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Partitioning the use of precipitation- and groundwater-derived moisture by vegetation in an arid ecosystem in California

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Abstract

Demands on groundwater supplies in arid regions have increased interest in the importance of groundwater, relative to precipitation-derived moisture, to vegetation. Depth to water (DTW), precipitation (PPT), and vegetation (total perennial cover, TPC) data have been collected from 30 sites in the Owens Valley, California, since the 1980s. We used these data to construct water budgets for each site, and to calculate precipitation-use efficiencies (PUE) and amount of TPC supported by precipitation and by groundwater. We compared these values among five plant communities over different DTW and PPT regimes to determine relative importance of each water source. Our results confirm that both groundwater and precipitation are important sources of water to Owens Valley vegetation. In general, groundwater becomes more important as DTW decreases, but this relationship varies among communities. TPC increased as DTW decreased up to a point, after which TPC remained constant or declined. Some groundwater usage by shrub- and grass-dominated communities continued to DTW of 6–8 m. PUE was highest at low precipitation and decreased as precipitation increased. Our results indicate that vegetation preferentially used precipitation-derived soil moisture, even with abundant groundwater, and that successful management of groundwater-affected arid ecosystems must account for complex interactions among multiple factors.

Keywords: Depth to water; Greasewood; Rabbitbrush; Sacaton; Saltbush; Saltgrass

1. Introduction

Water is a primary resource limitation to plant growth in arid environments (Leffler et al., 2004; Le Houerou et al., 1988). There are three primary natural sources of water for plants in arid regions: surface flow, precipitation, and groundwater (Chimner and Cooper, 2004; Flanagen and Ehleringer, 1991; Schlesinger and Jones, 1984). Supply from surface flow (e.g., surface runoff, rivers, streams, lakes) is generally very limited, spatially or temporally. Most arid vegetation must therefore rely on precipitation, groundwater, or a combination of the two.

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Groundwater has long been a valuable resource for direct human use in arid regions. It is becoming increasingly so as urban and agricultural growth in these regions continues (Groom et al., 2000a; Seyfried et al., 2005). The Owens Valley of California provides a classical example of the allocation of a limited resource between native vegetation and human use. The Owens Valley is a narrow (4–10 km wide) valley between the Sierra Nevada Mountains on the west and the Inyo and White Mountains on the east. Dissecting the valley is the Owens River flowing out of the eastern Sierras and supporting, along with subsurface flows from the mountains, a high water table (0–10 m) over portions of the valley floor. Annual mean precipitation varies from about 15 cm in the north to 9 cm in the south. Riparian vegetation typical of many river systems in the western United States occurs immediately adjacent to the river, and numerous meadow and shrubland communities form a mosaic between the river and the upland slopes at the base of the mountains.

In addition to in-valley agricultural, aquacultural, and urban uses of the groundwater, the Owens Valley supplies a large part of the water requirements of the City of Los Angeles. These human demands, both in-valley and export, have been supplied from both diversion of water from the Owens River and from groundwater pumping. A primary management issue in the Owens Valley is how to balance human use with the requirements of the native vegetation. Central to that issue is a correct understanding of the impact of both groundwater and precipitation on vegetation dynamics.

Although precipitation and groundwater are potential sources of water to much of the vegetation of the valley floor of the Owens Valley, it is unlikely that these two sources are equally important because plants, in general, do not equally utilize precipitation-derived soil moisture and groundwater (Chimner and Cooper, 2004; Dawson and Pate, 1996; Flanagen and Ehleringer, 1991; Mensforth et al., 1994; Mueller et al., 2005; Penuelas and Filella, 2003; Schulze et al., 1996; Schwinning et al., 2002, 2005; Sekiya and Yano, 2002; Smith et al., 1997; Snyder and Williams, 2003; Zencich et al., 2002). These utilization differences include (1) differences among species relative to potential use of groundwater and (2) differences within species relative to groundwater usage at varying levels of precipitation-derived soil moisture. Consequently, the presence or absence of groundwater at a particular depth does not necessarily imply a specific response by the vegetation because of the confounding effect of differential usage. Because of this differential usage by plants, a simple depth-to-water (DTW) management plan to protect vegetation is not viable. Similarly, the efficiency by which vegetation utilizes precipitation is not constant. Precipitation-use efficiency (PUE = amount of vegetation per unit of precipitation received) varies in response to a number of factors, two very important of which are vegetation type (more particularly, species and life forms) and amount of precipitation (Huxman et al., 2004; Le Houerou, 1984; Le Houerou and Hoste, 1977; Mueller et al., 2005; Paruelo et al., 1999; Schwinning et al., 2002, 2003).

The Los Angeles Department of Water and Power (LADWP) and the Inyo County Water Department (ICWD) began a joint monitoring program in the late 1980s to collect data on DTW (monthly) and vegetation (annually) at 30 permanent monitoring sites located along 100 km of the valley floor. This program, combined with precipitation data from 8 recording stations, provides a reasonably long (14–18 years) data set which can be used to investigate the relative importance of precipitation and groundwater in supporting arid vegetation under field conditions.

Our objective in this study was to utilize these data to estimate the relative amounts of groundwater and precipitation-derived water used by the vegetation in the Owens Valley over the 15–18 years covered by the data. Partitioning vegetation water use into precipitation-derived and groundwater-derived components will contribute to our understanding of the basic ecological functioning of these types of arid ecosystems. Such a partitioning will also substantially improve the ability of managers to allocate groundwater resources to human requirements while maintaining sufficient groundwater to meet the needs of the vegetation.

2. Methods

2.1. Permanent monitoring data

The LADWP/ICWD Permanent Monitoring Program collects data from 30 sites, 22 at which the vegetation has been affected by groundwater pumping in at least some years during data collection and eight at which it is believed that the vegetation has not been affected by groundwater pumping, based on results of hydrological modeling. The former are designated wellfield sites and the latter are designated control sites. The sites were established between 1987 and 1991. There is a monitoring (non-production) well associated with each site, at which DTW data are collected on a monthly basis. In some cases, the DTW data were collected at 3-month intervals for limited periods. There are eight precipitation recording stations associated with the permanent monitoring sites, equipped with continuous data recorders. A 100-m permanent line transect is located within 500 m of each monitoring well. Vegetation data (live leaf cover, by species) were collected along each transect in June. A point-frame is used and leaf intercept data (first-contact and all contacts) are recorded at 30-cm intervals (Bonham, 1989, pp. 21–22). First-contact data were used in this paper.

Percent total perennial cover (TPC) is the primary vegetation variable used in wellfield management by LADWP. This is the sum of number of hits by any perennial species along the transect divided by 334 and multiplied by 100. We used this as the vegetation variable in our analysis. We used mean annual DTW, calculated as the average of the 12 months including and previous to the vegetation sampling date. These data were taken for each site from the monitoring well associated with that site. The precipitation (PPT) variable used was precipitation received in the 12 months prior to the June in which the vegetation data were collected, with the data collected from the nearest of the 8 recording stations to the site.

