

INTERSPECIFIC HYBRIDIZATION IN A NATURAL OAK POPULATION WITH PARTICULAR REGARD TO INTROGRESSION

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A population of oaks, consisting of *Quercus stellata*, *Q. prinoides*, their interspecific hybrid, *Q. x stelloides*, and apparent backcrosses to the parental forms, was examined. An effort was made to determine existing relationships and locate possible introgression within the population.

Nine descriptive variables were analyzed and, as a set, could be used to accurately classify individuals by subgroups.

Character segregation, perhaps introgressive hybridization, is evident in the population. The effects of this are manifested in an increased adaptability and exploitation of the habitat by introgressants. Modification of the parental species type is negligible.

INTRODUCTION

Hybridization in oaks may involve individual trees, or small hybrid populations. Reports of such populations include the hybrids of *Quercus marilandica* Muench. and *Q. ilicifolia* Wang. (1), *Q. alba* L. and *Q. montana* Willd. (2), and recently, a hybrid population produced by three parent taxa, *Q. muehlenbergii* Engelm., *Q. prinoides* Willd., and *Q. bicolor* Willd. (3).

This study involves a small population of post oak (*Q. stellata* Wang.) and dwarf chinquapin (*Q. prinoides* Willd.), both of the white oak group, and their suspected interspecific hybrid *Q. x stelloides*. The hybrid was first described by Palmer (4) with collections reported from Massachusetts, New Jersey, Missouri, Kansas, and Oklahoma. In a later work Palmer (5) stated:

The leaves of the parent species are quite different from each other and the hybrid is well-marked in its intermediate characters. The plants are usually shrubby, from one to two meters tall, but rarely they become arborescent and up to four meters or more. The leaf patterns vary between those of the parent species, but usually they resemble more closely those of *Quercus stellata*, being obovate in outline, with 3-4 pairs of shallow rounded or pointed lateral lobes, simple or rarely enlarged and indented at the apex. At maturity they are green and nearly glabrous above and pale stellate-pubescent beneath.

The population under consideration is located in a wooded section of Mohawk Park, a 1,140-hectare, vegetationally diverse area along Bird Creek on the north side of Tulsa (Sec. 14-15, T20N, R13E).

Members of this population may be separated, with visual examination, into four groups on the basis of leaf type and plant height:

- (1) *Quercus stellata* leaf type
- (2) *Q. prinoides* leaf type, 2 m or less tall
- (3) *Q. prinoides* leaf type, 2-6 m tall
- (4) Intermediate leaf type

Morphological characteristics were studied and an effort was made to determine relationships among existing individuals. Particular attention was given to indications of introgressive hybridization or the infiltration of germplasm from one species into another due to hybridization and back-crossing to parental types (6). Examinations of morphological, biometrical, and ecological characteristics were made as suggested by Heiser (7) and Baker (8). Due to the length of *Quercus* life cycles, progeny testing as carried out by MacDougal (9) and Yarnell (10) was not attempted.

MATERIALS AND METHODS

The oak population under consideration is restricted to an area roughly 75 by 150 m. The elongated southern boundary is sharply delineated by a vertical cut and soil bank produced by a paralleling railroad. The

land slopes sharply away on the east, west, and north boundaries. It could not be ascertained whether this slope is natural or man-made. Post oak is found in the low areas, on the slopes, and at the top, whereas the dwarf chinquapin is restricted to the upper, more xeric soils. The soil is that of an upland prairie and overlies gray shale of the Holdenville formation (11).

The vegetation in the study area, particularly along the railroad tracks, has been subjected to occasional burning and has been treated with herbicides at least twice since 1955 (personal communication, Dr. Albert P. Blair, University of Tulsa).

Within this area sixty-two mature trees were chosen for study, maturity being based on the production of flowers and fruit. Data collected from these trees included leaf characters, flowering times, heights, leaf and twig color patterns, and gall types present.

