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Decline in alkali meadow vegetation cover in California: the effects of groundwater extraction and drought

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Summary

1. Throughout arid regions of the world, groundwater is extracted for human population centres. In the Great Basin and Range region of the USA, we lack basic information regarding some plant communities detailing the extent to which vegetation is threatened by groundwater extraction. This is particularly true for alkali meadow vegetation, which is restricted to zones of shallow groundwater yet is not a riparian plant community with obligate wetland properties.
2. To increase our understanding of the relative importance of groundwater and precipitation in maintaining alkali meadow vegetation cover, we used a 16-year record of plant cover derived from satellite data of Owens Valley, California, USA, in conjunction with concurrent depth-to-water and precipitation measurements, to analyse vegetation response to anthropogenic and climatic changes in water availability.
3. Groundwater decline varied from 0·5 to 5·0 m throughout the study area, with the largest changes occurring at sites closest to pumping wells. The entire region experienced a 6-year drought (1987–92), during which annual precipitation remained below the 50-year median.
4. Meadow plant cover over the 16-year study period was correlated with groundwater depth, but plant cover was generally unresponsive to annual precipitation variability. Sensitivity to groundwater decline was greatest for plots with a higher cover of herbaceous perennials.
5. The results showed that this plant community is groundwater dependent, and that this characteristic buffers the system from the effects of drought. However, at sites with extensive groundwater decline, the remaining plant cover became weakly correlated with precipitation only after groundwater declined below a threshold depth located at 2·5 m, representing the average plant rooting depth.
6. *Synthesis and applications*. Sustainable water development that seeks to pump groundwater without adversely affecting vegetation cover and plant assemblages must recognize the maximum rooting depth of groundwater-dependent plant species. When groundwater is within the root zone, management decisions can be made to either increase or decrease vegetation cover through modification of groundwater depth. When groundwater is below the root zone, vegetation cover is low and susceptible to changes in precipitation. Quantitative satellite measurements of vegetation cover might aid the monitoring and sustainable management of water resources.

Key-words: alkali meadow, desert vegetation, groundwater pumping, phreatophytic vegetation, precipitation, remote sensing, water resource management

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Introduction

Understanding the ecological effects of water management is key to sustainable development world-wide (Postel 2000; Jackson *et al*. 2001). Semi-arid and arid environments are particularly vulnerable to water-related land-use practices and are currently threatened by rapid population and socio-economic changes. A clear challenge to future development and management of water resources is abating tension between human and ecosystem requirements for fresh water (Postel, Daily & Ehrlich 1996; Steen 1998). In many locations, surface-water runoff is already utilized, and cities and agricultural centres have turned to groundwater aquifers to augment supply during drought (National Research Council 1993). The practice of recharging shallow aquifers during wet years, and then pumping these stored resources during dry years, has benefits over water storage in surface reservoirs because of lower evaporation rates. However, cycles of recharge and pumping result in increased fluctuation of the water table, which has ecological consequences for plant communities that are composed of groundwater-dependent (phreatophytic) species. Furthermore, pumping has led to the drying of springs and seeps in many regions, and this trend is likely to continue as water resources become further allocated to increasingly large urban centres.

In basins and valleys of the intermountain western USA, some zones between wetland and upland vegetation have been described as grass-dominated meadows (West & Young 2000). Plant species occupying these meadows are sometimes characterized as facultative wetland (Reed 1988), i.e. they are intermediate between obligate wetland species and species occurring only in upland (precipitation-dependent) zones. Facultative species generally benefit from shallow groundwater but can exist where groundwater is inaccessible. The relationships between plant species composition, distribution and cover, and groundwater depth, can be complex; nevertheless, clear patterns have been identified (Stromberg, Tiller & Richter 1996). An obvious pattern is related to rooting depth. Herbaceous meadow species with shallow roots thrive in regions of shallow groundwater (Allen-Diaz 1991; Castelli, Chambers & Tausch 2000). Roots of facultative phreatophytic shrubs reach groundwater at greater depths (Sorenson, Dileanis & Branson 1991; Groeneveld & Or 1994; Stromberg, Tiller & Richter 1996).

Sustainable water management of vegetation occupying zones with intermediate groundwater depth requires knowledge of the degree to which groundwater change affects plant cover or floristic composition. It also requires knowledge of how plant cover responds to water inputs directly from precipitation. To study these responses, simultaneous measurements are required for vegetation cover and the hydrologic parameters: groundwater depth and precipitation. Planning and foresight are necessary to ensure these measurements occur in the correct locations to capture the vegetation response to groundwater decline from pumping and, in the past, few water diversion projects included monitoring of biotic resources. Fortunately, quantitative remote-sensing methods can be used to determine the percentage plant cover from images acquired over the past two decades (Elmore *et al*. 2000). Remote measurements of plant cover have been shown to provide useful information for a variety of applications (Okin *et al*. 2001; Rogan, Franklin & Roberts 2002). Total plant cover from remote sensing provides an integrated valuation of the extent to which vegetation cover is altered by environmental factors such as depth to groundwater, precipitation, grazing and disturbance (Dube & Pickup 2001; Asner, Borghi & Ojeda 2003; Elmore, Mustard & Manning 2003). When used in conjunction with detailed field data, remote measurements of plant cover also highlight the regional significance of changes observed at smaller scales.

This study analysed the vegetation response within a plant community termed ‘alkali meadow’, which exists in scattered locations throughout the Great Basin and Range but is restricted to zones of shallow groundwater. In eastern California, USA, alkali meadow is an important plant community for conservation because (i) plant cover is dominated by facultative wetland species, (ii) it is essential habitat for numerous rare and endangered species, and (iii) groundwater extraction for water export is practised or proposed throughout much of the region. In previous work we used remote-sensing technologies to identify and classify regions of Owens Valley, California, where vegetation was affected by groundwater pumping (Elmore, Mustard & Manning 2003). With the present study we focused on plots of alkali meadow vegetation for which measurements of groundwater depth through a 16-year period were available. The data set included periods of drought and groundwater pumping that were sufficiently decoupled to allow separate analyses (Elmore, Mustard & Manning 2003). Our objectives were to: (i) understand the absolute and relative importance of groundwater and precipitation in influencing plant cover within alkali meadow vegetation; (ii) identify a maximum effective rooting depth that is generally characteristic of alkali meadow vegetation; and (iii) determine if a general model of plant cover response to groundwater decline is applicable across plots, or if plot characteristics, such as the proportion of herbaceous and woody plants, also influence vegetation cover response.

