Taxonomy of Hill's Oak (*Quercus ellipsoidalis* E.J. Hill) in the Chicago Region: Preliminary Molecular Evidence

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Hill's oak (*Quercus ellipsoidalis* E. J. Hill) is arguably the most problematic member of the black oak section (*Quercus* L. section *Lobatae* Loudon) in the upper Midwest. In a genus renowned for taxonomic difficulties, one that Coyne and Orr have gone so far as to label a "worst case scenario for the biological species concept" (Coyne and Orr 2004), Hill's oak is distinguished by the sheer number of workers who have puzzled over its taxonomic status and proper identification (Hokanson et al. 1993; Jensen 1977; Jensen 1979; Jensen et al. 1984; Maycock et al. 1980; Overlease 1977; Shepard 1993; Trelease 1919). These researches, which focus mostly on whether Hill's oak is distinct from scarlet oak (*Q. coccinea* Münchh.), have been inconclusive. Hill's oak was described based on a specimen from Chicago's Calumet area (Hill 1899), and the region around the type locality is the focus of the most taxonomic difficulty. Representing one side of the issue, *Flora of North America* (Jensen 1997) recognizes Hill's oak as distinct from scarlet oak and shows both as present in northeast Illinois (this treatment follows Jensen 1977; Jensen 1979; Jensen et al. 1984; Trelease 1919). Representing the other side of the issue is the most widely used flora for the Chicago region (Swink and Wilhelm 1994), which does not distinguish Hill's oak from scarlet oak and recommends application of the latter name because it has precedence (following Overlease 1977; Shepard 1993; Voss 1985). Most botanists familiar with the flora of the upper Midwest see greater similarity between oaks of northeastern Illinois and populations in Wisconsin, Michigan, and Minnesota than between the Chicago region oaks and scarlet oak from the south and east. It is not clear whether Hill's oak and scarlet oak are best recognized as distinct at the varietal, subspecific, or specific level, or whether they should be considered variants of a single, wide-ranging and variable taxon.

The identity of the type population for Hill's oak and trees similar to it throughout the Chicago region were long assumed to be scarlet oak (Trelease 1919). Subsequent to the description of Hill's oak, many botanists accepted the argument that Hill's oak is found throughout the upper Midwest to the exclusion of scarlet oak. Hill's oak has deeply lobed leaves that are, in their most typical form, highly distinctive, with C-shaped sinuses; ellipsoid, often longitudinally striped acorns, the caps glabrous on the inner surface or very sparsely pubescent, the cap scales tightly imbricated; and relatively small terminal buds that range from glabrous to sparsely silky-pubescent or occasionally densely pubescent, at least on the distal one-half to two-thirds (Figures 1 and 2). Range maps in *Flora of North America* (Jensen 1997) and specimens housed in the major herbaria documenting the flora of the Chicago region (WIS, MOR, and F) show the greatest overlap between Hill's oak and scarlet oak in northwest Indiana and the lower peninsula of Michigan, with a few collections of the latter scattered in northeast Illinois and southern Wisconsin.

In the upper Midwest, Hill's oak is readily confused with black oak (*Q. velutina* Lam.), although individuals at the morphological extremes are highly distinctive (Jensen 1977; Jensen et al. 1984). Typical black oak is characterized by large, sharply-angled buds with densely canescent scales (Figure 3); acorn caps

Figure 1. Hill's oak leaf. The deep lobing, C-shaped sinuses, and approximately circular outline of this leaf are typical of Hill's oak. However, the leaves of Hill's oak, like the acorns, are highly variable, with some individuals having less deeply divided leaves, reminiscent of black oak; lobes narrower and more nearly perpendicular to the midrib, reminiscent of pin oak; and / or leaves larger, not at all circular in outline. Photo: A. Hipp, Taltree Arboretum, Valparaiso IN, September 2006.

Figure 2. Hill's oak acorns. Acorn shape in Hill's oak is highly variable. More reliable for distinguishing the species from black oak are the imbricated acorn cap scales (cf. Figure 4, Black oak acorn). The striations on the acorn body are not uncommon in Hill's oak, but also not the rule. Photo: A. Hipp, Taltree Arboretum, Valparaiso IN, September 2006.

Figure 3. Black oak terminal buds. The dense pubescence and angular cross-section of the terminal buds are characteristic. Photo: A. Hipp, Taltree Arboretum, Valparaiso IN, September 2006.

Figure 4. Black oak acorn. The pubescence and loose, fringed appearance of the acorn cap scales are characteristic. Photo: A. Hipp, Taltree Arboretum, Valparaiso IN, September 2006.

that are densely pubescent on the inner surface, with loose scale margins (Figure 4); and leaves that are frequently pubescent, even at maturity, especially on the major veins on the leaf undersides (the latter characteristic appears to be more pronounced south and east of the Chicago region). Intermediates between Hill's oak and black oak are not uncommon. Hybridization involving some mixture of black oak, red oak (*Q. rubra* L.), pin oak (*Q. palustris* Münchh.) and scarlet oak has been implicated in the origins of *Q. ellipsoidalis* (Hill 1899; Jensen et al. 1984), though Hill (1899) rejected this idea on grounds that the species is too numerous and widespread for hybridization to be a satisfying explanation for the origin of the species.

