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Hydrologic niches explain species coexistence and abundance in a shrub-steppe system

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Abstract

1. Differences in vertical root distributions are often assumed to create resource uptake tradeoffs that determine plant growth and coexistence. Yet, most plant roots are in shallow soils, and data linking root distributions with resource uptake and plant abundances remain elusive.

2. Here we used a tracer experiment to describe the vertical distribution of absorptive roots of dominant species in a shrub-steppe ecosystem. To describe how these different rooting distributions affected water uptake in wet and dry soils across a growing season, we used a soil water movement model. Root traits were then correlated with plant landscape abundances.

3. Deeper root distributions extracted more soil water, had larger unique hydrological niches and were more abundant on the landscape. Though most (> 50%) root biomass and tracer uptake occurred in shallow soils (0-32 cm), the depth of 50% of tracer uptake varied from 11 to 32 cm across species and species with deeper rooting distributions were more abundant on the landscape ($R^2 = 0.95$). The water flow model revealed that deeper rooting distributions should extract more soil water (i.e., a range of 60 to 113 mm of soil water) because shallow roots were often in dry soils. These potential water uptake values were well correlated with species' abundances on the landscape ($R^2 = 0.90$). Finally, each species' rooting distribution demonstrated a depth and time at which it could extract more soil water than any other species, and the size of these unique hydrological niches was also well correlated with species' abundances ($R^2 = 0.89$).

4. *Synthesis*. Our results demonstrate not only a correlation between root distributions and species abundance, but also the mechanism through which differences in rooting

distributions can determine resource uptake and niche partitioning, even when most roots are found in shallow soils.

Introduction

Understanding how species coexist remains a central problem in ecology (Ellner *et al*. 2019). Trade-offs among resource acquisition strategies are one important mechanism of coexistence (Silvertown *et al*. 2015; Letten, *et al*. 2017). For example, there are likely to be trade-offs in resource uptake between plants that invest in shallow roots or deep roots (Sala *et al*. 1997; Fargione and Tilman 2005; Silvertown *et al*. 2015). Walter's two-layer hypothesis suggests that trees can coexist with grasses because deep roots provide trees with unique access to deep soil water (Ward *et al*. 2013). This hypothesis was developed for xeric savannas but has been applied to a wide range of semi-arid systems (Nippert & Knapp 2007; Fort *et al*. 2017; Li *et al*. 2018).

Walter's two-layer hypothesis was developed from observations of differences in vertical root biomass distributions among species (Ward *et al*. 2013). As a result, this hypothesis relies on the assumption that root biomass distributions are well correlated with resource uptake (Walker & Noy-Meier 1982; Germino & Reinhardt 2014). However, there are reasons to expect that root biomass distributions may not be well correlated with water uptake (Gambetta *et al*. 2017; Kulmatiski *et al*. 2017; Jesch *et al*. 2018). Root biomass data are likely to be biased toward shallow roots because large, suberized roots (which do not absorb water) are more abundant in shallow soils and are easier to collect than fine roots and mycorrhizae (Chen 2004). Measurements of fine instead of coarse roots can avoid this problem (Craine *et al*. 2003), but water uptake in fine roots can vary several fold as a function of both aquaporin activity and water availability (e.g., fine roots cannot absorb water from dry soils; Schenk 2008; Gambetta *et al*. 2017).

In addition to potentially poor correlations between root biomass distributions and water uptake, there are other factors that may limit or obscure the relationship between root biomass distributions and plant abundance (Nippert & Holdo 2015). Most plant roots are found in shallow soils (i.e., 0-30 cm) and large overlap in rooting depths has led some researchers to suggest that differentiation of water-use niches is unlikely to explain species coexistence or productivity (Jeltsch et al. 2000; Rodriquez et al. 2007; Mommer *et al.* 2010; Ravenek *et al.* 2014). Further, other physiological (water use efficiency, hydraulic conductivity, and nitrogen-limitation: Schwinning *et al.* 2002) and community-level (disease, herbivory, competition; Staver *et al.* 2011; Mueller *et al.* 2013) factors could either obscure or exaggerate relationships between root water uptake and landscape abundance.

