

MORPHOMETRIC VARIATION IN OAKS OF THE APOSTLE ISLANDS IN WISCONSIN: EVIDENCE OF HYBRIDIZATION BETWEEN *QUERCUS RUBRA* AND *Q. ELLIPSOIDALIS* (FAGACEAE)¹

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The Apostle Islands in Lake Superior are populated by trees that are clearly related to *Quercus rubra* L. However, several islands have trees with morphological characteristics suggestive of hybridization with *Q. ellipsoidalis* Hill. Leaf specimens were collected from trees in five locations: the outermost island, an intermediate island, the nearest-shore island, the northeast shoreline, and an inland forest about 24 km from the shoreline. Seventeen landmarks were digitized for two to five leaves per tree. These landmarks were used to generate nine linear characters and three angles. These characters, along with the number of bristle tips per leaf, were used in various combinations for several principal component analyses. In addition, the landmark configurations were examined using rotational-fit methods. The patterns observed in both types of analysis indicate phenotypic variation coincident with a line connecting the two most distant sample sites. The location nearest the geographic center of this line is also nearest the center of the two-dimensional view of phenotypic variation. Trees at each site illustrate a distinctive pattern in the rotational-fit analyses, and patterns of co-variation in the morphometric characters are different for each site. The observed morphometric variation is consistent with the hypothesis that there is hybridization between these two species, most likely in the form of introgression from *Q. ellipsoidalis* into *Q. rubra*.

Quercus is a wide-ranging genus of trees and shrubs comprised of up to 500 species worldwide (Nixon, 1989). In eastern North America, the genus is represented by approximately 50 species rather evenly divided between two reproductively isolated subgenera: *Quercus* subg. *Quercus*, the white and chestnut oaks, and *Quercus* subg. *Erythrobalanus*, the red and black oaks.

Within *Quercus*, a definitive view of taxonomic relationships among species has been difficult to achieve. To date, oak classifications have been based almost exclusively on morphological characteristics (Trelease, 1924; Jensen, 1988). However, the apparent ease of hybridization among species (Palmer, 1948), particularly in *Erythrobalanus*, renders such an approach problematic, especially where species ranges overlap. In areas of species sympatry, many trees may have morphologies intermediate between species types. These "hybrid" oaks often defy precise identification (Overlease, 1964; Jensen, 1977b). However, the ability to resolve the problem of identification of putative hybrids is, in part, a function of the number of species that must be considered as potential parent species. In areas where only a few reproductively compatible species are sympatric, as in northern Wisconsin, we might expect the problem to be more tractable.

Three species of *Quercus* subgenus *Erythrobalanus* occur in Wisconsin, but only two of these are found in the

northernmost reaches of the state: *Quercus ellipsoidalis* Hill and *Q. rubra* L. (Costello, 1931; Little, 1971). These two species are quite different morphologically, in both leaf and fruit characters (Jensen, 1977a, b), and are often found growing in the same communities (e.g., Braun, 1967; Miller and Lamb, 1985). Despite their frequent co-occurrence in forests throughout the upper Midwest, there has been no formal documentation of hybridization between these species.

There have, however, been occasional references to evidence of hybridization between *Q. ellipsoidalis* and *Q. rubra*. Palmer (1948) mentioned the existence of herbarium specimens suggesting such hybridization, and Overlease (1964, 1975) referred to gene exchange between these species. Swain (1972) found evidence of morphologically intermediate trees in several Minnesota stands, but chose not to invoke hybridization as the sole explanation of the observed variation. One of the authors (RJJ) has seen several herbarium specimens from Minnesota and Wisconsin that clearly suggest hybridization between these species. Given the rather large area of sympatry of *Q. ellipsoidalis* and *Q. rubra* and the apparent ease of hybridization among such closely related oaks, it would seem most surprising if these two species did not occasionally hybridize.

An opportunity to test the hypothesis of hybridization between *Q. ellipsoidalis* and *Q. rubra* arose as the result of JGI's observations of the oaks on the Apostle Islands in Lake Superior (northern Wisconsin). This archipelago consists of a number of islands extending about 30 km into Lake Superior. The larger islands are forested, and one species common in these forests is *Q. rubra*. While *Q. ellipsoidalis* is a common component of mainland forests to the south and west of the Apostle Islands, it is not thought to occur near the perimeter of the adjacent main-

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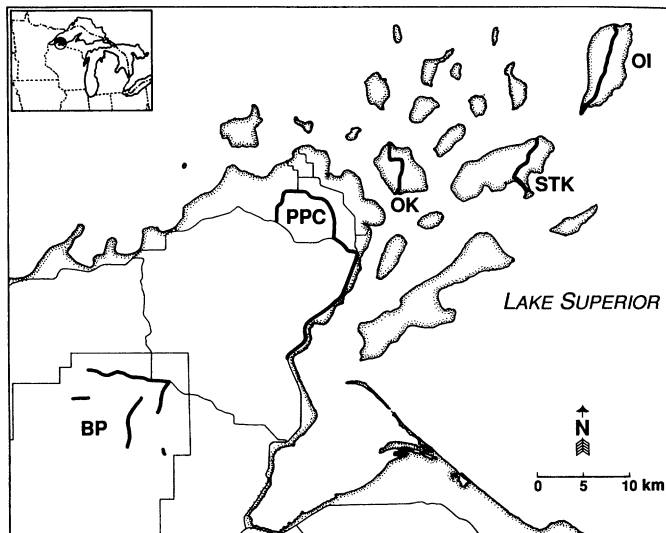


