Fine root growth dynamics of four Mojave Desert shrubs as related to soil moisture and microsite

Carolyn S. Wilcox[a], Joseph W. Ferguson[a],
George C.J. Fernandez[b], Robert S. Nowak[a,*]

[a] *Department of Environmental and Resource Sciences, University of Nevada, Reno,
Mail Stop 370, Reno, NV 89557 USA*
[b] *Nevada Agricultural Experiment Station, University of Nevada, Reno, Mail Stop 204,
Reno, NV 89557 USA*

Abstract

Water is generally considered to be the major limiting factor for perennial shrub growth in the Mojave Desert, USA. However, the responses of active fine roots to soil moisture and microsite differed among *Ambrosia dumosa*, *Ephedra nevadensis*, *Larrea tridentata*, and *Lycium pallidum*, suggesting differences in root foraging strategies. *Ambrosia* and *Ephedra* had a positive linear relationship between active fine root lengths and soil moisture and more roots under the canopy, whereas *Larrea* had a negative linear relationship and more roots in the interspace. *Lycium* did not show a significant root/water relationship or significant differences between canopy and interspace microsites.
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1. Introduction

Desert shrubs are often exposed to long periods of drought, and during these periods water is a limiting factor for growth and survival (Nobel and Huang, 1992;

Smith et al., 1995; Nobel, 1997). In order to utilize soil moisture following small-to-moderate rainfall events, plants have developed distinct root foraging strategies (Lauenroth et al., 1987). Foraging in plants has been defined as the production or placement of structures, such as roots, to enhance the acquisition of a limited or patchy resource (de Kroon and Hutchings, 1995). Desert shrubs produce both coarse (>2 mm diam.) and fine (<2 mm diam.) roots that differ in function but are both essential to survival and foraging. Coarse or woody roots provide support and anchorage, persist well through time, are the source for fine root production, and can absorb small amounts of water and nutrients. However, those roots that are the most active in the absorption of water and nutrients are the ephemeral fine roots. Although the majority of root foraging studies have studied root responses to nutrients (Mordelet et al., 1996; Humphrey and Pyke, 1997; Einsman et al., 1999; Farley and Fitter, 1999; Fransen et al., 1999), soil moisture is also unevenly distributed around individual plants (Jackson and Caldwell, 1993) and across arid ecosystems (MacMahon and Schimpf, 1981, pp. 114–171; Rundel and Gibson, 1996). Fewer root foraging studies have addressed fine root responses to soil moisture (Fitter, 1994, pp. 305–323; Bell and Sultan, 1999; North and Nobel, 2000).

Correlating the fine root lengths of Mojave Desert shrubs to soil water-contents may lead to a greater understanding of how different shrubs respond to heterogeneity in soil moisture and provide a better understanding of fine root growth dynamics. Previous studies in mesic environments have examined the relationship between roots and soil moisture and reported that during periods of drought, low root densities may correspond to low soil moisture levels (Stone et al., 1976; Bohm et al., 1977). However, fine root length densities of maize (*Zea mays* L.) and soybean (*Glycine max* (L.) Merr.) were compared to soil-water depletion, and although the depth of maximum water depletion corresponded well with the zone of maximum root length density, a clear correlation between fine root length densities and soil-water depletion was not apparent over time (Kirkham et al., 1998). Unlike south-eastern Kansas where the above study was conducted, southern Nevada is more likely to experience long periods of drought and may therefore exhibit stronger correlations between root growth patterns and soil-water depletion. However, the sparse nature of arid plant communities (fewer plants per hectare) relative to mesic systems may result in few to no fine roots both spatially and temporally (Wallace et al., 1974; Reynolds et al., 1999).

Although soil moisture is generally considered the primary factor influencing root growth in arid ecosystems, factors such as microsite relations, nutrients, and soil temperature can also influence fine root growth (Kinbursky and Steinberger, 1989; Boot and Mensink, 1990; Fitter et al., 1998). These factors are generally regarded as secondary limiting factors to root growth in arid ecosystems and were also addressed in the current study to assess their relative importance. The unvegetated bare space between two shrubs, or the interspace, is different from the area in and around a shrub canopy, which has also been referred to as a fertile (Schlesinger et al., 1996) or resource (Reynolds et al., 1999) island. Canopy microsites often contain more nutrients and organic matter when compared to the interspace (Gutierrez et al., 1993; Evans and Ehleringer, 1994; Breshears et al., 1998), which may also influence

the fine root growth dynamics of desert shrubs. Fine roots in either microsite may be affected by neighboring shrub roots depending on which species are interacting (Caldwell et al., 1991; Mahall and Callaway, 1992; Brisson and Reynolds, 1994). Finally, root growth generally increases with increasing soil temperature until an optimum is reached, above which root growth is reduced (Drennan and Nobel, 1996; McMichael and Burke, 1998; Pregitzer et al., 2000). Heterogeneity in soil moisture as well as these secondary factors can influence desert shrub root growth differently, leading to spatial and temporal root segregation, or 'niche separation', and enables shrubs to coexist with neighboring shrubs when resources are scarce (Davis and Mooney, 1986; Nobel, 1997; Pechackova et al., 1999; Schenk et al., 1999).