The need for more and better data on patterns of resource uptake by plants in field conditions, as opposed to root biomass distributions, has been recognized as a key gap in understanding plant growth, species coexistence and water and nutrient cycling (Smithwick *et al.* 2014; Silvertown *et al.* 2015; Grant & Dietrich 2017). Quantifying species-level water uptake by depth and time is a necessary step toward understanding whether or not water uptake and water uptake niches are primary determinants of plant abundance and coexistence relative to other factors (Holdo & Nippert 2015; Silvertown et al. 2015; Guderle et al. 2018). Hydrological tracer approaches provide a powerful tool for distinguishing where absorptive roots are present and absent (e.g., not present, dead, or non-absorbing; Schwinning *et al.* 2002; Rothfuss & Javaux 2017). However, because absorptive roots can absorb injected tracers in otherwise dry soils, tracer uptake data are likely to provide information on the location of absorptive roots, but not necessarily how much water moves through those roots (Jackson *et al.* 2000; von Felten *et al.* 2009). The functioning of absorptive roots in dry soils can be inferred using soil water flow

simulation models, and model simulations can be validated using soil moisture observations (Simunek *et al*. 2005; Schenk 2008; Mazzacavallo and Kulmatiski 2015; Zheng et al. 2018).

We hypothesized that plant root distributions determine plant growth and coexistence because tradeoffs in rooting strategies will provide different amounts of water uptake as well as depths or times of unique access to certain soil water pools (i.e., niches). To test this hypothesis, we produced a standardized measurement of the effect of root distributions on water uptake. A hydrologic tracer experiment was used to describe the proportion of absorptive roots by depth for common species in a largely undisturbed native plant community. Next, a soil water movement model (Hydrus 1D) was used to simulate soil water flow from wet and dry soils into absorptive rooting distributions across a growing season. All other plant traits (e.g., leaf area, stomatal conductance) were held constant among model simulations so that only the effects of absorptive rooting distributions on water uptake were considered. To be clear, this approach produced an estimate of the depth, timing and extent of water uptake that a stereotypical plant monoculture (e.g., alfalfa) would be expected to absorb if it had each of the plant root distributions revealed by the tracer uptake experiment. In addition to estimating the total amount of water a rooting distribution could be expected to absorb across a growing season (i.e., total potential water uptake), the simulations also identify any depths or times at which one species' rooting distribution should extract more soil water than any other species' rooting distribution (i.e., a unique hydrological niche). We emphasize that while this approach does not consider the effects of other species traits (e.g., leaf area or stomatal conductance) or interspecific competition for water as it flows through the soil profile, it is based on the rooting distributions of species observed in natural communities. Strong correlations between hydrologic niche size (i.e., total potential water uptake and unique hydrological niche size) and plant landscape abundance would

suggest that hydrologic niches are a primary determinant of plant growth and coexistence. Weak correlations would suggest that other factors such as stomatal conductance, disease or herbivory are more important determinants of plant abundance.

Materials and methods

Research was conducted at the US Sheep Experiment Station, Dubois, ID, USA. Mean annual precipitation is 328 mm and mean annual temperature is 6.1 °C (Adler *et al*. 2012). Plant growth typically occurs between April and July and is limited by water between June and October and by freezing temperatures from October to April. Compared to the long-term mean of 262 mm, the study season was drier than normal with 170 mm of precipitation between October 2012 and July 2013. The five most common species represented 87% of total leaf area and were the focus of this study. These include the shrub, *Artemisia tripartita* Rydberg (13.5 ± 3.0 % season average leaf area; mean ± SE), the taprooted forb *Balsamorhiza sagittata* Hooker ex Nuttall (7.2 ± 2.3 %) and the perennial grasses *Pseudoroegneria spicata* Pursh A. Love (5.0 ± 1.3 %), *Agropyron cristatum* L. Gaertner (4.3 ± 1.3 %), and *Poa secunda* J. Presl (2.0 ± 0.5 %). Ground cover was determined during each of three sampling periods: early- (4 May), mid- (25 May) and late-season (18 June, 2013). More specifically, during each sampling period, vegetation in each of 12 quadrats (1m^2; located 5 m west of randomly-selected injection plots; see below) was clipped and sorted by species. Leaf area from these plots was digitally scanned to determine the leaf area by species. Sagebrush systems cover an extensive area in the western US and have analogs in semi-arid systems around the world (Schlaepfer *et al*. 2012).

