

Hydrologic, abiotic and biotic interactions: plant density, windspeed, leaf size and groundwater all affect oak water use efficiency

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ABSTRACT

Plant water use in drylands can be complex due to variation in hydrologic, abiotic and biotic factors, particularly near ephemeral or intermittent streams. Plant use of groundwater may be important but is usually uncertain. Disturbances like fire contribute to complex spatiotemporal heterogeneity. Improved understanding of how such hydrologic, abiotic, and biotic factors affect plant water use is needed not only to address management issues related to land use but also due to climate change, particularly for drylands projected to become warmer and drier such as much of the southwestern USA. Here we focus on the interactive roles of hydrologic, abiotic, and biotic factors in determining plant water use of Gambel oak in ephemeral and/or intermittent riparian areas of ponderosa pine forest in central New Mexico, USA along a fire disturbance gradient with varying oak densities. More specifically, the purpose of this research is to determine: (1) depth to and frequency of groundwater associated with intermittent and ephemeral streams, (2) isotopic indications of whether or not groundwater is used by plants, and (3) plant water use (conductance, transpiration, and water use efficiency) interactions with groundwater. Depth to groundwater, which could be as shallow as 1 m or less, increased with plant density but plant water use efficiency decreased. Photosynthesis:transpiration ratios maximizing water use efficiency for a given successional stage appeared to be also affected by windspeed and leaf size, highlighting interactive effects of hydrologic, abiotic and biotic affects—a finding that may be ecohydrologically relevant for other dryland riparian systems. Published 2010. This article is a US Government work and is in the public domain in the USA.

KEY WORDS Gambel oak; *Quercus gambelii* Nutt.; conductance; transpiration; water use efficiency; groundwater; ephemeral stream; intermittent stream

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INTRODUCTION

The presence of water defines riparian ecosystems, which can have water flow all year (perennial), part of the year (intermittent) or only following rain storms (ephemeral) (Kauffman and Krueger, 1984; Cockman and Pieper, 1997). Intermittent and ephemeral streams are important components of arid and semi-arid ecosystems as they make up the majority of stream systems in semi-arid environments. Within interior United States alone, intermittent and ephemeral streams comprise approximately 59% of all streams and over 81% in the arid and semi-arid Southwest (U.S. Geological Survey (USGS), 2006; National Hydrography Dataset website, <http://nhd.usgs.gov/index.html> (NHD), 2007). Although intermittent and ephemeral drainages do not always contain saturated soil conditions, the limited but relevant research has shown that they are an important source of groundwater in arid and semi-arid ecosystems and support plant species that do not grow on other sites (Parissopoulos and Wheeler, 1992; Cockman and Pieper, 1997). Additional research indicates that riparian areas associated with intermittent water (1) remain cooler than

uplands, (2) enable riparian vegetation to extend close to ridge tops, (3) act as nursery areas for amphibians where fewer predators exist than in perennial systems, (4) are important to fish resources and (5) contribute nutrients to downstream reaches (Erman and Hawthorne, 1976; Reid and Ziemer, 1994). Ecosystem structure and function likely rely heavily on these attributes, especially as global change converts perennial streams into ephemeral or even intermittent streams. Other research suggests that species of riparian vegetation may differ in the depth to which they access groundwater. Sedges and willows, for example, have been associated with depths to groundwater within 1 m of the soil surface (Law *et al.*, 2000). Particularly uncertain, however, are local spatial variations in depth to groundwater beneath the soil surface adjacent to ephemeral and intermittent streams. In addition, how plants respond to ephemeral and intermittent streams and their associated groundwater remains highly uncertain. For example, are plants more abundant near ephemeral and intermittent streams compared to nearby upland areas? Such information is needed to assess how ecosystem structure, function, plant distribution and abundance could be altered as global temperatures rise, less precipitation falls and perennial streams become ephemeral or even intermittent (IPCC, 2007).

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Understanding the distribution and abundance or density of species and the mechanisms that maintain distribution and density patterns is essential to ecology (Jackson *et al.*, 2009), and, in such dryland riparian systems, is a fundamental ecohydrology question. We hypothesize that intermittent and ephemeral streams play a crucial role linking plant abundance and physiology with associated dynamics of groundwater, an issue within the realm of ecohydrology. We also hypothesize that the presence of intermittent and ephemeral streams and associated groundwater will change plant behaviour by altering plant conductance, transpiration and water use efficiency (WUE). Maximizing WUE is a mechanism whereby plants use scarce water resources more efficiently to chemically reduce CO₂ to photosynthate and, to some extent, likely determines the distribution and density by providing a competitive edge. WUE can be high when transpiration rates are low relative to the rate of photosynthesis, or when photosynthetic rates are high relative to transpiration rates or both (Farquhar *et al.*, 1989; Chaves *et al.*, 2004). McDowell *et al.* (2008) suggest that plant water loss via transpiration is initially regulated by stomatal conductance and over time, leaf area, plant height, plant density and climate play a larger role in the regulation of transpiration. The objectives of this study were to (1) determine whether groundwater associated with intermittent and/or ephemeral streams can be within a meter of the soil surface and therefore support certain riparian species across a gradient of plant succession, (2) determine how often the groundwater remains within a meter of the soil surface along the successional gradient, (3) determine if plants associated with intermittent and/or ephemeral streams are more or less water use efficient than plants not associated with intermittent and ephemeral streams and groundwater beneath them and (4) determine how plant density interacts with groundwater to alter plant physiological behaviour, i.e. WUE. In particular, we test whether Gambel oak (*Quercus gambelii* Nutt.), a ubiquitous species in the southwestern United States, has lower stomatal conductance and less transpiration and uses water more efficiently when away from a groundwater source, and how that relationship changes with plant density. Gambel's oak provides a good test species because of its ubiquity throughout the semi-arid Southwest, its ability to inhabit both wet and dry areas, dominate a site and coexist with many other species from early to late succession.

