

3-2011

## Hybrid Oaks: Full of Vexation and Wonder

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### Recommended Citation

Hayden, W. John. "Hybrid Oaks: Full of Vexation and Wonder." *Bulletin of the Virginia Native Plant Society* 30, no. 1 (March 2011): 1, 6-7.

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A publication of the VIRGINIA NATIVE PLANT SOCIETY

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Conserving wild flowers and wild places

## Hybrid oaks: Full of vexation and wonder

Distinguishing different species of oak in the forests of eastern North America can be challenging. For one thing, there are simply a lot of different species to sort out. A recent reference (Stein et al. 2003), describes 50 species in the genus *Quercus* occurring naturally east of the 100th meridian, and 90 species are distinguished for all of North America north of Mexico (Nixon 1997). With so many species to parse, confident identification requires careful study of leaves, stem and leaf hairiness, and fully mature acorns with their caps. But care is not always enough, because in addition to the identification challenges inherent in any species-rich group, many oaks hybridize

with closely related species, and hybrids, by their nature, blur what should be clear-cut distinctions between species.

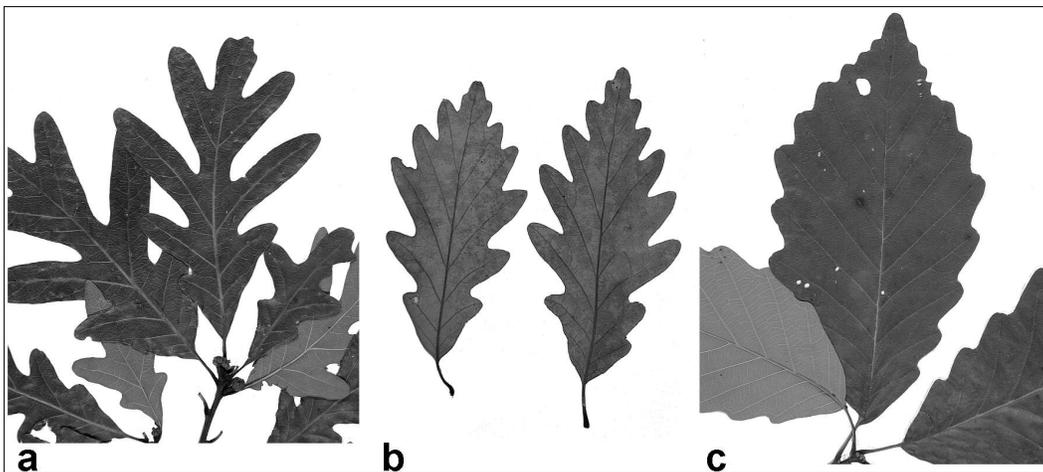
Hybrids parented by the VNPS Wildflower of the Year for 2011, white oak (*Quercus alba*), offer a case in point. White oak is known to hybridize naturally with post oak (*Q. stellata*), overcup oak (*Q. lyrata*), bur oak (*Q. macrocarpa*), chestnut oak (*Q. montana*), chinkapin oak (*Q. muehlenbergii*), dwarf chinkapin oak (*Q. prinoides*), swamp

white oak (*Q. bicolor*), and swamp chestnut oak (*Q. michauxii*). Further, given the opportunity in gardens and arboreta, our native white oak will hybridize with the English white oak (*Q. robur*). Reproductive promiscuity is not unique to white oak; post oak will also form hybrids with most of the species known to cross with white oak, and most of those species can parent multiple hybrid lineages as well. Many of these hybrids have been given formal scientific names, the most up-to-date

listings of which can be found in Nixon (1997).

As one might expect, hybrid oaks blend the characters of their parent species. Typically, one finds mixed combinations of the

(See *Hybridizing*, page 6)



One example of hybridization among species of the white oak group; a. white oak, *Quercus alba*; b. hybrid oak, *Q. x saulei* (= *Q. alba* x *montana*); c. chestnut oak, *Q. montana*.

