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A discriminant analysis of introgression between *Quercus prinus* L. and *Quercus alba* L.

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LEDIG, F. T., R. W. WILSON, J. W. DUFFIELD, and G. MAXWELL (Yale Univ., New Haven, Conn. 06511). A discriminant analysis of introgression between *Quercus prinus* L. and *Quercus alba* L. Bull. Torrey Bot. Club 96: 156–163. 1969.—A discriminant function based on leaf morphology was used to separate seedling rock chestnut oak, *Q. prinus*, and white oak, *Q. alba*. The values of the function were calculated for the progeny of a putative hybrid *Q.* × *saulii* growing in a mixed stand of the parental species and the frequency distribution was compared with that of the parents. It was concluded that *Q.* × *saulii* backcrosses to both parents but the majority of the introgression is toward *Q. prinus*. Based on external seedling morphology, many backcross progeny are not distinguishable from the latter parent and might be overlooked or misclassified in a study of naturally occurring populations.

The natural hybrid between rock chestnut oak, *Q. prinus*, and white oak, *Q. alba*, was named *Q.* × *saulii* by Schneider (1904). The nomenclature used herein follows that of Little (1953). *Q.* × *saulii* is frequently identified throughout the area of sympatry of the parental species. It has occurred in Vermont, Massachusetts, Rhode Island, New Jersey, Pennsylvania, the District of Columbia, North Carolina, Illinois, and Alabama according to Sargent's Manual (1922) and in Virginia according to Allard (1949).

Hybrids are important because they represent avenues of gene exchange between populations. Introgression may enhance genetic variability and maintain evolutionary flexibility. The significance of introgressive hybridization has been discussed many times (*e.g.* Anderson, 1949; Anderson and Stebbins, 1954). Though hybridization was common between *Q. marilandica* Muench. and *Q. ilicifolia* Wang., the role of introgression was considered relatively unimportant (Stebbins, Matzke, and Epling 1947). However, introgressants may often be difficult to recognize and the differential survival of introgressed genes which affect non-morphological traits may be nearly impossible to demonstrate. Stebbins (1959) has argued in favor of the importance of the rare event in evolution.

While the major species of oaks, such as *Q. prinus* and *Q. alba* form well-differentiated entities, new combinations of genes may provide raw material on which selection could act to produce populations adapted to

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changing environments or new habitats. Tree breeders may find oak hybrids or introgressants useful as cultivars in reforestation.

A hybrid colony of *Q.* × *saulii* has been described (Silliman and Leisner, 1958). However, studies of such colonies can only indicate the relative distribution of segregant or backcross individuals among recognizable population deviates; *i.e.* they indicate the affinities of obviously hybridized individuals but are inefficient in detecting types closely resembling the parents.