There is considerable evidence that alkali meadow vegetation in Owens Valley is phreatophytic (Sorenson, Dileanis & Branson 1991; Manning 1997; Steinwand, Harrington & Or 2006) but a specific understanding of plant cover response to water table changes has been elusive. Because the depth to which plants can acquire groundwater is limited (Jackson *et al*. 1996; Jackson *et al*. 1999; Sperry *et al*. 2002), we hypothesized that a response threshold exists, exhibited by the depth-to-water

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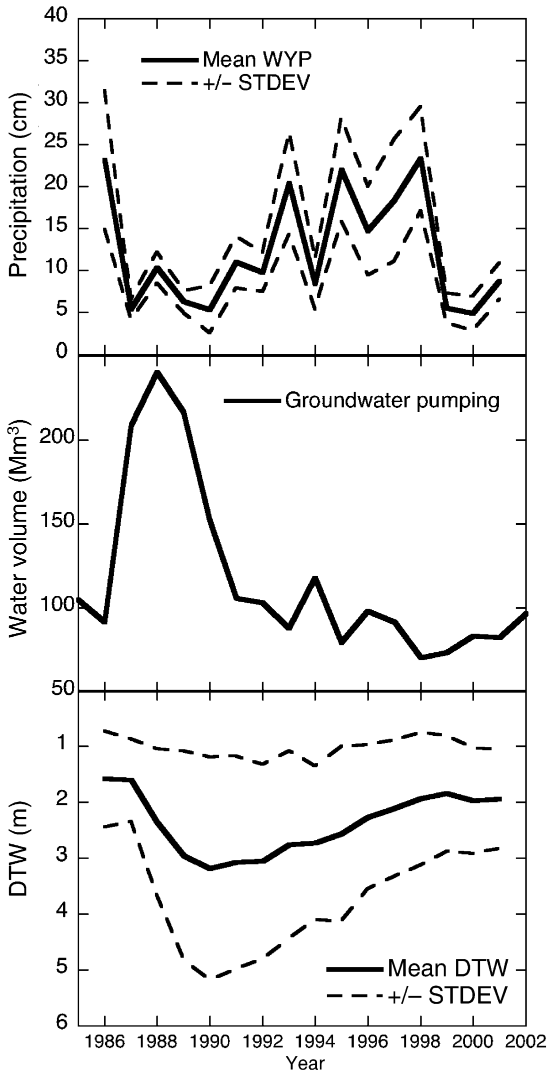

Fig. 1. Mean Owens Valley water year precipitation, annual pumping, and, for the study plots, mean depth to groundwater (DTW) for the period 1986–2001.

(DTW) beyond which plant cover ceases to respond to fluctuations in groundwater depth. We view the identification of this threshold DTW to be critical to the sustainable management of alkali meadow vegetation.

Materials and methods

SITE DESCRIPTION

This work was conducted in Owens Valley, a north–south running basin located east of the Sierra Nevada and west of the White-Inyo range, in eastern California, USA (Fig. 1). Precipitation falls mostly during the cool winter months and averages 13 cm year^{-1}. In addition to precipitation inputs, water recharges the valley aquifers each spring and summer as a result of snowmelt runoff from the Sierra Nevada. Historically, high groundwater tables occurred across the valley floor (Hollett *et al.* 1991). As a result, alkali meadow is relatively extensive throughout Owens Valley. Within the Great Basin region of the western USA in general, meadows occur infrequently and are often disturbed by activities ranging from grazing to water diversions (West & Young 2000). Although small in spatial extent, these communities are important biologically because they harbour rare plant species and provide habitat for local and migratory animals.

A vegetation map prepared in the mid-1980s showed areas of alkali meadow, characterized by the dominant perennial, native phreatophytic grass species saltgrass *Distichlis spicata* and/or alkali sacaton *Sporobolus airoides*, covering approximately 20 000 ha of the valley floor (City of Los Angeles and County of Inyo 1991). *Distichlis spicata* and *S. airoides* have wetland indicator classifications of facultative wetland and facultative wetland+, respectively (Reed 1988). Shrubs, especially rabbitbush *Chrysothamnus nauseosus* (wetland status disputed) and Nevada saltbush *Atriplex lentiformis* ssp. *torreyi* (facultative), and other species also occur in this broadly defined plant community (Sorenson, Dileanis & Branson 1991; Manning 1997). Pumping can in some cases be associated with an increase in deeper-rooted woody plants and/or invasive, non-native annual species that do not require groundwater (Manning 2001; Elmore, Mustard & Manning 2003). The two aforementioned native shrubs in particular, rabbitbrush and Nevada saltbush, are well adapted to colonizing disturbed alkali meadows. Total plant cover in Owens Valley meadow varies spatially; data from field sites showed a range from 8% to 85% (vertically projected) (Manning 1997). The dominant grass and shrub species have a maximum effective rooting depth of about 2 m and 4 m, respectively, and the estimated distance of capillarity above saturated groundwater varies with soil type but is typically about 1 m (City of Los Angeles & County of Inyo 1991; Sorenson, Dileanis & Branson 1991; Groeneveld 1992). Native annuals are relatively uncommon in Owens Valley alkali meadow (Manning 1997). In contrast, non-native annuals, such as Russian thistle *Salsola tragus* and *Bassia hyssopifolia* often contribute measurably to total cover in disturbed meadows in higher than normal precipitation years (Elmore, Mustard & Manning 2003; Inyo County Water Department, unpublished data).

