



# Should Hybridization Make Us Skeptical of the Oak Phylogeny?

**Andrew L. Hipp**

The Morton Arboretum  
4100 Illinois Route 53  
Lisle, IL 60532-1293, USA  
[ahipp@mortonarb.org](mailto:ahipp@mortonarb.org)

The Field Museum  
Department of Botany  
1400 S. Lake Shore Drive  
Chicago, IL 60605-2496, USA

“*Quercus macrocarpa* in fact, looks and acts very much like any good species; the only criterion in which *Q. macrocarpa* fails as a modern concept is in the area of gene flow.”

**Burger 1975, *Taxon* 24**

“It may well be that *Quercus macrocarpa* in Quebec exchanges many more genes with local *Q. bicolor* than it does with *Q. macrocarpa* in Texas.”

**Van Valen 1976, *Taxon* 25**

“All [eastern North American white oak] species have maintained their distinctiveness in face of this local ‘contamination,’ and I see no justification for considering the entities anything less than good taxonomic species.”

**Hardin 1975, *Journal of the Arnold Arboretum***

Hybridization in oaks has long been of interest to botanists and evolutionary biologists. In the first edition of his *Manual of the Botany of the Northern United States*, Asa Gray (Gray and Sullivant 1848) included two hybrids in the genus *Quercus*, both reported to be “founded on” a single tree or individual. In the 1857 through 1862 editions (Gray 1857, 1859, 1862) this number increased to three, which Gray described as “the following remarkable forms, by some regarded as species.”<sup>1</sup> The 1867 edition (Gray 1867) increased the number to five, and Wiegand (1935) notes that in this edition, “we find hybrids scarcely mentioned except in one genus, *Quercus*” (Wiegand 1935). Oak hybridization – or at least our perception of it – as a taxonomic phenomenon is familiar to every good field botanist and reader of this journal (Fig. 1).

Beyond the taxonomic implications, the effects of interspecific hybridization on oak species’ origins, coherence and evolutionary trajectories have been a research topic for more than 140 years: Palmer notes that Engelmann was aware that species could be too “distinct” to produce viable hybrid offspring (Engelmann 1876; Palmer 1948). Muller (1952) similarly wrote that “Remotely related oaks... apparently do not hybridize.” Between the 1940s and the early 1960s, plant biologists such as Edgar Anderson (reviewed in Anderson 1948), G. Ledyard Stebbins (1950), and Verne Grant (1971, 2004) undertook serious quantitative research into hybridization and its role in plant speciation. During this same period, rigorous specimen-based research into oak character evolution got a foothold, and several studies were published on oak hybridization and its consequences for populations and species (e.g. Allard 1932; Stebbins, Matzke, and Epling 1947; Palmer 1948; Allard 1949; Muller 1952; Tucker 1963; Ledig et al. 1969). But I think of a trio of now-classic papers from the mid 1970s as setting the stage for modern studies of oak evolution. In 1975, James Hardin published an article in the *Journal of the Arnold Arboretum* showing patterns of potential gene flow among 16 White Oaks of Eastern North America (Hardin 1975). His first figure (reproduced in the current article as Fig. 2) says it all: among the group, only two species were thought at that time to be reproductively isolated from the others: *Quercus oglethorpensis* W.H. Duncan and *Q. chapmanii* Sarg., both regional endemics. We now know that not even those two are isolated: *Q. oglethorpensis* is believed to be capable of hybridizing with *Q. margarettae* (Ashe) Small (Coombes and Coates 1997), and a hybrid between *Q. chapmanii* and *Q. minima* (Sarg.) Small is distributed on the coastal plain along eastern Florida (Muller 1961). Hardin’s work in characterizing patterns of hybridization among all the potentially hybridizing White Oaks of Eastern North America, demonstrating that none are reproductively isolated, is still one of the most taxonomically thorough studies of oak hybridization in a system of interbreeding oak species.

At about the same time, a pair of articles in *Taxon* by Chicago scientists William Burger (The Field Museum) and Leigh Van Valen (University of Chicago, best known for his description of the Red Queen Hypothesis: Van Valen 1973) argued that gene flow in oaks is dominated by local gene flow among individuals that are closely enough related to exchange genes, rather than among populations within species (Burger 1975; Van Valen 1976). These papers argue that our concept of species needs to be fundamentally rearranged to account for oaks. Because of hybridization and gene flow between oak species, Burger and Van Valen argue, the criterion of reproductive isolation cannot

---

1. Perhaps not coincidentally, Gray’s language changes between 1848 and 1862 – years flanking the publication of *Origin of Species* – from suggesting that these hybrids are mere sports to suggesting that they might be species of hybrid origin. Darwin had, in fact, sent a letter to Asa Gray in 1857 outlining his theory of natural selection. Does Gray’s change in language reflect a change in his view of the evolutionary implications of hybridization?