Our current research investigates several questions: (1) Can Hill's oak, scarlet oak, and black oak be distinguished from one another using molecular genetic data? If so, (2) is recognition of Hill's oak as a species distinct from scarlet oak warranted, and (3) which taxon is more widespread in the Chicago region, where the two taxa are said to overlap and where the nomenclature of the two is in greatest flux? Given the frequency of individuals that have morphological characteristics of both black oak and Hill's oak, an additional question of interest is (4) whether molecular data are compatible with the hypothesis of gene flow between Hill's oak and other black oak species in the Chicago region. These four questions are basic to understanding the taxonomy of Hill's oak, the relationships among oak species of the upper Midwest, and the potential for gene flow between populations and between taxa. Ultimately, answering these questions will allow us to address the ecological role of the different taxa interacting in the Midwest, where their taxonomy is a barrier to understanding the community ecology of upland forests, and increase our understanding of species boundaries in oaks.

Summary of Research to Date

Methods. We collected specimens from 154 oak trees from three southern populations of *Q. coccinea* (southern Illinois, southern Ohio, and eastern Missouri), eleven populations of *Q. velutina*, and eleven populations of *Q. ellipsoidalis* (nine from northeastern Illinois, one from northwestern Indiana, and one from Wisconsin). The 154-individual total includes four pin oaks, nine red oaks, and one cherrybark oak (*Q. pagoda* Raf.). We identified specimens using the key characters presented in *Flora of North America* (Jensen 1997), placing each identified plant into one of four categories: exhibiting morphological characteristics of one species only ("pure"); predominantly exhibiting characteristics of one species, but with morphological evidence of introgression from other species ("introgressed"); presenting an admixture of morphological characters from two or more species, but unclear which is dominant ("hybrid"); or unable to be identified with certainty due to inadequate material or unclear morphological affinities. We excluded individuals in the last category from analysis, leaving a total of 120 individuals of *Q. coccinea*, *Q. ellipsoidalis*, and *Q. velutina*. Analyses discussed in this report include only these three taxa.

We used amplified fragment length polymorphisms (AFLPs), a molecular fingerprinting technique, to estimate population genetic structure and genetic relationships among individuals. The results discussed here are based on analysis of a single AFLP primer pair, which amplified 253 scorable markers across all 154 individuals. We scored markers as present (1) or absent (0) for each individual in the study and analyzed as independent loci. Data for individuals were first analyzed using clustering algorithms (neighbor joining and UPGMA) and ordination (non-metric dimensional scaling) to identify major groupings and degree of genetic differentiation between populations. A Bayesian population-assignment method (Pritchard et al. 2000) was then employed to evaluate population genetic structure and test whether morphological intermediacy predicts genetic admixture (i.e., whether morphological "hybrids" bear the genetic imprint of introgression).

Results 1: Scarlet oak is genetically distinct from the other taxa analyzed. All analyses conducted suggest that scarlet oak is strongly differentiated from the other taxa investigated. This result is especially significant given the limited ability to discriminate taxa found in some genetic studies in the genus (e.g., Aldrich et al. 2003). This finding is compatible with either (1) a more recent divergence between black oak and Hill's oak than between Hill's oak and scarlet oak, as we would expect if the two are separate taxa; or (2) more gene flow between black oak and Hill's oak than between black oak and scarlet oak. These hypotheses are not mutually exclusive.

Results 2: Black oak and Hill's oak are less distinct from one another than either is from scarlet oak. Black oak and Hill's oak accessions overlap in clustering analyses (i.e., neighbor joining and UPGMA trees and ordinations), though they separate more cleanly in the Bayesian analyses (discussed below). While there may be hybridization between scarlet and Hill's oak, if and when these two grow at the same site, the greater confusion in the Chicago region appears to be hybridization between black oak and Hill's oak. Jensen (1977) similarly noted in a morphometric study of black oak species of Michigan and Wisconsin numerous hybrids whose parents appeared to be *Q. ellipsoidalis* and *Q. velutina* (see his Figure 2).

We have identified numerous individuals in our work in northeastern Illinois that appear to be intermediate between Hill's oak and black oak. However, individuals categorized in our study as "introgressed" or "hybrid" fall primarily among the pure Hill's oaks, suggesting that Hill's oak may exhibit greater morphological plasticity than black oak or scarlet oak. These individuals do not exhibit a greater degree of genetic admixture than the "pure" individuals in this study. If admixture of morphological characters were a good indicator of genetic admixture, inferred percentages of each population (*Q. ellipsoidalis* and *Q. velutina*) in the hybrid genome should be more even than in pure individuals. In fact, we find the opposite to be the case. The maximum percentage of the genome inferred to belong to one of the three populations detected in this study is 0.922 ± 0.011 [S.E.M.] for "pure" individuals, 0.920 ± 0.017 for "introgressed" individuals, and 0.966 ± 0.005 for "hybrid" individuals. This is the opposite of our expectation.

