Evolutionary divergence in closely related populations of *Mimulus guttatus* (Scrophulariaceae)

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EVOLUTIONARY DIVERGENCE IN CLOSELY RELATED POPULATIONS OF MIMULUS GUTTATUS (SCROPHULARIACEAE)

Karen W. Hughes and Robert K. Vickery, Jr.

Abstract. — The evolutionary divergence of five closely related populations of the yellow monkey flower, *Mimulus guttatus*, was compared with the length of time the populations could have occupied the site and with the ability of the populations to intercross. Populations from the younger sites were found to be morphologically intermediate to populations from the older sites. Ability to intercross was not correlated with morphological divergence at this stage of evolution.

Glaciation patterns of the Wasatch Mountains of Utah provide an estimate of the geological age of existing plant populations. If evolutionary relationships between isolated populations can be determined, an estimate of rates of evolution for these populations may be obtained. The purpose of this investigation is to determine the amount of divergence between populations from previously glaciated and unglaciated sites and to relate this divergence to the age and possible origin of the populations. Divergence is estimated by calculating a Prim network (Prim, 1957), based on morphological characteristics of the populations, and by analyzing the ability of the populations to intercross. The Prim network was calculated for 24 morphological traits and for 6 selected traits to determine whether larger numbers of characters make a significant difference in the network.

Methods and Materials

Five populations of *Mimulus guttatus* Fischer ex D.C., the yellow monkey flower, from two adjacent canyon drainages were selected for investigation (Table 1). *M. guttatus* grows in small isolated populations near streams or springs and is thus ideal for studies of evolutionary divergence. Plants were grown from seeds in the greenhouse. Quantitative data were gathered for 24 morphological traits on an average of 16 plants per population. We were unable to select a larger number of traits because of the close morphological relationships of the populations. Traits selected include height, dry weight, degree of pigmentation, timing and extent of flowering and seed set, etc. (Crook, 1964).

Plants from each population were intercrossed in all combinations but one, i.e., diallel design.

The estimated age of the populations was determined from the period of time each site was available, geologically, for occupation by the populations. The Thousand Springs and Storm Mountain sites have never been glaciated and apparently have been available for occupation for 50,000 years or more, while the remaining three sites were glaciated and have been available only since the retreat of the Wisconsin period glaciers (Table 2). Populations may not be as old as the site and may have migrated up and down the mountainsides with changing environmental conditions at the end of the glacial epoch.

Table 1. Populations of *Mimulus guttatus*

<table>
<thead>
<tr>
<th>Culture number</th>
<th>Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>6648</td>
<td>Big Water Gulch, Millcreek Canyon. Along stream south of parking lot at end of road. Altitude 7,680 feet.</td>
</tr>
<tr>
<td>5840</td>
<td>Thousand Springs, Millcreek Canyon. Hillside adjacent to road. Site is marked with a road sign. Altitude 7,200 feet.</td>
</tr>
<tr>
<td>6649</td>
<td>Brighton Loop, Big Cottonwood Canyon on Clayton Peak drainage. East edge of Brighton Loop at top of canyon. Altitude 8,760 feet.</td>
</tr>
<tr>
<td>5839</td>
<td>Spruces, Big Cottonwood Canyon. Stream and marsh areas of Spruces Campground. Altitude 7,360 feet.</td>
</tr>
<tr>
<td>6127</td>
<td>Storm Mountain, Big Cottonwood Canyon. Stream in small canyon south of Storm Mountain Campground. Altitude 6,240 feet.</td>
</tr>
</tbody>
</table>

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The 24 morphological traits were analyzed by the principal components method of factor analysis as outlined by Harman (1964) to obtain factors composed of mutually correlated groups of traits. Six major factors were obtained with eigenvalues greater than one (Crook, 1964).

The morphological similarities of the populations were determined by calculations of a shortest distance network developed by Prim (1957) and adapted to evolutionary studies by Edwards and Cavalli-Sforza (1964). In this method the sum of the normalized character differences between the populations is the estimate of the difference. Populations with large numbers of differing traits are widely separated on the network and vice versa. The assumption implicit in the use of the Prim network for evolutionary studies is that the sum of the character differences is proportional to the evolutionary differences between the populations. It should be noted that Edwards and Cavalli-Sforza made assumptions of independence and selective neutrality not made here. The assumption of neutrality is not necessary, as we are interested in divergence, whether random or the result of selective pressures. The 24 morphological traits are clearly not independent, as they may be combined into 6 groups of mutually correlated traits by factor analysis. Some of the 24 variables are represented in more than one factor (Crook, 1964). The 6 traits are as independent as can be obtained in that they represent high factor loading on one factor and very low loadings on the other factors. Prim networks were calculated for all 24 characters and for the 6 characters obtained from factor analysis.

