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Ronald P. Neilson
University of Utah

L. H. Wullstein
University of Utah

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MICROHABITAT AFFINITIES OF GAMBEL OAK SEEDLINGS

Ronald P. Neilson[1,2] and L. H. Wullstein[1]

ABSTRACT.—Previous work suggested that Gambel oak seedlings are rare in the northern parts of its range in Utah where summer rainfall is relatively low but should be abundant in southern parts of the range where summer rainfall is usually high. Gambel oak grades from a relatively minor component of a ponderosa pine/mixed conifer assemblage in the south to a virtually monotypic formation in the north, where it exists as long-lived clones.

Quadrat analysis in Arizona and New Mexico, within the oak zone, revealed a seedling density ranging from 120 to 1320 per hectare. We found a significant tendency of seedlings to be located on the NE (cool, shady) side of sheltering objects in the environment. Mature ponderosa pine ranged in density from ca 40 to 500 stems per hectare, whereas mature Gambel oak ranged from ca 10 to 20 genets per hectare with ca 1 to 7 ramets per clone. These results support our previous conclusion that Gambel oak in northern Utah probably became established as a minor component of a mixed pine/oak woodland at a time in mid-Holocene when summer rainfall was much higher than today.

Gambel oak (*Quercus gambelii* Nutt.), a deciduous, white oak, is the dominant oak of the southern Rocky Mountain region. Its distribution is primarily encompassed by the states of Utah, Colorado, Arizona, and New Mexico. We previously demonstrated that the northern limits of Gambel oak in Utah appear to be constrained by the combined effects of two distinct airmass gradients (Neilson and Wullstein 1983). Probabilities of late spring freeze as determined by the polar front gradient and summer drought as determined by the "Arizona Monsoon" gradient appear to covary during global warming and cooling trends and appear to have synergistically produced a relatively sharp northern boundary (Neilson and Wullstein 1983). At present, seedling establishment of Gambel oak is rare in the northern part of its range (Neilson and Wullstein 1983). Our transplant studies (seeds and seedlings, Neilson and Wullstein 1983) and physiological studies (Neilson and Wullstein 1986) indicate that natural seedling establishment may be expected to occur only in the parts of the range where summer rains are sufficient for seedling survival.

Gambel oak persists at its northern limits today by virtue of rhizomatous, asexual reproduction (Neilson and Wullstein 1983). We believe that these oaks became established at their northern limits through sexual reproduction and seed dispersal at some time during the mid-Holocene thermal maximum when limiting stresses would have been reduced (Neilson and Wullstein 1983). At that time the shrub and tree community composition in northern Utah, near the northern limits of distribution for this species, might have been similar to that where the species is capable of sexual reproduction and seedling establishment today. Near its northern limits today, where it reproduces asexually, Gambel oak forms an essentially monotypic plant formation, or "mountain brush community" (Ream 1963). In the southern part of its range, where it reproduces sexually, Gambel oak is a relatively minor component of a mixed pine-oak woodland. The purpose of this study is to document the density of Gambel oak seedlings in regions of high summer rainfall, their microhabitat affinities and the general canopy composition of their associated plant communities.

METHODS

In September 1979, 15 quadrats were established in Arizona and New Mexico to ascertain the density of Gambel oak seedlings in various habitats. Excavation of root systems revealed that seedlings can usually be distinguished from suckers on the basis of clustering. Suckers tend to occur in tight clusters, while seedlings are widely dispersed. In many

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[1] Department of Geography, University of Utah, Salt Lake City, Utah 84112.

[2] Present address: University of Utah Research Institute, Salt Lake City, Utah 84108.

cases the spent acorn was still attached to the seedling. It was also found that true seedlings possessed a readily extractable, vertically oriented taproot, which exhibited well-defined taper, whereas suckers were always attached to a horizontally oriented rhizome within a few cm of the surface, which exhibited little or no taper. Thereafter, seedlings were distinguished from suckers by counting shoots that exhibited isolation from other shoots by more than two meters. In doubtful instances plants were examined for tap roots. All oaks less than 30 cm in crown height were arbitrarily classified as seedlings unless otherwise determined to be suckers. Fourteen large seedlings were collected at random for estimations of age and taproot growth rates.

