Depth of water acquisition by invading shrubs and resident herbs in a Sierra Nevada meadow

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Abstract

Woody plant encroachment into semiarid ecosystems has become a global trend in recent decades. Due to stream channel incision, the semiarid riparian montane meadows of the southern Sierra Nevada Mountains, USA are experiencing long-term declines in soil moisture. A woody shrub, *Artemisia rothrockii* A. Gray (Rothrock sagebrush, Asteraceae) is invading these herbaceous meadows. We used an analysis of the stable oxygen isotope ratios of plant and soil water to measure the depth of plant water acquisition during the early stages of this woody plant encroachment. Sagebrush used deeper water on average than most herbs, but it also acquired 10–30% of its water from shallow (<30 cm) soil. Most of the young sagebrush seedlings (1–3 years old, <15 cm) that we sampled used deep water like the older shrubs. Many, but not all of the herb species we sampled were also able to acquire deep water. These findings are consistent with a scenario of shrub encroachment in which channel incision causes shallow-water-dependent herbs to die back, allowing shrub seedlings to establish in disturbed areas during wet years. At least during the early stages of the invasion, some herbs appear to coexist with sagebrush by using deep root systems to cope with the declining shallow soil moisture.

Introduction

Over the past 150 years, trees and shrubs have invaded many of the world's arid and semiarid grasslands, a phenomenon known as woody plant encroachment (Archer, 1994; Arnalds and Archer, 1999; Roques et al., 2001; Van Auken, 2000; West, 1983). In these dry ecosystems, low water availability limits plant growth (Briones et al., 1998; Noy-Meir, 1973; Shmida and Burgess, 1988). The natural or anthropogenic alteration of these limited water resources may in some cases be the direct cause of encroachment (Berlow et al., 2003; Chambers et al., 2004; Polley et al., 1997; Schwinning and Ehleringer, 2001; Stromberg et al., 1996; Wright and Chambers, 2002). Several authors have theorized that the coexistence of woody and herbaceous plants relies on the vertical partitioning of soil water (Noy-Meir, 1973; Shmida and Burgess, 1988; Walter, 1979). In dry habitats, shrubs and trees often grow long tap roots, allowing them sole access to deep soil water while herbaceous species develop their shallow roots and compete strongly for shallow soil water (Cline et al., 1977; Gibbens and Lenz, 2001; Ludwig et al., 2004; Polley et al., 1997; Schwinning and Ehleringer, 2001). This two-layer model predicts that a decline in shallow soil moisture would favor woody plants.

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In the field, partitioning of water between woody and herbaceous plants is often not such a clean dichotomy. Root architecture varies widely both among and within species, often in predictable spatial patterns (Breshears and Barnes, 1999; Gibbens and Lenz, 2001; Schlesinger et al., 1996). Furthermore, depth of water acquisition changes as plants grow. Plants that are deep-rooted as adults must rely on shallow soil water as seedlings or saplings (Dawson, 1996; Hutchings and John, 2003; Robinson et al., 2003). In the context of shrub encroachment, partitioning of water between woody and herbaceous plants may vary among different invasion sites or shift over the course of the invasion. Thus, plant-water relations and water partitioning during shrub encroachment must be investigated on a system-specific basis in which each plant species is considered separately. In this study, we used an analysis of the stable oxygen isotope ratio of plant and soil water to assess the depth of water acquisition by woody and herbaceous plants during the encroachment of Rothrock sagebrush (*Artemisia rothrockii* A. Gray, Asteraceae) into montane meadows of the Kern Plateau in the southern Sierra Nevada Mountains, California, USA.

Meadows on the Kern Plateau that have historically been dominated by graminoids and forbs are being invaded by *Artemisia rothrockii*, a native shrub (Albert, 1982; Berlow et al., 2002; Berlow et al., 2003; Odion et al., 1988). As in other semiarid riparian systems (Castelli et al., 2000; Stromberg et al., 1996), species composition in Kern Plateau meadows is strongly correlated with soil moisture availability (see Ratliff, 1985; Swartz, 2004 for Kern Plateau meadows; Allen-Diaz, 1991 for meadows farther north). Over the last 100 years, these meadows have undergone drastic changes in hydrology. Where streams used to wind across low-gradient meadows, incised channels with little sinuosity have cut into the alluvium causing water tables to drop and shallow soil moisture to decline.

Sagebrush was historically restricted to the dry meadow edges (Dull, 1999; Odion et al., 1988) and expansion into the meadows began in the late 1800's (Dull, 1999). At around that same time, grazing operations allowed cattle and sheep to defoliate and compact soil in most meadows on the Kern Plateau (Kinney, 1996; Knapp and Matthews, 1996). While not necessarily causally linked, numerous studies explain that channel formation, dropping water tables, and sagebrush invasion occurred subsequent to this intense grazing (Albert, 1982; Kattelmann and Embury, 1996; Kirchner et al., 1998; Knapp and Matthews, 1996; Odion et al., 1988). Repeat aerial photographs and analysis of sagebrush growth rings show that sagebrush invasion continues today (Bauer et al., 2002; Swartz, 2004). Between 1994 and 2001, sagebrush invaded ~10% of Mulkey Meadow (Swartz, 2004).