In addition to common, dominant species, Owens Valley alkali meadow harbours several species of conservation concern (Tibor 2001; California Department of Fish and Game 2004), including Owens Valley checkerbloom *Sidalcea covillei*, Inyo County star tulip *Calochortus excavatus*, Owens Valley vole *Microtus californicus* ssp. *vallicola*, northern harrier *Circus cyaneus* and red shouldered hawk *Buteo lineatus*. In addition to biodiversity values, the abundant grass cover on the valley floor provides economic benefits related to tourism and livestock production (Hickman 1993).

WATER MANAGEMENT IN OWENS VALLEY

The abundance of water in Owens Valley led to its development in the early 20th century as a municipal watershed by the City of Los Angeles. The Los Angeles Department of Water and Power (LADWP) diverts water from mountain streams into the Los Angeles aqueduct. Surface water supply is augmented by groundwater pumping, especially during dry years. During wet years, reduced pumping and intentional spreading of surface water over porous soil result in some recharge to the shallow aquifer. From 1987 to 1992, below-average precipitation conditions prevailed in the central Sierra Nevada and Owens Valley. LADWP responded to this drought by increasing groundwater extraction in many areas of the valley, leading in some cases to > 5 m declines in groundwater tables (Fig. 1).

LADWP expects to increase pumping to about $1{\cdot}36 \times 10^8$ m^3 $year^{-1}$ (City of Los Angeles and County of Inyo 1991) but the United States Geological Survey (USGS) has reported that a sustainable pumping rate is a third lower, at around $8{\cdot}64 \times 10^7$ m^3 $year^{-1}$ (Danskin 1998). The disparity between these two numbers has resulted in considerable tension between LADWP and the people of Owens Valley. An additional source of tension occurs at the state level, where California is being allotted a smaller fraction of Colorado River water, thus forcing local water managers to increase instate production. Population growth in Los Angeles, continued use of water for high valued crops in the central valley, and a series of low precipitation years (1987–92 and 1999–2004) all lead to the prediction that water extraction in Owens Valley will continue to be of high concern to Los Angeles. However, a water management agreement was signed in 1991 that commits LADWP to managing water resources in Owens Valley to avoid causing certain described decreases and changes in vegetation and to cause no significant effect on the environment that cannot be acceptably mitigated. Since the signing of this document, deciding whether measurable changes in vegetation were caused by water management, and agreeing on what constitutes 'avoidance', have been primary concerns of Los Angeles and residents of Owens Valley. Addressing this conflict and attributing vegetation change to variations in precipitation or groundwater extraction was the focus of this study.

PLOT SELECTION: PRECIPITATION AND GROUNDWATER MEASUREMENTS

We developed criteria to obtain spatial control between measurements of alkali meadow vegetation cover and depth to the water table from 1986 to 2001. LADWP maintains about 300 5-cm diameter monitoring wells throughout Owens Valley, and DTW in each well is measured at least twice annually. We identified a subset of monitoring wells that were located within vegetation mapped as alkali meadow and had DTW records dating back to April 1986. Using aerial photographs and plot observations, we then determined whether a plot 0·73 ha in size (size determined by remote-sensing data resolution as discussed below) could be placed in undisturbed vegetation surrounding, or within 100 m of, the monitoring well. Wells were excluded if roads, ditches, changes in topography, visible vegetation ecotone transitions or recent surface disturbances affected plot homogeneity. In this way, a set of 47 plots associated with monitoring wells was identified for the study (Fig. 1). Data on DTW, precipitation and vegetation cover were then assembled for each plot.

DTW measurements obtained in April of each year between 1986 and 2001 were acquired for each of the 47 monitoring wells. April marks the transition between winter precipitation and the onset of high evapotranspiration rates, and water levels are typically the shallowest then (Lee 1912). Therefore, April groundwater measurements were used to represent the annual extent of groundwater recharge, and thus the water available to potentially subirrigate the plants throughout the growing season.

Groundwater pumping was highest in 1987–89 (Fig. 1). Groundwater levels were relatively shallow in 1986, lowest in the early 1990s, and recovered to varying degrees during the late 1990s. In 1986, before the most intensive groundwater pumping and following high runoff years (e.g. 1998), DTW among the plots generally ranged from 0·2 to 3·5 m (data not shown). During dry years, 1987–92, when water was pumped extensively, 15 plots experienced groundwater below 3·5 m, and in six plots it dropped below 6·0 m. Among the plots, rates of water table decline between 1986 and 1992 ranged from 0 to approximately 0·8 m $year^{-1}$. Plots distant from groundwater pumping exhibited the smallest variation in DTW overall and were probably negligibly influenced by groundwater extraction.

LADWP, Inyo County Water Department (ICWD) and National Oceanic and Atmospheric Administration operate 14 precipitation gauges in Owens Valley. Precipitation data for each of the 47 plots was acquired from the nearest gauge. Seven of the precipitation gauges only became operational in 1993. To develop an estimate of precipitation for plots nearest one of the newer gauges, we regressed precipitation (1993–2001) for the new and a close-by older gauge and then used the parameters to calculate 1986–92 precipitation estimates for the new gauge. Data from all Owens Valley precipitation gauges are highly covariant. For this study, total water year precipitation (WYP), the precipitation that falls from October to September, was used as the plot precipitation value. During our study period, precipitation was below the Owens Valley average in 10 years (1987–92, 1994 and 1999–2001), and above average in at least five years (Fig. 1).

VEGETATION MEASUREMENTS

Cloud-free Landsat Thematic Mapper and Enhanced Thematic Mapper plus satellite data covering the visible and near infrared wavelengths at 28·5 m spatial resolution were acquired during September of each year.

Processing of these data followed methods described by Elmore *et al*. (2000). Pre-processing included detailed image co-registration (within one pixel) and georeferencing. These procedures assured that individual image elements (pixels) could be compared among years at specific geographical coordinates. Spectral alignment using temporally invariant surface features was performed to normalize for sensor and atmospheric changes between data acquisition events. No absolute corrections were made for the effects of atmospheric scattering and absorption. Atmospheric corrections of multispectral data amount to a simple linear transformation of the data, and the linear model we used to measure vegetation cover (see below) is invariant under such transformations.

