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Horizontal and vertical zones of influence for root systems of four Mojave Desert shrubs

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Abstract

Horizontal and vertical zones of influence for root systems of four Mojave Desert shrubs were characterized using ^{32}P as a nutrient tracer. *Larrea tridentata*'s horizontal zone of influence was sparse near the plant's stem base, with a maximum probability of accessing ^{32}P (P_{\max}) of 41%. However, its horizontal zone of influence extended beyond 5 m, and the distance from the stem base at which the probability of accessing ^{32}P was half P_{\max} ($L_{50}\sim 3$ m) was significantly greater than the other three shrubs. *Ambrosia dumosa*'s zone of influence was dense near the plant's stem base ($P_{\max}\sim 78\%$), but was rare at distances >2 m ($L_{50}\sim 1$ m). Zones of influence for *Lycium andersonii* and *Lycium pallidum* were intermediate between those of *L. tridentata* and *A. dumosa*. For vertical zones of influence, *L. tridentata* was more likely to obtain ^{32}P from 5 m soil depths than *A. dumosa*, but *L. pallidum* was not significantly different from either *A. dumosa* or *L. tridentata*. Horizontal zones of influence did not change with treatments that altered soil water and nitrogen availability, but vertical zones of influence increased with a flood irrigation treatment that increased water availability to 5 m soil depth. These differences among species likely reflect compromises between their shoot growth

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strategies and their need to acquire spatially and temporally limited soil resources, especially through competitive interactions.

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1. Introduction

Above-ground observations of plants are often used to make inferences about mechanisms that influence interactions among plants within a community (Fonteyn and Mahall, 1981). However, ecological interactions in arid ecosystems, such as competition, resource acquisition, and other factors that control plant distributions, primarily occur below-ground (Brisson and Reynolds, 1997). Thus, extrapolating from above-ground observations to below-ground functions can be misleading (Casper and Jackson, 1997). For example, roots of chaparral shrubs occupied an area 6–40 times greater than the area occupied by the plant canopy, which effectively precluded the establishment of new plants despite the abundance of bare soil (Kummerow et al., 1977).

Unfortunately, little is known about the rooting and other below-ground characteristics of desert plants. Among below-ground studies, some have examined a limited number of individuals very intensely using excavation techniques (Cannon, 1911; Chew and Chew, 1965; Brisson and Reynolds, 1994; Gile et al., 1998; Gibbens and Lenz, 2001) and rhizotrons (Mahall and Callaway, 1991, 1992, 1996), while others have measured below-ground biomass throughout the soil profile (Wallace et al., 1980). These studies provided detailed information concerning root growth patterns and improved our understanding of how individual plants interact under various conditions. However, root excavation and observation studies have three major shortcomings: (1) they rarely incorporate more than a few individuals or more than one or two species; (2) they cannot verify that the observed roots are physiologically active; and (3) fine roots and mycorrhizae, which are important for resource acquisition from the soil, are difficult to quantify using excavations or rhizotrons. Thus, these studies do not always provide definitive, quantitative information about resource acquisition by root systems at any given time and location, which is information critical to understanding ecological interactions.

Casper et al. (2003) proposed a concept of below-ground “zones of influence” for plants that focuses on the volume of soil from which a plant extracts resources, rather than on more typical measures, such as the presence of large roots or the quantity of roots in a soil volume. The zone of influence for a plant’s root system is defined as “the area over which a plant alters the environment” (p. 2313). They argue that the concept of a zone of influence is more useful than the location of roots because the ecologically important factors are the interactions of the plant with the soil and its resources, not the presence or absence of plant tissue. For example, a biologically inactive root is not ecologically important to a nutrient uptake question,

but the presence of mycorrhizal hyphae is important even if the host root is several centimeters from the nutrient and hence incapable of directly accessing the nutrient itself. Casper et al. (2003) advocate the use of nutrient tracers as a method to quantify below-ground zones of influence and use the results of a nutrient analog tracer study along with a literature review to show that: (1) horizontal and vertical limits of zones of influence for many plants are much greater than previously thought; (2) patterns of horizontal zones of influence are complex shapes that cannot be simplified into perfect circles around a plant stem; and (3) the relationship between a plant's ability to access soil resources at a particular distance from its stem is different for different types of plants using different strategies.

Below-ground zones of influence also have practical applications to the construction and monitoring of hazardous and radioactive waste sites (Klepper et al., 1985). For example, many desert species possess highly efficient below-ground root systems that have the capability to preclude percolation of surface water into buried waste materials (Anderson et al., 1987, 1993; Gee et al., 1994; Yoder and Nowak, 1999). Nutrient tracers have also been important tools to determine the potential for root depth and lateral spread to disrupt buried waste materials (Reynolds and Fraley, 1989; Abbott et al. 1991). Thus, the below-ground zones of influence for desert species provide an important criterion for waste site construction in arid systems.