Figure 1/ Herbarium specimen of a putative hybrid between *Q. macrocarpa* Michx. and *Q. alba* L., collected by Michael Nee, Wisconsin. Botanists commonly look for hybrids where the parents are both found, especially in oaks. On this specimen label, Nee writes: "Growing in yard of farmhouse, but undoubtedly natural and not deliberately planted. Both *Q. macrocarpa* and *Q. alba* are common in the vicinity and are the common trees of the broad, often sandy, Pine River valley here, formerly in prairie – oak savanna until European settlement in the 1840's and cessation of prairie fires. *Q. alba* is more abundant on hillslopes; *Q. macrocarpa* on alluvial soils and rocky hilltops. This tree [is] intermediate between the two parents in bark, leaf and acorn characters. The acorns have been on the ground for a few weeks." Scan courtesy of The Wisconsin State Herbarium (WIS) and Michael Nee.

work for these species. Rather, oak species represent ecologically discrete lineages with distinct evolutionary trajectories. “Species,” Van Valen writes, “are maintained for the most part ecologically, not reproductively.” They both argue that local gene flow among species may well exceed gene flow between populations of a single species, and that reproduction cannot therefore be the hallmark of oak species. Burger goes so far as to suggest erecting subgenera or sections that are equivalent to reproductive species, but allowing our named species in oaks to represent ecologically and morphologically defined evolutionary lineages. The idea that gene flow might be insufficient to cause species to cohere across their range had been discussed previously (Ehrlich and Raven 1969), but these papers were novel in stating that oak species are not reproductively defined entities but ecologically defined entities. What is troubling about this is that it is not clear what mechanism might shape species coherence in the face of ongoing local gene flow. A measured skepticism about oak species is not uncommon among botanists even today.

We now know, however, that while there is certainly hybridization and introgression among oak species (Whittemore and Schaal 1991; Dumolin-Lapegue et al. 1997; Dumolin-Lapegue, Kremer, and Petit 1999; Petit et al. 2003; Dodd and Afzal-Rafi 2004; Tovar-Sánchez and Oyama 2004; Lexer, Kremer, and Petit 2006; Curtu, Gailing, and Finkeldey 2007; Hipp and Weber 2008; Chybicki and Burczyk 2010; Moran, Willis, and Clark 2012), gene flow *among* species appears to be swamped by gene flow *within* species (Gerber et al. 2014). As Hardin (1975) wrote, “Rather extensive hybrid swarms or introgressed populations... are generally localized.... Neither Baranski (1975) nor I agree with Minckler (1965), who thinks that hybridization may mask evidence of races within white oak.” Moreover, much of the variation in oaks that has been interpreted as evidence of hybridization appears to be morphological variation within highly variable species. As Muller wrote in 1952, “The species of *Quercus* are notoriously variable in trivial characters. This variability has given rise to the belief that the oak species hybridize freely. It is quite evident from a study of herbarium specimens, however, that the bulk of claims of hybridity are based upon trivial variations of the sort one may encounter in a relatively pure population of a single species.” (Muller 1952). The result is that oak species are genetically coherent across wide geographic and even ecological ranges (Muir, Fleming, and Schlötterer 2000; Hipp and Weber 2008; Cavender-Bares and Pahlich 2009). This is what we expect of organisms with long-distance gene flow (Petit and Excoffier 2009). Oaks, with their great stature and volumes of wind-borne pollen, certainly fall in this category (Whittemore and Schaal 1991; Dow and Ashley 1998; Gerber et al. 2014). The concerns raised 40 years ago by Van Valen and Burger, that oak species do not constitute genetically coherent systems of populations, appear not to have been borne out. Oak species, we can say confidently against the backdrop of the last 20 years of oak research, are real.