The current study is motivated not only by an interest in plant ecology but also by one in landfill design in arid environments, as desert shrubs have the potential to successfully impede deep moisture infiltration and decrease surface erosion (Abbott et al., 1991; Anderson et al., 1993; Gee et al., 1994). A major concern of landfill design is moisture infiltration through the landfill covers, potentially causing leakage of contaminants into ground-water. Therefore, a basic understanding of shrub fine root dynamics in relation to soil moisture is essential for the appropriate selection of species to be planted on or near landfill covers. For example, a plant community over a low-level radioactive waste landfill should completely exploit all available soil moisture to reduce water movement into radioactive zones. However, plants with deep roots have the potential to disturb radioactive wastes by entering the waste zone and translocating radionuclides to the surface of the soil (Kalisz et al., 1988). This study will help assess which desert shrubs are most appropriate for landfill covers given their potential for both positive and negative landfill effects.

Overall objectives of the current study were to investigate the extent that soil moisture influences root growth of desert shrubs and to determine if the roots of the species preferentially utilized different microsite locations. Root length, soil moisture, inorganic nitrogen, and soil temperature were measured for four species in two microsites in order to answer the following questions: (i) Are fine root growth dynamics correlated to soil moisture or soil temperature? (ii) Does fine root growth generally match inorganic soil nitrogen levels? (iii) Do the four shrub species differ in their fine root responses to soil moisture, temperature, or nitrogen? (iv) Are the fine roots of the shrub species influenced by microsite location? (v) Do these differences suggest variable root foraging strategies and/or spatial root segregation of the four shrub species?

2. Methods

2.1. Site and study species

The study was conducted at the United States Department of Energy's Nevada Test Site (NTS). The NTS is located approximately 130 km north-west of Las Vegas, Nevada, and encompasses plant communities representing both the Mojave and Great Basin Desert ecosystems (Hansen et al., 1999 pp. 148–158). *Larrea tridentata*

(D.C.) Cov. (creosote bush), *Ambrosia dumosa* (A. Gray) Payne (white bursage), *Ephedra nevadensis* S. Wats. (Mormon tea), and *Lycium pallidum* Miers (desert-thorn) were the four perennial shrub species selected. These species were chosen based on the results of previous studies (Yoder and Nowak, 1999a, b), relatively high frequency at the NTS (Romney et al., 1973), differences in leaf phenologies and root distributions, and that each species exists in virtual monocultures.

The Mojave Desert typically receives most precipitation in the winter and experiences severe annual droughts during the summer months. A significant rainfall event in the winter will result in successful vegetative and reproductive growth of desert shrubs in the spring (Beatley, 1974). Winter precipitation tends to be regional and of relatively low intensity, whereas summer thunderstorms are intense, infrequent, and localized. Thirty-year precipitation means for the hydrologic year (October 1–September 30) in locations adjacent to the study sites were between 129 and 179 mm/year, and yearly precipitation from 1998 to 2001 ranged between 96 and 367 mm/year (Fig. 1) (www.sordx.nv.doe.gov, www.unlv.edu/Climate_Change_Research). Air temperatures on the site are extreme and range from a minimum of $-15°C$ during the winter to a maximum of $47°C$ during the summer (Ackerman, 1979). Soils at each site were Entisols, and bulk densities ranged from 1.3 to 1.7, sand ranged from 72% to 92%, silt ranged from 3% to 34%, and clay ranged from 3% to 15% (Yoder and Nowak, 1999a).

Within the Mojave Desert portion of the NTS, two replicate sites of mature *Larrea*, *Ambrosia*, *Ephedra*, and *Lycium* shrubs were used (Yoder and Nowak, 1999a). Each site contained four plots, and each plot consisted of a target shrub with one neutron probe access tube under a target shrub's canopy and an additional access tube in the interspace between the target shrub and the nearest neighbor of the same species (Fig. 2). The target plant and the nearest plant of the same species were between 1 and 3 m apart, and other plants were removed within a 2 m radius of the access tube placed in the interspace. At one site for each species, we utilized existing sets of two Peltier thermocouple psychrometers (J.R.D. Merrill Specialty Equip.
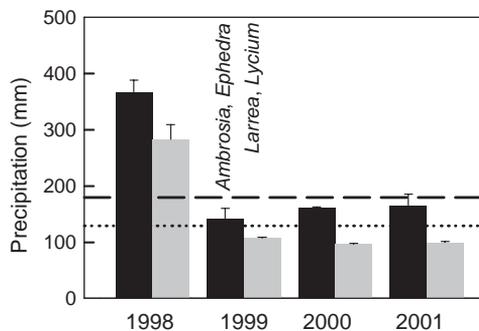