Sagebrush can grow in flooded conditions (Swartz, 2004) and it shows stronger recruitment in wet years (Bauer et al., 2002), but it cannot establish in dense mats of herbs (Berlow et al., 2002). These dense mats of herbs can be disturbed by gophers on a small scale (Berlow et al. 2002) or by the hydrologic changes described above on a large scale (Odion et al., 1988). This suggests a competitive scenario in which sagebrush is kept out of wet areas by competition from herbs, relying on disturbance of the dense mats of herbs before invading. Based upon this scenario, and upon the idea of a two-layer shrub-herb partitioning model, this study tests the following hypotheses about depth of water acquisition during the early stages of sagebrush invasion: (1) Young sagebrush shrubs rely on shallow water to establish; (2) older sagebrush shrubs use water from the water table; and (3) herbs rely primarily on shallow water.

Stable oxygen isotope ratios (reported as $\delta^{18}O$) in root and stem water have been used to distinguish among various possible sources of plant water uptake (Dawson and Ehleringer, 1991; Dodd et al., 1998; Ehleringer et al., 1991; Flanagan and Ehleringer, 1991; Flanagan et al., 1992; Le Roux et al., 1995). For reviews of the technique, see Ehleringer and Dawson, (1992) and Dawson et al. (2002). In this study, we make use of the marked vertical gradient in $\delta^{18}O$ throughout the soil profile to explore if plants obtained soil water from different soil layers. Allison et al. (1983) show that evaporation often leads to significant isotope enrichment (more positive $\delta^{18}O$ values) in shallow soil, giving it a different isotope value than deep soil water. This type of pattern in the soil can be used to measure depth of water acquisition because plants do not fractionate water upon uptake from the soil (Wershaw et al., 1966). Thus, the plant $\delta^{18}O$ can be directly compared with soil $\delta^{18}O$ to determine the zone(s) of water uptake.

We used a mixing model (see Dawson et al., 2002) to apportion plant water into shallow (<30 cm) and deep (>30 cm) soil water zones. Studies of rooting depths across many systems show that herbs often have maximum rooting depths that exceed 30 cm (Canadell and Jackson, 1996; Schenk and Jackson, 2002). We chose 30 cm as the separation between shallow and deep because these sources could be readily separated in our mixing model. Furthermore, herbaceous roots are often found to be most dense in the upper 30 cm. Two-layer models such as the one in Noy-Meier (1973) have hypothesized that shrubs will start dominating water uptake below 30 cm. We collected plant stems at a point in the season when shallow soil water had declined and deeper soil water was presumably most important for growth and survival. We also collected herbaceous plants from plots with intact sagebrush seedlings and plots in which sagebrush seedlings had been removed two seasons prior to our study; this allowed us to evaluate whether the presence of sagebrush seedlings affected the depth from which herb species acquired water. To gauge the relevance of the depth of water acquisition to the progress of the sagebrush invasion, we examined plants that were growing in areas that were in the early stages of sagebrush invasion.

Materials and methods

Study system

Our study took place in two connected Kern Plateau meadows: Mulkey Meadow (36°24′ N, 118°12′ W, 2750 m, 2.9 km^2) and its tributary Bullfrog Meadow (36°24′ N, 118°13′ W, 2750 m 0.55 km^2). These meadows are in the southern Sierra Nevada Mountains and are part of the Golden Trout Wilderness in Inyo National Forest, Inyo County, California, USA. Mulkey Meadow and Bullfrog Meadow are part a network of meadows that are the largest in the Sierra Nevada. (Monache Meadow, the largest, is 30 km^2.) The gently sloped alluvial valleys where the meadows form are 2500–3200 m in elevation and they drain into the north and south forks of the Kern River. Kern Plateau meadow soils are sandy entisols with weakly defined horizonation aside from occasional horizons of buried peat. Soils in the area have been classified as mixed typic cryopsamments (Soil Survey Staff, 2004).

Mulkey Meadow and Bullfrog Meadow receive an average of 50–70 cm precipitation yr^{-1} (USDA Forest Service, 1998). Of this, 7 cm falls in summer rainstorms; the rest is snow (California Department of Water Resources, 2004). The meadows are typically covered in snow from November to May. In the meadows and on the surrounding ridges, melting snow sinks into the porous sandy soils and flows downhill. On the steep mountain slopes that surround the meadows, the shallow soil dries quickly, but in the low-gradient meadows, the water collects and flows through the shallow subsurface until it reaches a stream or a flooded area. Soils near the active channel in the meadow are saturated with water and the water table depth increases toward the meadow edges (Sarr, 1995). The water table percolates up to keep the shallow soil much wetter than it is on the surrounding slopes. Summer rain also provides some surface recharge, but not enough to keep the meadows as wet as they are kept by the subsurface hydrology. Historical accounts and current observations suggest that before 1850, water flowed through most meadow areas within 1 m of the surface (Kinney, 1996; Micheli and Kirchner, 2002a, b; Odion et al., 1988). Since then, deep channels have cut into many Kern Plateau meadows, and water tables have dropped. Even after channel incision, these meadows still have a high water table (~1–2 m) compared to other areas around the globe in which shrubs are encroaching. Very similar hydrologic changes accompanied by encroachment are well documented in riparian ecosystems of the Great Basin (Jewett et al., 2004).