Yet the phenomenon of hybridization in oaks still troubles our ideas of what we mean by “the phylogeny of oaks.” Phylogenetic studies in oaks using a few nuclear markers (Manos, Doyle, and Nixon 1999; Oh and Manos 2008; Denk and Grimm 2010; Deng, Zhou, and Li 2013; Hubert et al. 2014) have illuminated many relationships, but these studies have not resolved many of the fine-scale relationships among oaks, nor even recovered deep splits that are generally recognized (e.g., the split between the Eurasian and American White Oaks). We do know broad-scale phylogenetic patterns based on these studies. For example, we know that the American oaks form a distinct clade comprising the sections *Quercus* (the White Oaks), *Lobatae* (the Red Oaks), and *Protobalanus* (the

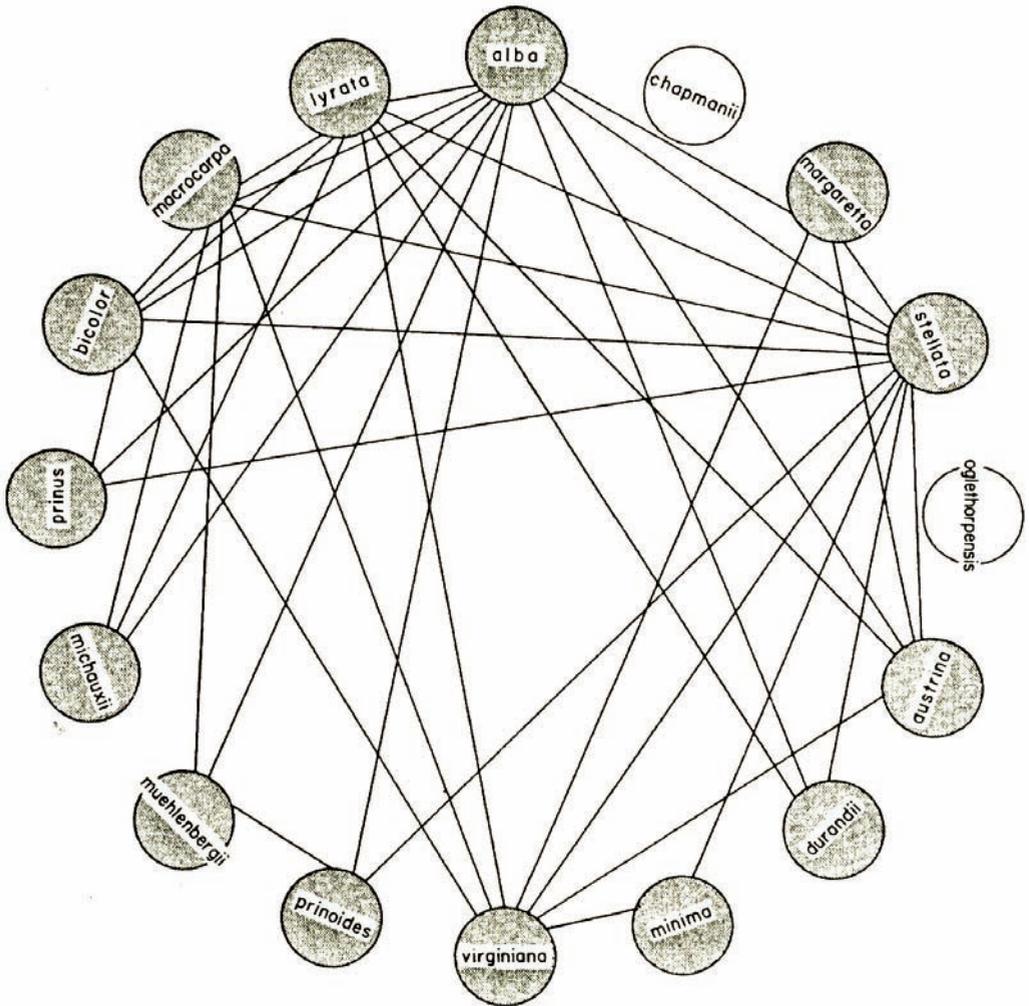


Figure 2/ “The white oak syngameon of eastern North America (shaded areas)”, reproduced from Hardin (1975), Figure 1. Hardin focused his study on white oak (*Quercus alba*), but in this figure he summarizes all crosses that are known between any species of White Oak believed at the time to be indigenous to North America east of Oklahoma and Texas. Crosses were inferred from literature, Hardin’s own collections, and herbarium specimens. Figure courtesy of *Journal of the Arnold Arboretum*, released by the Missouri Botanical Garden, Peter H. Raven Library under Creative Commons Attribution-NonCommercial-ShareAlike 4.0 (CC BY-NC-SA 4.0) license; non-commercial reuse is permitted under the same license, with source attribution.