2.2. Conceptual model

Vegetation is the product of the interaction of the available species with all aspects of the local environment, including biotic, abiotic, and historic. Consequently, vegetation dynamics, along with any attribute used to measure these dynamics (such as TPC), are controlled by a complex set of interacting factors. Any attempt to limit these factors will result in an over-simplification of reality. Conversely, an attempt to study all, or even substantial numbers, of these factors simultaneously is likely to be largely unproductive because of the inherent "noise" in the system. Our approach was to use a very simple conceptual model, understanding the limitations of such a model, to develop a first-approximation of the relative importance of groundwater and precipitation as factors controlling vegetation change at the 30 permanent monitoring sites.

Our basic predictive equation took the form of

$$\mathrm{TPC} = \mathrm{TPC}_{\mathrm{GW}} + \mathrm{TPC}_{\mathrm{PT}},$$

where $\mathrm{TPC}_{\mathrm{GW}}$ is the amount of TPC supported by groundwater and $\mathrm{TPC}_{\mathrm{PT}}$ the amount of TPC supported by precipitation.

The sources of all moisture available to vegetation at a site was assumed to be only precipitation and groundwater (which included the capillary fringe above the water table). Even from a water-balance standpoint this predictive equation was simplistic. Residual soil moisture was not included as a separate term. In general, it was assumed that all soil moisture was accounted for as part of the $\mathrm{TPC}_{\mathrm{PT}}$ or $\mathrm{TPC}_{\mathrm{GW}}$ terms and, in effect, there was no residual plant-available soil moisture from one year to the next. Although this is not an unreasonable assumption in most years in arid and semiarid ecosystems (Cable, 1980; Cline et al., 1977; Donovan and Ehleringer, 1994; Frasier and Cox, 1994; Gebauer and Ehleringer, 2000; Schwinning and Sala, 2004; Schwinning et al., 2005; Seyfried et al., 2005; Zencich et al., 2002), it certainly is not always the case (e.g., Dodd et al., 1998; Schulze et al., 1996; Snyder and Williams, 2003). At some sites and in some years, our data clearly indicated that there was a substantial portion of the precipitation received that was not utilized in evapotranspiration (ET) in that year. In other instances, where the water table declined over a period of several years in response to groundwater pumping or natural groundwater declines during low runoff years, the data clearly indicated residual soil moisture from one year to the next. In both of these cases, a residual soil moisture term was added to the predictive equation. Surface flow (runoff) onto, or off of, a site was assumed to be zero. This was probably a valid assumption for most of the sites because they are all located on relatively level terrain and runoff is generally minor on these lower topographic locations in the Owens Valley (Steinwand et al., 2006). However, surface runoff has been shown to be a significant source of water on other sites in arid eastern California (Schlesinger and Jones, 1984).

No attempt was made to quantify the amount of water extracted by evaporation. Our calculations of precipitation-use efficiency (PUE) included evaporation along with transpiration. Similarly, we assumed that there was no groundwater recharge from precipitation at any of the sites. DTW at most of the sites was greater than 1 m and field capacity of most of these soils was estimated to be 8–10%, resulting in a capacity of the soils to hold about 10 cm of water per meter of soil. Very few precipitation events in the Owens Valley, including snowmelt, are likely to exceed 10 cm and the resulting soil moisture is likely to be extracted through ET before it can accumulate sufficiently to percolate into groundwater. Lack of deep percolation of soil moisture because of low input amounts and high extraction rates is common in arid ecosystems (Cable, 1980; Cline et al., 1977; Joffre and Rambal, 1993; Nowak et al., 2004; Seyfried et al., 2005), although downward movement of precipitation-derived water by roots to depths of over 3 m has been reported in an arid shrub community (Ryel et al., 2003).

Our water-balance approach was to assume that all change in TPC from one year to the next could be partitioned into a component resulting from the vegetation response to the amount of precipitation received during the previous 12 months and a component resulting from the use of groundwater by the vegetation. The precipitation- and groundwater-factors were assumed to be site-specific. Therefore, calculations were made for each site individually over the 15–18-year period of record for that site.

We assumed that, in general, TPC would increase as DTW decreased (i.e., groundwater came nearer to the soil surface). However, we did not assume that this was always true or that the relationship between TPC and DTW was linear. There are a number of factors that can cause TPC to decline as groundwater rises or TPC to increase as groundwater declines (Ganskopp, 1986; Groeneveld and Crowley, 1988; Martin and Chambers, 2001; Naumburg et al., 2005; Van Bodegom et al., 2006). This is especially true for arid shrubs and perennial grasses, which formed the majority of the vegetation of our study sites. We also assumed that TPC would increase as precipitation increased, but that this relationship would not be linear because PUE was expected to decrease as precipitation increased.

2.3. Determination of precipitation factor

Our first step was to estimate the amount of TPC supported by precipitation. To estimate the proportion of TPC supported by precipitation, we tabulated the TPC, DTW, and PPT data, by year, in order of decreasing DTW. We divided the TPC value (%) for each year by the PPT value (cm) for the same years to determine an annual PUE for that site (Table 1). For purposes of determining the precipitation factor, we excluded the PUE values for those years where the data indicated that either (1) groundwater was being utilized or (2) there was apparent use of residual soil moisture. Groundwater utilization was indicated when the PUE value was substantially higher ($>150\%$) than the PUE values at the deeper groundwater depths and DTW was relatively low (i.e., high groundwater). The signature for residual soil moisture was similar, i.e., the PUE was substantially higher ($>130\%$) than the PUE values at similar DTW in other years. In addition, PPT in the previous year would be especially high (residual soil moisture from precipitation) or DTW declined in the previous 3 or more years (residual soil moisture from declining groundwater). Precipitation factor (PUE) values were calculated separately for each of the 30 permanent monitoring sites (Table 1).

2.4. Determination of groundwater factor

The amount of PPT-supported TPC ($\mathrm{TPC_{PT}}$) was estimated for each year by multiplying the appropriate precipitation factor times the amount of precipitation received in the previous 12 months for the respective year. The $\mathrm{TPC_{PT}}$ was then subtracted from the amount of TPC sampled in each respective year. The remainder was assumed, on the basis of the simplified conceptual model, to have been the amount of TPC supported by groundwater ($\mathrm{TPC_{GW}}$).

