

IDENTIFYING OAKS: THE HYBRID PROBLEM

by Richard J. Jensen

Anyone who has spent time trying to identify oaks (*Quercus* spp.), especially in the forests of eastern North America, has encountered trees that defy classification into any of the recognized species. Such trees commonly are treated as putative hybrids and often are taken as evidence that species of oaks are not as discrete as species in other groups. On the other hand, some (e.g., Muller, 1941) have argued that many, if not most, putative hybrids are nothing more than stump sprouts or aberrant individuals of a species. Muller (1941) did not deny the existence of hybrids; he was cautioning against an inflated view of the frequency of hybridization as a result of cavalier claims. As he put it (Muller, 1951), "The freedom of hybridization ascribed to oaks is immensely overrated." While I don't disagree with these sentiments, I do believe that hybrids are a common component of forests throughout North America.

Virtually all oak species in North America have been claimed to produce hybrids with one or more related species. Hardin (1975) presented a diagram illustrating hybrid combinations for the common white oak (*Quercus alba* L.) and Fig. 1 provides a similar view for northern red oak (*Quercus rubra* L.). Because these two species have very broad geographical ranges and come in contact with a large number of related taxa, there is ample opportunity for hybrid combinations to arise naturally. These two examples also reflect the fact that instances of hybridization are restricted to taxa within a section: *Quercus* section *Quercus* (the white and chestnut oaks) and *Quercus* section *Lobatae* (the red and black oaks), respectively. There have been no reports of naturally occurring intersectional hybridization, presumably because of marked genetic (e.g., Manos and Fairbrothers, 1987) and life history differences, especially annual (section *Quercus*) versus biennial (section *Lobatae*) fruit maturation.

