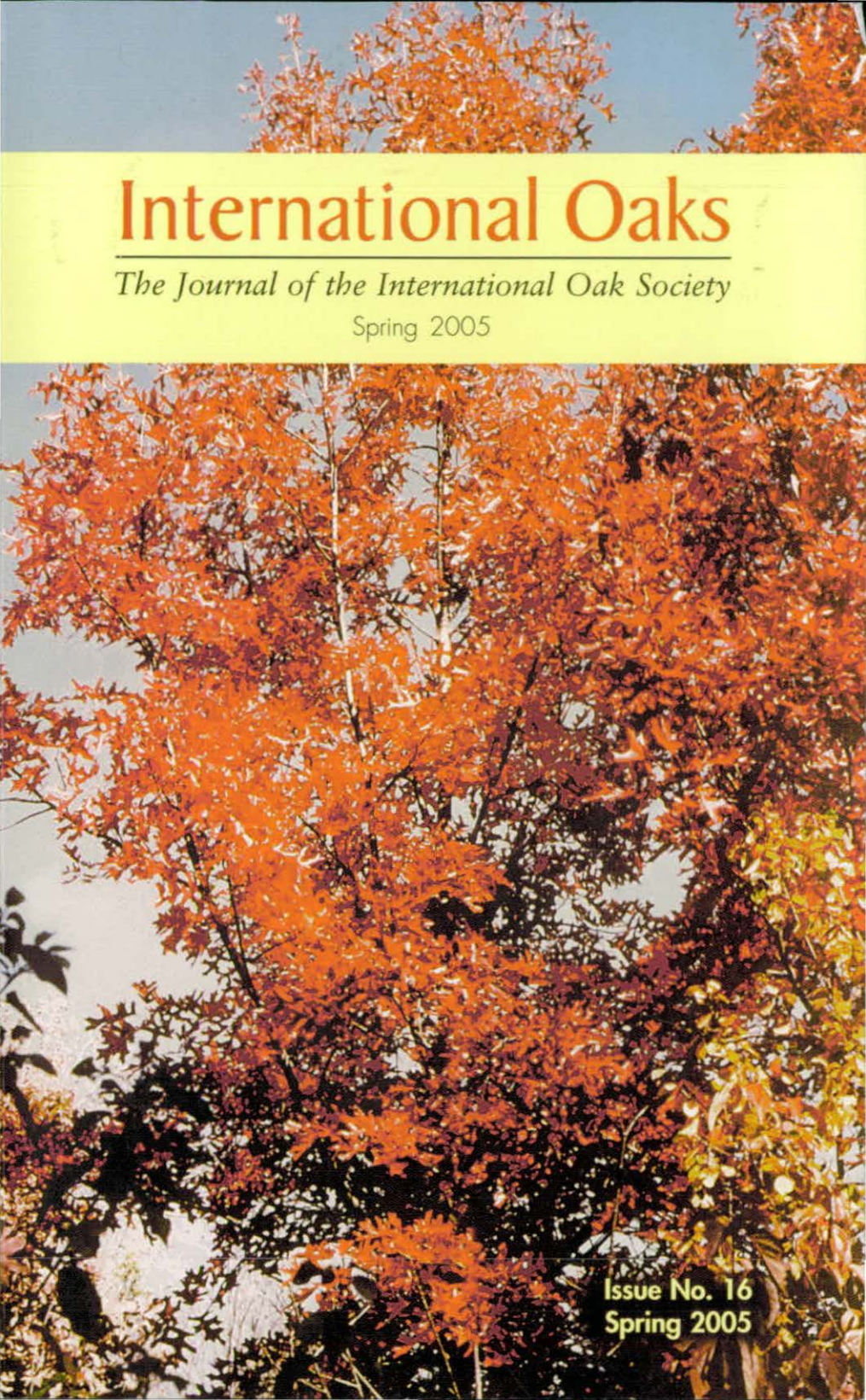

International Oaks

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Anyone interested in joining the International Oak Society or ordering information should contact the membership office. Membership dues are U.S. $25 per year, and benefits include *International Oaks* and *Oak News and Notes* publications, conference discounts, and exchanges of seeds and information among members from approximately 30 nations on six continents.

International Oak Society Website:
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Cover Photos:

Front: Fall color on a large *Quercus coccinea*, Tinley Creek Forest Preserve in northern Illinois. photo © David Shepard

Back: A Tibetan fodder cutter with a large bundle of *Quercus pannosa* cuttings. Photo © Guy Sternberg

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Notes from the President

Dear Members of the International Oak Society,

I am glad to present the current issue of our society's yearbook, "International Oaks," to you. This is already the 16th volume, with a wealth of interesting information about our favorite plant, the oak. Without members writing about oaks or oak-related issues, this publication would not be possible. I would like to express my gratitude to all contributors of this current issue, and hope that you will continue to share your knowledge and your experiences with oaks in future issues of "International Oaks."

This issue contains a lot of diverse information about oaks. You will read about historical oaks in Belgium and Germany; about the sometimes-confusing hybridization within the genus *Quercus*; about oak forests in Illinois and the Himalayas; about the difficulty to determine the age of an oak, and a report about the Oak Open Days in France. Finally, a photo gallery of *Q. macrocarpa* gives us a good idea of the habit of this majestic oak.

I am sure you will enjoy reading. We also owe many thanks to the tremendous work of Ron Lance, Doug McCreary and Guy Sternberg, who did all the work connected with this publication. In fact, "International Oaks" is a continuous link between the Oak Society members worldwide; especially for those who could not afford to join one of the events we had the past year. Two very successful meetings in Europe took place. I was fortunate enough to attend both of them. In England, Joe Earle organized a one-day "Oak Open Day" at one of our member's collections, in the garden of The Lord Michael Heseltine. Some 65 oak enthusiasts gathered together to see a marvellous oak collection. Later in the year, Thierry Lamant called for a four-day tour to visit French gardens and arboreta, and about 35 members attended. Thanks to Joe and Thierry for all their input in organizing these meetings. I know that many of our members do like these meetings as much as I do. It is not only to see the collections and to see new oaks. It is also the feeling of being part of a world community, or, as many members do express, of being part of a family. And, of course, the traditional plant swap or seed exchange always will add more oak treasures to your collection. I hope that many of you will have the opportunity to attend one of our next events. One of them is scheduled for September this year in Southern England. I also like to encourage more members in other regions to find time and energy in organizing a similar event. For sure there are interesting oak stands or collections in your region which will be of interest to other members too.

Also, our next Triennial Conference is approaching, in November 2006, in Texas, U.S.A. Make plans already that you will be able to attend, as for sure it will be another invaluable event. The Oak Society's website will keep you informed about this upcoming International Oak Conference and other meetings.

With the help of all members and their contributions, the International Oak Society supports work on oaks and oak-related subjects. Members of the International Oak Society take part in conferences and workshops, where the latest research about SOD and other oak diseases is told. You will find the latest information about SOD at our web page. Also, the IOS could sponsor Chinese students to attend an Oak Conference. I personally hope that we as a Society become more involved in the conservation and protection of oak forests worldwide.

Writing these lines, I am just thinking of all the acorns I just planted a few days ago. Without the Oak Society and its members, I would never have the chance testing oaks from all around the world in our Luxemburgish climate. I would have never gotten the idea of trying to grow oak species from regions such as Mexico or Southern China! Sometimes it surprises me to find out that certain oak species do grow vigorously here despite the meaning of many books I consulted before planting. This is one more example of a benefit you may have from being a member of the International Oak Society!

Eike Jablonski
President
International Oak Society

Past Hybridization Between *Quercus macrocarpa* and *Quercus gambelii* in Colorado

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all photos courtesy of the author

Summary

Apparent introgression between two allopatric species, *Quercus gambelii* Nutt. and *Quercus macrocarpa* Michx., has been observed in several locations along the foothills of the Rocky Mountains from the city of Denver, Colorado southward to the state of New Mexico. *Q. gambelii* is native to Colorado and other western states. *Q. macrocarpa* is not found in Colorado and native populations of these species are separated 300 km. Since *Q. macrocarpa* and *Q. gambelii* are currently allopatric, it is presumed that hybrids were formed during a period of past sympatric association, and the explanation of long range pollen transport is highly unlikely. *Q. macrocarpa* would have been capable of existing in Colorado during a period when climatic conditions were moister, and would have likely been eliminated during a period of increased aridity. It is quite possible that oaks were able to survive in the southern High Plains and low elevations of the Southwest (New Mexico, Arizona and Mexico) during the pluvial glacial periods of the Pleistocene. There is indication that during the earlier part of the post-glacial warming period (12,000-9,000 yr B.P.) that temperature and moisture were adequate for *Q. macrocarpa* and *Q. gambelii* to migrate north to lower elevations in Colorado. The post-Pleistocene Altithermal Period from about 8,000-5,000 yr B.P. when the climate became warmer and dryer, could have been the time of extirpation of a scattered and dispersed population of *Q. macrocarpa* in Colorado that slowly died off as the dry period intensified. During its terminal period in Colorado hybridization would have occurred. *Q. gambelii* and its hybrid with *Q. macrocapra* (*Quercus* x*mazei* Lueb.) have better tolerance of drought, and would have been able to survive this severe climatic period. In addition, the root suckering clonal nature of *Q. gambelii* and the majority of *Q.* x*mazei* would have enabled them to be much more resilient to fire and bark beetle attack, which often occur during an extended period of drought, than the single-stemmed *Q. macrocarpa*. *Q.* x*mazei* appears to have backcrossed extensively with *Q. gambelii*, and in several areas of Colorado a hybrid swarm of highly variable individuals has resulted.

Q. gambelii appears to have remained a good species and has maintained its general distinctness in the face of this "genetic infiltration." Almost all published descriptions of this species are quite broad (i.e. small shrub to large tree), and very likely include the description of *Q.* x*mazei*. It is suggested by the information presented in this paper that *Q. gambelii* is a colony forming shrub of around 1 m height with several other distinguishing features. It occupies a habitat that includes the top and side of hills and mesas in the foothills zone. Larger oaks in the *Q. gambelii* range in Colorado are very likely *Q.* x*mazei*. They occupy a niche on lower hill-

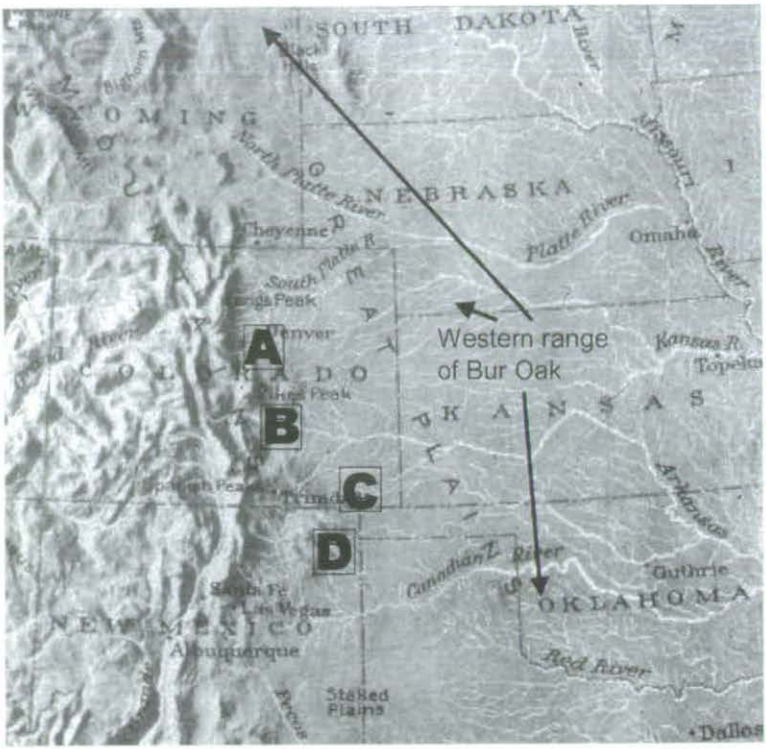

Figure 1 A. Castle Rock study area (CR) B. Green Horn Creek study area (GHC)
C. Cottonwood Creek Canyon D. Tramperos Creek Canyon

sides down to the gulches and streams. At higher elevations the hybrid occurs in *Pinus ponderosa* Dougl. forests.

In addition to putative *Q.* x*mazei* observed in the foothill region, apparent hybrid trees have also been found in southeast Colorado that appear to be good examples of *Q. macrocarpa* entering into the *Quercus* x*undulata* Torr. complex. These southeast Colorado trees likely represent a mix of *Q. macrocarpa*, *Q. gambelii* and *Quercus grisea* Liebm. It is logical to assume that if *Q. macrocarpa* existed in the west during the past that it should also be involved in the *Q.* x*undulata* complex.

Introduction

The following theory is explored in this paper.

- *Q. macrocarpa* once occurred in Colorado during a time of greater climatic moisture.
- Hybridization between *Q. gambelii* and *Q. macrocarpa* occurred during a period of sympatry resulting in a hybrid swarm of *Q.* x*mazei* with intermediate characteristics, which are found today in the foothill and mountain zones of the state.

- *Q. macrocarpa* gradually had its range reduced from increased aridity. It finally was eliminated due to the stress caused from a prolonged drought period, and the possible impact of wildfire and bark beetle attack. *Q. gambelii* and *Q.* x*mazei* with their clonal nature and better drought tolerance were able to survive.
- The recurrent parent *Q. gambelii* has remained a good species and occurs in the foothills zone. To be distinct from the hybrid it has to be smaller, occupy a harsher site, and be different in most other morphological characteristics. *Q.* x*mazei* has backcrossed with *Q. gambelii*, so the majority of hybrids have a closer resemblance to the smaller parent.
- The largest *Q.* x*mazei* are found in groves and not as single specimens. These groups of the largest trees are located in the best habitats, and are the likely spots where the last holdout *Q. macrocarpa* existed. The genetic influence from *Q. macrocarpa* is greatest in these groves.

Q. gambelii and *Q. macrocarpa* are in the same section: *Quercus* section *Quercus* (the white and chestnut oaks). *Q. macrocarpa* occurs along river banks and bottomlands in eastern and central United States and Canada. In the western part of its range it is often found in dry gulches and draws. In the Black Hills it occupies several habitats, including hillsides where it is often associated with *Pinus ponderosa*. *Q. macrocarpa* is a large tree in eastern North America, but becomes a small to medium sized tree in its northwest range. It has very distinct leaf lobing (Figure 5) and prominent long awn-like acorn scales that extend above the top of the cap (Figure 9), which make it quite distinguishable from other oaks. The extreme western range of *Q. macrocarpa* occurs in the Black Hills of northeast Wyoming, southwest Nebraska and western Oklahoma (Figure 1). *Q. macrocarpa* is found in dry areas in the western part of its range, where it receives 39 cm of annual precipitation in North Dakota, and 50 cm in the Black Hills and southwest Nebraska. *Q. gambelii* occurs in Colorado, extreme southern Wyoming, Utah, southern Nevada, Arizona, New Mexico, western Texas and northern Mexico (Sonora, Chihuahua, Coahuila). In Colorado it is abundant and in places covers whole hillsides. In the dryer parts of its range it receives only 30 cm of annual precipitation. *Q. gambelii* has been described as variable in size (Figure 2), being either a shrub 1-2 m high, often forming thick, dense thickets, small trees, or trees to 17 meters high (Powell 1998). Harrington (1964) describes it as being a complex and variable species. Jennings (2001) states that "*Q. gambelii* is actually easy to identify if one ignores leaf shape or whether the specimen is a tree or shrub or an oak scrub". The national champion Gambel Oak is 32 m tall, 175 cm diameter, and is found in Arizona's Coconino National Forest. All of these descriptions are no doubt accurate for the plants observed, but the extreme variation does raise the question if these can all be a single species.

Q. gambelii is the predominant oak species recorded in Colorado. *Q.* x*undulata* is found only in the southern counties near New Mexico. *Q. grisea* with likely introgression is very rare and occurs in the mesa lands of the southeast area of the state. *Quercus turbinella* Greene is found only in a few isolated spots in the southern half of Colorado. Hybrids between these taxa have been recorded (Jennings 2001).

Evidence that *Q. gambelii* has hybridized with various white oaks in the west has been presented by Tucker (1961). Artificially produced hybrids between *Q. macrocarpa* and *Q. gambelii* (*Q.* x*mazei* Leub.) were made at the University of Utah in the 1960's (Cottom, Tucker and Santamour 1982). Tucker (1990) describes past hybridization in Utah between *Q. gambelii* and *Q. turbinella* where the current colder climatic period has eliminated *Q. turbinella* from the area, leaving *Q. gambelii* and the hybrid. Maze (1968) describes putative *Q.* x*mazei* growing along Tramperos Creek in northeast New Mexico (Figure 1). He documents several intermediate characteristics between the parent species, which indicate past introgression with *Q. macrocarpa* has occurred. Maze (1968) also examined *Q. macrocarpa* in the Black hills and observed introgression with *Q. gambelii* was obvious.

