HYBRIDIZATION IN CALIFORNIA OAKS

by John M. Tucker

from *Fremontia*, July 1990

In California the first hybrid oak was recognized well over 100 years ago when, in 1863, Albert Kellogg gave the name *Quercus morehus* to the cross between the California black oak (*Q. kelloggii*) and the interior live oak (*Q. wislizenii*). But questions were sometimes raised as to whether these early examples were indeed hybrids or were actually species. This was certainly the case with *Q. morehus*. Jepson included it as a hybrid in his "Flora of California," but later, in his widely used "Manual of the Flowering Plants of California" (1923), included *Q. morehus* as a species, with no indication of its being a hybrid. How, then, are such questions to be resolved?

Over the vears students of the oaks have noted that suspected hybrids usually fit a certain patte: : they usually occur as single, isolated individuals; they differ significantly from any of the well-known species of the area, but are morphologically intermediate between two species that *could* be the parents; and they are growing with (or in the vicinity of) these presumed parents.

In regard to the distribution of hybrids, E.J. Palmer, in "Hybrid Oaks of North America" (1948), noted that, "Hybrids are most likely to occur in nature along the margins of the range of one of the parent species or where one is locally rare and the other abundant. . . the chance for the production of natural hybrids between compatible species increases in proportion to the numerical inequality of the parent species in the immediate vicinity . . . *it is not absolutely essential that both parent be found growing with it* [emphasis added], providing they are natives of the region and are known at no great distance. For if one of the parents was a lone individual, it may well have disappeared from the locality." Also, it has long been noted that hybridization in North American oaks occurs only within sections. That is, white oaks cross only with other members of the white oak group (the section *Quercus*), black or red oaks with other members of their group (the section *Erythrobalanus*), and the so-called intermediate oaks (the section *Protobalanus* --*Q. chrysolepis* and its relatives) only among their group.

In the Old World, however, a few natural hybrids have been reported between members of the white oak group and the section *Cerris*, a Eurasian group. And, interestingly enough, a case of spontaneous intersectional hybridization occurred at Kew Gardens in England in the 1930s.

The criteria noted above which characterize hybrids are generally reliable. But skeptics have pointed out that, since oaks are often notoriously variable, some supposed hybrids may be merely extreme variants of a species. This is certainly a valid argument; and a few critics have suggested other means -- presumably more reliable or objective -- for establishing the true nature of suspected hybrids.

Verification of Suspected Hybrids

In 1907 MacDougall suggested that suspected hybrids could be verified by several experimental procedures:

1. By performing progeny tests. Seedlings of a suspected hybrid (if it is fertile) should show segregation of characteristics of the presumed parents.

2. "Synthesizing" the hybrid by experimentally cross-pollinating the presumed parental species.

3. By making anatomical comparisons of the suspected hybrid with its parents.

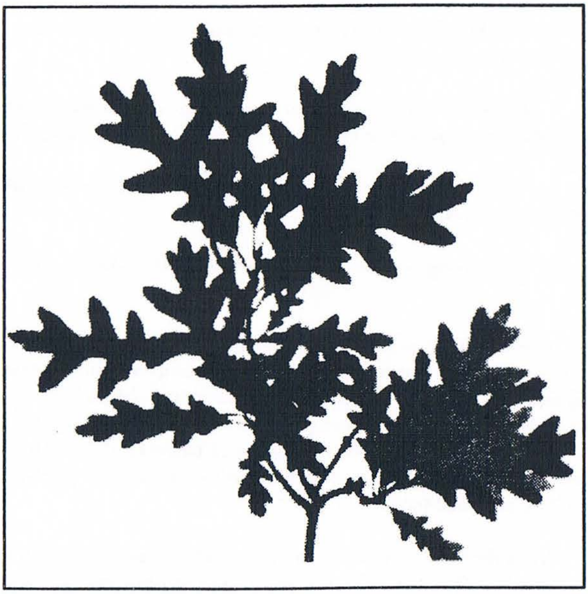
To comment on this third procedure before considering the other two, I have found in my own studies that very detailed morphological comparisons (even using the scanning electron microscope) -- rather than anatomical comparisons -- are easier to perform and probably provide more abundant data. Indeed, by analyzing as many characters as possible in which the two presumed parents differ, and by determining whether or not the suspected hybrid is intermediate on each of these points, a sound basis can usually be provided for such judgments.