Mulkey and Bullfrog Meadows have both low-growing (<20 cm) herbaceous vegetation patches and sagebrush-dominated patches. Relative to other meadows, Mulkey Meadow is heavily invaded by sagebrush. Bullfrog Meadow, until recently, was less invaded than most meadows in the region. A diverse assemblage of herbs grow in the herbaceous patches (Berlow et al., 2003; Sarr, 1995). There are more than 15 graminoid species, including at least 12 grasses, several sedges, and an abundant rush, *Juncus balticus* Willd. There are also more than 50 forb species, the most diverse families being Asteraceae, Rosaceae, Gentianaceae, and Polygonaceae.

The phenology in these meadows is constrained by the short growing season, but there

are some differences among species. When the snow melts in late May, plants of nearly all species start growing. Herbs bloom at slightly different times, but, depending on annual conditions, most herbs bloom about 1–2 months after snowmelt. Sagebrush remains active later in the season than most herbs, typically blooming into September. This study took place during the time we would most expect water partitioning to be important – peak herb physiology, which in the year of this study was about five weeks after snowmelt.

This study took place in and near plots set up to study the effects of sagebrush removal on soil moisture and herb abundance. The results from this removal experiment, including the difference in soil moisture between treatments, will be reported in Darrouzet-Nardi et al. (in preparation). We located six meadow patches that were in the early stages of sagebrush invasion and set up blocks containing paired plots. In each of the six blocks, we delineated two 3.5×3.5 m plots: one with all sagebrush individuals left intact, and one where we removed all sagebrush individuals (hereafter, $+S$ and $-S$). Most of the removed sagebrush plants were young (<8 years old) and small or medium in size (<30 cm tall). The plots within each pair were separated by 1 m and chosen to be as similar to each other as possible. On 24–25 May 2001, we removed all sagebrush plants from the $-S$ plots by clipping the aboveground shrub biomass. Any recruiting sagebrush individuals were removed each year. Since resprouts were rare, most of the sagebrush root systems likely died. The few resprouts were removed when found.

Volumetric soil moisture and water table depth

On 29 May 2003, at the beginning of the season, and on 5 July 2003, three days before the plant and soil samples for this study were collected, we measured volumetric soil moisture using a multi-segmented time domain reflectometry (TDR) probe (Environmental Sensors Inc., British Columbia). No late season data is available in 2003 because the dry conditions prevented the insertion of the TDR probe. We made three measurements in each of the six blocks. In each of the six blocks, a 2.54 cm diameter PVC water

well was inserted into the ground to measure the depth to ground water.

Plant tissue collection and oxygen isotope analysis

To quantify the reliance of sagebrush and meadow herbs on shallow (<30 cm) soil water, we compared stable oxygen isotope ratios (reported as $\delta^{18}O$) in soil water to $\delta^{18}O$ in plant tissue water collected on 8 July 2003, the approximate peak of herb activity for the 2003 season. In each of the six blocks, we collected samples of three sagebrush shrubs: one small (<15 cm tall), one medium (15–30 cm tall), and one large (>30 cm tall). Sagebrush individuals were collected slightly outside the $+S$ plots so as not to disrupt the ongoing study of sagebrush removal. In each block, we collected two samples of each common herb species – one sample from each treatment plot. The herb species sampled were *Carex* sp. A, *Carex* sp. B, *Juncus balticus* Willd., *Aster occidentalis* Nutt., *Ivesia campestris* Rydb., and *Muhlenbergia richardsonis* Rydb. In total, we took 18 sagebrush and 34 herb tissue samples. Herbaceous plants were sampled in both sagebrush removal and control plots.

Plant uptake of soil water causes no isotopic fractionation (Wershaw et al., 1966), but transpiration does (Dongmann et al., 1974), so plant tissue samples were taken from plant tissue that hydraulically precedes any photosynthetic tissue following Corbin et al., (2005). For sagebrush, we collected tissue from the lower stem. For forbs and grasses, we dug up and collected the root crown. At each block, we used a soil auger to collect soil samples from 5 to 8 soil depths (the depths are shown on the vertical axis of Figure 1). At block 5, deep soil water was collected from the PVC water well due to the difficulty of using an auger at that block; all other samples were collected with the soil auger.

We extracted the water from plant and soil samples using cryogenic vacuum distillation (Ehleringer et al., 2000). The $\delta^{18}O$ of extracted water was determined using the standard CO_2–H_2O equilibration method where 10 mL vials received 200 μL of water that were filled with 2% CO_2, capped and the head-space gas analyzed 48 h later using the GasBenchII/

o - *Aster occidentalis* a - *Carex* sp. A   i - *Ivesia campestris*   L *Artemisia rothrockii* large   S *Artemisia rothrockii* small

