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SEXUAL REPRODUCTION OF GAMBEL OAK (*QUERCUS GAMBELII*) NEAR ITS NORTHEASTERN LIMIT

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Gambel oak (*Quercus gambelii* Nutt.) is a deciduous, clonal, white oak that ranges in size from shrub to small tree (Harper et al. 1985). It occurs throughout much of Arizona, New Mexico, Utah, and Colorado, with small ranges in Nevada, Wyoming, Oklahoma, and northern Mexico (Little 1971). In the southern part of its range the oak has wide elevational limits, and these limits narrow in the north (Neilson and Wullstein 1983). It generally grows with ponderosa pine (*Pinus ponderosa;* Harper et al. 1985), pinyon pine (*Pinus edulis;* Neilson and Wullstein 1986), or just below the lower limit of pinyons and junipers (personal observation).

Neilson and Wullstein (1983) showed that Gambel oak in northern Utah likely migrated to its present range using sexual reproduction during the mid-Holocene hypsithermal and that the species now persists there through asexual reproduction. They found mortality of planted 1-yr-old *Q. gambelii* to be very high in northern Utah and low in Arizona and New Mexico. Neilson and Wullstein (1983) found no more than 20 natural seedlings in northern Utah in 4 yr of fieldwork, but reported a high density in Arizona and New Mexico (range 120–1320 ha^{-1}, generally 300–900 ha^{-1} [Neilson and Wullstein 1986]). Neilson and Wullstein (1983) concluded that young, sexually reproduced individuals in northern Utah died due to late spring freezes and especially summer/fall drought caused by absence of Arizona summer monsoons in northern Utah. This explanation is consistent with relatively high survival of individuals planted at and north of *Q. gambelii* limits in Wyoming, where summer monsoons extend farther north than in Utah (Neilson and Wullstein 1983). In west central Colorado, Brown (1958) found sexual reproduction "less evident" than vegetative reproduction.

There is no published information on occurrence of sexual reproduction in northeastern parts of *Q. gambelii*'s range. In this study we asked whether sexual reproduction occurs near the northeastern limit of the species, and we discuss ages and microhabitat preferences of individuals we did find.

We searched for seedlings (<1 yr old) and saplings (small stems >1 yr old) in areas with mature oaks in October 1997 at 3 sites from Colorado Springs to Canon City, Colorado. Site 1 is immediately west of Colorado Springs along Lower Gold Camp Road (38°48′N, 104°53′W, 2440 m elevation), about 70 km south of the northern limit of the species in this portion of its range. Colorado pinyon (*Pinus edulis*), one-seed juniper (*Juniperus monosperma*), and mountain-mahogany (*Cercocarpus montanus*) mix with Gambel oak on steep (40°–45°) colluvial slopes with many large boulders. Site 2 is in Aiken Canyon Preserve (38°37.5′N, 104°52.5′W, elevation 2070 m), about 30 km south of Colorado Springs. We searched gentle slopes several hundred meters east of the abrupt transition between the Great Plains and the Front Range where clearly defined groups of *Q. gambelii* stems are separated by meadows. Site 3 lies 4 km north of Canon City (38°24′N, 105°15′W, 1710 m). Moderate oak cover occurs among *J. monosperma* and *P. edulis* on 15°–20° slopes.

When searching for seedlings and saplings, we walked all habitats within 20–30 m of mature oaks and pushed vegetation aside when necessary to ensure no individuals were missed. Small stems beneath mature oaks were not examined due to the very large number of

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small, vegetatively produced stems there. Candidate stems were identified as being sexually reproduced by the spent, attached acorn or by long, tapering taproots and lack of horizontal rhizomes (Neilson and Wullstein 1986). For each seedling/sapling or cluster of these, we noted its relative shading during summer and early fall in 3 categories: little shade (<20% of the day), intermediate shade, and nearly continuous shade (>80%). We estimated ages of individuals by counting terminal bud scale scars. We generally could do this with high confidence to about 4 yr and with reasonable confidence on older stems.

All seedlings and saplings occurred in bare soil, and none were within herbaceous vegetation. Sexual reproduction occurred close to edges of mature clones, with 64% of seedlings and saplings within 3 m, 30% within 3.1–5.0 m, and the remainder within 7.7 m. Seedlings and saplings generally showed strong preference for sites receiving partial summer shade; at Aiken Canyon and Canon City 80% of clusters or single individuals occurred in this type of microsite. At the Colorado Springs site all individuals were in full sun and were 1–2 yr old in a recently eroded area.

For all individuals with acorns still attached (roughly 50% of those found), acorns were several cm below the surface. Seventy-three percent of seedlings and saplings occurred in clusters of >1 stem with stems <1 cm from each other (Table 1). These originated from groups of 2–20 acorns that were touching each other several cm below the soil surface.