Linear spectral mixture analysis (LSMA; Adams, Smith & Johnson 1986; Smith *et al*. 1990) was used to measure the fractional cover of photosynthetic vegetation. The LSMA model assumes the Landsat-measured surface radiance within each pixel to be a linear combination of basic surface materials such as vegetation and soil, called spectral endmembers. The endmember spectra used were extracted from the Landsat images: (i) photosynthetic vegetation from a high-cover alkali meadow, (ii) a high reflectance alkaline soil, (iii) a dark organic-rich soil and (iv) dark surface (shade) from a lake on the valley floor. Through LSMA we calculated the fraction of each of these four endmember spectra necessary to model the radiance of each pixel. The fraction of the photosynthetic vegetation (%PV) endmember was retained as our estimate of percentage vegetation cover (Elmore *et al*. 2000; Elmore, Mustard & Manning 2003). In previous work we compared LSMA measurements of vegetation cover with field-based measurements. Results showed that absolute measurements of vegetation cover were accurate to within ±4·0% and measurements of change were associated with an uncertainty of ±3·8% (Elmore *et al*. 2000).

Each of the 47 plots was represented in the remote-sensing database as nine contiguous pixels arranged in a square 0·73 ha in size. We estimated that this size was large enough to reduce any error attributed to annual georeferencing, yet small enough to assume that DTW measured in the monitoring well was representative of the plot. Therefore, the vegetation cover estimate for each plot was the average of the 9%PV values, and this measurement was made each year between 1986 and 2001.

In this analysis using remote-sensing data, it was not possible to differentiate plant cover by species or life form. Plots were assessed in the field during late summer in 2003 (at the end of the 16-year remote-sensing time series). Plant cover was measured within each plot along two 50-m north–south running transects located parallel to each other, separated by 50 m, and centred within each plot. From these data we calculated the percentage cover of the three dominant life forms: perennial herbaceous species, shrubs and annuals.

DATA ANALYSIS

Least-squares means regressions were used to assess the relationship between the environmental variables and vegetation cover (from remote sensing) in the 47 plots. For all regressions, both DTW and vegetation cover were log transformed after adding a constant (1 and 10, respectively) to normalize the distribution of residuals. With precipitation highly covariant among plots it was not possible to include precipitation and sampling year in the same model. Therefore, we initially ran a model of cover that included DTW, the identity of year and their interaction to test whether there were different relationships between DTW and cover among years. Neither year nor the interaction between DTW and year were significant ($P = 0{\cdot}07$, $P = 0{\cdot}16$, respectively). Therefore, it was concluded that data from all years could be grouped in subsequent models. It was also noted that the primary difference between years was the range in groundwater depth at each of the sites (Fig. 1) and not the response of vegetation to that range.

We modelled cover with regressions using data from all years. The first regression tested the influence of DTW and WYP on cover, and all data were used. We then excluded site measurements where DTW was shallower than a threshold value of 1·5 m and repeated the DTW and WYP regression. In an attempt to identify the maximum rooting depth we successively moved the threshold depth deeper from 1·5 m at 0·1-m intervals. We continued this repetitive process until only data with DTW deeper than 4·5 m were modelled. From the literature on Owens Valley species, we viewed the range 1·5–4·5 m to include the average maximum rooting depth for alkali meadow (Sorenson, Dileanis & Branson 1991; Groeneveld & Or 1994).

A useful task in water management is to collect information required to predict the response of individual plots to groundwater decline. Our final model tested whether the effects of DTW or WYP on vegetation cover differed among plots, or if a single model could be used for all plots. In this model, plot was used as a surrogate for characteristics that might modify the DTW–vegetation relationship, such as soil texture, nutrient availability and plant assemblage characteristics. For this retrospective analysis using satellite data, it was not possible to include each of these characteristics individually. In this model, DTW, WYP, a categorical plot identity and all pairwise interactions were included. The interaction term of DTW and plot identity tested whether the relationship between DTW and vegetation cover depended on the plot identity. To maximize the significance of plot level response to groundwater, we restricted this analysis to plots that varied at least twofold in the log-transformed DTW (13 plots). Finally, we examined differences in the relationship between DTW and vegetation cover, and related these differences to plot characteristics from the 2003 plot transect data of plant community composition.

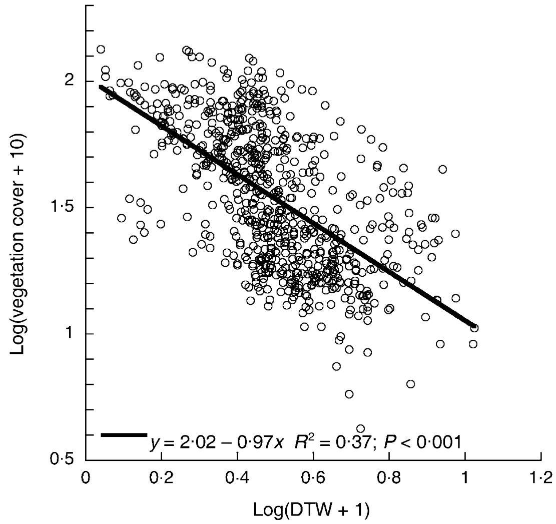

Fig. 2. Log-log relationship between groundwater depth (DTW) and vegetation cover with model parameters from Table 1.

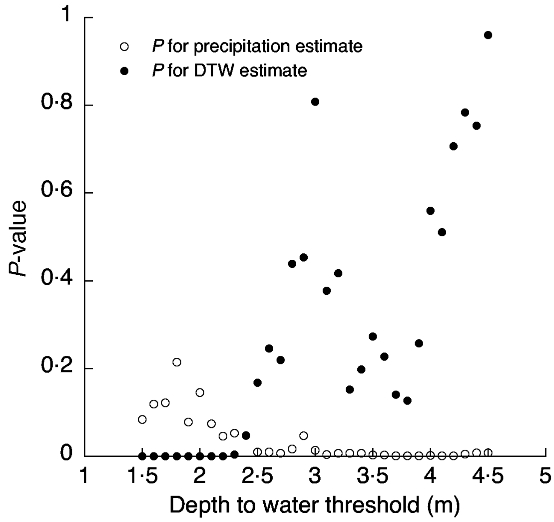

Fig. 3. Results of sequential multiple regression trials for models using all data, with groundwater (DTW) below a designated depth shown on the *x*-axis. Significance levels (*P*-values) for the precipitation and DTW estimates are plotted on the *y*-axis. When DTW was ≥ 2·5 m, DTW no longer had a significant effect on cover and the effect of precipitation became significant.