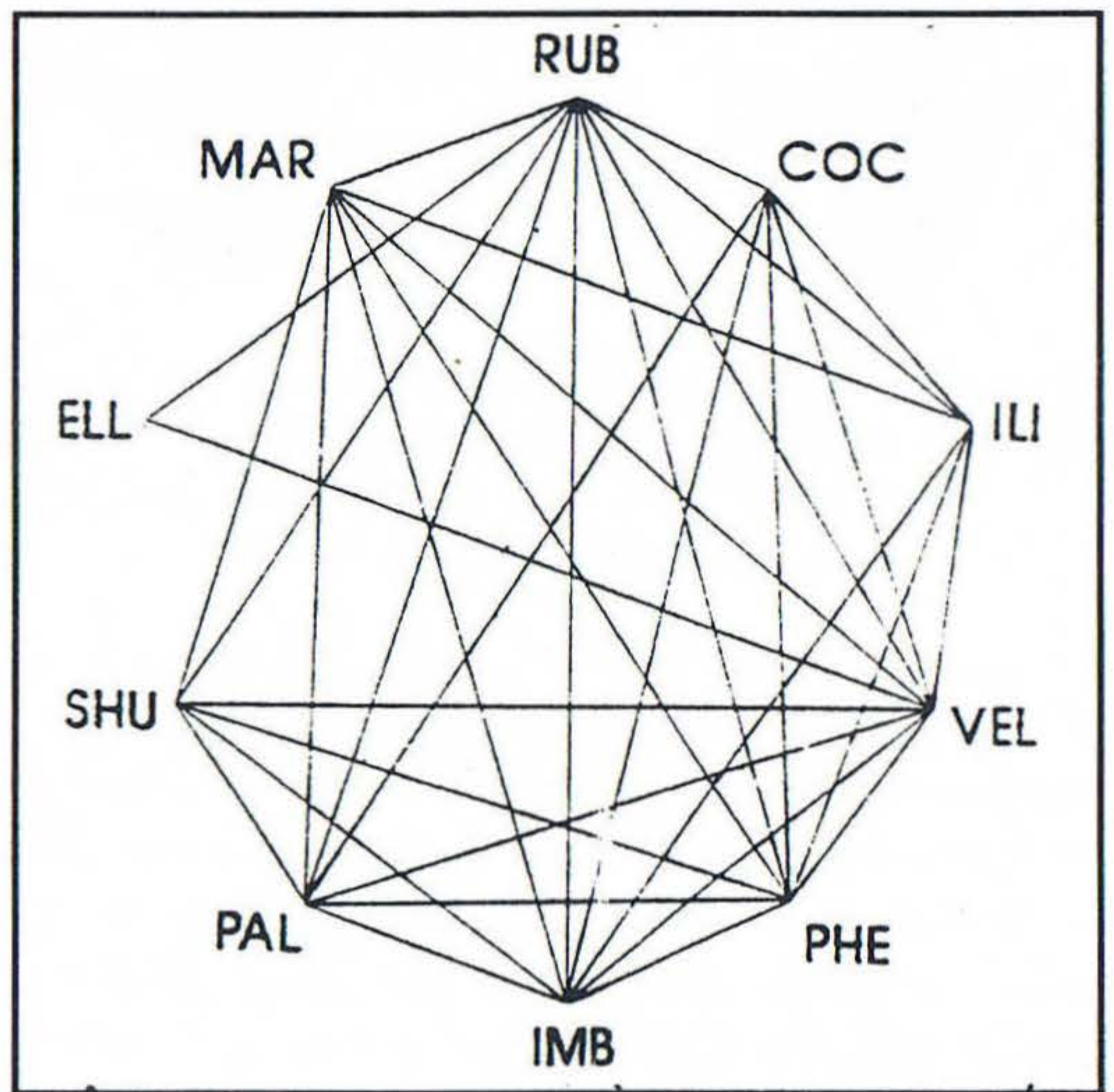


Figure 1 Patterns of hybridization for *Q. rubra*, and those species with which it is reported to hybridize. COC = *Q. coccinea*, ELL = *Q. ellipsoidalis*, ILI = *Q. ilicifolia*, IMB = *Q. imbricaria*, MAR = *Q. marilandica*, PAL = *Q. palustris*, PHE = *Q. phellos*, RUB = *Q. rubra*, SHU = *Q. shumardii*, VEL = *Q. velutina*.

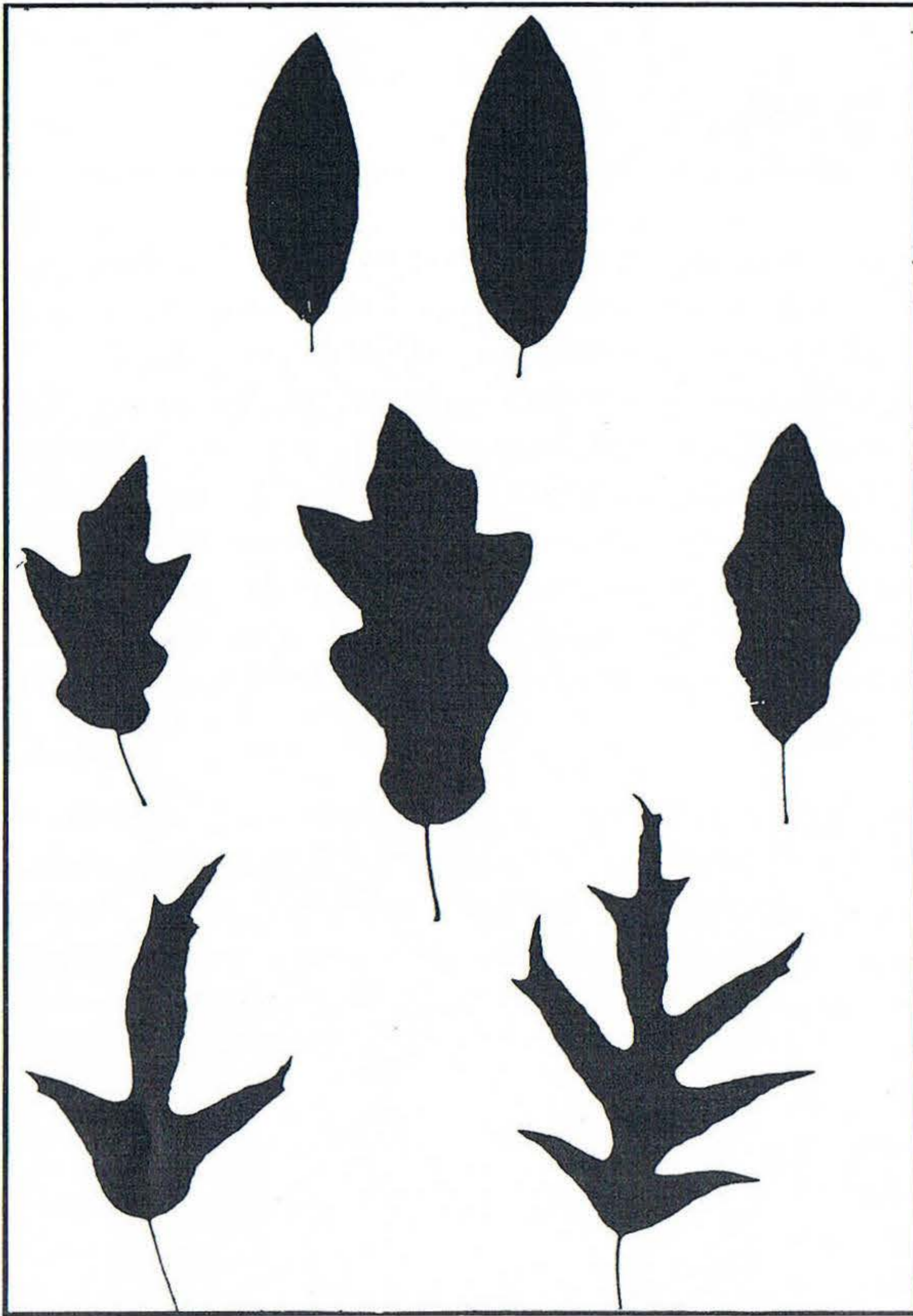


Figure 2 Leaf forms for two species and their putative hybrid. Top row = *Q. imbricaria*; middle row = putative hybrid (*Q. x anceps*); bottom row = *Q. falcata*.