Estimates of $\mathrm{TPC_{GW}}$ were made for each DTW for which data were available for that site. These estimates were arranged in descending order from the shallowest GW (smallest DTW value) to the deepest GW (largest DTW value) available for that site. This process provided $\mathrm{TPC_{GW}}$ estimates for those DTW values for which historic data were available. There were numerous DTW values for which no historic data were available at a particular site because DTW was not at those levels in the years that data were collected. $\mathrm{TPC_{GW}}$ was estimated for the DTW values without historic data by extrapolating between those points where data did exist. This assumed a linear relationship between DTW and $\mathrm{TPC_{GW}}$ between the two points, but it did not assume linearity past those two data points. This process produced a $\mathrm{TPC_{GW}}$ matrix for each site that

Table 1
Precipitation (PPT) factor [PUE = total perennial cover (%)/previous 12-months precipitation (cm)] values by dominant plant community for the 30 permanent monitoring sites

	TPC (%)	PPT level (cm)	PPT factor (%/cm)	PPT level (cm)	PPT factor (%/cm)	PPT level (cm)	PPT factor (%/cm)	PPT level (cm)	PPT factor (%/cm)
Nevada saltbush									
BG-2	16	<11	1.50	11–19	1.00			>19	0.71
BG-C	17	<11	1.28	11–19	0.95			>19	0.48
BP-1	18					<22	1.01	>22	0.71
BP-2	16	<10	1.53	10–12	1.27	12–22	1.00	>22	0.72
BP-4	17					<22	1.02	>22	0.75
BSC1	24					<20	1.67	>20	0.98
IO-2	11	<12	0.48	12–25	0.69			>25	0.33
IOC1	22	<8	1.40	8–17	0.80	17–21	0.68	>21	0.42
SS-1	18	<10	1.86	10–16	1.00			>16	0.77
SS-2	15					<21	0.76	>21	0.56
SS-3	16	<10	1.69	>10	0.69				
SS-4	16	<10	1.56	10–25	1.04			>25	0.81
TA-3	17	<11	1.60	11–20	1.25			>20	0.85
TA-C	44	<10	1.10	10–20	1.00	20–29	0.84	>29	0.41
Greasewood									
BP-3	10			<20	0.81	20–27	0.51	>27	0.37
LW-1	7	<12	0.42	12–20	0.36			>20	0.18
Rabbitbrush									
BSC2	24	<10	0.92	10–20	0.78			>20	0.45
TA-6	26	<10	2.00	>10	1.04				
Sacaton									
IO-1	33	<8	4.14	8–25	1.67			>25	1.27
IOC2	5	<9	0.44	9–20	0.25			>20	0.18
LW-2	13	<10	1.16	10–20	0.77			>20	0.49
LW-3	27	<10	2.00	>10	0.89				
TA-4	18	<10	0.67	10–20	0.95	21–30	0.75	>30	0.50
TA-5	7	<10	0.60	10–19	0.49	19–29	0.33	>29	0.30
TS-1	30	<8	1.30	8–20	1.85			>20	1.43
TS-2	20					<27	0.93	>27	0.61
TS-3	34	<8	1.12	8–20	1.40			>20	1.00
TS-4	30	<9	1.08	9–25	0.55			>25	0.40
TS-C[a]	8								
Saltgrass									
BSC3	38					<21	0.94	>21	0.65

Sites containing a C in their designations are control sites. Sites without a C are wellfield sites.

[a] TS-C had shallow GW (<3 m) in all years and TPC showed no response to fluctuations in PPT.

extended from the shallowest recorded DTW to the first DTW at which TPC_{GW} equaled zero. This zero TPC_{GW} point was considered to be the maximum depth at which the plant community at that site extracts groundwater.

An example of this process is presented for the BP-4 site in Table 2. In this example, the vegetation was estimated to utilize groundwater to a maximum depth of 5.6 m. This is the maximum DTW at which TPC_{GW} values are positive, without the influence of residual soil moisture. Negative values are estimation errors, as are different TPC_{GW} values in different years that had the same mean DTW. If there were no estimation errors, the TPC_{GW} values for 2001 and 2000 would be the same, the values for 2002 and 1999 would be the same, and the values for 1992–95 and 1997 would be zero. Precipitation in 1995 and in 2003 was relatively high and TPC in the two immediately preceding years was too low to utilize all of the PPT that followed. Therefore, some of

Table 2
Example of the water-balance approach of calculating TPC_{GW} using data from BP-4

Year	DTW (m)	PPT (cm)	PPT-factor (%/cm)	TPC_{PT} (%)	Sampled TPC (%)	TPC_{GW} (%)	Residual soil moisture
2001	4.5	7.6	1.02	7.8	21.0	13.2	None
2000	4.5	8.4	1.02	8.6	17.7	9.1	None
2002	4.9	5.7	1.02	5.8	10.2	4.4	None
1999	4.9	8.9	1.02	9.1	15.3	6.2	None
1998	5.5	29.1	0.75	21.8	22.2	0.4	None
2003	5.6	22.8	0.75	17.1	18.3	1.2	None
1997	5.7	21.2	1.02	21.6	20.1	−1.5	None
2004	5.9	11.8	1.02	12.0	15.6	3.6	Yes; from 2003 PPT
1996	6.1	18.7	1.02	19.1	25.8	6.7	Yes; from 1995 PPT
1995	6.5	33.3	0.75	25.0	23.7	−1.3	None
1994	6.7	11.2	1.02	11.4	11.1	−0.3	None
1989	6.9	8.9	1.02	9.1	20.4	11.3	Yes; declining GW
1993	7.1	24.9	0.75	18.7	17.7	−1.0	None
1992	7.1	12.5	1.02	12.8	12.0	−0.8	None
1990	7.2	6.4	1.02	6.5	11.4	4.9	Yes; declining GW
1991	7.3	14.3	1.02	14.6	16.8	2.2	Yes; declining GW

DTW = mean depth to groundwater (previous 12 months).
PPT = previous 12 months precipitation.
PPT-factor = PUE ratio taken from Table 1.
TPC_{PT} = (PPT)(PPT-factor) = amount of TPC supported by PPT.
TPC_{GW} = sampled TPC–TPC_{PT} = amount of TPC supported by groundwater.
Negative TPC_{GW} values are estimation errors. These values should equal zero.

this surplus soil moisture carried over into 1996 and 2004, respectively. Based on the residual soil moisture equation of this site (not presented in this article), we estimated this residual soil moisture to be approximately 71% of the surplus PPT. Similarly, the water table was declining from 1989 through 1991. As the water table declined, soil moisture became available in the previously saturated zone. This soil moisture was available to plants in the soil profile above the DTW depths of 1989–91, and the utilization of this upper profile soil moisture resulted in the positive TPC_{GW} calculated for those years.

2.5. Allocation of precipitation and groundwater contributions to TPC

For each of the 30 sites, estimations of precipitation- and groundwater-supported TPC were made for each mean DTW for which data were available for that site. TPC_{PT} and TPC_{GW} values for years with the same mean DTW were averaged. At each DTW for which data existed for a particular site, TPC was allocated into at PPT and a GW percentage by dividing the TPC_{PT} and TPC_{GW} values by the respective annual TPC value.