As for the first procedure, a classic example of a progeny test that established the hybrid nature of *Quercus* x *morehus* (an "x" between two terms of a botanical name indicates hybrid) beyond any doubt was performed by Carl B. Wolf in the 1930s. From several large collections of acorns from trees of *Q.* x *morehus*, Wolf obtained about 900 young plants. "Of these, many were so weak that they only produced a few pairs of leaves and survived only a few months. Others closely resembled seedlings of *Q. kelloggii* and *Q. wislizenii*, while a few from nearly every lot were typical *Q. morehus*. In addition, many seedlings were of variable leaf types and could not be regarded as any of the above three types."

One problem with the progeny test is that although young plants grown from a single tree obviously all have the same female parent, the pollen parentage may differ among the seedlings if more than one other compatible species is growing in the vicinity. Since oaks are largely self-incompatible, it can be assumed that the seedlings are the result of out-crossing, and not the result of self-pollination of the mother tree. Thus, wind-borne pollen from two or more other species could produce seedlings of diverse male parentage. Such a test could give controversial results, to say the least.

Another problem stems from the fact that, if the suspected hybrid is growing with only one of the presumed parents (with no other oaks in the neighborhood, as sometimes happens), at flowering time the hybrid will be showered with pollen from this one species. And the absence of any other pollen source, the resulting progeny of the hybrid would be back-crosses. Such seedlings would be highly variable -- attesting to the hybrid nature of the mother plant -- but they would provide few clues, if any, to the identity of the "absent" parent of the hybrid, if this was in doubt.

This point is borne out in a progeny test I performed some thirty-odd years ago (although not with a Californian hybrid). In the fall of 1957, I received a large collection of acorns from a graduate student (Rudy Drobnick) at the University of Utah. These were from a hybrid between *Q. turbinella* and *Q. gambelii* growing in the Oquirrh Mountains in Utah, near Salt Lake City. The hybrid was surrounded by shrubs of *Q. gambelii*, but there was no *Q. turbinella* in the vicinity. The identity of the parental species of the hybrid was

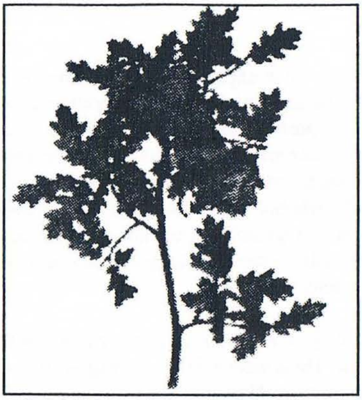
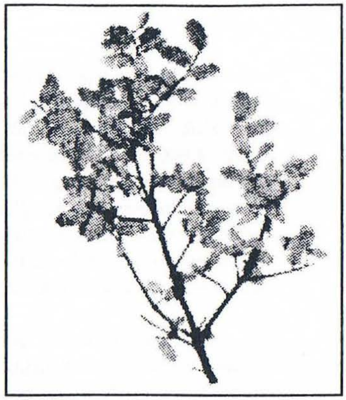


not in doubt, but the progeny test was performed out of curiosity as to what the results might be.

A detailed morphological analysis of the whole progeny (183 survivors at the end of the test, out of 900 acorns originally sown) clearly showed several general points: the plants were variable, but in general were intermediate between the parents; at one extreme, several individuals were so similar to *Q. gambelii* as to be scarcely distinguishable from it; at the other extreme, several plants were very similar to *Q. turbinella*. If there had been any question as to the identity of the absent parent, this progeny test would have provided no more clues than would a careful analysis of the mother plant, itself.