# Hybridizing tendencies can be perplexing

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parents' characteristics, or intermediate character states, or both; rarely, an extreme expression of one parental character can be observed. So, when identifying oaks, one needs to be prepared to encounter specimens that scramble the usually encountered character patterns. It could be worse, though. For one thing, oaks hybridize only within closely related groups of species. White oaks hybridize only with other species classified in the white oak group, i.e., trees with rounded leaf lobes and acorns that mature in a single year (several of which are listed in the previous paragraph). Similarly, various species from the red/black oak group, trees with bristle-tipped leaf lobes and acorns that mature over the course of two seasons, hybridize with each other. But hybrids between the white oak group and the red/black oak group simply do not occur. Further, many plant groups with rampant hybridization also exhibit additional complexity resulting from polyploidy, whole-genome multiplication in which complete sets of chromosomes become duplicated in hybrids and their offspring. Mercifully, polyploidy is virtually unknown in the oaks, even among the hybrids. In fact, chromosome numbers throughout the oak family (oak, beech, chestnut, etc.) are monotonously uniform: 12 chromosomes in each pollen and egg cell and, hence, 24 chromosomes in all other cells (half of which came from the pollen parent and half from the egg parent).

Clearly, at a practical level, the existence of oak hybrids can complicate species identification. Oak hybrids also present some theoretical issues. In theory, species maintain their genetic integrity by reproducing within closed gene pools. Said another way, breeding populations of a species remain isolated from the breeding populations of other species. The integration of ideas about gene flow within species and barriers to gene flow between different species are at the heart of what has become known as the biological species concept, developed largely by Ernst Mayr and colleagues in the 1930s and 1940s. In essence, the biological species concept posits that one or more aspects of the biology of two different species should operate to prevent their in-

terbreeding or, more subtly, to minimize gene flow between them even if occasional hybrids do form. These biological factors have come to be known as reproductive isolating mechanisms. These isolating mechanisms are credited with great theoretical significance because, in the absence of genetic isolation, species would lose their distinctiveness, hybridizing rampantly, and blending insensibly with others.

So-called external (or extrinsic) reproductive isolating mechanisms prevent interbreeding from occurring in the first place; several of these (or their breach) can be illustrated (or postulated) with white oak and its known hybrids. For example, in nature, the English (*Q. robur*) and North American (*Q. alba*) white oaks occupy different continents, a distance more than sufficient to isolate the wind-blown pollen of each from reaching the stigmas and ovules of the other. However, when English oaks are cultivated in the U.S. and our white oaks are cultivated in Europe, their natural geographic barrier is breached and hybrids, called *Q. x bimundorum* ("of two worlds"), form. In this case, under natural conditions, the geographic barrier is sufficient to provide genetic isolation between these two species, and hybrids form only as a consequence of human activity.

Within its native geographic range—which is most of eastern North America—the ecological range of *Q. alba* is also quite broad. But white oaks don't grow everywhere. Sites with nutrient-poor and droughty soils tend to support the growth of post oaks better than white oaks, and swamp white oaks are much better adapted to soggy wet bottomlands than ordinary white oaks. To some extent, then, despite broad overlap in their geographic ranges, ecological factors tend to segregate the parent trees by their preferred habitat, and that may help to limit whole-sale cross-pollination between these species—limit it, but not totally prevent it, because we do have hybrid trees as testimony to the occasional failure of these ecological barriers. It is not difficult, for example, to imagine white oak pollen blowing to droughty ridgetops or swampy bottomlands. Of course, the further a given pollen grain travels from its source tree, the greater its probability of dropping out of the air, so ecological separation may offer some partial measure of genetic isolation, even among wind-pollinated oaks.

The timing of pollen release and stigma receptivity may well be another external mechanism that imperfectly separates the breeding pools of species within the white oak group. Sometimes called seasonal isolation, this factor for oaks might be better described as temporal isolation because most oaks shed pollen more or less coincident with spring bud break, and the timing differences between different oaks are likely to be on the order of just a few days or weeks. I know of no detailed comparative phenological data for the hybridizing white oak group species discussed above. By analogy, however, there is some evidence that live oak (*Q. virginiana*) and sand live oak (*Q. geminata*) from the same general region shed their pollen a few weeks apart from each other, so it is conceivable that timing differences could serve to separate white oak from its nearest relatives at least some—maybe most—of the time.