Palmer (1948) provided both an historical overview of this topic and an accounting of all then recognized North American hybrids. That number has grown over the past 40+ years and I suspect new hybrid combinations will continue to be recognized for some time to come, especially as newer biosystematic tools are brought to bear on the problem. Historically, hybrids were recognized on the basis of their unusual morphological features. Perhaps, the most commonly recognized aspect of hybridization is seen in the clearly atypical leaves that arise when species characterized by entire leaves (e.g. *Q. imbricaria* Michx., shingle oak) hybridize with species that have deeply-lobed leaves (e.g. *Q. falcata* Michx., southern red oak). Figure 2 illustrates leaf forms for these two taxa as well as

for a tree identified as their hybrid, *Q. x anceps* Palmer. The leaves of the putative hybrid are clearly asymmetrical and irregularly-lobed. Similar examples are illustrated in Wagner and Schoen (1976) and Jensen (1994). While leaf morphology often is a good indicator of hybridity, it may not provide obvious evidence. Jensen (1994) provided an illustration of the leaves from a tree identified as *Q. x riparia* Laughlin, a hybrid of *Q. rubra* and *Q. shumardii* Buckl. In this case, the two putative parental taxa have leaves that are rather similar in their general features (large, lobed leaves) and the leaves of the hybrid do not appear to be much different from many leaves found on trees of either species.

However, aberrant leaf morphologies alone do not provide evidence of hybridization. Many claims of hybridization have, on closer inspection, proved to be erroneous. In some cases, the putative hybrid is nothing more than a tree belonging to a species not familiar to those making the claim of hybridity. Palmer (1948) discussed the status of *Q. x benderi* Baenitz, supposedly a hybrid of *Q. coccinea* Muenchh. (scarlet oak) and *Q. rubra*, based on a tree in cultivation in Austria. Palmer believed the tree in question most likely was an individual of *Q. ellipsoidalis* Hill (northern pin oak), a species probably then (in 1902) unknown to European botanists.

Two other causes of erroneous claims of hybridization involve a misunderstanding of the origin of the specimen in question. Oaks quite often produce second (and even third) flush leaves during the growing season. This is especially common in *Q. palustris* Muench. (common pin oak). Figure 3 illustrates two sets of leaves: the three upper leaves are rather typical pin oak leaves; the three lower leaves are of a type I have often seen described as being of hybrid origin. The interesting thing about these leaves is that they represent first and second flush leaves from a single branch on one tree. The striking morphological differences are clearly developmental variants and are not evidence of hybridization. Yet, there are many specimens in herbaria, with leaves like these, claimed to be hybrids of pin oak and one of its entire-leaved relatives. Similarly, many species that have entire leaves, e.g. bluejack oak (*Q. incana* Bartram) and willow oak (*Q. phellos* L.), produce second flush growth in which the leaves are irregularly lobed or toothed and are misidentified as hybrids. Second flush leaves of willow oak also may be decidedly pubescent on the abaxial surface, a characteristic often interpreted as evidence of hybridization because willow oak leaves are known to be glabrous on the abaxial surface.

