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

Tim Buchanan
737 Blue Mesa Avenue
Fort Collins, Colorado, USA
E-mail *tebuchanan@hotmail.com*
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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-

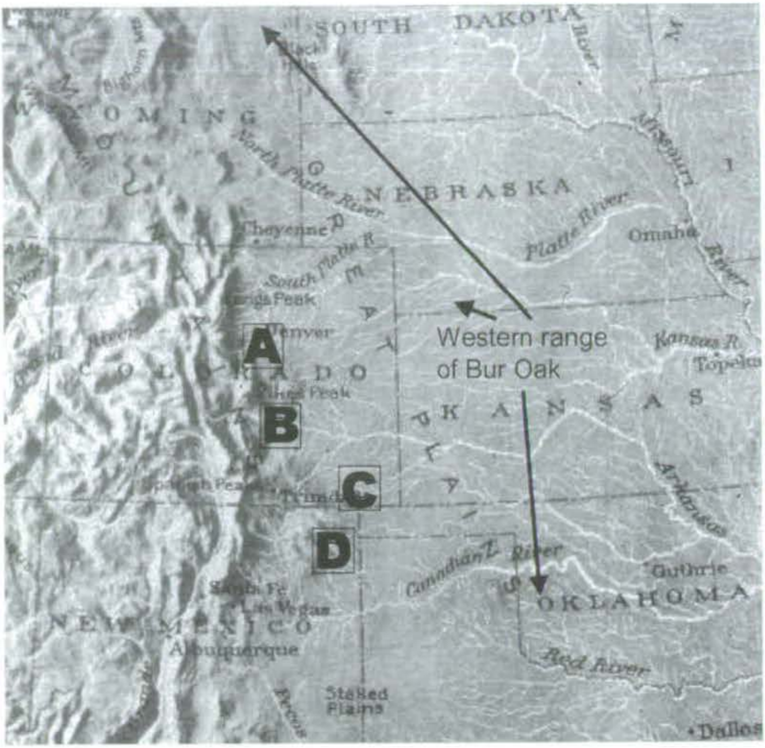

Figure 1 A. Castle Rock study area (CR) B. Green Horn Creek study area (GHC)
C. Cottonwood Creek Canyon D. Tramperos Creek Canyon

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

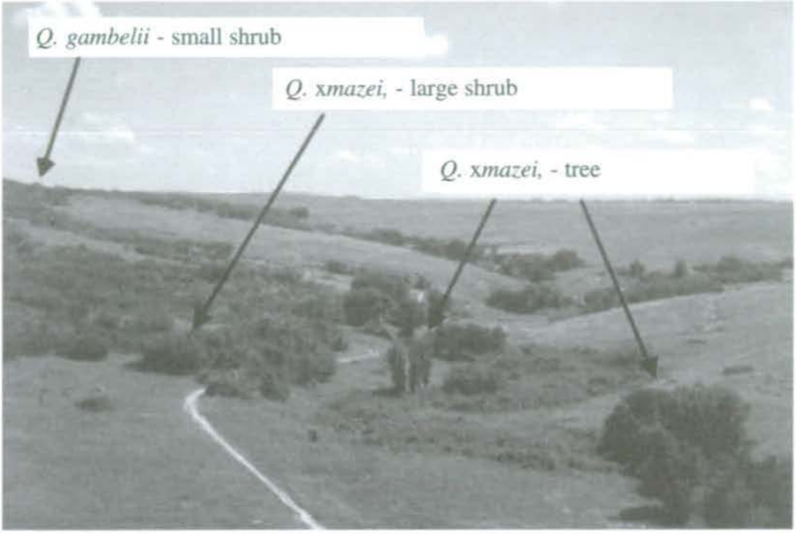

Fig 3. Habitats of *Q. gambelii* and *Q.* x*mazei*, Size and habit variation for *Q.* x*mazei*

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.

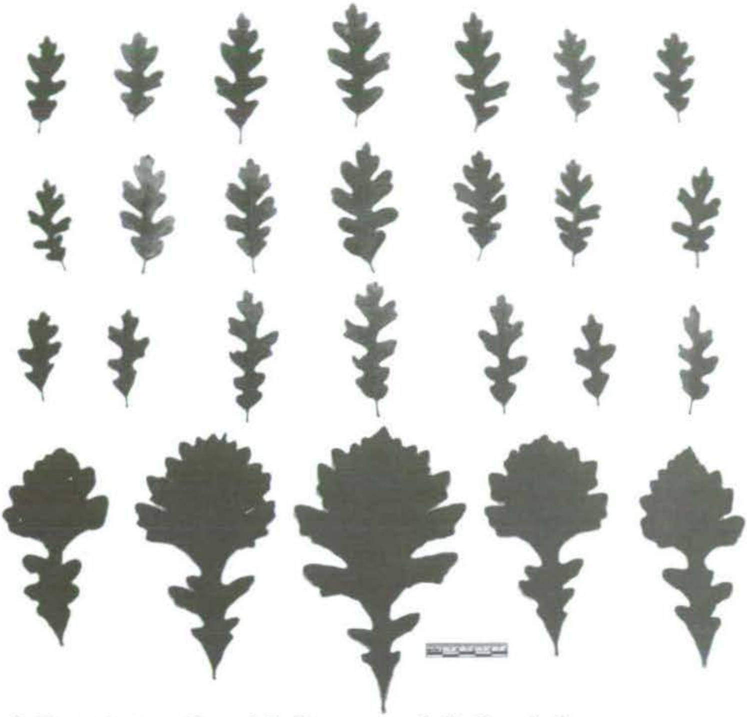

Fig 5. Top to bottom: Rows 1-3, *Quercus gambelii*, Row 4, *Quercus macrocarpa* SW Nebraska