As an interesting sidelight in this particular case, when Mr. Drobnick, in 1954, first discovered this interesting and seemingly unique oak, *Q. gambelii* was the only species known in north-central Utah . He and his major professor (Walter P. Cottam) decided it must be a new species. But first they sent specimens to C.H. Muller (at U.C., Santa Barbara), an authority on oak taxonomy, who then sent them to me. Both of us, independently, expressed the same opinion: this was a hybrid between *Q. gambelii* and *Q. turbinella* -- not an undescribed species.

As the nearest *Q. turbinella* was some 260 miles away in southwestern Utah, how could this possibly be a hybrid? This intriguing phytogeographic riddle set in motion a lengthy program of investigation by Drobnick, Cottam, and me, that included, among other things, an experimental crossing of *turbinella* and *gambelii*. The attempt at experimental hybridization was surprisingly successful, with no significant differences between the "artificial" hybrids and those found in the Oquirrhs and along the

The hybrid (center) between Gambel oak (Q. gambelli), left and desert scrub oak (Q. turbinella),(right).

in his M.S. Thesis, University of Utah, 1958, found many more of them extending southward along the Wasatch Range and all the way to the Pine Valley Mountains in extreme southwestern Utah. Here the two parents often occur cheek-by-jowl, and hybrids are frequent.

Puzzling Occurrences of Hybrids

The hybrids between *Q. gambelii* and *Q. turbinella* discussed in the preceding section obviously pose some puzzling questions. Several hybrids are known in California and adjacent Oregon that occur with one parental species but with the nearest occurrence of the other parent being many miles away.

How can such cases be explained? In every instance known to this writer, one *general* explanation seems to be the most probable, namely, that the "absent" parent has actually existed at the site of the hybrid at sometime in the past, that climatic change has occurred in that region of sufficient severity to eliminate one parent but not the other, and that the last lingering one or two individuals of the more sensitive species will be the parent of any hybrids produced. These last survivors will receive ample pollen from the other species, and, being largely self-incompatible, if they reproduce at all, their progeny will be hybrids with the other species.

To be sure, there is no dearth of other possible explanations: long-range pollination from the nearest trees of the "absent" parent -- wherever they happen to be; transport of hybrid acorns by traveling Indians, or even migrating birds (*hybrid* acorns? From what source?).

Long-range pollination might have some rational appeal, but I look upon it with extreme skepticism. Effective pollination would require the close coordination of flowering of the oaks in the separate areas, wind sufficiently strong and sustained and *in the proper direction* to transport pollen the required distance, and most improbable of all (after the immense dispersion and settling out over such a long distance), some of the pollen settling precisely upon the minute stigmas of the female flowers of the second species. Possible? In a theoretical sense, perhaps. But the probability of all these requirements being met would seem to be infinitesimal in the cases we are considering.

Back to the Utah hybrids -- our explanation, then, assumes a northward migration of *Q. turbinella* at least as far as the northernmost hybrids, at some time in the past. This was most likely during the post-Pleistocene Altithermal Period, from about 7,500 - 4,000 years ago, when the climate was warmer and drier than at present. As the climatic pendulum swung back to cooler conditions since that period, the winter became too severe for the evergreen *Q. turbinella* but not for the deciduous *Q. gambelii*, nor for the occasional hybrids (mostly semi-evergreen) that became established. Since these are usually single, isolated individuals (occuring with *gambelii*), and in most cases appear to be F_1 s, such individuals may be very old.

Closer to home, trees of *Q.* x *morehus* were discovered in the 1940s in Josephine County, southern Oregon. These were in areas of Douglas fir woodland, with the one parent, *Q. kelloggii*, being common. However, the nearest known *Q. wislezenii*, the other parent, is approximately seventy-five miles to the southeast in Siskiyou County, California. Since the latter prefers warmer and drier conditions than *Q. kelloggi*, these hybrid occurrences -- as with the hybrids in Utah -- argue for a period in the past when regional climate was warmer and drier than at present. And again, the Altithermal Period could have been the time.