Table 1. Model results analysing effects of depth to groundwater (DTW) and water year precipitation (WYP) on vegetation cover in 47 plots, 1986–2001

Parameters (n = 705, R^2 = 0·37)	SS*	Estimate	P
Intercept		2·00 ± 0·03	< 0·001
log DTW	20·3	–0·97 ± 0·05	< 0·001
WYP	0·2	0·002 ± 0·001	0·07
log DTW × WYP	0·1	0·009 ± 0·007	0·18

*Model SS 20·8.

Table 2. Model results including plot identity for plots exhibiting greater than twofold variation in log DTW

Parameters (n = 200, R^2 = 0·80)	SS*	Estimate	P
Intercept		1·76 ± 0·06	< 0·001
Plot	2·47		< 0·001
log DTW	1·28	–0·71 ± 0·08	< 0·001
log DTW × plot	0·97		< 0·001
WYP	0·31	0·008 ± 0·002	< 0·001
WYP × plot	0·40		0·037
log DTW × WYP	0·03	0·02 ± 0·01	0·171
log DTW × WYP × plot	0·26		0·244

*Model SS 9·19.

Results

In the model of cover that included DTW and WYP, 37% of the variation in cover could be explained by DTW (Table 1 and Fig. 2). Cover was high when DTW was shallow and low when DTW was deep ($P < 0{\cdot}001$). Variation in precipitation did not show a statistically significant correlation with cover ($P = 0{\cdot}07$) in this model, nor was there a significant interaction between precipitation and DTW ($P = 0{\cdot}18$) (Table 1).

The significance of the DTW and precipitation effects was dependent on the range of DTW at the modelled sites. Models that included data from sites where DTW was shallower than *c.* 2·5 m exhibited a significant effect from DTW, and precipitation was not a significant effect (Fig. 3). When the data were restricted to plots and times where DTW was deeper than *c.* 2·5 m, cover was significantly correlated with precipitation ($P < 0{\cdot}05$) but was unaffected by further fluctuations in DTW ($P > 0{\cdot}05$).

Including plot identity as an explanatory variable in the regression model greatly increased the variation explained by the model ($r^2 = 0{\cdot}80$; Table 2). Plots differed in mean cover beyond what could be explained by DTW or WYP, therefore plots with approximately the same DTW exhibited different cover values ($P < 0{\cdot}001$; Table 2). There were also different relationships among plots between cover and DTW ($P < 0{\cdot}001$; Table 2). In some plots, there was little influence of DTW on cover, while for other plots cover declined strongly with increasing DTW (Fig. 4, inset). This result led us to investigate whether a plot feature that was simple to measure could account for the contribution of plot identity to the overall model explanatory power. The variation among plots in the relationship between DTW and cover could not be explained by maximum groundwater depth ($P = 0{\cdot}30$), total plant cover in 2003 ($P = 0{\cdot}13$) or shrub cover in 2003 ($P = 0{\cdot}34$) (data not shown). Among the parameters we tested, the best predictor of total plant cover sensitivity to DTW was the 2003 perennial herbaceous cover. Plots with a greater cover of the more shallowly rooted perennial herbaceous plants were more sensitive to fluctuations in DTW ($r^2 = 0{\cdot}63$, $P = 0{\cdot}001$; Fig. 4).

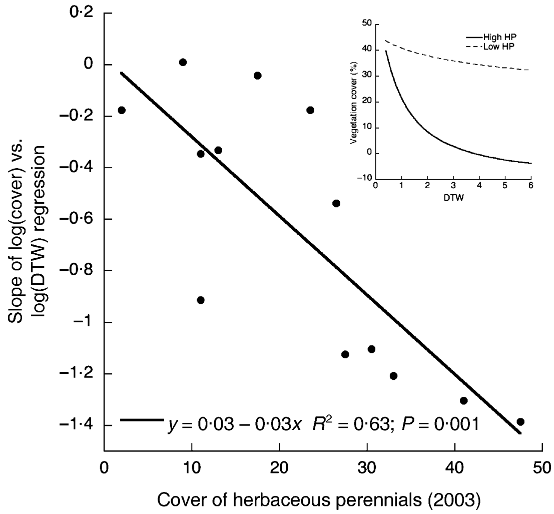

Fig. 4. The slope of the groundwater (DTW) vs. vegetation cover regression for selected plots (see text) plotted against the total cover of perennial herbaceous species (including grasses) measured in the plot in 2003. Inset: vegetation response to DTW for two plots with the highest and lowest cover of herbaceous perennials (HP), demonstrating the differences in response for these plots.