Of the 15 quadrats, 13 were 0.1 ha and square. The remaining two quadrats were 0.04 and 0.05 ha, respectively, and roughly square. The quadrat sites were chosen to reflect apparent extremes of habitat within an area. In areas exhibiting little variation in topography (e.g., two flat sites south of Flagstaff), the quadrat placement was essentially random. In areas of diverse topography, the quadrats were chosen to encompass previous seedling plantings (Neilson and Wullstein 1983), selected to reflect mesic and xeric extremes within the region.

Three quadrats were placed in each of two flat sites on the Mogollon Rim south of Flagstaff near the headwaters of Oak Creek Canyon. Three contiguous quadrats on Humphrey Peak (near Flagstaff, Arizona) sampled a gradient from swale to ridge on an east-facing slope. Three quadrats were established in the vicinity of Pinedale, Arizona, on the Mogollon Rim. Two of these were on flats separated by several kilometers. The third was on a south-facing slope. There were no previous plantings in this vicinity. Three quadrats were placed in the Sandia Mountains of New Mexico. Two of these were on east-facing ridges of differing moisture regime located near Cold Spring Picnic Ground (see Table 1). The third was on a southfacing slope. Latitude, longitude, elevation, slope, aspect, general canopy composition and density were noted. These data are summarized in Table 1.

As the natural seedlings were counted, they were marked with orange paint to eliminate double counting and to insure a complete count. The location of each seedling was noted with regard to surface drainage patterns, whether it was sheltered or unsheltered from the sun (by trees, shrubs or rocks), and, if sheltered, its compass orientation (in 4 quadrants) with respect to the sheltering object. Seedling distribution with regard to sheltering objects was analyzed with a Chi-square test. In 3 of the 15 quadrats seedlings were simply counted, since the canopy was essentially closed, i.e., all seedlings in these quadrats were sheltered from the sun.

RESULTS

The general physical characteristics of the 15 quadrats are presented in Table 1. The communities ranged from dominant ponderosa pine (*Pinus ponderosa*) to mixed conifer communities. Gambel oak was usually a relatively minor component. More complete descriptions of these communities may be found in Layser and Schubert (1979).

The three contiguous quadrat sites on Humphrey Peak (Table 1) were of low-density ponderosa pine averaging 43 ± 35 pines/ha with an average dbh of ca. 40 cm. Gambel oak density on each quadrat was ca 20 genets/ha with 1–2 stems per clone and an average dbh of 17 cm/stem. These quadrats represent a gradient from a swale to a neighboring ridge. This is most evident by a combined increase in *Cowania* sp. and *Cercocarpus* sp. from zero in quadrat 1 to 8 in quadrat 2 and more than 100 in quadrat 3. Gambel oak seedling density was relatively high (range 360–590) and without apparent pattern along this steep environmental gradient.

Quadrats 4–9 were located on the flat Mogollon Rim south of Flagstaff in mature ponderosa pine forest averaging 350 ± 112 stems/ha with an average dbh (in each quadrat) ranging from 31 to 46 cm. Mature oak density was low in these quadrats, averaging ca 10 genets/ha with 1–7 stems per clone and an average dbh of ca 16 cm per stem. Seedling density in these six quadrats ranged from 240 to 860 ha. Quadrat 9, which had the highest seedling density (860/ha) of this group, was flanked by five large oaks.

Quadrats 10–12 represent three distinct habitats in the Pinedale area of the Mogollon Rim, a south-facing slope (No. 12), a relatively

TABLE 1. Site characteristics for the 15 quadrats (redundant data are not repeated within a geographic region).

Quadrat number	Geographic region	Latitude (decimal)	Longitude (decimal)	Elevation (meters)	Slope	Aspect	Soil WHC[1]	Canopy species[2]
1	Humphrey Peak	35.27	111.6	2226	17°	S 80° E	32-88/45-60	PIPO/QUGA
2					25°	N 70° E		PIPO/QUGA
3					25°	N 75° E		PIPO/QUGA
4,5,6	Flagstaff	35.03	111.73	2165	0°		40-90/50-77	PIPO/QUGA
7,8,9		35.00	111.67		8°	N 65° E	40-90/50-77	PIPO/QUGA
10	Pinedale	34.3	110.25	1982	4°	N 45° W	unknown	PIPO/QUGA
11				2012	0°			PIPO/QUGA/JUXX
12				1982	20°	S 10° E		PIPO/QUGA/JUXX
13	Sandia Mountains	35.13	106.53	2226	15°	S 80° E	46-122/58-65	PIPO/PIED/JUXX/QUGA
14					10°	S 60° E	40-85/42-46	PIPO/PIED/JUXX/QUGA
15		35.15	106.53	2165	23°	S 30° W	54-66/60-62	PIPO/PIED/JUXX/QUGA

[1] WHC = Water Holding Capacity (%). A range of water holding capacities is reported for the soil surface layer and at a depth of 30 cm (Neilson and Wullstein 1983).