Tracer experiment

A grid with 60 points, each separated by 15 m was established. During each of the early-, mid- and late-season samplings, 20 plots (7 m^2 circles) were randomly assigned to a point in the grid. Of the 20 plots, four replicate plots were assigned to each of three shallow depths (10, 20 and 45 cm), three replicate plots were assigned to 75 cm depths, two replicate plots were assigned to 150 cm depths and three plots did not receive injections and were used to collect 'control' samples. Deep plots (75 and 150 cm) received fewer replicates because deep injections are more difficult and tracer uptake from these depths tends to be small with little variability (Kulmatiski et al. 2010; Mazzacavallo & Kulmatiski 2015). In each 7 m^2 plot, a 15 cm by 15 cm grid with 314 'pilot' holes was drilled to the target depth using a hammer drill (TE-60, Hilti North America, Texas, USA). We used custom-made syringes (16 gauge thin-walled hypodermic tubing; Vita Needle Company, MA, USA) to inject 1 ml of 70% ^2H_2O followed by 2 mL of tap water as a rinse into each pilot hole (Kulmatiski *et al*. 2010). While injections likely resulted in a temporary and localized increase in plant available water at the point of injection, they represented roughly 2% of daily reference evapotranspiration in the plot and so were not expected to stimulate plant growth. Injected tracer was expected to be constrained to a roughly 10 cm depth increment by the time of plant sampling (Kulmatiski *et al*. 2010; Mazzacavallo & Kulmatiski 2015; Warren *et al*. 2015; Berry & Kulmatiski 2017).

Two days after injections, two to four samples of non-transpiring tissue from one to several individuals were collected from all common (i.e., > 5% of community composition)

species. We collected samples using clippers that were triple rinsed with tap water between each sample. Clipped samples were immediately sealed with paraffin wax film in 19 mm, medium-walled borosilicate sample tubes (Corning Inc., NY, USA) and placed on ice until they were moved to a freezer later in the day. Water from plant tissues was extracted by cryogenic distillation within two weeks (Kulmatiski et al. 2010). We analyzed extracted water samples for hydrogen and oxygen isotopes on a wavelength scanned cavity ring-down spectrometer (Picarro L-2120*i;* Picarro Instruments, CA, USA). Isotope values [in delta notation (δ)] were converted to deuterium excess values (δ_e) to control for natural isotope enrichment caused by evaporation as follows: $\delta_e = \delta^2H - [(8 * \delta^{18}O) + 10]$(Kulmatiski *et al*. 2010, Mazzacavallo & Kulmatiski 2015).

Soil samples

We collected soil grab samples to measure soil moisture and soil texture. Soil moisture data were used to initialize and validate soil water movement model (Hydrus 1D) simulations. Gravimetric soil water was measured in roughly 300 g grab samples from 20, 40, 60, and 80 cm depths in three randomly selected plots during the early-, mid- and late-season samplings as well as from a pre-season (April) sampling. We took additional mid-season samples from 150 cm. Soil texture was measured from these grab samples using the Bouyoucos hydrometer method.

We collected soil cores to measure root biomass and soil bulk density. Root biomass data were used to provide a comparison to previous studies and as comparison to tracer uptake profiles. Soil cores (5-cm wide, 75-cm deep) were taken from five randomly selected plots during each sampling period. Sections (15 cm) were cut from the cores to determine root

biomass at 10, 20, 40 and 75 cm depths. Additionally, during the mid-season sampling, soil cores were extracted from 150 cm from three walls in each of two soil pits. Collected soil samples were dried to constant weight (70˚ C), passed through a 2 mm sieve and all roots were collected by hand, weighed and reported as grams of dry roots kg^{-1} of fine (< 2 mm) dry soil. These cores were also used to estimate soil bulk density, which was used to convert gravimetric to volumetric soil water content and to estimate hydrological parameters in the soil water movement model.