This study used two experiments to characterize the horizontal and vertical zones of influence for four Mojave Desert shrubs: *Ambrosia dumosa* (A. Gray), Payne (white bursage), *Larrea tridentata* (D.C.) Coville (creosote bush), *Lycium andersonii* A. Gray (Anderson boxthorn), and *Lycium pallidum* Miers (pale desert-thorn). These species were selected based on their relatively high frequency on the Nevada Test Site (Romney et al., 1973) and in the Mojave Desert. The experiments examined below-ground zones of influence under both natural conditions and conditions where soil resource availability was manipulated. The first experiment (horizontal zones of influence) was conducted on the Mojave Global Change Facility (MGCF), which is a large field experiment designed to evaluate some effects of global environmental changes on the Mojave Desert ecosystem. The MGCF is a factorial experiment that increases summer precipitation, disturbs the biological soil crust, and increases N deposition. Thus, the MGCF provided the venue to examine horizontal zones of influence under conditions of varying water and N availability. The second experiment (vertical zones of influence) examined the abilities of *A. dumosa*, *L. tridentata*, and *L. pallidum* to vertically access soils at a depth of 5 m in response to three variations in the vertical distribution of water in the soil: natural distribution (which typically wets the soil to 0.5–1.0 m deep), soil contiguously wetted from the surface to at least 5 m deep, and soil with natural distribution at the soil surface but wetted below ~5 m deep. This second experiment also examined how the proximity of *A. dumosa* and *L. tridentata* to each other affects their ability to access soil resources at a depth of 5 m. Results from Mahall and Callaway (1991, 1992) suggest that *L. tridentata* defends a root territory from other *L. tridentata* and from *A. dumosa* roots (Schenk et al., 1999). We hypothesized that if these two species were in close proximity, defense of root territories would prevent *A. dumosa* roots from

extending horizontally and force roots to extend vertically, thus increasing the vertical zone of influence for *A. dumosa*.

2. Methods

2.1. Horizontal zones of influence

Horizontal zones of influence for four Mojave Desert shrubs were characterized in an experiment performed at the MGCF on the Nevada Test Site (NTS) (36°46′07″N by 115°59′16″W). The MGCF is a long-term study site that examines the impacts of three global change factors: elevated summer precipitation, biological soil crust disturbance, and two levels of elevated nitrogen deposition. The elevated summer precipitation treatment received three 25 mm sprinkler irrigations in July and August of each year, with the control treatment of natural precipitation only. The biological soil crust disturbance treatment was imposed by personnel lightly shuffling their feet over the entire plot after the annual plants died every fall. The control treatment left the soil surface undisturbed. Adding nitrogen at a rate of 0, 10, and 40 kg N ha⁻¹ yr⁻¹ provided a control treatment and simulated increased atmospheric nitrogen deposition at two levels of N addition. Additional details on the treatment are available at http://www.unlv.edu/Climate_Change_Research/. Treatments were initiated 2 years before our study was conducted.

The MGCF consists of 96 plots of naturally occurring vegetation, where each plot measures 14 m × 14 m and is separated by a buffer of at least 20 m between any two plots. These 96 plots are split into eight blocks of 12 plots, and treatment combinations were randomly assigned to the plots in each block yielding a 2 × 2 × 3 completely randomized block design. This study used all of the plots in four of the eight blocks, or a total of 48 plots with four replicates per treatment.

Four perennial shrub species found at the MGCF were studied: *A. dumosa*, *L. tridentata*, *L. andersonii*, and *L. pallidum*. These species were selected based on their relatively high frequency on the Nevada Test Site (Romney et al., 1973). All individuals sampled were mature shrubs and were of similar size within each species.

Horizontal zones of influence were characterized using ³²P as a radioactive nutrient tracer. ³²P was chosen because: (1) phosphorous is an essential nutrient, hence, plants need to acquire it; (2) it is relatively immobile in the soil; (3) it is relatively safe to handle; and (4) it has a short (~2 week) half-life. First, a neutron probe access tube was installed to a depth of 1.8 m near the center of each plot to monitor soil water. To inject the radioactive tracer, nine 1-cm diameter steel tubes were installed in a square pattern in a canopy interspace near the neutron probe access tube. Each injection tube was 0.5 m from each other, and the bottom of each tube was at 0.35 m soil depth. When approximately 75% of the soil water was extracted from the 0.35 m soil depth in the spring, 0.2 mCi of ³²P as NaH₂PO₄ was injected into each steel tube (a total of 1.8 mCi per plot) followed by 40 ml of a 0.1 M HCl solution to wash the ³²P solution into the soil. This application was repeated three times on April 7, May 2, and May 22, 2003.

Vegetation samples were collected at 7-day intervals starting one week after the first injection of the tracer until 2 weeks after the last injection and were tested for the presence of ^{32}P . Approximately 0.5 g of leaf, flower, and seed material was collected from any plants of the four target shrubs that were accessible from the footpaths in each plot. In total, 247 *L. tridentata*, 165 *A. dumosa*, 84 *L. pallidum*, and 67 *L. andersonii* plants were sampled. Radioactivity of vegetation samples were determined following the procedures used in Black et al. (1994). If measured ^{32}P content on any sampling date was greater than the 99.95% confidence interval of background radiation, the plant was designated as “ ^{32}P positive”. If the measured ^{32}P content on all sampling dates was within the 99.95% confidence interval of background radiation, the plant was designated as “ ^{32}P negative”.

The distance of each sampled shrub from the injection point was calculated using geo-rectified aerial photographs of each plot. The shrub's position was defined as the center of its stem base. The injection point was defined as the tube that was nearest to the plant being sampled.