Intermediate Oaks) (Manos, Doyle, and Nixon 1999). We know that the Eurasian White Oaks (*Quercus robur* L. and relatives) are derived from a North American White Oak ancestor (Denk and Grimm 2010; Hubert et al. 2014). More recent work using genome-scale data (Pearse and Hipp 2009; Hipp et al. 2013; Hipp et al. 2014) has been successful in resolving relationships at a variety of depths throughout the phylogenetic tree, including relationships much closer to the tips of the tree. The Eurasian White Oaks are now resolved as monophyletic (Pearse and Hipp 2009), though their placement relative

to the White Oaks of Eastern North America is ambiguous (Hipp et al. 2013; Hipp et al. 2014). An out-of-Mexico scenario for the American oaks appears to be rejected (Pearse and Hipp 2009; Hipp et al. 2013; Hipp et al. 2014). Fine-scale relationships appear to be within reach.

These successes notwithstanding, in the face of hybridization, even limited in scale, one must ask, what are we finding in our phylogenetic inquiries? The methods we are constrained to using at this point are extremely broadbrush, genome-scale methods that, at least to date, have not resolved the histories encoded by genes individually, but have relied on analysis of the data in combination. Even if we get single, well-resolved phylogenies, what do they mean against the backdrop of oak hybridization and introgression? Should we trust the phylogenies that we see? It seems to me that the reality may be one or more of at least three scenarios:

- *Perhaps we are being misled: our phylogeny may really represent local gene flow masquerading as the history of species divergence.* In the worst case, our estimate of the oak phylogeny might just be a representation of local gene flow. We know, in fact, that chloroplast phylogenies in oaks tend to track geography rather than species boundaries (Whittemore and Schaal 1991; Dumolin-Lapegue et al. 1997), and in the beginning, there was some concern that multi-locus nuclear markers might do likewise. However, the fact that oak species cohere genetically at wide geographic ranges in both fine-scale population-level studies (Hipp and Weber 2008; Cavender-Bares and Pahlich 2009) and our first phylogenetic studies (Pearse and Hipp 2009) suggests that the patterns we are recovering are *not* patterns of local gene flow between populations. Rather, we are tracking a population history that is separate from, if not independent of, localized gene flow between species.
- *Gene flow may be sufficient to homogenize species and lineages.* Based on what we know from species-level studies, intraspecific gene flow (the gene flow among members of a single species) dominates the pattern of genetic variation that we find in and among oaks. This idea has been presented convincingly as a mechanism for species coherence in introgressing lineages (Petit and Excoffier 2009), and if true, such intraspecific gene flow might just as easily retain the history of population divergence even in the face of interspecific hybridization. Despite the known patterns of introgression and hybridization among oak species, high rates of gene flow within species should homogenize species genetically and transfer among individuals of those species the history of species divergence encoded in mutations and changing allele frequencies. Given the high rate of species coherence in both microevolutionary studies (at the species and population level) and macroevolutionary (phylogenetic) studies, this scenario seems plausible.
- *Divergence history may be stored preferentially at selected regions of the genome.* Genomic “islands of divergence” are putative regions of the genome at which species or populations diverge, even as hybridization may homogenize the genome as a whole (Michel et al. 2010). Such islands of divergence require either very strong selection (Beaumont and Balding 2004; Via and West 2008) or chromosomal rearrangements (Rieseberg 2001; Noor and Bennett 2009). While the genome of *Quercus* is believed to be rather stable (Duffield 1940; Aykut, Uslu, and Babaç 2011; Kremer et al. 2012), genomically heterogeneous selection is known in the genus (Sork, Stowe, and Hochwender 1993; Bodénès et al. 1997; Dodd and Afzal-