Data analyses

Standardizing root distributions: To parameterize Hydrus 1D and to allow comparisons among root biomass and tracer uptake profiles from different species, all root biomass and tracer uptake values were standardized as proportional values by depth (0-188 cm; Kulmatiski *et al*. 2010, Mazzacavallo & Kulmatiski 2015). For example, tracer uptake values were converted to proportional tracer uptake as a function of soil depth as follows: $\frac{S_n - C}{\sum_{n=1}^{j}(\tilde{S}_n - C)}$, where S_n is the mean δ_e value of samples from injection depth n in a plot (*e.g.*, *P. secunda* samples at 5 cm depth in the first replicate plot), $\tilde{S}_n$ were the mean δ_e value across plots for a target depth 1 to j (*i.e.*, 10 - 150 cm). C were δ_e values of control samples. This proportion was calculated for each plant species in a plot, producing one replicate proportional uptake value for each species in each field plot.

Testing for differences among tracer uptake profiles: To test for differences among tracer uptake profiles, we fit generalized additive mixed models (GAMMs). These models approximated the continuous soil profiles of tracer uptake with depth using a beta likelihood with a logit link for

the linear predictor (soil depth; Kulmatiski *et al*. 2017). We let the GAMMs have four "knots" to allow for a smooth interpolation between the five sample depths. We fit subsets of the mixed models with either all root distributions together or all root distributions separate. All models were fit in R (R Core Research Team 2004) using the gam function from the mgcv package (Wood 2004). We used Akaike's Information Criterion (AIC) to rank models in terms of their support by the data. The model with the lowest AIC is the model that best balances goodness-of-fit against parsimony.

Water uptake: The purpose of the water uptake modeling was to translate observed differences in tracer uptake distributions into simulated differences in the depth, time, and amount of each species' water uptake. We used Hydrus 1D, a numerical model that simulates interception, infiltration, evaporation, water flow through the soil matrix, and water uptake from a root distribution (Simunek et al. 2005). Model simulations were first performed using the observed root biomass distribution. This was a single distribution because it was not possible to distinguish root biomass of different species. Hydrus 1D normalizes root distributions in calculations, so the use of normalized root distributions as an input parameter does not affect model simulations. Hydrus 1D was initialized with observed soil moisture data from April 2013. Evapotranspiration was estimated using the Hargreaves equation with radiation estimated for the site and hourly temperature data collected 1 km from the study site. Hourly precipitation data were also collected 1 km from the study site. Model parameter definitions and climate input data are provided in detail Tables S1 to S5; here we provide a brief description. Hydrus 1D is based on the van Genuchten-Mualem water flow model. Hydraulic parameters within this submodel (e.g., saturated hydraulic conductivity, saturated and residual water content and tortuosity) were

derived from soil texture and bulk density data observed at the study site and the neural network

prediction option in Hydrus. The root water uptake submodel used the 'Feddes' model

parameterized for alfalfa. Plants were not allowed to compensate for low soil water availability

(i.e., the critical stress index value = 1.0). Plant height was assumed to be 60 cm and leaf area

was calculated by Hydrus from plant height associated with an alfalfa crop. Model predictions of

soil moisture were compared to observed volumetric soil data (Fig. S1). This simulation, using

the root biomass distribution, provided reasonable estimates of soil moisture across the growing

season, but underestimated deep water uptake (Fig. S1). All parameters used for the root biomass

simulation were then used for remaining simulations (i.e., for each species' rooting distribution).

A separate simulation approach using several different parameters (i.e., the Penman-Monteith

model of evapotranspiration, observed instead of assumed leaf area index and compensated root

water uptake) produced qualitatively similar results to those reported below (Fig. S2), but was

not used because it underestimated evapotranspiration relative to observed soil moisture.