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

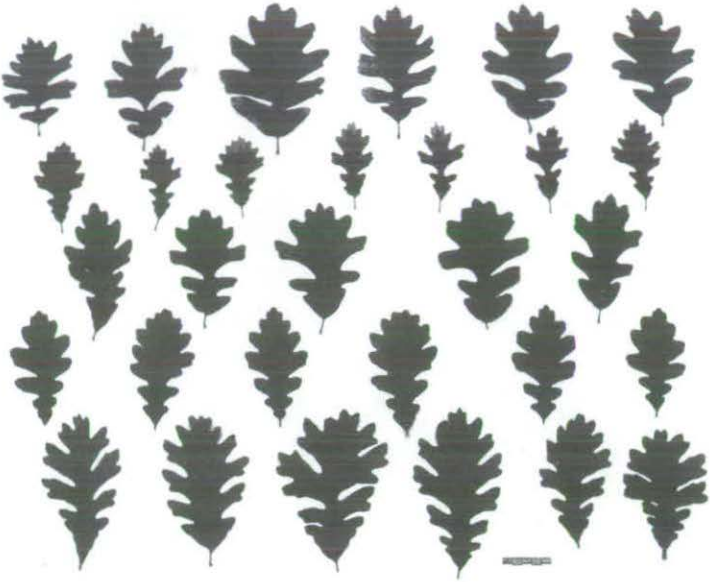

Fig 6. *Q.* x*mazei* with strong *Q. macrocarpa* introgression.

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

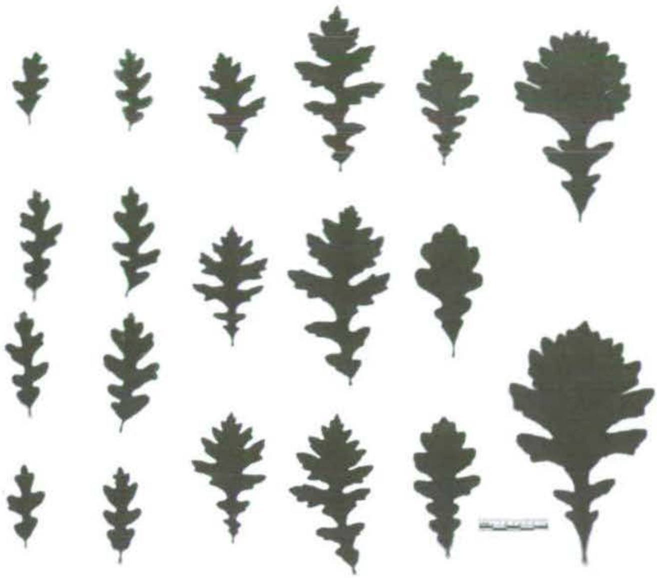

Fig 7. Left to Right: Row 1 and 2, *Q. gambelii*, Rows 3-5 *Q.* **x***mazei*, Row 5, *Q. macrocarpa* SW Nebraska

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

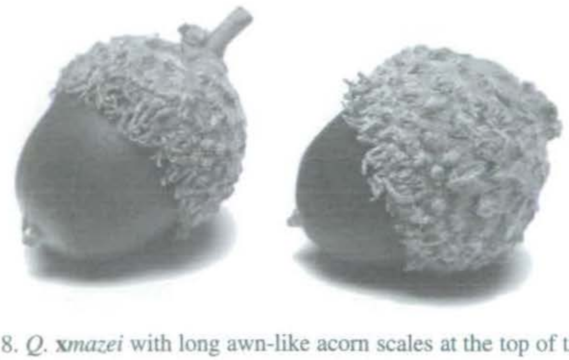

Fig 8. *Q.* x*mazei* with long awn-like acorn scales at the top of the cap.

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*).

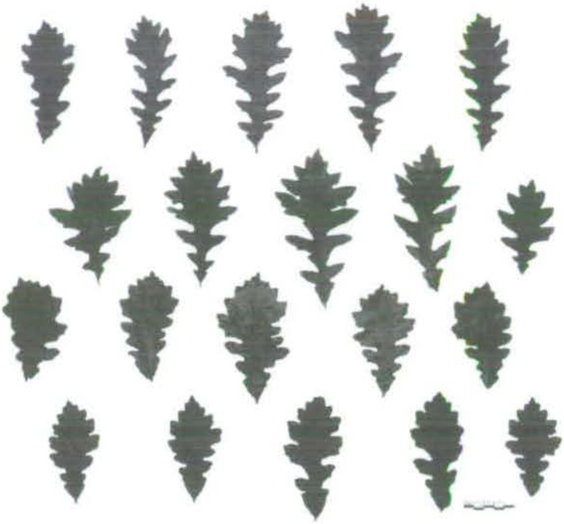

Fig 10. *Q. macrocarpa* x *Q.* x*undulata;* 2 year old half-siblings from Cottonwood Creek Canyon

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.* xundulata** (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 (flat-headed 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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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.

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