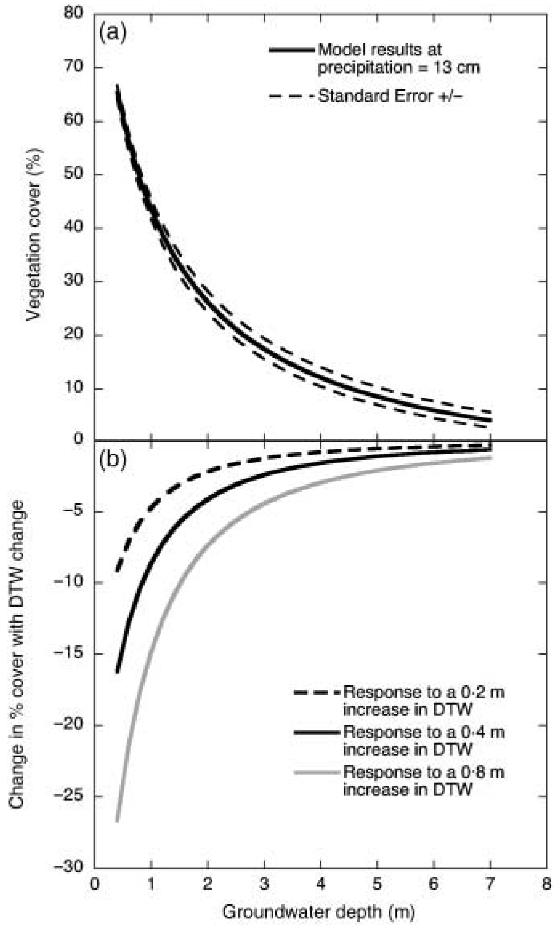

Fig. 5. A graphical presentation of the results of the general model, the coefficients of which are presented in Table 1. (a) Model results showing the vegetation cover relationship to DTW, with standard error. (b) The impact of changing groundwater depth modelled as the difference in vegetation cover for two groundwater values separated by 0·2, 0·4 or 0·8 m DTW.

Discussion

The 16-year data set of precipitation, DTW and remote-sensing derived vegetation cover showed that vegetation cover was highly responsive to variation in groundwater depth (Table 1 and Fig. 2). Vegetation cover is most sensitive to groundwater change initially, when groundwater is close to the surface, and sensitivity tapers off as DTW increases (Fig. 5). This indicates that cover response to declining groundwater is largest at the initiation of groundwater pumping. One explanation for this response is that vegetation is adapted to groundwater fluctuation within the range established previously (Shafroth, Stromberg & Patten 2002). When groundwater declines below this range, water availability decreases for some individuals or species and, as a result, total vegetation cover declines.

Owens Valley meadow cover response patterns are controlled by effective rooting depth. For the 47 plots used in this study, the average maximum effective rooting depth was located at 2·5 m. This estimation was based on three observations: (i) the range of DTW in 1986 prior to pumping in most areas was within the range of 0–3·5 m, and 66% of the plot DTW data was in the range 0·75–2·5 m (Fig. 1); (ii) vegetation cover was correlated with groundwater fluctuation only when modelled data included sites where DTW was within 2·5 m of the surface (Fig. 3); and (iii) vegetation cover was reduced and significantly correlated with precipitation when DTW was below 2·5 m (Figs 2 and 3).

The plot data revealed only a weak plant cover response to precipitation across the entire range of groundwater depths ($P = 0{\cdot}07$; Table 1). This result indicates that of the two water input sources, groundwater exerts a stronger influence on cover in Owens Valley meadows. Similarly, other studies have shown that groundwater availability in arid regions affects plant distribution patterns across the landscape (Allen-Diaz 1991; Stromberg, Tiller & Richter 1996; Castelli, Chambers & Tausch 2000). Our inability to detect a strong precipitation influence on meadow cover underscores some important characteristics of meadow systems in desert regions. First, within our data and within these systems in general, when plants have access to groundwater the roots of dominant Owens Valley meadow species potentially have access to water through as much as 2·5 m of saturated soil. This large volume of water is available to plants throughout the entire growing season. Precipitation, in contrast, averages 13 cm, rarely exceeds 30 cm (Fig. 1) and partly evaporates before being absorbed by plants or soil. Therefore precipitation is a sparse and unreliable water source relative to groundwater.

Undoubtedly, Owens Valley meadow plants absorb precipitation water, but the contribution of precipitation to the characteristic we measured, late summer total vegetation cover, is negligible where groundwater occurs within the root zone. Research on species in similar systems and habitats has shown precipitation to stimulate physiological activity but not contribute measurably to canopy growth (Snyder & Donovan 2004). Others have shown plants using groundwater and precipitation (Torres *et al*. 2002), plants switching from groundwater to precipitation (Chimner & Cooper 2004) and different species at the same site using different water sources (Yepez *et al*. 2003). We also recognize the role of late summer annual plants in increasing the response of vegetation cover to annual precipitation (Elmore, Mustard & Manning 2003). Finally, precipitation has other roles, such as mobilizing soil nutrients (Burke *et al*. 1998) and temporarily washing salts from the soil surface (Guler & Thyne 2004). Any or all of these mechanisms could be responsible for the observed (albeit weak, $P = 0{\cdot}07$; Table 1) relationship between plant cover and precipitation.

Terrestrial vegetation depends on precipitation consistently across biomes, and sensitivity to precipitation change is largest when mean annual precipitation is lowest (Huxman *et al*. 2004). In contrast, Owens Valley meadow exhibits stable high plant cover in a highly variable, low-rainfall environment, suggesting this ecosystem has more in common with wetlands than upland systems. Large volumes of mountain snowmelt maintain a stable shallow groundwater aquifer that buffers plant communities from the effects of drought (Danskin 1998; Elmore, Mustard & Manning 2003). Similar to other intermountain settings (Schulze *et al*. 1996), the availability of these groundwater resources has allowed for the establishment and survival of plants that are not dependent on precipitation within these localized regions. Throughout arid regions, vegetation dependent on groundwater resources might be more widespread than previously estimated if plant assemblages functionally similar to Owens Valley meadows are included.

Cover response to declining groundwater availability can be explained mechanistically. When groundwater begins to decline beneath alkali meadow vegetation, the most shallowly rooted plants (grasses and forbs) are the first to respond. As individual plants and plants in more sensitive microhabitats (e.g. on elevated locations or in more coarse-textured soils; Sperry & Hacke 2002) lose contact with the groundwater table, total plant cover declines as a result of mortality of those groundwater-disconnected plants. In locations where there is a high total cover of shallow-rooted plants, the decrease in total cover is more rapid. Where cover of deeper-rooted species (shrubs) is greater, the response to groundwater decline can be slower, but nevertheless the response generally follows a logarithmic decline. As groundwater declines below the rooting depth of most plants, precipitation becomes the primary water source for plants remaining on the site, and cover switches from responding to groundwater declines to responding to precipitation fluctuations. The weak response between precipitation and cover at deep DTW suggests that perennial meadow vegetation is not well adapted to switching to precipitation in these conditions. However, where seeds are available, annual plants can respond to precipitation, particularly during the first wet years following drought (Elmore, Mustard & Manning 2003).