Rafii 2004; Saintagne et al. 2004; Lexer, Kremer, and Petit 2006; Goicoechea, Petit, and Kremer 2012; Guichoux et al. 2013; Lind-Riehl, Sullivan, and Gailing 2014) and may well play a role in both speciation and species coherence (Morjan and Rieseberg 2004). If so, phylogenetic estimates might be expected to track selected genes better than neutral regions of the genome. In the most recent phylogenetic study in the genus (Hipp et al. 2014), my colleagues and I investigated this question by mapping genomic markers back to a functional gene database (more formally, an expressed sequence tag or EST collection for plants), and found that EST-linked markers (which we expect to be enriched for genome regions under selection, because they code for genes) are no more phylogenetically conclusive than non-EST-linked markers. The only other genome-scale study of oak phylogeny was based on amplified fragment length polymorphisms, AFLPs (Pearse and Hipp 2009), which are presumed to sample mostly from neutral regions of the genome. But these relatively coarse analyses only suggest that phylogenetically informative sites are relatively widespread across the genome rather than localized. It may still turn out that divergence is concentrated in selected regions of the genome. For example, genes contributing to drought resistance may have a fundamentally different history from those contributing to freezing tolerance. It might also turn out that lineage diversification is encoded heterogeneously and in a predictable manner, such that common regions of the genome tend to harbor the history of lineage diversification while other regions tend to share readily among lineages. Fine-scale genomic data, coupled with multilocus phylogenetic data at a range of phylogenetic scales, will be needed to investigate the genomic architecture of differentiation, and ultimately to understand what genes shape the oak tree of life.

Given recent successes in fine-scale oak phylogenetics and past success in resolving species boundaries in oaks using molecular markers, a phylogenetic reconstruction for oaks, representing a meaningful history of species divergence, appears an achievable goal. It is not clear, however, how hybridization may still tamper with our understanding of oak species divergence. Even if there is strong phylogenetic structure in oaks, hybridization may drag branches of the tree around, and such effects may be difficult or impossible to detect. Moderate levels of hybridization and introgression may be detectable, but widespread interspecific gene flow is likely to be a history-effacing process (Sober 1991). Will we fully tease apart evolutionary history from ongoing introgression? Can we distinguish between ancient introgression events and shared ancestry? Recent statistical methods will certainly help (Eaton and Ree 2013; Eaton 2014), but as we attack the evolutionary history of oaks on a large scale, identifying histories of hybridization will be increasingly complex and essential to our understanding of the oak phylogeny. The history of oak evolution – the phylogeny of oaks – is certainly real, and largely understandable. How far we can go remains to be seen.

## ***Acknowledgments***

The author wishes to acknowledge his numerous colleagues in oak systematics for insights that have informed his views of oak phylogeny and population genetics, including Deren Eaton, Oliver Gailing, Antoine Kremer, Dick Jensen, Paul Manos, John McVay, Rémy Petit, Jaime Weber, and collaborators in the Oaks of the Americas project

(<http://tinyurl.com/americanoakgroup>). Béatrice Chassé, Rachel Davis, Oliver Gailing, Marlene Hahn, Paul Manos, and Nick Stoyloff provided comments on a first draft of this manuscript. Mark Wetter and Ken Cameron at the Wisconsin State Herbarium (WIS) provided the herbarium scan presented in Figure 1, and Michael Nee noticed and collected this excellent specimen. Figure 2, from Hardin (1975), is reproduced from the *Journal of the Arnold Arboretum* with permission of the Library of the Arnold Arboretum. I extend particular thanks to Béatrice Chassé for her work in editing the journal, and for inviting me to submit this article. This work was supported by NSF DEB Award #1146488 and a Fellowship from the Fulbright and Franco-American Commission (2014).