Extreme variation in size has been described for *Q. gambelii* (Powell 1998), and is a good indicator that more then one taxon may be involved. Since size is such a variable and distinct characteristic, it was initially used in this study during 2002 in examining *Q. gambelii* in the foothills of the Rocky Mountains from Denver, Colorado south to New Mexico. Different habitat patterns based on size were noted (Figures 3 and 4), and pockets of the largest trees and smallest shrubs were identified for additional study of characteristics. The range of sizes found in this survey varied from a .75 m shrub to an 18 m tall single-stem tree 74 cm diameter (Figure 2). Many of the larger specimens exhibited characters that suggested hybridization with *Q. macrocarpa* (Figures 2, 6 and 8). These larger oaks were found growing in more mesic areas along streams and in gulches (Figures 2 and 3). The smallest 1 m colony-forming shrubs were found in very xeric habitat on the top and side of hills and mesas (Figures 3 and 4). They did not have any characteristics that suggested introgression with *Q. macrocarpa.*

In making a determination if a valid hybrid has occurred, it is first important to understand the range of intraspecific variation that can be found for each of the possible parents (Spurr and Barnes 1989). This information is available in the literature for *Q. macrocarpa*, but there is a serious question about usefulness of information that has been published for *Q. gambelii*. It is possible that most of the literature that describes this species in Colorado and other areas includes the description of more than one taxon. The variation within characteristics is very broad, and extreme variation can occur in plants growing together (Figures 2 and 3).

Intraspecific variation should be expected to occur in *Q. gambelii*, but the range in variation for characteristics that have been described (1 meter shrub-32 meter tree, etc.) can not easily be explained within the species concept. Members of the same species should share many characteristics in common, and should have recognizable, consistent and persistent discontinuities from other species (Hardin, Leopold, and White 2001). Taking just leaf shape, it is easy to observe that there is a lack of common characteristics and recognizable discontinuity between other species (Figures 5, 6 and 7). Considering the number of synonyms for *Q. gambelii*, it apparently was difficult for Rydberg (naming authority for synonyms) to apply the species concept to this diverse group (*Q. utahensis*, *Q. stellata* var. *utahensis*, *Q. gunnisonii*, *Q. alba* var. *gunnisonii*, *Q. nitescens*, *Q. vreelandii*, *Q. leptophylla*, *Q. novomexicana*. *Q. douglasii* var. *novomexicana*, and *Q. submossis*). By default, as the explanation of multiple species was rejected, this grex-like group was consolidated under *Q. gambelii*. Since the current classification does not appear compatible within the species concept, one is led to look for another explanation.

A hybrid population could have variable characteristics similar to those described for *Q. gambelii*. Applying the theory of past hybridization from *Q. macrocarpa* to this problem, one would still be uncertain as to degree of introgression. If a swarm of *Q.* x*mazei* does exist in Colorado, then pure *Q. gambelii* should still be found as a good species distinct from its hybrid (Hardin, Leopold and White 2001). What does true Q. *gambelii* look like? This is a critical question that needs to be answered before the hybrid theory can be fully explored. An accurate description of *Q. gambelii* is necessary to make a valid comparison to the putative hybrid. Logically it could be assumed that the smallest plants growing in the more xeric habitats are the least likely to have any influence from *Q. macrocarpa*, and without reservation be identified as *Q. gambelii* (Figures 2, 3 and 4).

Methodology

For the purpose of having a definitive description of *Q. gambelii*, which the putative hybrid can be compared to, the smallest oaks on xeric habitat (.75-1.5 m clonal shrubs) have been use to describe the species (see Morphological and Habitat Analysis). They represent the extreme form away from *Q. macrocarpa* within the "Gambel Oak" population, and display many characteristics in common with consistent discontinuities from other species. Larger plants that deviate from the typical characteristics of *Q. gambelii* are considered putative *Q.* x*mazei*, and have been compared to the parental species. The use of this binomial (*Q.* x*mazei*) is for convenience in identifying this highly variable group, and is not necessarily meant as a confirmation of the theory of past hybridization. (See Discussion section for interpretation of findings)

To be able to analyze the morphological characteristics of the putative hybrid and its smaller parent, two study areas were selected where evaluations and collections could occur. The criteria used in selecting these areas were an abundance of large hybrid specimens (larger than 5 m), and open access to oaks in all sizes. The two study areas are Castle Rock (CR) and Greenhorn Creek (GHC), and are named for prominent geographic features. They are both located in the foothills of the Rocky Mountains between Denver, Colorado and New Mexico (Figure 1). The CR area represents the northern extension of *Q. gambelii* in the Colorado foothills. The elevation is 1,585 m at GHC and 1859 m at CR.

CR and GHC each receives 36 cm of annual precipitation and have very similar habitats. CR is 160 km north of GHC. They both contain Q. gambelii shrubs and hybrids of varying sizes. These are the only oak taxa present. CR and GHC have growing seasons of around 150 days, are located in USDA hardiness zone 5 and have recorded winter temperatures below -35 degrees C. The study areas are each around 155 square km in size, and include the location of all evaluations and collections.

At GHC and CR the largest hybrids at 5 different locations within each of the study areas were evaluated. In all around 200 trees (5 m height or greater) were studied. Small .75-1.5 m *Q. gambelii* shrubs were evaluated only at the CR site, although they were noted to occur at GHC. There were around 50 of these oak shrubs that were examined. Several putative *Q.* x*mazei* of smaller size (2 m shrubs to 5 m multi-stem trees) were studied at each site. Numerous leaf, acorn and twig collections from representative specimens of all forms and sizes were made in each study area in 2002-2004. Aberrant leaf morphologies were avoided when collecting leaves.

A morphological analysis of characteristics was conducted on all the trees and shrubs evaluated in the study areas, to see if there is a pattern of intermediacy in the putative hybrid. To compensate for subjectivity, large numbers of hybrids of varying size from two geographic locations were studied. Jensen (1995) suggests that the presence of hybrids can be determined with the use of scatter diagrams and multivariate analysis. These methods have not been used in this study, but are recommended for future research on this hybrid problem.

The characteristics of large size, lobing pattern of the leaf, single-stem habit, leaf size and awn-like acorn cap scales found in *Q. macrocarpa* are so distinctly different from *Q. gambelii* that when most of these features are apparent in Colorado specimens they can be used to provide strong evidence of hybridity (Figures 2, 6 and 8). All of these characteristics plus leaf color, twig size and color, and habitat can be useful in distinguishing *Q. gambelii* from *Q.* x*mazei* and have been used in the morphological analysis.

The use of progeny tests is another method that can be used to determine hybrids (Tucker 1990). Seedlings have been grown for two years from acorns collected from trees with apparent *Q. macrocarpa* introgression at GHC and CR. After two growing seasons there are twenty remaining seedlings for each of the study areas (40). Progeny were grown the first year in 3.78 L containers and the second in 7.56 L. A commercial grade potting mix was used.

Horticultural origin *Q.* x*mazei* have been identified growing in Fort Collins, Colorado. There are several hybrid trees that range from 5-18 m tall. The characteristics of these man-made hybrids have been compared to the putative ones of wild origin.

Morphological and Habitat Analysis

The analysis of morphological features can be used to determine hybrids. One should analyze as many characters as possible in which the two parents differ and determine if the suspected hybrid is intermediate on each of the features (Tucker 1990). Leaf morphology can often be a good indicator of hybridity, but may not always provide obvious evidence. Aberrant leaf morphologies alone do not provide evidence of hybridization (Jensen 1995).

The following analysis of putative *Q.* x*mazei* characteristics is made from specimens that have been evaluated at GHC and CR. Comparisons are made to the parental species characteristics. Characteristics for *Q. gambelii* are from clonal shrubs (.75-1.5 m) studied at CR. Those for *Q. macrocarpa* are from Hardin, Leopold and White (2001) and from landscape trees in Fort Collins, Colorado.

Relative degree of leaf lobing (Figures 5, 6 and 7)

Most hybrids display some variation in sinus depth, in which case the upper lobes are shallower than the bottom lobes. Some specimens that have lobing closest to *Q. macrocarpa* display one pair of sinuses deeper than all the others. Many other hybrids have 2 or 3 deep pairs of sinuses of about equal size in the lower portion of the leaf, with those in the upper portion being noticeably shallower. Sinuses on *Q. gambelii* leaves are approximately equal in depth.

Q. macrocarpa has one pair of sinuses deeper than the others, with the upper portion of the leaf shallowly lobed and larger than the deeply lobed lower portion.

Leaf size and shape (Figures 5, 6 and 7)

Leaf blade length

Q. gambelii	5-8.5 cm
Q. x*mazei*	8.5-15 cm (most 9-11.5 cm)
Q. macrocarpa	10-30 cm

Leaf width

Q. gambelii	2.5-4 cm
Q. x*mazei*	4.5-10 cm (most 5-8 cm)
Q. macrocarpa	7.5-15 cm

Leaf shape

Q. gambelii	elliptical to oblong
Q. x*mazei*	oblong to mostly obovate
Q. macrocarpa	distinctly obovate

Leaf color

There is a distinct difference in leaf color between *Q. gambelli* and *Q.* x*mazei*. The leaves of *Q. gambelli* are noticeably a lighter shade of green in comparison to most hybrids, that are darker green. This is quite noticeable as one traverses the habitats from the top of hills where *Q. gambelii* is found, down the hillsides to the gulches where *Q.* x*mazei* becomes dominant (Figure 3). The leaf color difference is noticeable from a panoramic view when masses of plants can be observed at a distance. When the hybrid is found near to the recurrent parent the leaf color difference is often distinct. *Q. macrocapa* has dark green and lustrous leaves on the upper surface.

Q. gambelii, 1 meter shrub

Q. x*mazei*, 5 meter multi-stem tree

Q. x*mazei*, 15 meter single-stem tree

Figure 2. Size and form variation between *Q. gambelii* and *Q. xmazei*.

Size, form and clonal nature (Figures 2 and 3)

The characteristic of mature size is often most notable and variable between the hybrid and its parents. There are numerous examples of *Q.* x*mazei* specimens from 2-4 m height in the study areas. The number of hybrids larger than 4 m decreases dramatically as height increases, and those over 10 meters size are rare. The largest *Q.* x*mazei* found in the study areas has a height of 18 m. There appears to be good correlation between height and the degree of root sucker production (clonal nature). As height increases the clonal nature decreases and the single-stem habit increases. Single-stem trees are found in both study areas, but are rare. They are in most cases the tallest trees. The largest examples of *Q.* x*mazei* are found in groups of several individuals and not as isolated trees. Some smaller plants may be interspersed in these groups, but the majority are large. These groves of large *Q.* x*mazei* gradually transition to smaller size hybrids in surrounding zones. Some of the tallest *Q.* x*mazei* have several clonal stems but they are larger, fewer in number and further apart, compared to smaller specimens. In areas where smaller *Q.* x*mazei* occur, it is common to see a 2-meter plant growing near one that is 4-5 m tall.

There is considerable variation in habit or form of the hybrid. *Q.* x*mazei* can be very upright with vertical stems (Figure 3) or much more horizontal with crooked stems that grow outward forming a round canopy edge. The upright form is found more often in larger hybrids.

Q. macrocapa is a medium-size to large tree with a single-stem habit and upright form that develops a broad crown of stout branches. Its mature height can reach 20-25 m with a maximum over 38 m. Trees within the northwest part of the range are smaller.

Q. *gambelii* is a small colony forming shrub of .75-1.5 m height. The width of a single shrub colony is often 4-7 meters (Figure 2).

Acorns (Figures 8 and 9)

The acorn caps of *Q. macrocarpa* and *Q. gambelii* are very different. *Q. macrocarpa* has awn-like scales that are long at the top of the cap. *Q. gambelii* does not have this feature. Hybrids should display intermediacy for this character. Of the 200 large *Q.* x*mazei* examined only 5 trees clearly display awn-like scales that extend beyond the top of the acorn cap (Figure 8). Examples are found in both of the study areas. There are about 25 other trees with a distinct tendency toward this character. Many of the others show a slight tendency toward awn-like scales, but they are not significantly different from the cap scales of *Q. gambelii*. The majority of *Q.* x*mazei* do not have distinct awn-like scales that extend beyond the top of the cap.

Acorn length

Q. gambelii	10-13 mm
Q. x*mazei*	14-22 mm (most 16-18 mm)
Q. macrocarpa	19-51 mm

Habitat (Figures 3 and 4)

Q. x*mazei* dominates on the lower portion of the hills and extends onto the edge of the valley at the base of hills. It is also found in the bottom of some of the gulches and along streams. At higher elevations in the montane zone it mixes with *Pinus ponderosa* where it is found in forest openings and in the understory. It appears to

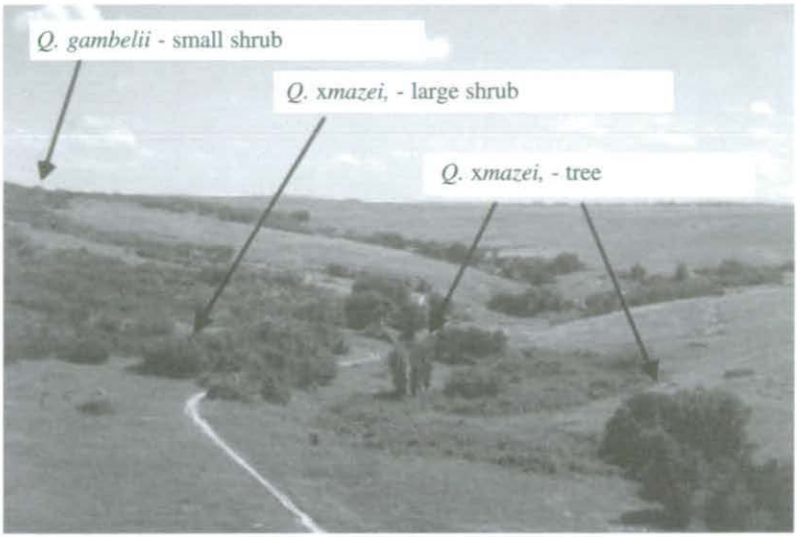

Fig 3. Habitats of *Q. gambelii* and *Q.* **x***mazei*, Size and habit variation for *Q.* **x***mazei*

Fig 4. *Quercus gambelii* habitat

have intermediate tolerance. Often there is an oak-free zone of short grass prairie between the hybrid trees growing in gulches or near streams, and those found near the base of hills. The habitat of *Q.* **x***mazei* is generally the intermediate area between where *Q. gambelii* is found and where *Q. macrocarpa* would have likely occurred when it existed in the area. The larger size hybrids which are toward *Q. macrocarpa* are found in more mesic low areas, and the smaller hybrids are found near *Q. gambelii*.

The habitat of *Q. gambelii* is the top and side of hills and mesas in the foothills zone (Figure 4). It appears to thrive on steep slopes, but is also found in flatter areas. These sites are xeric and often have rocky ridges and cliffs. Where hill tops are wide and flat this shrub species is usually found on the side of the hill where there is greater slope. It is occasionally found at the base of a hill but is not dominant there.

Q. macrocarpa prefers a habitat of river banks and bottoms. In its western range it is found in dry gulches and draws. In the Black Hills it is found on hillsides with *Pinus ponderosa*.

Progeny

Seedlings from GHC and CR have been grown for 2 years with 20 remaining from each area. Around 20% of the seedlings are noticeably taller than the others. The other 80% are smaller and tend to have strong low branches and sprouts at the base. A few plants are shrublike and small. One tree has grown .3 m taller than all others, and is very straight without any major branches. Six parent trees provided acorns for the 40 seedlings. There is a strong resemblance of seedling leaf shape to that of the female parent. Major differences were not observed between seedlings from GHC and CR.