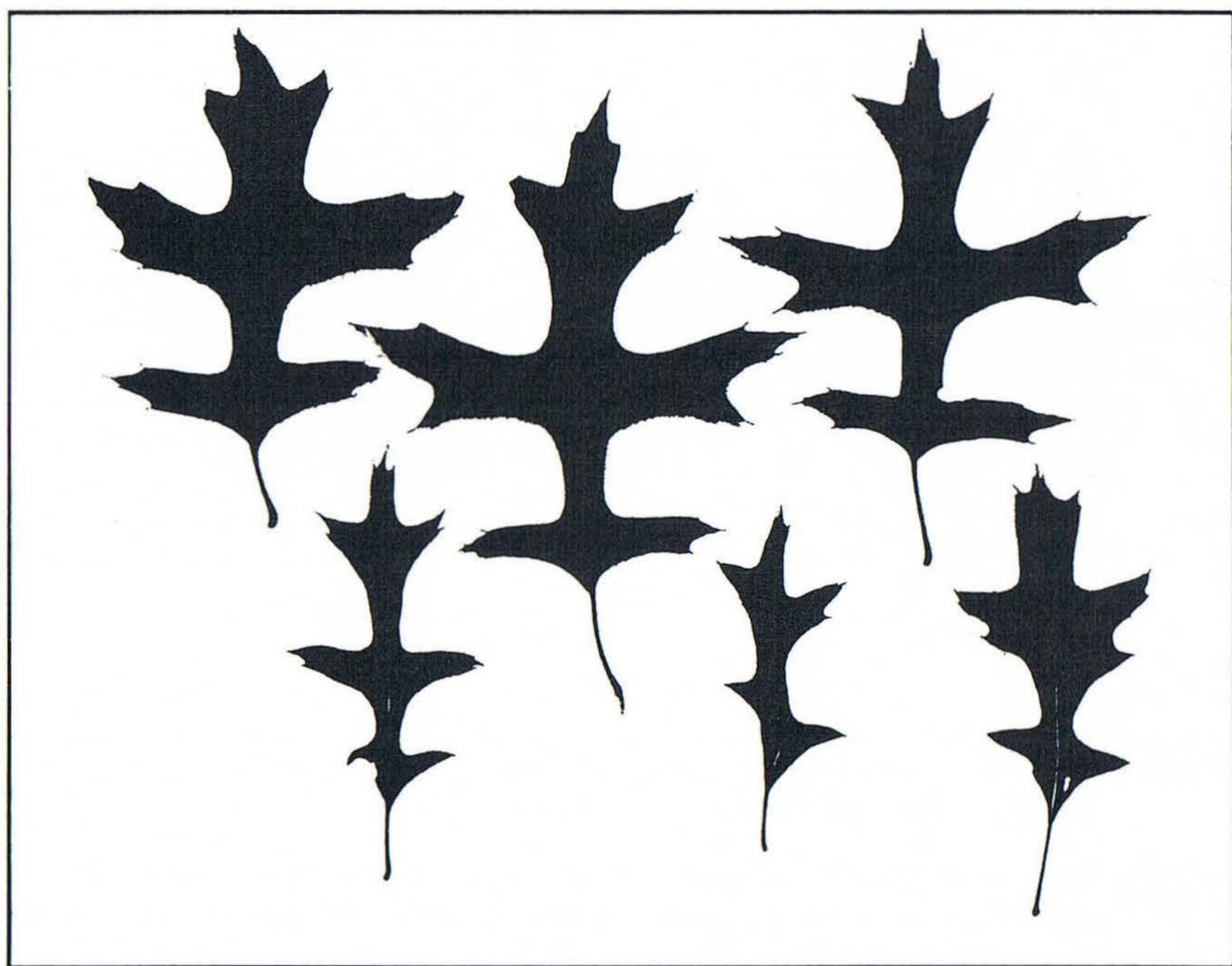


Figure 3 Leaf forms of *Q. palustris*. Top row = mature first flush leaves; bottom row = mature second flush leaves on the same branch as the first flush leaves.

Finally, many instances of putative hybrids are nothing more than misidentified stump sprouts, epicormic sprouts, or juvenile specimens of a species. In each of these cases, the leaves fall outside the range of variation expected for typical individuals of the species in question. What must be remembered is that the descriptions provided in floras are almost always based on mature specimens. There is no realistic way to provide, in a standard flora, an accounting of all possible leaf forms likely to occur in a given species. A good

rule of thumb is this: don't use aberrant leaf morphology as an indicator of hybridity unless you can reasonably rule out second flush growth, stump or epicormic sprouting, and juvenile specimens as the explanation. If the aberrant leaves come from first flush twigs on mature trees and are typical for the entire tree, then there is good reason to make a claim of hybridity.

There are several classic approaches to documenting the presence of hybrids. Perhaps foremost among these are the use of scatter diagrams and the hybrid index. Good examples of these techniques are found in Silliman and Leisner (1958) and Cooperrider (1957), respectively. Implicit in both approaches is the idea that hybrids will exhibit morphological features intermediate with respect to those that can be used to differentiate the parental taxa. While this may often be the case, it certainly is not going to be true for all characters and for all hybrids.