Standard niche overlap index: To allow a comparison with other niche partitioning studies, a

standard measure of niche overlap among the five species was calculated for the proportion of

tracer uptake using EcoSim ver. 7 (Entsminger 2014). Pianka's standardized overlap value is

defined as: $O_{jk} = \frac{\sum e_{ij}e_{ik}}{\sqrt{\sum e_{ij}^2 e_{ik}^2}}$, where O_{jk} is a measure of overlap between species j and k, the

electivity index $e_{ij} = p_{ij}/R_j$, where p_{ij} is the proportion that resource i is of the total resource used

by species j, and Rj is a measure of the availability of resource state j. This unitless measure

ranges from 0 to 1, where 0 indicates complete niche separation. To determine if observed

overlap values were likely to result by chance, the species utilization matrices were compared to

predictions from a randomized null model. Randomization algorithm three in EcoSim ver. 7, in

which niche breadth is retained and zero states are reshuffled, was used because niche breadth

did appear to differ by species, zero uptake did not appear to be a fixed species trait for any depth

(*i.e.*, all plants accessed some tracer from every depth sampled during one time period or

another), and this approach is usually superior in detecting non-random overlap (Winemiller &

Pianka 1990). Niche overlap was calculated for the three sampling periods using both tracer

uptake and water uptake values.

Hydrological niches: We defined hydrological niche size two ways. First, we defined the total

hydrological niche as the total sum of simulated water uptake by each rooting distribution, across

all depths and sampling periods (i.e., potential water uptake). Second, we defined the unique

hydrological niche as the sum of soil water uptake that was unique to a rooting distribution:

$\sum_{d=1}^{188}\{if [U_{id} - Max (U_{ad}, U_{bd}, ...)] > 0\}$, where U_{id} is water uptake in mm by species *i* at depth

d, for species *a* through *i* and soil depths from 1 to 188 cm. To describe the relationships between

species' abundances and these niche measurements, we regressed abundance against either

potential water uptake or unique hydrological niche size.

Results

Total root biomass decreased from a maximum of 2.7 g kg^{-1} at the surface to a minimum of 0.04

g kg^{-1} at 150 cm. When converted to the proportion of root biomass per cm of soil depth, root

biomass decreased from 2.7% cm^{-1} to 0.04% cm^{-1} from the surface to 150 cm (Fig. 1a). The

cumulative proportion of root biomass with depth indicated that 50% of total root biomass occurred in the top 24 cm of soil.
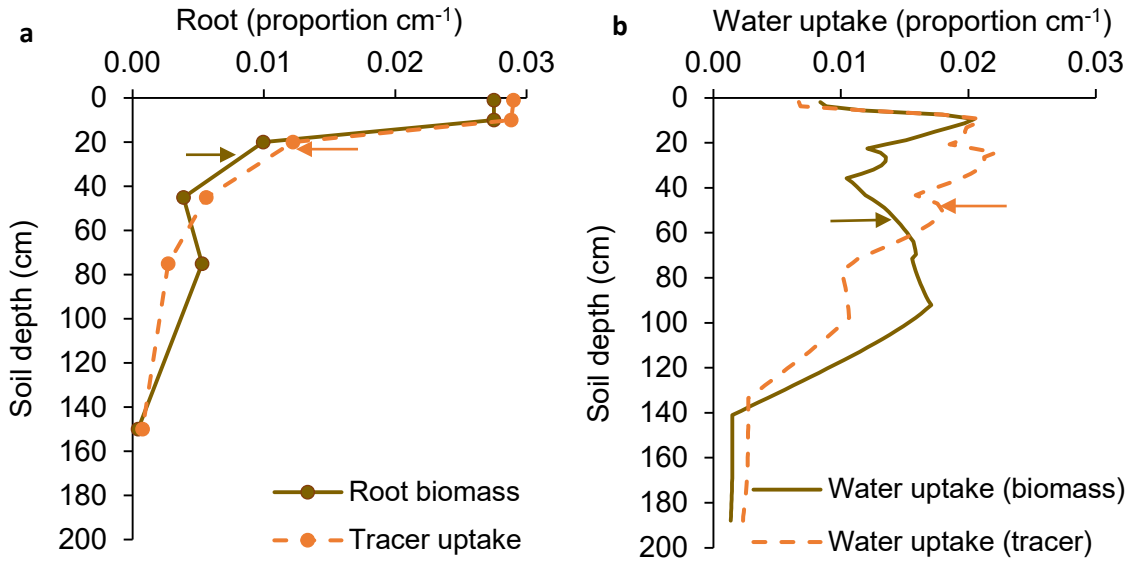
Fig. 1*. (a) Root biomass and tracer uptake by depth and (b) water uptake simulated using root biomass or tracer uptake by depth in the Hydrus soil water movement model. The depth at which the cumulative proportion of the indicated value reaches 50% is indicated with a color-coded arrow. All values reported as a proportion of total (summed across depths) per cm of depth.*