These results show that alkali meadow attains high plant cover only when groundwater is well within the root zone of the perennial grasses and shrubs. The data set was limited in that the remote-sensing data did not indicate whether plant community floristic composition is maintained through a period of groundwater decline and recharge. However, evidence from Owens Valley suggests that periods of low groundwater aid the recruitment success of deeper-rooted shrub species and annuals that are not phreatophytic (Elmore, Mustard & Manning 2003). If this trend were to continue and prove to be a robust feature of the Owens Valley landscape, it would have the effect of decoupling vegetation cover from changes in the shallow groundwater aquifer. Such a change in system functioning (a change in the maximum rooting depth or a switch to precipitation dependence) would represent a threshold response to an alternative state. Research in a variety of systems has highlighted the fact that alternative states can be stable, result in the degradation of ecosystem services, and can be very costly to manage for the return of the previous ecosystem structure and functioning (May 1977; Scheffer *et al*. 2001; van de Koppel *et al*. 2002).

The vegetation response model and remote-sensing methods described here can be used to guide management of groundwater levels and vegetation cover within Owens Valley meadows, and perhaps management of other plant communities that are dominated by facultative wetland species. If sustained plant community composition and resistance to drought (i.e. the capability of utilizing groundwater as a buffer from drought) is a management objective, then groundwater must remain within the root zone of these plants. Management options (decisions on whether to pump groundwater or to allow natural recharge) are available when groundwater is within approximately 2·5 m of the surface. Below this depth, precipitation dynamics dominate and further changes in DTW have no effect on plant cover. Remote-sensing data can play an important role when interpreting vegetation changes in areas where DTW has not been monitored. Its primary strengths are to identify the regional extent of vegetation change measured at field sites, and to highlight areas that over time become sensitive to precipitation variability. This might assist managers in determining where further pumping should be avoided. Through a combination of remote-sensing data analysis, targeted field monitoring and informed groundwater management, it might be possible to balance the water needs of humans with environmental resources.

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References

Adams, J.B., Smith, M.O. & Johnson, P.E. (1986) Spectral mixture modeling: a new analysis of rock and soil types at the Viking Lander I Site. *Journal of Geophysical Research*, **91**, 8098–8112.

Allen-Diaz, B. (1991) Water-table and plant species relationships in Sierra Nevada meadows. *American Midland Naturalist*, **126**, 30–43.

Asner, G.P., Borghi, C.E. & Ojeda, R.A. (2003) Desertification in central Argentina: changes in ecosystem carbon and nitrogen from imaging spectroscopy. *Ecological Applications*, **13**, 629–648.

Burke, I., Laurenroth, W., Vinton, M., Hook, P., Kelly, R., Epstein, H., Aguiar, M., Robles, M., Aguilera, M., Murphy, K. & Gill, R. (1998) Plant–soil interactions in temperate grasslands. *Biogeochemistry*, **42**, 121–143.

California Department of Fish and Game (2004) Special animals. *California Natural Diversity Database, Wildlife and Habitat Data Analysis Branch*. p. 55. California Department of Fish and Game, CA.

Castelli, R., Chambers, J.C. & Tausch, R.J. (2000) Soil–plant relations along a soil–water gradient in Great Basin riparian meadows. *Wetlands*, **20**, 251–266.

Chimner, R.A. & Cooper, D.J. (2004) Using stable oxygen isotopes to quantify the water source used for transpiration by native shrubs in the San Luis Valley, Colorado USA. *Plant and Soil*, **260**, 225–236.

City of Los Angeles and County of Inyo (1991) *Water from the Owens Valley to Supply the Second Los Angeles Aqueduct: 1970–90, and 1990 Onward, Pursuant to a Long Term Groundwater Management Plan.* Final Environmental Impact Report. State Clearing House No. 89080705. Department of Water and Power, Los Angeles, CA.

Danskin, W.R. (1998) *Evaluation of the Hydrologic System and Selected Water-Management Alternatives in the Owens Valley, California.* Water-Supply Paper 2370-H. US Geological Survey, Washington, DC.

Dube, O. & Pickup, G. (2001) Effects of rainfall variability and communal and semi-commercial grazing on land cover in southern African rangelands. *Climate Research*, **17**, 195–208.

Elmore, A.J., Mustard, J.F. & Manning, S.J. (2003) Regional patterns of plant community response to changes in water: Owens Valley, California. *Ecological Applications*, **13**, 443–460.

Elmore, A.J., Mustard, J.F., Manning, S.J. & Lobell, D.B. (2000) Quantifying vegetation change in semiarid environments: precision and accuracy of spectral mixture analysis and the normalized difference vegetation index. *Remote Sensing of Environment*, **73**, 87–102.

Groeneveld, D. (1992) Owens Valley, California, plant ecology: effects from export groundwater pumping and measures to conserve the local environment. *The History of Water: Eastern Sierra Nevada, Owens Valley, White-Inyo Mountains* (eds C.A.J. Hall, V. Doyle-Jones & B. Widawski), pp. 128–155. White Mountain Research Station, Bishop, CA.

Groeneveld, D.P. & Or, D. (1994) Water-table induced shrub–herbaceous ecotone: hydrologic management implications. *Water Resources Bulletin*, **30**, 911–920.

Guler, C. & Thyne, G.D. (2004) Hydrologic and geologic factors controlling surface and groundwater chemistry in Indian Wells-Owens Valley area, southeastern California, USA. *Journal of Hydrology*, **285**, 177–198.

Hickman, J.C. (1993) *The Jepson manual: higher plants of California*. Berkeley: University of California Press.

Hollett, K.J., Danskin, W.R., McCaffrey, W.F. & Walti, C.L. (1991) *Geology and Water Resources of Owens Valley, California.* Water Supply Paper 2370-H. US Geological Survey, Washington, DC.