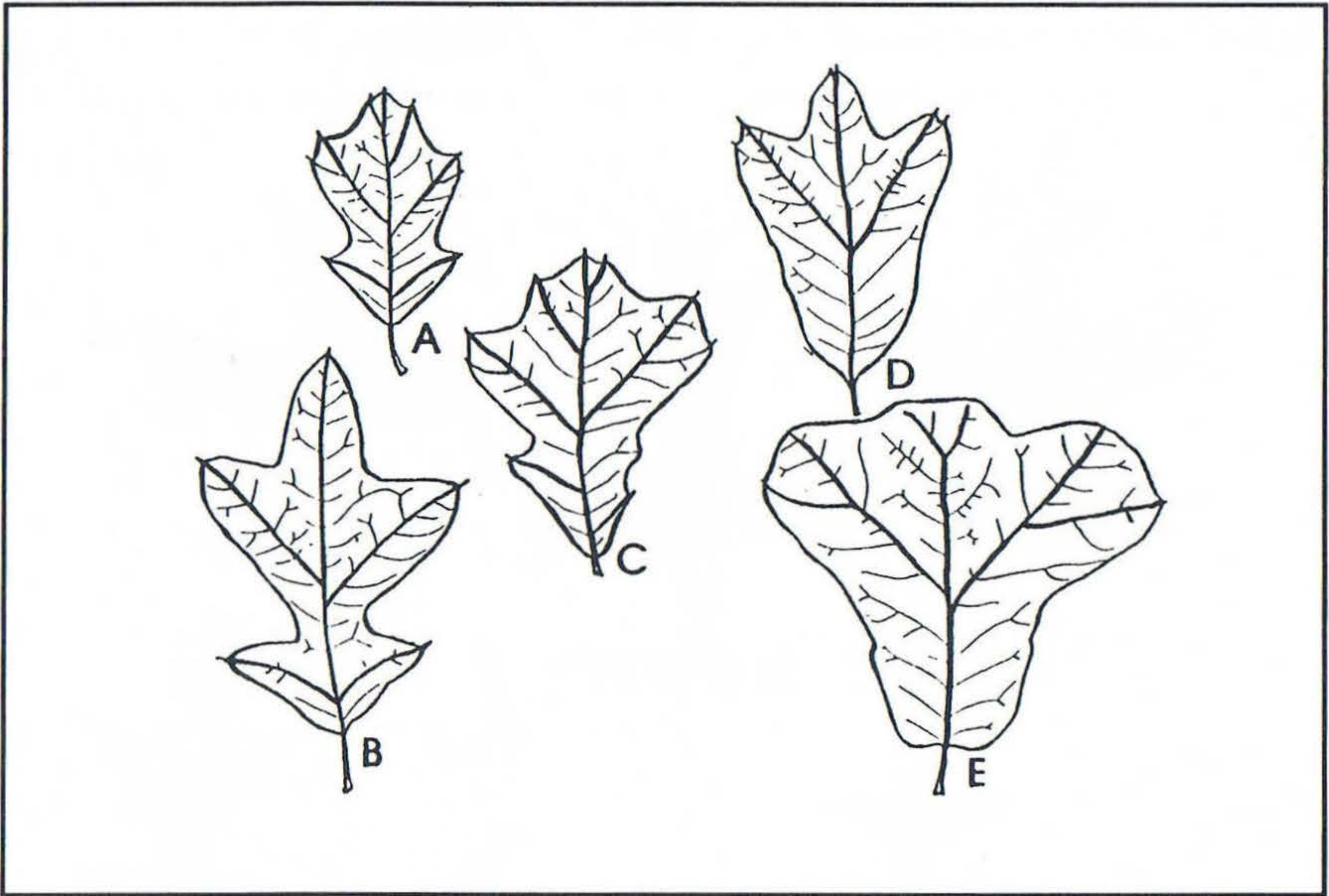


Figure 4 Leaves of two species and three putative hybrids. A = *Q. ilicifolia*; B, C, D = putative hybrids (*Q. x brittonii*); *Q. marilandica*.

Figure 4 illustrates leaf morphologies for two species, *Q. ilicifolia* Wang, (bear oak) and *Q. marilandica* Muenchh. (blackjack oak), and several putative hybrids (*Q. x brittonii* W. T. Davis). The occurrence of hybrids between bear oak and blackjack oak was inferred from morphology and was supported by biochemical analysis of leaf phenolics (Knops and Tensen, 1980). While the hybrids were often intermediate for morphological characters, this was not always the case. Figures 5 and 6 represent scatter diagrams for trees representing bear oak, blackjack oak and their hybrids. In both scatter diagrams, the two morphological characters allow easy separation of the two species. The hybrids, on the other hand, occupy positions from one extreme to the other. Notice, especially, hybrids H1, H3, and H6. In Fig. 5, H1 falls beyond the extreme for blackjack oak, H3 is somewhat intermediate, and H6 falls within the bear oak cluster. However, in Fig. 6, H1 is clearly intermediate (as is H3) while H6 now falls near the extreme for the blackjack oak cluster.

