

Limited uptake of summer precipitation by bigtooth maple (*Acer grandidentatum* Nutt) and Gambel's oak (*Quercus gambelii* Nutt)

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Abstract. Winter and spring precipitation that saturates to deep soil layers precedes summer droughts in the Intermountain West. Occasional summer convection storms relieve summer drought, but are infrequent and unreliable from year to year, leading to the hypothesis that dominant tree species might not invest limited carbon reserves to surface roots to take up summer precipitation in these regions. We compared the hydrogen (δD) and oxygen ($\delta^{18}O$) isotope ratios of winter, spring and summer precipitation to that of xylem sap water in *Acer grandidentatum* and *Quercus gambelii*, two dominant trees of this region. By this method we could identify water sources utilized throughout the growing season. Xylem δD and $\delta^{18}O$ values changed significantly when each species leafed-out; this change was not associated with changes in either soil or plant water status (as measured by predawn and midday water potentials). This shift is apparently related increased transpirational flux, which may flush out residual stem water from the previous growing season. δD values of xylem sap of both species matched winter precipitation input values throughout most of the summer, indicating a reliance on deep-soil moisture sources throughout the growing season. Mature *Q. gambelii* did not take up summer precipitation, whereas *A. grandidentatum* responded slightly to the largest summer rain event. Small trees of both species, particularly *A. grandidentatum*, showed a limited uptake of summer rains.

Key words: Hydrogen isotope ratio – Oxygen isotope ratio – Water source – Rooting patterns – Drought stress

Introduction

Several recent studies have indicated that a number of perennial plant species in the Intermountain West do not significantly utilize summer precipitation (Ehleringer et al.

1991; Gregg 1991; Flanagan et al. 1992; Donovan and Ehleringer 1994). Instead these species appear to rely on deep soil water that originates from winter recharge of the soil profile. Identification of plant water sources in these systems is possible because the hydrogen (δD) and oxygen ($\delta^{18}O$) isotope ratios of precipitation differ between seasons and because there is no fractionation of isotopes during water uptake (see Ehleringer and Dawson 1992 for a review). Ehleringer and Dawson (1992) hypothesized that in habitats with a low probability of summer precipitation, long-lived perennials might have a greater net carbon gain if they did not invest in fine roots in the upper soil layers, but instead allocated carbon to develop roots for uptake from more reliable deeper soil depths.

Precipitation varies significantly along elevation gradients in the Intermountain West region of the United States, and at the lower elevations water is the primary limiting factor to plant growth (see Comstock and Ehleringer 1992 for review). In the transition zone between the lower-elevation grass-shrublands and the higher-elevation fir forests is shrub woodland, which is dominated by deciduous hardwoods including *Quercus gambelii* Nutt. and *Acer grandidentatum* Nutt. (Cronquist et al. 1972; Welsh et al. 1987).

Although taxonomically unrelated, *Q. gambelii* and *A. grandidentatum* are physiognomically similar. On dry slopes, individuals of both species grow as clonal shrubs with numerous, densely spaced ramets, and large underground biomass (Clary and Tiedemann 1986). In riparian zones, both exhibit a tree life form. However, morphological and ecological differences between these two species may result in temporally different patterns of water source utilization. *A. grandidentatum* has diffuse porous, and *Q. gambelii* has ring porous xylem anatomy, and consequently different foliar phenologies (Wang et al. 1992). *A. grandidentatum* may leaf out several weeks earlier than *Q. gambelii*, at a time when the soil moisture profile is charged by highly predictable winter and spring storms (Caldwell 1985; West 1988; Dobrowolski et al. 1990). *Q. gambelii* typically leafs out in late spring, closer to the beginning of the summer drought (Dina 1970), which is

potentially relieved by convective thunderstorms that often wet only the upper soil layers (Caldwell 1985, West 1988; Comstock and Ehleringer 1992).

In this study, we examined the δD and $\delta^{18}O$ values of stem water to evaluate water use by *Q. gambelii* and *A. grandidentatum* in northern Utah. We ask the following: what water sources do these shrub species use throughout their growing season? Do they use summer precipitation? Is variation in foliar phenology related to water source? Do water availability and water stress relate to water source? Since the growing season of *A. grandidentatum* occurs in spring when upper soil layers are charged with adequate moisture, and because it tends to occupy the more mesic portions of their shared range, we hypothesized that *A. grandidentatum* may be more likely to utilize surface water than *Q. gambelii*.

