

## Root turnover and relocation in the soil profile in response to seasonal soil water variation in a natural stand of Utah juniper (*Juniperus osteosperma*)

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**Summary** Juniper species are noted for long-lived foliage, low and persistent gas exchange activity and drought tolerance. Because leaves and roots of the same species are thought to be similar in structure and life history, we hypothesized that *Juniperus osteosperma* (Torr.) Little (Utah juniper) fine roots would reflect the persistent aboveground foliage characteristic of this species. We monitored fine roots, less than 1 mm in diameter, by minirhizotron imaging to a depth of 150 cm over two growing seasons from April 2002 to December 2003. We measured fine root numbers, lengths and diameters, and noted the time of birth and death of root segments. We correlated our root data with soil water potential measured by thermocouple psychrometry and ecosystem evapotranspiration measured by ecosystem eddy flux. Median fine root lifespan, determined by the Kaplan-Meier product-limit method, was about one year, much less than foliage lifespan estimates of more than five years. Yet, roots of juniper live much longer than those of other Great Basin species. The median survivorship of shallow and deep roots was 144 and 448 days, respectively. Production of new roots was observed during periods of favorable soil water potential and there was a seasonal progression of increased new roots and root length during the warm season toward lower soil depths with root loss in the upper soil layers. This was also reflected in water extraction which progressed to greater soil depths later in the warm season. Aboveground, rates of ecosystem evapotranspiration decreased with decreasing soil water potentials in a similar manner in both 2002 and 2003, reflecting the relocation of roots to available water at depth. Juniper exhibited a flexible root depth distribution throughout the 20 months of this study, indicating the potential to respond to shifting soil water resources despite long fine root lifespans.

**Keywords:** eddy flux, fine root dynamics, minirhizotron, root length, root diameter, survival analysis.

### Introduction

The traits of leaves and fine roots are purported to have similarities in structure, growth rates, physiological activity and lifespan (Ryser 1996, Schlapfer and Ryser 1996, Eissenstat et al. 2000, Comas et al. 2002). Thus, plants with long-lived leaves are expected to have long-lived fine roots. We explored this correlation in a widely distributed *Juniperus* species with very long-lived foliage.

Juniper needles grow slowly and remain on the trees for long periods (Reich et al. 1999), leading to constant foliage mass through the year (Grier et al. 1992, Miller et al. 1992, Hicks and Dugas 1998). For example, mean longevity of needles on *Juniperus monosperma* (Engelm.) Sarg., a species closely related to *J. osteosperma* and occurring in similar sites, can be greater than 70 months (Reich et al. 1999). Juniper foliage has a high construction cost and low assimilation rates (Reich et al. 1999) typical of the foliage of plants adapted to dry, nutrient-poor environments (Reich et al. 1992). Junipers are drought tolerant (Linton et al. 1998) and have a low carbon acquisition rate for much of the snow-free portion of the year. For example, Leffler et al. (2002) reported that a population of Utah Juniper (*Juniperus osteosperma* (Torr.) Little) maintained positive leaf-level CO<sub>2</sub> assimilation even at soil water potentials below –5 MPa. Eddy covariance, stand-level flux data for these woodlands also indicate positive net uptake of CO<sub>2</sub> for much of the year, even on warm winter days (Ivans et al. 2006). Thus, given the expectation of similar life-history characteristics of leaves and fine roots, slow turnover and long life spans of fine roots should be characteristic of juniper species.

Shifting soil water resources alter the availability of water to different soil layers. Between significant precipitation events, vegetation tends to remove soil water preferentially from the upper layers because the roots of most plants are denser in the

upper layers (Schenk and Jackson 2002). This is the case for vegetation in cold deserts in the Intermountain Region, including junipers (Leffler and Caldwell 2005). Therefore, a root system with long-lived fine roots might not be sufficiently flexible when soil water becomes limited to the deeper soil layers, unless junipers can maintain uniform root depth distribution through the periods of soil water decline and recharge.

This study examined fine root dynamics of a Utah juniper stand in northern Utah. Root length, diameter, births and deaths were monitored with minirhizotron tubes from April 2002 to December 2003. We tested the hypothesis that belowground dynamics are a reflection of aboveground growth and physiology. We predicted that fine roots of Utah juniper are long lived, as with other evergreen species (Black et al. 1998, Matamala et al. 2003), and root depth distributions are constant through the drying and rewetting cycles because of the long root lifespans. Furthermore, we predicted root births and deaths are constant throughout the growing season because water appears to be continuously supplied to the shoot to maintain positive gas exchange rates for much of the year (Leffler et al. 2002). Additionally, we monitored soil water potential ( $\Psi_s$ ) and ecosystem evapotranspiration to evaluate water use patterns in the context of fine root dynamics.