b - *Carex* sp. B   r - *Muhlenbergia richardsonis*   j - *Juncus balticus*   M *Artemisia rothrockii* medium   —o— Soil water
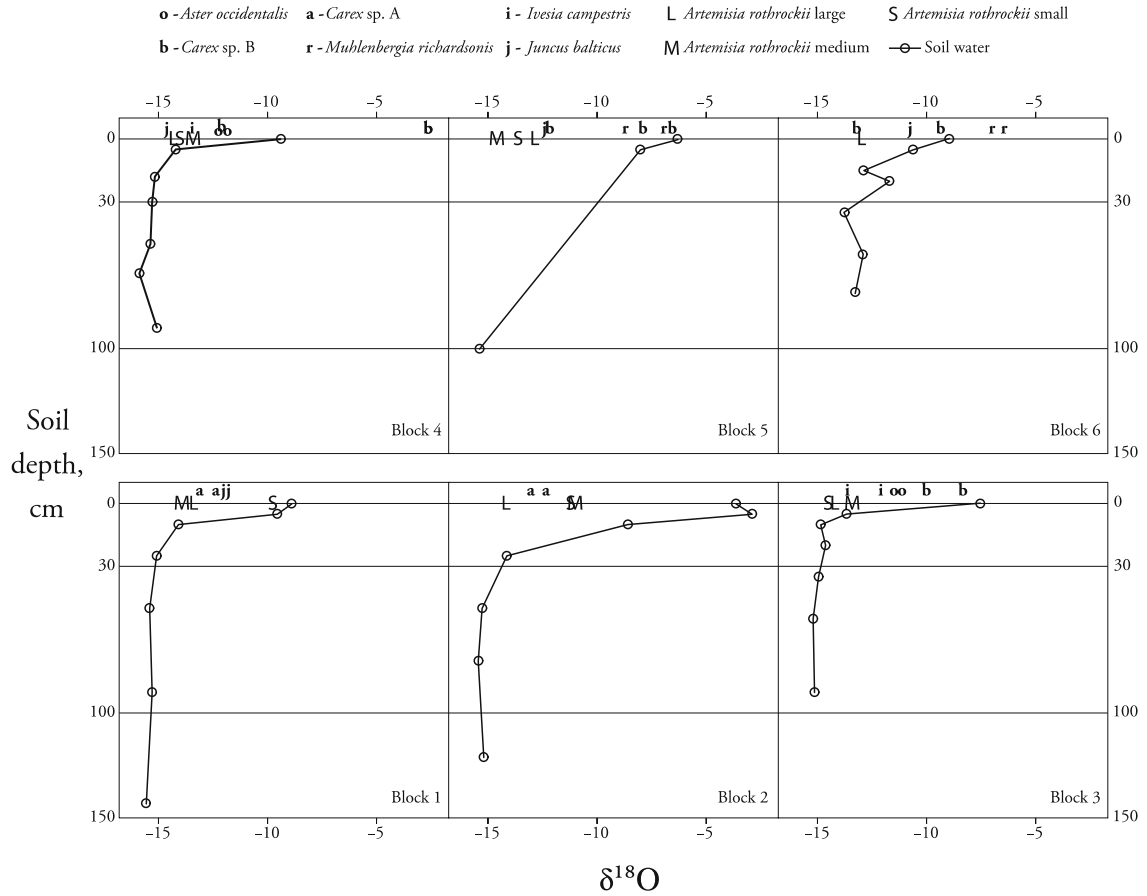
Soil depth, cm

Figure 1. Stable oxygen isotope ratios ($\delta^{18}O$) of (1) soil water by depth (open black circles connected by lines), (2) the most abundant herbs (serifed lower case letters), and (3) three sizes of sagebrush (sans-serif upper case letters): small (<15 cm tall), medium (15–30 cm tall), and large (>30 cm tall). Blocks are located in areas that sagebrush is beginning to invade.

autosampler interfaced with a Finnigan-MAT Delta + XL Mass Spectrometer (Bremen, Germany) at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley. The $\delta^{18}O$ values are expressed in standard delta-notation in units of parts per thousand (‰) relative to the internationally accepted reference standard, Vienna Standard Mean Ocean Water (V-SMOW; see Dawson et al., 2002). Long-term (3 years) external precision for this analysis is ±0.13‰.

We used a two-source mixing model (after Dawson et al., 2002) to determine the fraction of water that each plant had acquired in shallow (<30 cm) soil:

$$\delta^{18}O_{plant} = (F_{SSW}\delta^{18}O_{shallowsoil}) + ((1 - F_{SSW})\delta^{18}O_{deepsoil}) \qquad (a)$$

where $\delta^{18}O_{shallowsoil}$ is the highest soil $\delta^{18}O$ ratio at the block in which $\delta^{18}O_{plant}$ was measured, and $\delta^{18}O_{deepsoil}$ is the average of the below-30 cm soil $\delta^{18}O$ ratios. The fraction of shallow soil water acquired (F_{SSW}) was calculated as follows:

$$F_{SSW} = (\delta^{18}O_{plant} - \delta^{18}O_{deepsoil}) / (\delta^{18}O_{shallowsoil} - \delta^{18}O_{deepsoil}) \qquad (b)$$

This mixing model assumes that each of the two water sources is homogenous. Because shallow

soil $\delta^{18}O$ was graded instead of homogenous, we cannot estimate the exact fraction of soil water that each plant acquired from shallow soil. However, the deep soil was homogenous so we can estimate the *minimum* fraction of water that each plant obtained from the shallow (<30 cm) soil surface (minimum F_{SSW}). For example, if exposed surface soil shows a $\delta^{18}O$ of $-7\permil$, deep soil is $-15\permil$, and a plant is $-11\permil$, it is possible that the plant got all of its water from shallow soil at 15 cm depth, where $\delta^{18}O$ would be $-11\permil$ (F_{SSW} would equal 1); at the other extreme, the plant may have obtained half of its water from deep soil and the other half from exposed surface soil (F_{SSW} would equal 0.5); thus, we can say that this plant's *minimum* F_{SSW} is 0.5. We used the mixing model to compare minimum F_{SSW} in adult sagebrush shrubs to minimum F_{SSW} in young sagebrush shrubs and each meadow herb.