Twig size and color

Twig color

Q. gambelii	reddish-brown; few lenticels
Q. x*mazei*	reddish-brown to yellowish-brown; some to many lenticels
Q. macrocarpa	usually yellowish brown or buff color and rather light; abundant lenticels

Twig diameter

Q. gambelii	2-3 mm
Q. x*mazei*	3-4 mm
Q. macrocarpa	4-7 mm

Comparison to artificial hybrids

Several *Q.* x*mazei* of horticultural origin have been identified in Fort Collins, Colorado. They range from 5-18 m in height and are found in city parks and parkways. Native *Q.* x*mazei* have been compared to these artificial hybrids. Generally the horticultural hybrids are larger in all comparative characteristics. None are producing any root suckers. They have a light colored bark that is white-tan to silver-tan, which is very similar to the wild *Q.* x*mazei*. The bark color of *Q. macrocarpa* is noticeably darker than that of the hybrids. The awn-like acorn scales are more developed on the artificial hybrids than the natives, but are shorter than most *Q. macrocarpa*. Some have only rudimentary awn-like scales. The horticultural hybrids have larger acorns than the natives, but generally smaller than most *Q. macrocarpa*. Their acorns ripen in early September, before those of *Q. macrocarpa*. The native hybrids ripen from August 20 to September 10. For all these characteristics, the horticultural hybrids show intermediacy closer to *Q. macrocarpa*, compared to most of wild origin.

Apparently the hybrid trees in Fort Collins were grown from acorns selected from superior tree forms of *Q.* x*mazei*. There are several *Q.* x*mazei* in Fort Collins thriving on un-irrigated sites that have an excellent shape and form. Many are producing acorns. Progeny from these trees are fairly consistent to the female parent. They have potential to be used as a seed source for the production of superior medium-size shade trees that are highly adapted to the arid-alkaline High Plains and Rocky Mountain west.

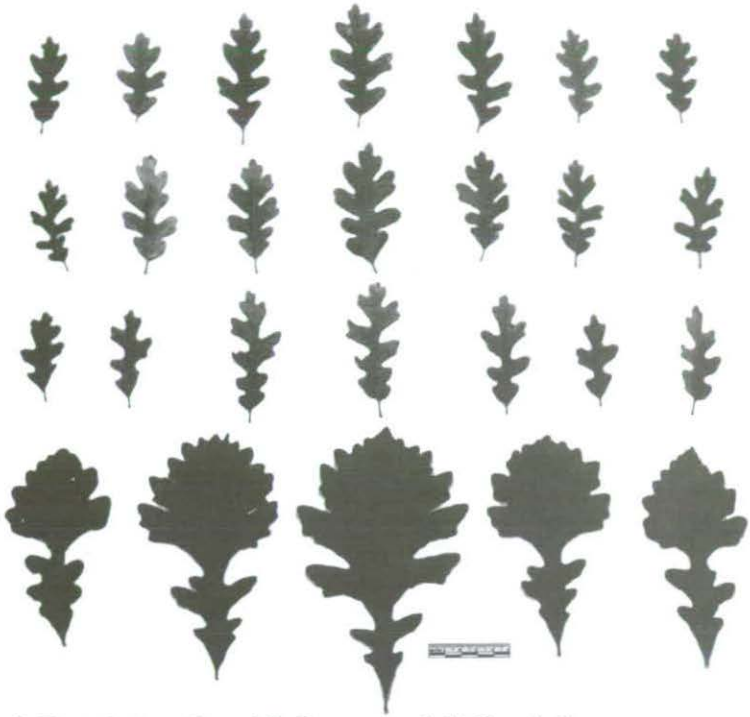

Fig 5. Top to bottom: Rows 1-3, *Quercus gambelii*, Row 4, *Quercus macrocarpa* SW Nebraska

Discussion

Morphology and habitat

The morphological analysis of characters (leaves, acorns, size and clonal nature) conducted in this study on putative *Q.* x*mazei* shows a consistent pattern of intermediacy when compared to its parents (Figures 2, 6 and 8). These results support the theory of past hybridization between *Q. gambelii* and *Q. macrocarpa* in Colorado. The degree of diversity that occurs, and the large amount of area that intermediates cover, suggest a hybrid swarm. *Q.* x*mazei* ranges in size from a colony forming shrub to a large single-stem tree. Most specimens are 2-5 m in height and clonal. The full range of intermediate characteristics are found throughout the population. The majority of *Q.* x*mazei* are toward *Q. gambelii*, which is expected from repeated backcrosses.

The groves of the largest *Q.* x*mazei* are found on good sites that are the likely locations of the last holdout *Q. macrocarpa* before it was extirpated in the area (Figures 2 and 3). Cottam (1959) suggests that normal interspecific hybridization in oaks occurs only when interspecific pollination greatly exceeds intraspecific pollination. When stands of *Q. macrocarpa* had been reduced to only a few remaining trees, they would have been showered with pollen from *Q. gambelii* resulting in F1 hybrids. It is likely that F1 hybrids were formed over an extended period of time

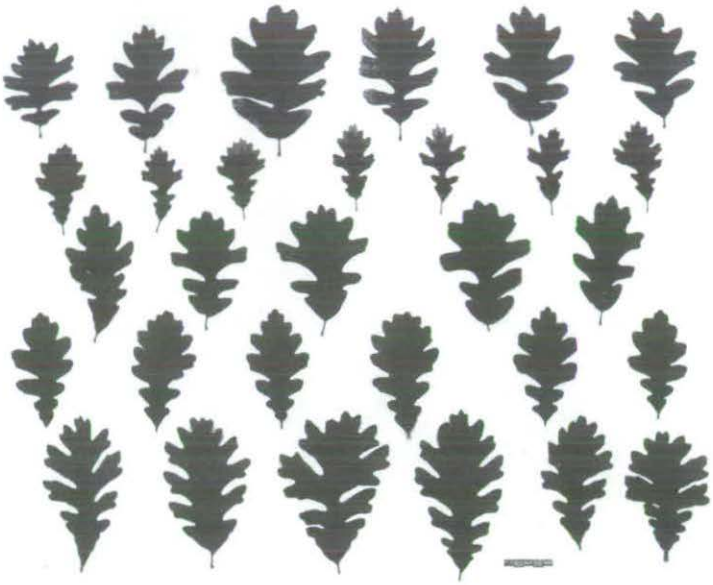

Fig 6. *Q.* x*mazei* with strong *Q. macrocarpa* introgression.

as *Q. macrocarpa* gradually died out in different locations. This would help to explain the abundance and extent of *Q.* x*mazei* found today. A few of the largest hybrids appear closer to *Q. macrocarpa* than to *Q. gambelii*, which indicates there was a period where *Q.* x*mazei* backcrossed with its larger parent before it was eliminated. After it died out, hybrids with the strongest *Q. macrocarpa* introgression would have received the most pollen from similar trees nearby. Those that survived incorporated enough *Q. gambelii* genes to resist the ravages of the drought period. Today these groves display the highest level of *Q. macrocarpa* introgression and mark the location where it last remained. The strength of introgression in some trees suggests that a few *Q. macrocarpa* may have persisted in isolated locations until more recent times.

Q. x*mazei* occupies a range of habitats between its parents. The degree of intermediacy found in the hybrid is generally related to which parental habitat it is found closest to. If *Q. macrocarpa* was the initial F1 female parent during its terminal period in Colorado, then it would be expected that the concentration of its genes would dissipate, away from its prime habitat. As sites become harsher there is selective pressure against hybrids closest to *Q. macrocarpa*, which would also affect habitat pattern. F1 hybrids formed with *Q. gambelii* as the female parent would not likely have survived on xeric sites. It appears that most of the original F1 population occurred with *Q. macrocarpa* as the female parent. Gradually, successive hybrid generations moved further away from the original habitat, and had diminishing levels of *Q. macrocarpa* introgression as they crossed with each other and *Q. gambelii*. Selective pressure occurred as hybrids encountered more xeric habitat, favoring those that were closest to *Q. gambelii*. With its different habitat adaptability *Q.* x*mazei* expanded into areas that did not have *Q. gambelii*, resulting in closed

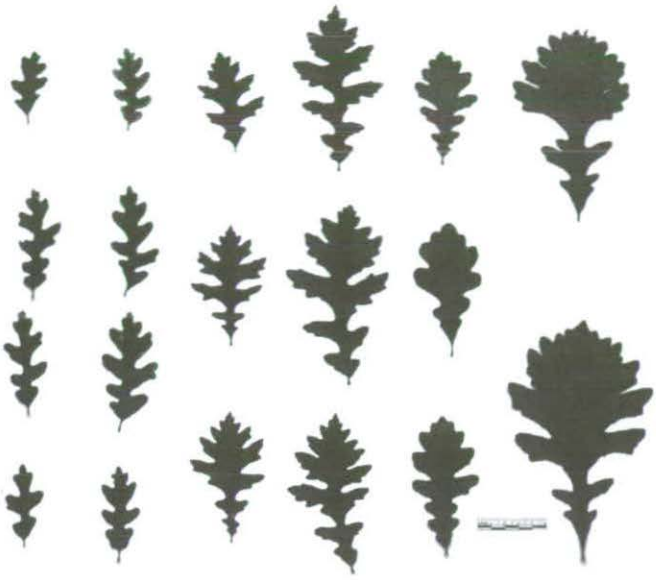

Fig 7. Left to Right: Row 1 and 2, *Q. gambelii*, Rows 3-5 *Q.* x*mazei*, Row 5, *Q. macrocarpa* SW Nebraska

hybrid populations. The diverse hybrid swarm that has resulted is adapted to a much larger range of habitats than either of its parents, which has allowed it to occupy a large area.

When examining *Q. gambelii* and *Q.* x*mazei* growing together it can be difficult to determine degree of previous hybrid origin in individuals. Large specimens usually have several intermediate characteristics and can be easily identified as *Q.* x*mazei*, but small specimens are problematic. *Q. gambelii* has been identified as a small .75-1.5 m colony- forming shrub. The smallest plants on the more xeric habitats, which also display the other characteristics recorded for this species (see Morphological and Habitat Analysis), will likely be *Q. gambelii*. Specimens of *Q.* x*mazei* will be larger, display other intermediate characteristics and be on less xeric habitat. Mature height is usually the first characteristic that is noticeably different in hybrids. Populations that display significant size variation likely include *Q.* x*mazei*. Leaf size, lobing pattern, and leaf color are other characteristics that can easily be used to help identify the hybrid. *Q. gambelii* may not always be found in association with *Q.* x*mazei*. There are cases of dispersed introgression where the genetic influence of one species is detected far from the site of original hybridization (Hardin, Leopold and White 2001).

Q. gambelii may display a greater size range than .75-1.5 m, as described in this paper. Some size variation should be expected to occur throughout its range. Although, it would seem unlikely that average size would vary more than 2 xs between the largest and smallest populations. An extreme form might occasionally be 3 xs larger. Since the dominant pattern of genetically based variation is more or less continuous, it would be expected that mature height difference would change slowly over distance, and not much within a region.

Only *Q. macrocarpa* has the constellation of characters different from *Q. gambelii* that are found in the hybrid. Geographically *Q. macrocarpa* is the closest occurring representative in the section *Quercus* that could have imparted the size characteristic found in the larger specimens. It is capable of growing and reproducing in areas that receive as little as 39-50 cm annual precipitation. The GHC and CR study areas receive 36 centimeters annual precipitation. A climatic period that was moister by 3-15 cm per year could have sustained *Q. macrocarpa* in Colorado. *Q. macrocapa* found as outliers in western Kansas and Nebraska, 300 kilometers east of the range of *Q. gambelii*, likely represent some western migration since the Altithermal or Middle Holocene dry period, when *Q. gambelii* and *Q. macrocarpa* became allopatric (Figure 1).

Q. macrocarpa has prominent, long, awn-like acorn scales that extend above the top of the cap. *Q. gambelii* does not have this characteristic. Only five specimens were found in the study areas that clearly display awn-like scales that extend beyond the top of the cap (Figures 8 and 9). There were several others that show some tendency toward this character. The majority of *Q.* x*mazei* in Colorado do not have cap scales distinctly different than *Q. gambelii*, although cap size is larger. Finding only a few trees that produce a fringed acorn cap is significant evidence of *Q. macrocarpa* introgression. The only other explanation for its occurrence is abnormal or mutational variation. Since five specimens were found with this feature distinctly expressed in intermediate form, and several others had a tendency toward it, the explanation of mutational variation is unlikely. It is surprising that more *Q.* x*mazei* do not display this characteristic. Perhaps repeated back crossing with Q. *gambelii*, or that multiple genes are involved, could be plausible explanations. In the Black Hills population of *Q. macrocarpa* (420 km northeast from stands of *Q. gambelii*) are occasional individuals that don't display the fringed acorn cap characteristic.

It is documented that many species of oaks show significant size variation from the top of hills to the valleys below. Could the range of sizes and variation in other characteristics observed for *Q.* x*mazei* be the result of phenotypic variation (i.e. environmentally induced variation)? Does *Q. gambelii* have a highly plastic general purpose genotype? The range and pattern of characteristics observed, even when size is not considered, suggests introgression. Size and clonal nature can be highly variable in plants growing side by side. A 3- to 4- fold difference in height is not uncommon in putative hybrids growing near each other. Size variation in the

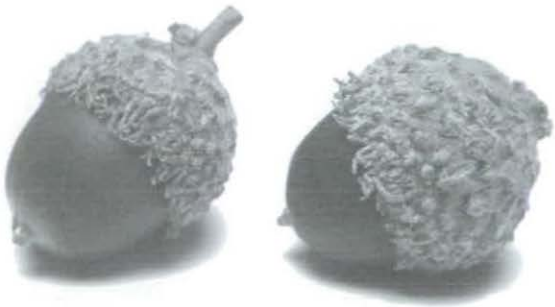

Fig 8. *Q.* x*mazei* with long awn-like acorn scales at the top of the cap.

Fig 9. Left to right: 1, *Q. macrocarpa* NE Wyoming; 2, *Q. gambelii* Castle Rock; 3, *Q. macrocarpa*; 4, *Q. macrocarpa* x *Q.* x*undulata* Cottonwood Creek Canyon; 5, *Q.* x*mazei* Castle Rock

study areas ranged from .75 m to 18 m. This represents a 24-fold difference in height. Many of the *Q. gambelii* examined had vigorous shoots. Vigor did not appear to change mature height or leaf morphology from what has been described for this species. The region is semiarid, so even the better sites are still fairly droughty. These observations suggest introgression and not phenotypic variation. Long term progeny tests conducted on *Q. gambelii* and *Q. xmazei* could be used to evaluate the range of phenotypic variation and is recommended for future study.

North versus south range differences in *Q. gambelii*

The range of characteristics and habitat patterns observed in the two study areas (CR and GHC) are generally similar to what is found throughout the northern range of *Q. gambelii* in Colorado, Utah and northern New Mexico. In the southern part of the described range of *Q. gambelii*, which includes southern New Mexico and adjacent areas, many of the specimens are larger single-stem trees that resemble *Q. macrocarpa*. The national champion "Gambel Oak" is 32 m tall and 175 cm diameter, and is found in Arizona. This is very different to what is seen in the north where plants are smaller and mostly clonal in nature. The information presented in this paper is generally considered applicable to the range areas in the north. The large trees in the southern range that have been identified as *Q. gambelii* should be studied as a separate problem. The following two hypotheses are presented as possible explanations, but will need to be investigated through research. (See time of sympatry in Discussion section)

Hypotheses

There could be separate shrub and tree species with a close phylogenetic relationship within the current classification of *Q. gambelii* (e.g. *Q. muehlenbergii* and *Q. prinoides*).

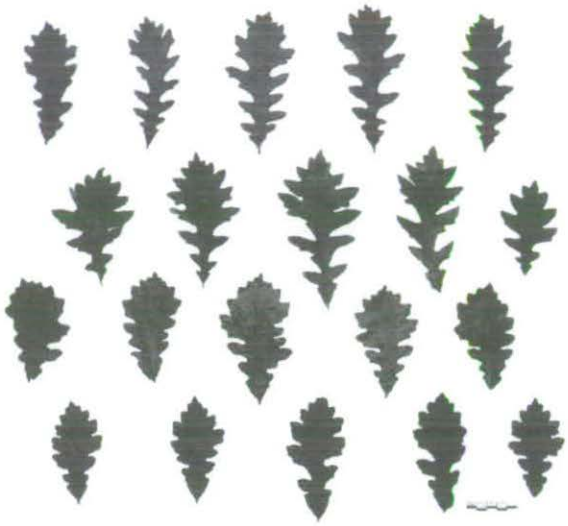

Fig 10. *Q. macrocarpa* x *Q.* x*undulata;* 2 year old half-siblings from Cottonwood Creek Canyon

In southern New Mexico and adjacent areas the large trees that have been classified as *Q. gambelii* could actually be an isolated population of *Q. macrocarpa* with introgression displaying the early stage of genecological differentiation where this divergent population is only slightly distinct form the parental form. *Q. macrocarpa* could have migrated westward to the southern High Plains and low elevations of the Southwest during pluvial periods of the Pleistocene. During the post-glacial warming period it was able to migrate to higher elevations that were cooler and moister, which allowed it to survive the dramatic climate change. Selective pressure from the new environment would have reduced its range, encouraged genecological differentiation and the survival of introgressants.