Fig. 1. Mean precipitation with standard error bars for the hydrologic years 1998–2001 (October 1–September 30) for study sites with *Ambrosia* or *Ephedra* (black bars) and with *Larrea* or *Lycium* (gray bars). Dashed line is long-term (30-year) mean precipitation for *Ambrosia* or *Ephedra* study sites and dotted line is for *Larrea* or *Lycium*.
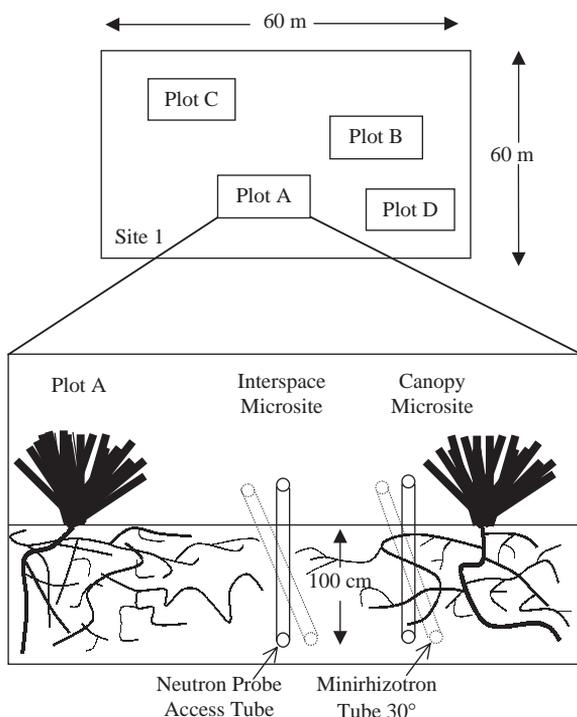
Fig. 2. Schematic of a field site and plot design that is not drawn to scale. At the top is a bird's eye view of field site, and a blown-up side view of plot design is at the bottom. Each plot has a neutron probe access tube and minirhizotron tube in the interspace and canopy.

Logan, UT, USA) that had been installed at two soil depths (0.35 and 0.75 m) near each of the three plants that were within a few meters of the plots with access tubes (Yoder and Nowak, 1999b). Thermocouples in each psychrometer and an electronic thermocouple reference junction (model BAT-12, Physitemp, Clifton NJ, USA) were used in the current study to measure soil temperature at the time of minirhizotron and soil water data collection.

2.2. Root and soil measurements

Transparent plastic minirhizotron tubes offer a non-destructive method to track fine root growth over an extended period of time for the determination of fine root growth patterns (Hendrick and Pregitzer, 1996). Sixty-four minirhizotron tubes (44 mm O.D., 38 mm I.D.) were installed with a pneumatic rock-drill adapted to drill casing (Phillips et al., 2000). These clear plastic tubes were buried at a 30° angle off vertical (Bragg et al., 1983) to a depth of 1 m and were located adjacent to the access tubes in each of the 32 plots (Fig. 2). A minimum distance of 0.30 m separated the minirhizotron tubes from the neutron probe access tubes. The above-ground portion

of each tube was painted with a layer of black paint, a layer of white paint, and then covered with a white closed-cell foam rubber cap to minimize moisture and heat exchange between the tube and above-ground air (Tingey et al., 1997). Minirhizotron images were recorded on S-VHS tapes using a minirhizotron camera (Bartz Technology Company, Santa Barbara, CA). The indexing handle used in conjunction with the minirhizotron camera locked into position in an index hole in each minirhizotron tube, and regularly spaced indentations advanced the camera from one field of view (frame) to the next (Johnson and Meyer, 1998). For each minirhizotron tube, approximately 24 minirhizotron images were collected, with a gap of approximately 44 mm between each frame.

RooTracker 1.1 (Duke University Phytotron, 1995) was utilized to create a database of root lengths and root locations in each image. Roots were analysed by comparing images from monthly samplings that were taken in the same tube and at the same depth. Viewing the images in this manner provided accurate measurements of each root over time. Minirhizotron images were more numerous than measurements of soil moisture and soil temperature; therefore, root length data were summed to match the depth increments of the soil moisture or temperature data, which included five depths for soil moisture and two depths for soil temperature. Due to the possible effect of less active or suberized roots masking a correlation between root length and soil moisture, fine root length data were divided into two categories: active fine roots and all fine roots (Fernandez and Caldwell, 1975). Fine roots with root hairs and white fine roots were considered 'active' and analysed separately from the remaining darker fine root data (Franco and Nobel, 1990; Wan et al., 1994; Nobel, 1997). Although many of the minirhizotron frames had zero root growth, these data were included in the analysis because the fact that active roots were not present was significant to the study.

Root images, soil water and soil temperature measurements were taken monthly from January to July of 2000 and of 2001. A neutron probe (Model 503 Hydroprobe, Campbell Pacific Nuclear Corporation, Martinez, California) was used to measure volumetric soil water-content (θ_V). Field counts were collected at 0.2 m soil depth and continued at 0.2 m increments to 1 m in depth. The neutron probe was calibrated at four representative sites, and the slopes and the intercepts of the soil moisture regression lines did not differ significantly between the sites (Yoder and Nowak, 1999a). The lines were therefore pooled with a resulting R^2 of 0.91, and this equation was used to convert field counts to percent moisture. Additionally, soil samples were collected at the soil surface on January 19, 2001 (following a 22 mm rainfall event on January 11, 2001) from each site in order to assess the general influence of inorganic nitrogen between the microsites of the different shrub species. Soil samples were collected from the soil surface to 0.05 m soil depth under the canopy and in the interspace of three shrub associations within a site and then pooled into one canopy and interspace sample per site (Evans and Ehleringer, 1994). A total of 16 samples (8 sites × 2 microsites) were collected and extracted with 2 M KCl (Maynard and Kalra, 1993, pp. 25–38). The samples were analysed for NO_3–N^- and NH_4–N^+ on a QuickChem 8000 Automated Ion Analyzer Continuum Series (Zellweger Analysis Inc. Milwaukee, WI).