[2] PIPO = *Pinus ponderosa*, QUGA = *Quercus gambelii*, PIED = *Pinus edulis*, JUXX = *Juniperus* sp.

flat lowland area (No. 10), and a flat plateau area. All three areas possessed a high density of seedlings, with the plateau exhibiting the greatest number (1,080/ha). All three areas had been artificially thinned, but still possessed a fairly dense canopy. Quadrats 10 and 12 were primarily mature ponderosa pine with ca 500 stems/ha and an average dbh of 18 and 27 cm, respectively. Quadrat 11 was mixed conifer/oak woodland.

Quadrats 13–15 in the Sandia Mountains, New Mexico, were characterized by mixed conifer forest with a Gambel oak component. Quadrat 15, on a south-facing slope, was similar in seedling density to most other quadrats, with 513 seedlings/ha. Quadrats 13 and 14 were on east-facing ridges. These quadrats were of the same elevation and aspect and were within 1 km of each other. Quadrat 14 was located on a primary ridge separating major drainage basins. It was at a lower angle than No. 13 and contained more bare ground. Quadrat 13, by contrast, was located on a ridge within a major drainage basin, was at a steeper angle, and contained less bare ground than No. 14. By virtue of their close proximity, the two quadrats would be expected to receive similar amounts of rainfall. Because of its position as a drainage divide, the primary input of moisture to Quadrat 14 was likely limited to incident rainfall. Quadrat 13, however, received moisture from both rainfall and runoff from the surrounding basin within which it occurred. This was particularly evident from extensive rill development, which was absent on Quadrat 14. Quadrat 13 possessed 1,320 seedlings/ha in contrast to 120 seedlings/ha in Quadrat 14.

Table 2 indicates the number of seedlings in sheltered and unsheltered positions for each of the quadrats. Quadrats 11, 13, and 15 were too dense to allow judgements of sheltering. Sixty percent (341/571) of the seedlings in 12 quadrats (i.e., excluding quadrats 11, 13, and 15) were scored for their orientation with regard to a sheltering object (Table 2, Fig. 1). The distribution is significantly skewed ($X^2 = 33.74$, $P \ll .01$) to the NE quadrant.

Age estimates of 14 randomly collected seedlings (<30 cm crown height) ranged from 6 to 17 years. Regressions of root length against root diameter indicated root taper ranging from −.06 to −.19 mm/cm (r^2 ranged from .81 to .99). Since these measurements were obtained from broken taproots, total root length was extrapolated from the regression equations and found to range from 40 to 114 cm. Root growth rates were estimated to range from 2.7 to 11.4 cm/yr.

Discussion

Several points are apparent from these data. First, Gambel oak seedlings are abundant and widely distributed in the southern part of the range of this species and are rare in

TABLE 2. Total seedlings (sheltered and unsheltered) per quadrat.

Quadrat no.	Sheltered	Unsheltered	Seedlings/ hectare
1	40	19	590
2	16	20	360
3	32	16	480
4	24	20	440
5	29	6	350
6	14	10	240
7	19	20	390
8	12	13	250
9	58	28	860
10	50	37	870
11	unknown	unknown	1080
12	35	41	760
13	unknown	unknown	1320
14	12	0	120
15	unknown	unknown	513

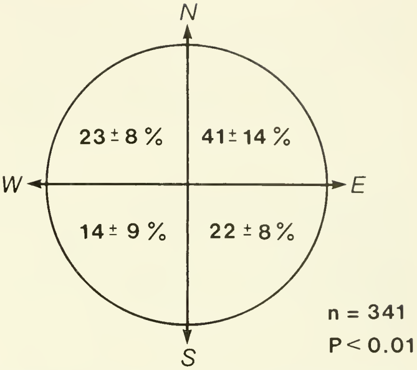

Fig. 1. Compass orientation of seedlings (% per quadrant) associated with a sheltering object in all quadrats, excluding quadrats 11, 13, and 15 (see text for explanation).