Q. macrocarpa* x *Q.* x*undulata (Figures1, 9 and 10)

Apparent hybrid trees have also been found in southeast Colorado, which appear to be a good example of *Q. macrocarpa* entering into the *Q.* x*undulata* complex. If *Q. macrocarpa* existed in the west during the past it is logical to assume that it is also involved in this hybrid complex. There is a grove of around 60 medium-size trees in Cottonwood Creek Canyon that display distinct *Q. macrocarpa* and *Q.* x*undulata* characteristics. The influences of these taxa are apparent in leaf morphology (Figure 10). The hybrid trees are located by a perennial creek and natural spring. The grove has some specimens that display a remarkable resemblance to *Q. macrocarpa*. Cottonwood Creek Canyon is located 150 km southeast of GHC and 105 km north of Tramperos Creek Canyon in New Mexico where Maze (1968) first described apparent *Q.* x*mazei* (Figure 1).

Other oaks found in Cottonwood Creek Canyon include the typical shrub form

of *Q.* x*undulata*, *Q.* x*mazei* and a few *Q. grisea* with likely introgression. Hybridization with *Q. macrocarpa* is obvious in some of the larger oaks in the Canyon, and is presented here to further support the theory of its past existence in the west. The strength of introgression in some trees suggests *Q. macrocarpa* may have remained in this area until more recent times.

Period of sympatry in Colorado

The climate during the last glacial period was much colder, and it is unlikely that either *Q. macrocarpa* or *Q. gambelii* could have survived in Colorado. The time of sympatry between these species must have been when the temperature had become warmer and there was more moisture available than today. There is evidence that the glacial periods were correlated with increased moisture in the Great Plains and Southwest, and that the biotas of these areas were modified. Maze (1968) suggests *Q. macrocarpa* migrated westward during pluvial periods associated with the glaciers. It is quite possible that oaks were able to survive in the southern High Plains and low elevations of the Southwest (New Mexico, Arizona and Mexico) during the last glacial period. Oak pollen is reported from the High Plains of southwest Kansas and northwestern Oklahoma were oaks do not occur today (Kapp 1965). At the end of the Pleistocene (16,500-10,000 yr B.P.) the Southwest was much wetter and cooler than today (Thompson and Anderson 2004). The Laurentide Ice Sheet began to retreat at 18,000 yr B.P. The climate began to warm around 16,500 yr B.P. and by 12,500 to 8,000 yr B.P. major climate amelioration had occurred (Barnes, Zak, Denton and Spurr 1998). During this period of dramatic global warming, but before the drying of the Altithermal (8,000-5,000 yr B.P.), there was adequate temperature and moisture for *Q. macrocarpa* to have migrated from the southern High Plains and Southwest northward to lower elevations in Colorado. Hardwoods extended further west into the Great Plains at 10,000 yr B.P., indicating a wetter period. The migration of *Q. macrocarpa* into Colorado could have coincided with Oaks migrating north through the Midwest and reaching Canada by 10,000 yr B.P. (Barnes, Zak, Denton and Spurr 1998). The post-glacial warming period is also the likely time that *Q. gambelii* migrated northward into Colorado. Sympatry between these species could have first occurred in the Southwest and then later in the north, as both species migrated. The period of sympatry in Colorado likely began during 12,000 to 9,000 yr B.P.

Extirpation of *Q. macrocapa* in Colorado

Q. macrocarpa would likely have been eliminated during a period of increased aridity. The climate began to dry during the first half of the Holocene and between 6,500-5,000 yr B.P. the maximum in dryness in the last 12,000 years occurred (Barnes, Zak, Denton and Spurr 1998). The environmental period between 8,000-5,000 yr B.P. is often known as the Altithermal or Middle Holocene. Studies indicate an environment characterized by low moisture, hot temperatures, and overall instability. The analysis of organic remains reveals a climate in which the majority of rainfall occurs during the summer season, a shift from the earlier Pleistocene pattern of high winter precipitation. The effect of these changes on flora in the High Plains and western regions were quite dramatic. Woodlands retreated to higher and higher elevations, while desert scrub and grassland habitats expanded to the east

and to the north (Kantner 2004). Potato Lake on the Mogollon rim in Arizona almost dried up at 5,000 yr B.P. (Anderson 1993). Archaeological remains indicate from 6,800-5,300 yr B.P. early inhabitants of the Colorado Plateau made radical changes in settlement and subsistence patterns in response to a dry period (Kantner 2001). At 5,000 yr B.P. prairies in the Midwest had advanced eastward into areas that had been forested. In its western-most range, *Q. macrocarpa* is found in dry areas that receive 39-50 centimeters of annual precipitation. A prolonged and severe drought would have been required for its elimination. By 6,500-5,000 yr B.P. *Q. macrocarpa* would have been subjected to a much dryer climate in Colorado than when it first migrated into the area 3-6 thousand years earlier. The more drought tolerant *Q. gambelii* and *Q.* x*mazei* would have been able to survive under such conditions. Even if their stems were killed to the ground they could regenerate by their clonal nature.

Drought periods in the west are known for increased occurrence of fire. Drought also predisposes trees to bark beetle attack. Both of these phenomena could have further contributed to the die-off of *Q. macrocarpa*, while the clonal *Q. gambelii* and *Q.* x*mazei* would have been able to recover. During the last 4 years of drought in Colorado (2000-2004) there has surfaced new evidence related to the Gambel Oak Borer (*Agrilus quercicola*) that indicate it could have played a role in the extirpation of *Q. macrocarpa* in Colorado. This insect is a member of Buprestidea (flatheaded borers) and feeds under the bark, girdling stems of all sizes.

Agrilus quercicola was considered a secondary insect problem in Colorado where it was occasionally found in weak or declining native oaks. During the recent drought period it has become much more abundant, and is the cause of major die-down of stressed *Q. gambelii* and *Q.* x*mazei* in the state. It has benefited from the increased number of stressed oaks, and the warmer temperatures that provide for multiple generations per year. Many oak colonies have several of the larger stems killed. Most of these damaged oaks will recover by producing and releasing root suckers. The insect has also become much more aggressive then previously documented, and has moved into the cities of Denver and Colorado Springs where it is killing planted *Q. macrocarpa*. A nursery in a high impact area lost all of their Bur Oak. During the period when *Q. macrocapa* existed in Colorado a similar epidemic could have contributed to its extirpation. In its terminal period *Q. macrocarpa* would have likely been scattered and dispersed as lone trees and small groves, which would have been vulnerable to an insect epidemic or regional wild fire. Not having the ability to coppice, the species would have been eliminated from the area as the last trees succumbed to the ravages of the drought period. The extirpation of *Q. macrocarpa* in Colorado likely occurred from the stress of a prolonged drought, an *Agrilus quercicola* epidemic, and increased incidence of fire.

Conclusion

The information presented supports the theory of past hybridization between *Q. gambelii* and *Q. macrocarpa* in Colorado. It is hoped that this paper will lay a foundation that will begin to bring scientific order to this taxonomic problem. Further study should occur on *Q. macrocapa* in the Black Hills and the large "*Quercus gambelii*" trees in southern New Mexico and adjacent areas. Morphological analysis should be conducted in other regions within the range of *Q. gambelii*. Ultimately a rework of the taxonomy of *Q. gambelii* appears needed.

Apparent hybrids between *Q. macrocarpa* and *Q.* x*undulata* have been observed in southeast Colorado. A review of the theory that supports the *Q.* x*undulata* complex is suggested, for possible inclusion of a new taxon.

There is a large potential benefit to horticulture from Colorado Foothills Oak (*Q.* x*mazei).* It appears to be one of the most adapted shade trees to the High Plains and Rocky Mountain regions. Through progeny tests, seed trees can be identified that produce the least variation. A protocol should be developed for selecting superior quality seedlings during the first two years. This will insure that seedlings sent to production will result in a high percentage of quality shade trees. In the water-poor areas of the United States, where restrictions are likely to increase, Colorado Foothills Oak could become an important part of the urban forest. With its medium size, desirable form, and low water requirements, it is a shade tree that can work effectively in most western landscapes.

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Acknowledgements

Don Bowman of PuebloWest, Colorado allowed me access to his property on Greenhorn Creek to study and make collections of *Q.* x*mazei*. The largest tree found in the study areas is on his land. Having a trained eye for nature from his own extensive entomological collections, he had concluded his trees must be hybrids prior to our acquaintance. I am glad that I can provide the information in this paper to assist in our understanding of the origin of the oaks on Greenhorn Creek.

Gratitude needs to be extended to Ellen Buchanan for her understanding and encouragement.

Oak Open Days - France 24-26 September 2004

Béatrice Chassé
Arboretum des Pouyouleix
St. Jory de Chalais, France

A documentary-producer friend of mine, after listening to my verbal account of this my first oak journey (Oak Open Days, France 24-26 September), said, "This is incredible... who would have thought... we'll have to film this one day." So, if his second-hand, completely vicarious experience of this is that exciting, you can well imagine what it was like for me to be there.

Was it that this mixture of "professionals" and "amateurs" projected us back to a time when science, botany in particular, flourished in large part due to the close collaboration of those two groups? Was it the stimulus provided by the feeling that never in a million years could one know oaks as well as certain of those present? Or just the sight of so many incredible, botanical marvels? the passionate discussions? The freedom and satisfaction of being able to ask all your questions... and always get good answers?

An oak by any other name

Stéphane Brame, Allen Coombes, Eike Jablonski and Thierry Lamant huddled in consultation, agreeing or disagreeing with the name on the label or proposing a name in the absence of the latter, is perhaps not just an epiphenomenon of taxonomic deficiencies or systematic incoherencies. It seemed rather the perfect illustration of what it means to be an oak tree. If all classification systems are a synthetic view of man's understanding of life, maybe the genus *Quercus* is trying to tell us something!

The author, Beatrice Chassè, measuring the height of a tree

photo © Eike Jablonski

The tour organizer, Thierry Lamant photo © Eike Jablonski

Antoine le Hardy de Beaulieu pointed out to me, and he certainly has seen a great number of individuals of a great number of species of oak, that even when an oak tree does very well outside of its natural zone, differences in leaf, habit, etc… are almost always expressed.

Perhaps then, the most important thing I have come away with after these Oak Open Days, is a greater appreciation of the incredible plasticity of these trees and an even firmer conviction that while genetics can deepen our understanding of many things, many of its deterministic paradigms hinder rather than help.

Le Jardin des Plantes

Louis XVI said, walking up the flight of stairs that were to be his last, "A-t-on des nouvelles de Lapérouse?" ("Do we have any news from Lapérouse?"). Famous last words that mark the importance French monarchs accorded to voyages of discovery and exploration of the world. Though their motives were certainly not of the order of natural history, the impact on botany is nevertheless spectacular: today *le*

Jardin des Plantes manages an eight million specimen rich herbarium plus several thousand living plants.

When you plant an oak tree that you know will not be extraordinary - like only oak trees can be extraordinary - until, say, 100 or 150 years have gone by, there is always something astounding about looking at an oak that was planted... 100 or 150 years ago. It buys you a little piece of eternity. Suddenly, a plant opens the door to an otherwise humanly incomprehensible lapse of time.

And so, *le Jardin des Plantes* is awesome if only for this reason: *Quercus haas*, 1855, the first of its kind to be planted in France; *Quercus infectoria*, 1850, the oldest specimen in France today; *Quercus ithaburensis* subsp. *macrolepis*, 1814; *Quercus macrocarpa*, 1811, that we did not see for lack of time - so you all must go back to *le Jardin des Plantes*!

On one of the corners of *l'Allée Alfred Lacroix* (I think) can be found an interesting specimen of *Quercus myrsinaefolia*. As I have only ever seen it growing as a tree, here at last was a *Quercus myrsinaefolia* that looked like a *Myrsine* shrub border.

Before leaving *le Jardin des Plantes*, Michel Avishai, generously distributed the acorns he had come with: *Quercus ithaburensis*, *Quercus alnifolia*, *Quercus look* and *Quercus libani*. These are the first acorns that I will attempt to grow. Sincerest thanks to you, Michael Avishai. Other acorns that were distributed during our voyage were *Q. copayensis, Q. costa-ricansis, Q. seemanii* and *Q. insignis*, from Christian Spinelli (Costa Rica) and *Q. salicina, Q. serrata and Q. acuta* from Shaun Haddock (France).

French "Farewell" at Arboretum LeCoulèes, with owner Michael Angeard serving the wine

photo © Eike Jablonski

Q. afares in the Arboretum National Des Barres. This specimen was introduced from Algeria in 1880. photo © Eike Jablonski

Les Coulées

Leaving *le Jardin des Plantes*, our next stop was 250 km to the southwest, near the city of Angers at the Arboretum, *Les Coulées*. Our host, Michel Angeard, an immediately likeable individual, with a sort of mad-scientist look about him, began planting here about 30 years ago.

As a scientist, Michel Angeard began by taking core samples across his 40 acres to have a good overview of the different soil conditions present. To a certain extent, he organised which plants would go where based on this information. But, as an artist (painter and sculptor), the planting was also based on pure aesthetic inspiration and the desire to create a pleasant garden with nice surprises around every corner.

His first passion with botany was with the genus *Rosa*. He planted over 450 species/varieties of roses - that today have graciously receded their dominion as the trees he had planted grew. Their presence is still largely felt with numerous species that have clung on to life while often clinging to the trees, rising five, six or more metres from the ground and flowering abundantly. Among the many other notable species: *Rosa palustris* (a rose with no thorns), *Rosa sericea omeinsis* f. *pteracantha* (with beautiful translucent red thorns), *R. pimpinellifolia* (with dark purple, black hips).

There are many, many different kinds of trees at *Les Coulées*: oaks, maples, willows, ashes, alders, horse chestnut, and more, not to mention the coniferous species. But there are 200 oak trees, the majority of which are American along with numerous cultivars, mostly European. Michel admits to having a weakness for the American oaks because of their wonderful colour transformations. He has no par-

ticular personal explanation for his passion for oak trees. He attributes it to the mythology of the oak tree: majestic and charged with history, as well as to the fact that it is a dominant element of the natural environment that he has grown up with.

There are so many oak trees to see at *Les Coulées* that I am somewhat at a loss to point out one or another from anything other than a purely anecdotal point of being mislabelled; *Q. graciliformis*, *Q. rysophylla* and *Q. macranthera*, because I had never seen any of them; *Q. lobata*, in quite good health, although many say that this tree is usually unhappy in this part of the world; *Q. pagoda* with bright reddish-pink leaves, because mine were still green; *Q. macranthera* 'Fastigiata', because I didn't even know that it existed!

In style, Michel and his wife Simone bid us farewell with numerous bottles of a regional wine called *chaumes* and wonderful *hors-d'œuvres* hot out of the oven. Just what we needed to keep us going after a long, too-many-things-seen, too-much-information-to-absorb, day. A quick ride to our hotel near Angers, and as Caroline Brown (from California) said to me, our daily programme of walk, walk, walk, walk, talk, talk, talk, talk, eat, eat, eat, eat, sleep, was entering its final stages.

L'Arboretum Gaston Allard (Angers)

M. Gaston Allard started planting in this arboretum, now run by the city of Angers, about 150 years ago.

Having read, as many of you I am sure, the Proceedings of the Fourth International Oak Conference (Fall 2003, Winchester, England), I was eager to see M. Gaston Allard's famous "trademark" as explained by Thierry Lamant: "...trees planted high, not being fully inserted into the soil, so that the upper part of the root system is exposed." A good lesson to learn: there are 50 ways to make chocolate mousse, and most of them are quite good. So what is the essential ingredient?

Probably the most spectacular thing I saw during this trip was here: an alley of enormous *Q. frainetto* and *Q. palustris* (planted in 1875). Some of these trees are 25 m tall and the effect is astounding. There is also a very large *Quercus suber* (80 cm in diameter) - the sole survivor of this species here after the harsh winter of 1985/86. A very beautiful specimen of *Quercus ilex*, with numerous young *ilex* having germinated underneath, attracted my attention. Various cultivars of this species can also be seen here.

A remarkable 35 m tall *Quercus* x *schochiana* (a natural hybrid between *Q. phellos* and *Q. palustris* was the backdrop to a very interesting conversation with M. Hervé LeBouler that started with different methods of propagating oaks that he has been studying in his experimental nursery for several years and that ended with a general discussion about taxonomy and the evolutionary biology of oaks in particular.

There is a very large specimen of *Torreya taxifolia*, which Thierry explained is an endangered species in its natural environment.