Most individuals from sexual reproduction (71%) were 1–2 yr old, and only 1 sapling was >7 yr old (Table 1). Heights for seedlings ranged from 2 to 15 cm, and for 2-yr-old saplings from 2 to 20 cm. The tallest sapling found was a 60-cm-tall, 6-yr-old stem. Occasional short, old saplings were found, e.g., a 15-yr-old, 16-cm-tall stem.

Occurrence of seedlings and saplings in partially shaded sites agrees with results of Neilson and Wullstein (1986), who found most seedlings on the northeast side of sheltering objects. In most situations apparently only individuals experiencing moderate shade can withstand summer drought stress (Neilson and Wullstein 1983).

Competition with herbaceous vegetation could conceivably limit sexual reproduction to bare soil since young *Q. gambelii* presumably experience the same competition with herbaceous vegetation as another oak in southwestern North America (Weltzin and McPherson 1997). However, even if this were an important limiting factor, it seems likely we would have found at least some seedlings or saplings within herbaceous vegetation. It is likely that animals dispersing acorns to bare soil contribute to the pattern we found.

Means of acorn dispersal for *Q. gambelii* are not clear from our data and likely include more than 1 vector. More research is necessary to definitively determine vectors, but possibilities will be considered here. Acorns that germinated on the soil surface may be simply gravity-dispersed. Several animal species could bury acorns in soil. Western Scrub Jays (*Aphelocoma californica*) were commonly observed caching Gambel oak acorns, and 96% of 211 caches were of single acorns on the west side of Colorado Springs in 1983–1986 (R. Bunn unpublished data). Western Scrub Jays usually pushed acorns into the soil until they were from just below the surface to 1.5 cm deep. They most often chose to place acorns into the soil in small bare areas within clumps of the short-grass blue grama/hairy grama (*Bouteloua gracilis/B. hirsuta*), but when caching near mid-grasses jays tended to place them in bare soil at the edges of clumps (R. Bunn unpublished data). It is these caches, when not recovered, which seem likely to produce some of the single seedlings and saplings we observed. Steller's Jays (*Cyanocitta stelleri*), which also disperse acorns (Vander Wall 1990), are markedly less common at our study sites then Western Scrub Jays.

Based on ranges and information on foods and storage habits (Fitzgerald et al. 1994), several small mammals could bury acorns in clusters. Rock squirrels (*Spermophilus variegatus*) commonly eat acorns when they are available (Ortega 1987) and carry large stores of acorns in cheek pouches (J. Ortega written communication). Other mammals that eat seeds and might bury clusters of acorns include golden-mantled ground squirrels (*Spermophilus lateralis*), Colorado chipmunks (*Tamias quadrivittatus*), least chipmunks (*T. minimus*), and deer mice (*Peromyscus maniculatus*).

Sexual reproduction does occur in the northeastern portion of the range of *Q. gambelii*, though apparently it is not common. We caution against inferring from our limited data on

TABLE 1. Gambel oak (*Quercus gambelii*) seedling and sapling numbers by site, by occurrence singly or in clusters, and by age.

Site	Search time (h)	Seedlings and Saplings: Total no.	Single	In clusters	No. / cluster (min, max)	No. clusters	Age in yr: 1–2	3–7	>7
Colorado Springs	4	31	8	23	3, 20	2	10	0	0
Aiken Canyon	25	33	9	24	2, 4	6	12	3	0
Canon City	6	25	7	18	2, 11	3	3	6	1

age structures (Table 1) that essentially no sexually reproduced individuals successfully mature. Larger stems, which may have originated from acorns, were less likely to be excavated by us to determine seedling status. Variation through time in successful sexual reproduction is also unknown based on our observations in a single season. In spring 1998 a small number of Gambel oak seedlings were observed in an area ca 0.3 ha of western Colorado Springs while none were observed in unirrigated parts of the same area the previous 8 yr (personal observation). Since sexual reproduction of *Q. gambelii* in northern Utah is limited primarily by late summer and fall drought (Neilson and Wullstein 1983), the above-average precipitation for June through October 1997 at Colorado Springs (NOAA 1997) caused by an El Niño event (Webster and Palmer 1997) may have increased seedling survival compared to most years. Thus, while sexual reproduction commonly occurs in the southern part of the *Q. gambelii* range (Neilson and Wullstein 1986), sexual reproduction is rare, or possibly episodic, in the northwestern (Neilson and Wullstein 1983) and northeastern (this study) portions of the range. The species apparently maintains itself in the northern part of its range primarily vegetatively; and occasional sexual reproduction creates possibilities of new clones, genetic variation, and dispersal to new areas.

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