Twenty leaves were taken from each tree, from all exposures on each plant to allow for environmental variation due to light, moisture, and temperature (12). In all cases, leaves were chosen from nonfertile branches.

Using the methods of Tucker, Cottam, and Drobnick (13), the following measurements in mm were made on each of the 1,240 leaves (Fig. 1): length (including the petiole), vein length from the longest vein on the right hand of the abaxial surface, and depth of the lobe adjacent to the measured vein.

Flowering time was established from field observation of the winter buds and based upon the date the buds began to break rather than the degree of opening or pendulance of the aments.

Tree height was measured directly for those members of the population less than 150 cm tall. The remaining trees were measured via triangulation.

Coloration of twigs and abaxial leaf surfaces was determined using the color standards of Ridgway (14). One twig, at least two years old, from each tree sampled, was assigned a color. Individual trees demonstrated a consistency of coloration in the twigs if the current year's growth was not considered. The coloration of the leaf surface was taken from a single representative leaf. All comparisons between living material and color plates were made in full sunlight to minimize error.

The presence of insect galls on the trees was investigated. Gall frequency and density were not considered. Gall identification was made, using the classification of Felt (15). The two types widely encountered were produced by the gall wasps *Callirhytis clavula* O.S. (Type A) and *Disholcaspis globulus* Fitch (Type B.) Trees having neither gall type A nor B were combined for statistical purposes.

Discriminant analysis was chosen to determine suitability of specific variables for predictive classification. The DISCRIMINANT subprogram of the SPSS (Statistical Package for the Social Sciences) system of

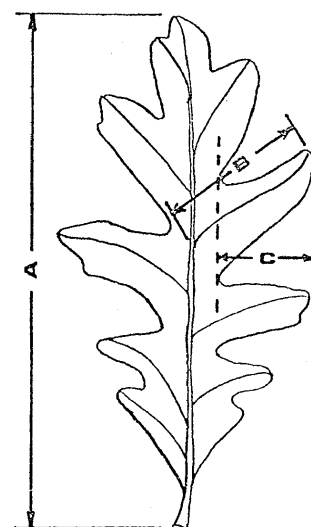


FIGURE 1. Leaf measurements
A = length, B = vein, C = lobe

TABLE 1. Characters selected for discriminant analysis.

Code	Characters
Length	Leaf length with petiole in mm
Vein	Length of longest vein from midrib in mm
Lobe	Depth of lobe adjacent to vein in mm
Nolobe	Number of lobes per leaf
Flower	Day of the year of bud break
Height	Height of the tree in cm
Color T	Color of a representative twig
Color L	Color of abaxial leaf surface
Gall	Gall type present

computer programs (16) was used for this analysis.

Nine variables (Table 1) were analyzed as to the probability of their correctly classifying, singly or in combination, trees of the population into the four arbitrary groups, i.e. *Quercus stellata* leaf, *Q. prinoides* leaf from either shorter or taller trees, and intermediate leaf form. The prediction results of this analysis are presented in Table 2.

Four characteristics in the study population were chosen to construct a hybrid index (6), or graphic representation of relationships (Fig. 2). These characters were chosen because variation in the population, with respect to these characters, fell along a continuum, with the typical post oak at one end and the typical dwarf chinquapin at the other.

The assignment of "typical" characteristic values for post oak and dwarf chinquapin oak was made from the descriptions of Steyermark (17) and Sargent (18) and from examination of specimens in the herbaria of the University of Tulsa and Oklahoma State University.

Each of the 62 trees in the population was assigned a score for the four characteristics. The scores were obtained by inserting each of the individuals along the continuum, relative to each of the four characteristics (Table 3). The total of these scores was used as an index of hybridity.

RESULTS

When the nine selected variables were considered as a group, analysis revealed an ability to correctly classify individuals in 98.39% of the cases studied. Of special note is the high relative F value for the depth of lobing and the absence from the scheme of the variable for leaf color. The subsets listed in Table 4 are the groups into which individuals can be classified according to a particular variable. The number of lobes per leaf is the only variable which can be used to classify individuals into four clear groups.