METHODS

Study sites

To adequately test the hypotheses and meet the objectives of this study, we chose study sites spanning a gradient of densities caused by wildfire events in central New Mexico that vary in time since burn (Table I). We use space for time substitutions by using different wildfire sites in Gambel oak for time since disturbance and to incorporate variation associated with secondary succession and Gambel oak density. Fires used in this study burned across a range of time periods and locations. We controlled for the natural abiotic and biotic variation between fires, to the extent possible, by selecting fires that occurred within similar elevations of ponderosa pine stands within the Cibola National Forest, New Mexico. Within each of these burns, four to five intermittent and/or ephemeral corridors were chosen for monitoring that were spatially segregated and assumed to be independent. All of the corridors were located within an associated fire perimeter and contained riparian vegetation (indicative of shallow groundwater), showed physical evidence of intermittent or ephemeral surface water and/or had forest service maps indicating water. An area near the Tajique fire that had not been burned for at least 80 years served as a relatively unburned, high density site (Table I). In addition, Tables I and II give site characteristics such as soil texture and rainfall for each of the three study sites. In most of the drainages used in this study the soils are classified as fine, mixed, frigid, Typic Argiboroll and fine silty, mixed mesic Ustollic Haplargid (Bourlier *et al.*, 1970).

Depth to water table

To measure growing season depth to groundwater, we installed water wells near each studied stream location. At each general stream location a 2.5 cm × 183 cm perforated steel pipe was randomly located in the streambed center if live water was not present or at a distance of 1 m from the stream center if live water was present. Each pipe was driven into the soil as near to a 100 cm depth as possible and capped. A Solinst 101 mini water level meter (Solinst Canada Ltd., Georgetown, Ontario, Canada) was used to measure the depth to groundwater in each well every 2 weeks beginning in May and ending in November (2005–2007).

Table I. Wildfire study sites on the Cibola National Forest near Albuquerque, New Mexico.

Fire	Year of fire	Elevation (m)	Burned area (ha)	Soil texture
Sedgwick (E) 34.18°N108.13°W	2004	2497	3,478	Sandy loam
Tajique ^a (M) 34.79°N106.34°W	1988	2218	1,041	Sandy loam
Knight ^a (M) 34.79°N106.35°W	1987			
Cañon de Tajique ^b (L) 34.78°N106.39°W	Not burned	2358	N/A	Loam

(E), (M) and (L) signify early, mid and late succession, respectively.

^a These two fires were combined and studied as one fire.

^b This site served as a reference and has not experienced fire for over 80 years.

Table II. Abiotic and biotic characteristics of the study sites and their associated upland and stream locations.

Time since disturbance	Location	Cover (%)	Composition (%)	Water table depth (m)	Detection (%)	Light/quantum ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Windspeed (m s^{-1})	Rain pre- and post-monsoon (mm) ^a	Leaf size (cm^2)
Early succession	Upland	0.6 ± 0.6	4.69 ± 4.69	N/A	N/A	1325.4	0.96	23.53, 165	10.83
	Stream	4.4 ± 1.7	61.29 ± 18.1	0.42	36	935			12.45
Mid succession	Upland	8 ± 1.7	72.14 ± 6.5	N/A	N/A	1048.9	0.91	68.93, 229.53	7.62
	Stream	11.6 ± 3.3	52.8 ± 14.6	0.49	51	833.7			13.2
Late succession	Upland	18.1 ± 6.7	28.1 ± 11.9	N/A	N/A	176.8	0.4	68.93, 229.53	15.25
	Stream	27.3 ± 6.3	25.2 ± 6.2	0.68	16	239.04			15.67

^a Pre-monsoon was April through June and post-monsoon was July through November.

Plant cover measurements

Two 100-m transects randomly located on either side of each water well and perpendicular to the drainages were used to measure upland overstory cover. A GRS densiometer (Geographic Resource Solutions, Arcata, CA, USA) was used to measure overstory cover at 1-m intervals along each transect. A modified Whitaker plot (Stohlgren *et al.*, 1995) was centered on each well and parallel to the drainage and was used to measure riparian overstory plant cover.

