

Spatial distribution of roots across three dryland ecosystems and plant functional types

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ABSTRACT.—Roots play a critical role in carbon storage, carbon cycling, and resource acquisition in dryland ecosystems, yet their distribution and production patterns are poorly understood. We aimed to compare the vertical and horizontal distribution of roots of the dominant plant functional types across 3 dryland ecosystems in the western Great Plains of the United States. We collected consecutive soil cores from directly under plants to 29 cm away from the center of plant individuals (horizontal plane), to a 20-cm depth (vertical plane). Across the 3 ecosystem types, grass root biomass decreased with depth and, for the sagebrush steppe, at a distance beyond 6.5 cm from the center of the plant. At the 10–20 cm depth increment, there was no horizontal pattern in root biomass. Uniformity in root biomass in the 10–20 cm depth and at distances >6.5 cm from the plant center is best explained by the overlap of roots of individual and neighboring plants to maximize belowground resource uptake. There was much lower root biomass in the surface 20 cm adjacent to shrubs than adjacent to grasses in the sagebrush steppe, and while grass root biomass decreased significantly with depth and distance as described above, shrub roots were uniform in both planes. Our study confirms that root distribution in drylands differs among plant functional types, with grasses exploiting surface soils both horizontally and vertically to capitalize on surface resources, and shrubs capitalizing less on those resources.

RESUMEN.—Las raíces desempeñan un papel fundamental en el almacenamiento de carbono, en el ciclo y en la adquisición de recursos en los ecosistemas de tierras áridas, aunque sus patrones de distribución y producción sean poco conocidos. Nuestro objetivo fue comparar la distribución vertical y horizontal de las raíces de plantas dominantes en tres ecosistemas de tierras áridas en las Grandes Llanuras occidentales de Estados Unidos. Recolectamos núcleos de suelo consecutivo extraídos debajo de las plantas a 29 cm del centro de las plantas (plano horizontal) y a 20 cm de profundidad (plano vertical). En los 3 tipos de ecosistemas, la biomasa radicular del pasto disminuyó con la profundidad y, en el caso de la estepa de la artemisa, a una distancia de más de 6.5 cm del centro de la planta. Cuando la profundidad aumentó de 10 a 20 cm no se encontró un patrón horizontal en la biomasa radicular. La uniformidad en la biomasa radicular a una profundidad de 10 a 20 cm y a distancias superiores a 6.5 cm desde el centro de la planta se explica mejor por la superposición de raíces de plantas individuales y vecinas que maximizan la captación de recursos subterráneos. La biomasa radicular fue mucho menor en la superficie cuya distancia a los arbustos adyacentes fue de 20 cm que las adyacentes a los pastos de la estepa de artemisa. Mientras que la biomasa de la hierba disminuyó significativamente con la profundidad y la distancia como se describió anteriormente, las raíces de los arbustos fueron uniformes en ambos planos. Nuestro estudio confirma que la distribución radicular en las tierras áridas difiere entre los tipos funcionales de las plantas, donde los pastos explotan las superficies de los suelos tanto horizontal como verticalmente para aprovechar los recursos superficiales, y los arbustos explotan menos tales recursos.

Net primary production in dryland ecosystems is limited by water and nitrogen (Lauenroth et al. 1978, Burke 1989, Hooper and Johnson 1999, Yahdjian et al. 2011, Stevens et al. 2015), both of which can be considered “belowground resource constraints.” Water and nitrogen availability vary temporally and spatially within dryland ecosystems (Burke 1989, Sala et al. 1992, Burke et al. 1999, Austin et al. 2004), and a plant’s ability to sur-

vive is dependent on its ability to acquire these belowground resources. While previous literature has focused on defining species-specific root characteristics (Coupland and Johnson 1965), the effects of soil characteristics on root distribution (Weaver and Darland 1949, Fox et al. 1953, Burke et al. 1998), and belowground competition (Coffin and Lauenroth 1991, Hook et al. 1994), few studies have addressed the spatial distribution of the roots

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of individuals by plant functional types and in surface soils where belowground resources are most likely to be available.