DISCUSSION

The population of oaks in this study fits Anderson's (19) description of a "mongrel population", in that it is composed of parental species forms, their F_1 intermediates, and apparent backcrosses to the parental forms. The exact hybrid nature of much of the population is still a matter for speculation.

Stebbins (20) suggested that discontinuity between hybrid parents is effectively maintained, even though free intercrossing of parents and hybrids is permitted, when extreme morphological and physiological divergence has evolved. The genetic differences between the parents are so great in these cases that most of the genic recombinations which appear in the second generation are weak or inviable. In *Q. stellata*

TABLE 2. Discriminant analysis classification matrix. *Quercus stellata* type leaf (1), *Q. prinoides* type leaf, shorter tree (2), Intermediate type leaf (3) and *Q. prinoides* type leaf, taller tree (4).

Identified Group Membership	Predicted Group Membership				% Correctly Placed
	1	2	3	4	
1	10	0	0	0	100.0
2	0	25	0	0	100.0
3	0	0	12	0	100.0
4	0	1	0	14	93.3

TABLE 3. Assignment of values to four population characteristics for construction of a hybrid index structure.

Characteristics	Basis of Assigned Scores			
	0	1	2	3
Vein:lobe	2	2-4	4+	
Lobe number	5-8	8-11	11-22	
Height	6 m +	4-6 m	2-4 m	0-2 m
Gall type	None	A	B	

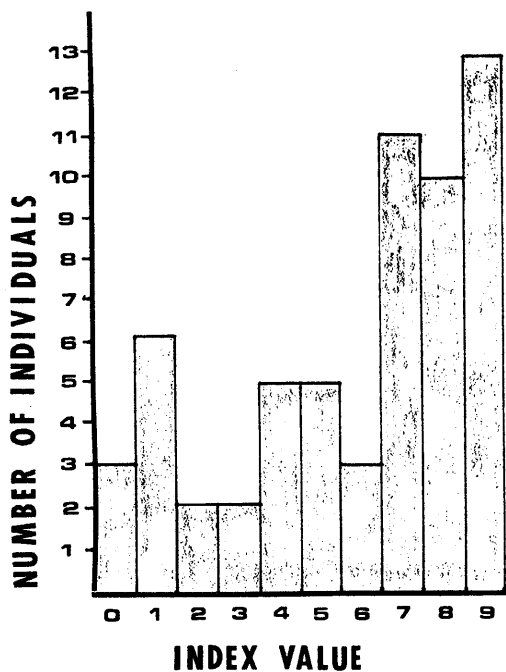


FIGURE 2. A hybrid index of the population based on number of leaf lobes, leaf vein:lobe ratio, tree height, and gall type present.

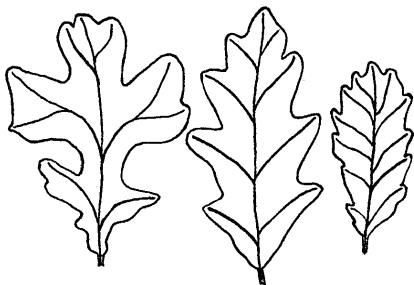


FIGURE 3. Leaf types in population (L-R: *Quercus stellata*, *Q. x stelloides*, *Q. prinoides*)

and *Q. prinoides* crosses, the morphological differences in the parental species are most evident. There is a definite intermediate leaf type in the hybrids examined (Fig. 3) which has been compared with a specimen from Harvard's Arnold Arboretum. The specimen (no. 14285), collected by E. J. Palmer in 1918 in Muskogee, Oklahoma, was called *Quercus x stelloides*. The leaf type of this specimen compares favorably with that of the twelve intermediate types occurring in the study area.

Other than the intermediate types, surviving individuals in the supposed F₂ and succeeding generations seem to be those that are most similar to the parents in many characters. There is not a representation of all possible recombinations.