Weather and Gambel oak water use

Midday (~10:00 am–2:00 pm) weather data were recorded above each well at a height of 3 m using a Kestrel 3000 handheld weather meter (KestrelMeters.com, Sylvan Lake, MI, USA); measurements included temperature, relative humidity, windspeed and dew point temperature. All of the weather data were measured each time the depth to groundwater was measured from May through November 2005–2007. Permanent weather stations were also placed in an open area at mid-slope within the boundary of the fire sites and were used to continuously measure rainfall, temperature, relative humidity and dew point temperature. Onset rain gauges, Hobo data loggers and radiation shields (Onset Computer Corporation, Bourne, MA, USA) were used in the weather stations to measure the weather variables on a per millimeter basis for rainfall and per hour basis for relative humidity (%) and temperature (°C). The rain gauges were set 1 m above the soil surface and the temperature and humidity hobo data loggers, in the radiation shields, were placed 0.5 m above the soil surface. The weather station data were downloaded continuously throughout the duration of the study. All of the weather measurements were used to calculate the 1-h time step potential evapotranspiration for a grass reference crop as explained by Allen *et al.* (1998). Light (quantum in $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured along with the weather variables using a Li-Cor Li-250A quantum meter (Li-Cor, Inc. Lincoln, NE, USA). Gambel's oak stomatal leaf conductance ($g_{\text{H}_2\text{O}}$) was measured at the same time as the light and the weather variables. One streamside Gambel oak plant adjacent to each water well was selected and tagged and an associated Gambel oak plant ~10 m

uphill from the water well was also selected. Five randomly selected leaves were measured on each plant using a Steady State Diffusion Porometer (Decagon Devices, Pullman, Washington). Leaves from the upper canopy to the lower canopy, in the shade and in the sun, were measured. Light and conductance were measured for each tagged Gambel oak from May 2007 through July 2007 every 2 weeks between 10:00 and 14:00 h. Leaf size was measured by selecting three leaves per plant and tracing them onto paper every 2 weeks. The area of each leaf was then measured using a Lasico model L-10 planimeter (Los Angeles Scientific Instrument Co., Inc. Los Angeles, CA, USA). Carbon isotope ratios were measured in July and October by randomly selecting mature leaves from each tagged Gambel's oak plant and sending them to the Analytical Chemistry Laboratory at the Odum School of Ecology, University of Georgia, for carbon isotope analysis. Carbon 12:13 ratios were measured relative to the Pee Dee Belemnite standard (Craig, 1957). Carbon dioxide and ¹³C concentrations for May through July 2007 and May through October 2007 were obtained from published data from the Carbon Dioxide Information Analysis Center (NOAA/CMDL Flask Network, White and Vaughn). From the ¹³C measurements we calculated carbon isotope discrimination (Δ) and intrinsic water use efficiency (iWUE). The variable Δ (expressed as ‰) was defined using Equation (1):

$$\Delta = \frac{\delta_{\text{air}} - \delta_{\text{plant}}}{1000 + \delta_{\text{plant}}} \times 1000, \quad (1)$$

where δ_{air} and δ_{plant} are the carbon isotope ratios of the air and plant, respectively (Farquhar *et al.*, 1989). We relate Δ to iWUE ($A/g_{\text{H}_2\text{O}}$) by Equation (2):

$$\Delta = a + (b - a) \left(1 - \frac{1.6A}{C_a g_{\text{H}_2\text{O}}}\right), \quad (2)$$

where a is the fractionation of carbon isotopes during diffusion through the stomata (4.4‰, O'Leary, 1981), b is the fractionation associated with carboxylation (27‰, Farquhar and Richards, 1984), C_a is the concentration of CO₂ in the air and 1.6 is the ratio of leaf conductance to water vapour and CO₂ ($g_{\text{H}_2\text{O}} = 16g_{\text{CO}_2}$) (Miller-Rushing *et al.*, 2009). The variable Δ provides a measure of how much the leaves of Gambel's oak discriminate against

^{13}C relative to the more common ^{12}C isotope. The iWUE reflects the ratio of the amount of carbon assimilated to water conducted through the stomata. In a broad sense, an increase in Δ signifies a decline in iWUE (Miller-Rushing *et al.*, 2009).

Transpiration (E) was derived from Equation (3):

$$E = g_{\text{H}_2\text{O}} \frac{es(T_L) - ea}{Pa}, \quad (3)$$

(Campbell and Norman, 1998) where $e_s(T_L)$ in kilopascals is the vapour pressure at the leaf surface and is derived from the Tetons formula (Buck, 1981) given in Equation (4):

$$(es(T_L) = a \exp(\frac{bT}{T+c}))/Pa, \quad (4)$$

where a , b and c are constants: $a = 0611$ kPa, $b = 17.502$, $c = 240.97^\circ\text{C}$, T = the leaf surface temperature ($^\circ\text{C}$) given from the steady state porometer and Pa is the atmospheric pressure derived from Equation (5):

$$Pa = 101\,325/e^{[(Z/29.3)/T_K]}, \quad (5)$$

where Z is the altitude in metres and T_K is the air temperature in Kelvin (Marshall and Zhang, 1994).