In a semiarid dryland region, the structure and function of an ecosystem is determined by the distribution and production of plant functional types, which include C₃ grasses, C₄ grasses, C₃ forbs, C₄ forbs, and shrubs. The most important functional types and the ones that are the most likely dominants are grasses and shrubs. Grouping species into plant functional types based on their morphological and physiological characteristics provides an important tool for assessing plant-ecosystem interactions (Epstein et al. 1997, Sala et al. 1997). The coexistence of C₃ grasses, C₄ grasses, and shrubs in drylands may be partially explained by their ability to access different pools of belowground resources, which vary in time and space. For instance, studies on shrub and grass resource partitioning suggest that shrubs rely on deep-soil water stores, while grasses acquire water from the top 30 cm of soil (Walter 1971, Sala et al. 1989).

Previous studies that have taken place across climate gradients have provided us with evidence that annual belowground resource availability is a function of mean annual temperature, mean annual precipitation, seasonality, and soil texture (Epstein et al. 1996, 1997, Paruelo and Lauenroth 1996, Sala et al. 1997). For instance, mean annual temperature, mean annual precipitation, and soil texture explained 67% to 81% of the variance in production of grasses across the Great Plains (Epstein et al. 1996, 1997). The location of available water in the soil profile is determined by soil texture and the overlap between monthly precipitation and monthly temperature (Sala et al. 1997), while nitrogen availability in drylands decreases with depth, is highest in fine-textured soils, and has horizontal patterning such that it is higher close to individual plants than in interspaces (Vinton and Burke 1995, Burke et al. 1999).

It was previously thought that aboveground plant cover could be used to predict belowground biomass distribution patterns, but studies have demonstrated that aboveground plant cover is not a reliable indicator (Sims and Singh 1978). Bare ground and low plant cover are common in water-limited ecosystems due to low regeneration rates and high intraspecific competition (Coffin and Lauenroth 1991,

Aguilera and Lauenroth 1993). The average root span is often larger than bare ground openings (Hook et al. 1991), resulting in root presence below the bare ground. For instance, in the shortgrass steppe, plant basal cover is approximately 20%–40%, with frequent bare ground openings averaging <15 cm in diameter (Milchunas et al. 1989, Coffin and Lauenroth 1992, Hook et al. 1994, Hook and Lauenroth 1994), while the average total root span of the common grass *Bouteloua gracilis* is 22 cm (Lee and Lauenroth 1994). Plants adjacent to openings extend roots horizontally under bare ground to maximize uptake of belowground resources (Hook et al. 1994).

Aboveground biomass and net primary production have been well studied in relation to temporal and spatial belowground resource availability; however, few studies have identified horizontal and vertical root distribution patterns, despite the fact that 50% or more of the total net primary production of semiarid ecosystems occurs belowground (Sims et al. 1978, Milchunas and Lauenroth 2001). Our objective in this study was to describe the spatial distribution of the root systems of individual plants of the dominant grasses as they vary with depth and distance across 3 types of semiarid ecosystems in the western Great Plains of the United States: the shortgrass steppe, the northern mixed-grass prairie, and the sagebrush steppe. Because the shrub *Artemisia tridentata* is codominant along with grasses in the sagebrush steppe, we included it in our sampling. We had 2 key questions:

- (1) How does the spatial distribution of roots of an individual plant change with depth and distance from the plant center?
- (2) How does root biomass change with plant functional type and across sites of each ecosystem type?