## Materials and methods

We examined roots in a stand of *J. osteosperma* in Rush Valley, UT (40°17' N, 112°28' W, 1660 m elevation). This study area is typical of the Great Basin with hot, dry summers and sporadic, but generally small summer rain events (Figure 1; Caldwell 1985). The winters are cold, with a mean of 2 °C (40-year average, Vernon, UT weather station) and the majority of soil water recharge is derived from snow in the winter and rains in the spring (Dobrowolski et al. 1990). Plant biomass is dominated by *J. osteosperma*, with occasional *Artemisia tridentata* Nutt. shrubs intermixed. Soil in the study area is a Borvant gravelly loam (Tooele County, Utah Soil Survey 1993), with coarse rock fragments (up to 80%) in the upper 1 m and a petrocalcic layer at depths ranging from 1 to 3 m (Lowe 1999).

Roots were examined with eight cellulose acetate butyrate (CAB) minirhizotron tubes. We inserted the tubes (183 cm long; 5 cm inner diameter (ID); 5.4 cm outer diameter (OD)) at an angle of 30° from the vertical so that the vertical depth reached 158 cm. Tubes were installed in 1999 and imaged during 2002–2003; thus, minimizing any disturbance effects. Because of the rocky soil, 5.7 cm holes were drilled with a power soil auger. Two of the eight tubes were doubled in length and extended to a vertical depth of more than 300 cm; however, water extraction was not evident below 150 cm and roots were not imaged in these tubes (see Figure 2). The portion of the minirhizotron tube extending above the ground (roughly 10–20 cm) was painted white and capped to prevent light and rainfall from entering. Tubes were anchored to 0.5 m-long iron bars inserted in the soil to prevent horizontal or vertical movement. A 10-cm-diameter (OD) rubber flashing was placed

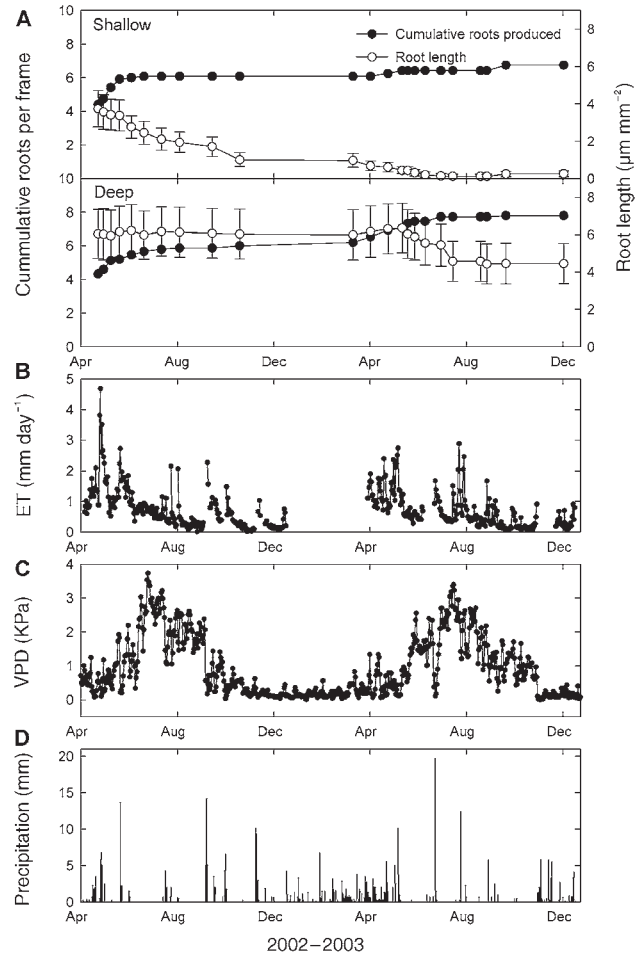


Figure 1. Seasonal patterns of (A) cumulative fine roots per frame and length per  $\text{mm}^2$  of image area; (B) evapotranspiration (ET); (C) vapor pressure deficit (VPD); and (D) precipitation from April 23, 2002 to December 2, 2003. The top panel (A) shows data for root length and cumulative number of roots pooled across 5 to 30 cm depths (shallow panel) and across 45 to 150 cm depths (deep panel). The upper-middle panel (B) represents ET and each value is a cumulative daily total measured by eddy flux from a single tower 50 m from our observation tubes. The lower-middle panel (C) shows the daily mean VPD calculated from humidity and temperature data from our weather station. The bottom panel (D) is precipitation represented as cumulative daily totals.