The ambient vapour pressure (e_a) in kilopascals was also derived from Equation (4), the Tetons formula (Buck, 1981), with T being the ambient air temperature ($^\circ\text{C}$).

STATISTICAL ANALYSIS

All of the ANOVA analyses were performed via a mixed procedure in SAS 9.1 (SAS Institute INC., Cary, NC). In many cases, the dependent variable was log or square root transformed to meet homogeneity and/or normality assumptions of ANOVA analysis. For clarity, nevertheless, the results are given as non-transformed data. Descriptive statistics were performed in Excel (Microsoft Corp., Bellevue, WA). Regression analyses were performed using SPSS V. 11.0 (SPSS Inc., Chicago, IL). In some cases, when assumptions of ANOVA analysis were not met, a nonparametric Friedman's rank test was used to determine significance. Significant results were determined at an alpha level of 0.1.

RESULTS

Above and below ground water

The results of this study apply to spring, summer and fall when vapour pressure deficits range from 4.4 KPa in June prior to the monsoon rains to 0.51 KPa in July during the monsoon rains. Mean rainfall pre- and post-monsoon for each of the three study sites is listed in Table I. Rain intensity at the early and late succession sites was on average 1.17 mm h⁻¹ while the mid succession site rain intensity was on average 1.33 mm h⁻¹. Midday potential evapotranspiration for a grass reference crop on the late succession site was less than that for the mid

succession site with a mean of 0.52 mm h⁻¹ compared to a mid succession mean of 0.56 mm h⁻¹. The midday potential evapotranspiration was intermediate at the early succession site with a mean of 0.54 mm h⁻¹ and was not different from the mid or late succession sites.

The mean depth to water was deepest at the late succession site at 0.68 m below the soil surface (Table II). Depth to groundwater at the mid and early succession sites did not differ but was shallower than at the late succession site with an average depth of 0.46 m. The frequency of detecting water during the growing season at these depths or within 1 m below the soil surface was 36% for early, 51% for mid and 16% for late stage succession.

Percent cover and composition

Percent Gambel oak cover increased with time since fire disturbance but percent of Gambel oak relative to total percent vegetative cover (% species composition) decreased with time since disturbance (Table II). More specifically, at the stream locations percent oak cover increased along the time since fire gradient from 4.4 to 11.6 to 27.3% from early, mid and late succession sites, respectively. Similarly, in the upland locations, percent oak cover increased from 0.6 to 8.0 to 18.1% along the time since fire gradient. Relative to other plant species in the same vicinity, percent composition of Gambel oak decreased with time since disturbance at the stream locations but not in the upland ones. At the stream locations, the percent composition of Gambel oak was 61.29, 52.83 and 25.21% at the early, mid and late succession sites, respectively, whereas at the upland locations the percent composition decreased from the mid to late succession sites (from 72.1% to 28.1%) but was lowest at the early succession site (4.7%).

Total overstory cover was not different between the stream locations and the adjacent uplands for the early and mid succession sites (means of 13.69 and 22.60%, respectively). There was a difference in total overstory cover between the riparian zones and the adjacent upland locations for the late succession site. The late succession stream locations had a mean of 111.22% overstory cover while the late succession upland locations had a mean of 63% overstory cover. Overall, the late succession site had significantly more vegetative cover compared to the early and mid succession sites. The increase in total percent cover with time since disturbance was also reflected by the decrease in percent Gambel oak composition (Table II).

Stomatal conductance and transpiration

Overall mean midday stomatal conductance (g_s) did not differ among the three successional stages (mean = 228.43 $\mu\text{mol m}^{-2}\text{s}^{-1}$) (Figure 1A). However, for the late succession site midday stomatal conductance was nearly twice as high at the upland locations (218.66) than the stream (163.79) locations. Alternatively, stomatal transpiration (E) did differ between the three