Materials and methods

Study site

This study was conducted in the Red Butte Canyon Research Natural Area near Salt Lake City, Utah, USA (latitude 40°48'N, longitude 111°47'W; see Ehleringer et al. 1992 for a complete description). Two field sites were a xeric "slope" site (1890 m) on a south-facing hillside approx 60 m above perennial Red Butte Creek, and approximately 2 km SW of the slope site, a "streamside" site (1680 m), where all sampling was done within 3 m of Red Butte Creek. Soils at the slope site were sandy and gravelly loam overlying shale and mudstone. Those of the streamside site were an undifferentiated floodplain alluvium of the same. On the slope, an open-canopy scrub grove site was sampled where *Q. gambelii* and *A. grandidentatum* were the dominant species (perennial grasses occupied the open areas). Both species were in nearly equal abundance, with 53% of the live ramets oak and 47% maple within the 120 m² study area. Five adjacent pairs of each species were chosen for study. Individuals within each pair were of similar size, ramet number and density. The streamside site had a closed canopy, with *Acer negundo*, *Betula occidentalis* and *A. grandidentatum* dominant. *Q. gambelii* occurred at much lower frequency at the streamside site, therefore only three unpaired trees of each of the study species were sampled in an unpaired design.

Phenology

The timing of phenological events was recorded for each individual at approximately 12 day intervals from mid March to late September 1991. Eight phenological stages were identified: buds resting, buds swollen, flower bud break and immature flowers, mature flowers and leaf buds breaking, leaves flushed and expanding, leaves fully expanded and fruits maturing, leaves yellowing and fruits dispersing, leaves yellowed and falling.

Water potentials

Midday xylem pressure potential (Ψ_{md}) measurements ($n = 2$) were made with a pressure chamber (PMS Instruments, Corvallis, Ore., USA) on each of ten sampling dates between early April and late September. Predawn xylem pressure potentials (Ψ_{pd} , $n = 2$) were also measured on the same sampling dates from May to September. Before bud break, Ψ_{md} was also measured with a stem psychrometer (Dixon and Tyree 1984) for comparison with the pressure chamber data.

Stable isotope ratios of stem water, precipitation, and stream water

A random sample of suberized stems for hydrogen isotopic analysis was collected from at least three ramets of each individual on seven sampling dates between March and September 1991. Stems were cut from trees, immediately sealed in glass vials, and stored frozen until stem water was extracted via a cryogenic vacuum distillation technique (Ehleringer and Osmond 1989). A portion of the waters distilled from samples collected from slope trees of each species ($n = 2$) on the April, June, and July sampling dates were also used for oxygen isotopic analysis.

Daily precipitation collections were made nearby (12 km S, 1545 m) for isotopic analysis. Daily precipitation amounts were reported by the National Oceanic and Atmospheric Administration. The monthly average δD value of precipitation was determined by measuring the isotopic composition of each storm event and weighting by the amount of precipitation in a storm. Stream water samples were collected from Red Butte Creek.

Water samples were prepared for hydrogen isotopic analysis by reducing the hydrogen to its diatomic form with zinc (Coleman et al. 1982). A subset of the water samples was prepared for oxygen isotope analysis by equilibration of the water with CO₂ (Epstein and Mayeda 1953; Socki et al. 1992). Isotopic composition was measured on a Finnigan MAT delta-S isotope ratio mass spectrometer (San Jose, Calif. USA). Results are expressed in delta notation (δD and $\delta^{18}O$), which is the sample isotope ratio relative to that of Standard Mean Ocean Water (SMOW). Measurement precision, based on repeated measurements of two secondary standards, was $\pm 1.1\%$ for δD and $\pm 0.4\%$ for $\delta^{18}O$.

Size comparison

We established two additional sites, adjacent to the sites described above, to determine if ramet size was related to the plants' ability to use summer precipitation. Three days after a very large summer precipitation event in early September, we sampled 12 *A. grandidentatum* individuals of varying size on the slope, six individual *Q. gambelii* on the slope and six *A. grandidentatum* by the stream. Stems were collected for hydrogen isotopic analysis (as described above) and trunk diameter was measured at a height of 1.5 m.

Statistics

Repeated measures analysis of variance (SAS 1985) was used to determine if Ψ and δD differed based on species. Differences in the mean values of both Ψ and δD for each species between sampling dates were compared with a Waller-Duncan K -ratio test.