around the tube flush with the ground to prevent preferential water flow down the outside of the tube following rain events. Color images were taken every 10–15 days throughout the spring (April–June), and less frequently during the remainder of the year (July–December, every 20–30 days) with a digital camera and software (Bartz Technology, Santa Barbara, CA) at depths of 5, 10, 15, 30, 45, 60, 90, 120 and 150 cm. At each depth, three images were taken, creating an interval of 0.8 cm around each depth. For example, at the 5 cm depth, the actual sampling depth was 4.2–5.8 cm. Twenty-seven images were taken per tube, three at each depth to increase the number of root segments at each depth.

Digital images were processed with a Windows-based root

tracing software package (WinRhizotron MF, Regents Instruments, Quebec, Canada). Grass roots were distinguished from juniper roots based on color: juniper roots turn from white to red during the summer whereas grass roots do not redden. Root length and diameter were determined by cursor tracings calibrated against a standard image at each date. All observed roots were less than 1 mm in diameter. Individual observation frames were 226 mm<sup>2</sup> and root images located within those frames were root segments, or branches from root segments, although actual branching was seldom observed in these small frames. Each visible root segment was classified as alive or dead. Root color changes were used for classification, white and red roots were considered alive and black or disappeared roots were classified as dead. Because black roots of other woody species exhibited no physiological activity in other studies (e.g., Comas et al. 2000), those roots as well as roots that had disappeared were classified as dead.

Precipitation was measured with an automated rain gauge associated with a weather station located about 3 km from the experimental site. Additionally, soil water potential ( $\Psi_s$ ) was recorded hourly throughout the study, with individually calibrated screen-cage thermocouple psychrometers (J.R.D. Merrill Specialty Equipment, Logan, UT; Wescor, Logan, UT) connected to a Campbell Scientific data logger (Model CR7, Logan, UT). Psychrometer arrays were established in three trenches containing two to three psychrometers at depths of 30, 45, 60, 90, 120, 150 and 180 cm in each trench. Psychrometers were installed horizontally into the trench wall (~15 cm) and the trench was refilled when installation was complete. Monitoring depths less than 30 cm was not possible because of diurnal temperature fluctuations (Rundel and Jarrell 1989).

Ecosystem evapotranspiration (ET) was measured by the eddy covariance technique (Baldocchi 2003). A single flux tower was located about 50 m from the minirhizotron tubes and consisted of a 3-D sonic anemometer (Model CSAT3, Campbell Scientific) and an open-path CO<sub>2</sub>/H<sub>2</sub>O infrared gas analyzer (Model 7500, Li-Cor, Lincoln, NE). The sensors were mounted 7 m above the 4- to 5-m tall canopy. Data were collected at 10 Hz and 30-min means were stored in a data-logger (Model 23X, Campbell Scientific). The planar-fit coordinate rotation was employed to define a more appropriate coordinate system and remove effects of tilt error of the sonic anemometer (Wilczak et al. 2001). Data were corrected for density effects on the fluxes, as described by Webb et al. (1980). High frequency corrections for sensor frequency response, path averaging and spatial separation of sensors were also conducted (Massman 2000, 2001).

#### *Statistical analyses*

Precipitation data collected in 2002 and 2003 at our Rush Valley site (analyzed separately for the annual October–September, summer (June–August) and fall through spring (September–May) periods) were compared to the 40-year average from the Vernon, UT weather station (40°05′ N, 112°27′ W; 1672 m elevation) by *t* tests.