Data analysis

To quantify the differences in F_{SSW} between the mature sagebrush and the other meadow plants, we used Hodges–Lehmann estimators with confidence intervals approximated using the normal distribution. Variance in F_{SSW} was non-homogenous among different species, so we used the non-parametric Hodges–Lehmann estimators to produce estimates of the differences. (The non-homogenous variances were too extreme to be normalized using data transformations.) This analysis was performed using the function wilcox.exact in the exactRankTests package in R 2.0.1 (Hothorn and Hornik, 2004; R Development Core Team, 2004). Since we are not interested in comparing herbs to one another (only herbs with sagebrush), we did not use an all-pairwise comparisons method. Instead, we made multiple comparisons with a control (Hsu, 1996), the "control" in this case being the large and medium sagebrush plants (whose distributions we combined due to their similarity). We used the Bonferroni inequality to estimate a corrected α for each comparison, making the overall $\alpha = 0.05$. Each confidence interval was calculated with $\alpha = 0.05/7$.

Results

Soil moisture and soil $\delta^{18}O$

The size of the April snowpack preceding our sampling was in the 31st percentile among the last 75 years of recorded data (California Department of Water Resources, 2004). The meadows were snow-free by the fourth week of May and aboveground plant growth was apparent by early June. In 2003, the year of this study, the soil moisture at the beginning of July was quite low compared to the post-snowmelt period in late May (Table 1) and compared to measurements we made over three seasons (Darrouzet-Nardi et al., in preparation). At the time of sampling, there had been no rainfall for several weeks. Plants were beginning to flower and were presumably close to peak physiological activity. Though sagebrush reached its peak physiological activity later in the season than most of the herbs, it was growing and setting

Table 1. Water table depth and shallow and deep volumetric soil moisture percentages measured using TDR for each block we sampled

Block	Water table depth (cm)	Soil moisture percentage (0–30 cm) 29 May 2003	Soil moisture percentage (30–60 cm) 29 May 2005	Soil moisture percentage (0–30 cm) 8 July 2003	Soil moisture percentage (30–60 cm) 8 July 2005
1	>100	23.4	23.2	3.5	7.5
2	>100	19.7	35.2	3.8	21.9
3	91	22.1	26.0	7.9	14.9
4	115	34.5	41.9	12.0	21.5
5	122	14.6	12.9	3.5	6.7
6	138	21.4	35.0	5.2	11.9

These measurements were taken at the beginning of the season (29 May 2003) and then again three days before the $\delta^{18}O$ samples were collected. Soil moisture percentage data were measured in the plots with intact sagebrush (+S). The water table in blocks 1 and 2 had descended below our 100 cm wells by an unknown amount.

seed at the time we sampled. The TDR soil moisture data showed that meadow soil was substantially drier at 0–30 cm than at 30–60 cm in all replicates (Table 1). This was always the case across 3 years of soil moisture measurements. In late July and August 2003, when the dry conditions prevented the insertion of our multi-segmented TDR probe, the soil moisture levels were presumably very low. Among the replicates, water table depth and soil moisture percentage exhibited substantial variability. Blocks 3 and 4 were wetter than the other blocks in the shallow soil moisture zone.

Below 30 cm, the soil had a consistent $\delta^{18}O$ value in all of the blocks; above 30 cm, evaporation depleted ^{16}O (Figure 1; cf. Allison et al., 1983). The $\delta^{18}O$ of exposed surface soil was −3‰ to −9‰. The $\delta^{18}O$ values we observed in the surface soil were likely due to evaporation instead of rain input because (1) it had not rained for 2 weeks, and (2) we took similar samples on other dates, but the data were unusable due to the irregular $\delta^{18}O$ soil profiles caused by the recent rainfall. When it rained, we were able to see the rain signature in the soil, but we did not see such a signature at this sampling date. As soil depth increased, $\delta^{18}O$ declined gradually to approximately −15‰. At every block, the $\delta^{18}O$ at the deepest soil depths we measured (at or near the water table), matched the $\delta^{18}O$ at 30 cm. At the block where we measured the deep soil using a PVC water well instead of the auger, the deep soil was also

close to −15‰, suggesting that the use of the water well instead of the auger did not alter the results from this block.

Differences in F_{SSW} among meadow plants

As hypothesized, large and medium sagebrush shrubs acquired water from a lower average depth than did the herb species (Figure 2; Table 2). Of the 18 sagebrush shrubs we sampled, all but two showed minimum F_{SSW} values of less than 30%. These two were young (probably <3 years old) sagebrush plants. The other four small sagebrush individuals were within the range of the medium and large shrubs. Minimum F_{SSW} by adult sagebrush ranged from 10% to 30%. This suggests that sagebrush relies on its deep taproot for water, even where there is an appreciable amount of shallow soil moisture, as in blocks 3 and 4. However, sagebrush is not restricted to using deep water and must have some roots capable of acquiring water in the shallow soil.