2.2. Vertical zones of influence

A second experiment to characterize the vertical zones of influence of Mojave Desert shrubs was conducted in an area south of the MGCF site. Eighteen study plots were located that contained at least one mature, full-sized individual of each of the target species: *A. dumosa*, *L. tridentata*, and *L. pallidum*. To determine if the proximity of *A. dumosa* and *L. tridentata* affected vertical zones of influence, half of the plots were chosen such that an *A. dumosa* shrub was located within the canopy of a *L. tridentata* shrub, and the other half were chosen such that the *A. dumosa* and *L. tridentata* shrubs were separated by at least 1 m. Four tubes were installed in each plot. A 5 cm diameter steel neutron probe access tube was installed in the center of each plot to monitor soil water to a depth of 6 m. Three PVC tubes (2-cm diameter) were evenly spaced in a radius of 1.5 m from the neutron probe access tube and installed such that the bottom of the tube was at 5 m soil depth.

Plots were randomly assigned to control, deep irrigation, or flood irrigation treatments. The control treatment received surface soil water from natural precipitation only. Natural precipitation typically wets only the top 0.5–1.0 m of soil, although the wetting front can extend to >2 m in very wet years (Yoder and Nowak, 1999). The deep irrigation treatment had the same naturally wetted surface soil as the control treatment, but also a wet soil patch starting at 5 m depth and continuing down. This wet soil patch was created by injecting water through the three PVC tubes until the neutron probe measurements indicated that soil water at a depth of 5 m was near field capacity. The flood irrigation treatment was a contiguously wetted soil column brought to near field capacity from the surface to a depth of at least 5 m. This wet soil column was maintained by flood-irrigation whenever soil water content between 2 and 5 m dropped below 50% of field capacity. Treatments were started 16 months prior to the first ^{32}P injection.

When approximately 75% of the soil water was extracted from the 0.35 m soil depth of the control plots in the spring, 1.1 mCi of ^{32}P as NaH_2PO_4 was injected

into each PVC tube (a total of 3.3 mCi per plot) followed by 250 ml of a 0.1 M HCl solution to wash the ^{32}P solution into the soil. This application was repeated three times on April 7, May 2, and May 22, 2003. Vegetation samples from all plants of the target species whose stem bases were located within a 3 m radius of the neutron probe access tube were collected and analysed for ^{32}P as described above for the horizontal zones of influence study.

2.3. Statistical analysis

Binary logistic regression analysis is a powerful method to determine the relationship between binary responses (e.g., the ^{32}P positive or negative content in our study) and both continuous and categorical predictor variables (Fernandez, 2002a). Thus, logistic regression models were used to analyse the data of both the horizontal and vertical zones of influence experiments, and all relevant statistical model assumptions were tested. Because the horizontal zones of influence models had only one continuous predictor variable and the vertical zones of influence models did not have any, multicollinearity could not be a problem. Overdispersion was checked using the Deviance Goodness-of-Fit test (SAS Institute Inc., 1995), and none of the models used for either the horizontal or vertical data tested significant for overdispersion. Finally, no outliers or highly influential observations were found in any of the models used.

All models used the ^{32}P positive/negative designations as the response variable and were analysed using the SAS macro-application “LOGISTIC” (Fernandez, 2002b). For each experiment, we first used a full logistic regression model that consisted of all potential predictor variables, and Type III analysis of effects tests determined which predictor variables were significant. A forward selection method was then run to check the results of the Type III analysis of effects tests. All forward selection procedures produced the same list of significant variables as the Type III analysis of effects tests. Finally, we then re-ran the logistic regression model using the reduced model of only the significant predictor variables.

In the horizontal zones of influence study, the full model had shrub species, distance from the injection point, MGCF block, irrigation, crust presence, and nitrogen deposition level as predictor variables. The final, reduced model had only species and distance as significant predictor variables. A species \times distance interaction term and a distance \times distance quadratic term were also tested but were not significant ($p = 0.922$ and 0.522 , respectively). Significant differences among shrub species were determined using analysis of maximum likelihood estimates derived from the reduced logistic regression model. In addition, a power analysis was generated to determine if the sample sizes were reasonable in relation to the other treatment variables (irrigation, crust disturbance, and nitrogen deposition level).

The reduced model was also used to compute the predicted probability scores for each of the data points in the horizontal zones of influence experiment. The predicted probability score provides information concerning the likelihood that a given data point will be positive or negative depending on the predictor variables (SAS, 1995). For example, results in Fig. 2 show that a *L. tridentata* plant at 3 m from the

injection tubes has a predicted probability score of approximately 0.21. Consequently, if a *L. tridentata* shrub that was 3 m from an injection point was selected at random, there is a 21% chance that the shrub would test positive for ^{32}P .

The predicted probability scores for each species from the horizontal zones of influence experiment were fit to the logistic decay curve:

$$P_l = P_{\max}/(1 + [L/L_{50}]^f), \quad (1)$$

where P_l is the probability for any location l to be part of the underground zone of influence for a plant; P_{\max} is a constant characterizing the maximum probability of a location being part of the below-ground zone of influence; L is the distance from the stem base to a particular location; L_{50} is a constant characterizing the distance from the stem base at which the probability is half of P_{\max} ; and f is a curve shape constant characterizing how rapidly the probability (P_l) decreases with the distance from the stem base (L). PROC NLIN in SAS Institute Inc. (2003) was used to fit Eq. (1), and all non-linear regressions were highly significant ($p < 0.001$).