2.3. Statistical analysis

Soil water-content, soil temperature, and root length measurements were integrated over the January–July period in each year (2000 and 2001) using the trapezoidal rule (SigmaPlot, 2001) for two time periods (January–July 2000 and 2001) for each depth increment. Integrations were performed for two main reasons: (a) integrations captured both the amount of roots present and how long they were present, i.e. two-way plants can vary their abilities to extract soil moisture; and (b) integrations removed any potential time delay of root growth responses to soil moisture. The experimental unit consisted of the specific depth interval averaged over four plots per site for each microsite and each year. Integrated root length and soil moisture data were averaged by site (8), microsite (2), depth (5), and year (2) for a total of 160 data points (40 data points per species). Root length and soil temperature data were averaged by site (4), depth (2), and year (2) for a total of 16 data points (8 data points per year).

Integrated data for all of the species were first analysed together using SAS in a three-way ANOVA procedure with species as a qualitative factor, microsite as a qualitative factor, and soil moisture as a quantitative factor that is expressed through a linear term (Fernandez, 2001a). The linear term was devised to test the linear relationship between the response of root length and the quantitative factor of soil moisture (Fernandez, 2001a). Two-way ANOVAs with microsite as a qualitative factor and soil moisture as a quantitative factor were also run for each separate species (Fernandez, 2001b). Violations of normality and/or equal variance assumptions were remedied when necessary by using a log–log transformation and/or a robust ANOVA with iteratively re-weighted least squares based on Hubers's weights (Neter et al., 1996). Significant outliers were removed for *Ambrosia* and *Ephedra* two-way ANOVA analyses; however, these outliers did not change the nature of the linear relationship between soil moisture and root length for these species. The outliers are marked in Fig. 3 and represent large unexplainable increases in root lengths at the 0.6 m depth during the 2001 growing season. Soil depth and soil nitrogen data were analysed using a robust two-way ANOVA with species and depth as factors for the former and species and microsite as factors for the latter (Fernandez, 2001c). Lastly, simple linear regressions (Fernandez, 2002) were fitted to the soil temperature and root length data.

3. Results

3.1. Fine root growth and soil moisture dynamics

The main effect of species was highly significant in the three-way ANOVA (Table 1), with mean integrated active root lengths (mm day) of 306 for *Larrea*, 637 for *Lycium*, 1120 for *Ephedra* and 1530 for *Ambrosia*. At the species level of comparison, *Larrea* had significantly fewer active fine roots when compared to *Ephedra* and *Ambrosia* when averaged over the canopy and interspace microsites. Additionally,
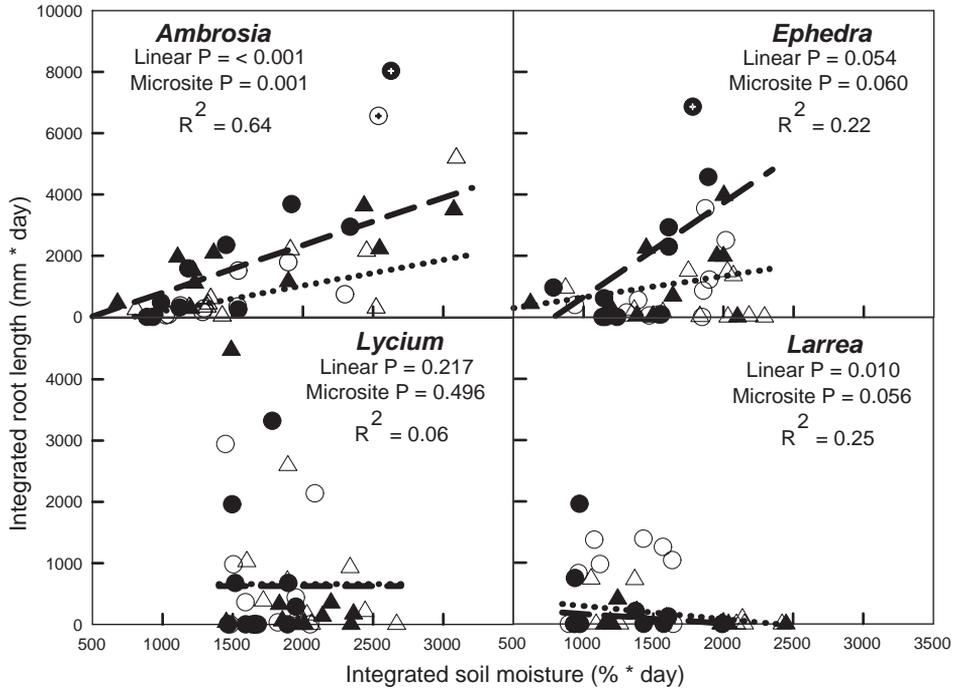
Fig. 3. Integrated soil moisture and integrated fine root lengths for *Ambrosia*, *Ephedra*, *Lycium* and *Larrea* in the canopy and interspace. Filled symbols represent the canopy microsite and open symbols represent the interspace microsite. Triangles are data for 2000 and circles are data for 2001. The *y*-axis scaling was adjusted for *Lycium* and *Larrea* graphs when compared to *Ambrosia* and *Ephedra* graphs. Circles with crosses represent data points at 60 cm depth for 2001 that were significant outliers. The *P*-values, R^2, and linear lines came from data adjusted by the two-way ANOVAs represented in Table 1.