Differences in root length per frame area through 23 sampling periods from April 2002 to December 2003 at each depth (5–150 cm) were tested by a repeated measures analysis of variance. The depth in each tube was used as the repeated measurement. Individual root segment diameter was tested with a repeated measures ANOVA to determine diameter changes through time and by depth. In this analysis, the individual root segment was the repeated measurement. The tubes were modeled as random effects to satisfy non-independence. The homogeneity of variance assumption was tested, and met, for each analysis. All pairwise comparisons were adjusted for experiment-wise error using Tukey's adjustment. Changes in root length are presented as relative changes for ease of interpretation. We used ANCOVA to regress the log of ET against  $\Psi_s$  in both years. Measurements of  $\Psi_s$  were condensed into one daily value by averaging the hourly measurements, then averaging the six depths. Equality of slopes was examined by *F* tests with the pooled variance estimates (Sokal and Rohlf 1995). Tests of the difference of slopes from zero were conducted with *t* tests.

We conducted a parametric survival analysis to examine median survival time of root segments (PROC LIFEREG, SAS, Cary, NC). Because some root segments were present at the start of the measurements, at the end of the measurement, or both, the actual survival of some roots was unknown. These data are considered to be censored (Allison 1995, Black et al. 1998). For these root segments, those that were present for the duration of the study were designated as "interval censored;" those root segments that were present at the start of the season, but died before the end of the season were designated as "left censored;" and roots that appeared after the start of the season, but were still alive at the time of the last measurement were "right censored." In total, 199 roots were analyzed, and 32% of those roots were censored. Our analysis utilized maximum likelihood estimation for the appropriate treatment of censored data (Lee 2004).

We modeled the survival (in days) of the population of juniper roots pooled across all tubes with a parametric probability distribution function (see Black et al. 1998 for a discussion of survival analysis on roots). The major assumption of this survival analysis is that the shape of the survival distribution is known (e.g., Weibull, Exponential, Gamma, Lognormal, etc.). Because we had no prior knowledge of the distribution for juniper root longevities, we chose the flexible Weibull distribution, which is described with two parameters—a scale ( $\theta$ ) and a shape ( $\gamma$ ) parameter (Black et al. 1998). The scale parameter signifies the degree of hazard (defined in our model as root death) and is analogous to mean lifespan. To obtain meaningful estimates of lifespans (the Weibull scale parameter is unitless), we modeled median root survival (in days) using the Kaplan-Meier product-limit method (Kaplan and Meier 1958). The shape parameter corresponds to the change in the degree of hazard through time. When  $\gamma = 1$ , the hazard is constant so that the probability of a root being present at one time and the next is the same. Values less than one indicate a decreasing risk with age, whereas values greater than one indicate an increasing risk with age.

## Results

Weather at our study site during 2002–2003 was typical of the Great Basin ecosystem (Figure 1). The summer months are characterized by lower evapotranspiration (ET) and higher vapor pressure deficits (VPD) than the spring months. For the October–September period of 2001–2002, precipitation was 228 mm compared with 202 mm in 2002–2003. The temporal distribution within the years of our study was significantly lower for the summer months (June–August) than the long-term mean based on 40 years of data obtained from the Vernon, UT weather station about 20 km south of our field site. During this time, summer precipitation was 13 and 44 mm in 2002 and 2003, respectively, whereas the long-term mean was 87 mm. Precipitation in the fall through spring period (September–May) in 2001–2002 was 215 mm and in 2002–2003 it was 158 mm.

When examining cumulative root numbers, new roots only appeared during the spring months in both years, with few new roots appearing during the remainder of either year (Figure 1). Spring was also the time of year with the most favorable soil water potential for growth, usually above  $-1$  MPa (Figure 2). Despite the appearance of new roots, there was an overall reduction in root length from the start of data collection on April 23, 2002 to the last sampling on December 2, 2003 (Figure 1). The greatest reduction in root length occurred in the upper soil layers (5–30 cm), from  $3.7$  to  $0.2 \mu\text{m mm}^{-2}$ . Root length loss at the lower soil depths (45–150 mm) involved only a net loss of  $1.5 \mu\text{m mm}^{-2}$  of root length, but twice as many new roots appeared at these greater depths.