La Forêt Domaniale de Bercé

A two and a half hour bus ride to the north west (with lunch in the middle) brought us to *la Forêt Domaniale de Bercé*, (3000 hectares of oak - *Quercus petraea* - and 2400 hectares of pine) for a guided tour of what is considered to be one of the best run forests in France. The oak trees live to be... 240 years old before they are cut down. Well, of couse, not all of them, but certainly enough of them to create that

unique atmosphere that only comes from a deciduous forest with very, very old, rather tall trees.

The forest is managed on the principle that every year 12.5 hectares must be exploited and regenerated. The old trees provide the seed and are eliminated progressively to leave space for the young trees. It takes about ten years to complete view: a magnificent *Q. rugosa*, which I was very proud to correctly identify without hesitation; a tree labelled, *Q. acerifolia*, which I was very proud to identify as this cycle and so it is estimated that approximately 125 hectares are permanently in the progress of being exploited/regenerated.

Since the winter of 1999/2000 and the great storms that swept across France destroying uncountable hectares (140 million cubic metres of wood) there is great controversy (both political and ecological) over how forests have been and should be managed. There is much criticism regarding today's policy makers' accused of paying little real attention to sound ecological principles while basing decisions primarily on commercial considerations. As often is the case…

Arboretum National des Barres

Considered to be one of the crown jewels of French botanical gardens, this arboretum is located in the village of *Nogent sur Vernisson*, near the city of *Orléans*. One of three arboreta created by the very wealthy and powerful Vilmorin family, the botanical collections at *Les Barres* cover about 40 hectares. The national collection of oak trees is here: 83 botanical species and 18 cultivars and hybrids.

The only specimen outside of China of *Quercus gracilis* can be found here - except that it shouldn't be called *Q. gracilis*, but *Q. liboensis* ! In 1998, Professor Zhou Zhekun, visited *Les Barres* specifically to verify the dubious identity of this tree which, at the time, was labelled, *Quercus oxyodon*. Fruiting only three times between 1995 and 2001, our voyage was definitely blessed: Eike Jablonski found

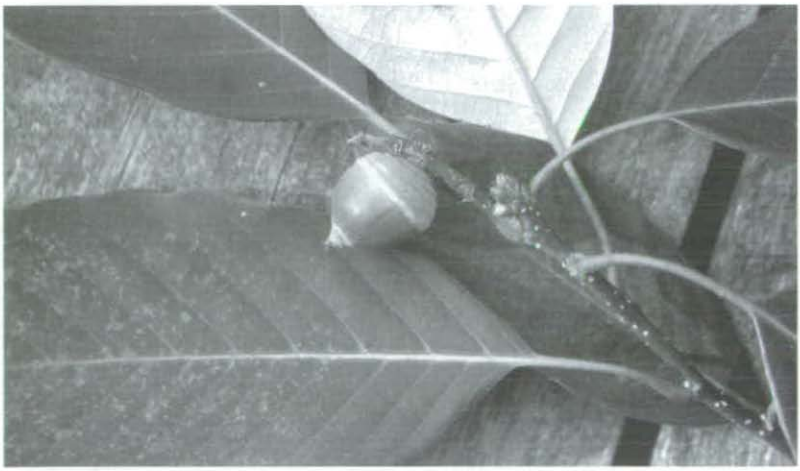

photo © Eike Jablonski

Q. liboensis (or *Q. gracilis*). Raised from seed collected by Father Paul Farges in 1901, this rare Chinese species is found in the wild only in a small reserve in Kweichow, and this is the only cultivated specimen outside China. In one hundred years, only six acorns have been found on this tree!

an acorn! Today, unfortunately, *Quercus oxyodon* is still the name that visitors will read, and the *Quercus gracilis/Quercus liboensis* taxonomical battle is apparently not quite resolved.

Alongside a curious hybrid - with no label - between *Quercus cerris* and *Quercus no-one-was-quite-sure*, Michael Avishal explained that *Quercus afares, castaneifolia* and *cerris* all have a common origin but have differentiated with time and their geographical distribution. We all had the opportunity to admire a beautiful *Quercus afares* planted in 1920 with a trunk measuring, today, 2.50 m in diameter.

Throughout our journey I was quite distressed by many *Quercus nigra* representatives that we saw because the leaves definitely did not resemble the leaves of my *Quercus nigra* specimens. Thierry Lamant tried to reassure me saying that it was only a question of age. Thank goodness here at last was a fairly young one and the leaves were exactly like mine!

There is a remarkable stand of *Quercus ilicifolia* (half an hectare, planted in 1828 on the outskirts of the park). The trees are impressively tall for this species, 6.5 metres for example, much taller than in their natural habitat. Allen Coombes was quite interested in collecting acorns from a specimen that was not far from a *Quercus rubra* in hopes of being able to obtain a *Quercus* x *fernaldi*. As all of us frantically collected those pretty little acorns with their distinctive pink-orange spot, perhaps one day one of us will be able to exhibit this apparently very hard to find hybrid.

Q. aliena (planted in 1929, 15 m); *Q. myrsinaefolia* (planted in 1931, 10 m); *Q. palustris* (35 m); *Q. x hickelli* (first-known specimen of this hybrid between *Q. petraea* and *Q. pontica); Q. baronii* (the only one present in any European collection); *Q.* x *vilmoriniana* (the first specimen of this artifivial hybrid between *Q. dentata* and *Q. petraea*)....

There are many magnificent trees here - and not just oaks - but, I must say, the overwhelming impression is that they are all planted much too near to one another and so, especially when they are old, it is difficult to really see them. Additionally, many labels are missing or, what is worse, incorrect. I do not wish to belittle those who - past or present - have devoted their time and energy into maintaining the aesthetic and botanical interest of the place, but the present state of affaires is a bit distressing.

One can buy plants at *Les Barres*: of the 22 species of *Quercus* present in the catalogue for 2004, the general origin - United States - of only 4 of them is indicated. A year or so ago, at the beginning of my interest in this genus, I tried to find out how many species and which ones were in the *Quercus* national collection. When I finally managed to speak to someone who would talk to me about this, I was told that this information could not be given out to the public...! At the time I laughed at what I took to be yet another mystery of French bureaucracy, but, very sadly, one has to ask: what is going on here?

In conclusion

One of the most interesting voyages of discovery I have ever been a part of; it was a shame that it only lasted two and a half days. Two and a half weeks would have been better! I can't wait for the next opportunity to participate in such an adventure and wish to thank all of my new *Quercus*-lover friends for the wonderful moments spent together.

The "Femeiche" - A Historical Oak of Germany

Eike Jablonski
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Like many European countries, Germany has a long affinity to oaks. Tales and legends about old oaks, together with mysterious stories about pre-christian tribes, are still alive. The ancient Germans, history informs us, had oak castles as well.

Loudon, in his *Arboretum et Fruticetum Britannicum* (1844) wrote about these old oaks of Germany: "...lately standing in Westphalia, one was 130 ft. high, and reported to be 30 ft. in diameter; another yielded 100 loads of timber; and a third served both for a castle and a fort" He also cited Googe´s *Four Bookes of Husbandrie* (published in 1586): "We have at this day an oke in Westphalia, not far from the castle of Alsenan, which is from the foote to the neerest bowe, one hundred and thirtie foote, and three elles in thickness; and another, in another place, that, being cutte out, made a hundred waine load. Not farre from this place there grew an other oke of tenne yardes in thicknesse, but not very hie".

It is fascinating, that some of these witnesses of ancient times survived until today. The old oak at Erle, a tiny northwestern village near Raesfeld in Westphalia, is such a tree. Perhaps Loudon told about it already in 1844.

Close to the old church of the village, this oak grows there for some 1500 years. As different reports tell us, this should be the eldest tree in Germany still alive. Despite its real age, which may be only a several hundred years up to a millenium, the tree stands for living history. It is a *Quercus robur*, the native oak of this region. The old name for it was "Raven Oak", which refers to the Raven, the holy bird of the Nordic god "Odin". This old designation and the name of the parish where the oak is growing show that this locality must have been a sacrificial place for the Germanic. As names often last for centuries, it is believed that therefore the oak was already growing here as a remarkable tree in heathen times. Christianity was brought to this remote region in the middle of the 8th century. Also at this time the first wooden church was build just next to the oak. The "heathen" tree was now growing on parish grounds, which may have saved the tree. Other holy oaks of the old Germanic were cut down by early missionaries, if they were growing on common land. Later, a stone church replaced the wooden one, and the oak is still alive.

Today, the oak is known under the name "Femeiche" or "Vehme-Oak". The "Feme" (or "vehme") was a jurisdiction; where a judge presided over a vehmic court. This secret lynchlaw was typical for certain regions in Westphalia in the late Middle Ages. The place underneath the oak served as the court. An old document from 1441 tells of the vehmic judge Bernt de Dücker, who passed a sentence of death upon Gert van Diepenbrock and his bondmen; the judgment was spoken under this oak.

In 1750, the parish priest ordered the removal of the rotten wood inside the massive trunk. Now the tree was hollow, and perhaps this saved the tree a second time. A doorlike passing with a height of two meters, and a width of 80 cm must have been there in 1819, when the hollow trunk had a diameter of some 2,75 m. That year, on September 26, the Prince Royal Friedrich Wilhelm of Prussia (later

The ancient "Femeiche" (*Quercus robur*) in the village of Erle, Germany, is said to be 1500 years old. photo © Eike Jablonski

King Friedrich Wilhelm IV) visited the oak. 36 infantry soldiers had to stand in the trunk with complete armament in marching order. The Prince Royal liked the tree so much that he had his breakfast with two of his generals inside the oak the other morning.

In 1851, the Bishop of Munster, Johann Georg, came to see the parish and the oak. It is reported that (after a night visit) he had a glass of wine in the oak, where a table for 12 persons including chairs were situated for him and his fellows.

The last of this kind of report dates from 1897, when a group of 40 members of the regional Forestry Commission arranged themselves inside the tree, singing a huntsman song. Nothing is written about it, but it seems that this event did not harm the tree too much.

The local population from villages nearby celebrated most of their important holidays like weddings and births under the tree, and did so for several centuries.

Today, law protects this oak, still growing vigorously on fresh, sandy diluvial soil. A fence keeps the Forestry Commission, Royal Princes, and Bishops away. Despite a height of perhaps 14 meters, the oak is nevertheless a giant. In 1953, a circumference of 14 meters at soil level, and of 12 meters at two-meter level was measured (Buerbaum, 1954). The first branches are sprouting three meters above the soil, forming a secondary crown. It is still clearly visible that the whole former crown was completely destroyed by storms and lightning during the last centuries. Only in single years, acorns are produced. In 2004, after the hot 2003 summer, the tree bore an excellent crop with masses of viable acorns. The trunk is not only hollow; several parts of the old trunk are not connected together any more. Wooden and iron posts support the remaining branches. In 1965, the first treatment of this kind was done. A second treatment was done in 1987.

Let´s hope that this impressive living monument of history will survive for several more decades. Visiting this tree, one still can feel the history connected with it.

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photo © Eike Jablonski

Author standing near "Femeiche."

photo © Eike Jablonski

Fodder and Burning Material - The Use of Oaks in Nepal and Adjacent Himalayan Regions

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Nowadays the higher regions of the Himalayas see a growing population with all its pressures. This includes a rising number of livestock, like cattle, sheep and goats. The forests of the Himalayan midlands, which lie between 800-3000 Meters (2400 - 9000 feet), become more and more fragile and over-utilized. Besides the cutting of trees for firewood, the practice of coppicing and pollarding trees for fodder is common.

The Nepali population has a long tradition of mixed farming, with animal husbandry being interdependent components. Livestock is also an integral part of the cultural life in Nepal. About 50% of the forested area in Nepal is used for fodder production from trees. The other half of the forested area is out of reach of settlements, or grows in steep gorges or other places where any fodder production is too difficult.

Animals in Nepal derive ca. 35% of their feed from trees. The annual production of fodder from trees in Nepal is estimated to 3.5 to 4 tons of dry leaves. The production of fodder from trees is possible through various methods. Trees, which are believed to have high quality fodder or special medicinal power, are lopped very carefully; only the leaves are stripped off by hand. The people own most of these trees, and they are growing in close proximity to the villages.

Trees in the forests, belonging to no one in general (called "everybody's trees" in Nepal), are more or less heavily lopped by the "Khukuri" - a knife, or by axe. In this case, twigs and branches are also cut, and this is often done down to the main trunk. Thus, firewood can also be harvested (Jablonski, 1993). According to Wormald et al. (1983) twigs and branches can make up to 30% of the weight of the whole harvest. This practice can cause heavy injury to the trees. If this practice is repeated frequently, and more annually, the trees hardly can produce flowers or fruits. Natural rejuvenation becomes more and more unlikely in such forests. Already in 1937, stated Gorrie, oaks in Northern India became increasingly weak because of annual lopping, instead of the formerly common lopping in a three-year-cycle. He also noted that not only did the trees produce less fodder, but that oaks became more and more displaced by *Pinus wallichiana*.

Livestock face maximum nutritional stress from January to May, which is the dry season in Nepal. Only in the rainy season is there sufficient fodder for animals. Consequently, only milk-producing animals like buffaloes get well fed, whilst others are grazed on the limited pasture areas, fallow land, and in the forests. In the dry season, animal fodder is in very short supply, and during this period trees provide a valuable source of nutrition.

Around a dozen oak species are growing in the forests of the Himalayas. The rural population utilizes more than one hundred species of trees (Amataya, 1991;

Gorrie, 1937; Shabnam, 1959). Although they know little about their chemical composition, they have considerable knowledge of their nutritional qualities (Amataya, 1990). The farmers do prefer special fodder tree species, including several species of oak. Some of the species coppice well, others have both coppicing and pollarding powers.

Authors from Nepal and India (Behari et al., 1968; Gupta, 1963) count *Quercus floribunda, Q. glauca, Q. lanata, Q. leucotrichophora* and *Q. semecarpifolia* as the most valuable fodder trees in the mountains. In Eastern Nepal, Sikkim and Darjeeling also name *Q. lamellosa* as heavily lopped.

Quercus glauca has a wide distribution throughout the Himalayas, growing from the mid-hills (1800 m) to about 3100 m elevation. This species coppices well, and it is extensively lopped for fodder. Lopping starts from April and continues until July. The new flush appears in March, varying from region to region. The leaves contain 9.6 % crude protein and the total of digestive nutrients amount to 39 % (Singh, 1982). Panday (1992) estimates a mean annual fodder yield of 80-100 kg per tree, fresh material.

Quercus lamellosa grows from about 1800 m to about 2700 m elevation, but only in regions with high annual rainfall. This moderate to large-sized tree demands light. It is quite sensitive to fire. It coppices well, but does not produce root suckers. It is extensively lopped for fodder. Lopping starts from March and continues until October. The dry leaves contain 10 % crude protein.

Quercus lanata grows from the Nepali mid-hills (1800 m) to about 2400 m elevation. This light-demanding species coppices well. It produces a massive root system and grows on a variety of soils. In some regions in Nepal *Quercus lanata* yields 78% of the whole fodder leaf harvest (Hawkins et al.; 1983). Lopping starts from October and continues to April. The old leaves shed during summer, and the new flush appears before winter, between July and Oc-

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A couple in northwestern Yunnan, Peoples' Republic of China, returns from an oak forest with bundles of fodder for their livestock

© Eike Jablonski

Heavily lopped *Quercus lamellosa*, growing in a forest near Yoksum, Sikkim, at nearly 3000 m.

tober. One tree is estimated to produce 50-80 kg of fresh fodder per annum (Panday, 1982)

Quercus leucotrichophora occurs mostly in the Western Himalayan belt up to an elevation of 2100 m, although it has a wide range of distribution throughout the country, except in the eastern Himalayas. It is a moderate to large-sized evergreen tree with a characteristic rounded crown. This light-demanding species can tolerate shade to a certain amount, coppices well, but is susceptible to drought. In some regions of Nepal it is the most heavily lopped fodder tree, and local farmers rate it as a high quality fodder tree. Lopping starts from October and continues until August. The new leaves appear in March or April. They contain a high percentage of crude fibre (30-32 %) and tannin. Because of the high tannin content it is not advisable to use leaves of *Quercus leucotrichophora* as a sole feed for livestock.

Quercus semecarpifolia grows in high elevations, ranging from 1500 - 3600 m. In many regions it forms large stands in the upper forest belt. The medium to large-sized tree develops a spreading crown. It is a strong, light-demanding species. It coppices and pollards quite well. According to Panday (1982), farmers in the higher regions of the Himalayas regard *Quercus semecarpifolia* as the fodder tree with highest qualities. Amataya (1990) also counts *Quercus semecarpifolia* in the five most important fodder trees in Nepal. The tree is lopped extensively in the northernmost districts of Nepal. The leaves of this species are preferred as a good fodder source. Lopping starts from November and continues until March-April, before the old leaves start shedding. The new flush appears immediately in April-May; therefore it has an evergreen appearance. The leaves contain 4-5 % ash and 1.4 % nitrogen. Annual harvest of fodder leaves per tree can be up to 120-200 kg of fresh material.