Table 1
P-values and degrees of freedom for three-way qualitative (species), qualitative (microsite), quantitative (soil moisture) and two-way qualitative (species or microsite), quantitative (soil moisture) ANOVAs for integrated root length data

Source of variation	All three-way	Canopy two-way	Interspace two-way	*Ambrosia* two-way	*Ephedra* two-way	*Lycium* two-way	*Larrea* two-way
Linear (*L*)	0.629	0.924	0.441	<0.001	0.054	0.217	0.010
Species (*S*)	<0.001	<0.001	0.018	—	—	—	—
Microsite (*M*)	0.084	—	—	<0.001	0.060	0.500	0.056
$S \times M$	0.037	—	—	—	—	—	—
$L \times S$	0.011	0.114	0.085	—	—	—	—
$L \times M$	0.177	—	—	0.342	0.162	0.820	0.320
$L \times S \times M$	0.869	—	—	—	—	—	—
df. error	144	68	68	36	36	36	36

Note that the 'Linear' term tests the relationship between responses of root length and soil moisture.

Ambrosia had significantly more integrated active fine roots when compared to *Lycium*. Because the $S \times M$ term was also significant in the three-way ANOVA, we examined differences among species for each microsite with two-way ANOVAs (Table 1). The order of species within each microsite was the same as that over both microsites, but the statistical groupings of species changed slightly (data not shown).

The correlation between active fine root length and soil moisture was significant, but the correlations differed among species (i.e. the $L \times S$ term in the three-way ANOVA, Table 1). Thus, data were analysed separately by both species and microsite in two-way ANOVAs to better understand the interaction between linear and species. When the data were divided into four species, *Ambrosia* and *Ephedra* had a positive linear relationship between active fine root lengths and soil moisture; however, the linear relationship for *Ephedra* was significant only at the 0.06 level (Table 1, Fig. 3). Active fine root data for *Ambrosia* had the greatest number of images with fine roots overall and the highest R^2 with soil moisture. *Larrea* had a significant negative linear relationship between active fine root lengths and water, and *Lycium* did not have a significant relationship. When the data were divided into the two microsites, the interaction between linear and species was no longer significant.

The results discussed above only involved the active fine roots as opposed to all of the fine root data (see Methods section). The ratios of active fine roots to all fine roots varied among the species: *Larrea* (34%), *Ambrosia* (53%), *Ephedra* (61%), and *Lycium* (82%). When all fine roots were analysed, the trends were similar for all species but the significant linear relationships for *Ephedra* and *Larrea* were lost (data not shown). The complete absence of roots in many of the minirhizotron frames was an interesting result. For example, on certain sampling dates, all the images in some of the minirhizotron tubes had zero active fine root growth. Removing data such as the 1 m depth increment for *Larrea*, which had zero fine root growth throughout both seasons, also did not change the nature of the relationship between root lengths and soil moisture (results not shown).

3.2. Fine root growth: microsite and soil depth influences

Although the main effect of microsite was not significant, the interaction between species and microsite was significant when all the species were analysed in a three-way ANOVA (Table 1). This interaction indicated that the active fine roots of the species respond differently to the canopy or interspace microsites regardless of soil moisture. When comparing the linear relationships for *Ambrosia*, *Ephedra*, and *Larrea* in separate ANOVAs (Fig. 3), differences between microsites were found for the intercepts but not the slopes. However, the responses for both *Ephedra* and *Larrea* were only significant at the 0.06 level. *Ambrosia* and *Ephedra* had significantly more active fine roots under the canopy relative to the interspace over all soil moisture levels, whereas *Larrea* had significantly more active fine roots in the interspace relative to the canopy.

Differences among species, depths, and the interaction between species and depth were not significant in a two-way ANOVA with site replicated (results not shown).
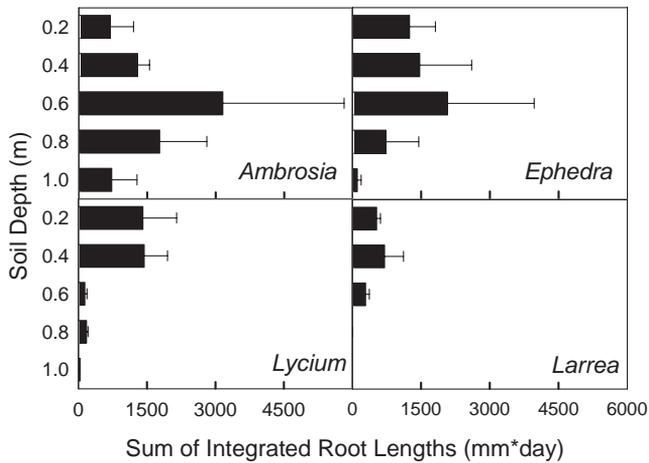
Fig. 4. Integrated root lengths summed by depth increment for the four species over both 2000 and 2001. The numbers along the *y*-axis indicate the midpoint of the depth increment.

The large error bars observed in Fig. 4 contributed to these non-significant differences. Generally one site for the same species had higher root activity, leading to greater error between sites, especially when considering the *Ambrosia* and *Ephedra* sites. Nonetheless, the most fine root growth centered around 0.6 m in depth for *Ambrosia* and *Ephedra*, and around 0.2–0.4 m for *Larrea* and *Lycium* (Fig. 4).