In the vertical study, the full model had species, irrigation type, proximity of *A. dumosa* and *L. tridentata*, and number of species replications per plot as predictor variables. The proximity variable tested if plots with *L. tridentata* and *A. dumosa* in close proximity were statistically different from those where the shrubs were separated by at least 1 m. The last predictor variable (“number of species replications per plot”) tested if the density of individuals of a species in a plot affected their frequency of accessing ^{32}P at 5 m depth. A shrub species \times irrigation type interactive term was also tested, but was not significant ($p = 0.754$). The final, reduced model only had shrub species and irrigation type as significant predictor variables. Significant differences among shrub species and irrigation types were determined using analysis of maximum likelihood estimates derived from the reduced model.

3. Results

3.1. Horizontal zones of influence

For the horizontal zones of influence experiment, only two predictor variables, shrub species and the distance from the injection point, were significantly related to the probability that a given shrub would acquire ^{32}P in the full and the reduced logistic regression models (Table 1a). None of the other predictor variables in the full model (MGCF block, summer irrigation treatment, crust disturbance treatment, and nitrogen deposition treatment) were significant. Overall, the reduced model was significant using the log likelihood ratio test ($p < 0.001$). Analysis of maximum likelihood estimate tests indicated that no significant differences occurred between the overall likelihood of *L. tridentata* and *L. pallidum* shrubs to be designated ^{32}P positive at any particular distance from the injection point, nor between *A. dumosa* and *L. andersonii*. However, all other pairings of species were significantly different from each other (Table 1b). For all species, ^{32}P negative plants occurred up to ~ 3 m

Table 1

Binary logistic regression analysis of horizontal zones of influence based on the frequency of plants that acquired ^{32}P

Variable	df	Wald χ^2	Pr > χ^2
<i>(a) Horizontal zones of influence models^a</i>			
Full model: individual variables			
Shrub species	3	13.97	0.003
Distance from injection point	1	51.58	<0.001
MGCF block	1	0.83	0.363
Summer irrigation	1	0.16	0.691
Crust disturbance	1	0.17	0.681
Nitrogen deposition	1	0.05	0.828
Reduced model: individual variables			
Shrub species	3	14.31	0.003
Distance from injection point	1	61.09	<0.001
<i>(b) Species differences using reduced model^b</i>			
<i>A. dumosa</i> vs. <i>L. pallidum</i>	1	-9.77	0.002
<i>A. dumosa</i> vs. <i>L. tridentata</i>	1	-4.11	0.043
<i>A. dumosa</i> vs. <i>L. andersonii</i>	1	0.64	0.425
<i>L. pallidum</i> vs. <i>L. tridentata</i>	1	2.20	0.138
<i>L. pallidum</i> vs. <i>L. andersonii</i>	1	9.02	0.003
<i>L. tridentata</i> vs. <i>L. andersonii</i>	1	4.64	0.031

^aDegrees of freedom (df), Wald χ^2 values, and Pr > χ^2 values for individual variables for the full and the reduced logistic regression models. Pr > χ^2 values are based on the Type III analysis of effects.

^bComparison of species using analysis of maximum likelihood estimates and the reduced logistic regression model in "a".

beyond the most distal ^{32}P positive plant (Fig. 1), suggesting that the maximum horizontal zones of influence for these species was reasonably characterized.

The differences among species are related to differences in their probability of accessing the resource ^{32}P (which is located at a 0.35 m soil depth) at a certain distance from a plant (Fig. 2). Because the probability distributions in Fig. 2 represent the horizontal zones of influence as defined by Casper et al. (2003), we will refer to them as such for the remainder of this paper. For *L. tridentata*, the horizontal zone of influence declines slowly in a relatively linear fashion until the last ^{32}P positive *L. tridentata* shrub at 5.8 m from an injection point shows an 8% chance of having physiologically active roots in the soil located at 0.35 m deep and at a horizontal distance of 5.8 m from the plant's stem base. The horizontal zone of influence for *L. andersonii* is similar to that of *L. tridentata* near the plant's stem base, with a shrub at 0.5 m having a 40% chance of being ^{32}P positive, but *L. andersonii* drops at a faster rate than *L. tridentata* such that the last shrub at 4.1 m has only a 3% chance of being ^{32}P positive. The horizontal zone of influence for *A. dumosa* is different from these two species in that *A. dumosa* has an extremely high predicted probability (81%) of accessing ^{32}P close to the plant's stem base (0.2 m), but the probability drops very quickly to where *A. dumosa* at 1.7 m has only a 14%