METHODS

Site Description

Within each ecosystem type, we sampled the horizontal and vertical distribution of roots of the dominant plant functional types across the shortgrass steppe, the northern mixed-grass prairie, and the sagebrush steppe. We sampled the shortgrass steppe and the northern mixed-grass prairie between 21 August

and 28 August 2016, and the sagebrush steppe between 21 June 2017 and 25 June 2017, because we did not have access to the sagebrush site location in 2016. All 3 locations have a history of moderate cattle grazing during the growing season and are currently managed for this purpose. We controlled for soil texture by choosing sites with either sandy-clay-loam, sandy-loam, or loam soils and tested soil texture using a protocol based on Klute (1986) and Gavlak et al. (1994).

The shortgrass steppe at the Central Plains Experimental Range (CPER) is located 40 km south of Cheyenne, Wyoming, and 61 km northeast of Fort Collins, Colorado (40°49' N, 104°43' W). The CPER is managed by the United States Department of Agriculture (USDA) Agriculture Research Service (ARS) and was formerly part of the National Science Foundation Long-Term Ecological Research (LTER) network (Lauenroth and Burke 2008). The average elevation is 1650 m, and monthly temperatures range from -9.8 °C in December to 30.7 °C in July. Mean annual temperature is 8.7 °C, and mean annual precipitation is 341 mm (PRISM 2018). The majority of precipitation comes in short and intense thunder storms during the summer months, with rainfall events that drop typically <5 mm (Lauenroth and Sala 1992). The dominant plant species in the shortgrass steppe are the C₄ perennial grasses blue grama (*Bouteloua gracilis*) and buffalo grass (*Bouteloua dactyloides*), the subshrub prairie sagewort (*Artemisia frigida*), and plains prickly pear cactus (*Opuntia polyacantha*) (Lauenroth 2008) (nomenclature follows USDA-NRCS [2018]).

The northern mixed-grass prairie site is located within the High Plains Grassland Research Station (HPGRS) and is managed by the USDA-ARS. The site is located 8 km west of Cheyenne, Wyoming, (41°12' N, 104°54' W) and has an average elevation of 1930 m. Mean monthly temperatures range from -8.8 °C in December to 27.9 °C in July, and mean annual temperature is 7.4 °C. Mean annual precipitation is 393 mm (PRISM 2018). The vegetation is a mixture of C₃ perennial grass species including western wheatgrass (*Pascopyrum smithii*), needle and thread (*Hesperostipa comata*), and the C₄ perennial grass *B. gracilis* (Schuman et al. 2009).

The sagebrush steppe site is located within the Thunder Basin National Grassland (TBNG),

64 km northeast of Douglas, Wyoming (43°25' N, 104°56' W), and is managed by The Nature Conservancy. The average elevation is 1500 m. Mean monthly temperatures range from -11.1 °C in December to 31.7 °C in July, and mean annual temperature is 8.1 °C. Mean annual precipitation is 331 mm (PRISM 2018). The overwhelmingly dominant shrub is big sagebrush (*Artemisia tridentata*), and the understory consists of a mixture of several C₃ and C₄ perennial grasses and forbs including *B. gracilis*, *H. comata*, and *P. smithii* (Pennington et al. 2017).

Field Studies

At each site, we laid out a total of 5 transects (30 m long) that were placed 50 m apart. At each transect we identified 20 individuals of the dominant plant functional type and randomly selected 2 individuals for sampling. There were 10 samples associated with each individual: 5 distances (0, 6.5, 13, 19.5, and 26 cm), with each distance containing 2 depths (0 to 10 cm and 10 to 20 cm). At the shortgrass steppe, we sampled 9 individuals of the C₄ perennial bunchgrass *B. gracilis*; at the northern mixed-grass prairie we sampled 9 individuals of either *P. smithii* or *H. comata*, both C₃ perennial grasses; and at the sagebrush steppe we sampled 10 individuals of the shrub *A. tridentata* and 10 individuals of the perennial grasses *B. gracilis* or *H. comata* for a total of 10 individuals per functional type. Because our objective was to sample the dominant grasses in each of the ecosystems, we assumed functional plant type similarities and ignored species details (Sala et al. 1997).