Geography, ecology, and timing of pollen release may provide some genetic isolation between the various species of the white oak group, but the well-documented existence of hybrids indicates that these potential barriers are, at the very least, somewhat porous for oaks.

In addition to external isolating mechanisms, the biological species concept also incorporates so-called internal (or intrinsic) isolating mechanisms that operate as barriers to gene flow between species in spite of the occasional formation of hybrids. In essence, internal isolating mechanisms posit the existence of genetic incompatibilities between the two genomes combined via hybridization. For example, a hybrid embryo may form, but not survive to the point of birth (animals) or seed germination (plants); alternatively, hybrids may survive, but fail to form gametes, as in sterile mules and various sterile hybrid plants. In both cases, the opposing sets of genes from the two parent species fail to work together in a coordinated way and the hybrid is impaired in one way or another. In theory, then, such hybrids represent dead ends in terms of potential gene flow between their parent species. Clearly, in the case of oaks, hybrids do form and they can grow to become mature trees that shed pollen and bear

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## •Oaks

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acorns. So, it seems that the internal isolating mechanisms of hybrid inviability or hybrid sterility don't apply.

There is one last internal isolating mechanism that might apply to white oak species: hybrid breakdown. The core concept behind hybrid breakdown is the idea that while hybrids may form, grow, and reproduce, the hybrids themselves and their offspring simply may not be as well adapted to their environment as either of their parents and so the hybrids—and their offspring—simply fail to thrive and suffer higher mortality than either of their parent species, thus limiting the degree of genetic mixing that occurs between the parental species. Does hybrid breakdown serve to isolate species of oak known to form occasional hybrids? That's hard to say. Documenting hybrid breakdown requires detailed study of every pertinent individual of the two parental species and all their hybrid offspring within breeding (or crossbreeding) populations over multiple generations. That's a lot of work for annual plants which complete a generation every year; but nearly impossible when individual oak trees may take a few decades to reach reproductive maturity, and then continue to shed pollen and disperse acorns for a few hundred years. It would be interesting to know, for ex-

ample, if hybrids of white oaks ever attain great age similar to that commonly observed in "pure" white oaks.

So what does this all mean? For one thing, because of the multiple hybrid combinations known to occur among white oak group species in nature, application of the biological species concept might lead one to consider all members of the white oak group as a single interbreeding gene pool and thus one big, morphologically diverse species! And ditto for the red/black oaks prone to hybridization. This possibility was discussed formally by Burger (1975) but he and subsequent botanists have rejected such an extreme, although fully logical, deviation from traditional species concepts among the oaks. The key seems to lie in the numbers. Yes, white oaks do form hybrids with at least eight other species in eastern North America, but the vast majority of white oak trees encountered in any forest or woodlot fall easily within the traditional morphological concept of *Quercus alba*. Hybrid individuals, though certainly present here and there, are relatively rare, and oaks assignable to traditionally recognized species are extremely numerous. Even rarer are instances of hybrid swarms, populations composed of hybrids and all manner of intermediates between their parent species. Without a doubt some mixing of genes between differ-

ent oaks does occur, but not at a rate sufficient to threaten the genetic integrity of each species as a whole.

This essay opened by framing the existence of oak hybrids as a vexing roadblock to specimen identification; one often hears reference to hybrid oaks cast as an annoyance to straightforward identification and classification, and I'll admit that I have adopted that tone on occasion, myself. But maybe there is value in thinking about hybrid oaks from a different perspective. The white oak group species of the forests of eastern North America are sympatric over tremendously large areas, they all flower roughly at spring bud-break, they are passively pollinated by wind, and they are certainly capable of forming hybrids . . . so how is it that hybrids are relatively rare? How do the species involved remain reasonably distinct from each other? Rather than vexation, maybe we should adopt an attitude of awe and respect for the complexity of biological processes that, playing out on continental scales, involving untold millions of individual trees, and millennial time frames, challenge our best efforts at comprehension. White oaks are such common trees, who could imagine that their coherence as a species could be so wonderfully complex to contemplate?

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