3.3. Fine root growth: soil temperature influence

Fine root lengths were not significantly correlated to soil temperature when all species were combined together into one regression analysis (Fig. 5). Soil temperature data were combined for all the shrub species because psychrometers were only present within one site for each of the shrub species and were not originally positioned to measure differences between microsites (see Methods section). Integrated soil temperatures were consistently higher in 2000 than in 2001, but root lengths were consistently lower in 2000 than in 2001.

3.4. Soil nitrogen and microsite

The highest mean levels of inorganic nitrogen were associated with the canopies of shrubs, especially *Larrea* and *Lycium* canopies (Fig. 6). Differences between microsites, species, and the interaction between species and microsite were significant for nitrate (NO_3–N^-). Trends in ammonium (NH_4–N^+) were similar to the trends in nitrate but only the difference between microsites was significant (Table 2). Over all shrub species, significantly more ammonium and nitrate existed in the soil below the shrub canopy than in the interspace. Soil under the *Larrea* canopy contained significantly higher levels of nitrate than that of the other species. Additionally, the
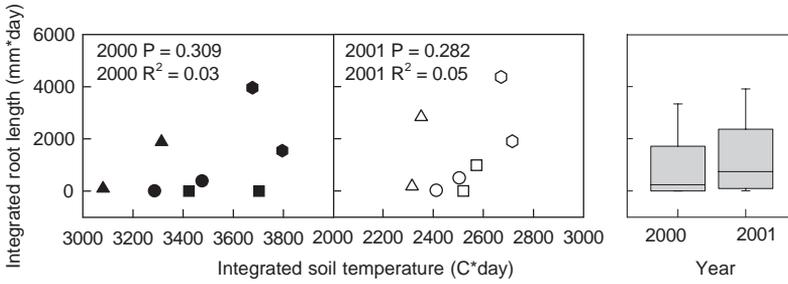
Fig. 5. Relationship between integrated soil temperature and integrated root lengths for all species. Pentagons represent *Ambrosia*; circles, *Ephedra*; squares, *Larrea*; and triangles, *Lycium*. Filled symbols represent data for 2000 and open symbols are 2001. The box plots (on right) are for integrated root lengths over all species for each year.
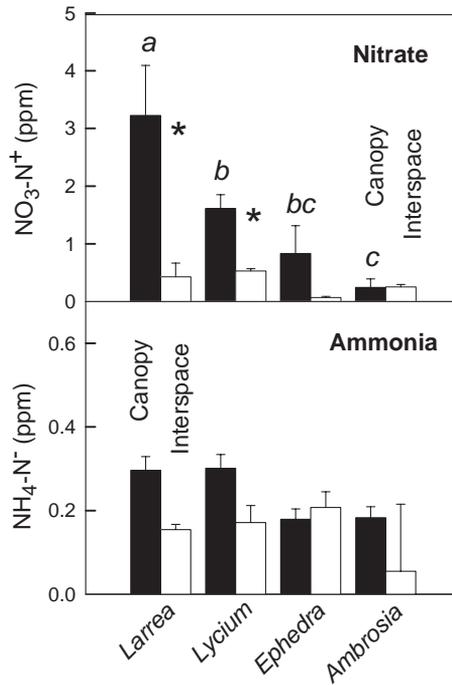

Fig. 6. Mean nitrate (NO_3–N^-) and ammonium (NH_4–N^+) levels with standard error bars in the interspace and canopy microsite for each species. Different letters represent significant differences among species for the canopy microsites. Asterisks indicate significant differences between canopy and interspace microsites of the same species. Determination of significance is from the two-way ANOVA (Table 2).

soil under the *Lycium* canopy had significantly higher levels of nitrate relative to the soil under the *Ambrosia* canopy. When considering both microsites, the mean values for nitrate were greatest in *Larrea* and then decreased, in order, from *Lycium* to *Ephedra* to *Ambrosia*.

Table 2
P-values and degrees of freedom for two-way qualitative (species), qualitative (microsite) ANOVAs for inorganic nitrogen (NH_4–N^+ and NO_3–N^-)

Source of variation	NO^3–N^-	NH^4–N^+
Species (S)	0.006	0.225
Microsite (M)	<0.001	**0.032**
$S \times M$	0.017	0.292
df. error	12	12

4. Discussion

4.1. Fine root foraging and soil moisture

The active fine root lengths of *Ambrosia*, *Ephedra*, and *Larrea* were significantly correlated with soil moisture during 2 years of slightly below-average precipitation (Fig. 1) in the Mojave Desert. However, a significant correlation between the active fine root lengths of *Lycium* and soil moisture was not found. *Ambrosia* and *Ephedra* showed a positive linear relationship between active fine root lengths and soil moisture and had more active fine roots under the canopy when compared to the interspace. The opposite trend was apparent for *Larrea*, which had significantly more active fine roots when less soil water was available and more fine roots in the interspace over the canopy. Although this result seems counter-intuitive, *Larrea* roots tend to favor well-drained soils that are generally drier. Furthermore, the above-ground growth of *Larrea* (as measured by new nodes) has been found to be largely independent of rainfall and to increase as soil moisture reached its lowest values (Chew and Chew, 1965).