Great variation exists within the study population based on leaf form. As indicated by Palmer (5), the leaves of the post oak and the hybrid intermediate are fairly standard within their groups and closely

TABLE 4. Summary statistics for discriminant analysis of nine characters as they relate to four groups of *Quercus*.

Step Number	Variable Entered	Means ^a					F to Enter	Wilk's ^b lambda
		Qst	Qps	Int	Qpt			
1	Lobe	30.65	4.64	20.32	4.11		246.78	.0727
2	Flower	85.20	83.84	82.33	67.67		79.47	.0140
3	Height	720.90	107.22	517.05	418.97		12.40	.0084
4	Gall	1.80	2.76	1.33	2.67		11.29	.0052
5	NoLobe	6.07	12.38	9.25	17.76		11.26	.0032
6	Color T	20.18	17.71	20.05	17.39		7.76	.0022
7	Length	123.74	98.50	133.69	115.19		8.58	.0015
8	Vein	57.10	30.28	51.51	33.77		2.72	.0013
Not entered	Color L	25.32	27.20	27.23	36.55			

^aQst = *Quercus stellata* type leaf, Qps = *Q. prinoides* short type, Int = Intermediate type leaf, Qpt = *Q. prinoides* tall type.
^bp < .05

resemble each other, whereas the dwarf chinquapin leaves demonstrate wide variation.

Anderson (19) emphasized that a loose, nonrandom association of various characters is critical evidence for hybridization. When species hybridize, normal isolating barriers continue to work, gradually being lessened in mongrel populations.

When graphed, the hybrid indexes display a bimodal character, skewed toward the *Q. prinoides* parent, strongly suggesting introgressive hybridization.

The shift in the index is due to the prevalence of the dwarf chinquapin and its taller form. Tucker and his associates (13) found that in areas where parental species occur sympatrically, hybrids have usually been found at sites where one species is infrequent or rare and the other abundant. Stebbins *et al.* (1) suggest shifts in a population index of this kind occur because individuals tend to backcross with the most prevalent parent — the parent usually better adapted to the habitat.

Engelmann (21) suggested that annual prairie fires cause the stunted growth form of *Q. prinoides*, while other species are not affected. Because of the interspacing of tall and short trees with the same leaf type, this is apparently not the case at the study site. More likely, the taller trees with the *Q. prinoides* leaf are products of backcrosses of the F_1 hybrid with the *Q. prinoides* parent stock.

If habitat preference is considered a heritable characteristic as valid as any other, it can be seen that an F_1 hybrid would prefer a habitat equal to that of one of the parents or a habitat which would be intermediate relative to that of the parents (22). An F_1 would yield individuals with preferences directly related to the number of genes needed to adapt the two parents to their particular habitats.

A high incidence of hybrid swarms of sympatric plant populations occur in disturbed areas (6) (23). Increased segregate survival in hybridized habitats exists while competition with the parent population on their own ground effectively screens establishment of hybrid populations. The study site is such a disturbed area. Railroad and highway construction and maintenance as well as burning and herbicide application have served as the disturbing influence.

Blair (24) emphasized hybridization within zones of stress, whether spatial or temporal. The population of oaks studied meet the criteria for existence in a zone of stress, either as a result of the disturbed nature of the site, or because the dwarf chinquapin is better adapted to the area than the post oak. The latter is found in the lower areas in greater numbers, while the dwarf is restricted to the uplift in larger numbers than the post oak. These species have the same general geographic distribution but are separated by slightly differing ecological requirements.

The hybrids at the site would have some economic advantage by being able to exploit the intermediate environment. Backcrosses to the better adapted parent would have an increased advantage because of the introduction of genetic material of the less adapted parent. The variation in the individuals with the *Q. prinoides* leaf is likely due to backcrossing of the intermediates with the *Q. prinoides* parents.

In the study population, introgression has only a local effect. It allows offspring produced by hybridization to exploit habitat areas in which either of the parental forms fail to compete well, but without altering the integrity of the parental species significantly at the site and not at all away from the site.

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