Fig. 1. Map of the Apostle Islands and adjoining Bayfield Peninsula in northeastern Wisconsin. Map abbreviations for the five populations studied are BP (Bayfield Peninsula), PPC (Peninsula Perimeter), OK (Oak Island), STK (Stockton Island), and OI (Outer Island). Heavy lines indicate sampling transects.

land peninsula nor on the islands themselves. However, some trees on the near-shore islands had leaves with fewer lobes and/or deeper sinuses than is typical for *Q. rubra*. When compared to trees on the outer islands, these trees tended to illustrate spindly, highly branched trunks (more typical for *Q. ellipsoidalis*), and the bark was coarse and blocky rather than having the network of broad, smooth plates seen in *Q. rubra*. In addition, the few fruits found associated with these trees had relatively smaller, more elliptic nuts and the cup scales were more pubescent than is typical for *Q. rubra*. Taken together, these qualitative aspects of growth form, bark characteristics, and leaf and fruit morphologies suggest evidence of introgression from *Q. ellipsoidalis* into *Q. rubra*.

We chose to test the hybridization hypothesis by conducting studies of both morphological and biochemical variation. Here we report the results of studies of variation in leaf morphology. Although evidence by hybridization was seen in other characters, we have focused on quantitative studies of leaf morphology 1) because we wished to avoid subjective evaluations of variation and 2) only a few trees yielded fruits during the time we conducted our sampling.

MATERIALS AND METHODS

During the summer and fall of 1989 and 1990, mature leaves were collected from trees in five locations: two mainland sites and on three islands. The collecting sites lie on a west-east transect, extending from the Bayfield Peninsula to Outer Island (Fig. 1). Leaf samples were collected in October 1989. Bayfield Peninsula collections were made along roads that defined the east and northern perimeters of the Chequamegon National Forest, and peninsula perimeter collections were made along the public roads that skirted the perimeter of Bayfield Peninsula. At both sites, we sampled the first mature oak of any taxon

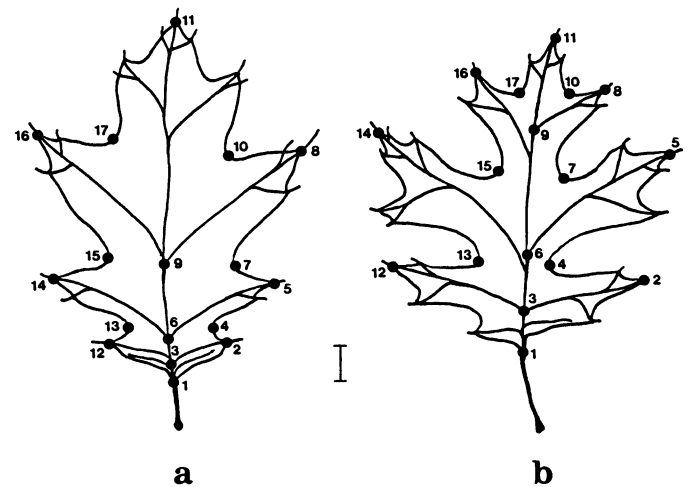


Fig. 2. Leaves of (a) *Quercus rubra* and (b) *Q. ellipsoidalis* illustrating landmarks. See text for explanation of how landmarks were defined. Leaves are drawn to scale (Bar = 1 cm).

sighted at 0.4-km intervals along the roads. Collections on Oak Island were made on a north to south trail that bisected the island. The Stockton Island and Outer Island collections were made along trails that ran from southwest to northeast the length of each island. These populations were sampled by walking vigorously for 5 minutes and collecting specimens from the first mature oak of any taxon sighted within 20 m of the trail. All trees were sampled by harvesting one or two twigs with mature leaves. The numbers of trees sampled per site were as follows: Bayfield Peninsula (BP) = 39; Peninsula Perimeter (PP) = 18; Oak Island (OK) = 10; Stockton Island (SI) = 20; Outer Island (OI) = 20 (total = 107). In order not to confound estimates of variation, only leaves lacking evidence of pathology or extensive insect damage were used for recording data. Most samples yielded three to five "usable" leaves per tree, although for a few trees only two such leaves were available.

After the leaves were pressed and dried, a GTCO DP5-1117 digitizing tablet interfaced with an IBM-PC was used to record 17 landmarks for each leaf (Fig. 2). Landmarks were chosen, as noted by Jensen (1990), to represent putatively biologically homologous points on each leaf (biological homology does not imply functional homology). The leaf was oriented with the abaxial surface up, and the landmarks were defined as follows: 1 = the juncture of blade and petiole; 2, 5, 8, 12, 14, 16 = the tips of lobes defined by the second, third, and fourth secondary veins on each side of the leaf; 3, 6, 9 = the intersection of the midrib with the veins used to define the three right lobes; 4, 7, 10, 13, 15, 17 = the bases of the sinuses immediately above each lobe (these landmarks are more appropriately referred to as computed homologies, sensu Bookstein et al., 1985); 11 = the apex of the leaf blade. The above landmarks were used to generate 12 morphological characters: nine linear measures and three angular measures (Table 1). In addition, the number of bristle tips on each leaf was counted. To reduce the data matrix to reasonable size, a vector of character means was calculated for each tree, resulting in a data matrix having 107 rows (= trees)

TABLE 1. Morphological characters used for multivariate analyses.

Character	Landmarks ^a
1. LBL ^b	1-11
2. LBWB ^c	2-12
3. LBWM ^d	5-14
4. LBWA ^e	8-16
5. INTB ^f	4-13
6. INTM ^g	7-15
7. INTA ^h	10-17
8. CENTER ⁱ	6- 9
9. APEX ^j	9-11
10. ANG1 ^k	1-3-2
11. ANG2 ^l	11-6-5
12. ANG3 ^m	11-9-8
13. NBT ⁿ	

^a For characters 1-9, the character represents the distance between the specified landmarks; for characters 10-12, the middle landmark is the vertex of the angle.