3. Results

3.1. Precipitation factor

Precipitation factor (PUE) values varied by site and by amount of precipitation received (Table 1). Changes in site-specific PUE values tended to occur as discontinuous shifts rather than as a continuous function. Overall, and for most sites individually, the PUE value increased (efficiency decreased) as precipitation increased (Fig. 1). PUE at low precipitation levels (<8–12 cm) tended to be about twice its value at high

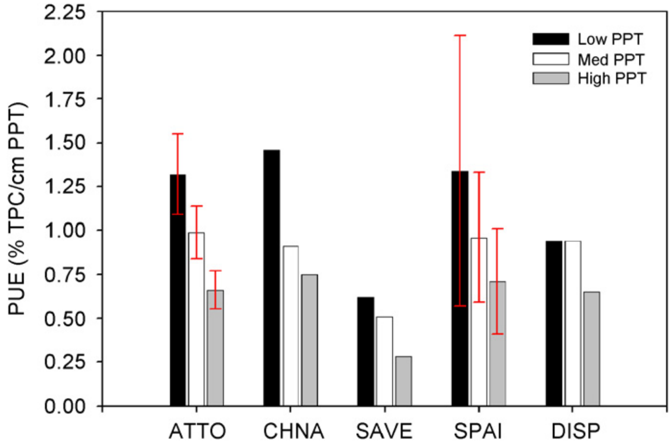

Fig. 1. Mean precipitation-use efficiency (PUE) at low, medium, and high precipitation (PPT) levels for each of five plant communities (ATTO = Nevada saltbush, CHNA = rabbitbrush, SAVE = greasewood, SPAI = alkali sacaton, DISP = saltgrass). Error bars indicate 95% confidence intervals of the means.

precipitation levels (>19–30 cm). With the exception of greasewood, PUE did not vary much among species or lifeforms. However, the small sample sizes for three of the species makes comparisons very tentative except for Nevada saltbush and sacaton.

3.2. *Groundwater utilization*

In general, the proportion of TPC supported by groundwater decreased as DTW increased (Fig. 2), which was expected on the basis of the conceptual model. When DTW was 3 m or less, change in DTW had little effect on TPC_{GW} in Nevada saltbush (ATTO) communities (Fig. 2A). At these depths, 60–70% of TPC was supported by groundwater. Below 3 m, the relative utilization of groundwater by vegetation decreased as DTW increased. Saltbush communities utilized some groundwater (<10% of total use) from as deep as 5–7 m.

Data were more limited for greasewood (Fig. 2C) and rabbitbrush (Fig. 2D) communities, but the available data suggested a similar groundwater-utilization pattern for greasewood communities as for saltbush communities, but a somewhat different pattern for rabbitbrush communities. TPC_{GW} decreased with increasing DTW in greasewood (SAVE) communities, but groundwater utilization was relatively constant (65–75%), and higher than for saltbush communities, at 2–4 m depth. Groundwater utilization by greasewood communities decreased dramatically (to 20%) at about 4 m, but then remained relatively constant from 4 to 8 m. Greasewood communities did not utilize groundwater below at DTW of 8 m. Between 3 and 4 m DTW, rabbitbrush communities (Fig. 2D) utilized a similar proportion of groundwater (35–40%) as did saltbush communities. However, TPC_{GW} almost doubled between 4 and 5 m, indicating a greater use of groundwater by rabbitbrush communities at 4–5 m than at 3–4 m. At 6–6.5 m DTW, groundwater utilization by rabbitbrush communities was intermediate between that of saltbush and greasewood communities.

Sacaton communities utilized a high proportion (80%) of groundwater at very shallow DTW (1 m or less; Fig. 2B). TPC_{GW} was variable in sacaton communities between 1 and 3.5 m DTW, but averaged 47% at these DTW, and between 3.5 and 5.5 m, TPC_{GW} was surprisingly stable (32–35%). Groundwater utilization decreased to 10–15% between 5.5 and 6.5 m, and then decreased to zero below 6.5 m. Data for saltgrass communities were available from only one site. These limited data suggested that saltgrass communities utilize proportionately more groundwater (about 25% more, Fig. 2E) than sacaton communities, and that groundwater utilization begins to decline below 2 m.

3.3. *Relationship between TPC and DTW*

The TPC_{GW} values are estimates of the relative amounts of groundwater-supported TPC at the various DTW. As such, they are indicators of the importance of groundwater in supporting the vegetation present at

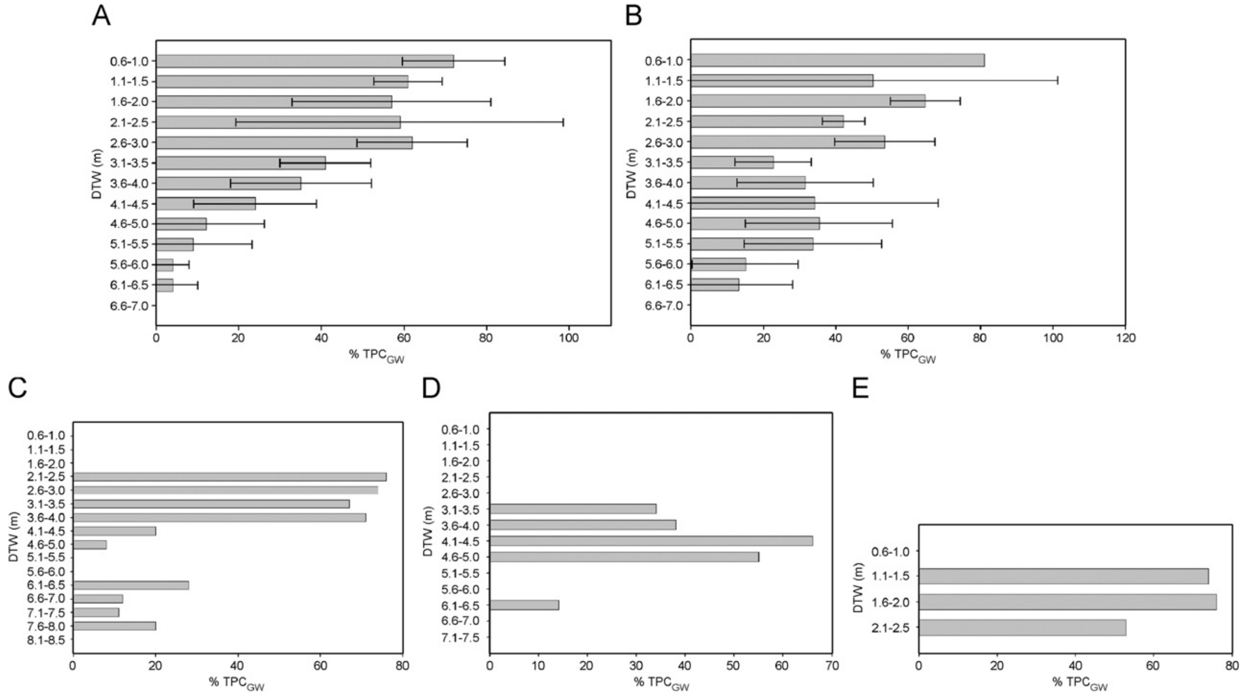

Fig. 2. Total perennial cover (%) supported by groundwater (TPC_{GW}) at various depth to groundwater (DTW) in communities dominated by Nevada saltbush (A), sacaton (B), greasewood (C), rabbitbrush (D), and saltgrass (E). Error bars indicate 95% confidence intervals of the means.

the site, but they do not provide any indication as to how productive the vegetation was at the various DTW or the effect of change in DTW on change in plant cover. To determine the effect of DTW on plant cover, we compared mean TPC by DTW for each of five plant communities. Mean TPC was calculated by averaging the TPC values for all years and all sites (within the respective five communities) that occurred within each 0.5-m range in DTW.