To estimate root biomass with depth (vertical plane) and distance away from an individual (horizontal plane), we used a 6.5-cm internal diameter core to a depth of 20 cm because approximately 75% of total root biomass is within the top 20 cm of soil (Leetham and Milchunas 1985). For each individual, we extracted 5 soil cores consecutively in a straight line of a random direction with the first core directly over the individual. We assumed, based on previous work (Hook et al. 1994), that the majority of the root biomass we sampled was from our target individuals, but we did not have a way to be sure that this was true.

At the sagebrush steppe, we collected cores for 10 *A. tridentata*. The soil core could not be

placed directly over the *A. tridentata* individual due to its size; therefore, we extracted the soil cores on a random side adjacent to the stem. We separated each core into 2 depths, 0 to 10 cm and 10 to 20 cm. We sampled 38 individuals, with each individual associated with 5 distances and 2 depths. In total, we processed 380 samples: 280 grass root samples across the 3 sites and 100 samples of sagebrush roots.

Laboratory Analysis

In the laboratory, we air-dried the soil samples when possible or oven-dried them at 55 °C for 48 h. Using water, we washed the soil away from the belowground biomass in accordance with the methods of Lauenroth and Whitman (1971). The resulting biomass was dried at 55 °C for 48 h and hand separated into crowns, fine roots, and coarse roots (>2 mm diameter) and weighed (Robertson et al. 2009). The washed and sorted samples were ashed in a muffle furnace at 450 °C for 4 h to eliminate contamination from residual soil particles (Harmon et al. 1999). The ash-free dry weight was expressed as grams of dry weight per meter squared (g/m^2).

Data Analysis

We conducted a 2-way analysis of variance to test whether root biomass differed with distance and depth from the center of plants. We fit a linear mixed-effects model with the R package lme4 v1.1.18.1 (Bates et al. 2015) using restricted maximum likelihood and including distance, depth, and the interaction as fixed effects. We calculated ANOVA tables with F statistics for the fixed effects with the package lmerTest v3.0.1 (Kuznetsova et al. 2017). We fit a model for each site separately for which we included individual plants as random effects of intercept and of slope of distance. Additionally, we fit a model for all sites combined for which we included sites and individual plants within sites as random effects. To test whether the mean root biomass at each distance and depth was significantly different from other units when the associated fixed effect was significant, we conducted a post hoc pairwise comparison test (Tukey's honest significant difference [HSD] with the package emmeans v1.2.4 [R Core Team 2018]).

We tested for differences in total root biomass and root biomass distribution patterns

between plant functional types at the sagebrush steppe site using paired-sample t tests (grasses vs. shrubs and C_3 grasses vs. C_4 grasses). An additional paired-sample t test was used to test for significant differences in total root biomass between fine and coarse root distribution for *A. tridentata*. All tests were conducted using the statistical software R (R Core Team 2018), and all references to significant differences are at the $P \leq 0.05$ level.

RESULTS

Depth, Distance, and their Interaction on Grass Root Distribution

Root biomass was consistently higher in the 0–10 cm depth than in the 10–20 cm depth on average for all distances and sites ($F = 144.2$, $P < 0.001$; Fig. 1, Tables 1, 2). On average across all sites, grass root biomass directly under a plant individual (distance 0) declined from $180 \pm 12 \text{ g}/\text{m}^2$ (marginal mean \pm SE) in the 0–10 cm depth to $94 \pm 12 \text{ g}/\text{m}^2$ in the 10–20 cm depth, a 48% decrease (Tukey's HSD: $P < 0.05$). On average, grass root biomass declined with distance in the 0–10 cm depth but not in the 20–30 cm depth (Fig. 1) based on a significant interaction term between distance and depth ($F = 8.04$, $P < 0.001$; Table 2). The highest amount of root biomass occurred within the 0–10 cm depth and within a 3.25-cm radius of individual plants (Table 1).