During each sampling period, 52 to 79 plant water samples were taken from each of the five dominant species, with the exception that *P. secunda* was not sampled in the late-season because it had senesced for the year. This sampling design resulted in 815 plant isotope samples for the season. When weighted by species abundance and summed across the growing season, patterns of tracer uptake were similar to patterns of root biomass: 50% of tracer uptake (across species) occurred in the top 21 cm (Fig. 1a).

Total water uptake simulated by Hydrus was deeper than root biomass or tracer uptake: 50% of Hydrus-simulated water uptake occurred at 66 and 68 cm, when parameterized with root biomass or tracer data, respectively (Fig. 1b). Root biomass-informed and tracer-informed

Hydrus model simulations of soil moisture were both reasonably well correlated with observed soil moisture by depth values (root mean squared deviation = 0.054 and 0.051 cm^3 cm^{-3}, respectively), though deep soil water uptake (i.e., 75 to 150 cm) was underestimated by both (Fig. S1).

Analyses of tracer uptake by depth at the species-level over time revealed important variation that was hidden in the annual-level data (Fig. 2). When GAMMs were used to approximate the continuous soil profiles of tracer uptake by species, there was no difference between models that separated uptake by all species or combined all species together for the early-season data (AIC = -1347 vs. -1347; Fig. 2a), but the 'all separate' model outperformed the 'all together' model for mid- (AIC = -1415 vs. -1423; Fig. 2b), and late- (AIC = -1046 vs. -1069; Fig. 2c) season data.

At the species level, across the growing season, the depth of 50% of tracer uptake was 11 cm for *P. secunda,* 13 cm for *A. cristatum,* 16 cm for *P. spicata,* 24 cm for *B. sagittata* and 32 cm for *A. tridentata*. There was a strong correlation between the depth of 50% of tracer uptake and plant landscape abundance (Fig. 3a).