These results indicated that TPC also decreased as DTW increased, but the decreases in TPC occurred more in response to DTW thresholds (Fig. 3) than did the changes in TPC_{GW} (Fig. 2). TPC in Nevada saltbush-dominated communities (Fig. 3A) remained fairly constant (26–33%) when DTW was 3 m or less. When DTW was between 4.5 and 9.5 m, TPC averaged 13–16%. Most of the change in TPC in these communities occurred between 3.5 and 4.5 m DTW. Response patterns below 9.5 m are unclear because of the small number of observations at these DTW. Change in TPC in greasewood communities (Fig. 3C) had a pattern similar to that in Nevada saltbush communities. TPC was relatively high (32–34%) when DTW was 3 m or less and low (5–13%) between 3.5 and 8.0 m, but showed no consistent pattern with increasing DTW below 3.5 m. TPC in rabbitbrush communities (Fig. 3D) was highest around 4 m DTW and was less at both lower (shallower) and higher (deeper) DTW.

In sacaton communities, TPC decreased with increased DTW when DTW was above 2 m (Fig. 3B). The same pattern occurred in the saltgrass community between 1 and 2.5 m (Fig. 3E). TPC was about 50% lower for sacaton communities when DTW was less than 2 m than when DTW was greater than 2 m, but otherwise there was only a weak relationship between change in TPC and change in DTW below 2 m. When DTW was between 2 and 5.5 m, TPC averaged 10–28%, compared to 10–28% when DTW was between 5.5 and 8.5 m.

4. Discussion

4.1. Relationship between TPC and DTW

Both precipitation and groundwater are important sources of water to the vegetation at these 30 sites in the Owens Valley. As predicted by our hypothesis, the relative importance of groundwater increased as DTW

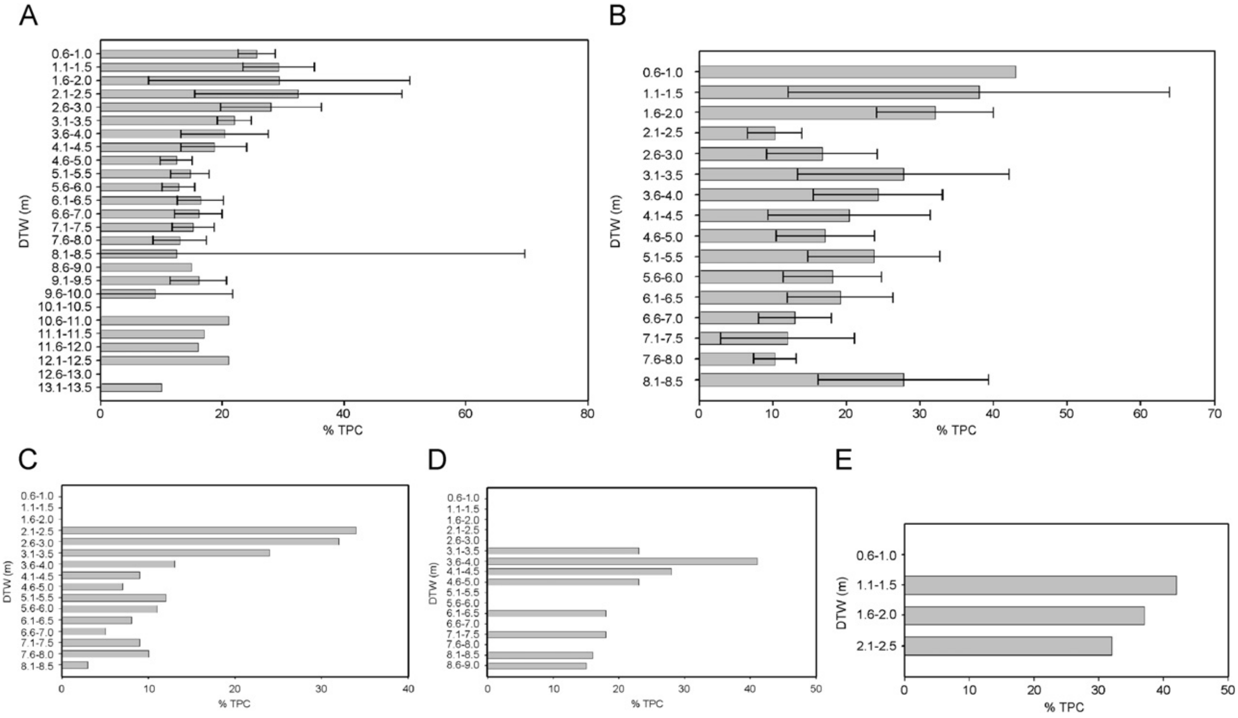

Fig. 3. Relationship between mean total perennial cover (TPC, %) and depth to groundwater (DTW) at communities dominated by Nevada saltbush (A), sacaton (B), greasewood (C), rabbitbrush (D), and saltgrass (E). Error bars indicate 95% confidence interval of the means.

decreased and the relative importance of precipitation increased as DTW increased. Although this pattern was true in general, the data indicate that neither the relationship between TPC and depth to groundwater nor between TPC and precipitation are linear.

For four of the five communities, TPC was highest when DTW was relatively shallow. In addition, with the exception of Nevada saltbush communities, TPC declined as DTW increased at these relatively shallow DTW. These high-TPC DTW thresholds were 3 m for greasewood communities, 2 m for sacaton communities, and 2.5 m for the single saltgrass community. All three of these communities are often considered to be groundwater-dependent (Miller et al., 1982). These relatively high water tables (2–3 m for greasewood and 1–2 m for the grasses) provide abundant water within the soil depths containing large amounts of plant roots. The high TPC zone for Nevada saltbush communities was 3 m DTW or less, but within this zone, TPC did not continue to increase as DTW decreased except at the shallowest DTW (0.6–1.0 m).