**Photographers.** Title page: Béatrice Chassé (*Quercus × bebbiana*). Photo 1: Guy Sternberg.

### Works cited

- Allard, H.A. 1932. A progeny study of the so-called oak species *Quercus saulii*, with notes on other probable hybrids found in or near the District of Columbia. *Bulletin of the Torrey Botanical Club* 59: 267-277.
- . 1949. An analysis of seedling progeny of an individual of *Quercus saulii* compared with seedlings of a typical individual of white oak (*Quercus alba*) and a typical rock chestnut oak (*Q. montana*). *Castanea* 14 (109-117).
- Anderson, E. 1948. Hybridization of the habitat. *Evolution* 2: 1-9.
- Aykut, Y., E. Uslu, and M. Tekin Babac. 2011. Cytogenetic studies on *Quercus* L. (Fagaceae) species belonging to *Ilex* and *Cerris* section in Turkey. *Caryologia* 64 (3): 297-301.
- Baranski, M.J. 1975. An analysis of variation within white oak (*Quercus alba* L.). Raleigh: North Carolina Agricultural Experiment Station.
- Beaumont, M.A., and D.J. Balding. 2004. Identifying adaptive genetic divergence among populations from genome scans. *Molecular Ecology* 13 (4): 969-980.
- Bodénès, C., S. Joandet, F. Laigret, and A. Kremer. 1997. Detection of genomic regions differentiating two closely related oak species *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. *Heredity* 78: 433-444.
- Burger, W.C. 1975. The species concept in *Quercus*. *Taxon* 24: 45-50.
- Cavender-Bares, J., and A. Pahlisch. 2009. Molecular, morphological, and ecological niche differentiation of sympatric sister oak species, *Quercus virginiana* and *Q. geminata* (Fagaceae). *American Journal of Botany* 96 (9): 1690-1702.
- Chybicki, I.J., and J. Burczyk. 2010. Realized gene flow within mixed stands of *Quercus robur* L. and *Q. petraea* (Matt.) L. revealed at the stage of naturally established seedling. *Molecular Ecology* 19 (10): 2137-2151.
- Coombs, A.J., and W.N. Coates. 1997. Oglethorpe and the Oglethorpe Oak. *Arnoldia* 57 (7): 25-30.
- Curtu, A., O. Gailing, and R. Finkeldey. 2007. Evidence for hybridization and introgression within a species-rich oak (*Quercus* spp.) community. *BMC Evolutionary Biology* 7 (1): 218.
- Deng, M., Z. Zhou, and Q. Li. 2013. Taxonomy and Systematics of *Quercus* subgenus *Cyclobalanopsis*. *International Oaks* 24: 49-60.
- Denk, T., and G.W. Grimm. 2010. "The oaks of western Eurasia: Traditional classifications and evidence from two nuclear markers." *Taxon* no. 59:351-366.
- Dodd, R.S., and Z. Afzal-Rafii. 2004. Selection and dispersal in a multispecies oak hybrid zone. *Evolution* 58 (2): 261-269.
- Dow, B. D., and M.V. Ashley. 1998. High levels of gene flow in bur oak revealed by paternity analysis using microsatellites. *Journal of Heredity* 89: 62-70.
- Duffield, J.W. 1940. Chromosome counts in *Quercus*. *American Journal of Botany* 27: 787-788.
- Dumolin-Lapegue, S., A. Kremer, and R.J. Petit. 1999. Are Chloroplast and Mitochondrial DNA Variation Species Independent in Oaks? *Evolution* 53 (5): 1406-1413.
- Dumolin-Lapegue, S., B. Demesure, S. Fineschi, V. Le Come, and R.J. Petit. 1997. Phylogeographic structure of white oaks throughout the European continent. *Genetics* 146: 1475-1487.
- Eaton, Deren A.R. 2014. PyRAD: assembly of de novo RADseq loci for phylogenetic analyses. *Bioinformatics*:doi: 10.1093/bioinformatics/btu121. doi: 10.1093/bioinformatics/btu121.
- Eaton, D.A.R., and R.H. Ree. 2013. Inferring Phylogeny and Introgression using RADseq Data: An Example from Flowering Plants (*Pedicularis*: Orobanchaceae). *Systematic Biology* 62: 689-706.
- Ehrlich, P.R., and P.H. Raven. 1969. Differentiation of populations: Gene flow seems to be less important in speciation than the neo-Darwinians thought. *Science* 165 (3899): 1228-1232.
- Engelmann, G. 1876. The oaks of the United States. *Transactions of the Academy of Sciences St. Louis* no. 3: 539-543.
- Gerber, S., J. Chadæuf, F. Gugerli, M. Lascoux, J. Buiteveld, J. Cottrell, A. Dounavi, S. Fineschi, L.L. Forrest, J. Fogelqvist, P.G. Goicoechea, J.S. Jensen, D. Salvini, G.G. Vendramin, and A. Kremer. 2014. "High Rates of Gene Flow by Pollen and Seed in Oak Populations across Europe." *PLoS ONE* 9 (1): e85130. doi: 10.1371/journal.pone.0085130.
- Goicoechea, P.G., R.J. Petit, and A. Kremer. 2012. Detecting the footprints of divergent selection in oaks with linked markers." *Heredity* 109 (6): 361-371. doi: <http://www.nature.com/hdy/journal/v109/n6/supinfo/hdy201251s1.html>.
- Grant, V. 1971. *Plant Speciation*. First ed. New York: Columbia University Press.
- . 2004. Plant speciation, the book: perspectives and paradigms. *New Phytologist* no. 161 (1):8-11. doi: 10.1111/j.1469-8137.2004.00964.x.
- Gray, A. 1857. *Manual of the botany of the northern United States. Including Virginia, Kentucky, and all east of the Mississippi: arranged according to the natural system*. New York: G. P. Putnam & Co.
- . 1859. *Manual of the botany of the northern United States: including Virginia, Kentucky, and all east of the Mississippi*