^b Leaf blade length.

^c Leaf blade width defined by basal lobe pair.

^d Leaf blade width defined by middle lobe pair.

^e Leaf blade width defined by apical lobe pair.

^f Interval between basal pair of sinuses.

^g Interval between middle pair of sinuses.

^h Interval between apical pair of sinuses.

ⁱ Interval between center vein intersections.

^j Interval between apical vein intersections.

^k Angle 1.

^l Angle 2.

^m Angle 3.

ⁿ Number of bristle tips.

and 13 columns (= characters). While we recognize the problems inherent with such data reduction, experience (e.g., Knops and Jensen, 1980) indicates this is an appropriate approach.

Patterns of variation among the trees were examined by principal components analysis (PCA; Sneath and Sokal, 1973) of several versions of the data matrix. First, the raw character matrix was standardized (0 mean, unit variance) by columns, and a matrix of character \times character correlations was generated. The latter was used as input for principal components analysis (PC1). Second, the three angular measures and the count of bristle tips were dropped from the raw matrix, and the nine remaining characters were converted to common logarithms. This 107×9 matrix was used to generate a 9×9 variance-covariance matrix. The latter was used as input for a second principal components analysis (PC2) based solely on linear measures. This analysis allows us to contrast patterns determined largely by general size differences with those derived from an analysis designed to remove the general size component. Burnaby's sweep (Rohlf and Bookstein, 1987) was used in an attempt to remove the effects of general size from the variance-covariance matrix. The size-adjusted matrix was used as input for a third principal components analysis (PC3). Finally, a separate principal components analysis, analogous to PC1 above, was performed on each of the five sample sites. These last PCAs were used to evaluate patterns of character correlation at each site. The above analyses were performed using NTSYS-pc, version 1.6 (Rohlf, 1990).

A second set of analyses was performed using the original sets of landmark configurations. A program developed by Rohlf and Slice (1990) was used to conduct ro-

tational-fit analyses of variation in the entire set of data as well as at each of the five sites. As demonstrated by Jensen (1990), these methods can be used to compare leaf "shapes" as determined by the landmarks. These comparisons are size free, so differences among sets of leaves may be viewed as shape differences. Because of the limitations of the program (only 150 objects can be processed in a single analysis), the leaves for each tree were used to generate a consensus configuration for that tree (the consensus configuration can be thought of as analogous to a set of character means). The generalized resistant fit (GRF) algorithm (without an affine transformation) was used to create plots of variation in landmark configurations. These plots were prepared to illustrate the major and minor axes and two-standard-deviation equal-frequency ellipses of variation for each landmark.

The number of landmarks, and the proximity of several of the landmarks, makes it difficult to envision variation in the entire set of trees. The following steps were used to create simple plots to indicate the differences among the five sample sites. First, a consensus configuration was calculated for the entire collection. Second, a consensus configuration was calculated for each sample site. Third, the sample site consensus was fit to the overall consensus using the GRF option. The resulting plots illustrate the vectors of change (residual vectors) required to fit each sample site consensus to the overall consensus. In these plots, if two sample sites have similar consensus configurations, then they will illustrate the same pattern of vectors. On the other hand, if two sample sites have dissimilar consensus configurations, the vector plots will allow recognition of these differences.

RESULTS AND DISCUSSION

As noted above, the island samples have fewer trees than the mainland samples and these trees by and large appear more like *Q. rubra* than *Q. ellipsoidalis*. Nevertheless, the Outer Island and Stockton Island collections appear to be more variable than collections from the other sites. This is especially evident in Fig. 3, a PCA based on the full set of characters. As the leaf images illustrate, there is a continuum of leaf morphologies extending from typical *Q. ellipsoidalis* on the left to typical *Q. rubra* on the right. The general pattern along Component 1 is that BP trees cluster to the left of center, OI and STK trees are found to the right of center, and OK trees are found near center. This pattern mimics the general geographic pattern seen in Fig. 1. The PP trees are also located right of center, completely surrounded by STK and OI trees.

As revealed in Table 2, Component 1 in Fig. 3 summarizes general size variation. Six of the nine linear measures have high positive correlations with Component 1. On the other hand, neither any of the angles nor the number of bristle tips are highly correlated with this Component. Component 2 of Fig. 3 emphasizes the basal width of the leaf blade and is moderately correlated with the middle width of the blade and angles 2 and 3. These patterns of variation are consistent with the observation that the island samples are dominated by trees with *Q. rubra* leaf morphologies while the BP sample is dominated by trees with *Q. ellipsoidalis* morphologies. However, as can be seen in Fig. 3, both OI and STK have individual

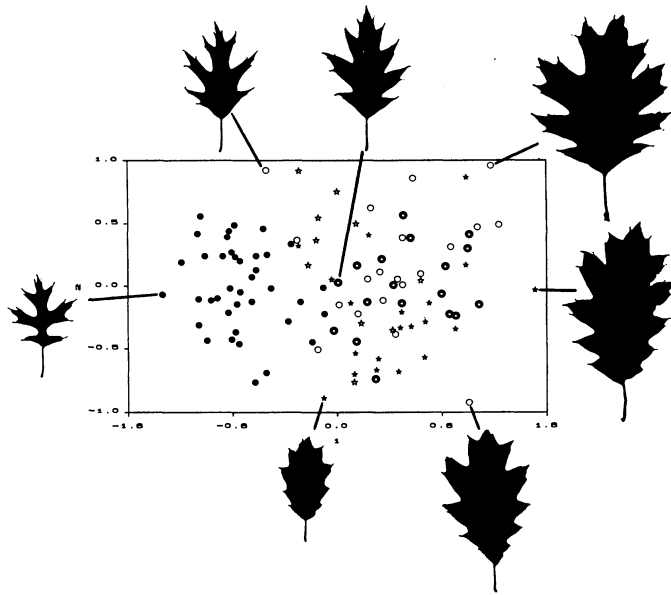


Fig. 3. Morphometric variation defined by components 1 and 2 of a principal component analysis of the full set of morphological variables (see text for explanation). Black circle = Bayfield Peninsula trees; black circle with star = Peninsula Perimeter trees; open star = Oak Island trees; black star = Stockton Island trees; open circle = Outer Island trees. Leaf images are typical for that tree and are reproduced to scale.