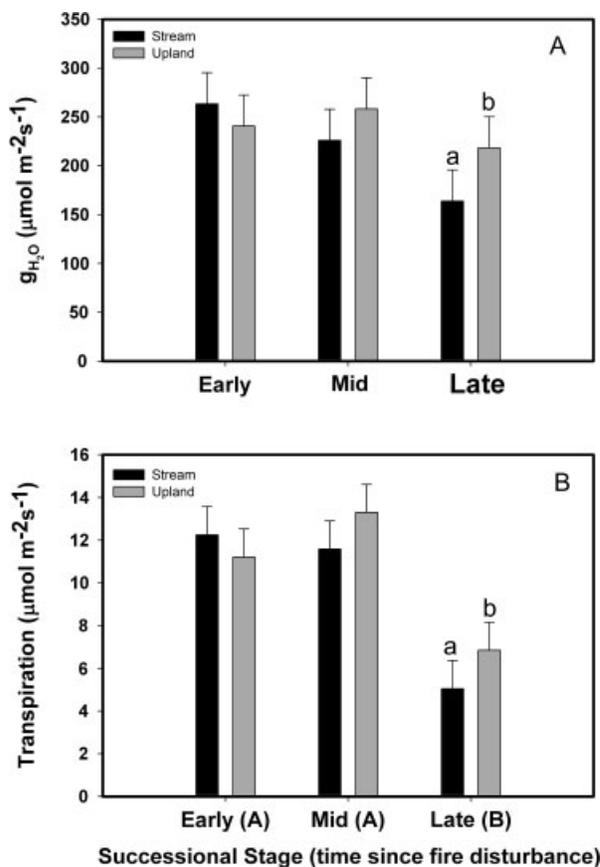


Figure 1. Differences in g_{H_2O} (A) and E (B) between upland and stream locations and along a successional gradient in a ponderosa pine forest near central New Mexico. The letters above the bars represent significant differences between the upland and stream locations for that particular successional stage. In addition, the letters in parenthesis along the x-axis indicate differences between the early, mid and late successional sites. The error bars represent one standard error from the means.

study sites. Stomatal transpiration was lowest at the late succession site with a mean midday transpiration rate of $5.94 \mu\text{mol m}^{-2}\text{s}^{-1}$, compared to 11.72 and $12.43 \mu\text{mol m}^{-2}\text{s}^{-1}$ at the early and mid succession sites, respectively (Figure 1B). Stomatal transpiration also differed between the stream and the upland locations at the late succession study site. The upland oaks had higher E rates than the stream oaks at 6.84 and $5.05 \mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. If we assume that g_s is the maximum potential rate of water loss from the stomata, then E makes up only a portion of that potential maximum. We found that E was a small fraction of the total potential water loss. The late succession site had the least water loss relative to the total potential amount of loss at just over 3% for both the stream and the upland locations. The mid succession site had the most water loss relative to its total potential loss at just over 5% for both the stream and the upland locations. The early succession site was intermediate, with a water loss at just over 4.5% of its potential loss for both locations.

Gambel oak Δ and $iWUE$

Overall, Gambel oak discriminated against ^{13}C significantly less during the first half of the growing season

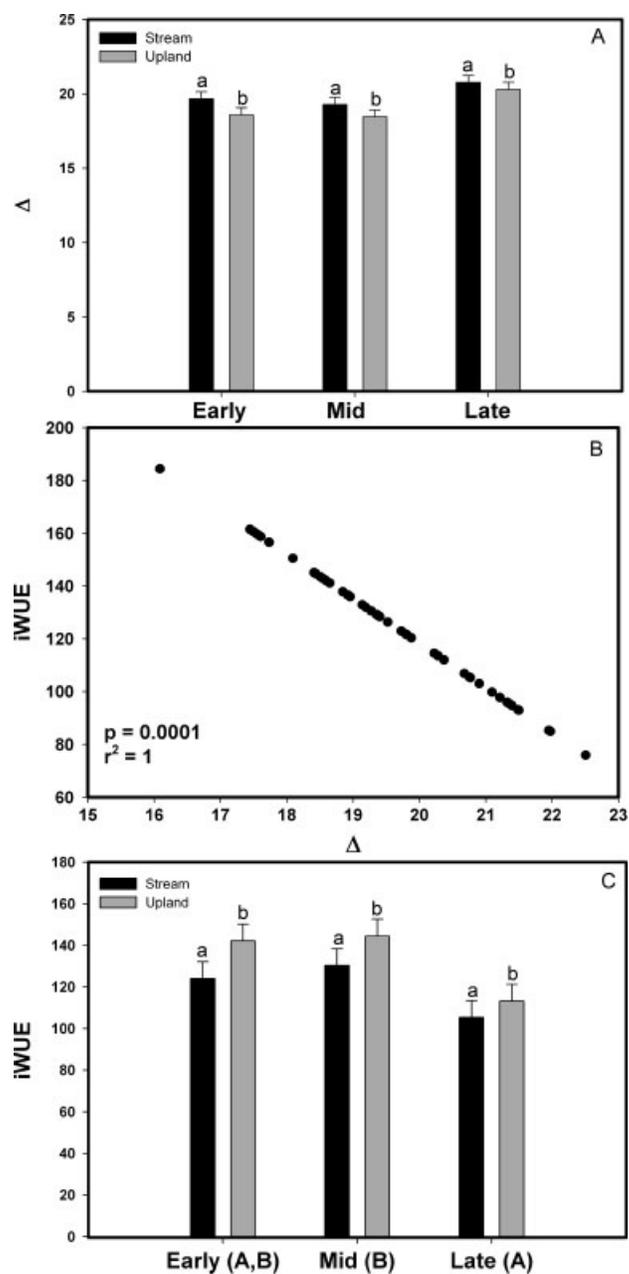


Figure 2. This bar graph shows differences in Δ (A) and E (C) and the relationship between the two (B). The letters above the bars represent significant differences between the upland and stream locations for that particular successional stage. In addition, the letters in parenthesis along the x-axis indicate differences between the early, mid and late successional sites. The error bars represent one standard error from the means.

than during the latter half (18.95% vs. 20.06%) regardless of time since fire whether in the upland or stream location. There were no significant Δ differences among oaks inhabiting the early, mid or late succession study sites during the whole growing season. Nevertheless, the oaks inhabiting areas adjacent to the streams discriminated against ^{13}C significantly more than those oaks in the upland locations during the whole growing season, with an average Δ of 19.90‰ for the stream oaks relative to 19.11‰ for the upland oaks (Figure 2A).