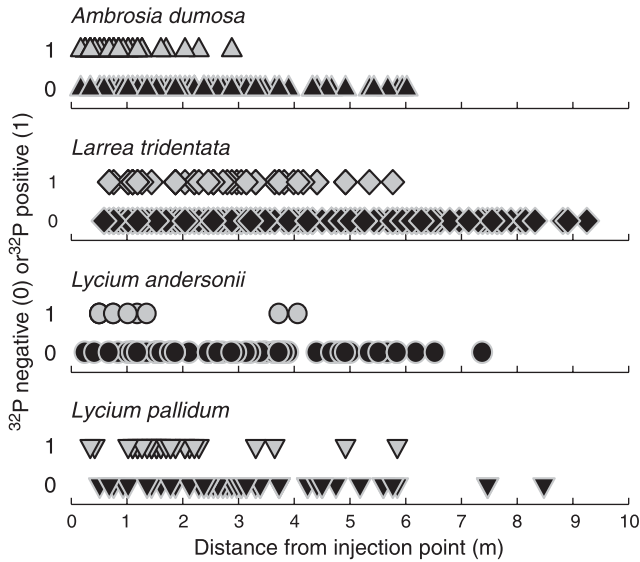


Fig. 1. Scatterplots of ³²P negative (0; black symbols) and ³²P positive (1; grey symbols) shrubs in horizontal zones of influence study for *A. dumosa* (triangles), *L. tridentata* (diamonds), *L. andersonii* (circles), and *L. pallidum* (inverted triangles).

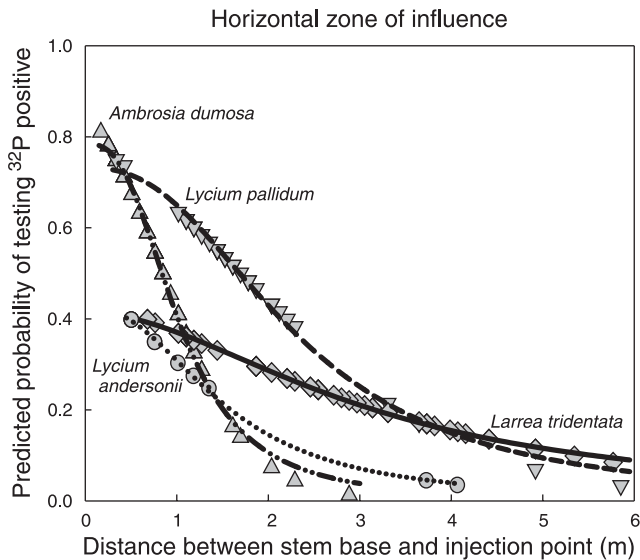


Fig. 2. Predicted probability of a root accessing a ³²P tracer at different horizontal distances from the shrub's stem base for *A. dumosa* (triangles), *L. pallidum* (inverted triangles), *L. andersonii* (circles), and *L. tridentata* (diamonds). ³²P was injected at 0.35 m soil depth. Different lines are the logistic decay functions for different species using the coefficients in Table 1 and Eq. (1).

Table 2

Values for the three constants in Eq. (1) that characterize the below-ground zones of influence of the four shrub species *L. tridentata*, *L. andersonii*, *L. pallidum*, and *A. dumosa*

Zone of influence equation constant	<i>L. tridentata</i>	<i>L. andersonii</i>	<i>L. pallidum</i>	<i>A. dumosa</i>
P_{\max}	0.414 <i>a</i> (±0.005)	0.425 <i>a</i> (±0.013)	0.732 <i>b</i> (±0.019)	0.784 <i>c</i> ±0.010
L_{50}	3.05 <i>d</i> (±0.05)	1.51 <i>b</i> (±0.07)	2.30 <i>c</i> (±0.07)	1.03 <i>a</i> (±0.02)
f	1.92 <i>a</i> (±0.05)	2.35 <i>b</i> (±0.21)	2.47 <i>b</i> (±0.17)	2.79 <i>c</i> (±0.14)

Significant differences among species are shown by lower case letters and are based on the 95% confidence intervals (shown in parentheses) that were estimated by PROC NLIN (SAS, 2003).

chance, and then tapers out more gradually until a shrub at 2.9 m has only a 1% chance of being ^{32}P positive. Finally, the horizontal zone of influence for *L. pallidum* starts out like *A. dumosa* with a shrub at 0.3 m having a 75% chance of being ^{32}P positive, but *L. pallidum* has a more gradual decline until a shrub at 5.9 m still has a 3% chance of being ^{32}P positive.

These differences among species in their probability of accessing resources located at various distances from the plant are also quantified by the three constants in Eq. (1) (Table 2). P_{\max} (i.e. the maximum probability of a location being part of the below-ground zone of influence) of *L. tridentata* and *L. andersonii* were not significantly different from each other, but were substantially and significantly lower than that of the other two species. For the other two species, P_{\max} of *L. pallidum* was slightly, but significantly, lower than that of *A. dumosa*. L_{50} , which is a constant characterizing the distance from the stem base at which the probability of being in the zone of influence is half of P_{\max} , differed significantly among all species, with *A. dumosa* having the shortest distance, followed in turn by *L. andersonii*, *L. pallidum*, and *L. tridentata*. Finally, the curve shape constant f , which characterizes how rapidly the probability of being in the zone of influence decreases with distance from the stem base, for *L. andersonii* and *L. pallidum* were not significantly different from each other, but were significantly larger than that for *L. tridentata* and significantly smaller than that for *A. dumosa*.