Contrary to our hypothesis, the isotope data reveal that herbs were in fact able to make use of deeper soil water. Of the herbaceous species, I. campestris and Carex sp. A, which can grow deep roots, were the least reliant on shallow soil water. J. balticus, Aster occidentalis, and Carex sp. B relied heavily on shallow water, but likely acquired some deep water. The four individuals of the grass M. richardsonis we sampled likely used shallow water exclusively. (Two M. richardsonis individuals and one Carex sp. B
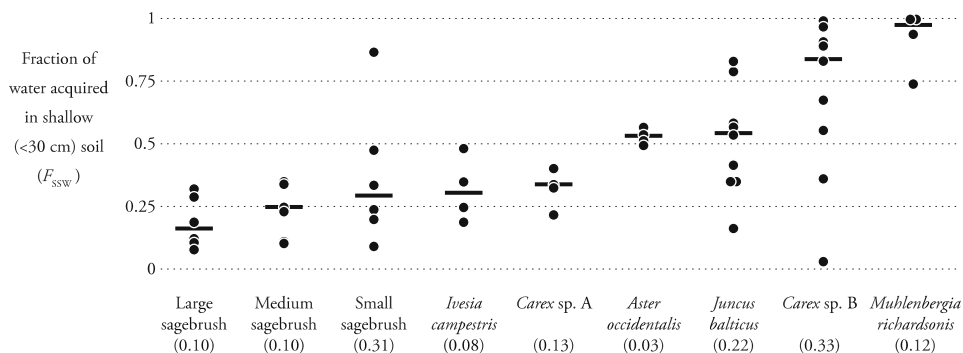

Figure 2. Results of the deep/shallow two-source mixing model. Each black circle shows the minimum fraction of water acquired in shallow (<30 cm) soil (F_{SSW}) for one plant. The three size classes of sagebrush and six herb species are ordered by median F_{SSW}. Standard deviations for the distributions of F_{SSW} values for each size class of sagebrush and herb species are shown in parentheses.

Table 2. The difference in median minimum fraction of water acquired in shallow (<30 cm) soil (F_{SSW}) between adult sagebrush plants and each other meadow species/sagebrush class (e.g., adult sagebrush minus *Muhlenbergia richardsonis*)

Species/sagebrush class	Mean difference in F_{SSW} [95% CI]
Small sagebrush	0.05 [−0.15, 0.69]
Ivesia campestris	0.11 [−0.10, 0.31]
Carex sp. A	0.11 [−0.13, 0.38]
Aster occidentalis	0.28 [0.06, 0.55]
Juncus balticus	0.31 [0.17, 0.47]
Carex sp. B	0.58 [0.08, 0.80]
Muhlenbergia richardsonis	0.71 [.044, 0.93]

The data used in this analysis are shown in Figure 2. The differences were calculated using Hodges–Lehmann estimators. The simultaneous confidence intervals ($\alpha = 0.05$ overall) were approximated using the normal distribution.
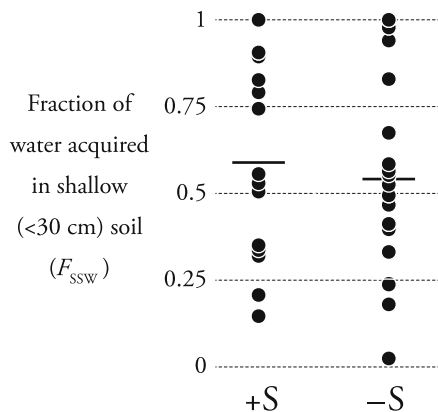

Figure 3. Comparison of F_{SSW} values between herbs growing in plots with intact sagebrush (+S) and plots in which sagebrush was removed (−S). The difference between the treatments is 0.05 ± 0.20 (mean ± 95%CI, $df = 31$, two-sample *t*-test).

individual were more depleted in ^{16}O than the exposed soil surface, which had perhaps experienced periods of greater evaporation than what had occurred immediately prior to our collections. We assume that these three plants acquired all of their water from shallow soil.)

In several species/sagebrush classes, we found a great deal of variation among different individuals in F_{SSW} values (Figure 2; Table 2). *J. balticus* (SD = 0.22), *Carex* sp. B (SD = 0.33), and small sagebrush shrubs (SD = 0.31) were particularly variable in their depth of water acquisition. Adult sagebrush shrubs (medium and large

sagebrush) were more consistent in the amount of shallow water they used (SD = 0.10 for each). *A. occidentalis* and *Carex* sp. A had little variation in F_{SSW}, but we only examined four samples of each, which may be inadequate to estimate population-level variation. The distribution of F_{SSW} values for *Carex* sp. B is skewed toward low values. Young sagebrush shrubs are skewed toward high F_{SSW} values.

There was too much variation and too few samples to effectively distinguish between the sagebrush removal treatments (Figure 3). The mean F_{SSW} for herbs in −S plots was 0.05 ± 0.20 higher than the mean F_{SSW} for herbs in +S plots (mean ± 95%CI, $df = 31$, two-sample *t*-test).

Discussion

Depth of water acquisition

In support of our first hypothesis, sagebrush shrubs acquired deeper water on average than the resident herbs. However, sagebrush still acquired a minimum of 10–30% of its water from shallow soil. Although we cannot tell from the data in this study if herbs dominated the uptake of shallow water, as would be predicted by a two-layer model, two-layer models do allow for overlap in shrub and herb water uptake in the shallow layers. Sagebrush acquired more shallow water than expected, but our data suggest that it relies primarily on deep water.