Site and Plant Functional Type

Root biomass was quite variable within each site, with coefficients of variation ranging from 23% to 85%. Mean grass root biomass averaged across distances and summed across the 0–20 cm depth was greatest at the northern mixed-grass prairie site ($257 \pm 49 \text{ g}/\text{m}^2$; observed mean \pm SD), followed by the short-grass steppe site ($213 \pm 63 \text{ g}/\text{m}^2$) and the sagebrush steppe site ($205 \pm 98 \text{ g}/\text{m}^2$; Table 1). There was significantly higher grass root biomass at the northern mixed-grass prairie than at the sagebrush steppe site (Tukey's HSD: $P < 0.05$), whereas root biomass at the short-grass site did not differ from either. ANOVAs of individual sites confirmed that root biomass declined significantly with depth (all values of $P < 0.001$; Table 2, Fig. 2). The analyses also showed that distance did not have a significant effect on root biomass at the shortgrass steppe

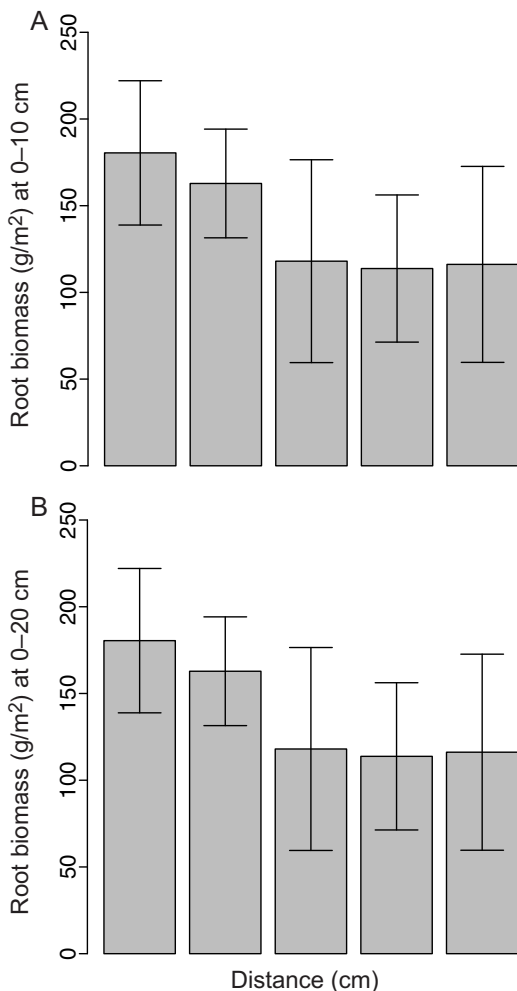


Fig. 1. Grass root biomass by distance and by depth (A, 0–10 cm; B, 10–20 cm) from individual plants across 3 dryland sites in the western United States: the short-grass steppe, the northern mixed-grass prairie, and the sagebrush steppe. The bars represent marginal mean root biomass and the error bars a 95% confidence interval from the linear mixed model with sites and individual plants (nested within sites) as random effects.

or the northern mixed-grass prairie sites (Fig. 2A–D). Root biomass declined significantly with distance and in interaction with depth, at the sagebrush steppe site (interaction term $F = 13.54$, $P < 0.001$; Table 2). We found a significant drop of root biomass between distances 6.5 cm and 13 cm in the 0–10 cm depth but not in the 10–20 cm depth (Fig. 2E, F).

We compared grass root distribution (C_3 and C_4 grasses) to shrub root distribution (*A. tridentata*) at the sagebrush steppe site and

found that depth and distance did not have a significant effect on *A. tridentata* roots (fine or coarse), while grass root biomass decreased with both distance and depth. Overall, there was significantly lower root biomass for roots of the shrub *A. tridentata* (28 ± 14 g/m²) than for grasses (108 ± 80 g/m²) within the 0–20 cm depth. We also compared the root distribution patterns of C_3 grasses with C_4 grasses within the sagebrush steppe site. There were no significant differences in total root biomass or root biomass distribution by depth or distance between the C_4 perennial bunchgrass *B. gracilis* and the C_3 perennial bunchgrass *H. comata*.

