributions which display the same type of deviation from the normal; (2) the correlation coefficients for different distances exhibit a very consistent trend of change (table 2); (3) mere inspection of the data without any computations demonstrates beyond any doubt that populations from

TAble 2
Correlations between the frequencies of blue flowered plants in populations
found at different distances.

| APPROXIMATE <br> DISTANCE | $\mathrm{r} \pm \mathrm{m}_{\mathbf{r}}$ | NUMBER OF <br> ENTRIES | BASED ON DATA <br> PRESENTED IN |
| :---: | :---: | :---: | :---: |
| 25 feet | $+0.899 \pm 0.037$. | 29 | page 323 |
| 75 feet | $+0.875 \pm 0.065$ | 27 | ditto |
| 250 feet | $+0.817 \pm 0.022$ | 224 | Table I |
| 750 feet | $+0.723 \pm 0.062$ | 61 | ditto |
| 0.5 mile | $+0.599 \pm 0.066$ | 95 | ditto |
| 1.0 mile | $+0.505 \pm 0.082$ | 82 | ditto |
| 1.5 miles | $+0.115 \pm 0.114$ | 77 | ditto |
| 2.0 miles | $+0.096 \pm 0.109$ | 84 | ditto |

closely adjacent localities tend to be more similar than those from more remote localities, thus giving common sense confirmation of the correlation coefficients which actually express a biological regularity present in the data.

Table 2 shows that the populations which inhabited territories 750 feet apart or less tend to have similar frequencies of the blue and the white flowered plants. This conclusion is confirmed by inspection of the data for the 30 samples on the transect at station No. 24. This transect shows a clear gradient in the frequency of blues; at one end of the transect the population is predominantly white, at the other end it is predominantly blue, and a gradual change occurs in the intervening zone. The resemblance of populations found within one-half mile and within one mile of each other is still perceptible. The correlation coefficients for distances of I .5 and 2 miles are no longer significant.

No relation between the composition of populations of Linanthus Parryae and the environment in which these populations live is detectable. As pointed out above, the region studied is homogeneous both with respect to physical factors and with respect to plant associations. The boundaries between the variable and the predominantly white areas do not coincide with any perceptible migration barriers. An attempt was made to relate the composition and the density of the populations examined. The outcome of this attempt was negative. The population density in the variable areas fluctuated from less than one to 26 plants per square foot, the average being 9.7 plants; in the predominantly white areas the fluctuation was from less than one to 48 , and the average 7.4 per square foot. Correlating the population density and the frequency of blues at different stations within the variable region, a non-significant correlation coefficient ( $\mathrm{r}=-0.08$ $\pm 0.16)$ was obtained.

## DISCUSSION AND SUMMARY

The apparent complexity of the distribution pattern of white and blue flower color in Linanthus Parryae can be reduced to a relatively simple scheme. The blue was found principally in three or four "variable areas." Outside these areas the blue was encountered only sporadically, as would be expected if it were introduced there only on rare occasions through mutation or through occasional transport of "blue" pollen or seed. Within the variable areas the white and blue occurred side by side, and the population was differentiated into an extremely fine mosaic of microgeographic races. Pure white and pure blue colonies occurred at distances as small as 500 feet (station No. 27 , table i). Nevertheless, populations found one mile or less apart, resemble each other more than do populations taken at random in the variable areas (table 2 ).

In the samples from the variable areas (fig. 3) the distribution curve of the frequencies of blue flowered plants resembles Wright's curves for the distribution of gene frequencies in effectively small populations. This resemblance, as well as the extremely fine geographic subdivision of the species in the region studied, furnishes an indication of the agency which is primarily responsible for this mosaic-like subdivision. As shown by Wright (193I and later work), the variable genes in small populations tend to become stabilized at values of zero and one-that is, tend to be lost or to reach fixation. The distribution curve for such populations consequently assumes a U-like shape which is symmetrical in the absence of mutation, selection, and interchange of migrants among the separate colonies. Introduction of one or more of these factors may cause the U-curve to become
skewed. The curve in figure 4 is definitely skewed toward the left. However, this curve represents phenotype frequencies and not gene frequencies. Since the mode of inheritance of the flower color is as yet unknown, we are unable to compute the gene frequencies in our material. If Linanthus Parryae is obligatorily or predominantly crossfertilized, if the difference in color is caused by a single pair of alleles, and if blue is recessive to white, the gene frequency curve would assume a nearly symmetrical $U$-shape. If blue is dominant to white, the gene frequency curve would be skewed even more toward the left than the phenotype curve shown in figure 4 .

## LITERATURE CITED

Dobzhansky, Th., 1937 Genetics and the origin of species. Ist edition. New York: Columbia University Press.
Snedecor, G. W., 1934 Calculation and interpretation of analysis of variance and covariance. Ames, Iowa: Collegiate Press. 1937 Statistical methods. Ames, Iowa: Collegiate Press.
Turesson, G., 1922 The genotypical response of the plant species to the habitat. Hereditas 3: 211-350.
Wright, S., 193r Evolution in Mendelian populations. Genetics 16: 97-159.
1937 The distribution of gene frequencies in populations. Proc. Nat. Acad. Sci. 23: 307-320. 1040 The statistical sequences of Mendelian heredity in relation to speciation. The New Systematics pp. 161-183. Oxford: Clarendon Press.