In Southern California a very interesting hybrid occurs under desert conditions in Joshua Tree National Monument, Riverside County. Although similar to the examples discussed above in that one parent is "absent," the climatic implications of the case are quite different. This tree, growing in a wash at Live Oak Tank, is a hybrid between the valley oak, *Q. lobata*, and the shrubby desert species, *Q. cornelius-mulleri*. The latter is abundant at the site, but the nearest valley oak is approximately 150 miles to the northwest, along the south side of Antelope Valley in northwestern Lost Angeles County. The two species are completely separated geographically at present, for *Q. cornelius-mulleri* reaches its northwestern limits in the Cajon Pass area in San Bernardino County.

The hybrid is essentially intermediate between the parents. Even so, in some characteristics it bears a clear resemblance to the valley oak: in the tree habit of growth, the medium-sized leaves with distinctly lobed margins, the medium-sized acorns, and moderately warty acorn cups. In two other characters, however, it is more similar to theshrubby parent: its evergreen habit and flaky bark (*Q. lobata* is deciduous and in mature trees has thick bark deeply fissured into cuboid segments).

For years the identity of this tree was controversial. Several different botanists had offered their opinions (all different) and made collections from it. Acorns collected from the tree in 1946 by the late Dr. P.A. Munz were propagated at the Rancho Santa Ana Botanical Garden. Munz noted that the young oaks differed markedly from one another. However, neither these nor seedlings from collections ten years later (by Ralph D. Cornell, Los Angeles architect) suggested *Q. lobata* parentage. Specimens sent to me from the plants surviving in 1963 all have leaves that are smaller and more spinose that the parent tree, i.e., tending toward the shrubby parent. Thus, they probably were back-crosses to *Q. cornelius-mulleri*.

After a visit to the site, and detailed morphological comparison, I was convinced that the tree is indeed a hybrid between *Q. lobata* and the shrubby, evergreen species at the site, and published a descriptive article in which I name the hybrid *Quercus* x *munzii*. The name I used for the shrubby parent, however, was *Q. turbinella* subsp. *californica*, which is the shrubby oak common in desert border habitats northwestward from the Cajon Pass region. It was not until some years later that this similar shrub of the lower desert was recognized as a distinct species. In 1981 two graduate students at U.C., Santa Barbara, Kevin Nixon and Kelly Steele, named it *Quercus cornelius-mulleri* for Professor Muller at that institution. I agree with their judgment completely. Thus, the parents of the Oak Tank hybrid, *Q.* x *munzii* must henceforth be stated, not as in my article, but as *Q. lobata* x *Q. cornelius-mulleri*.

In any event, the general point to be emphasized, as in the previous example, is that the range of the "absent" parent most likely extended as far as the hybrid site at some time in the past. In the case of *Q. lobata*, this must have been a period when climatic conditions were moister than at present in the southern Mohave. Some period within the last few thousand years, since the Altithermal (which was warmer and drier than at present), would seem to be a good possibility. Furthermore, considering the fact that the hybrid does not appear to be a very old tree -- perhaps no more than 100 to 150 years old -- the last tree of *Q. lobata* may have persisted at the site right up until the last century or two.

Evidence of this recent climatic change has been noted in Kern County, just to the north. Ernest Twisselmann ("A Flora of Kern County, California," 1967) reported the occurrence of old, long-fallen Jeffrey Pines several miles below the nearest living ones, in the Tehachapi Mountains.

Finally, the few "anomalous" occurences presented here are just some of the more dramatic examples known to the writer. A number of others come to mind in which the "absent" parent is much closer -- no more than a few miles away. In any such case, the curious-minded layman is always interested in an explanation and is often quick to propose one of his own -- long-range pollination, acorn transport by Indians, or by super-jays, or something even more fanciful. Of course, the evidence must be carefully considered in each case. But it is always good to keep in mind the observations of E.J. Palmer, noted at the beginning of this paper.