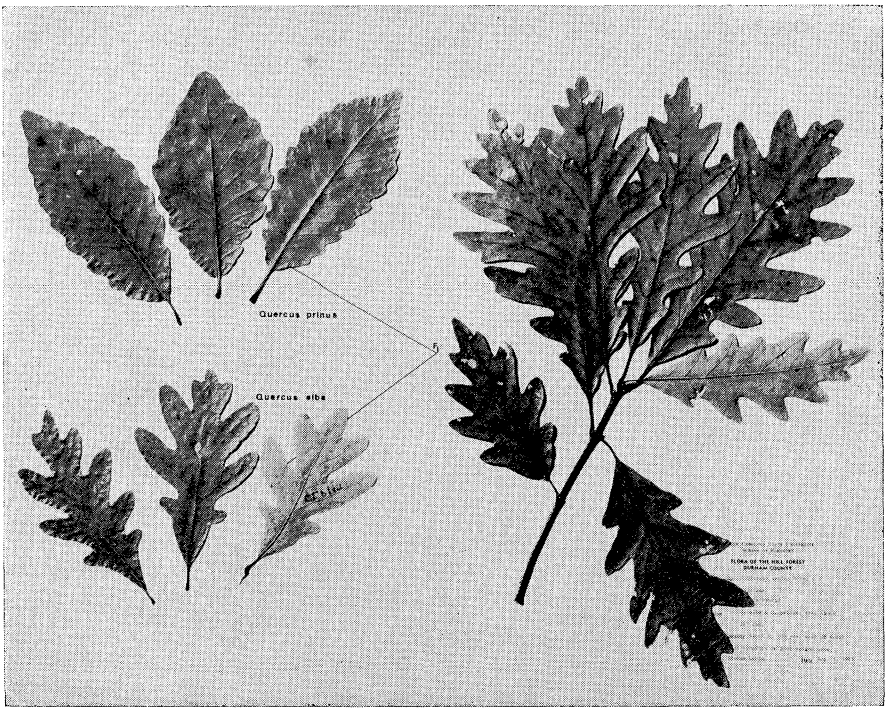

Figure 1. Leaves of the hybrid, *Quercus* × *saulii,* and representatives of the parental populations.

The present study describes the characteristics of the offspring of one putative hybrid and attempts to interpret its pattern of crossing in a mixed stand of *Q. prinus* and *Q. alba.* To accomplish this, the best combination of leaf characteristics for separation of the parental species was determined from discriminant analyses.

Methods.—DESCRIPTION OF THE HYBRID. A putative *Q.* × *saulii* was located on the Hill Forest, Durham County, North Carolina.[3] The site is of poor quality, has a history of fire and logging, and the soil is thin. The

[3] The Hill Forest is part of the School of Forest Resources, North Carolina State University.

hybrid colony investigated by Silliman and Leisner (1958) is located near Chapel Hill, approximately 20 miles from the hybrid individual considered here. Their description of that site as "barren" and "almost as though paved with stones" applies equally well to the present situation.

In outline the leaves of the hybrid have more lobes than those of *Q. alba* but deeper sinuses than those which separate the crenations of *Q. prinus* (Fig. 1). The leaves closely resembled the herbarium specimen pictured by Vasey (1883). Dr. Kingsley Taft of the Tennessee Valley Authority, Norris, Tennessee, supplied specimens of the foliage of artificial hybrids produced in 1936 by J. C. McDaniel from controlled crosses of *Q. alba* with pollen of *Q. prinus*. These specimens are nearly identical to those of the putative hybrid.

Acorns were collected between September 30 and October 9, 1965 in traps and from the ground within 20 ft of the hybrid. The tree appeared extremely fertile and over 900 acorns were easily collected. Collections were

Table 1. Acorn weight, length, and diameter of *Quercus prinus*, *Q. alba*, and *Q.* x *saulii*, their F_1 hybrid.

	Weight[1] ($g \pm S_x$)	Length[2] ($mm \pm S_{\bar{x}}$)	Diameter[2] ($mm \pm S_x$)
Q. prinus	7.92 ± 1.32	39.64 ± 1.27	30.18 ± 1.24
Q. alba	3.45 ± 0.84	22.77 ± 1.73	16.23 ± 1.20
Q. x *saulii*	5.20 ± 1.15	22.62 ± 1.86	19.34 ± 1.35

[1] Based on samples of 55, 35, and 502 respectively.
[2] Based on samples of 55, 35, and 316 respectively.

also made beneath trees of *Q. prinus* and *Q. alba* on the Hill Forest. Because the possibility of past introgression between these species exists throughout the area, defining the parental populations can only be subjective. Therefore, the only criterion applied to selection of trees from which collections were made was that they were individuals which a trained taxonomist would identify as obviously *Q. prinus* or *Q. alba*, respectively.

The acorns of the hybrid were highly viable; germination percent was 79% compared to 78% and 77% for *Q. prinus* or *Q. alba* respectively. A sample of these acorns was weighed and their length and diameter were measured. The hybrid was intermediate between the parental species in these characteristics and in the nature of the cup scales (Table 1).

The bark of the hybrid was also intermediate between its putative parents being neither as thick and deeply furrowed as typical *Q. prinus* nor as flaky as *Q. alba*.

Because of the intermediacy of the hybrid and its near-identity to specimens of *Q.* × *saulii* resulting from controlled hybridization, it was concluded that the Hill Forest specimen was a first generation hybrid of *Q. prinus* and *Q. alba*.