Root diameter increased with depth ( $F_{8,3730} = 126$ ,  $P < 0.0001$ ; Figure 3), but did not change significantly during the study ( $F_{176,3730} = 0.94$ ,  $P > 0.05$ ; data not shown). Root length changed both within years ( $F_{22,650} = 2.14$ ,  $P = 0.0019$ ; Fig-

ure 4a) and between years ( $F_{1,855} = 27.1$ ,  $P < 0.0001$ ; Figure 4b) and as a function of depth ( $F_{176,3730} = 7.4$ ,  $P < 0.0001$ ; Figures 4a and 4b). In 2002, a significant reduction in root length occurred in the upper 10- and 15-cm depths from the spring to the summer (10 cm:  $t_{650} = 5.2$ ,  $P < 0.001$ ; 15 cm:  $t_{650} = 1.2$ ,  $P < 0.05$ ), whereas at the 120-cm depth, there was a significant increase in root length from spring to summer ( $t_{650} = 3.4$ ,  $P < 0.01$ ). Presented as relative root length changes (Figure 4a), root length losses were evident at most depths in both years. Only a slight increase (5%) was observed in 2003 at 90 cm, although root length increased by 20% in 2002 at 120 cm (Figure 4a). Similarly between 2002 and 2003, root length decreased substantially in the upper 30 cm, with root losses ranging from 50 to 100% (Figure 4b). However, a slight increase in root length was observed at 120 cm (1%) and root length per frame increased by about 20% at 150 cm ( $t_{650} = 4.7$ ,  $P < 0.01$ ).

Observed fine root lifespan was from 7 to 581 days with a median of 368 days (95% CI = 322–413). Shallow roots had a shorter median lifespan than deep roots, 144 days (95% CI = 103–179) and 448 days (95% CI = 433–469), respectively. Fine root survivorship was reduced at a relatively constant rate for the first 200 days, suspended during the winter months and further reduced from 300 to 500 days after the roots first appeared for both shallow and deep roots. Deep roots, however, had a reduced risk of survival through time compared to shallow roots. The pattern of relatively constant death rate reflects the Weibull shape parameter of 0.9 (95% CI = 0.65–1.14) and 1.0 (95% CI = 0.80–1.27) for shallow and deep roots, respectively. Both shape parameters are not significantly different from unity indicating a constant risk of mortality through time.

Across the range of measured water potentials, evapotranspiration showed similar patterns between years despite substantial differences in seasonal precipitation (Figure 5). When

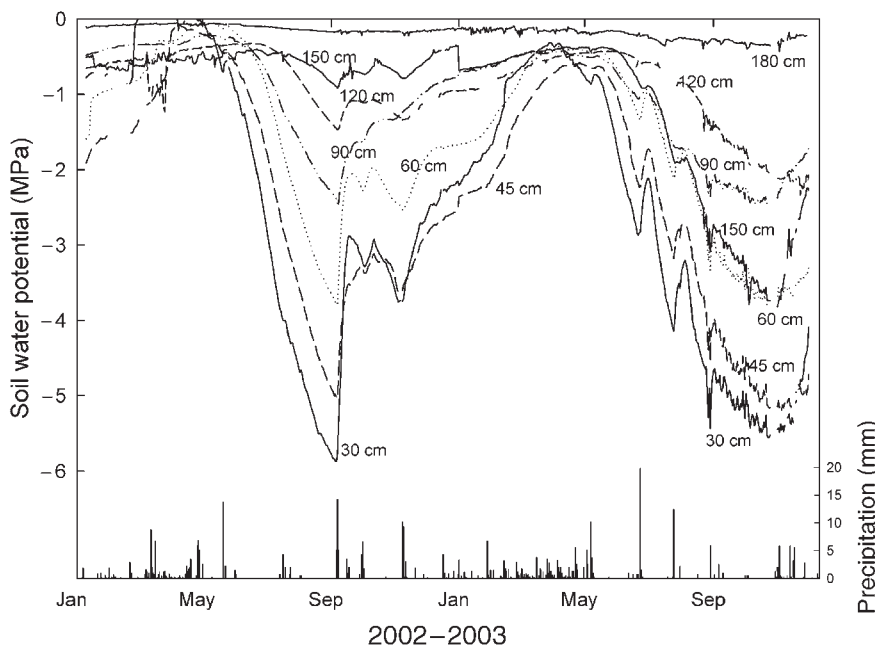


Figure 2. Seasonal patterns of soil water potential at depths from 30–180 cm. Vertical bars represent precipitation events.