Quercus kellogii

Quercus x morebus

Quercus wislizenii

Taxonomic Difficulties Related to Hybridization

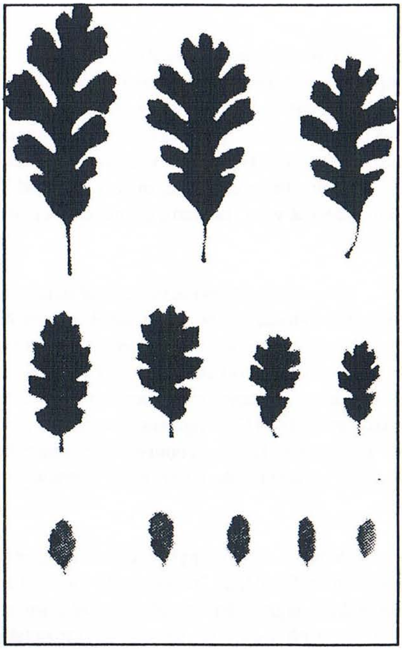
The simplest sort of difficulties are those experienced by anyone attempting to identify an unfamiliar oak that happens to be a hybrid. Especially frustrating to the amateur, hybrids can also be problematic to the professional. Keys in manuals or floras are seldom constructed to accommodate hybrids, and species descriptions don't fit very well, either.

More serious problems, however, may confront the taxonomist, for example, in compiling a local flora, if highly variable populations resulting from interspecific hybridization exist in the area, or intergrading populations occur where species ranges are contiguous. Difficult taxonomic judgments may be called for in such situations.

Even though well-differentiated morphologically, if two taxa interbreed freely where they co-exist, one school of thought would regard them as different *varieties* or *subspecies* of a single species. This mind-set is a legacy of pre-evolutionary beliefs, when it was thought that interbreeding simply didn't occur between "good" species. Occasional sterile hybrids, perhaps, but even these were rare. This viewpoint is illustrated graphically by remarks of George Engelmann in a paper in 1878, "The Oaks of the United States." Engelmann, one of the foremost students of the oaks in the nineteenth century, was describing a highly variable population on the Arkansas River, above Canyon City in southern Colorado. "We feel satisfied that we might have abundant material to characterize several distinct species, certainly four or five well-marked forms, and, indeed, they have been considered such." But he goes on to say: ". . . but, looking around us, the very abundance of material must shake our confidence in our discrimination: within the compass of a few hundred yards we find not only the forms [species] above distinguished, but numbers of others which are neither the one nor the other, but which are intermediate between them and clearly unite them all as forms of one single extremely polymorphous species." And he ends, rather plaintively: "If one oak behaves thus, why not others? Thrown into a sea of doubt, what can guide us to correct knowledge?"

Engelmann's species concept was doubtless rooted in pre-Darwinian ideas of special creation. But even modern evolutionary biologists sometimes rely on similar criteria for a practical definition of species. Their rationale assumes that in a lineage whose members are undergoing evolutionary divergence, the development of barriers to gene exchange between them proceeds at the same rate as morphological divergence. Translated into taxonomic practice, if two related taxa hybridize and exchange genes more or less freely, they have not yet attained the status of good biological species and should be treated as taxonomic subspecies (of a single species).