trees located left of center, very close to the *Q. ellipsoidalis* cluster.

The general patterns of character correlation in the full data set are depicted in Fig. 4. The vectors provide a concise visual representation of both the relationships among variables and the directions of change for each. It is clear that LBWB (see Table 1 for character acronyms) is oriented nearly at right angles to the majority of the linear characters, which are roughly parallel to Component 1. While Fig. 4 could be superimposed on Fig. 3 to provide a summary of patterns of character change, neither of these figures allows comparison among the different samples. For example, it is obvious that the dispersion of the OK trees in Fig. 3 (from upper left center

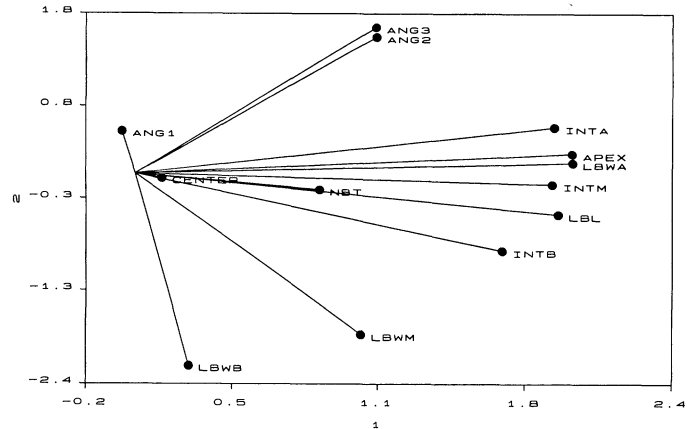


Fig. 4. Vectors illustrating patterns of character variation on components 1 and 2 of the principal components analysis shown in Fig. 1. Abbreviations as in Table 1.

to lower right center) is not the same as for the other groups (e.g., PP trees are dispersed from lower center to upper right). The differences among the five sample sites are depicted graphically in Fig. 5, derived from separate PCAs for each sample site. There are general similarities among the plots for BP (Fig. 5a), STK (Fig. 5d), and OI (Fig. 5e): LBL, LBWA, INTM, and APEX all are highly correlated with Component 1. However, the patterns for the other characters, especially CENTER, NBT, and the three angles, are quite different. On the other hand, PP (Fig. 5b) and OK (Fig. 5c) reveal distinctive patterns of character variation on the first two components. This may be evidence of hybridization if we make the assumption that, while there are similar strong correlations among certain characters in both species, these correlations break down in their hybrids, yielding patterns of character variation not observed in either parental species (Jensen, 1988; Wilson, 1992).

As seen in Fig. 3, general leaf size is an important aspect of variation among these trees. Because the three angles and the number of bristle tips do not make important contributions to the major component of variation (Table 2), we examined the data in a way that would allow us

TABLE 2. Correlations of each character with components 1 and 2 and percent variance explained by each component.

Character ^a	PC1		PC2		PC3	
	1	2	1	2	1	2
LBL	0.94	0.19	0.91	0.14	0.14	-0.19
LBWB	0.12	0.90	0.01	0.20	0.20	-0.94
LBWM	0.50	0.75	0.38	0.19	0.19	-0.80
LBWA	0.97	-0.05	0.96	0.00	0.00	0.05
INTB	0.82	0.36	0.85	0.12	0.12	-0.36
INTM	0.93	0.05	0.96	0.04	0.04	-0.06
INTA	0.93	-0.22	0.98	-0.01	-0.01	0.16
CENTER	0.06	0.02	-0.11	0.99	0.99	0.09
APEX	0.97	-0.09	0.97	0.02	0.02	0.09
ANG1	-0.03	-0.20	—	—	—	—
ANG2	0.54	-0.63	—	—	—	—
ANG3	0.54	-0.68	—	—	—	—
NBT	0.41	0.08	—	—	—	—
% Variance explained	47.4	19.3	67.4	19.8	60.6	23.2

^a Character abbreviations as in Table 1.