Results

The spring months (March through early June) experienced abundant rainfall of low, but increasing δD values. June through early August were dry until the onset of summer rains which had higher δD values (Fig. 1). The δD values of Red Butte Creek stream water did not show the same seasonal fluctuation as precipitation (Fig. 1), but maintained a narrow range of δD values similar to those of winter and early spring precipitation.

The timing of all phenological events occurred 11–15 days later for *Q. gambelii* than for *A. grandidentatum* (Fig. 1). Because of its earlier start, *A. grandidentatum* had finished flowering, breaking bud, and had almost fully-

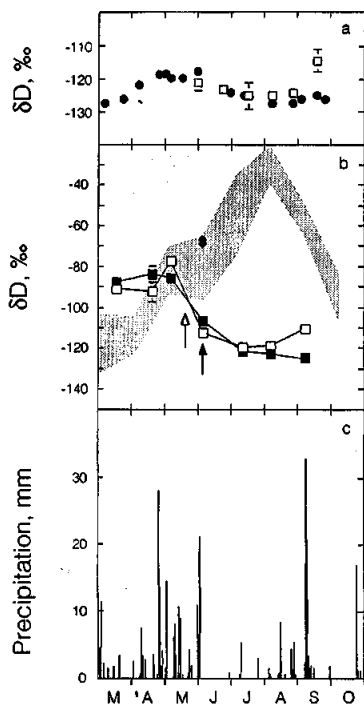


Fig. 1. **a** Mean δD values of xylem waters of streamside *A. grandidentatum* (open square) \pm standard error ($n = 3$) and stream water (shaded circle) throughout the growing season. **b** Mean δD values of xylem waters of slope *Q. gambelii* (closed square) and *A. grandidentatum* (open square) \pm standard error ($n = 5$) throughout the growing season. The shaded area connects the standard errors of the mean monthly weighted δD values of precipitation. Closed diamonds represent two *Q. gambelii* individuals that were phenologically later than the rest of those sampled, and at the June sampling had not yet flushed leaves. Open arrow represents date of leaf flush for *A. grandidentatum*, and closed arrow that of *Q. gambelii*. ■ Precipitation; □ maple; ■ oak. **c** Daily precipitation for the 1991 growing season at Salt Lake City, Utah

expanded leaves before the May rains ceased. In contrast, *Q. gambelii* had just broken leaf bud after most of the spring precipitation had occurred.

Once plants had leafed out at the streamside site, Ψ_{pd} changed little throughout the growing season in either species (Fig. 2). On the slope site, Ψ_{pd} of both species decreased throughout the growing season (Fig. 2). The water potentials of the two species began to diverge in spring and by late summer the Ψ_{pd} values of *A. grandidentatum* were significantly lower ($F = 5.0$, $P < 0.05$) than those of *Q. gambelii*. Intense summer rains occurred late in the summer, but did not affect Ψ_{pd} values for either species at either site.

The Ψ_{md} water potentials of both species at the slope site decreased throughout the season (Fig. 2). Following summer rains, the Ψ_{md} values for the *Q. gambelii* continued to decrease, whereas those of the *A. grandidentatum* increased slightly but significantly ($t = 0.7$, $P < 0.5$), possibly indicating a response to summer rains, or that midday conditions were less stressful.

As slope plants leaves flushed in the spring, the δD values of stem waters of both species showed a significant decline (for *A. grandidentatum*, $F = 70.5$, $P < 0.0001$, and

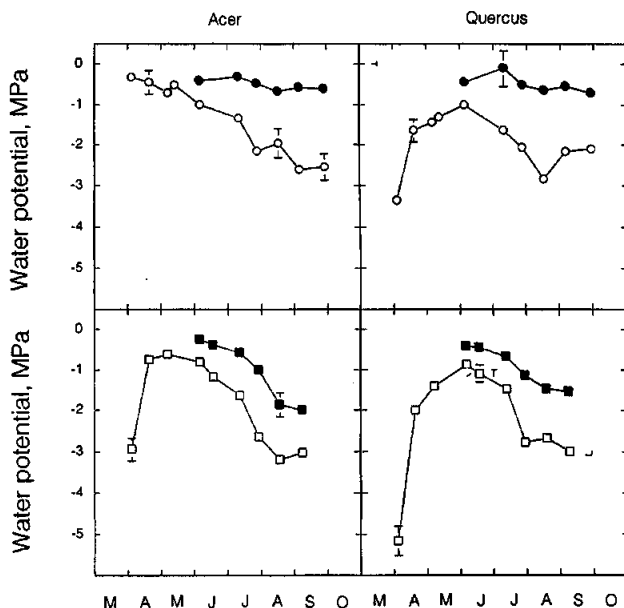


Fig. 2. Seasonal course of mean predawn (closed) and midday (open) water potentials of *Q. gambelii* and *A. grandidentatum* on streamside (circles) and slope (squares) sites, \pm standard error, $n = 5$