Huxman, T.E., Smith, M.D., Fay, P.A., Knapp, A.K., Shaw, M.R., Loik, M.E., Smith, S.D., Tissue, D.T., Zak, J.C., Weltzin, J.F., Pockman, W.T., Sala, O.E., Haddad, B.M., Harte, J., Koch, G.W., Schwinning, S., Small, E.E. & Williams, D.G. (2004) Convergence across biomes to a common rain-use efficiency. *Nature*, **429**, 651–654.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.

Jackson, R.B., Carpenter, S.R., Dahm, C.N., McKnight, D.M., Naiman, R.J., Postel, S.L. & Running, S.W. (2001) Water in a changing world. *Ecological Applications*, **11**, 1027–1045.

Jackson, P.C., Meinzer, F.C., Bustamante, M., Goldstein, G., Franco, A., Rundel, P.W., Caldas, L., Igler, E. & Causin, F. (1999) Partitioning of soil water among tree species in a Brazilian Cerrado ecosystem. *Tree Physiology*, **19**, 717–724.

van de Koppel, J., Rietkerk, M., van Langevelde, F., Kumar, L., Klausmeier, C.A., Fryxell, J.M., Hearne, J.W., van Andel, J., de Ridder, N., Skidmore, A., Stroosnijder, L. & Prins, H.H.T. (2002) Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. *American Naturalist*, **159**, 209–218.

Lee, C.H. (1912) *An Intensive Study of the Water Resources of a Part of Owens Valley, California.* Water Supply Paper. United States Geological Survey, Water-Supply Paper 294, Washington, DC: Government Printing Office.

Manning, S.J. (1997) *Plant Communities of LADWP Land in the Owens Valley: An Exploratory Analysis of Baseline Conditions.* Inyo County Water Department Report. Inyo County Water Department, Bishop, CA.

Manning, S.J. (2001) *Vegetation Conditions in Monitored Owens Valley Parcels in 2000.* Inyo/LA Technical Group Report. Inyo County Water Department, Bishop, CA.

May, R.M. (1977) Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, **269**, 471–477.

National Research Council (1993) *The Role of Terrestrial Ecosystems in Global Change*. National Academy Press, Washington, DC.

Okin, G.S., Roberts, D.A., Murray, B. & Okin, W.J. (2001) Practical limits on hyperspectral vegetation discrimination in arid and semiarid environments. *Remote Sensing of Environment*, **77**, 212–225.

Postel, S.L. (2000) Entering an era of water scarcity: the challenges ahead. *Ecological Applications*, **10**, 941–948.

Postel, S.L., Daily, G.C. & Ehrlich, P.R. (1996) Human appropriation of renewable fresh water. *Science*, **217**, 785–788.

Reed, P.B. (1988) *National List of Plant Species that Occur in Wetlands: California (Region 0)*. US Fish and Wildlife Service, Washington, DC.

Rogan, J., Franklin, J. & Roberts, D.A. (2002) A comparison of methods for monitoring multitemporal vegetation change using Thematic Mapper imagery. *Remote Sensing of Environment*, **80**, 143–156.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.

Schulze, E.D., Mooney, H.A., Sala, O.E., Jobbagy, E., Buchmann, N., Bauer, G., Canadell, J., Jackson, R.B., Loreti, J., Oesterheld, M. & Ehleringer, J.R. (1996) Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. *Oecologia*, **108**, 503–511.

Shafroth, P.B., Stromberg, J.C. & Patten, D.T. (2002) Riparian vegetation response to altered disturbance and stress regimes. *Ecological Applications*, **12**, 107–123.

Smith, M.O., Ustin, S.L., Adams, J.B. & Gillespie, A.R. (1990) Vegetation in deserts. I. Regional measure of abundance from multispectral images. *Remote Sensing of Environment*, **31**, 1–26.

Snyder, K.A. & Donovan, L.A. (2004) Extensive summer water pulses do not necessarily lead to canopy growth of Great Basin and northern Mojave Desert shrubs. *Oecologia*, **141**, 325–334.

Sorenson, S., Dileanis, P. & Branson, F. (1991) *Soil and Vegetation Response to Precipitation and Changes in Depth to Groundwater in Owens Valley.* California Water-Supply paper 2370-G. US Geological Survey, Washington, DC.

Sperry, J.S. & Hacke, U.G. (2002) Desert shrub water relations with respect to soil characteristics and plant functional type. *Functional Ecology*, **16**, 367–378.

Sperry, J.S., Hacke, U.G., Oren, R. & Comstock, J.P. (2002) Water deficits and hydraulic limits to leaf water supply. *Plant Cell and Environment*, **25**, 251–263.

Steen, E. (1998) Soil water: basis for conservation and management of the plant cover of dry areas. *Ambio*, **27**, 539–544.

Steinwand, A.L., Harrington, R.F. & Or, D. (in press) Water balance for Great Basin phreatophytes derived from eddy covariance, soil water, and water table measurements. *Journal of Hydrology*, in press.

Stromberg, J., Tiller, R. & Richter, B. (1996) Effects of groundwater decline on riparian vegetation of semiarid regions: the San Pedro, Arizona. *Ecological Applications*, **6**, 113–131.

Tibor, D.P. (2001) *Inventory of Rare and Endangered Plants of California.* California Native Plant Society, Sacramento, CA.

Torres, R., Squeo, F.A., Jorquera, C., Aguirre, E. & Ehleringer, J.R. (2002) Assessment of the seasonal ability to use precipitation events in three native Chilean shrubs species with different root systems. *Revista Chilena de Historia Natural*, **75**, 737–749.

West, N.E. & Young, J.A. (2000) Intermountain valleys, and lower mountain slopes. *North American Terrestrial Vegetation* (eds M.G. Barbour & W.D. Billings), pp. 255–284. Cambridge University Press, New York, NY.

Yepez, E.A., Williams, D.G., Scott, R.L. & Lin, G.H. (2003) Partitioning overstorey and understorey evapotranspiration in a semiarid savanna woodland from the isotopic composition of water vapor. *Agricultural and Forest Meteorology*, **119**, 53–68.

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