3.2. Vertical zones of influence

Only differences among shrub species and among irrigation treatments were significant in the full and reduced logistic regression models of the vertical zones of influence data (Table 3a). The other predictor variables from the full model (proximity of *L. tridentata* and *A. dumosa* plants; the number of species replications per plot) were not significant. Overall, the reduced model was significant using the log likelihood ratio test ($p < 0.001$). A series of analysis of maximum likelihood estimate tests (Table 3b) indicated that *L. tridentata* was significantly more likely to

Table 3

Binary logistic regression analysis of vertical zones of influence based on the frequency of plants that acquired ³²P

Variable	Full data set			Reduced data set		
	df	Wald χ^2	Pr > χ^2	df	Wald χ^2	Pr > χ^2
<i>(a) Vertical zones of influence models^a</i>						
Full model: individual variables						
Shrub species	2	7.61	0.022	1	5.02	0.025
Irrigation treatment	2	10.79	0.005	2	8.92	0.012
Proximity of <i>L. tridentata</i> and <i>A. dumosa</i>	1	0.70	0.402	1	<0.01	0.988
No. of Repetitions per plot	3	3.54	0.316	3	3.22	0.359
Reduced Model: individual variables						
Shrub species	2	11.41	0.003			
Irrigation type	2	10.69	0.005			
<i>(b) Species and irrigation type differences using reduced model^b</i>						
<i>L. tridentata</i> vs. <i>A. dumosa</i>	1	11.10	0.001			
<i>L. tridentata</i> vs. <i>L. pallidum</i>	1	3.68	0.055			
<i>L. pallidum</i> vs. <i>A. dumosa</i>	1	1.41	0.235			
Flood irrigation vs. deep irrigation	1	8.97	0.003			
Flood irrigation vs. control	1	6.17	0.013			
Control vs. deep irrigation	1	0.54	0.464			

^aDegrees of freedom (df), Wald χ^2 values, and Pr > χ^2 values for individual variables for the full and the reduced logistic regression models. The full data set included all three species tested (*L. tridentata*, *A. dumosa*, and *L. pallidum*), whereas the reduced data set used only *L. tridentata* and *A. dumosa*. Pr > χ^2 values are based on the Type III analysis of effects.

^bComparisons of species and irrigation treatments using analysis of maximum likelihood estimates and the reduced logistic regression model in “a”.

access soil at a 5 m depth than *A. dumosa* (Fig. 3, left panel), i.e. the vertical zone of influence for *L. tridentata* was significantly greater than that of *A. dumosa* at 5 m soil depth. Vertical zones of influence for *L. tridentata* and *L. pallidum* were not significantly different at the 95% confidence level, but were at the 90% confidence level. Finally, vertical zones of influence for *A. dumosa* and *L. pallidum* were not significantly different. Comparing the three irrigation treatments, vertical zones of influence for shrubs that received the flood irrigation treatment was significantly greater than either the deep irrigation or control treatments (Fig. 3, right panel). However, the vertical zones of influence for the deep irrigation treatment was not significantly different from the control treatment.

4. Discussion

The vertical and horizontal zones of influence for root systems of *A. dumosa*, *L. tridentata*, *L. andersonii*, and *L. pallidum* are different from each other and likely represent different ecological strategies. Following closely the Casper et al. (2003)

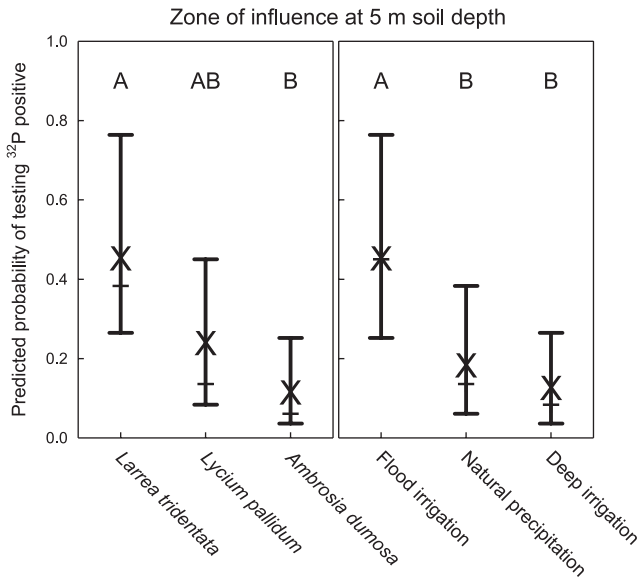


Fig. 3. Predicted probability of a root accessing a ^{32}P tracer that was injected at 5 m soil depth for different shrub species incorporating all irrigation treatments (left panel) and for different irrigation treatments incorporating all shrub species (right panel). Upper and lower lines of each plot represent maximum and minimum values, horizontal line is the median, and “X” is the mean. Plots with the same upper case letter are not significantly different from each other.

definition of zones of influence, this study specifically measured the probability that a shrub was capable of accessing a patch of soil that was at known horizontal distances from its stem base or that was at a 5 m depth. It is important to note that our results do not necessarily indicate the presence, density, or efficiency of fine roots in any given soil patch. For example, all four shrubs in our study are known to host arbuscular mycorrhizae (Titus et al., 2002b). Thus, some of the ^{32}P that was present in the shrubs likely was obtained through mycorrhizal symbiosis. In addition, three of the four species that we studied have been demonstrated to hydraulically redistribute soil water (Yoder and Nowak, 1999), and studies in other ecosystems have demonstrated that neighboring plants parasitize hydraulically redistributed water (Caldwell et al., 1998). Although it is possible that ^{32}P in one shrub was obtained during the hydraulic redistribution of water by another shrub, this mechanism appears unlikely for our study, based on results from the vertical zones of influence experiment. First, hydraulic redistribution of water from deep to shallow soils should be more common in the deep irrigation treatment than in the control treatment, but the probability of obtaining ^{32}P did not differ between the two treatments (Fig. 3). Second, we would expect parasitism of hydraulically redistributed ^{32}P to be more common when *A. dumosa* and *L. tridentata* were in close proximity, but proximity was not a significant factor in the full logistic model (Table 3). Nonetheless, even if a plant obtained a significant portion of its ^{32}P from