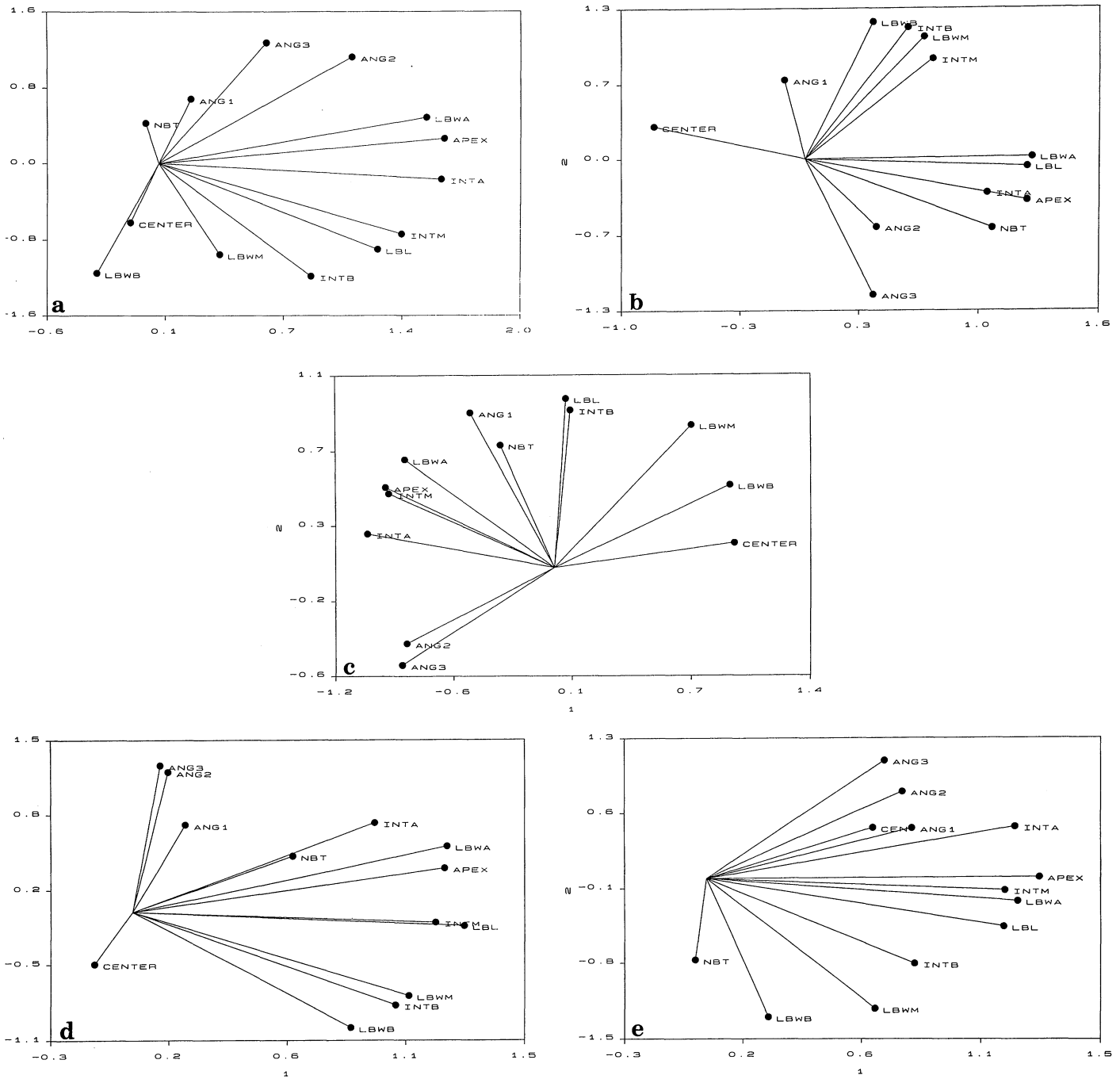


Fig. 5. Patterns of character variation derived from a principal components analysis for each sample locality. (a) Bayfield Peninsula, (b) Peninsula Perimeter, (c) Oak Island, (d) Stockton Island, (e) Outer Island. Character abbreviations as in Table 1.

to interpret size trends without the confounding effects of characters that appear to vary independently of size. A common approach to summarizing general size variation is to convert all linear measures to logarithms and then use PCA to analyze the character \times character covariance matrix (e.g., Rohlf and Bookstein, 1987). Figure 6 illustrates the results of PC2, produced by analyzing just the linear measures. As seen in Table 2, Component 1 of Fig. 6 has high positive correlations with six of the nine linear measures—the same six as for Component 1 in PC1. Again, Component 1 summarizes general size differences and the

island samples appear more variable, especially along Component 2, than the BP sample. Moreover, the OK trees are near the middle of the plot.

The second component of PC2 allows recognition of a rather distinct cluster of trees containing individuals from three sites: OI, STK, PP. This component is almost perfectly correlated with CENTER, all other characters having very low correlations. CENTER is a linear measure that would be expected to differentiate *Q. rubra* (small values) from *Q. ellipsoidalis* (large values), provided the leaves are of approximately equal size (as in Fig. 2). Figure

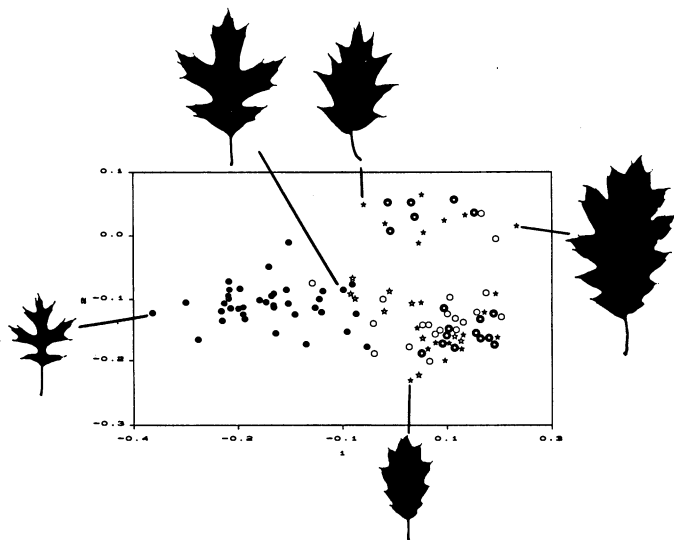


Fig. 6. Morphometric variation defined by components 1 and 2 of a principal component analysis based on linear characters only (see text for explanation). Symbols and leaf images as in Fig. 3.