It is not surprising that shallower DTW resulted in higher TPC. What was surprising was that the highest groundwater levels did not result in particularly high TPC values. TPC in sacaton communities averaged less than 20% when DTW was 2–3 m (Fig. 3B). When DTW decreased to 1.5–2.0 m, TPC increased by more than 50% (to 32%). Another 0.5-m decrease in DTW resulted in a further increase in TPC of only 20% (to 38%), and at 0.6–1.0 DTW, TPC averaged 43%, or only slightly more than twice what it averaged at 2–8 m DTW. Nevada saltbush is a shrub capable of producing thickets with well over 100% canopy cover and 2–3 m high (personal observation). TPC of communities dominated by this species doubled when DTW decreased from 4–5 to 2–3 m, then did not increase further even as DTW decreased to less than 1 m (Fig. 3A). Eight control sites were included in the 30 permanent monitoring sites of this study. DTW was shallow (mean of 2.5 m) and remained fairly stable at these control sites, varying by an average of less than 1 m over the 14–18 years of data collection. Yet TPC averaged less than 23% on these control sites and TPC exceeded 50% only 6 of 129 times [(number of years) (number of sites)].

Although high groundwater did favor higher TPC in four out of the five communities, the upper limit of productivity of these plant communities appears to be determined by something other than water availability.

Either shrubs or deep-rooted perennial grasses (e.g., sacaton), and generally both, are present at all of the 8 control sites. These species are fully capable of extracting large amounts of water from depths of 2.5 m or less and 14–18 years is a sufficiently long period of time for these species to develop mature stands under adequate to optimum conditions. However, TPC averaged less 23% on these sites when groundwater was abundant.

Such a lack of increased productivity with shallower groundwater has been reported in other studies. Schulze et al. (1996) discussed conditions in Patagonia where vegetation along an aridity gradient from desert to forest did not effectively utilize high soil moisture within 2–3 m of the surface. Similarly, Scott et al. (2006) found that sacaton grassland in Arizona were unable to effectively utilize groundwater within their rooting zone (<3 m).

Nutrient, in particular nitrogen, availability may be an important factor limiting the upper productivity of the vegetation in the Owens Valley. Higher nutrient levels are often found in upper soil layers, especially under arid conditions, with levels rapidly decreasing with depth (Gebauer and Ehleringer, 2000; Seyfried et al., 2005; Walvoord et al., 2003). If the lack of nutrients is limiting productivity, an abundant supply of water would not be expected to increase productivity. Under such conditions, the vegetation might utilize increased amounts of groundwater without a corresponding increase in canopy cover.

Rabbitbrush communities did not display the same TPC-DTW pattern as did the other four communities. TPC in rabbitbrush communities was higher between 3.5 and 4.5 m DTW than at shallower depths (3–3.5 m). Rabbitbrush has been reported to extract water more efficiently at deeper rather than shallower DTW (Leffler et al., 2004) and this has been attributed to the lack of live fine roots in rabbitbrush at shallower soil depths (Leffler et al., 2004). Rabbitbrush has been reported to be mostly unaffected by changes in moisture content in upper soil layers, extracting soil moisture from lower layers instead (Donovan and Ehleringer, 1994). Chimner and Cooper (2004) indicated that rabbitbrush in the San Luis Valley of Colorado used groundwater almost exclusively when DTW was about 2 m or less and during dry seasons. When precipitation-derived soil moisture became available following summer rains, rabbitbrush utilized this moisture source but only if DTW was >4 m. The 4-m threshold reported by Chimner and Cooper (2004) corresponds closely with the 3.5–4.5 m threshold indicated by our data. The higher TPC at these DTW in the Owens Valley rabbitbrush communities could be the result of a combined precipitation and groundwater usage, whereas the lower TPC at shallower DTW might be the result of groundwater usage only and the lower TPC at deeper DTW might be the result of precipitation usage only.

4.2. Groundwater utilization

Our data indicate that groundwater is the major source of water for Nevada saltbush communities when DTW is 3 m or less (Fig. 2A) and then decreases in importance with increasing DTW. These communities utilize little groundwater at depths below 5 m and none below 6.5 m. Both greasewood and rabbitbrush communities utilize more groundwater at most depths than do saltbush communities. Groundwater is utilized particularly heavily by greasewood communities at DTW down to 4 m and by rabbitbrush communities between 4 and 5 m DTW. Toft and Fraizer (2003) reported a similar range in DTW (3.7–5.8 m) for groundwater usage by rabbitbrush at their Mono Lake study site northwest of the Owens Valley.

Sacaton communities also utilize large amounts of groundwater (40–80% of total use) when DTW is 3 m or less (Fig. 2B). Groundwater remains an important source of water to sacaton (20–35% of total supply) to a DTW of about 5.5 m. This is deeper than indicated from other studies. Scott et al. (2000, 2006) reported that sacaton did not extract significant amounts of water below 2–3 m in Arizona. Our data indicated that sacaton utilizes some groundwater (10–15%) to a DTW of 6.5 m.

Saltgrass was dominant on only one of the 30 permanent monitoring sites. Based on these very limited data, saltgrass utilization of groundwater was 30% higher than it was for sacaton. At 1–2.5 m DTW, saltgrass averaged 68% TPC_{GW} compared to 52% for sacaton (Fig. 2E). At these DTW, groundwater utilization by saltgrass was 15% greater than by Nevada saltbush. This higher groundwater utilization by saltgrass was not unexpected. Saltgrass is generally considered to be indicative of sites where DTW is 2.5 m or less (Miller et al., 1982; Nichols, 1994) and species adapted to high water tables tend to utilize relatively large amounts of groundwater (Huxman et al., 2004; McDonald and Hughes, 1968; Mueller et al., 2005).

Groundwater utilization is not synonymous with groundwater dependency. In fact, they may be very different. An estimated 72% of the total water used by Nevada saltbush communities is from groundwater when DTW is less than 1 m, compared to 60% when DTW is 1–3 m (Fig. 2A). Nevada saltbush communities support an average of 26% TPC when DTW is less than 1 m and 30% when DTW is 1–3 m (Fig. 3A). These communities utilize a larger proportion of groundwater at the shallower DTW but produce less TPC in the process. This appears to be a case of luxury consumption of a readily available resource. On a per unit TPC basis, the community is merely transpiring more groundwater, with no increase in productivity. In this case, the community would be more productive (i.e., higher TPC) at a lower (deeper) DTW, and would use less groundwater in the process. A similar example is presented by sacaton. At DTW of 1 m or less, sacaton utilizes 81% groundwater to support 43% TPC. At a DTW of 1–2 m, sacaton utilizes 58% groundwater to support 35% TPC. At less than 1 m DTW, sacaton communities produce 23% more TPC but at a cost of a 40% increase in groundwater usage.