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Quercus leucotrichophora, with *Rhododenron arboreum*, on a hill above Kathmandu (ca. 2500 m). The trees are growing in a Royal Hunting Preserve si they are not lopped.

Trees play an important role for the feeding of livestock in the Himalayan regions, and oaks are a remarkable part of it. Despite the tremendous demand for fodder and the fodder deficit for livestock, there is little active production or planting of fodder trees being done. To protect and conserve Himalayan forests, including the oaks, there is a need for several measures (Amataya, 1990; Jablonski, 1993):

- Establishing of nurseries, which produce fodder trees in cooperation with the local population.
- Planting of "Fodder Forests."
- Planting of fodder trees on erosion-prone hill slopes and marginal areas of small farms. Unlike other fodder crops (clover, leucerne) trees do not deprive farmers of land capable of growing crops for human consumption.
- Education of the rural population; programs to improve the farmers' knowledge of fodder tree management.
- Fodder quality improvement.
- Reduction of animal populations, especially in monsoon season.
- Necessity of stall feeding in monsoon season.

It is urgent to make efforts in stabilizing the forests of the Himalayas and the oaks involved. Unfortunately, the recent political situation makes it unlikely that the people are able to make these efforts by themselves. Let's hope that there will be a wide consensus between all concerned parties, regional and worldwide, to save these forests, and to try to realize the above-mentioned measures.

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How Old Is This Oak? Determing the age of *Quercus virginiana*

By Coleen Perilloux Landry

Note: The words written are purely by personal observation and research and are not based on any scientific data.

Grown in only 14 states in the United States the live oak, *Quercus virginiana*, has long been a subject of controversy as to the determination of its age. It can be found in swamps, on coastlines of the Gulf of Mexico and the Atlantic and Pacific oceans, and on higher ground farther inland. It has been grown for its sculpture and beauty, for its food for wildlife and for its valuable timber in shipbuilding, furniture-making and flooring.

Let us discuss its growth habits first. Unlike many of the *Quercus* family the live oak is a sprawling oak. Its branches can reach out 150 feet from its trunk and curve along the ground then upwards again towards the sky. This is the most natural form of the live oak and if it is not pruned as a young oak it will automatically grow in that manner. The crown is usually rounded in form and does not reach the height of most oak species, preferring to spread itself on the earth rather than reach for the sky.

This particular characteristic is what makes the live oak such a popular place of salvation during a hurricane. It has been documented that during many destructive hurricanes in Louisiana residents took refuge in the branches of the oaks to escape the floodwaters. The people tied themselves to the massive branches and the rounded canopy buffeted the winds thus preventing them from being ripped into the force of the hurricane. In Louisiana, Mississippi, Georgia and Alabama the live oak is looked upon as a tree of protection. On the coast of the Gulf of Mexico in Louisiana there are oak trees still standing where there are no longer any towns because of destruction by hurricanes that occurred over a century ago. The strength and resiliency of the live oak in nature's fury cause it to be admired and revered.

The people of Louisiana have selected it as an icon of their own survival in a harsh and dangerous natural environment.

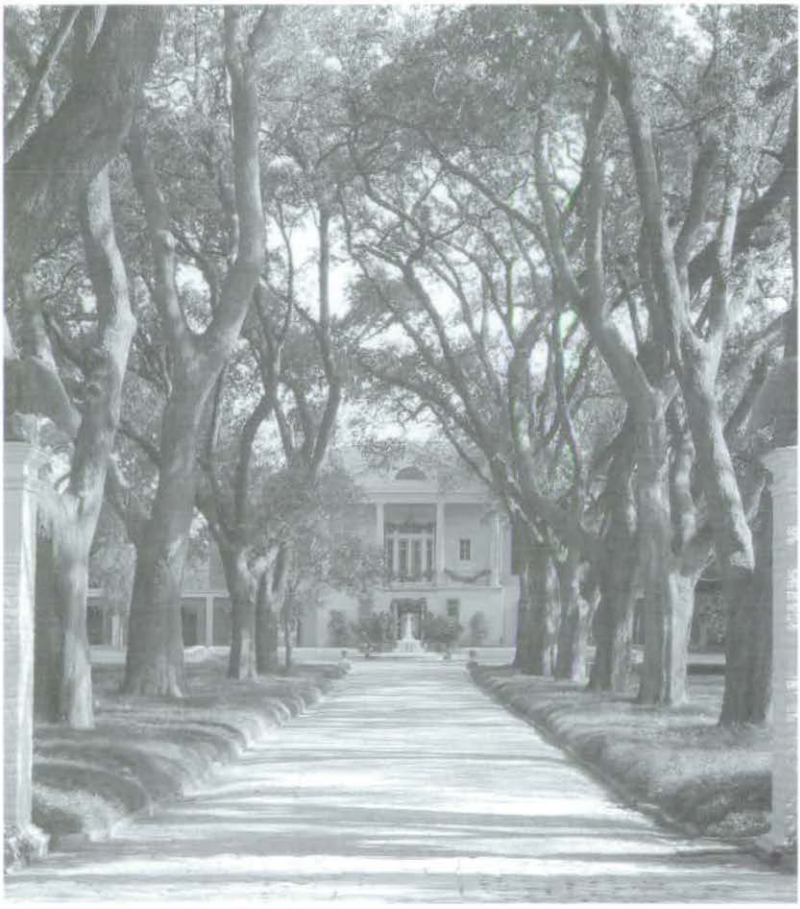
The federal government realized the value of the live oak for shipbuilding. President John Quincy Adams subsidized the first tree farm in the history of the United States in Florida in the 1820's. He estimated the growth from an acorn to a tree with desired wood heavy enough for shipbuilding would be 100 years. As in many government projects it was plagued with political intrigue and was eventually transferred to the Pensacola Navy yard commander where the project perished. However, the oak grove still stands today and because of someone's incompetency the oaks have enjoyed life these many years. Ships are no longer made of oak, but steel, and oak wood is used by the Navy only for restoration of their old and historic vessels.

There is a question that is almost unanswerable when it comes to the live oak- "how old do you think this live oak is?" The only true tests for the age of a live oak are cutting it down and counting the rings or core boring. Cutting it down to determine the age would be foolish. The only accurate way of dating any living tree is to

"core" it by removing a cylinder of wood from the interior of the tree in order to count the annual growth rings. Large live oaks are almost impossible to core because of the exceptional hardness of the woods. The cores break off within the tree before they can be removed intact and counted. Unless someone has planted the tree from an acorn or there is documentation of the tree when it was planted it is very difficult to determine the age.

Foresters have decided that the live oak national champion in Lewisburg, Louisiana, is over 1200 years old. It has a girth of over 38 feet. The founder of the Live Oak Society, Dr. Edwin Lewis Stephens, in 1934 declared through his studies of the live oak, that a tree 16 feet in girth was a century old. And, therein lies the continuing discussion.

Some live oaks in City Park in New Orleans have been growing for 200 years and have reached the girth of only 14 feet. Some live oaks in residential landscapes have been growing for only 25 years and have already reached the girth of 9 feet. And, the controversy goes on.



Longue Vue Gardens in New Orleans. The oaks were planted in 1850.

Many factors determine the growth of *Quercus virginiana*. Just like most trees the important combination of light, soil and water are needed. In the case of an oak in Jefferson, Louisiana, named Old Dickory, all three factors were exact. It lived in a little forest that enjoyed the natural mulching and nourishment of the other trees; it lived near the banks of a natural stream, and it enjoyed the warm, southern coastal light. It was left undisturbed for centuries until recently when it was saved from a roadway project by a driving force of preservationists. It is determined to be between 600 and 900 years old. Left to its own growth ways and nature a live oak is the king of the forest because its heavy, forceful branches push away other trees. Its roots are also heavy and spread as wide as the canopy. The sheer weight of a live oak makes it superior to most trees in a forest.

Live oaks have been used to line allees. The most famous world known allee is Oak Alley Plantation in Vacherie, Louisiana, and the age of these oaks are always debated though it is known that the house is over a century and a half years old. St. Charles Avenue in New Orleans has an oak allee of many miles and they have survived almost 80 years of autombile traffic, foot traffic and air pollution. History records when these oaks were planted but no one recorded how old the oaks were at the time of planting. And, the controversy continues.

City Park in New Orleans has the largest stand of live oaks in the world. An inventory in 1983 revealed that at least 250 of the oaks had a circumference of at least 10 feet. History proves that this forest of live oaks began hundreds of years ago when an old bayou was a tributary of the Mississippi River and flowed through the area feeding the oaks each year with alluvial soil. All of these oaks vary in size and it is believed that the smaller ones are probably the progeny of the older trees. Yet no one really knows the true age of each, yet in a few of the ancient ones estimates are very close.

Plans are underway to plant several young live oak seedlings at an Agricultural University in Louisiana and to study their growth for at least a century. Though you and I will never know the findings of this study it will perhaps help with the answer to the question "How old is this oak?"

Children are dwarfed by a single limb of "Old Dickory."

Live Oak grove in City Park in New Orleans. There are over 1000 ancient oaks in City Park varying in age from 200 years old to 700 years old.

"The Walking Oak" in City Park in New Orleans. It is believed to be 250 years old.

all photos courtesy of Coleen Perilloux Landry

The Land that Time Forgot: Southern Flatwood Oaks and Associates of the Tinley Creek Forest Preserve of Cook County, Illinois

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Abstract

Recent botanical study has revealed the discovery of eleven southern disjunct species including putative hybrids typical of flatwood forests of the lower Mississippi River valley growing in northern Illinois. *Celtis laevigata* var. *smallii* (sugarberry), *Liquidambar styraciflua* (sweetgum), *Tilia heterophylla* (white basswood), *Quercus shumardii* (Shumard oak), *Quercus montana* (chestnut oak), *Quercus lyrata* (overcup oak), *Quercus texana* (Nuttall's oak), *Quercus coccinea* (scarlet oak), *Quercus* x *guadalupensis* (post oak x bur oak), *Quercus* affn. *falcata* (southern red oak putatively introgressed with black oak), and *Quercus* affn. *pagoda* (cherrybark oak putatively introgressed with black oak) were found growing in flatwoods forest within the 324 hectare(800 acres) Tinley Creek Forest Preserve of southwestern Cook County Illinois. They are presumed native and their occurrence may be the result of post glacial migrations up the Mississippi River Valley. Their persistence to the present may be attributable to a unique combination of soil, drainage, and microclimatic effects of Lake Michigan.

The Tinley Creek Forest Preserve (TCFP) lies at the lower end of Lake Michigan at the eastern edge of what is called the Prairie Peninsula, an ectonal region originally typified by tall grass prairie, savannah and forest communities (Transeau, 1935). Glaciation, shifting climatic changes, and anthropogenic influences over millennia have shaped the region into a mosaic of plant biota originating from all points of a compass. The local microclimatic effects of Lake Michigan have also played a key role in providing refugium habitats for taxa with more southerly or easterly affinities. The Tinley Creek Forest Preserve represents a rare tract of land that blends these elements together. Special attention must be given to preserve and maintain these rare plant communities before they disappear.

Climate

The Chicago region has a humid continental climate. The TCFP lies 24 kilometers south west of Lake Michigan. The average mean annual temperature is 9×C with a mean annual precipitation of 96 cm. The last frost date is approximately April 30th (Ruffner,1978). The area exhibits a slight lake effect of moderating temperatures in winter, and slightly greater precipitation compared to outlying suburban areas. (Fizzel, 2002).

Cultural History

European settlement at TCFP began in the 1830's with several land owners managing tracts of land mostly near what is now Camp Sullivan in the northeastern part of the preserve. The forested portion was originally called Betchelder's Grove

and then presumably renamed by New Englander Steven Rexford as Bachelor's Grove in the 1840's. German settlement proceeded through the 1850's with establishment of a post office around 151st and Harlem (Bettenhausen, 2002). In the 1860's, Asa Turner, T. Moss, and R. Schilling were the predominate landowners of the study area (Flower, 1861). Between 1858 and 1884 the population migrated eastward toward the village of Blue Island leaving the area with few residents. Later, the settlement of Goeselville (1884-1906) was established near what is now Camp Sullivan until it was abandoned (Bettenhausen, 2002). By 1904 there were over 30 individuals owning land in the preserve with Schilling, Hunstock, Lyttle, and Moss in possession of the larger tracts (Mitchell, 1904).

According to Dan Weber, real estate and license engineer of the Cook County Forest Preserves, initial purchase of land began around 1925 and continued through its completion in the 1950's. Aerial photographs taken in 1939 and 1940 (Illinois Air Photo Image Base, 2004) show sections of the flatwoods area cleared with evidence of patches of agricultural activity south of Tinley Creek. The photo also reveals the preserve surrounded by farms and small tracts of forest. In the 1940's and 1950's Camp Sullivan and Camp Falcon, located in the northeast corner of the preserve, were built for the boy scouts and are still utilized today. A grove of *Pinus resinosa* Ait.(red pine) was planted 2 kilometers to the west of Harlem Avenue at 151st in the 1960's. In the 1980's and 1990's, Cook County Forest Preserves installed biking trails, planted ornamental trees, and Eurasian grass along sections of a bike path. (Dick Newhardt, District Forester, Cook County Forest Preserve, personal com.)

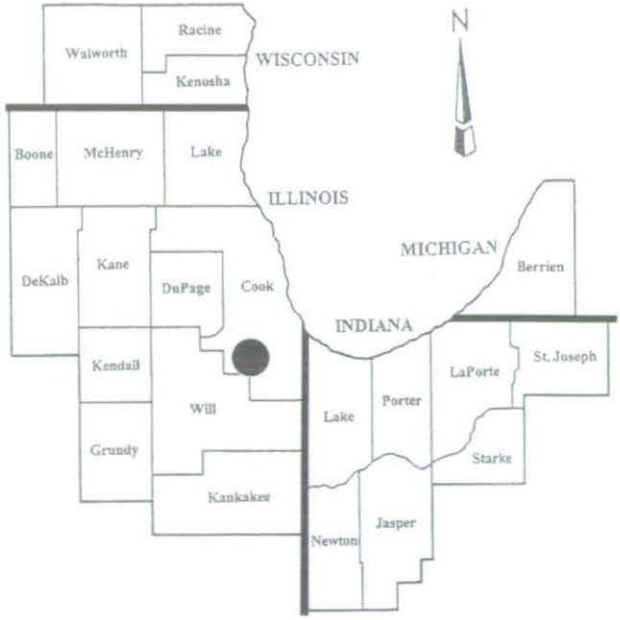


Figure 1. Map of the Chicago Region
Base Map: Swink and Wilhelm, 1994
Tinley Creek Forest Preserve highlighted

Table 1. List of southern taxa and putative hybrids of TCFP with Field Museum herbarium accession number given on left. (* indicates a southern form of the oak).

FM 2230274	*Celtis laevigata* Willd. var. *smallii* Beadl. (sugarberry)
FM 2230276	*Liquidambar styraciflua* L. (sweetgum)
FM 2230277	*Tilia heterophylla* Vent. (white basswood)
FM 2230278	*Quercus coccinea* Muenchh. (scarlet oak)*
FM 2246493	*Quercus* affn. *falcata* Michx. (southern red oak introgressed possibly with black oak)
FM 2252943	*Quercus* x *guadalupensis* Sarg. (post oak x bur oak)
FM 2230271	*Quercus lyrata* Walt. (overcup oak)
FM 2252945	*Quercus lyrata* Willd. x *Quercus macrocarpa* Michx. (overcup oak x bur oak)
FM 2230272	*Quercus montana* Willd. (rock chestnut oak)
FM 2246494	*Quercus* affn. *pagoda* Raf. (cherrybark oak introgressed possibly with black oak)
FM 2230275	*Quercus* x *saulei* Schneider (white oak x rock chestnut oak)
FM 2230273	*Quercus shumardii* Buckl. (Shumard oak)
FM 2252942	*Quercus shumardii* var. *stenocarpa* Laughlin (Shumard oak)
FM 2252941	*Quercus texana* Buckl. (Nuttall's oak)

Natural History/Ecology

TCFP harbors sixty five species of native Illinois arborescent taxa with eleven taxa having distinct southern Applachian and lower Mississippi River valley affinities (Table 1). Sixteen oak taxa including eight southern species with associated hybrids have been observed (Table 2). Notable Illinois endangered species are *Quercus texana* (Nuttall's oak) and *Quercus montana* (rock chestnut oak) (Herkert and Ebinger, 2002). Other southern taxa include *Celtis laevigata* var. *smallii* (sugarberry) and Illinois state threatened species *Tilia heterophylla* (white basswood). The area supports a mix of northern and southern elements in a mosaic of forest communities defined by topography, soil and moisture conditions. Over 350 native taxa have been found to exist (Shepard, 2001). The Illinois endangered species *Carex communis* Baily (common beech sedge), typically found in eastern forests, has been recorded from the ravines (Bowles and Radke, 1999). The southern taxa occur as scattered individuals and in groups occupying the flat to gently rolling forest communities outside the floodplain and ravines. These communities lie approximately 0.5 kilometer north of the creek floodplain and 1.5 kilometers to the south covering 90 hectares or twenty five percent of the preserve area (Figure 1). Individual populations of *Q. montana,* and *Tila heterophylla* are separated by as much as 2.2 kilometers.