With oaks, however, as well as a number of other woody plant groups (e.g., manzanitas and willows), a less doctrinaire species concept is called for. If the oak taxonomist were to treat as subspecies any pair of taxa that hybridize freely, he would often lump together oaks that are extremely different morphologically, belong to very different floristic assemblages, and have doubtless had long, separate evolutionary histories. One of the most striking examples of this sort known to the writer involves *Q. gambelii* and *Q. grisea* in the mountains of New Mexico. Morphologically they are poles apart. Floristically, *Q. gambelii* is a common element of the ponderosa pine association of the central and southern Rocky Mountains. *Quercus grisea*, by contrast, is a member of the North Mexican "encinal," or evergreen oak woodland, which occurs in parts of New Mexico and West Texas. In the Capitan, Sacramento, and Guadalupe mountains in south-central New Mexico, hybridization has been so extensive and the derivative populations so successful, that large areas -- sometimes whole mountain sides -- are clothed with brushy oaks of this origin. Extremely variable, but generally intermediate in character -- and often with a few individuals of one or both parental species present -- such populations are one element of the *Quercus undulata* complex, a widespread hybrid complex in the Southwest. Interestingly enough, in other parts of New Mexico one may find *Q. gambelii* and *Q. grisea* growing together with only an occasional F_1 hybrid, or none at all. This is the case in the Black Range in western New Mexico and on the lower western slopes of the Sandia Mountains immediately east of Albuquerque.



Leaves of hybrid (middle row), *Quercus lobata* (top row), and *Quercus cornelius-mulleri* (bottom row).

Cases of this sort point up an important principle that botanists have learned in recent decades, in focusing attention on *isolating mechanisms* between species. In many plant groups evolutionary divergence between species has resulted from the development of *internal* isolating mechanisms, such as chromosomal changes (e.g., translocations, inversions, and deletions). But in groups such as the oaks these internal barriers have not developed, and the different taxa have evolved in *geographical isolations* from one another. If subsequent climate (or other) change brings them together later on, hybridization and considerable gene exchange may result. But this hybridization is clearly a secondary phenomenon. And if such taxa in their typical forms are very different morphologically and floristically, the major objective of phylogenetic classification -- to show evolutionary relationships -- is best served by maintaining them as taxonomic *species*.

Horticultural Importance of Hybrids

Are oak hybrids of any horticultural importance? Yes -- they can be, certainly. Individual hybrids that have desirable traits for ornamental planting, such as vigorous growth, unusually attractive foliage, superior form, and good fall color, would surely be worth propagating. But vegetative propagation would obviously be required, because attempting to propagate a hybrid from its acorns (assuming it was fertile to some degree) would result in diverse, segregating seedlings. And possibly none of them would possess the desirable combination of traits of the parent tree.

Grafting is ordinarily the most feasible method with oaks. Propagation by cutting has been extremely difficult (or virtually impossible) in the experience of most plantsmen. Various attempts have been made to overcome this problem, since propagation from cuttings is ordinarily cheaper and more efficient that grafting. What limited success has been achieved has been accomplished by using cuttings from relatively young individuals one or two years old. The difficulty, of course, is that one can only guess at what the horticultural quality of such plants will be when they reach maturity.[1]

Considering hybrids in particular, one intriguing thought is the possiblity of creating "tailor-made" hybrids for use in special habitats or geographic in which oaks are rarely found at present. For decades plant breeders have developed new varieties of crop plants or garden ornamentals by hybridization and selection. Why not oaks, as well? For instance, consider the fact that in communities along the west side of the San Joaquin Valley, from Coalinga southward, one rarely sees oaks used in parks or as street trees. The limiting factor, of course, is the extremely dry climate. Indeed, in the native flora of the adjacent hills a number of Mohavean species extend into this semi-desert region.

What kind of oak hybrids could be grown successfully in such an inhospitable region? An artificial (i.e., "tailor-made") hybrid designed for landscape use here could combine the drought-tolerance of a species of the arid Southwest such as *Q. oblongifolia* or *Q. grisea* with some other species having outstanding horitcultural qualities such as *Q. gambelii, Q. macrocarpa*, or *Q. muhlenbergii*. Sound far fetched? Granted, this may be futuristic thinking, but consider the following: a vigorous program of experimental oak hybridization was carried on during the 1960s by the late Walter P. Cottam, and Rudy Drobnick at the University of Utah. One of the most remarkable of Cottam's achievements was his successful crossing of a black oak (the blackjack oak, *Q. marilandica*) with a white oak (*Q. turbinella*).