- arranged according to the natural system. New York: Ivison & Phinney.
- . 1862. *Manual of the botany of the northern United States, third revised edition*. Chicago: Ivison, Phinney, & Co.
- . 1867. *Manual of the Botany of the Northern United States, Including the District East of the Mississippi and North of North Carolina and Tennessee, Arranged According to the Natural System*. Fifth ed. New York: Ivison, Blakeman, Taylor & Co.
- Gray, A., and W.S. Sullivant. 1848. *A manual of the botany of the northern United States, from New England to Wisconsin and south to Ohio and Pennsylvania inclusive (the mosses and liverworts by Wm. S. Sullivant) arranged according to the natural system*. Boston and London: J. Munroe, J. Chapman.
- Guichoux, E., P. Garnier-Géré, L. Lagache, T. Lang, C. Boury, and R.J. Petit. 2013. Outlier loci highlight the direction of introgression in oaks. *Molecular Ecology* 22 (2): 450-462. doi: 10.1111/mec.12125.
- Hardin, J.W. 1975. Hybridization and introgression in *Quercus alba*. *Journal of the Arnold Arboretum* 56: 336-363.
- Hipp, A.L., D.A.R. Eaton, J. Cavender-Bares, E. Fitzek, R. Nipper, and P.S. Manos. 2014. A framework phylogeny of the American oak clade based on sequenced RAD data. *PLoS ONE* 9: e93975.
- Hipp, Andrew L., Paul S. Manos, Jeannine Cavender-Bares, Deren A. R. Eaton, and Rick Nipper. 2013. Using phylogenomics to infer the evolutionary history of oaks. *International Oak Journal* 24: 61-71.
- Hipp, A.L., and J.A. Weber. 2008. Taxonomy of Hill's Oak (*Quercus ellipsoidalis*: Fagaceae): Evidence from AFLP Data. *Systematic Botany* 33: 148-158.
- Hubert, F., G.W. Grimm, E. Jousselin, V. Berry, A. Franc, and A. Kremer. 2014. "Multiple nuclear genes stabilize the phylogenetic backbone of the genus *Quercus*." *Systematics and Biodiversity* 12: 405-423. doi: 10.1080/14772000.2014.941037.
- Kremer, A., A. Abbott, J. Carlson, P.S. Manos, C. Plomion, P. Sisco, M. Staton, S. Ueno, and G. Vendramin. 2012. Genomics of Fagaceae. *Tree Genetics & Genomes* 8: 583-610. doi: 10.1007/s11295-012-0498-3.
- Ledig, F.T., R.W. Wilson, J.W. Duffield, and G. Maxwell. 1969. A discriminant analysis of introgression between *Quercus prinus* L. and *Quercus alba* L. *Bulletin of the Torrey Botanical Club* 96: 156-163.
- Lexer, C., A. Kremer, and R.J. Petit. 2006. Shared alleles in sympatric oaks: recurrent gene flow is a more parsimonious explanation than ancestral polymorphism. *Molecular Ecology* 15: 2007-2012.
- Lind-Riehl, J.F., A.R. Sullivan, and O. Gailing. 2014. Evidence for selection on a CONSTANS-like gene between two red oak species. *Annals of Botany*. doi: 10.1093/aob/mcu019.
- Manos, P.S., J.J. Doyle, and K.C. Nixon. 1999. Phylogeny, Biogeography, and Processes of Molecular Differentiation in *Quercus* Subgenus *Quercus* (Fagaceae). *Molecular Phylogenetics and Evolution* 12 (3): 333-349. doi: 10.1006/mpev.1999.0614.
- Michel, A.P., S. Sim, T.H. Powell, M.S. Taylor, P. Nosil, and J.L. Feder. 2010. Widespread genomic divergence during sympatric speciation. *Proceedings of the National Academy of Sciences of the United States of America*. doi: 1000939107 [pii]10.1073/pnas.1000939107.
- Moran, E.V., J. Willis, and J.S. Clark. 2012. Genetic evidence for hybridization in red oaks (*Quercus* sect. *Lobatae*, Fagaceae). *American Journal of Botany* 99 (1): 92-100. doi: 10.3732/ajb.1100023.