These results suggest that the four desert shrub species have different root foraging strategies as related to heterogeneity in soil moisture and differences between microsites. *Ambrosia* and *Ephedra* concentrate a higher proportion of their active fine roots in areas of high soil moisture, whereas *Larrea* and *Lycium* are employing different foraging strategies. By increasing the surface area of absorptive fine root tissue, *Ambrosia* and *Ephedra* may be able to extract soil moisture more effectively depending on how long the soil moisture is available. In contrast, we speculate that *Larrea* and *Lycium* may have a more distributed, drought insensitive root foraging strategy to acquire resources, although their lower root growth may have fewer carbon costs when compared to *Ambrosia* and *Ephedra*. Indeed, a study of the competition for soil phosphorus between *Ambrosia* and *Larrea* (Yoder and Nowak, 2000) would be consistent with this difference in foraging strategies. Nonetheless, these shrubs also show similar rates of water extraction when all species are compared (Yoder and Nowak, 1999a). However, plant roots can respond to soil moisture by increasing rates of water uptake with or without structural modifications such as increased root lengths (North and Nobel, 2000). For example, existing or surviving roots of *Bouteloua gracilis* H.B.K. Lag. ex Steud. were able to absorb water

at approximately 40% of the rate of new roots (Lauenroth et al., 1987). Therefore, *Larrea* and *Lycium* may be able to maintain their rates of water uptake without producing new roots.

When comparing the results of the different shrub species, potentially confounding effects may contribute to the results. However, these effects did not appear to be profound enough to change the relationships described in this study. First, the sites that encompassed *Ambrosia* and *Ephedra* received more precipitation when compared to the *Larrea* and *Lycium* sites (Fig. 1). These differences in precipitation may have resulted in higher overall integrated root lengths when compared to the other sites. Second, one of the *Ambrosia* sites contained higher silt contents throughout the entire profile, which may have contributed to higher soil moisture retention and the associated increases in active fine root lengths when compared to both the other *Ambrosia* site and all the other sites. Third, foraging is a result of morphological plasticity and differences in foraging ability between species should ideally be examined at a common size instead of a common time (Fransen et al., 1999). Although mature *Larrea*, *Lycium* and *Ephedra* were all similarly sized, mature *Ambrosia* were less than half the size of the other shrubs. Lastly, *Lycium* displayed a high ratio of active fine roots to all fine roots (83%) when compared to the other species (34–61%). If *Lycium* roots had visually differed more in regards to color or root hairs and provided more evidence for including roots in the 'active' category, then perhaps a significant correlation to water might have been found.

4.2. Fine root distributions: canopy microsite and soil depth

Our results suggest that the fine root distributions among different depths (Fig. 4) and between microsites (Fig. 3) differ among the four species, suggesting some degree of spatial root segregation. Davis and Mooney (1986) also found that roots might become segregated by depth when the above-ground portions of shrubs are close together. Additionally, the horizontal dimension of roots also has been shown to affect how roots are distributed (Pechackova et al., 1999). The segregation of plant roots enables plants to occupy a larger amount of physical space in order to acquire more resources (McConnaughay and Bazzaz, 1992). *Larrea* and *Ambrosia* cover approximately 70% of the Mojave Desert, whereas *Lycium* and *Ephedra* are commonly associated with co-dominant *Larrea–Ambrosia* communities (Turner, 1994, pp. 156–168; Rundel and Gibson, 1996). Although the current study measured desert shrubs in virtual monocultures, these shrubs grow together in diverse communities and may be forced to share limited resources therein.

The results of the current study generally support previous studies involving coarse root distributions of *Ambrosia*, *Ephedra*, *Larrea*, and *Lycium*. The coarse rooting characteristics of *Ambrosia* have been found to depend largely on the size of the shrubs excavated. Small plants (<0.4 m) had narrow taproots that could extend more than 1 m into the soil and frequently penetrated layers of hard-packed gravel in the soil. However, large plants (>0.8 m) lacked these taproots and had dominant woody laterals at depths no greater than 0.5 m (Jones, 1984). The present study found that the fine roots of large *Ambrosia* plants were relatively abundant

throughout the soil profile, although the highest root length densities were centered around 0.6 m depth (Fig. 4). The coarse roots of *Ephedra* have been described as penetrating deeply but reaching only a small extent laterally (Cannon, 1870). The present study found that high densities of *Ephedra* fine root lengths were also centered around 0.6 m depth and were more prolific under the canopy than the interspace. The coarse root system of *Lycium* have been described as almost entirely horizontal (Markle, 1917), which is an observation supported in this study given that the highest number of roots were found between 0.2 and 0.4 m depth and as many roots were observed in the interspace as under the canopy. The coarse roots of *Larrea* were found to have well-developed tap roots and lateral roots in an excavation study, though the extent of the laterals depended on how deeply the tap root penetrated (Chew and Chew, 1965). In the current study, more active fine roots were found in the interspace than in the canopy, supporting the idea of well-developed lateral roots for *Larrea*. However, few *Larrea* roots were found below 0.6 m in depth, providing little information on tap root development.