4.3. *Precipitation utilization*

The patterns of precipitation-use efficiency were the same for all five communities (Fig. 1). PUE was higher when precipitation was low and lower when precipitation was high. Overall, PUE at high precipitation was about half the respective value at low precipitation. The PUE gradient exhibited by our data (highest at low PPT, lowest at high PPT) was different than that reported for grasslands by Paruelo et al. (1999). Those authors reported that PUE in grasslands is characteristically low at both low and high PPT levels, and highest at mid-PPT levels (around 50 cm). The fact that PUE was highest in our system at the low end of the PPT gradient may be an indication of adaptation to xeric conditions. Paruelo et al. (1999) used data from various grasslands, but predominantly semiarid grasslands. It is not surprising that semiarid vegetation would be most adapted, as indicated by PUE, to semiarid conditions (i.e., mid-precipitation range). Le Houerou and Hoste (1977) and Le Houerou (1984) also reported a decrease in PUE with an increase in aridity, but this was for different locations, i.e., vegetation in arid regions had lower PUE than vegetation in more mesic regions. Conversely, Huxman et al. (2004) indicated that PUE decreases as precipitation increases, which is consistent with the results of our study.

PUE values at all levels were similar for three of the communities (Fig. 1). This result was unexpected because these three included two shrub communities (Nevada saltbush and rabbitbrush) and one grass community (sacaton). Shrubs tend to be less efficient than perennial grasses in the use of water (Dwyer and DeGarmo, 1970; McGinnies and Arnold, 1939) and in the use of event-driven pluses of precipitation (Schwinning et al., 2003). All three of these species are arid species that, although frequently found in areas of high water tables or areas that accumulate surface runoff, are also found in areas with deep water tables and where surface runoff does not accumulate.

This pattern of decreasing PUE with increasing precipitation provides an upper limit to the productivity of these communities. Even though these three communities are most efficient at low precipitation levels, the net result is low TPC. At an average PUE of 1.3 at 10 cm of precipitation, the community would produce only 13% TPC. The average annual precipitation in the Owens Valley is about 12 cm. At a PUE of 0.9, this would support about 11% TPC. In a very wet year, 40 cm might be received. At a PUE of 0.7, this would support 28% TPC. An upper limit to the productivity of the vegetation, based entirely on precipitation, is therefore on the order of 30% TPC.

The PUE values for greasewood communities were substantially lower than those for the other communities, although these differences were not statistically significant ($P<0.05$) because of the small sample size for the greasewood communities. However, the patterns were consistent and may represent a biologically valid result. Greasewood communities are mostly found in areas of high water table or areas that receive substantial runoff (Donart, 1994; Miller et al., 1982; Nichols, 1994). Species well-adapted to the relatively high soil moisture conditions associated with these types of sites may not be as water-efficient as species adapted to more upland conditions.

4.4. *Interaction between precipitation and groundwater*

Numerous studies have shown that plants often preferentially utilize precipitation-derived soil moisture over groundwater (Chimner and Cooper, 2004; Dawson and Pate, 1996; Mensforth et al., 1994; O'Grady et al., 2006; Penuelas and Filella, 2003; Schulze et al., 1996; Sekiya and Yano, 2002; Smith et al., 1997; Snyder and Williams, 2003; Zencich et al., 2002) or deep soil water (Groom et al., 2000b; Leffler et al., 2004; Schwinning et al., 2002, 2005; Williams and Ehleringer, 2000) when both are available. Our data support these findings. Our data set contained 260 instances where the amount of precipitation received at a site differed among years that had the same mean DTW. A comparison of the calculated $\mathrm{TPC_{PT}}$ values among these pairs provides a method of estimating the relative importance of precipitation, compared to groundwater. If vegetation preferentially uses precipitation-derived soil moisture over groundwater, the $\mathrm{TPC_{PT}}$ value should be higher at higher precipitation levels when DTW remains constant because precipitation-derived soil moisture becomes more available. We compared paired observations (i.e., observations among years at the same site) to minimize the effect of intra-site differences. Sixty-five of the paired observations were at DTW of 6 m or more and these observations were not included in our analysis. This 6-m threshold assumed that groundwater was not utilized to any appreciable amount below this depth, and therefore the relative importance of precipitation would remain constant below this depth. The remaining 195 paired observations were compared overall and by community type (Fig. 4). Statistical significance of the differences between mean $\mathrm{TPC_{PT}}$ at lower precipitation versus greater precipitation level were determined by use of paired *t*-tests (Snedecor and Cochran, 1989).

Overall (i.e., all communities combined), mean $\mathrm{TPC_{PT}}$ was greater at higher precipitation levels than at lower precipitation levels (65% and 55%, respectively; Fig. 4), among observations paired by equal DTW. The same was true for Nevada saltbush (ATTO) communities and sacaton (SPAI) communities, when analyzed separately by community type. $\mathrm{TPC_{PT}}$ was also higher at higher precipitation levels in rabbitbrush (CHNA) and greasewood (SAVE) communities, but the differences were not significant ($P > 0.1$) for these two community types. The lack of statistical significance in these two community types could have been the result of a weaker relationship than in saltbush or sacaton communities, or it could have been the result of much smaller sample sizes.

The higher use of precipitation-derived soil moisture at higher precipitation levels, as evidenced by higher $\mathrm{TPC_{PT}}$ values, could have simply been an artifact of higher productivity at higher precipitation levels. If groundwater use was limited at deeper DTW levels and there were a sufficient number of these observations included in the data set, higher $\mathrm{TPC_{PT}}$ could have resulted from the higher precipitation-induced productivity, rather than the preferential use of precipitation that we hypothesized. To eliminate this possibility, we also compared $\mathrm{TPC_{PT}}$ values at higher and lower precipitation levels using only observations where DTW was 3 m or less. At these DTW, groundwater, including capillary fringe, would be well-within the rooting zone of the vegetation and therefore groundwater would not be limited to the plants. Any change in $\mathrm{TPC_{PT}}$ values would

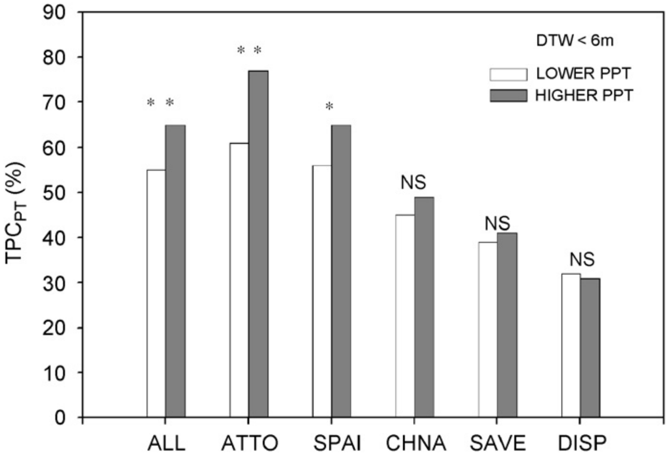

Fig. 4. Mean total perennial cover supported by precipitation ($\mathrm{TPC_{PT}}$) compared by relative precipitation (PPT) levels paired by equal depth to water (all paired observations where DTW < 6 m) overall (ALL) and by plant community (ATTO = Nevada saltbush, SPAI = alkali sacaton, CHNA = rabbitbrush, SAVE = greasewood, DISP = saltgrass). Paired *t*-tests were used to determine significance of differences between means (**$P < 0.01$, *$P < 0.05$, NS = $P > 0.1$).