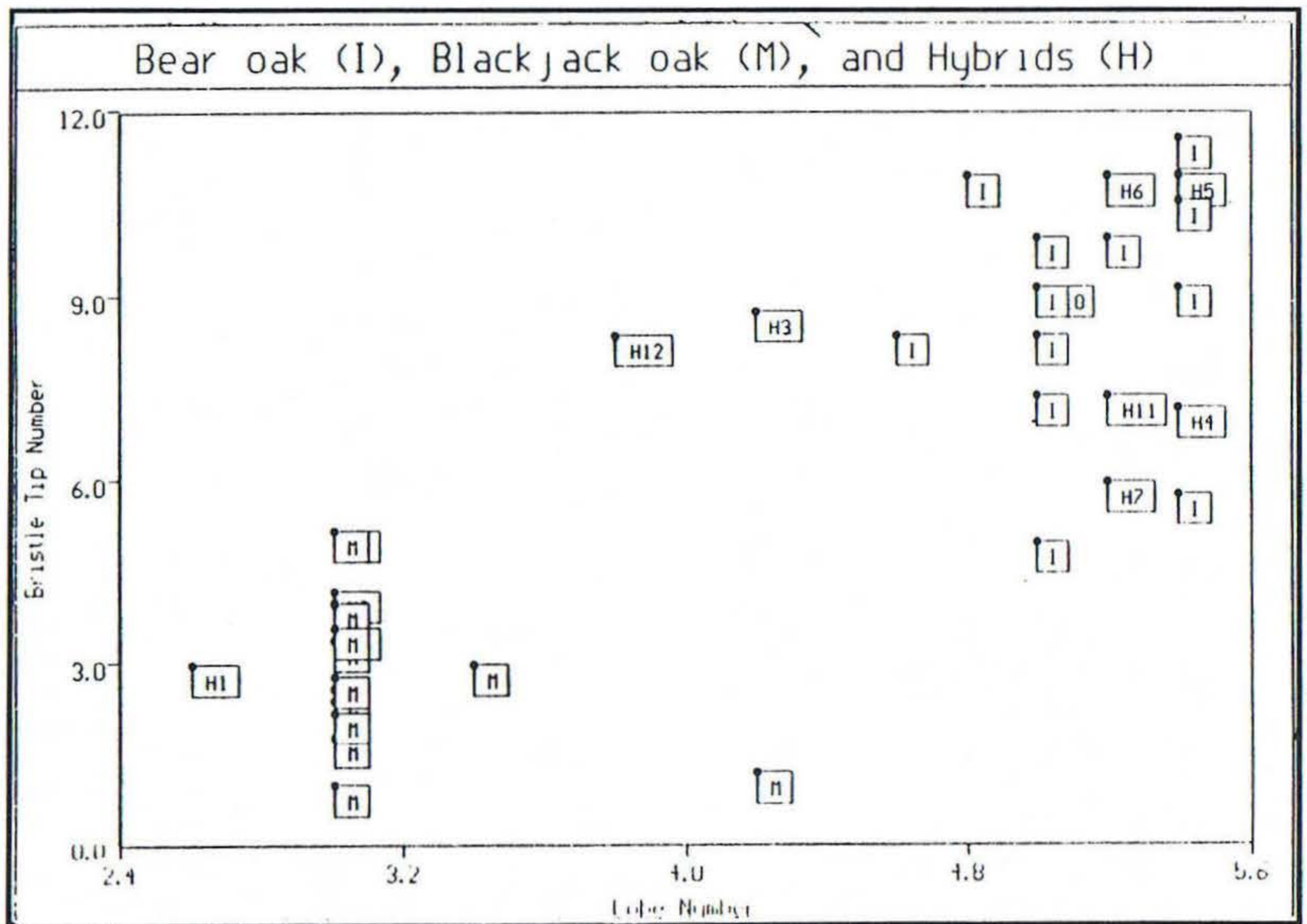


Figure 5 Scatter diagram based on mean number of lobes and mean number of bristle tips for trees representing *Q. ilicifolia* (I), *Q. marilandica* (M), and their putative hybrids (H1 - H12).

The idea of hybrid intermediacy should not be discounted. In a multivariate analysis, e.g. a principal components analysis (PCA) based on a number of morphological characters, hybrids reasonably might be expected to occupy positions intermediate between the two parents. One explanation for this has to do with the way the principal components are derived. The principal components are determined by the correlations among the characters. If there are several characters that can be used to distinguish the two species, as in Figs. 5 and 6, then these characters should have relatively high absolute correlations. This will be reflected in a plot of the individuals along the PCA axes with the parental taxa occupying different regions of the component space.

This is demonstrated in Fig. 7, based on the same trees used for Figs. 5 and 6. In this case, each tree was scored for 10 morphological characters. Figure 7 shows the position of each tree in the ordination space defined by the first two principal components. It is clear that the two species, bear oak and blackjack oak, are quite distinct. Notice that the three hybrids referred to earlier, H1, H3, and H6, are now all more or less intermediate between the two parents. However, some of the hybrids (e.g. H5, H8) clearly are more like one parent or the other while one (H2) appears quite different from all the other trees.

The patterns seen in Fig. 7 may be explained as follows. First, because hybrids will have combinations of characters not found in either parent, they will exhibit a different set of character correlations. Thus, some characters will "pull" the hybrid toward one parent while others will have the opposite effect. This could result in the hybrid appearing intermediate in the multivariate space. Second, hybrids that fall within the parental clusters could represent backcross or segregation progeny, or they may reflect dominant or additive inheritance in one or more characters. Finally, hybrids that appear quite distinct (e.g. H12) may be the result of transgressive hybridization (Grant, 1975) or may not