a specific soil patch by mechanisms other than direct uptake by roots (such as through mycorrhizae or hydraulic redistribution), that soil patch still falls within the plant's below-ground zone of influence, as defined by Casper et al. (2003). Thus, our experiments directly measure the species' below-ground zone of influence, i.e. the volume of soil from which a plant accesses resources.

L. tridentata has the most extensive below-ground zone of influence both vertically and horizontally of the four species that we studied. *L. tridentata* had the longest L_{50} (the distance from the stem base at which the probability of accessing a resource is half of the maximum probability) (Table 2) and the highest probability of vertically accessing soil at depths of 5 m (Fig. 3). Furthermore, the small value for the curve shape constant f , which characterizes how rapidly the probability of being in the zone of influence decreases with distance from the stem base, also indicates that *L. tridentata* horizontally extends its below-ground zone of influence. However, the low P_{\max} , which is the maximum probability of accessing a soil resource, indicates that although root systems (i.e. fine roots, mycorrhizae, etc.) regularly access soil near the stem base, they are not very dense. Other studies of *L. tridentata* have shown the presence of horizontal and vertical roots at distances greater than 5 m from the plant's stem base and extensive but not dense patterns of extending roots (Cannon, 1911; Chew and Chew, 1965; Brisson and Reynolds, 1994; Gile et al., 1998; Gibbens and Lenz, 2001). The relatively low P_{\max} and f for *L. tridentata* is also consistent with the results of Wilcox et al. (2004), who found that *L. tridentata* produced a greater quantity of fine roots in interspaces between shrubs than in canopies. Taken together, our zones of influence and previous fine root growth results suggest that *L. tridentata* extends its below-ground zone of influence over a very large soil volume but does not concentrate its root systems in the area immediately surrounding the plant. This dispersed, extensive belowground zone of influence for *L. tridentata* allows plants to access "remote" soil patches at greater depths or in the interspaces between shrubs as resources become available in those locations (Schenk et al., 1999) or as competition becomes too strong in other soil patches (Brisson and Reynolds, 1994). This strategy of an extensive below-ground zone of influence likely helps *L. tridentata* maintain its evergreen growth form, but the lack of an intensive belowground zone of influence under its own canopy, which represents one of the more fertile microsites in the Mojave Desert (Titus et al. 2002a), may reduce its ability to grow rapidly.

In contrast to *L. tridentata*, *A. dumosa* concentrates its below-ground zone of influence close to its stem base and only rarely extends it to greater depths and distances, which fits *A. dumosa*'s fast growing, concentrated, deciduous growth strategy. *A. dumosa* had the shortest L_{50} and the greatest f , but also the highest P_{\max} (Table 2). Although *A. dumosa* did access depths of 5 m, it only did so once under natural precipitation and only five times with the flood irrigation treatment, which was significantly less than *L. tridentata* (Fig. 3). Note that although the proximity of *L. tridentata* and *A. dumosa* was not significant in the vertical experiment, we cannot conclude that *A. dumosa* does not increase its vertical zone of influence when growing next to *L. tridentata*; we can only conclude that *A. dumosa* does not significantly increase its zone of influence at 5 m soil depth, i.e. the depth at which we

conducted measurements. Root excavation and minirhizotron studies of *A. dumosa* also found that roots extended beyond the drip line of the plant's canopy (Cannon, 1911; Rundel and Gibson, 1996), but *A. dumosa* produces more fine roots under the shrub's canopy than in the plant interspaces (Wilcox et al. 2004). These patterns suggest that *A. dumosa* has a concentrated root system in the soil zone surrounding the stem base and only rarely sends out longer roots into surrounding or drier soil areas. A dense zone of influence near the plant's stem base presumably allows *A. dumosa* to extract much of the soil resources over the short spring growth period before it drops its leaves for the summer drought period as well as helps explain why photosynthetic rate of *A. dumosa* is often twice that of co-occurring shrubs in the spring (Housman et al., 2003; Naumburg et al., 2003).

L. pallidum appears to use a hybrid of strategies that incorporates aspects of both the *A. dumosa* and *L. tridentata* strategies. The maximum horizontal zone of influence for *L. pallidum* is similar to that of *L. tridentata* (Fig. 2), but *L. pallidum* has a smaller chance of accessing deep soils (Fig. 3). Values of P_{\max} and f for *L. pallidum* are closest to those for *A. dumosa*, indicating that *L. pallidum* has a high ability to extract resources near the plant's stem base (Table 2). Wilcox et al. (2004) also found that the fine root growth pattern of *L. pallidum* was between that of *A. dumosa* and *L. tridentata*. Markle (1917) indicated that *L. pallidum* had a noticeably shallower root system than any other shrub species in his excavation study and that its roots extended horizontally to 4.6 m. Because *L. pallidum* is deciduous like *A. dumosa* but much larger in both leaf and canopy size, the more extensive horizontal zone of influence may be necessary to sustain the larger size.