The F_{SSW} values of the young sagebrush shrubs partially matched our second hypothesis that small shrubs would rely on shallow soil water. While two of the six shrubs appeared to have relied more heavily on shallow water as expected, four of the six small shrubs we sampled showed F_{SSW} values that were within the range of the adult shrubs. This suggests that sagebrush grows a deep taproot quickly and uses deep soil water as soon as it can. This is underscored by the image in Figure 4, which shows a rapidly growing taproot on a 1-year-old sagebrush seedling. We did not collect any young-of-the-year sagebrush seedlings, but presumably those plants would rely even more heavily on shallow water.

Contrary to our third hypothesis, most of the herb species we sampled also appeared to have access to deep soil water. Rooting depth studies

Figure 4. One-year-old sagebrush seedling with root cross section exposed on the side of a soil pit. Roots are digitally highlighted for visibility. The black line indicates the soil surface. Note the scale at left.

(Canadell and Jackson, 1996; Schenk and Jackson, 2002) show that deeply rooted herbs can exist though they may not rely on the deep water. *Carex* sp. A is one of the few herbaceous species present in the driest, most heavily sagebrush-invaded areas that we sampled. *Ivesia campestris* is typically found in more mesic parts of the meadow, but it has a deep taproot that presumably allows access to deep water. The ability of *I. campestris* and *Carex* sp. A to access deep soil water appeared similar to that of sagebrush. The graminoids *J. balticus* and *Carex* sp. B also appeared to be able to acquire deep water (though our methods for measuring *minimum* F_{SSW} cannot rule out the exclusive use of shallow water). *Carex* sp. B also showed a wide range of F_{SSW} values; however, the median is high because many individuals got water almost exclusively from shallow soil. This could result from a root system that preferentially acquires water from shallow soil but can facultatively use deeper water. Most *Carex* sp. B individuals growing in the drier blocks (5 and 6) senesced before setting seed during this season. The individuals of *Carex* sp. B that did have $\delta^{18}O$ values similar to the deep soil $\delta^{18}O$ likely

got most of their water from 25 to 35 cm. Likewise, the forb *A. occidentalis* acquired a minimum of half of its water from shallow soil, but because it is only found in the wetter parts of the meadow, we speculate that it is not deep-rooted. Finally, the grass *M. richardsonis* uses shallow water almost exclusively, as we might expect from the shallow root architectures of most low-growing grasses (Craine et al., 2003).

The plants we sampled were likely not acquiring water from the top few centimeters of the soil where the soil moisture approaches zero. Other studies that have used stable isotope methods to measure depth of water acquisition have excluded or considered excluding soil layers from their mixing models when those layers are too dry for plants to be physiologically capable of acquiring water (Brunel et al., 1995; Thorburn and Walker, 1993; Thorburn and Ehleringer, 1995). Though this would be the ideal approach in this study, we do not have sufficiently detailed data on soil moisture levels or soil water isotopic signature within the top 30 cm, nor do we have soil moisture release curves for these plants, which would tell us what soil moisture level is too low for plant uptake. Despite this, the isotopic signatures of the plants in this study demonstrate that all of them are getting at least some water from 0 to 30 cm, even in the plots where soil moisture is as low as 3.5%. Otherwise, the plant water signature would match the meadow-wide value for deep soil of $-15\permil$, and F_{SSW} would be zero. Whether or not we were to exclude the shallowest soil isotopic signature from our analysis, F_{SSW} would not be zero in any plant we measured. Thorburn and Walker (1993) similarly found that the woody plants they measured, *Eucalyptus camaldulensis*, were acquiring water from remarkably dry soil layers.

The consistent $\delta^{18}O$ signature in deep soil water among the blocks – which varied in soil moisture – suggests that water below 30 cm comes from an isotopically homogenous water table. The consistent isotopic ratio across the meadow in the deep soil suggests that the groundwater in different parts of the meadow is receiving inputs from the same or similar sources. Groundwater sources may include the snowpack, water percolating from long-term underground reservoirs, water flowing through the meadows, rain water that percolates to the water table, and possibly

others. We do not have information on these sources, but they are not essential for determining the depth of plant water acquisition, which relies only on the consistent deep-water signature.

Though depth of water acquisition has rarely been examined explicitly in semiarid montane riparian systems, evidence from other systems corroborates the flexibility in herb and shrub water acquisition that we documented on our sampling date. Meadows in the Great Basin (Toiyabe Mountain Range and Toquima Mountain Range) show a spectrum of herb communities – from wet meadow to xeric meadow – that correlate with seasonal trends in depth to water table (Castelli et al., 2000). In those meadows, some, but not all of the herbaceous species can be used as indicators of shallow water tables – that is, some of the herbs are more flexible in their water use than others. In the meadows along the San Pedro River (Arizona, USA), declines in the water table are predicted to extirpate or alter the abundance of some plants, but merely affect the size and productivity of others such as *Chrysothamnus nauseosus* and *Sporobolus wrightii* (Stromberg et al., 1996).