Most of the hybrids Cottam and Drobnick produced are still growing at the University of Utah and in the University Arboretum at U.C., Davis.

Several progenies from Cottam's hybrids are being grown at six widely separated localities in the United States, an important step in developing hybrid strains. One can safely assert that Cottam's numerous hybrids -- maintained at the University of Utah and the University of California, Davis -- will serve for years to come as a valuable resource in furthering increased use of oaks in international horticulture.

◊1 *Considerable progress has been made in the development of techniques for the cut ting propagation of oaks sinceDr. Tucker first published this paper in 1990.*

Named and Unnamed, naturally occuring hybrid oaks, with parent species

(from Munz, 1968 and Griffin, et. al. 1987)

Named Hybrids

Hybrid Species	Parents	
1. *Q.* x *morehus*	*Q. kelloggii*	*Q. wislizenii*
2. *Q.* x *chasei*	*Q. kelloggii*	*Q. agrifolia*
3. *Q.* x *ganderi*	*Q. kelloggii*	*Q. agrifolia var. oxyadenia*
4. *Q.* x *eplingii*	*Q. garryana*	*Q. douglasii*
5. *Q.* x *subconvesa*	*Q. garryana*	*Q. durata*
6. *Q.* x *howellii*	*Q. garryana*	*Q. dumosa*
7. *Q.* x *grandidentata*	*Q. engelmannii*	*Q. dumosa*
8. *Q.* x *alvordiana*	*Q. douglasii*	*Q. turbinella*
9. *Q.* x *jolonensis*	*Q. douglasii*	*Q. lobata*
10. *Q.* x *macdonaldi*	*Q. dumosa*	*Q. lobata* (and other white oaks)
11. *Q.* x *munzii*	*Q. lobata*	*Q. turbinella*

Unnamed Hybrids

Hybrid Species	Parents	
Unnamed hybrid 1	*Q. agrifolia*	*Q. wislizenii*
Unnamed hybrid 2	*Q. garryana*	*Q. lobata*
Unnamed hybrid 3	*Q. engelmannii*	*Q. lobata*
Unnamed hybrid 4	*Q. turbinella*	*Q. dumosa*
Unnamed hybrid 5	*Q. durata*	*Q. dumosa*
Unnamed hybrid 6	*Q. douglasii*	*Q. dumosa*
Unnamed hybrid 7	*Q. chrysolepis*	*Q. dunnii*
Unnamed hybrid 8	*Q. chrysolepis*	*Q. tomentella*
Unnamed hybrid 9	*Q. chrysolepis*	*Q. vaccinifolia*
Unnamed hybrid 10	*Q. sadleriana*	*Q. garryana*

J. Griffin, 1990

THE CALIFORNIA OAKS, BY SUBGENERA

WHITE OAKS Subgenus *Quercus*		BLACK OAKS Subgenus *Erythrobalnus*		INTERMEDIATE OAKS Subgenus *Protobalanus*	
◊TREE OAKS◊					
Blue	*Q. douglasii*	Coast Live	*Q. agrifolia*	Canyon	*Q. chrysolepis*
Engelmann	*Q. englemanni*	Black	*Q. kelloggii*	Island	*Q. tomentella*
Garry or Oregon white	*Q. garryana*	Shreve Oak	*Q. parvula* var. *shrevii*		
Valley	*Q. lobata*	Interior live	*Q. wislizenii*		
◊SHRUB OAKS◊					
Muller	*Q. cornelius-mulleri*	Island scrub	*Q. parvula*	Palmer	*Q. palmeri*
				Huckleberry	*Q. vaccinifolia*
Scrub	*Q. dumosa*				
Leather	*Q. durata*				
Brewer	*Q. garryana* var. *breweri*				
Deer	*Q. sadleriana*				
Desert scrub	*Q. turbinella*				