Results 3: Population genetic structure of Hill's oak and scarlet oak combined does not mirror population genetic structure of black oak alone. Because scarlet oak accessions sampled are from the Ozarks and the Appalachians, quite distant from the Illinois and Wisconsin samples of Hill's oak and black oak included in this study, the identification of scarlet oak as a separate genetic cluster in all analyses might be due to genetic divergence in distant populations of a single species rather than genetic divergence in separate species. In other words, the data for scarlet oak and Hill's oak, analyzed without reference to the other taxa in this study, cannot distinguish between two alternative hypotheses: (1) Hill's oak and scarlet oak are genetically divergent end points of a single, variable species; or (2) Hill's oak and scarlet oak are distinct species. The black oaks we analyzed include accessions that are syntopic with scarlet oak and Hill's oak accessions also included in the study, allowing a comparison of population genetic structure between black oak as one group versus Hill's oak and scarlet oak analyzed together as a second group. If Hill's oak were simply a regional variant of a widespread scarlet oak, we would expect population genetic structure in Hill's oak and scarlet oak analyzed together to resemble population genetic structure of black oak collected from the same range, analyzed alone.

All analyses we conducted failed to separate geographic populations of a given species from one another, suggesting a high rate of gene flow between intraspecific populations. This supports previous studies demonstrating that most of the genetic variance in oaks generally and red oaks and their allies (section *Lobatae*) in particular is among individuals within populations rather than among populations (Hokanson et al. 1993; Iakovlev and Kleinschmidt 2002). Similarly, geographically proximate accessions for the most part do not consistently cluster together in distance-based genetic clustering analyses (ordination and UPGMA / neighbor joining trees). The finding that geographically proximal individuals do not cluster with one another stands in contrast to the distinct scarlet oak cluster, supporting the hypothesis that scarlet oak is taxonomically distinct and not simply geographically distant from the populations of other taxa studied. Were the observed pattern simply due to geographic distance between scarlet oak and the other taxa investigated, we would expect black oak, which was sampled from essentially the same geographic range as scarlet oak and Hill's oak, to show a separation between southern and northern populations. Taxonomy in this study appears to explain much of the genetic variation while geography alone explains little.

Conclusions

The findings summarized in this paper support four conclusions relative to the questions posed at the outset of the study. (1) Scarlet oak, Hill's oak, and black oak can be distinguished from one another using molecular genetic data, provided enough loci are sampled. (2) Hill's oak and scarlet oak are taxonomically distinct, not simply regional variants of a single, widespread species. Whether these are better recognized at the specific, subspecific, or varietal level is to some extent a matter of taxonomic opinion. (3) Most of what has been referred to as scarlet oak in the Chicago region is in fact Hill's oak. (4) The apparent frequency of gene flow between Hill's oak and black oak based on morphological characters is belied by the molecular data. Admittedly, the fact that Hill's oak and black oak do not separate cleanly in distance-based clustering analyses may be due to ongoing gene flow. However, the Bayesian clustering technique employed is highly successful at distinguishing individuals of Hill's oak and black oak collected at the same site, suggesting that the two are genetically distinct, and there appears to be no correlation between degree of genetic admixture and degree of morphological admixture. Whether this unexpected result is an artifact of insufficient data or reflects a real biological phenomenon is not clear. The role of hybridization among *Quercus* section *Lobatae* species is unresolved in our work and is a focus of ongoing study.

While we advocate for the recognition of two separate taxa and application of the name *Q. ellipsoidalis* to most of the Chicago region populations, we do not deny the existence of true *Q. coccinea* in the Chicago region. There are a few Chicago region specimens at the major Chicago region herbaria (MOR and F) that appear to be distinct *Q. coccinea,* and a recent publication in this journal points to a significant population in Tinley Creek Forest Preserve in southern Cook County (Shepard 2005). One individual we sampled for the current study is an apparent scarlet oak from a spontaneous population at Taltree Arboretum (near Valparaiso, Indiana). This individual and Hill's oaks collected from the same site cluster with the Hill's oaks sampled for this study, suggesting that hybridization between Hill's oak and scarlet oak may not be restricted in the area of sympatry. Additional sampling in southern Michigan and northwestern Indiana is required to understand the dynamics between these taxa and to evaluate whether the contrast we found between population genetic structure in black oak versus Hill's oak and scarlet oak combined is still evident with the addition of sympatric populations.

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Figure 5. Scarlet oak acorn, showing concentric rings of pits at stylar end. Scarlet oak shows considerable variability in this characteristic, ranging from pitting absent to pits forming three or more concentric rings. Photo: A. Hipp, Albany Pine Bush Preserve, Albany NY, June 2006.

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