for *Q. gambelii*, $F = 7.15$, $P < 0.001$). This decline appeared to track the δD values of the source waters, from high δD values similar to spring precipitation, to more negative δD values that were similar to the δD values of winter precipitation (Fig. 1). This change was not concurrent with any obvious change in either Ψ_{pr} or Ψ_{md} values, but instead corresponded only with leaf flush for both species. On the June sampling date, three of the *Q. gambelii* individuals sampled had flushed leaves while two had not. The latter two, presented separately from the population mean in Fig. 1, had stem δD values that were more positive than those individuals that had flushed leaves. The two late individuals had δD values similar to current precipitation, until after they too flushed leaves. Once all trees of both species had leaves, their stem water δD values remained similar to those of winter precipitation despite several small rain events. After large storms in early September, the *A. grandidentatum* diverged from previous values δD ($F = 70.5$, $P < 0.0001$), while the *Q. gambelii* stem water was statistically identical to pre-storm δD values.

The δD and $\delta^{18}O$ values of precipitation collected during the study period are plotted in Fig. 3 in a linear regression known as the local meteoric water line (MWL). Figure 3 also shows the relationship between δD and $\delta^{18}O$ values of a subset of the xylem water samples taken from the slope population for three sampling dates: (1) late April, before leaf flush for each species, (2) early June, when all the *A. grandidentatum* and all but two of the *Q. gambelii* had flushed, and (3) mid-July, after all leaves had flushed. Xylem sap of every plant that had leaves did not deviate from the MWL, regardless of species or sampling date. This indicates that there was no difference in isotopic composition between the winter precipitation and xylem

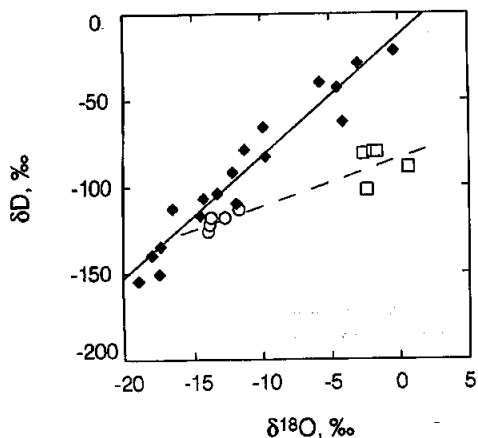


Fig. 3. The relationship between hydrogen and oxygen isotope ratios of 1991 precipitation water (closed diamond) and xylem water samples of both species before leaf flush (open square) and after leaf flush (open circle). The linear regression $\delta D = 7.0 * \delta^{18}O - 13.3$ (solid line) describes the MWL. The dashed line is the linear regression $\delta D = 1.1 * \delta^{18}O - 98.5$ that describes the stem water isotopic relationship. ♦ 1991 precipitation; □ stem water before flush; ○ stem water after flush

sap isotope values of plants in leaf, specifically that plant water sources were not subject to evaporative enrichment. On the other hand, the isotope ratios of xylem sap from plants that had yet to flush fell below the MWL. *Q. gambelii* individuals both with and without leaves that were sampled on the same day in early June exemplify this pattern. Xylem sap isotopic values taken from leafless plants were off the MWL in a manner that indicated they had been evaporatively enriched; the *Q. gambelii* individuals with leaves had xylem sap isotopic values matched both MWL values, and the values of samples taken in July.

The relationship between individual ramet diameter and the δD values of stem waters collected after a large summer storm was negative, indicating that smaller plants had a greater fraction of recent precipitation than did larger plants (Fig. 4). Using a two-ended linear model (White 1988) with end members of δD values of -125‰ (the weighted winter-spring precipitation value) and -59‰ (the weighted mean δD of the preceding summer storm of 47 mm), we calculated for the smallest trees (1.5 cm dbh) that approximately 62% of the water used by small *A. grandidentatum* was recent summer rain; for equivalent *Q. gambelii* individuals, it was 47%. On the other hand, large *A. grandidentatum* on the slope (dbh > 20 cm) used water that included approximately 2% recent precipitation, while the larger *Q. gambelii* (dbh > 10 cm) used none of that recent precipitation. At the stream site, however, the *A. grandidentatum* sampled showed a much smaller change in stem δD values with size; the smallest plants used water that contained 19% recent precipitation and the largest used none.