- Morjan, C.L., and L.H. Rieseberg. 2004. How species evolve collectively: implications of gene flow and selection for the spread of advantageous alleles. *Molecular Ecology* 13 (6): 1341-1356.
- Muir, G., C.C. Fleming, and C. Schlotterer. 2000. Species status of hybridizing oaks. *Nature (London)* 405: 1016.
- Muller, C.H. 1961. The live oaks of the Series *Virentes*. *American Midland Naturalist* 65: 17-39.
- Muller, C.H. 1952. Ecological control of hybridization in *Quercus*: a factor in the mechanism of evolution. *Evolution* 6 (2): 147-161.
- Noor, M.A., and S.M. Bennett. 2009. Islands of speciation or mirages in the desert? Examining the role of restricted recombination in maintaining species. *Heredity* 103: 439-444.
- Oh, S.H., and P.S. Manos. 2008. Molecular phylogenetics and cupule evolution in Fagaceae as inferred from nuclear CRABS CLAW sequences. *Taxon* 57: 434-451.
- Palmer, E.J. 1948. Hybrid oaks of North America. *Journal of the Arnold Arboretum* 29 (1): 1-48.
- Pearse, I.S., and A.L. Hipp. 2009. Phylogenetic and trait similarity to a native species predict herbivory on non-native oaks. *Proceedings of the National Academy of Sciences of the United States of America* 106 (43): 18097-18102.
- Petit, R.J., and L. Excoffier. 2009. Gene flow and species delimitation. *Trends in Ecology & Evolution* 24 (7): 386-393.
- Petit, R.J., C. Bodenes, A. Ducouso, G. Roussel, and A. Kremer. 2003. Hybridization as a mechanism of invasion in oaks. *New Phytologist* 161: 151-164.
- Rieseberg, L.H. 2001. Chromosomal rearrangements and speciation. *Trends in Ecology & Evolution* 16 (7): 351-358.
- Saintagne, C., C. Bodenes, T. Barreneche, D. Pot, C. Plomion, and A. Kremer. 2004. Distribution of genomic regions differentiating oak species assessed by QTL detection. *Heredity* 92: 20-30.
- Sober, E. 1991. *Reconstructing the Past: Parsimony, Evolution, and Inference*. Cambridge, MA: The MIT Press.
- Sork, V.L., K.A. Stowe, and C. Hochwender. 1993. Evidence for local adaptation in closely adjacent subpopulations of northern Red Oak (*Quercus rubra* L.) expressed as resistance to leaf herbivores. *American Naturalist* 142 (6): 928-936.
- Stebbins, G.L. 1950. *Variation and Evolution in Plants*. Edited by L.C. Dunn, *Columbia Biological Series*. New York: Columbia University Press.
- Stebbins, G.L., E.G. Matzke, and C. Epling. 1947. Hybridization in a population of *Quercus marilandica* and *Q. ilicifolia*. *Evolution* 1: 79-88.
- Tovar-Sánchez, E., and K. Oyama. 2004. Natural hybridization and hybrid zones between *Quercus crassifolia* and *Quercus crassipes* (Fagaceae) in Mexico: morphological and molecular evidence. *American Journal of Botany* 91 (9): 1352-1363. doi: 10.3732/ajb.91.9.1352.
- Tucker, J.M. 1963. Studies in the *Quercus undulata* complex. III. The contribution of *Q. arizonica*. *American Journal of Botany* 50: 699-708.
- Van Valen, L. 1973. A new evolutionary law. *Evolutionary theory* 1: 1-30.
- . 1976. "Ecological species, multispecies, and oaks." *Taxon* no. 25:233-239.
- Via, S., and J. West. 2008. The genetic mosaic suggests a new role for hitchhiking in ecological speciation. *Molecular Ecology* 17 (19): 4334-4345.
- Whittemore, A.T., and B.A. Schaal. 1991. Interspecific gene flow in sympatric oaks. *Proceedings of the National Academy of Sciences USA* 88: 2540 - 2544.
- Wiegand, K.M. 1935. A taxonomist's experience with hybrids in the wild. *Science* 81: 161-166.



1/ *Quercus macrocarpa*