Implications for sagebrush invasion dynamics

Though all of the plants we measured were actively growing at the time we made our measurements, we cannot predict from these data what water partitioning would be like at other times in the growing season or during wetter or drier seasons, which would be essential to achieve a full understanding of the water dynamics during sagebrush invasion, especially considering the slightly different phenologies of the species we examined. Despite our narrow window of observation, we can say that the data presented here are consistent with an encroachment scenario in which reduced herb cover is a prerequisite to sagebrush establishment, and in which sagebrush establishment occurs in wet years in sites that have previously been disturbed (Baeur, 2002; Berlow et al., 2002, 2003; Swartz 2004). The early invasion sites we sampled have likely already have lost some of the more shallow-water-dependent herbs. Grazing might also reduce herb competition for sagebrush, but grazing levels are low, and sagebrush invasion still occurs in a cattle exclosure in Mulkey Meadow (Berlow et al., 2002).

Berlow et al. (2003) demonstrated in a watering experiment on a high sagebrush terrace in Mulkey meadow that adult sagebrush could respond rapidly to soil watering treatments, suggesting a flexible strategy for living in these harsh environments where summer thunderstorms can replenish shallow soil water but in which the water table provides a steady source of moisture throughout the typical summer drought. During a sagebrush invasion, plants like *J. balticus* may also survive because they are flexible enough to have established themselves during wet conditions, while remaining able to survive when soil moisture declines. Other plants like *M. richardsonis* may die back when the shallow soil moisture declines. Studies that have classified meadow herbs by soil moisture requirements have placed the grass *M. richardsonis* in categories intermediate between flooded and xeric (Castelli et al., 2000; Ratliff, 1985). *M. richardsonis* is the only grass species (there are at least 12 in these meadows) that we found in these sagebrush-invasion plots. *M. richardsonis* individuals looked parched and were not observed to grow or set seed. Plants that are even less drought tolerant than *M. richardsonis* have probably already died back in these plots where sagebrush has begun to invade.

The pattern in which shrubs acquire water from both shallow and deep soil has been found in other studies. In *Artemisia tridentata* (closely related to *A. rothrockii*; see Kornkven, 1998 for *Artemisia* phylogenetics), shallow root growth can be substantial, and root growth can track the depth of water availability throughout the season (Fernandez and Caldwell, 1975). Many shrubs have such flexible root architectures. Extensive root excavations in the Chihuahuan desert show that shrub roots are developed in both shallow and deep soil (Gibbens and Lenz, 2001). Shrub distributions along a gradient of depth to groundwater also provide evidence that shrubs can tolerate a wide range of soil moisture conditions (Stromberg et al., 1996). Finally, plants in the shortgrass steppe of Colorado fit a two-layer model better than plants in our study system. In that system, shrubs use water from all depths as in our system, but herbs in the shortgrass steppe are more restricted to acquiring water from the uppermost soil layers (Dodd et al., 1998).

Juncus balticus, a clonal rush, is abundant in these meadows and occurs in a wide range of soil

moisture conditions. Unlike other semiarid riparian meadows where it has been reported to be restricted to very shallow water tables (Castelli et al., 2000; Stromberg et al., 1996), *J. balticus* grows in both flooded areas and within xeric (soil moisture <10% shallow soil volume in June) stands of sagebrush (Berlow et al., 2003). Each single-blade ramet of *J. balticus* is connected to a lateral root that is ~1 cm below the surface. This lateral root is the thickest part of the root system (~5 mm diameter), and descending roots grow out of it. In our study, *J. balticus* individuals ranged from 20% to 80% minimum F_{SSW}. This suggests that *J. balticus* has a flexible root architecture that allows it to use water throughout the soil profile, potentially explaining its success across a broad range of meadow conditions. As has been demonstrated for other clonal graminoids (De Kroon et al., 1998; Dong and Alaten, 1999), *J. balticus* may use its ramets to 'forage' in wetter areas for the benefit of the entire genet (see De Kroon, 1995, but also see Linhart and Gehring, 2003 for genetic evidence of small genet size in alpine clonal graminoids). *J. balticus* is not, however, found beyond the meadow edges, suggesting a limit to its depth of water acquisition (~2 m).

Even with the examination of the removal experiment, the effect of sagebrush on the depth of water acquisition by herbs during our measurement date is uncertain. The 95% confidence interval we calculated for the effect of sagebrush on herb F_{SSW} is −0.15 to 0.25. Within this interval, the true difference could be small and negligible or could be quite substantial. For example, even an effect of 0.05 could still indicate that sagebrush is depriving herbs of needed shallow water. Furthermore, it is difficult to translate change in depth of water acquisition to strength of sagebrush inhibition of herbs. If herbs are not able to change their depth of water acquisition, they may simply acquire less water in the presence of sagebrush. This may have been the case since herbs did increase by ~10% cover in sagebrush removal plots (Darrouzet-Nardi et al., in preparation). Other studies of shrub-herb interactions in semiarid habitat have likewise demonstrated competition for water (Briones et al., 1998; Kochy and Wilson, 2004). Competition for water in both shallow and deep soil cannot be ruled out.

Conclusion

Two-layer models suggest that when natural or anthropogenic disturbance causes long-term shallow soil moisture decline, there will be a soil moisture level at which vertical partitioning allows for the coexistence of herbaceous and woody plants. In contrast, our data are consistent with a model in which only herbs that are flexible enough to use deep water remain when the water table declines. When species such as *Carex* sp. B, *A. occidentalis*, and *M. richardsonis* die back due to their inability to access deeper soil water, it may allow sagebrush individuals to establish, send down deep taproots, broaden their canopy, and begin to dominate a site. The resulting early-invasion community then consists of newly established sagebrush shrubs growing among the deeper-rooted herb species.

Acknowledgements

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