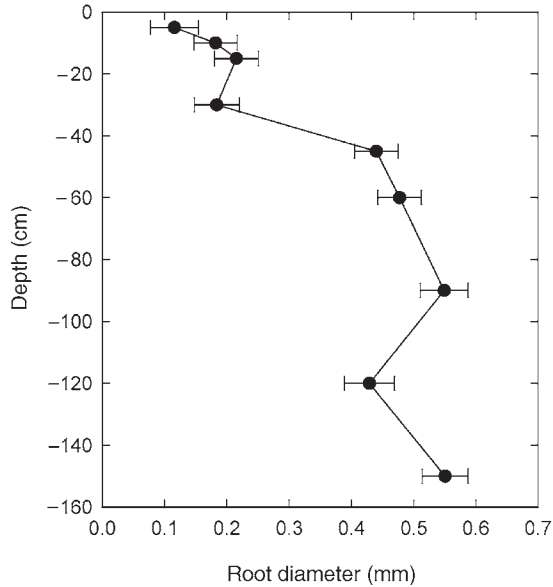


Figure 3. Variation with depth in the diameter of individual juniper fine roots. Values are means for all minirhizotron tubes across both years at each depth. The variability estimate is one standard error.

analyzed statistically, the slopes of the log-transformed ET regression lines between the two seasons were significantly different ( $F_{1,424} = 7.57$ ,  $P = 0.006$ ). This difference was 0.29 in 2002 and 0.22 in 2003; however, given the variability in the data, there was little functional difference in these relationships (2002:  $r^2 = 0.45$ ; 2003:  $r^2 = 0.51$ ).

## Discussion

Our initial hypothesis hinged on the assumption that there are similarities between foliage and fine roots (Ryser 1996, Schlapfer and Ryser 1996, Eissenstat et al. 2000, Comas et al. 2002). Two important results about lifespan were gleaned from our minirhizotron studies. First, median fine root longevity were approximately 1 year, far less than the reported values for lifespans of juniper foliage. Second, median lifespans were much greater than those of co-occurring Great Basin species. Furthermore, we predicted that long root lifespans would be necessary to supply water continuously throughout the year. Despite median lifespans of 1 year, juniper demonstrated a dynamic root system capable of relocating fine roots to reflect changes in soil water potential. Few new roots were produced in the upper soil layers, and an overall loss of root length was observed during this study (Figures 1 and 4). The lack of precipitation may partially explain these findings; however, studies in additional years with differing precipitation patterns would shed more light onto the fine root patterns in the upper layers.

Juniper species are noted for relatively low, but consistent daily mean photosynthetic rates and stomatal conductances over much of the snow-free portion of the year (Körner et al. 1979, Miller and Schultz 1987, Leffler et al. 2002). Addition-

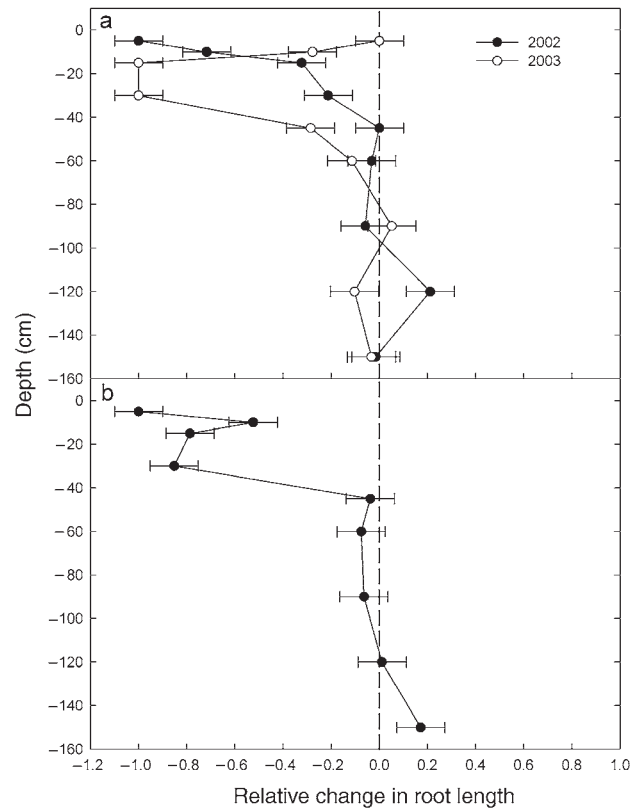


Figure 4. Relative change in root length between seasons (a) and between years (b). Panel (a) is the change in root length between the spring and summer of both years, 2002 (●) and 2003 (○). Panel (b) is the change in root length between 2002 and 2003. The vertical reference line at zero demarks no net change in root length between (a) the spring and summer in both 2002 and 2003 and (b) yearly means of root length between 2002 and 2003. For both panels, values to the left of the reference indicate a net loss in root length and values to the right indicate a net gain in root length. The estimate of variability is derived from the standard error of the difference and natural log transformed to reflect the percent change.