DISCUSSION

Root biomass decreased rapidly with soil depth by about 50% between the 0–10 cm depth and the 10–20 cm depth. Root biomass in the 0–10 cm depth did not vary with distance except for in the sagebrush steppe where it also dropped at a distance of 6.5 cm; we found no relationship with distances in the 10–20 cm depth. Our results indicate that mean total root biomass in the surface soil layers (0–20 cm) was highest at the northern mixed-grass prairie, and particularly high compared to the sagebrush steppe. Root distribution patterns were similar for the 2 grass-dominated sites, but differed for the sagebrush steppe. When examining differences between plant functional types at the sagebrush steppe, we found that grass root distribution decreased significantly with depth and distance up to 6.5 cm away, while shrub roots were uniform in both directions.

One expectation for how the spatial distribution of plant roots changes with depth and distance was that they would decrease smoothly away from the center of the plant both vertically and horizontally. The distributions we found did not consistently fit this expectation. At the sagebrush steppe, grass root biomass was strongly concentrated beneath plant individuals, with the highest amount of root biomass in the top 10 cm and within a 3.25-cm horizontal radius of the center of the plant. Evidence for a decreasing root biomass gradient existed only within the top 0–10 cm depth, as root biomass decreased with distance from the center of the plant to 6.5 cm away; however, this pattern did not hold true

TABLE 1. Means and standard deviations (in parentheses) of observed root biomass (g/m^2) by depth, distance, site, and plant functional type. At the shortgrass steppe we sampled 9 plant individuals of the C_4 perennial bunchgrass *Bouteloua gracilis*, and at the northern mixed-grass prairie we sampled 9 plant individuals of either the C_3 perennial bunchgrass *Hesperostipa comata* or *Pascopyrum smithii*. At the sagebrush steppe, we sampled 10 individuals of either the grass *Bouteloua gracilis* or the grass *Hesperostipa comata* and 10 individuals of the shrub *Artemisia tridentata*.

Site	Depth (cm)	Distance (cm)				
		0	6.5	13	19.5	26
Shortgrass steppe	0 to 20	235 ± 46	233 ± 59	207 ± 59	189 ± 56	201 ± 88
<i>B. gracilis</i>	0 to 10	159 ± 34	156 ± 51	133 ± 41	121 ± 48	120 ± 73
	10 to 20	76 ± 24	76 ± 18	74 ± 24	68 ± 18	81 ± 20
Northern mixed grass prairie	0 to 20	277 ± 45	274 ± 67	250 ± 55	240 ± 36	247 ± 36
<i>P. smithii</i> , <i>H. comata</i>	0 to 10	166 ± 38	168 ± 32	152 ± 42	142 ± 23	149 ± 50
	10 to 20	112 ± 28	106 ± 46	98 ± 39	98 ± 26	98 ± 32
Sagebrush steppe, grasses	0 to 20	311 ± 70	246 ± 103	148 ± 43	171 ± 95	149 ± 58
<i>B. gracilis</i> , <i>H. comata</i>	0 to 10	215 ± 64	164 ± 79	72 ± 18	81 ± 31	81 ± 38
	10 to 20	97 ± 37	82 ± 29	77 ± 30	90 ± 77	68 ± 27
Sagebrush steppe	0 to 20	52 ± 20	51 ± 27	53 ± 25	63 ± 25	66 ± 38
<i>A. tridentata</i> , roots ≤ 2 mm	0 to 10	30 ± 10	28 ± 14	27 ± 13	29 ± 14	30 ± 22
	10 to 20	23 ± 9	23 ± 12	26 ± 11	34 ± 10	36 ± 16
Sagebrush steppe	0 to 20	30 ± 50	10 ± 17	5 ± 15	5 ± 9	8 ± 20
<i>A. tridentata</i> , roots > 2 mm	0 to 10	11 ± 19	7 ± 13	5 ± 14	4 ± 6	6 ± 17
	10 to 20	18 ± 31	3 ± 5	0 ± 1	1 ± 3	2 ± 4