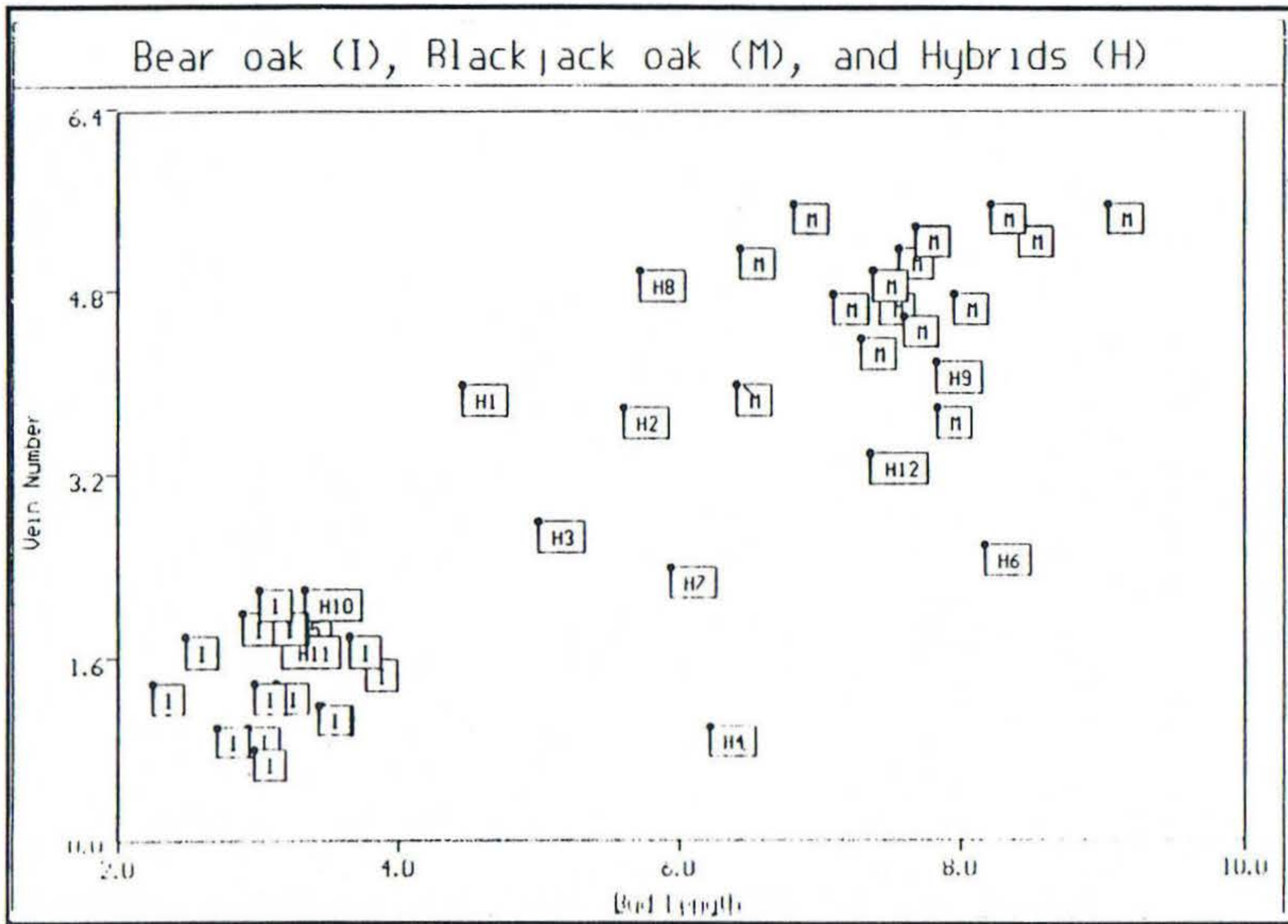


Figure 6 Scatter diagram based on mean bud length and mean number of veins (locate the first vein on the right abaxial surface that departs from the mid rib and ends at the leaf margin, then count the number of additional veins branching from the midrib below this vein) for the same trees as in Fig. 5.

belong to the complex in question. In the community where these trees were sampled, there is also evidence of hybridization between blackjack oak and black oak (*Q. velutina* Lam.). Tree H12 may represent such a hybrid.

The identification of hybrids is not an exact science. While morphological features often provide good evidence of hybridization, as shown above, morphology may be misleading. Other avenues can be used to provide additional evidence to support a claim of hybridity. In some cases, biochemical markers may prove informative. Knops and Jensen (1980) found evidence of hybridization by examining leaf phenolics. Manos and Fairbrothers (1987) and Guttman and Weigt (1989) found isozymes useful for recognizing sectional differences and for some species differences, but did not address the problem of identifying hybrids. Chechowitz et al. (1990) and Hokanson et al. (1993) found that isozymes did not confirm hybridization inferred from morphological studies; i.e., there were no isozyme markers for the species being compared. On the other hand, Whittemore and Schaal (1991), examining species of *Quercus* section *Quercus*, found evidence of species-specific DNA fragments. Two chloroplast DNA fragments were found only in *Q. alba*; one nuclear DNA fragment was found only in *Q. alba*, *Q. macrocarpa* Michx., and *Q. michauxii* Nutt. Such markers would be especially useful for determining the existence and extent of naturally occurring hybridization between species.

One other valuable, but prolonged, approach is to conduct studies of progeny of suspected or artificially created hybrids. If the progeny of the putative hybrid segregate into a range of types, varying from one parental extreme to the other, then there is strong evidence of hybridity. Examples of segregation consistent with the hypothesis of hybridization are found in Cottam et al. (1982) and Rushton (1993).