Discussion

Moisture available to plants growing in the Intermountain West is derived primarily from winter precipitation (Dobrowolski et al. 1990); approximately 80% of this precip-

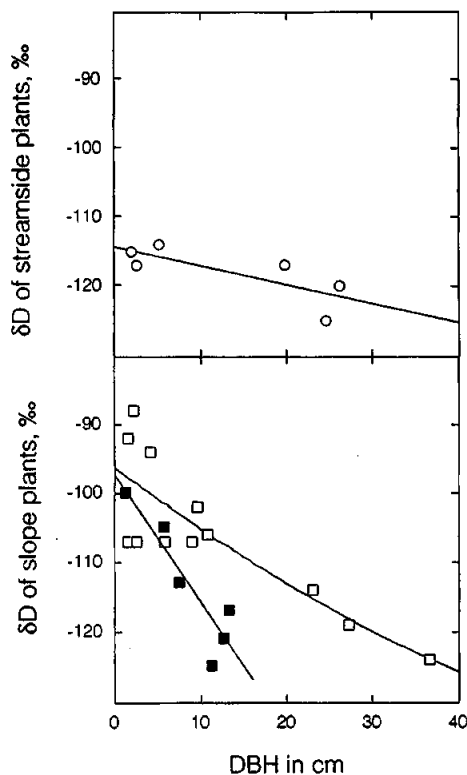


Fig. 4. The relationship between stem δD and DBH of streamside *A. grandidentatum* (upper panel) and slope individuals of both *A. grandidentatum* (open squares) and *Q. gambelii* (closed squares) sampled after early September rains

itation falls as snow. Precipitation in this region is marked by large seasonal variations in both isotopic signals and soil wetting patterns. Physically, these attributes result in the deposition of distinct water layers in the soil profile (Zimmermann et al. 1967). The deeper layers have the more negative isotope ratio values, characteristic of winter precipitation and snow melt. In the absence of additional precipitation, the upper soil layers are marked by the evaporation of this winter precipitation which enriches the isotopic composition (resulting in more positive isotope ratios). Late spring and summer precipitation adds isotopically heavier (more positive) layers to the soil surface (Craig et al. 1963; Barnes and Allison 1983). Plants capable of hydraulic lift might blur this layered pattern by releasing isotopically light water that was absorbed by deep roots in the upper soil layers (Caldwell and Richards 1989). Ecologically, these patterns result in several qualitatively different soil environments that deeply rooted plants could but do not necessarily exploit.

Both *A. grandidentatum* and *Q. gambelii* have lateral surface roots and deep tap roots (Christensen 1949, 1962; Muller 1951; Clary and Tiedemann 1986), yet the xylem sap isotope ratios suggest that surface roots of both species contribute little, if any, to the water supply of the mature trees studied. The surface roots of both species occupy soil layers which we would expect to have more positive δD values after summer rain than the values of -120‰ to 125‰ that represent typical winter precipitation values. Either the surface roots were inactive, or they contributed

so little to a plant's water supply that the isotopic signal of that water was not detected.

Other studies of *Quercus* from different ecosystems have yielded contrasting results. Other white oak species growing in regions with seasonal droughts have been shown to preferentially uptake water from surface layers if the entire soil profile is wet (Rambal 1984; Stringer et al. 1986; Kalisz et al. 1988). In these studies, deeper soil layers contributed increasingly more to the tree's water supply only as water stress developed and the surface layers dried out (Rambal 1984; Stringer et al. 1986; Kalisz et al. 1988). Taken alone, our δD values would initially appear to support the conclusion of surface moisture uptake in spring (Fig. 1). That is, one might conclude since xylem sap δD values match those of currently falling precipitation early in the growing season, but diverge as the season progresses, there is a switch in water sources. However, when both hydrogen and oxygen isotope ratios are considered, a different picture emerges. Comparing xylem sap $\delta^{18}O$ values in early spring to the local meteoric water line (Fig. 3), shows that the xylem water sampled from both species before their leaves flushed had been subject to evaporative enrichment (because the slope is less than that of MWL). It is unlikely that the surface roots were taking up winter recharge water that had been subject to evaporation in the upper soil layers because frequent, substantial rain events were continually wetting the soil surface (Fig. 1).