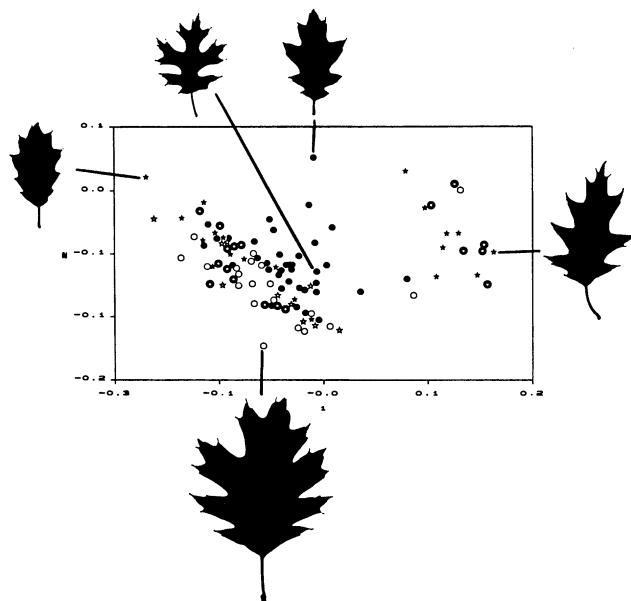


Fig. 7. Morphometric variation defined by components 1 and 2 of a principal component analysis of the size-adjusted data (see text for explanation). Symbols and leaf images as in Fig. 3.

6 indicates that many of the island and PP trees have relatively smaller values for this variable than do most BP trees. This pattern is emphasized in Fig. 7, depicting the results of PC3 (see above). Burnaby's sweep was used to subtract the first component of PC2 from the log-transformed data matrix. The result is a new data matrix that reflects residual variation after subtracting general size variation. Some have viewed this new matrix as one that emphasizes shape differences (see Somers, 1989), but that interpretation is not universally accepted (e.g., Bookstein, 1989).

Component 1 of PC3 (Fig. 7) is emphasizing something other than size. As the leaf illustrations indicate, leaves at both extremes of Component 1 are not conspicuously larger or smaller than those near the center. Examination of Table 2 reveals that Component 1 of PC3 has correlations with the characters identical to those seen for Component 2 of PC2. This result was expected; the effect of using Burnaby's sweep as done here is equivalent to plotting Components 2 and 3 of PC2. Whether the pattern seen in Fig. 7 can be interpreted as summarizing shape differences or not is debatable. Component 1 emphasizes differences in CENTER (increasing from left to right), and Component 2 emphasizes differences in basal width (LBWB) and middle width (LBWM) of the leaf blade (both increasing from top to bottom). There is a general trend for leaf shape to change from elliptic (near the top of Fig. 7) to ovate to almost circular (near the bottom of Fig. 7). However, this variation in shape appears to occur at each sample site.

Patterns of variation of leaf landmark configurations of trees at each site are summarized in Fig. 8. A common feature in each set of leaves is that landmarks 1, 3, 6, 9, and 11 have major axes of variability running parallel to the long axis of the leaf while all other landmarks have major axes oriented obliquely or at right angles to the long axis of the leaf. In addition, landmarks around the periphery of the leaves are more variable than those that are closer to the center of the leaf. And, variation in

landmarks 2, 4, 5, 7, 8, 10, 12, 13, 14, 15, 16, and 17 appears to be quite symmetric. This is not to imply that individual leaves are symmetric; rather, analogous landmarks on opposite sides of the leaf are approximately equally variable, in both direction and extent.

Figure 8 illustrates general shape differences between *Q. ellipsoidalis* (Fig. 8a) and *Q. rubra* (Fig. 8b, d, e). For example, imagine a line connecting the centroids of landmarks 2 and 8 and a second line connecting the centroids of landmarks 12 and 16. In Fig. 8a, these lines are converging toward the apex of the leaf, while in Fig. 8b, d, e these lines are diverging from the apex (as in Fig. 2). In addition, note the proximity of the centroids of landmarks 9 and 11 as well as the relative positions of landmarks 8, 10, 16, and 17. When Fig. 8b, d, e are contrasted with Fig. 8a, landmarks 9 and 11 are much farther apart and landmarks 8, 10, 16, and 17 are relatively farther away from landmark 11. These illustrations suggest that major shape differences between the leaves of *Q. ellipsoidalis* and *Q. rubra* emphasize the relationships among landmarks in the upper half of the leaf blade. This trend is consistent with the observation that characters derived from these landmarks (e.g., LBWA, INTA, APEX) have high correlations with Component 1 of both PC1 and PC2.

As seen in Fig. 8c, the OK leaves appear to be intermediate between BP on the one hand and PP, STK, and OI on the other hand. This intermediate morphology is illustrated most clearly in Fig. 9. These illustrations show the residual vectors required to fit the consensus landmark configuration at each site to the overall consensus landmark configuration. For example, Fig. 9a indicates that for the consensus leaf of BP to fit the overall consensus, landmarks 11 and 9 move toward each other, as do landmarks 8 and 16, 10 and 17, and 7 and 15. Landmarks 5 and 14 move obliquely toward the leaf apex while landmarks 2 and 12 move obliquely in the opposite direction.