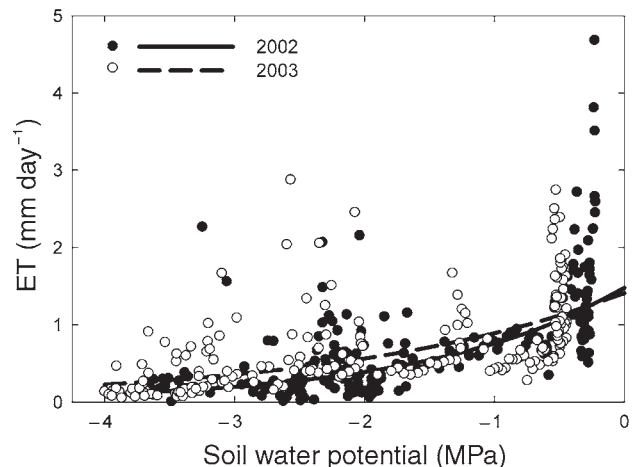


Figure 5. Cumulative daily evapotranspiration (ET) as a function of daily mean soil water potential measured in 2002 (●) and 2003 (○).

ally, aboveground foliage biomass remains relatively constant during the year and among years (Grier et al. 1992, Miller et al. 1992, Hicks and Dugas 1998), and leaf lifespan can be several years (Miller 1984, Reich et al. 1999). Reich et al. (1999) reported needle longevity of a closely related juniper species, *Juniperus monosperma* (Engelm.) Sarg., to be between 70 and 100 months (6–8 years), whereas Ryel and Ivans (unpublished data) found that new foliage lived for at least 3 years in the same stand of *Juniperus osteosperma* as our study. Belowground, however, we found that *J. osteosperma* root life spans were substantially shorter than juniper foliage duration (Miller 1984, Reich et al. 1999). Our reported root lifespans, however, are substantially longer than the reported values of about 1 month for the long-lived shrub *Artemisia tridentata* (Beetle & A. Young) Welsh and perennial tussock, *Agropyron desertorum* (Fisch. ex Link) J.A. Schultes (Peek et al. 2005). The foliage lifespan estimates for the drought deciduous shrub and the perennial tussock grass are only slightly longer than the fine root estimates reported by Peek et al. (2005). In *Artemisia tridentata*, leaf lifespan is about 4 months for deciduous leaves and 1 year for perennial leaves, whereas *A. desertorum* leaf blades live for about 2 months (Ryel unpublished data).

Root longevity varies substantially among species (Eissenstat and Yanai 1997, Anderson et al. 2003, Trumbore and Gaudinski 2003). Species most comparable in life form with juniper are conifers, but there are few data available on root longevity of conifer species. Over half of the roots of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) survived longer than 63 days (Black et al. 1998), but the study ended at that point, so actual life spans are unknown. Similarly, in Norway spruce (*Picea abies*) 50% of roots were reported to survive for at least 360 days (Majdi 2001); again the study was terminated shortly thereafter so ultimate life span remains unresolved. Fine roots of ponderosa pine (*Pinus ponderosa* P. & C. Lawson) were reported to have median longevity of 100 days in one study (Johnson et al. 2000), whereas Thomas et al. (1999) reported 2446 days (6.7 years) and 951 days (2.6 years) for cohorts of roots produced before and after midsummer.

Root growth in arid areas generally occurs when soil water is more abundant (Lyr and Hoffman 1967, Hayes and Seastedt 1987, Peek et al. 2005). Correspondingly, we observed that most juniper fine root production occurred between April and June in both years (Figure 1) when soil water was more available. In three other Great Basin species, *A. tridentata*, *Bromus tectorum* L. and *A. desertorum*, fine root production also peaked in the spring and declined during the hot and dry summers (Peek et al. 2005). In warm deserts, greater root growth of shrubs following precipitation at different times of the year has been reported (Reynolds et al. 1999, Wilcox et al. 2004). Although periods of root growth were limited to the three months when soil water was most available, root death and disappearance were continual throughout the year except during the cold winter period (Figure 6; Weibull shape parameter = 0.9 (95% CI = 0.65–1.14) and 1.0 (95% CI = 0.80–1.27) for shallow and deep roots, respectively).