METHODS OF ANALYSIS. Acorns collected on September 30, and October 9, 1965 were stored in plastic bags at 2–4°C until October 26, 1965 when they were sown in the nursery bed in completely randomized rows of 10–20 seeds with approximately 1 ft spacing between rows. At the end of the first growing season, October 1966, two leaves were harvested from each of 58 putative backcross or F_2 seedlings, 12 of *Q. prinus* and 9 of *Q. alba*.

Sixteen measurements (see Fig. 2) were made on the leaves or on trac-

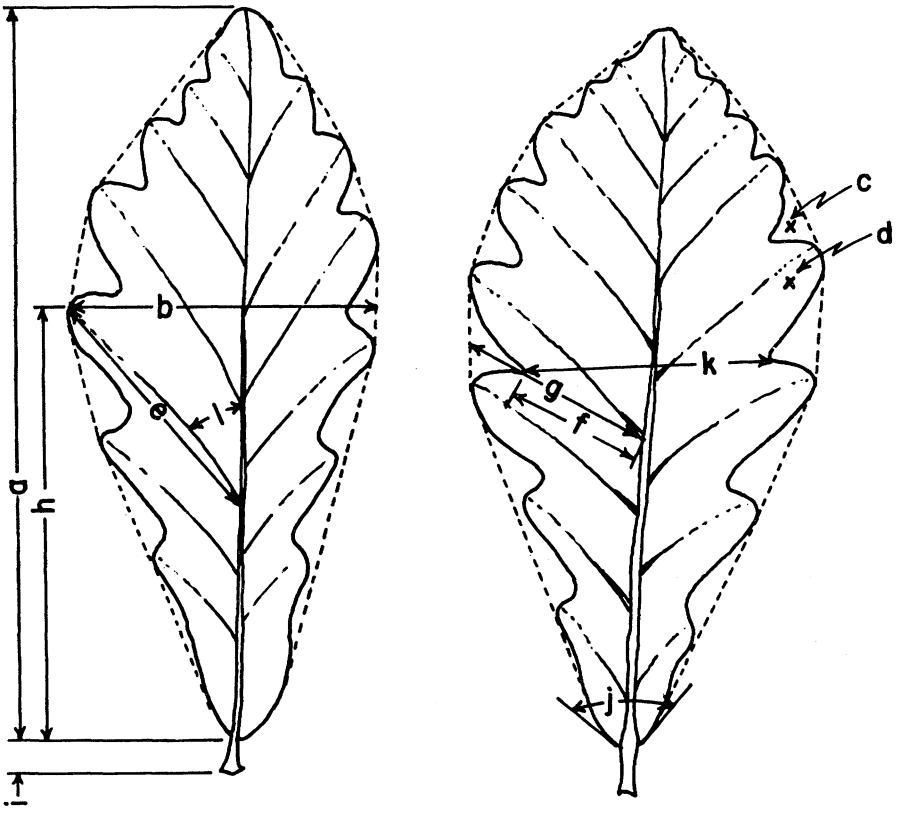

Figure 2. Diagram of two leaves from seedlings of wind-pollinated *Quercus* × *saulii* showing basic measurements and circumscribed convex polygons.

ings of the leaves. All linear measurements were made to the nearest millimeter and angles measured with a protractor to the nearest 5°. Areas were determined by planimeter. Reflectance of the leaf surface was measured with a Bausch and Lomb Spectronic 20 and reflectance attachment.

For analysis some of the basic measurements were transformed. The following variables were used (letters refer to Fig. 2): length (a), length ÷ width (a/b), polygon area ÷ leaf area (d/c), length ÷ distance from the

base to the widest point (a/h), intersinus width (k), width ÷ intersinus width (b/k), petiole length (i), basal angle (j), lobe angle (l), total number of lobes (m + n), asymetry or the difference between number of lobes on the right and number on the left (m − n), depth of incision ratio (g/f), reflectance of the top surface, reflectance of the bottom surface.

In addition three other measurements and ratios commonly used to express depth of incision or degree of dissection were analyzed. However, the ratio finally chosen (g/f) was best in discriminating between parental species as shown by a t-test.