RESULTS AND DISCUSSION

The 6 major factors derived from the factor analysis of 24 characters can be identified as follows. Factor 1 is a composite factor representing general bushiness of the plant, with high factor loadings on the number of leaves and branches and on measurements related to the age of the plant. Factor 2 represents dry-weight measurements, with emphasis on roots and runners. Factor 3 represents almost entirely pigment measurements, with negative loadings on age. Factor 4 is a general measure of height. Factor 5 is a general measure of flower size. Factor 6 has the highest loadings on duration of flowering and seed set. The characteristic with the highest factor loading in each factor was selected for analysis by the Prim network (Table 3).

The Prim networks based on 24 morphological characters and on the 6 selected morphological characters are given in Figures 1 and 2. Both networks are identical in pattern, but the distances between populations vary somewhat.
All populations tested intercrossed. In only two cases was the seed production reduced (Figure 3). Thousand Springs ♀ X Spruces ♂ produced an average of 89 seeds per capsule. Spruces ♀ X Brighton ♂ produced an average of 90.61 seeds per capsule. The average parental seed production for all populations in the study was 173.67. Big Water Gulch and Thousand Springs were not intercrossed.

The correlation of Prim network distances between populations and the number of seeds produced was not significant when Prim network distance was calculated from all 24 traits ($r = -0.026$) and barely significant when Prim network distance was calculated from 6 traits ($r = -0.443, p = .05$).

CONCLUSION

The similarity of the two Prim networks indicates that fewer characteristics may be used without distorting the observed pattern of relationships between the populations; however, the distances between populations do change somewhat. In this study the characteristics for the second network were selected by factor analysis; however, the factors represented broad generalized categories, and an investigator with an extensive knowledge of his/her organism might intuitively select similarly representative factors. Factor analysis might also be used in a preliminary study by investigators who lack resources for collecting large amounts of data.

In both Prim networks the oldest populations, i.e., populations occupying sites that have been available for the longest period of time, appear at either end of the network, while populations from the newer sites occupy intermediate positions. This finding is in agreement with the pattern of evolution expected if the younger populations received portions of their gene pool from the older established populations. Mimulus is an edible plant, and Lindsay (1960) has shown that seeds can pass undigested through the digestive tract of birds. It is thus possible that birds and mammals could carry the seeds from site to site. Seeds deposited in recently deglaciated sites would find little competition from other plants and would be likely to survive. Seeds carried to well-established older sites from the younger sites would have to compete with well-adapted genotypes. Thus the younger populations are likely to be a mixture of genotypes from the older populations, while the older populations would tend to maintain their well-adapted genotypes. If this pattern of evolution is correct, we would expect that the younger populations would be a mixture of genotypes from the older, well-established populations and would be intermediate to the older populations on the Prim network. The network suggests that older popula-

Table 3. Morphological traits selected by factor analysis.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Species</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total number of branches at end of seed production</td>
<td>Thousand Springs</td>
<td>4.45</td>
</tr>
<tr>
<td>Total dry weight recorded at end of seed production</td>
<td>Spruces</td>
<td>4.05</td>
</tr>
<tr>
<td>Number of internodes on main stem that show anthocyanin pigment</td>
<td>Prim</td>
<td>3.89</td>
</tr>
<tr>
<td>Length in mm of longest internode</td>
<td>Big Water Gulch</td>
<td>2.03</td>
</tr>
<tr>
<td>Length of last flower produced by the plant</td>
<td>Storm Mountain</td>
<td>2.10</td>
</tr>
<tr>
<td>Time in days of seed production</td>
<td></td>
<td>4.45</td>
</tr>
</tbody>
</table>

Fig. 2. Prim network for six morphological traits.

Total distance = 21.00
Fig. 3. Seeds produced by crosses between populations of *Mimulus guttatus*. The direction of the arrow is from male pollen donor to female. Crosses within populations are indicated by a bar within the circle. Self-pollinations are indicated by the thickness of the circle circumference.

Titions are more closely related to the younger populations in adjacent canyons than to younger populations in the same canyon. This may reflect the results of selection on a mixture of genotypes rather than patterns of population establishment.

The failure of crossing data to correlate with the Prim network results is not surprising. None of the populations have shown significant morphological differences, and barriers to gene exchange have not evolved. At such a point a random accumulation of gene differences might or might not cause a reduction in ability to intercross, depending upon which genes are involved.

**Summary**

Prim networks based on 24 and 6 morphological traits were identical with respect to order of the populations. However, the distances between the populations did vary from population to population. The two oldest populations appeared at either end of the network, while the more recently established populations ap-
peared in the middle. Probably the older, well-adapted populations donated a portion of their gene pools to the younger populations.

References Cited