Interestingly, the pattern of horizontal zone of influence for *L. andersonii* differs substantially from that of its congener *L. pallidum* (Fig. 2 and Table 2). Both P_{\max} and L_{50} for *L. andersonii* are significantly smaller than those for *L. pallidum*, suggesting that *L. andersonii* has both a sparser zone of influence near the stem base and a less extensive horizontal zone of influence. These characteristics of the below-ground zone of influence imply that *L. andersonii* has less access to soil resources than *L. pallidum*, which may help explain why *L. andersonii* has much smaller leaves that drop more quickly in response to drought than *L. pallidum*.

Although these Mojave Desert shrubs differ in their horizontal and vertical zones of influence, Yoder and Nowak (1999) found that *A. dumosa*, *L. tridentata*, and *L. pallidum* were capable of completely extracting soil water at depths measured up to 1.95 m. Anderson et al. (1993) found similar results for species in a semi-arid shrub steppe that also differ in their horizontal and vertical root profiles (Abbott et al. 1991). The soil moisture regulating abilities of these species make them critical elements in the design of soil caps for hazardous or radioactive waste sites, but plants can also penetrate and possibly damage the caps if their roots grow too deep (Bowerman and Redente 1998). Results from our vertical zones of influence experiment showed that *A. dumosa* and *L. pallidum* were significantly less likely to reach 5 m than *L. tridentata*, but they still occasionally accessed ^{32}P from 5 m soil depth (Fig. 3). This ability was significantly increased with the flood irrigation treatment, but not in the control or deep irrigation treatments (Fig. 3). Thus, long-term soil caps must be designed to account for all of these factors.

Surprisingly, differences in soil water and N availability caused by summer precipitation, crust disturbance, or nitrogen deposition treatments did not affect the horizontal zones of influence for the Mojave Desert shrubs. However, these treatment results need to be interpreted cautiously. The treatments had only been in effect for ~2 years at the time of the experiment, and the previous hydrologic year was the driest in the past 7 years, amounting to only 34% of the annual mean precipitation. The slow and sporadic growth patterns of these desert shrubs may simply require more time to develop significantly different responses to these treatments. A power analysis comparing the minimum distance differences required for statistical significance as a function of shrub species, treatment variables, and the number of replicates sampled showed that the sample sizes used in this study are able to detect treatment effects of ~0.3 m for *A. dumosa*, 0.8–0.9 m for *L. tridentata*, 0.8–1.1 m for *L. andersonii*, and 0.9–1.1 m for *L. pallidum*. Because the MGCF study site is intended to remain active for > 10 years, it would be useful to repeat this study at a later time to see if significant treatment effects develop over time.

Although we have largely followed the concepts of below-ground zones of influence as outlined by Casper et al (2003) in our treatment of data, our approach differs in one key aspect: we have fit our data to a logistic decay curve rather than the conditional exponential decay curve that they recommend (their Eq. (2)). The logistic decay curve has the same ecological features of the exponential decay curve that Casper et al (2003) consider to be important, such as exponential declines in the probability of accessing a resource with increasing distance from the stem base until zero is reached. However, the logistic decay curve has an important ecological feature that a simple exponential decay curve lacks, i.e. that there is a maximum probability of accessing a soil resource and that the maximum cannot exceed but does not necessarily have to equal one. Casper et al. recognized this constraint and thus constructed a conditional function where the probability of accessing a resource at a certain distance from the stem base had a maximum value of either the value from a simple exponential decay function or one. Although we recognize that the maximum probability approaches one for some plants, the maximum does not necessarily have to equal one. Indeed, the maximum may be substantially less than one for many species, as we observed in our study, for sound ecological reasons. In natural communities, root systems (including their associated rhizosphere) overlap such that roots of one plant are often found directly underneath the canopy of another plant. Furthermore, soil microbes also compete with plants for soil resources. Thus, some of the resources beneath the plant will not be used by that plant, which means that the maximum probability has to be less than one. By explicitly fitting the maximum probability, the logistic decay curve provides a more realistic ecological fit to the data.

Finally, just as extrapolating from above-ground observations to below-ground functions can be misleading (Casper and Jackson 1997), extrapolating from below-ground zones of influence to plant community structure can also be misleading. For example, the greater P_{\max} for *A. dumosa* relative to that for *L. tridentata* suggests that *A. dumosa* may be a better competitor for resources that are relatively close to it,

and indeed *A. dumosa* is able to acquire six times more P from soil interspaces than *L. tridentata* when both shrubs are competing with an annual grass (Yoder and Nowak, 2000). However unlike *A. dumosa*, the dense zone of influence near *L. pallidum* stem bases does not lead to greater P acquisition than *L. tridentata* when the shrubs compete against an annual grass (Yoder and Nowak 2000), suggesting that a dense zone of influence alone does not confer competitive advantage. Clearly, below-ground zones of influence for aridland plants are related to many factors, including temporal and spatial patterns of resource availability, plant phenology, plant ecophysiology, plant size, and competitive interactions. To paraphrase Schenk and Jackson (2002), the intriguing question is whether these factors shape the below-ground zones of influence or whether the below-ground zones of influence shape these factors.

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