Leaf level $iWUE$ was significantly negatively correlated with Δ (Figure 2B) such that oaks were much more

water-use efficient during the first half of the growing season (135.96) compared to the latter half (117.21). Leaf level *i*WUE was greater at the upland (133.29) than stream locations (119.89) regardless of successional stage (Figure 2C). In addition, oaks were significantly more water-use efficient at the mid succession (137.39) than at the late succession (109.29) stages.

Abiotic measures and correlations

Windspeed was more than two times greater at the early and mid succession sites compared to the late succession site (Table II). In addition, windspeed was significantly correlated with percent overstory cover (Figure 3A) and *E* (Figure 3B). Light was also significantly different between the early and late succession sites and between the upland and stream locations for all the sites (Table II). Light was more than five times higher on the early succession site compared to that at the late succession site. Notably, the largest leaves were found at the late successional site while the smallest leaves were found at the early successional site. Leaf size was also significantly correlated with *i*WUE (Figure 3C).

DISCUSSION

We document examples where, in semi-arid ponderosa pine stands, ephemeral or even intermittent streams can have water tables associated with them. The depth to these water tables can be within as little as 1 m from the soil surface and in some cases can remain within 1 m below the soil surface for a significant portion of the growing season (Table II). The presence of this shallow groundwater apparently affected Gambel oak water use. In addition, plant water use of early seral oaks differed from that of late seral oaks.

In similar systems, Gambel oak has been shown to use deep water sources even when soil surface water is freely available. A high ratio of Gambel oak reproductive structures to feeding rootlets near the soil surface may result in less soil water used at the soil surface (Baker and Korsian, 1931). Williams and Ehleringer (2000) discovered that Gambel oak primarily used deep soil water (~50 cm below the soil surface), even after substantial rainfall, at sites where the mean summer precipitation was relatively low. In this study, the measured water table depths were within the vicinity of use by Gambel oak roots, which apparently resulted in higher discrimination against ^{13}C for oaks near the ephemeral and intermittent streams compared to the upland oaks as indicated by the significantly higher Δ . Oaks at the upland sites, which were drier, fixed more ^{13}C to maintain photosynthesis while the stomates were closed and the ratio of $^{12}\text{C}:^{13}\text{C}$ decreased in the stomatal cavity. Therefore, the upland oaks used water significantly more efficiently than those oaks adjacent to ephemeral and intermittent streams and associated groundwater as shown in Figure 2B. These results are consistent with other results of WUE studies performed