the northern part of the range. Second, mature Gambel oak is a relatively minor component of the ponderosa pine–mixed conifer forest. Third, although Gambel oak does clone in Arizona and New Mexico, the apparent number of ramets per clone is relatively few (1–7 in the quadrats sampled, although larger numbers can be found) compared to the hundreds to thousands of ramets per clone that are common in the northern parts of the range (Brown 1958, Ream 1963). A corollary to this point is that mature ramets are much larger in the south than in the north, where dbh is typically in the range of 5–8 cm (Brown 1958, Ream 1963) compared to 16–17 cm in the south. Fourth, although seedlings are widespread across a range of microhabitats, their distribution and abundance does appear to reflect some dependence on soil moisture.

This last point is most interesting. We previously reported (Neilson and Wullstein 1983) that seedling survival in the southern parts of the range was largely independent of microhabitat, being high in all situations from sheltered to unsheltered. The three contiguous quadrats on Humphrey Peak are in support of this contention. Whereas the shrub distribution indicated considerable edaphic and/or hydrologic differences between the swale and ridge habitats, the seedling density across this gradient indicated no trend. Nevertheless, 60% of the seedlings in these and the other quadrats did exhibit a strong pattern of sheltering, apparently favoring mesic microhabitats. This is further supported by the two ridge quadrats in the Sandia Mountains. One ridge was apparently swept frequently by surface flow, as indicated by the extensive rill development and the location of the ridge within a major drainage basin. Intense summer thunder showers are common in this region (Bryson and Lowry 1955). This ridge contained the highest density of seedlings observed in any of the quadrats, notwithstanding the apparently high surface wash. A neighboring ridge, a major drainage divide, apparently received little to no runoff from the surrounding landscape, as indicated by the absence of rills. This ridge contained the lowest density of oak seedlings observed (all of which were sheltered) in any of the quadrats. In almost every respect but hydrology, the two ridges appear to be similar. This suggests that even in a region where summer rain is relatively high, a consistently mesic microhabitat may be required to provide adequate soil moisture for seedling survival.

The six quadrats on the relatively flat Mogollon Rim south of Flagstaff present some evidence that the density of seedlings is not entirely independent of the density of adults. Five of these quadrats possessed seedling densities ranging from 250 to 440 per hectare (quadrats 4–8), whereas one (quadrat 9) possessed a seedling density of 860 per hectare (Table 2). All these quadrats contained a similar density of mature oaks. However, quadrat 9 with the highest seedling density in this region, was flanked by five large oaks, suggesting some dependency of seedling density on the local density of seed–bearing trees.

Since seedling density was found to be relatively high throughout the oak zone in the southwest, why are mature oaks relatively rare in these forests? It may be that conifer seedlings, which are also abundant in these forests, grow much more rapidly than the oaks and gain dominance through competition for light and moisture. Several oak seedlings (of less than 30 cm stature) were aged on the basis of taproot rings and were judged to be from 6 to 17 years old. By contrast, ponderosa pine raised in several provenance gardens in the Great Plains grew between 0.7 and 3.9 m in 10 years (Read 1983). Thus, overtopping of oak seedlings by ponderosa pine seedlings may competitively inhibit the growth of oaks.

Once past the establishment phase, the position of oaks in the landscape is apparently independent of minor differences between microhabitats. The density of mature oaks was relatively uniform between all the quadrats, which varied considerably in topography. The ultimate fate of seedlings, once established (i.e., taproot developed), is likely determined by biotic factors, including competition with pines and herbivory from insects and vertebrates (primarily rabbits and cows) (Neilson and Wullstein 1983).

In conclusion, where Gambel oak is least abundant in its geographic range, it is capable of sexual reproduction, seed dispersal, and seedling establishment. Conversely, where Gambel oak is most abundant in its geographic range, near the northern limits, its mode of reproduction is primarily asexual. The establishment of Gambel oak seedlings is dependent on consistent soil moisture, even in areas where summer rainfall is high. These results support the hypothesis that Gambel oak in northern Utah, existing today by asexual reproduction, was likely established as a relatively minor component of a mixed pine/oak woodland under a mid-Holocene climate with more favorable summer moisture conditions in northern Utah than presently occur (Cottam, Tucker, and Drobnick 1959, Neilson and Wullstein 1983).

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