Discriminant analyses of *Q. prinus* and *Q. alba* were run using many combinations of these variables. The discriminant analysis is a multivariate statistical procedure pioneered by Fisher (1936). It is basically simple but was rarely applied before the development of electronic computers. In the case of two species it is analogous to the regression of a dummy dependent variable on the independent variables (see ch. 44 in Kendall and Stuart, 1966, for the statistical approach to discriminant analysis). In this investigation the dummy dependent variable stands for the parental species and the independent variable is an arbitrary constant; *e.g.* +1 for *Q. prinus* and –1 for *Q. alba*. The regression coefficients obtained are the weights assigned to the characters in the discriminant function. The values of the function can be calculated for each individual and plotted on a scale similar to that used with a hybrid index. Scales established by discriminant functions have been used by Namkoong (1966) for the analysis of introgression in forest trees.

Results. The discriminant function was chosen which resulted in the widest separation of seedlings of the parental types. The function was:

$$Z = 0.049610(a) - 0.437192(i) - 0.033963(k) - 0.241377(m+n) + 1.0(g/f)$$

The Rao-Mahanolobis coefficient for the function was 339.8. It is a generalized distance coefficient (see Rao, 1952). The larger its value, the greater the power of the function to discriminate between groups. Parental types were classified perfectly by the function (*i.e.* without overlap). The variables in order of their contribution to discrimination were number of lobes (m + n), leaf length (a), petiole length (i), intersinus width (k), and incision ratio (g/f). All models which included number of lobes as a criterion were significant. This is expected since there is no overlap between the parental species in number of lobes.

When values of the discriminant function were calculated, divided into convenient classes, and plotted as a frequency polygon for the parental types and the offspring of the hybrid, an interesting distribution appeared (Fig. 3). The frequency distribution for the hybrid's progeny is denser toward the *Q. prinus* parent than toward the *Q. alba* parent. This verifies the visual observation that most of the progeny tended to resemble seedlings of *Q. prinus*. The function yields a low frequency of types exactly inter-

mediate between parental means. The two modes suggest that the hybrid crosses with both parents. There is more gene flow toward the *Q. prinus* population as shown by the high frequency of types halfway between the midpoint and the parental mean. In addition, a proportion of the progeny lie well within the parental range of *Q. prinus* and some even resemble extreme *Q. prinus* types.

Discussion. A striking characteristic of the progeny of the hybrid is the resemblance of many individuals to the *Q. prinus* parent. The major mode of the frequency distribution lies in a position corresponding to a backcross

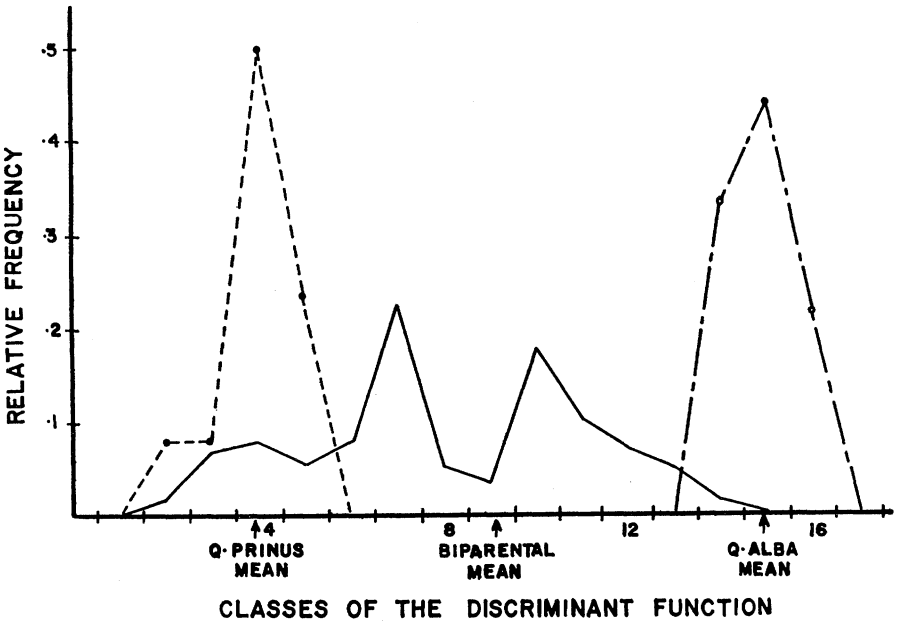

Figure 3. Location and relative frequency of progeny of the putative hybrid and the parental populations by discriminant function.