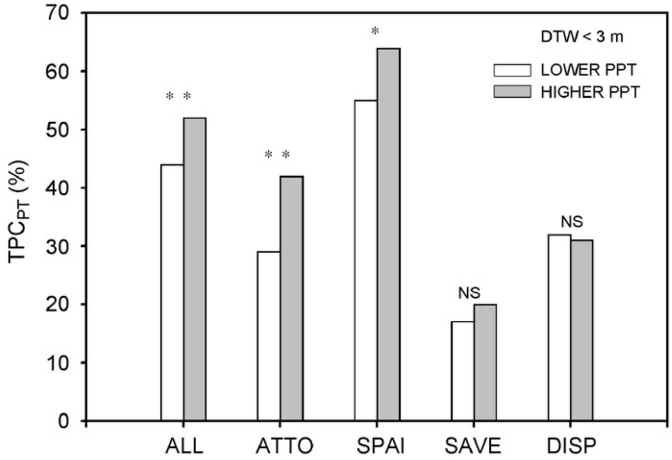

Fig. 5. Mean total perennial cover supported by precipitation (TPC$_{PT}$) compared by relative precipitation (PPT) levels paired by equal depth to water (only paired observations where DTW = 3 m or less) overall (ALL) and by plant community (ATTO = Nevada saltbush, SPAI = alkali sacaton, CHNA = rabbitbrush, SAVE = greasewood, DISP = saltgrass). Paired *t*-tests were used to determine significance of differences between means (**$P<0.01$, *$P<0.05$, NS = $P>0.1$).

be the result of preferential use of precipitation and not an artifact of productivity response to changes in water availability. The results using observations where DTW was 3 m or less were the same as when observations where DTW was <6 m (Fig. 5). There was a significant increase in TPC$_{PT}$ at higher precipitation levels for all sites combined and for both Nevada saltbush and alkali sacaton communities. The statistical levels of significance were also the same as when the deeper DTW values were used.

These TPC$_{PT}$ results indicate that these plant communities (overall, and saltbush and sacaton in particular) preferentially utilize precipitation over groundwater. As precipitation becomes more abundant, and groundwater remains constant, the relative amount of TPC supported by precipitation increases and the amount supported by groundwater decreases.

5. Conclusions

The results of our study confirm that both groundwater and precipitation are important sources of water to the valley-floor vegetation of the Owens Valley. In general, groundwater becomes more important as depth to water decreases but this relationship is not linear and is not consistent among vegetation communities. Groundwater usage by Nevada saltbush communities was relatively constant when DTW was 3 m or less, but decreased with increasing DTW below 3 m. Groundwater usage by greasewood communities was relatively constant between 2 and 4 m, but increased with decreasing DTW above and below these levels, with a rapid decrease below 4 m. Greatest groundwater usage by rabbitbrush communities was between 4 and 5 m, with lower amounts utilized both above and below these DTW. Grass-dominated communities utilized much more groundwater at shallow DTW than did shrub-dominated communities, but also extracted substantial amounts of groundwater at relatively deep DTW (e.g., 5.5–6.5 m).

Productivity of the vegetation, as measured by total perennial cover, generally increased as depth to water decreased, but only up to a limit. As groundwater became increasingly more shallow, productivity either remained constant or decreased. This response was likely the result of a number of factors, including loss of root biomass in saturated zones, limited root architecture plasticity, relatively low upper productivity limits in arid species, and nutrient limitations.

Some groundwater usage occurred at relatively deep depths to groundwater. Our data indicate that Nevada saltbush communities continued to utilize some groundwater (<10% of total use) at depths of 5–7 m, greasewood continued to utilize some groundwater down to 8 m, and rabbitbrush utilized some groundwater at 6–6.5 m. Sacaton communities, the major grass-dominated community, continued to utilize 10–15% groundwater at depths of 5.5–6.5 m, with groundwater-usage decreasing to zero below 6.5 m. Maximum potential DTW for utilization of groundwater is largely a function of two factors: maximum root depth of the species and height of capillary rise from the groundwater surface. Schenk and Jackson (2002) reported that maximum rooting depths of xeric shrubs are often on the order of 5 m. Potential capillary rise in coarse-textured soils is on the order of 0.5–0.75 m (Kohnke, 1968, p. 21) and DTW fluctuations at the 30 monitoring sites were often on the order of 1 m annually. These dynamics of rooting depth, height of capillary rise, and fluctuations in DTW combine to support our findings of maximum groundwater utilization at DTW of 5–8 m.

The vegetation, both shrublands and grasslands, was most efficient in utilizing precipitation at low precipitation levels, and this efficiency decreased as precipitation increased. Differences among communities were relatively minor compared to the differences among precipitation levels (low, medium, high). An exception was greasewood communities, which had lower PUE values than the other four communities. These high precipitation use efficiencies at low precipitation levels and low efficiencies at high levels suggest a high-level of adaptation of this vegetation to arid conditions. These patterns are in contrast to those reported from more mesic regions, but strongly support the convergent rain-use efficiency model proposed by Huxman et al. (2004).

A large amount of experimental data indicate that arid and semiarid vegetation preferentially utilize precipitation-derived soil moisture over groundwater-derived soil moisture. Our study provides a strong field validation of these results that includes multiple plant communities, a moderately long period of time (14–18 years), and wide fluctuations in both precipitation and depth to water. Averaged over the 30 locations included in our data set, the relative use of precipitation-derived soil moisture increased by almost 20% when precipitation-derived soil moisture became more available. Somewhat surprisingly, the increase was greater for the major shrub community, Nevada saltbush, than it was for the major grass community, sacaton (45% and 16%, respectively).

Water is the primary limiting resource in arid ecosystems. In large part, the productivity and structure of plant communities in arid environments are limited by its scarcity. Even so, the dynamics of these plant communities are much too complex to be understood on the basis of single-factor approaches. Our results support the concept that both precipitation and groundwater can be important sources of water to arid valley plant communities, but that these two sources are not precise ecological equivalents. This has important ramifications both in management scenarios (e.g., precipitation is a more effective source of water for vegetation than is groundwater) and research scenarios (e.g., experimental irrigation applications may not be the ecological equivalent of rainfall). Our results also provide another example of where an increase in supply of the most limited resource (e.g., water) only increases productivity to a point where it now becomes limited by another factor (e.g., nutrients). These findings provide confirmation that successful management programs, even in arid ecosystems, can not be single-factor programs, but must account for complex interactions among multiple environmental and ecological factors.

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