The flatwoods represent a second-growth forest that has had a history of agriculture, logging, clearing, grazing, and in presettlement times, fire (Bowles and Radke, 1992; McClain and Elzinga, 1994). The biodiversity of the area is hidden and masked by the Eurasian weeds and shrubs that proliferate in sections of the understory and ground layers. Disturbance has brought invasive buckthorn (*Rhamnus cathartica* L.), oriental bittersweet (*Celastrus orbicularis* Thunb,), and multiflora rose (*Rosa multiflora* Thunb.) into the understory, choking out natural recruitment of native trees. Field garlic (*Allium vineale* L.) and more recently garlic mustard (*Alliaria petiolata* (M. Bieb) Cavara and Grande) have invaded the ground layer.

Table 2. List of oak taxa and putative hybrids found at Tinley Creek Forest Preserve

Quercus alba L.	(white oak)
Quercus bebbiana	C. K. Schneider (white oak x bur oak)
Quercus bicolor Willd.	(swamp white oak).
Quercus coccinea Muenchh.	(scarlet oak)
Quercus ellipsoidalis E.J. Hill.	(Hill's oak)
Quercus affn. *falcata* Michx.	(southern red oak introgressed possibly with black oak)
Quercus x *guadalupensis* Sarg.	(post oak x bur oak)
Quercus x *jackiana* Schneider	(swamp white oak x white oak)
Quercus lyrata Willd.	(overcup oak)
Quercus macrocarpa Michx.	(bur oak)
Quercus montana Willd.	(rock chestnut oak)
Quercus muhlenbergii Englm.	(Chinkapin oak)
Quercus affn. *pagoda* Raf.	(cherrybark oak introgressed possibly with black oak)
Quercus x *paleolithicola* Trel.	(Hill's oak x black oak)
Quercus palustris Muenchh.	(pin oak)
Quercus x *riparia* Laughlin	(Shumard oak x northern red oak)
Quercus rubra L.	(northern red oak)
Quercus x *saulei* Schneider	(white oak x rock chestnut oak)
Quercus shumardii Buckl.	(Shumard oak)
Quercus shumardii var. *stenocarpa* Laughlin	(Shumard oak)
Quercus texana Buckl.	(Nuttall's oak)
Quercus velutina Lam.	(black oak)

Native species characteristic of these wet woods still persist, however. Sweet scented bedstraw (*Galium triflorum* Michx.), Greendragon (*Arisaema dracontium* (L.) Schott), lady fern (*Athyrium filix-femina* L., sensitive fern (*Onoclea sensibilis* L.), yellow violet (*Viola pensylvanica* Michx.) and Missouri violet (*Viola missouriensis* Greene) are prevalent in the herbaceous community. Downy serviceberry (*Amelanchier arborea* (Michx. f.) Fern.) and Allegheny shadblow serviceberry (*Amelanchier laevis* Weig.), more typical of eastern and southern forests, are occasionally found in clearings and the understory (Shepard, 2001).

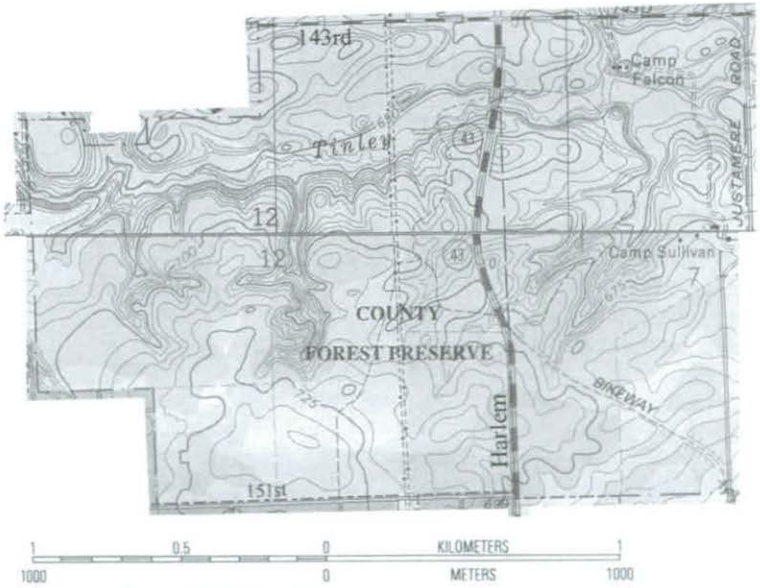
Glacial History/Topography/Forest Soils

The topography of northeastern Illinois is the result of the Wisconsinan Glacier that arrived 75,000 ybp and departed 12,000 ybp. This glaciation left the Chicago region with a complex of ancient beach ridges, outwash plains and a complex morainal system forming the periphery around the southern end of Lake Michigan. TCFP is situated on the Tinley Moraine of the Northeastern Morainal Division of Illinois (Schwegman *et al.*1973;Willman and Frye, 1970). During the last stages of Wisconsinan glaciation, four meltwater lakes were dammed by the Tinley Moraine. One of these lakes, glacial Lake Tinley, cut a drainage outlet through Tinley moraine east to Stony Creek and the Sag Channel forming Tinley Creek. A series of steep bluffs and ravines rising from 650 feet at the stream bed to 700 feet at the ravine edge illustrate the erosional effect of the meltwater (Bowles and Radke, 1992).

The ravines are surrounded by flat to gently rolling topography with perched water tables and generally poor drainage described as flatwoods.

Soils of the TCFP formed over an ancient glacial lake bed under wetland, prairie, and forest conditions. Flatwood soils are underlain with a rather semi- impervious layer of clayey glacial till promoting vegetation adapted to periodic high water tables and wet/dry conditions. Trees growing in these soils must adapt to seasonal water availability because both flooded and droughty conditions occur during the growing seasons (Mapes, 1976). Knolls and slightly elevated topography can support species associated with better drainage. The flatwoods are represented by Morley/Ashkum and Beecher/Markham silt loams on mostly two to five percent topography.

Minor topographic, drainage, and soil patterns segregate the flatwoods into a mosaic of forest associations. The species compositions found at TCFP are similar to those found in the lower Mississippi River Valley, Appalachian forests and forests of more eastern distribution, albeit on a much more fragmented, smaller scale. The Society of American Foresters lists several forest types with species associations found in southern bottomland forests, southern Appalachians and northern wet forests. Remnants of these forest associations that have been observed in the flatwoods area are Type 93 (sugarberry – American elm – green ash; Beecher/ Markham silt loams 0-5% slope), Type 52 (white oak – black oak – red oak – scarlet oak – chestnut oak; Markham silt loam 5-10% slope), and Type 39 (black ash, - American elm – red maple; Morley/Ashkum 2-5% slope with perched water table) (Erye, 1980; Mapes, 1974). Braun (1950) and Bryant (1990,1999) discuss Tennes-



CONTOUR INTERVAL 5 FEET
NATIONAL GEODETIC VERTICAL DATUM OF 1929
Tinley and Palos Park Illinois Quadrangles, 7.5 Minute Series
USDI Geological Survey, 1993

Figure 2. Topographic map of the study site and areas of botanical interest.

see and Kentucky bottomland forests dominated by *Celtis laevigata* with component species *Q. lyrata, Q. shumardii, Q. palustris, Q. pagoda, Q. stellata,* and *Q. falcata. Quercus coccinea* and *Q. montana* are also mentioned but are more typical of surrounding uplands (Fralish and Snyder, 1993; Bryant, 1999). The bottomland forests of the Middle Tennessee, and Kentucky discussed by Bryant (1990, 1999) and Chester and Schibig (1997) possess many species seen on TCFP silt loam soils. Among those found at TCFP are *Celtis laevigata* var. *smallii* (sugarberry), *Celtis occidentalis* L. (hackberry), *Ulmus americana* L. (American elm), *Fraxinus pennsylvanica* Marsh (green ash), *Fraxinus americana* L. (white ash), *Tilia heterophylla, Q. palustris, Q. bicolor, Q. muhlenbergii,* and *Platanus occidentalis* L. (sycamore).

Southern Oaks

Among the TCFP oaks found growing with *Celtis laevigata* var. *smallii* is *Quercus lyrata.* It is found in southern Illinois and in scattered disjunct populations along the Mississippi River in west-central Illinois (Mohlenbrock, 1986). At TCFP, there are over one hundred trees of this species represented in all size classes spread out over a 1.5 square kilometer area. The tallest trees range between 20-23 meters in height. The oldest tree examined was 112 years old, aged with a resistograph coring device handled by forester Jim Tresouthick. The tree's DBH was 28in (0.7m), the largest of the southern oaks (see photograph). Putative hybrids between *Q. macrocarpa* (bur oak) and *Q.lyrata* have been found in the preserve with specimens deposited at the Field Museum of Natural History in Chicago. *Quercus* x *megaleia* Laughlin, another hybrid, has been reported from TCFP, but is now thought to be just a form of *Q. lyrata. Quercus lyrata* also associates with *Q. texana, Q. macrocarpa, Ulmus americana, Fraxinus nigra* Marsh (black ash), and *Acer rubrum* var. *trilobum* K. Koch. (red maple), in the northern part of the preserve in a wet forest analogous to American Society of Foresters type 39 (Eyre, 1980).

Many trees growing in the flatwoods appear to be genetically mixed with *Q.macrocarpa* as one of the parents. One of the more confusing is the putative hybrid *Q.* x *guadalupensis* Sarg., involving a cross between *Q. stellata* and *Q. macrocarpa. Quercus* x *guadalupensis* is known only from populations in Texas where it was first discovered (Nixon and Muller, 1997). The range of variation in this apparent hybrid swarm tends to both extremes. Their more stunted growth, smaller outer diameter of the acorn cupules (<20mm), and more cruciform leaf morphology identify these trees. Field observations indicate that these putative hybrids may be found scattered across southern Cook County in wet forests. *Quercus stellata* is typically a southern species occurring in habitats ranging from dry sterile soil to hardpan clay flatwoods. It has been found as far north as central Illinois and north central Indiana (Mohlenbrock, 1986; Nixon and Muller, 1997).

Quercus shumardii is a species of floodplain terraces and moist alluvial bottomlands of the southern U.S. (Braun. 1950). It is found in the southern third of Illinois growing as far north as Jersey County (Shepard, 1993). Disjunct populations of the species purportedly grow in Lower Michigan and northern Indiana (Jensen, 1997). At TCFP, the *Q. shumardii* population numbers under 30 mature trees where it is found on Beecher silt loam. Individual trees frequently attain 22-24m, and 0.6 DBH (see photo). One tree was aged at 85 years with a resistograph. Acorn variation is seen within the population including an ellipsoid shaped form with a shallow cupule resembling the description of *Q. shumardii* var. *stenocarpa*

Laughlin. Leaf forms range from typical forms to those resembling *Quercus acerifolia* (E.J. Palmer) Stoynoff & Hess.

A common tree growing with *Juglans nigra* L. (black walnut) on the poorly drained Beecher soil is the putative hybrid *Q. rubra* x *Q. shumardii* (*Q.*x *riparia* Laughlin). Like flatwood populations of *Q. macrocarpa, Q. rubra* populations are genetically mixed. Many display bark, leaf, and acorn morphology intermediate with *Q. shumardii*. *Quercus rubra* populations growing in the better drained ravines represent typical northern expressions of the taxon.

Photo © David Shepard

Quercus lyrata 112 years old growing in wetland

Quercus montana has the widest range of the southern oak taxa within the preserve covering 2.2km between populations. It is found in American Foresters type 93 and 52 associations. It grows with *Celtis laevigata* var. *smallii, Q. lyrata,* and *Q. shumardii* on Beecher silt loam and *Acer saccharum* Marsh (sugar maple) and *Tilia heterophylla* on the better drained sites of Morley/Ashkum. On more upland Markham silt loam, *Q. montana* occurs with *Q. rubra, Q. coccinea, Q. alba, Q. velutina,* and *Q.* x *guadalupensis*. Although it numbers fewer than 40 mature trees, seedling recruitment is frequently observed. *Quercus montana* is on the endangered species list in Illinois where it grows stunted on dry slopes in the Shawnee National Forest. The nearest population to Tinley Creek is in unglaciated Brown County, Indiana where it grows with *Q. coccinea.* A tree of the hybrid *Quercus x saulei* (*Q. montana* x *Q. alba*) aged at 93 years was found growing with *Q. coccinea, Q. alba,* and *Q. bicolor* (see photo).

Photo © Guy Sternberg

The author standing next to *Quercus shumardii* in flatwoods

Among the most interesting and controversial oak taxa of the Chicago region is *Q. coccinea.* Populations of this taxon at TCFP represent a southern form or variety of the species whose center of distribution lies predominately in the southern Appalachians and Ozark Mountains. The closest populations reside in the Shawnee National Forest of extreme southern Illinois. Data from studies of *Q. coccinea* (Shepard, 1993, 2001) reveal major morphological differences between southern Appalachian/Ozark forms of this species and those identified as *Q. coccinea* or *Q. ellipsoidalis* (Hill's oak) in northern Illinois. These more southern forms are typified by larger 6 to 8mm long buds with pubescent tips, acorns with prominent concentric rings, and greater height. The trees also illustrate more southern characteristics by holding their brilliant red foliage through late November (cover photo).

While *Q. coccinea* is generally associated with dry upland sites in the Appalachians, it occasionally can be found in flatwoods or low mesic forests of alluvial terraces (Bryant, 1990) (see photo below). At TCFP it grows in a mixed mesophytic forest community with *Q.bicolor, Q. alba, Fraxinus pennsylvanica, Fraxinus americana, Tilia americana* L. (American basswood), *Tilia heterophylla* and *Acer saccharum* Marsh.(sugar maple) (see photo on opposing page). In another part of the preserve individual trees grow with a 100 year old *Liquidambar styraciflua*. On 5-10% slope Markham soil it forms a component of a remnant white oak - black oak - red oak- scarlet oak – chestnut oak association (Eyre, 1980).

Growing with *Celtis laevigata* var. *smallii, Q. palustris,* and *Quercus* x *riparia* are single specimens of *Q.* affn. *pagoda* and *Q.* affn. *falcata.* Both trees show distinct introgression with *Q. velutina* particularly in bud pubescence, and the more glabrous abaxial surface of the leaf. Leaf forms of both trees are unique and stand out among the other oaks. *Quercus* affn. *pagoda* is one of the larger diameter species of the southern disjuncts measuring just over 0.6m DBH. Putative hybrids of both taxa can be found at TCFP with most involving either *Q. rubra* or *Q. velutina.* Both *Q. pagoda* and *Q. falcata* can be found in the extreme southern Illinois counties (Mohlenbrock, 1986).

Most unusual among the oaks is the occurrence of *Q. texana,* represented by eleven trees. At TCFP it grows alongside *Q. lyrata, Fraxinus pennsyvanica, Ulmus americana, Acer rubrum* var. *trilobum,* and *Fraxinus nigra* on Morley silt loam with a perched water table. The trees average between 20 to 24 meters in height and hold their leaves green through late November. It wasn't recognized as a species until 1927 and was formerly known as *Q. nuttallii* (Jensen, 1997). It is a bottomland species typical of the lower Mississippi River Valley occurring in Tennessee, Arkansas, Louisiana, and Texas. The acorn and leaf morphology are unique in this species.

Photo © David Shepard

Wet flatwood forest with a 30-meter *Quercus coccinea* at center.