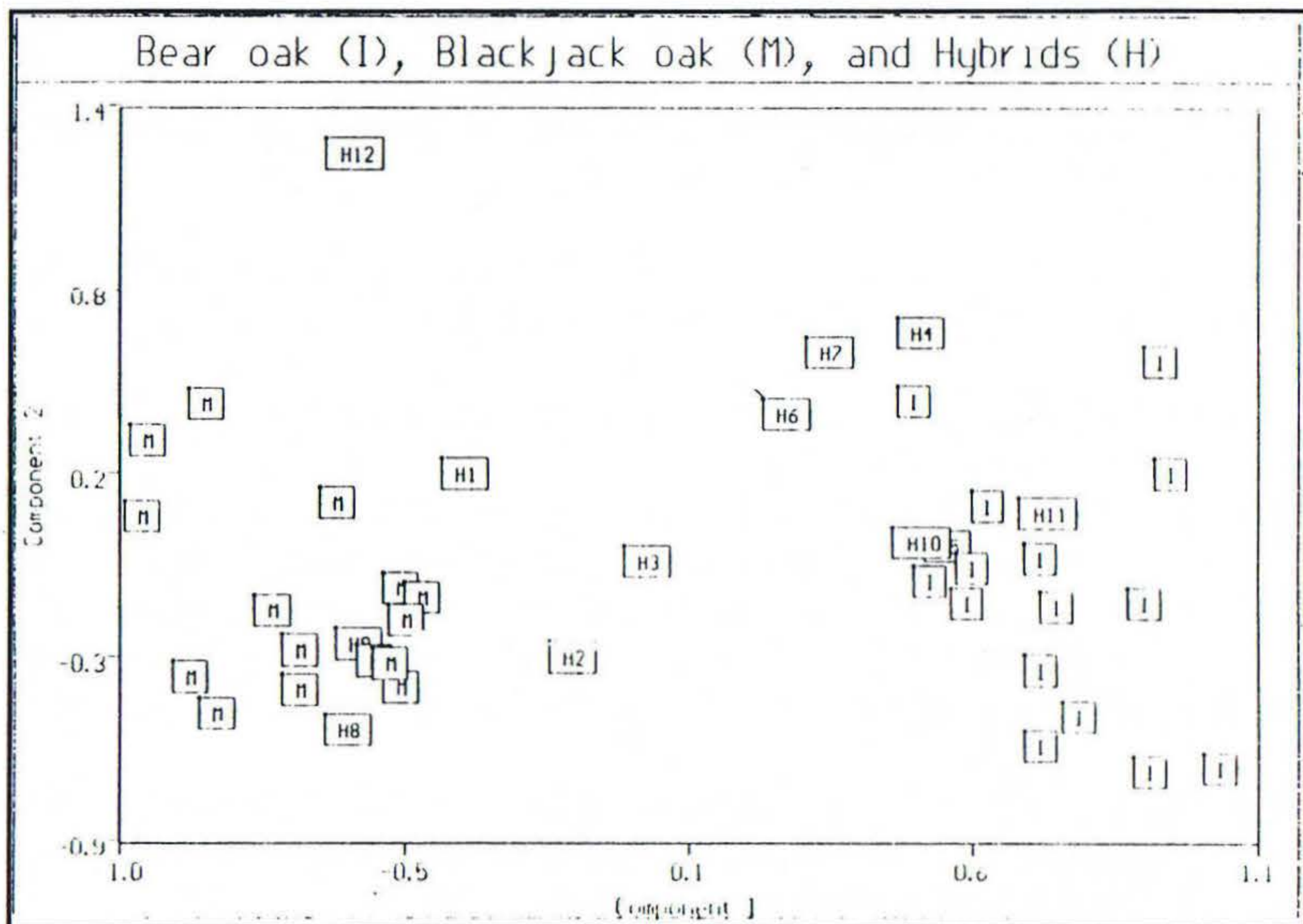


Figure 7 Projection of trees onto the ordination space defined by components one and two of a principal components analysis based on 10 morphological characters. Trees as in Fig. 5.

Hybrid oaks, rare in an absolute sense, are a common component of forests where closely related species are sympatric. Whether there are only two species present, e.g. in parts of Europe where only *Quercus robur* L. (English oak) and *Q. petraea* (Matt.) Leibl. (sessile oak) occur (Rushton, 1979), or there are four or more closely related species in the same community (Jensen, 1988), one thing is clear: there is ample opportunity for and evidence of localized hybridization. The long-term implications of these hybridizations are poorly understood. While there is evidence to suggest that some species may be of hybrid origin (e.g. Jensen et al., 1984), most wide-ranging oak species illustrate a consistent set of phenotypic characters, despite local hybridization with a variety of different taxa (Burger, 1975). It would seem that hybridization between oaks may be locally important (e.g. Overlease, 1975), but there is no clear evidence of its broader systematic/evolutionary significance.

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