Despite median life spans of about 1 year, juniper roots demonstrated sufficient turnover to accommodate a shift in

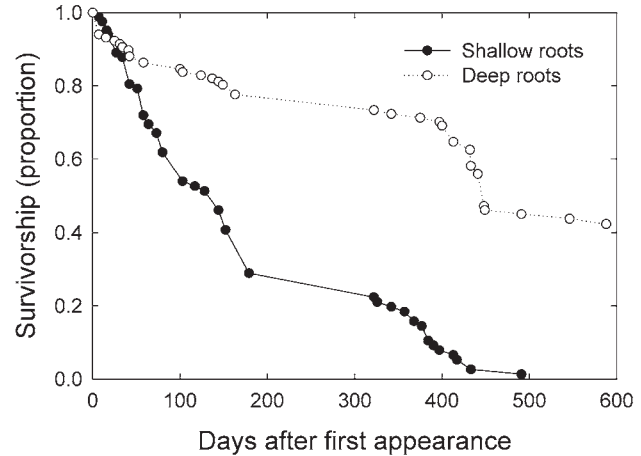


Figure 6. Probability of juniper individual fine root survivorship expressed as a proportion for roots in shallow soil (0–30 cm) and roots in deep soil (45–150 cm). Roots were followed from birth to death between April 23, 2002 and December 2, 2003.

overall fine root length to deeper soil layers (Figure 4). These changes in fine root distribution corresponded with the progressive downward shift in use of soil water during the growing season (Figure 2) and the reduced lifespan of shallow roots (144 days) compared with deeper roots (448 days). A similar shift in root growth activity to deeper soil layers was reported in three desert shrubs as the growing season progressed (Fernandez and Caldwell 1975) and deeper roots are generally longer lived (Eissenstat and Yanai 1997).

Evapotranspiration exhibited an exponential decline with decreasing  $\Psi_s$  in both years (Figure 5), despite differences in root depth allocation and seasonal precipitation between 2002 and 2003. The majority of soil water recharge is derived from snow in winter and rains in spring (Caldwell 1985, Dobrowolski et al. 1990). The cool-season precipitation in the second year (2002–2003) was 26% less than in the first year. Shifts in the depth distribution of root length may have contributed to maintaining water supply for transpiration in the second year with less cool-season precipitation. In both years, water extraction occurred down to 150 cm (Figure 2), but the degree of extraction differed at the deepest depths. For example, in 2002 at 120 and 150 cm,  $\Psi_s$  reached minimum values of  $-1.5$  and  $-1$  MPa, respectively; however, in 2003, roots at these depths extracted water to water potentials of  $-2$  and about  $-4$  MPa, respectively. This pattern corresponded to the increase in root numbers and length at 150 cm depth in 2003 (Figures 1 and 4).

During the study, summer precipitation was below normal (only 13 and 44 mm in 2002 and 2003, respectively, compared with the average of 87 mm). These small, summer rain events were observed as abrupt increases in water potential at 30, 60 and even at 90 cm depths (Figure 2) where considerable root length increases occurred (Figure 4). These simultaneous increases at significant depths are considered to be the result of downward hydraulic redistribution because rain events of this size cannot infiltrate to such depths by gravity or film flow

(Leffler et al. 2002, Ryel et al. 2002). Ryel et al. (2004) conducted simulations of downward hydraulic redistribution and demonstrated a net gain of water at depth for an *Artemisia* shrub population and this redistributed water acted to sustain transpiration later in the summer. In 2002, the meager summer precipitation (13 mm) was not reflected in water potential increases at even 30 cm depth, indicating that these rain events were likely rapidly lost to evaporation. Later in September, however, large storms resulted in large increases in  $\Psi_s$  at several depths, probably as a result of hydraulic redistribution.

*Juniperus osteosperma* demonstrated flexibility in root depth allocation despite a median fine root life span of 1 year. This flexibility may have contributed to the similar relationship between ET and  $\Psi_s$  during the study despite differences in seasonal precipitation. Although most of the annual soil recharge is due to cool-season precipitation, water from summer rains can be moved effectively to the rooting zone by hydraulic redistribution. These dynamic properties of roots of *J. osteosperma* combined with its drought tolerance (Linton et al. 1998), long-lived foliage and conservative aboveground gas exchange (Leffler et al. 2002) contribute to the success of this species in this water-limited environment. These properties should also help it cope with future conditions if the regional climate changes.

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