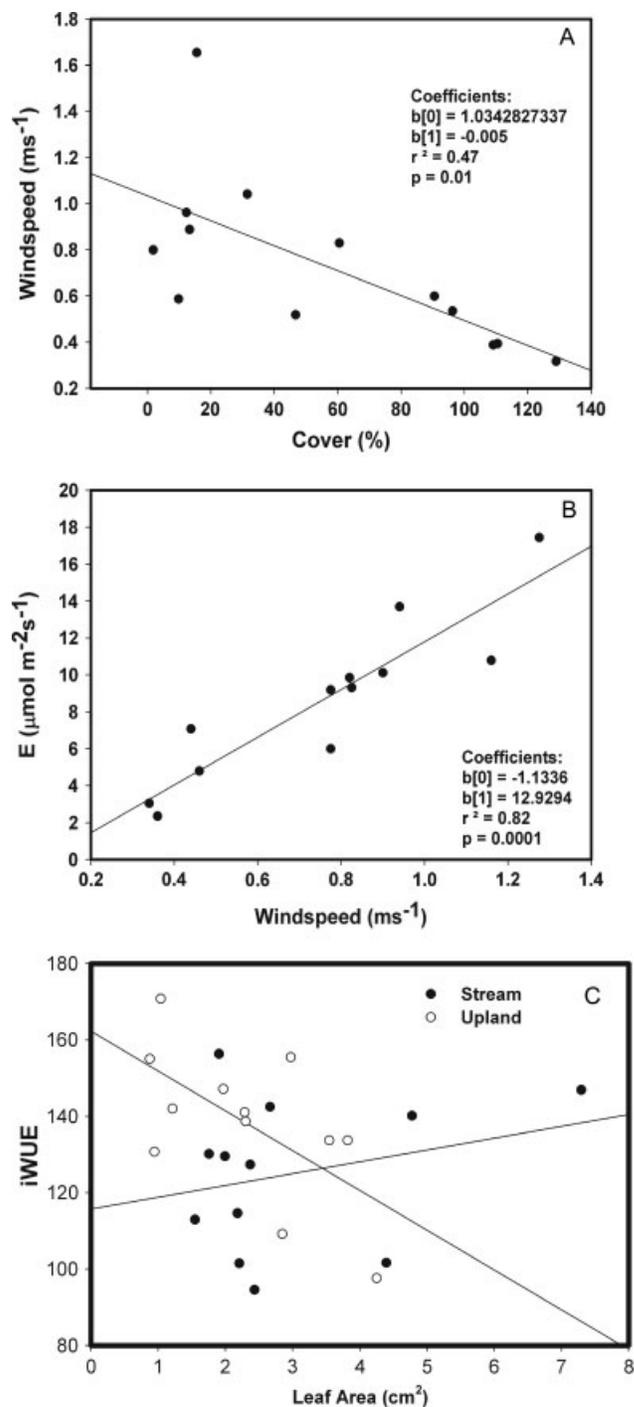


Figure 3. The panels in this figure show significant relationships between windspeed and the biotic factors of % cover and *E*. (A) Shows that increased cover can reduce windspeed. (B) Shows that decreased windspeed plays a role in the reduction of *E*. (C) Shows that leaf area may help determine WUE, especially at the upland locations where the relationship is significant.

in the Southwest where drier sites have more water-use-efficient vegetation (i.e. Lajtha and Getz, 1993). This is further supported by low Δ and high *i*WUE during the early drier part of the growing season prior to the arrival of the monsoon rains. Following the monsoon rains there was a significant increase in Δ and drop in *i*WUE. The 3-year mean total rainfall from April through June was

53.8 mm while rainfall from July through November was 208.0 mm.

Interestingly, g_{H_2O} and E were not different between the stream and upland locations during midday for the early and mid succession study sites which appears to be inconsistent with the Δ and $iWUE$ results. Other studies suggest that slight reductions in instantaneous transpiration result in significant reductions in water loss over the long term while CO_2 uptake does not change and WUE increases (Yoo *et al.*, 2009). Our ability to detect slight differences in E and g_{H_2O} may have been limited because of sample size. However, we did detect that the oaks near the streams at the late succession site had lower g_{H_2O} and E rates compared to the upland oaks even though $iWUE$ was lower and Δ was higher at the stream site compared to the upland site. It seems counterintuitive that oaks would be conducting and transpiring more water at the upland locations compared to the stream locations but still be more water use efficient. Nevertheless, in this study we found that there were significant correlations among total cover, windspeed and E (Figure 3). The only significant difference in percent cover between the upland and stream locations was found at the late succession site where stream cover was significantly higher than upland cover (Table II). It may be that higher cover at the stream location decreased windspeed sufficiently to minimize E over the long term so that stomates could remain open or partially open longer during a diurnal period and discriminate more against ^{13}C during photosynthesis (A), which would have resulted in lower $iWUE$ as per the equation relating Δ and $iWUE$. In addition, we also noted a significant difference in leaf size between the stream and upland locations at the late succession study site (Table II). An increase in leaf area usually results in higher boundary layer thickness restricting water loss (Nobel, 1974, 1999; Yoo *et al.*, 2009). It may be that a lower boundary layer conductance to water vapour, especially in low windspeed conditions, allowed the stomates to remain slightly more open or open longer, resulting in higher Δ and lower $iWUE$ over the long term at the late succession stream locations compared to the upland locations. Late succession stream oaks may have had more open stomata but less water loss due to lower boundary layer conductance and reduced windspeed resulting in lower $iWUE$ per Equation (2). Higher shade due to increased cover would have also influenced light and photosynthesis altering $iWUE$ at the late succession stream locations. The photosynthetic part of $iWUE$ (Equation (2)) and its relationship to E will be discussed below.

Along the successional gradient Gambel oak cover increased, total cover increased, water tables dropped, $iWUE$ declined, Δ did not change, g_{H_2O} did not change and E decreased. It makes sense that both g_{H_2O} and Δ did not change as Δ should primarily be a function of g_{H_2O} (i.e. stomatal aperture). But, it is again not intuitive why $iWUE$ is lowest at the late succession site when there was a drop in water table. $iWUE$ is usually much higher in drier locations compared to more moist locations (i.e. Lajtha and Getz, 1993) as was detected