Not until after leaf flush had occurred for each species did the isotopic values of xylem waters return to the MWL (Fig. 3). Indeed, this shift from high to low isotope ratio values was not related to any apparent decline in soil water availability or increase in water stress (as measured by predawn and midday water potentials), neither of which occurred until later in the growing season. A more likely explanation is that xylem sap sampled before leaf flushing contained residual stem water subjected to evaporation throughout the previous winter. The extent of winter drying can be significant (Richards 1984; Richards and Bliss 1986), and depends on the relative humidity and the number of freeze/thaw cycles that occurred throughout the winter.

The oxygen isotope ratios we observed also suggest, but do not prove, that *Q. gambelii* and *A. grandidentatum* were not using hydraulic lift throughout most of the growing season. Caldwell and Richards (1989) showed that water with distinct δD values absorbed by deep roots can be deposited at the upper soil layers at night, then reabsorbed by surface roots during the day. Had this occurred, the δD values in deep and shallow layers may have been similar, but the $\delta^{18}O$ values of the water that was deposited in otherwise dry soil should show evaporative enrichment (Barnes and Allison 1983). Although our sampling of $\delta^{18}O$ values was limited, the results show no indication of hydraulic lift, since summer xylem water falls on the MWL.

The reliance of *Q. gambelii* on deep, winter recharge water throughout the summer period, and the lack of response to summer precipitation events reported here agrees with several recent studies that use stable isotopes to identify water sources of semi-arid plants. These studies,

from a variety of communities, have all found that some of the dominant woody perennial plants in these communities showed no response to summer precipitation (Ehleringer et al. 1991 in the Colorado Plateau, Flanagan and Ehleringer 1991 and Flanagan et al. 1992 in pinyon-juniper woodlands in southern Utah, Valentini et al. 1992 in the Mediterranean macchia of Italy, and Busch et al. 1992 in riparian communities of the lower Colorado Basin). However, each of these studies also observed that other woody perennials showed at least partial response to summer rain. The smallest dbh *A. grandidentatum* sampled here did show a slight increase in xylem sap δD values following a large summer storm in early September (Fig. 1). No corresponding change in the predawn water potential was observed, so the effect of the storm was at best minor, and probably not ecologically significant (Sala and Lauenroth 1982).

The limited response to a large summer storm by *A. grandidentatum* was related to trunk size (Fig. 4). Similar to previous observations on *A. negundo* by Dawson and Ehleringer (1991), we found that smaller diameter trees had significantly higher δD values than larger ones even though the smallest trees used as much as 47% of the summer rain water. Utilization of summer-moisture was more pronounced for *A. grandidentatum* than for *Q. gambelii*; the δD values were higher at a given stem diameter, and a larger range of sizes were affected in *A. grandidentatum*. Since the stems collected for the seasonal course data set represented a random sample of ramets within a clone, an integrated sample of stems from the *A. grandidentatum* may have included more stems from trunks small enough to respond to summer rain. The degree of clonal integration in these species is unknown.

The functional rooting patterns of the species studied here are largely similar. Both species have roots capable of using water from deeper soil layers, and both are largely unaffected by surface inputs. The use of this strategy supports the hypothesis of Ehleringer and Dawson that perennials do not appear to maintain surface roots for water uptake if summer rains are unpredictable. However, the slight response to summer rain, the differences in the size versus δD relationship, and the significantly lower predawn water potentials in *A. grandidentatum* in midsummer support the suggestion that *Q. gambelii* relies more on deep water than *A. grandidentatum* (Keddington 1970; Dina et al. 1973).

The implications of any subtle difference in rooting depth between the two species might be most apparent in years in which the growing seasons are either extremely wet or extremely dry. Over the long-term, total spring precipitation has varied substantially, from 33 mm in 1961 to 212 mm in 1986, and summer precipitation has varied from 6 mm in 1956 to 258 mm in 1982. In extremely dry years, *Q. gambelii*'s roots might be deep enough to buffer the effects of soil surface desiccation, whereas the *A. grandidentatum* might be more susceptible to water stress. Indeed in during the extremely dry summer of 1988, Ehleringer (unpublished data) measured midday water potentials of -5.5 MPa for *A. grandidentatum*, but nearby *Q. gambelii* did not fall below -4.0 MPa. These infrequent climatic extremes may be one of the critical factors influencing the local distribution of these two

species, and to the dieback observed following the drought of 1988 and 1989 (Ehleringer et al. 1992).

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