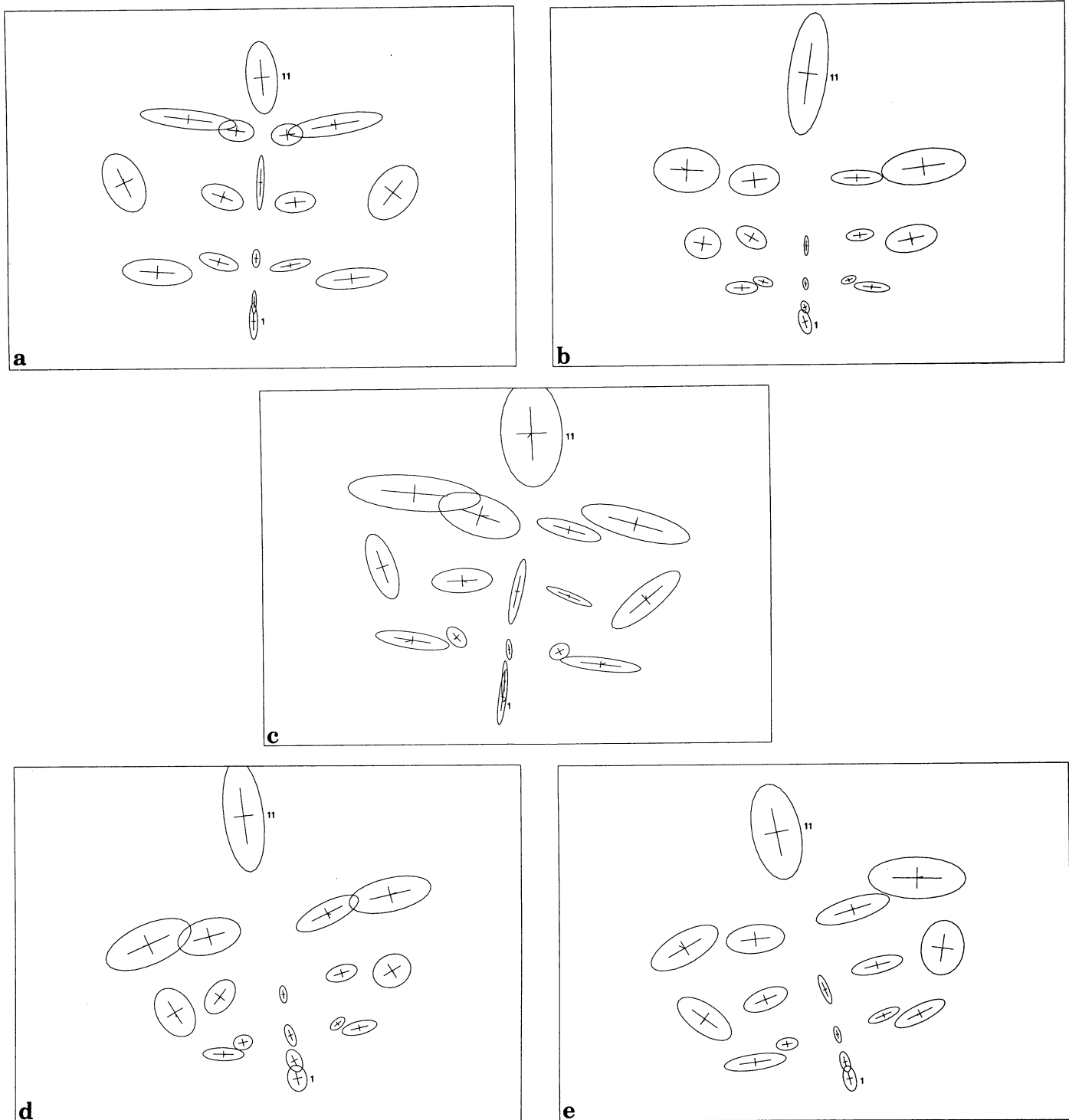
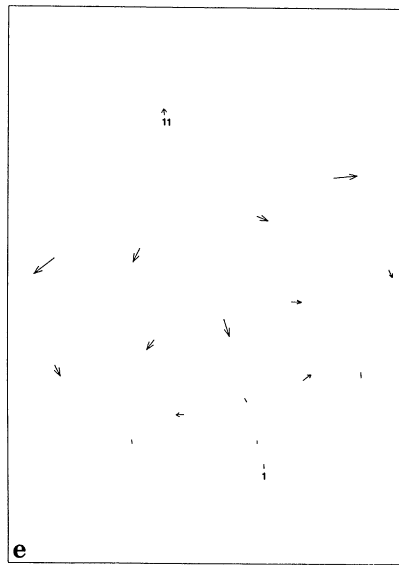
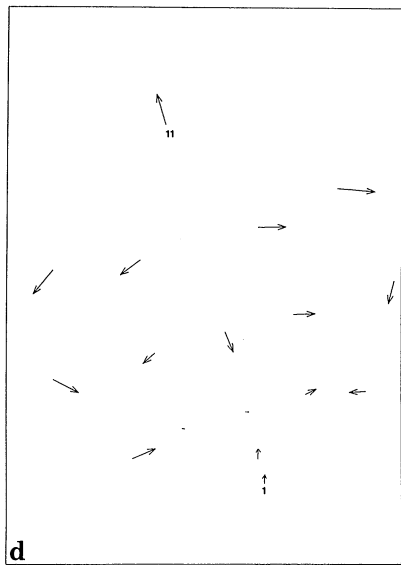
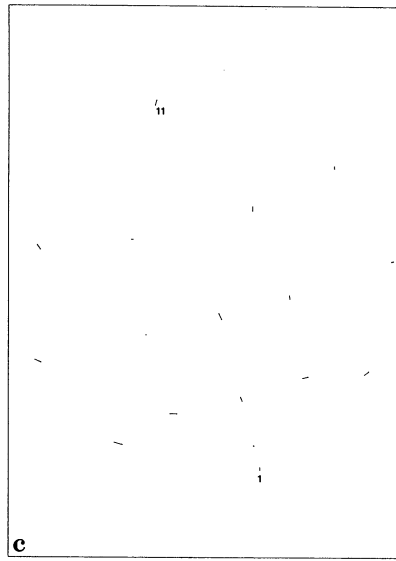
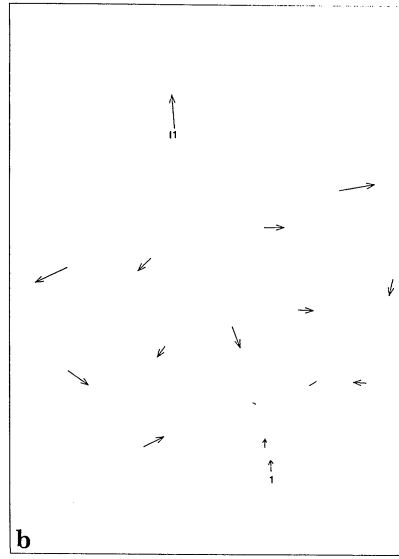
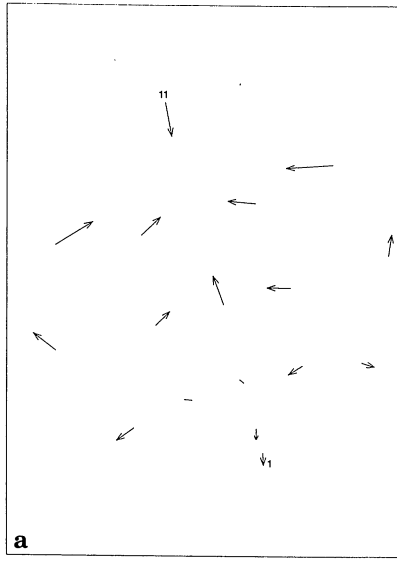