Analysis of southern species

The historical information, species diversity, distribution, forest ecology, hybridization, and age coring presented in this paper concerning the southern forest species at TCFP suggest that they are native and not planted or introduced. There are no records of these trees being planted by the Cook County Forest Preserve District, (Dan Weber, personal com.) or by individual land owners dating back to the 1860's (Bettenhausen, 2002). The southern oak taxa occurring at TCFP are not and have not been typical trees used in forestry or the landscape industry in the Chicago area or elsewhere in Illinois. (Central Illinois Tree Council, 1998; Paul

Photo © David Shepard

The upper crown of the 93 year old *Quercus xsaullii.*

Deizmann, Illinois Department of Natural Resources, Forester, personal com.). Most are difficult to identify let alone grow several hundred kilometers north of their range (Dirr, 1983). Aerial photos from 1939 and 1940 reveal some land clearing and agricultural activity, but lack sufficient detail to identify any nursery plots or the existence (or non existence) of individual trees. Moreover, many of the southern species growing in the purported agricultural and cleared sites have existed since 1925 with at least one dating back to the late 1890's. The degree of hybridization and introgression observed between northern and southern taxa points to their intermixing over many generations. Horticulturally establishing and maintaining such a complex flatwoods forest following precise species associations, soil variations, and moisture gradients is unlikely.

The occurrence of these southern disjuncts should not be unexpected. Species with typically southern and eastern affinities are not uncommon to the southern Lake Michigan region and have been well documented. Migrational paths of southern species have been discussed by various botanists. Peattie (1922), and Catling and Spicer (1988) have cited populations of coastal plain flora occurring throughout various localities. Evidence of migrations of southern forest taxa into the upper Midwest is apparent when one looks at the number of disjunct species seen at the lower end of Lake Michigan from southern Cook County Illinois across northern Indiana to southern Michigan. *Styrax americanum* Lam.(American snowbell), *Populus heterophylla* L.(swamp cottonwood), and *Fraxinus profunda* Bush (pumpkin ash) occur as disjunct populations in the Kankakee River valley of northern Indiana and Illinois (Phillippe et al., 2003). Disjunct populations of *Q. shumardii* occur scattered throughout northwest Indiana and lower Michigan (Jensen, 1997). Microclimatic effects of Lake Michigan have allowed *Sassafras albidum* Nutt.(sassafras) and *Nyssa sylvatica* Marsh.(black gum), more typical of forest communities much further south, to grow on sandy ridges in southern Cook County Forest Preserves (Shepard, 2001).

So how did all these southern trees get up into northern Illinois, if someone didn't plant them? The same way bogs, prairies, and deciduous trees got there - migration during major climatic shifts. It is known that deciduous trees migrate up river valleys. The range distributions of *Carya illinoensis* (Wang.) K. Koch (pecan) and *Q. lyrata* are good examples (Mohlenbrock, 1986). One possible hypothesis suggests a Gulf Coastal Plain route (Reznicek, 1994).

The deciduous Forests of the Northeastern Morainal section of Illinois developed sometime between 8-11,000 ybp in waves of migration from the unglaciated forests of the Coastal Plain, Appalachian, and Ozark Mountains following the retreat of the Wisconsinan glacier 12,000 ybp (King, 1981; Anderson, 1991). Forest ecosystems began colonizing the morainal regions probably around 11,000 ybp beginning with cool and wet ash/elm/maple communities and ending with the progressively warmer and drier oak/ hickory associations. Migrations of southern deciduous forests with Appalachian/Ozark affinities may have developed around the lower end of Lake Michigan just prior to or during the early stages of the Hypsithermal Period which was the warmest period beginning about 8,000ybp (Fuller, 1935). These southern bottomland species may have followed a migratory path of extensive alluvial silt loam deposits along the postglacial Mississippi – Illinois - DesPlaines - Kankakee River – Stony Creek (Cal Sag Channel) – Tinley Morainal Lakes/Creek bed (Wilman, 1971; Reznicek, 1994). The warmer temperatures, higher relative humidity and ample soil saturation levels contributed by ancient glacial morainal lakes may have provided the habitat for species that flourish on silty clay loams . Progressively drier climatic conditions (grassland formation of 5-8000ybp) of the period, coupled with annual burning by native Americans may have prevented further development and expansion of these taxa (Anderson, 1970). An 1834 land survey indicated that the Tinley Creek forest was surrounded by tall grass prairie in presettlement times (Bowles and McBride, 2002).

As the climate shifted again to cooler temperatures of the present day, widespread hybridization with northern species such as *Q. macrocarpa*, *Q. rubra*, and *Q. velutina* may have begun to occur. This may have resulted in the subsequent disappearance of genetically "pure" forms of *Q.stellata, Q. pagoda,* and *Q. falcata*

which left only their genes behind (no pun intended). Sensitive forbs, shrubs, and grasses typical of southern wetlands would have been the first to disappear leaving only the deeper-rooted hardy trees. The most adaptable species survived by incorporating themselves into the savannah/forest ecosystems around suitable sites of the Tinley moraine. Their persistence may be due to the milder microclimatic effects of Lake Michigan, higher moisture levels in the soil, and delay in urban development of the region. Land clearing may have actually helped regeneration of these oak species when the native Americans and their fires were gone (Fralish and Snyder, 1993; Mclain and Elzinga, 1994). The dense second growth of the present day flatwoods indicates a substantial seedbank of biodiversity after disturbance. The heights of the canopy trees and their reproductive capacity illustrate the richness of the soil and the acclimatization of these southern species to the area as a whole. Recruitment is impeded by exotics not by soil oxidation or erosion caused by agricultural practices.

The origin of the southern species can only be hypothesized at this point. They may exist as last vestiges of forest communities long since gone. The initial remoteness of the area coupled with the taxonomic confusion of oak species in general may have kept the trees hidden from botanists for years. Just as northern Illinois bog species are considered examples of a previous colder climatic age, so are these southern species representatives of a warmer age. Their presence truly makes them ancient relicts in a land that time forgot.

Acknowledgements

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A Gallery of Bur Oaks

Guy Sternberg
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Petersburg, Illinois USA
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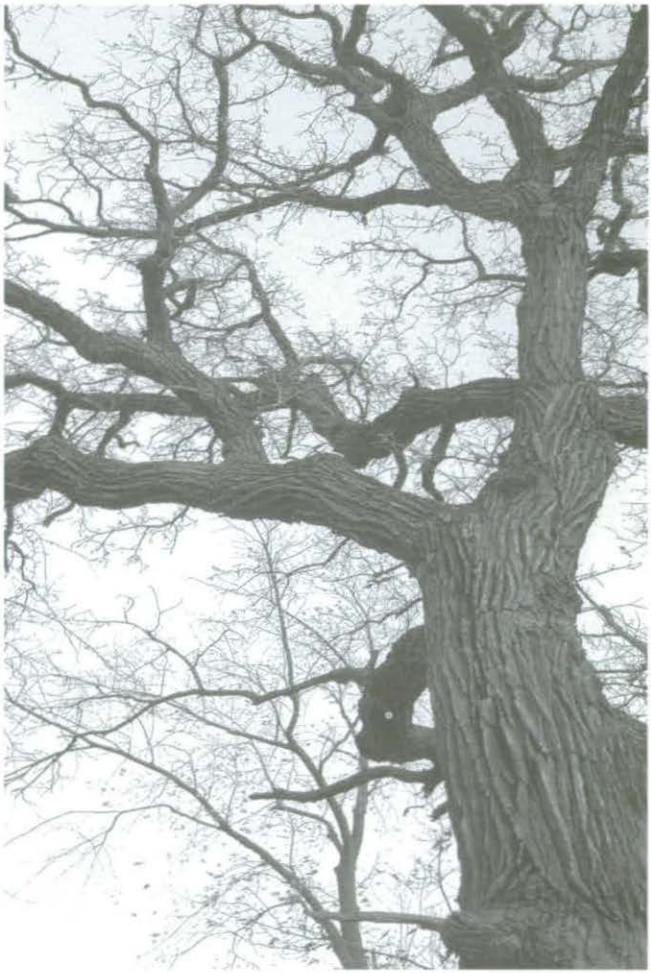
with artwork by Bernd Schulz



Quercus macrocarpa in a riparian forest in Livingston County, Illinois, approximately 250 years old

Buds of *Quercus macrocarpa*
© Bernd Schulz

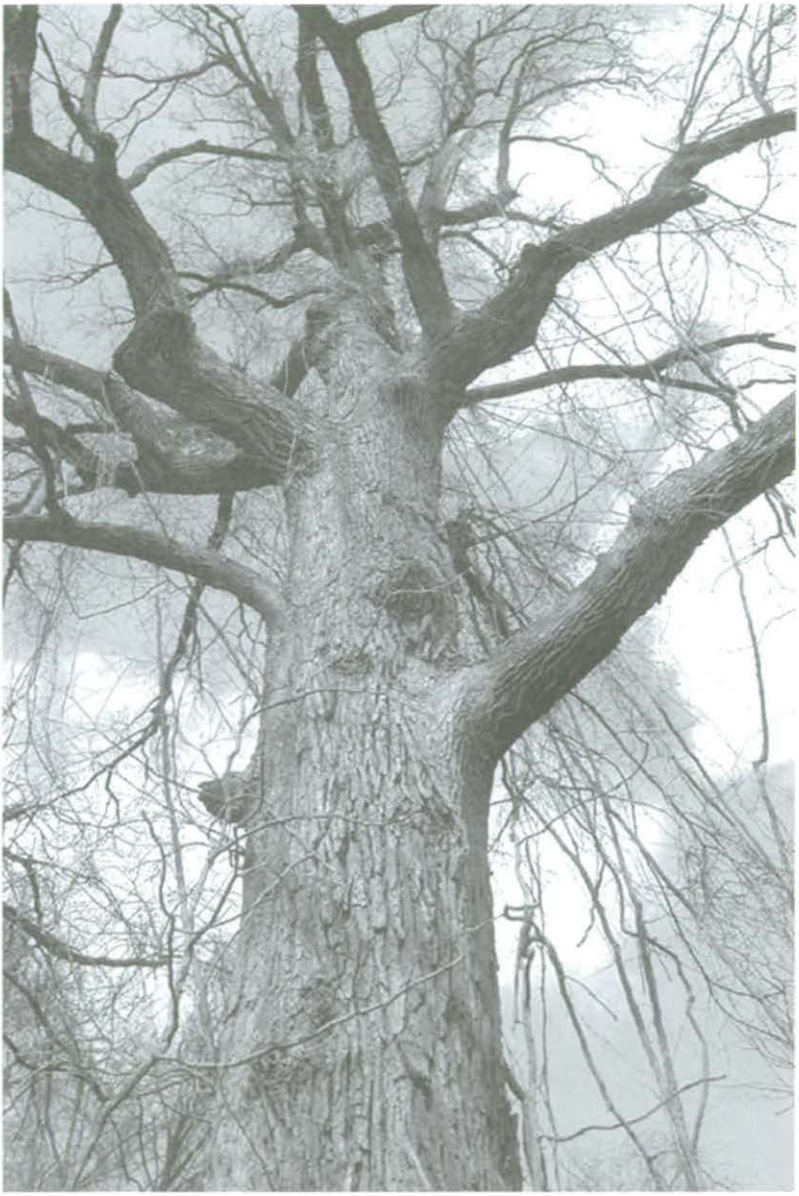
This bur oak at Starhill Forest in Menard County, Illinois was 35 years of age at the time of the photo.

A remnant of old growth upland forest, this bur oak in DeWitt County, Illinois is 5 meters in circumference

One of the most massive bur oaks in North America, this tree in Warren County, Indiana was 8.5 meters in circumference and 400 years old when examined by Guy and Edie Sternberg

This hollow bur oak 400 years old in Warren County, Indiana, is large enough to serve as shelter for Edie Sternberg and several friends

The Missouri co-champion bur oak, in a bottomland forest in Mississippi County, is 43 meters tall

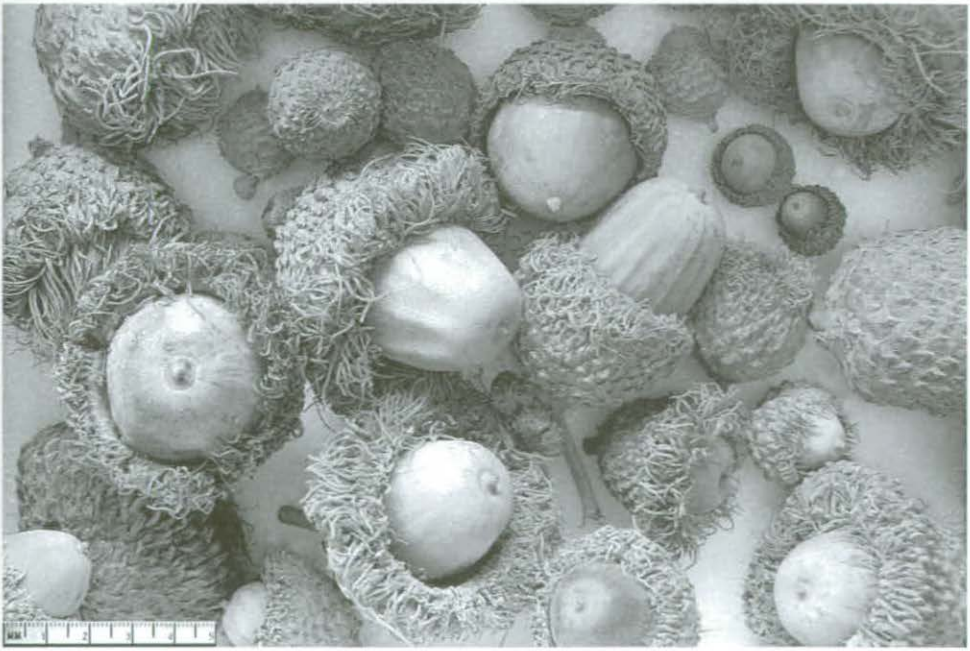


An old-growth *Quercus macrocarpa* 5 meters in circumference in a floodplain forest in Sangamon County, Illinois

An old savanna bur oak in a horse pasture in Macon County, Illinois, 6 meters in circumference

A massive presettlement savanna bur oak in McLean County, Illinois, 7 meters in circumference with a branch spread of 40 meters

Edie Sternberg is dwarfed by this 7-meter bur oak in McLean County, Illinois

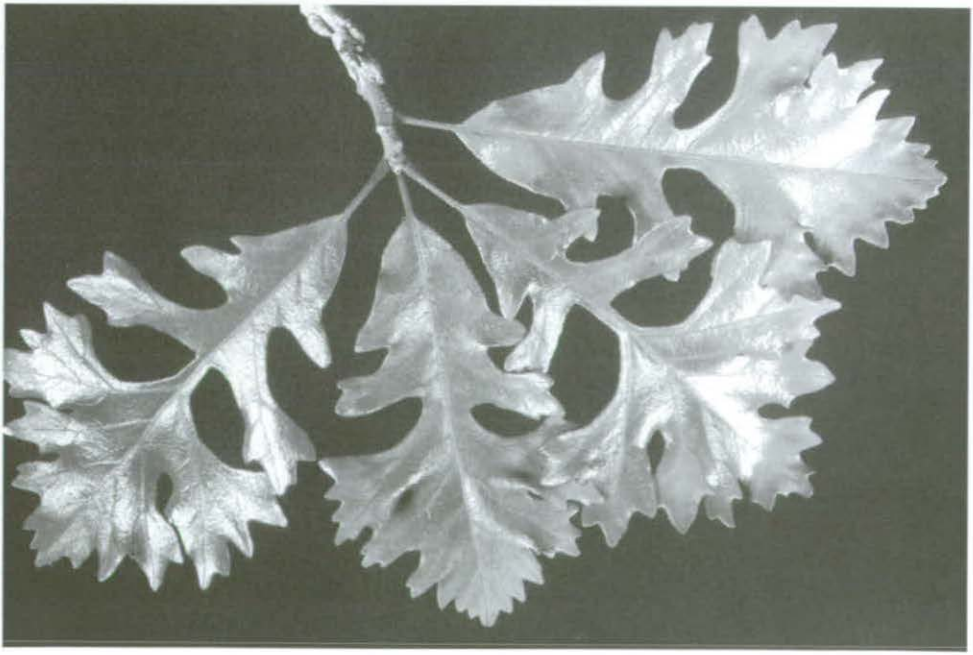


Acorns collected from throughout the native range of *Quercus macrocarpa* show extreme clinal variation in size and shape

The US national champion *Quercus macrocarpa* in Jessamine County, Kentucky is 8.5 meters in circumference

Quercus macrocarpa twigs can vary from nearly smooth to extremely corky, like this specimen in Porter County, Indiana

Staminate (catkins) and pistillate (axillary) flowers on *Quercus macrocarpa*



Foliage of *Quercus macrocarpa*

An old savanna bur oak in McHenry County, Illinois displays the rugged habit typical of the northern portion of its range

Part of an old bur oak savanna in Carroll County, Illinois

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