of an F_1 with *Q. prinus,* interpreted according to Anderson (1949) and the theory of quantitative characters correlated by linkage. It is probable that most gene flow through the hybrid is in the direction from *Q. alba* to *Q. prinus*. This agrees with the results of Silliman and Leisner (1958) whose hybrid index suggested a clustering of the individuals in their hybrid colony close to the parental mode of *Q. prinus*. Their study included only mature trees. Because there may be differential survival of backcross or segregant types due to natural selection, it is more likely that the method employed in this study indicates the pattern of crossing and the initial distribution of backcross types. Though the results of Silliman and Leisner's

study are similar to those reported here, this analysis indicates substantial backcrossing to *Q. alba* also. These types may be selected against on such poor sites, accounting for their absence in the stand investigated by Silliman and Leisner.

The distribution of the values of the discriminant function is remarkably similar to the frequency chart of Allard (1949) for progeny of a single tree of *Q.* × *saulii* growing in Virginia. Allard's chart is based only on the number of lobes, but it too has two peaks, the largest lying near the *Q. prinus* parent, the other near *Q. alba,* and with some individuals within the range of and even more extreme than *Q. prinus.* The discriminant function used here includes number of lobes, so the similarity may be expected.

No other hybrid individuals were observed in the neighborhood of the study tree and in the absence of other hybrids, an F_2 or segregating generation could be produced only by selfing. Oaks in general are known to be rather self-incompatible (Irgens-Moller, 1955; Piatnitsky, 1960) so that selfing would probably be rare. Therefore, the low frequency of intermediates midway between parent species is anticipated. Because of the improbability of any but a very low level of selfing, the extreme individuals in the hybrid progeny, closely resembling *Q. prinus,* are felt to be backcrosses and not segregants.

The close resemblance or apparent identity of many hybrid offspring to *Q. prinus* indicates the great difficulty of recognizing and fully assessing the extent of introgression in natural stands. No simple hybrid index based on leaf characteristics could separate and identify these individuals as backcrosses.

The apparent fertility of the hybrid plus frequent reports of its occurrence suggest that introgression between *Q. prinus* and *Q. alba* could be important. If not of significance in the past evolution of these populations, it represents a potential store of variability for the future. The relative ease of crossability and high fertility[4] of the F_1 are also characteristics of value to tree breeders should hybrid progeny be shown to have utility in reforestation.

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[4] Personal communication with Dr. Kingsley Taft indicated that the hybrids resulting from controlled cross-pollination of *Q. alba* with *Q. prinus* also produced an abundance of acorns in 1965, a good mast year.

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Ecological role of *Talinum* (Portulacaceae) in cedar glade vegetation

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WARE, STEWART. (College of William & Mary, Williamsburg, Virginia 23185). Ecological role of *Talinum* (Portulacaceae) in cedar glade vegetation. Bull. Torrey Bot. Club 96: 163–175. 1969.—Field and greenhouse studies were made of the life cycle and distribution within its habitat of *Talinum calcaricum* Ware (Portulacaceae). This succulent perennial herb is endemic to limestone cedar glades of middle Tennessee and northern Alabama, where it is confined to a shallow soil ecotone between bare rock and grass-dominated vegetation on soil deeper than 10 cm. Strongly drought resistant, it grows through the driest, hottest part of the summer, but major events of its life cycle are timed so that environmental conditions during critical periods of the cycle are near optimum for growth, survival, and reproduction. Distribution and abundance of *Talinum* within the glade habitat, and thus its role in the vegetation, are limited by soil depth, severe drought, and interspecific competition.

The cedar glades of middle Tennessee and northern Alabama are characterized by a unique flora and vegetation. The glades are open areas

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