Fig. 8. Generalized resistant fit analyses of landmark variation at each sample locality. (a) Bayfield Peninsula, (b) Peninsula Perimeter, (c) Oak Island, (d) Stockton Island, (e) Outer Island. For each landmark, the major and minor axis of variation and a two-standard-deviation equal-frequency ellipse are plotted. Orientation as in Fig. 2 with landmarks 1 and 11 marking the base and apex of the blade, respectively.

Fig. 9. Residual vectors from a generalized resistant fit of the consensus landmark configuration at each site to the overall consensus landmark configuration. (a) Bayfield Peninsula, (b) Peninsula Perimeter, (c) Oak Island, (d) Stockton Island, (e) Outer Island. Orientation as in Fig. 2 with landmarks 1 and 11 marking the base and apex of the blade, respectively.



On the other hand, for these same landmark pairs, PP (Fig. 9b), STK (Fig. 9d), and OI (Fig. 9e) generally illustrate opposite residual vectors of fit. And, as shown in Fig. 9c, the consensus leaf for the OK collection has a landmark configuration almost identical to that of the overall consensus; the residual vectors are so slight as to be almost nonexistent.

These results, derived from several distinctly different methods of examining morphological variation, indicate that there is a continuum in leaf morphology approximating a line connecting the BP site to OI. This continuum is reflected in general leaf size (Figs. 3, 6) and in leaf shape as defined by the configurations of landmarks (Fig. 9). In each of these analyses, the OK specimens occupy an intermediate position, coincident with the intermediate position of OK itself. The observed continuum is consistent with the hypothesis that there has been hybridization between *Q. ellipsoidalis* and *Q. rubra*.

Initially, we expected that trees on OI would be most like *Q. rubra* and that trees in BP would be most like *Q. ellipsoidalis*. While the latter is substantiated by these analyses, it is obvious that each site has trees that are more or less typical for *Q. rubra*. The wider scatter of trees from OI in Figs. 3 and 6 and the rather small vectors required to fit the OI consensus landmark configuration to the overall consensus landmark configuration (Fig. 9e) indicate that Outer Island has trees approaching both extremes in phenotypes. While it might make sense for OK to be intermediate, it appears that the OI sample has a greater number *Q. ellipsoidalis*-like trees than do the PP and STK samples, both of which are closer to the mainland.

When Swain (1972) found evidence of a morphological continuum between *Q. ellipsoidalis* and *Q. rubra*, she hesitated to identify individual trees as hybrids, suggesting that the patterns of variation observed could also be environmentally induced. Our interpretation of the analyses presented here is that there is gene flow between these two species, a hypothesis supported by analyses of electrophoretic markers (Hokanson et al., 1993). The morphological continuum observed is consistent with that seen in mixed oak communities in which other types of data (e.g., phenolic variation; Knops and Jensen, 1980) indicated the existence of hybrid trees.

Unfortunately, we do not believe we can point to an individual tree and identify its hybrid status, i.e., F_1 or F_2 or backcross. The existence of species-specific markers would permit recognition of hybrids, but we have not uncovered any species-specific markers in leaf morphology (e.g., a certain angle, length, or count). Rather, it is the existence of a morphological continuum that we view as support for the hypothesis of hybridization. The nature of the patterns of morphological variation and our field observations suggest that there is unidirectional gene flow: from the mainland population of *Q. ellipsoidalis* to the island populations of *Q. rubra*. The most likely pattern of pollen drift, given the prevailing wind directions on the mainland and near islands, is from the southwest to the northeast. Thus, if the islands were originally colonized by *Q. rubra*, we would expect that later generations of trees would show evidence of subsequent "contamination" from mainland *Q. ellipsoidalis*. While no species-

specific alleles have been identified to allow a direct test of this hypothesis, isozyme analysis indicates the species are genetically very similar (Hokanson et al., 1993).

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