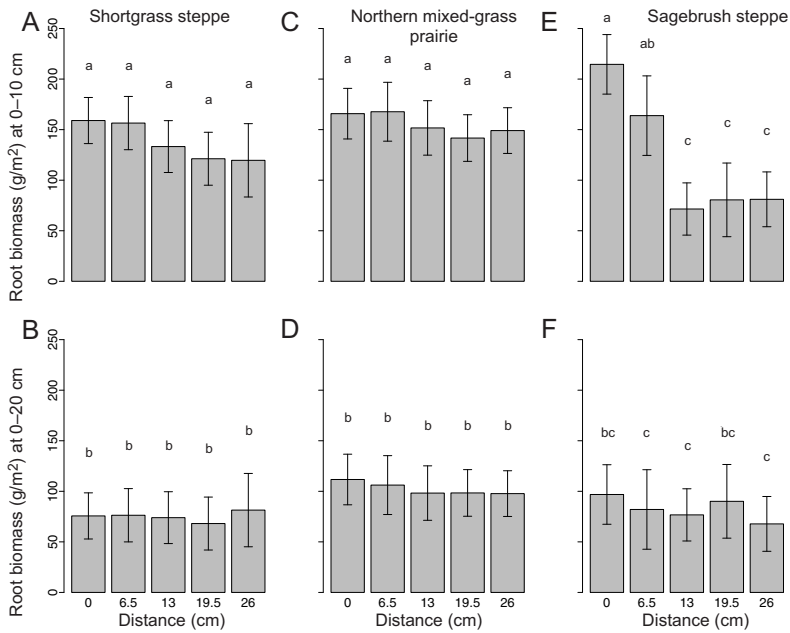


Fig. 2. Mean grass root biomass by distance and by depth (A, C, E: 0–10 cm; B, D, F: 10–20 cm) for individual plants at the shortgrass steppe (A, B), the northern mixed-grass prairie (C, D), and the sagebrush steppe (E, F). The bars represent marginal mean root biomass, and the error bars represent a 95% confidence interval from the linear mixed model for each site with individual plants as random effects. The letters above the bars (a, b, and c) signify statistically significant differences ($P \leq 0.05$) from Tukey’s HSD tests per site (but for depth \times distance).

TABLE 2. Two-way ANOVAs of fixed effects distance and depth for all sites combined (sites and plants as random effects) and for each site separately (plants as random effects). SS = sum of squares; MS = mean squares; Num-df/den-df = numerator/denominator degrees of freedom (Satterthwaite’s method for “all sites”; Kenward-Roger’s method for analyses per site).

		SS	MS	Num-df	Den-df	F	P
All sites	Distance	8719	2180	4	2.2	1.71	0.389
	Depth	184,221	184,221	1	214.7	144.20	<0.001
	Distance \times depth	41,087	10,272	4	214.7	8.04	<0.001
CPER	Distance	3407	852	4	5	0.66	0.648
	Depth	88,828	88,828	1	40	109.37	<0.001
	Distance \times depth	6450	1613	4	40	1.99	0.115
HPGRS	Distance	4404	1101	4	5	0.67	0.638
	Depth	62,599	62,599	1	40	61.31	<0.001
	Distance \times depth	770	193	4	40	0.19	0.943
TBNGG	Distance	46,023	11,506	4	6	6.39	0.024
	Depth	39,244	39,244	1	45	32.72	<0.001
	Distance \times depth	64,981	16,245	4	45	13.54	<0.001

for distances past 6.5 cm or at any distances in the 10–20 cm depth. An important explanation for why we found a spatial distribution that did not meet the smoothly decreasing expectation is illustrated in Fig. 3. The smoothly decreasing expectation is what we might expect for an isolated plant (Hook et al. 1994,