4.3. Variation in soil nitrogen among microsites

The results of the nitrogen analyses suggest that inorganic nitrogen is not the primary limiting factor to fine root growth. The results for fine root growth dynamics generally did not match differences in surface soil nitrogen levels. The shrub canopies of *Larrea* contained lower levels of root growth but significantly higher levels of nitrate than the interspace. *Lycium* did not have significant differences in fine root growth between the microsites, but had significantly more nitrate in the canopy than the interspace. The nitrate levels for *Ephedra* and the ammonium levels for *Ambrosia* were the only matches between fine root growth dynamics and nitrate levels. The shrub canopies of *Ephedra* contained both significantly more nitrogen and higher root lengths when compared to *Ephedra* interspaces. Additionally, the shrub canopies of *Ambrosia* contained more ammonium and higher root lengths when compared to the interspace. Although we only sampled nitrogen once in 2001, similar results were found in *Larrea*, *Lycium* and *Ambrosia* microsites in 1999 (Titus et al., 2002), suggesting that trends in inorganic nitrogen levels between species and microsites may be more or less consistent over time. However, these results should not be extrapolated to diverse shrub communities because studies have generally found stronger correlations between root lengths and the acquisition of nitrogen when plants are growing in interspecific competition (Hodge et al., 2000).

4.4. Fine root growth and soil temperature

Our results support the idea that soil temperature is a secondary factor influencing root growth. A significant correlation was not found between integrated fine root lengths and integrated soil temperatures. Although lower fine root lengths in 2000 may be partially explained by higher soil temperatures that year, other factors could have also contributed to differences observed between the years 2000 and 2001. For

example, 2001 had higher soil moisture levels, and the minirhizotron tubes had been in place for a longer time period. Additionally, fine root responses to soil temperature may be species specific (i.e. some species have higher temperature tolerances than others) and therefore cannot be fully teased apart unless more replications are performed for each individual species.

4.5. Implications for landfills

The results of this study suggest that a shrub community including *Ambrosia* would be most appropriate for a landfill. The active fine roots of *Ambrosia* are best able to respond to soil moisture in both the canopy and interspace (Fig. 2) to a depth of 1 m, suggesting that this shrub would be most suitable as a landfill cap cover species (Anderson et al., 1993). If a landfill is to include plants, the landfill should be located under the environmental conditions (i.e. climatic and geographic) conditions where that plant is most likely to survive and persist for long periods of time. Individual *Ambrosia* plants have been shown to survive from 36 to over 100 years and have about a 43% mortality rate per century (Bowers et al., 1995). A greenhouse study that complimented this study transplanted young *Ambrosia* seedlings to greenhouse pots and only had a 3% mortality rate after 2 years. Additionally, *Ambrosia* seedlings were able to rapidly recover in a denuded area on the Nevada Test Site, indicating the tenacity of this shrub (Hunter, 1989). Although the potential for adult *Ambrosia* to spread roots deeply into the soil profile and potentially enter into contaminated zones is unlikely, this potential needs to be further explored for *Ambrosia* seedlings. The inclusion of Mojave Desert shrubs in landfill caps would involve short-term planning and costs but would provide a more stable and therefore safer long-term solution to the disposal of wastes (Andraski, 1997).

4.6. Future studies

Although mosaics of pure stands of *Larrea*, *Lycium,* and *Ephedra* were common in certain areas at the Nevada Test Site, pure stands of *Ambrosia* were less common. In fact, both of the *Ambrosia* sites utilized in this study still had a few large *Larrea* plants intermixed (these *Larrea* plants were not adjacent to the *Ambrosia* plots utilized in this study). Although shrub community dynamics was not directly assessed in the current study, the potential absence of pure *Ambrosia* stands is interesting. Future studies should address why certain desert shrubs are more likely to form pure stands and whether or not *Ambrosia* commonly exists in pure stands in other areas of the Mojave Desert. Additionally, some evidence suggests that the roots of *Ambrosia* may be able to grow beyond 1 m in depth, and studies should address this potential in relation to landfill design. Lastly, root/water relations could change when monocultures of certain species are compared to diverse mixed communities that include the same species.

5. Summary

Larrea, *Ambrosia*, *Ephedra* and *Lycium* often grow in close proximity to one another in mixed communities in the Mojave Desert. The results of the current study suggest that the active fine roots of the four shrub species have different root foraging strategies and potentially have their own niches within the soil profile. *Ambrosia* showed a positive correlation between active fine roots and soil moisture and produced significantly more fine roots in the canopy relative to the interspace. The results for *Ephedra* root dynamics were similar to the results for *Ambrosia*, although less statistically strong, whereas a correlation between fine roots and soil moisture was not found for *Lycium*. Further, *Larrea* had a negative correlation between active fine roots and soil moisture and more fine roots in the interspace than under the canopy. When considering all the species, the presence of soil moisture did not necessarily indicate the presence or absence of active fine shrub roots due largely to the sparseness of desert plant communities. The current study also provided some information on secondary limiting resources including inorganic nitrogen and soil temperature. Nitrate levels were significantly different among the four species, whereas, both nitrate and ammonium levels were significantly different between the microsites. However, differences in inorganic nitrogen did not appear to explain the differences in fine root lengths. Further, the regressions between fine root lengths and soil temperature were not significant, suggesting that fine root growth may be largely independent of soil temperature when integrated over a growing season. This study supports the hypothesis that water is the main limiting factor to desert shrub fine root growth.

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