between the stream and upland locations for the early and midsuccession study sites. This may be explained by the equation $iWUE = A/g_{H_2O}$. WUE can be low when photosynthesis (A) is low (Chaves *et al.*, 2004). If there is a drop in g_{H_2O} , WUE remains high unless there is also a subsequent drop in A along with a drop in g_{H_2O} . Light was significantly less at the late successional site compared to the early and mid successional sites, which would reduce carbon assimilation, and appears to be related to increased cover at the late successional site (Table II). In addition, windspeed was negatively correlated with increased cover and positively correlated with E , which was again particularly significant at the late succession site where we noted higher cover (Table II). As a result, it appears that shade increased (drop in A), leaf size increased and E decreased, which makes a reasonable explanation of why WUE at the late successional site is relatively low. Yoo *et al.* (2009) suggest that g_{H_2O} , E and carbon assimilation are linearly related to a point, and then carbon assimilation levels off while E continues to increase. At the late succession site carbon assimilation may level off owing to less light making production low relative to water loss, which could explain why $iWUE$ is low and E and g_{H_2O} are also relatively low. Yet, this does not explain why Gambel oak cover increased along the successional gradient when its $iWUE$ went down and why it is able to tolerate shady conditions when it is known to be a pioneer species, being one of the first to sprout and re-grow following fire (Brown, 1958; Jefferies, 1965; Hanks, 1966; Marquiss, 1973; Mullette, 1978; Engle and Bonham 1980; Engle *et al.*, 1983; Kufeld, 1983; Montenegro *et al.*, 1983; DeVelice *et al.*, 1986; Tiedemann, 1987; Biondi *et al.*, 1992; Klemmedson, 1992; Huston, 1994). Leaf size was much greater at the late succession site. This may be key to its success along a successional gradient. An increase in leaf size may compensate for lower light, along with a decrease in E owing to reduced windspeed and decreased boundary layer conductance to water vapour (Nobel, 1974, 1999; Yoo *et al.*, 2009) may allow Gambel oak to maintain a proper ratio between A and g_{H_2O} in order to remain competitive and coexist with other shade-tolerant species like the big-toothed maple (*Acer grandidentatum* Nutt.) that made up a substantial part of the vegetative cover near the stream locations at the late successional study site. Other factors that may have played a role include soil texture (Table I), which would have changed soil water holding capacity and soil moisture conditions between the late and early seral sites and should be considered in future studies.

Collectively, our results highlight the importance of ecological and hydrological interactions. These interactions are summarized in Figure 4. Figure 4 is a conceptual figure suggesting possible mechanisms and interactions that control WUE . This figure or model suggests that as plant density increases and depth to water table increases WUE decreases. This is likely due to reduced windspeed, increased leaf size and boundary layer resistance and decreased light (less photosynthesis).

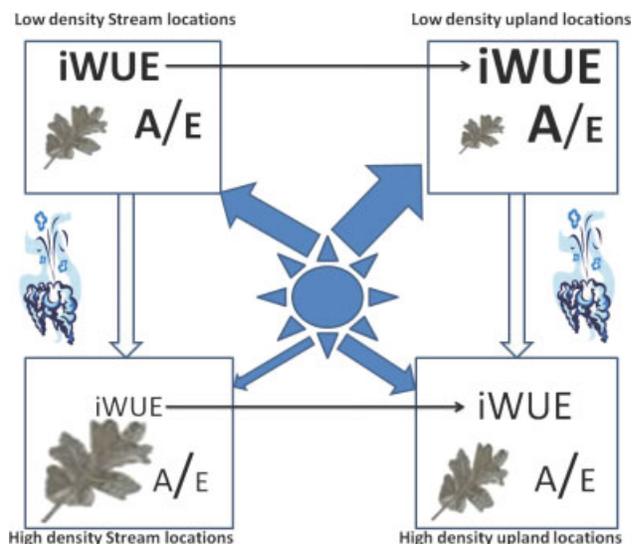


Figure 4. A conceptual figure suggesting possible mechanisms and interactions that control WUE of Gambel oak in ponderosa pine forests of Central New Mexico, USA. Primarily this model shows how the photosynthesis:transpiration ratio and leaf size changes to maximize WUE for a given scenario.

Increased vegetative cover may lower water tables and, in the process, decrease light and photosynthesis. As cover increases windspeed decreases, and combined with a high boundary layer resistance (large leaf size), E is decreased, allowing stomates to open larger or stay open longer, which increases Δ and decreases $iWUE$. In addition to changes with plant density, changes also occur along a gradient of groundwater depth. Plants near intermittent and ephemeral streams have access to groundwater, have relatively larger leaves, experience lower light and have less carbon assimilation relative to water loss compared to upland plants.

In addition, this model (Figure 4) shows a process that can be generally applied across a broad range of species that are associated with intermittent and ephemeral groundwater. This model also demonstrates how we might expect plants to respond over time as plant community composition changes, canopies close and understory shade increases. Although we tested Gambel oak response to groundwater and succession we suggest that the processes and mechanisms that are summarized in Figure 4 may also assist other scientists and land managers in predicting what might happen with a different semi-arid plant species.

CONCLUSIONS

We document plant water relationships for locations where ephemeral and intermittent streams have groundwater associated with them and that groundwater can be within 1 m of the soil surface. Groundwater at this depth is within the range of uptake by Gambel oak and therefore, modifies Gambel oak behaviour by changing the ratio of photosynthesis to transpiration ($iWUE$). Although this ratio should always be above 1, this research shows that plants near groundwater sources

have a different $A:E$ ratio or $iWUE$ value than plants away from a groundwater source. This ratio also changes from early seral, recently disturbed areas to late successional plant communities. It may be that maintaining a proper ratio between carbon gain and water loss is key to plant success and that plants may modify their leaf size, stomatal conductance and photosynthetic rate to achieve a competitive balance between carbon assimilated and water transpired in high or low wind and high or low light environments. More generally, the results highlight interactive effects of hydrologic, abiotic and biotic effects—a finding that may be ecohydrologically relevant for other dryland riparian systems. These feedbacks between groundwater, abiotic and biotic characteristics are important for furthering the relatively young field of ecohydrology and associated disciplines.

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