Lee and Lauenroth 1994). We sampled undisturbed plant communities in which we assumed the presence of the maximum number of plants that can be supported by the average resource availability (Coffin and Lauenroth 1991, Sala et al. 1997). Overlapping root systems likely explains why we observed a



Fig. 3. Conceptual drawing of the vertical and horizontal root distribution patterns of grasses in drylands. Roots of adjacent plants overlap to maximize belowground resource use. Scale is in centimeters.

relatively complex vertical and horizontal spatial distribution of roots at each site and as an average across sites (Figs. 1, 2). Further, differences in how bunchgrasses exploit belowground resources compared to rhizomatous grasses may have contributed to the complexity of the spatial distributions of root biomass we observed. Uniformity in root biomass increased with depth and with distances >6.5 cm, suggesting that the shallow soil profile and spaces next to plant individuals are being fully exploited by the roots of the individual and the neighboring plants to maximize belowground resource uptake.

At the sagebrush steppe site, root biomass distribution patterns differed between grasses and the shrub *A. tridentata*. Root biomass was uniform across all depths and distances for *A. tridentata*, while grass root biomass decreased

with both depth and distance. Similar results have been found in the shortgrass steppe (Lee and Lauenroth 1994), the Patagonia steppe (Sala et al. 1989), and the African savanna (Walter 1971). The morphological differences between grass and shrub root systems allow the 2 functional types to utilize water at all depths of the soil profile. For instance, grasses concentrate their roots in the upper 30 cm of soil (Coupland and Johnson 1965, Bartos and Sims 1974) to exploit frequent and short-duration pulses of precipitation (Sala et al. 1992), while shrub root systems are generally deeper to allow them to tap into water in deep soil layers (Walter 1971). We also compared root distribution patterns between the C_3 and C_4 perennial bunchgrasses in the sagebrush steppe site, although we did not detect any significant differences between the 2 root

systems. We likely did not see a significant difference between the root distribution patterns of the 2 grass types because they both rely on belowground resource pools in the top 20 cm of soil (Percy and Ehleringer 1984). The shrub *A. tridentata* produces roots in the deeper soil layers to access deep water stores, while also developing roots in the upper soil layers to optimize belowground resource uptake of summer precipitation as well as the mineral nutrients that are concentrated in surface soils and beneath plants (Burke 1989). Surprisingly, sagebrush root distributions did not match well-known resource island patterns for sagebrush, and a majority of the *A. tridentata* roots sampled in the 0–20 cm depth were thicker than 2 mm.

Our study provides additional knowledge of plant-soil interactions in drylands by describing the root distribution patterns of 3 plant functional types across 3 types of semiarid dryland ecosystems. This study revealed that the spatial distribution of roots varies between grasses and shrubs, but not between C₃ and C₄ perennial bunchgrasses. For each of the ecosystem types, root biomass was concentrated beneath individual plants and in the surface soils, while below the 10-cm depth, there was no influence of distance from the center of a plant. Representation across 3 different types of dryland ecosystems provides strong inference for drylands in this region, a strength of regional studies across large spatial gradients (Burke et al. 1991, Vinton and Burke 1997, Gill et al. 1999, Barrett and Burke 2002, McCulley et al. 2005). However, lack of replication within the ecosystem types in this study limits inferences about the individual ecosystem types. The significance of root distribution patterns to ecosystem processes is an important consideration for understanding environmental and climatic change. Changes in precipitation and its seasonality, subsequent changes in soil water distribution in time and space, and changes in nitrogen deposition will very likely differentially influence plant functional types based on root distribution.

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