Across the growing season, the depth of 50% of simulated water uptake differed for each species' rooting distribution: 24 cm for *P. secunda,* 43 cm for *A. cristatum,* 50 cm for *P. spicata,* 62 cm for *B. sagittata* and 72 cm for *A. tridentata*. There was a strong non-linear correlation between the depth of 50% of tracer uptake and plant landscape abundance (Fig. 3b).
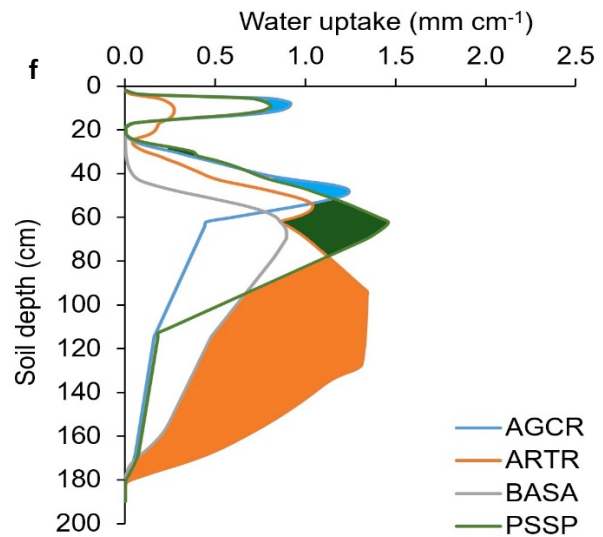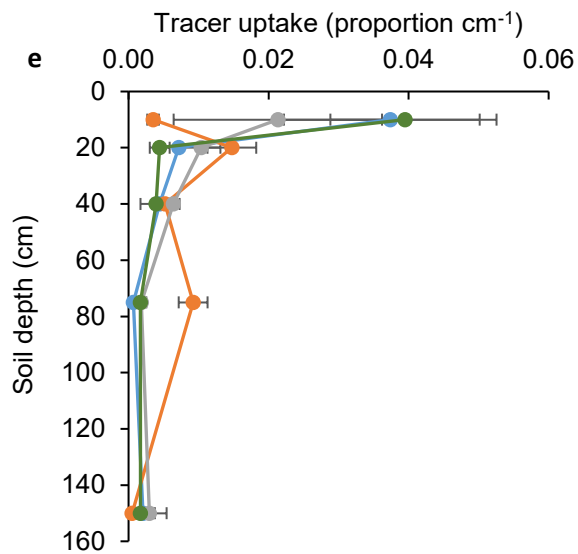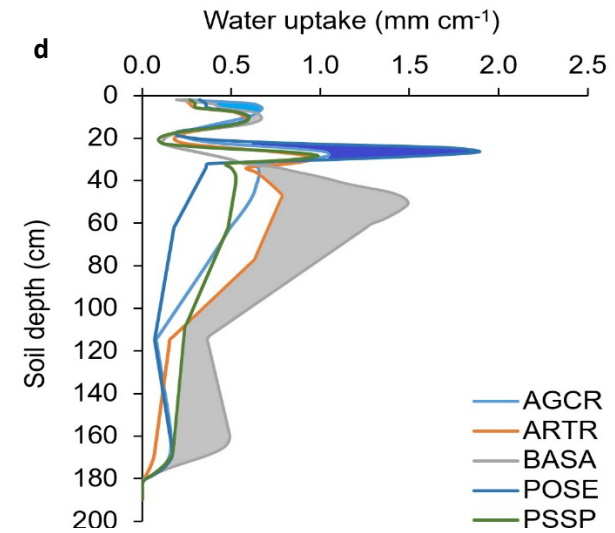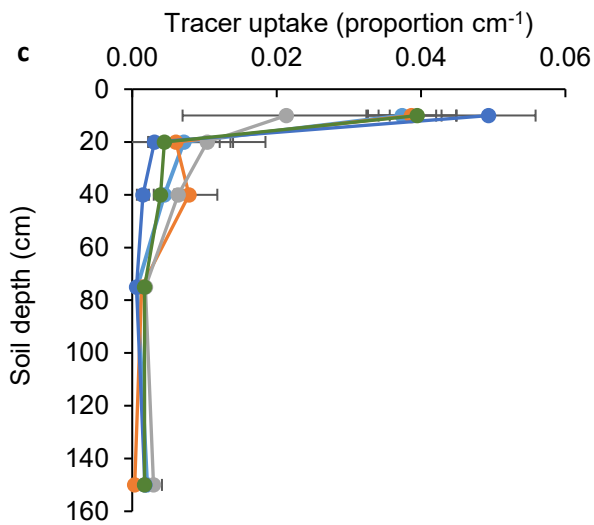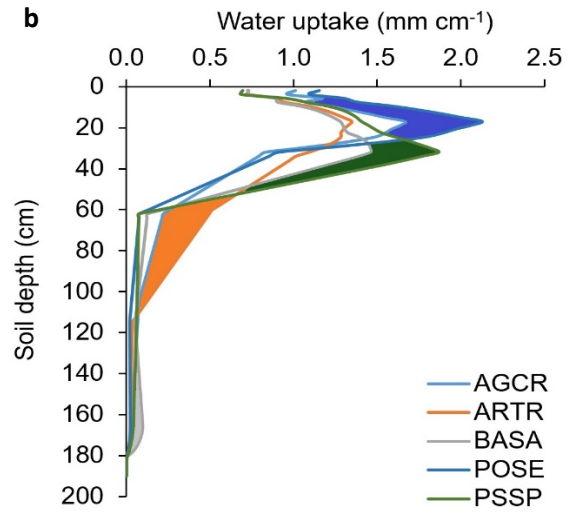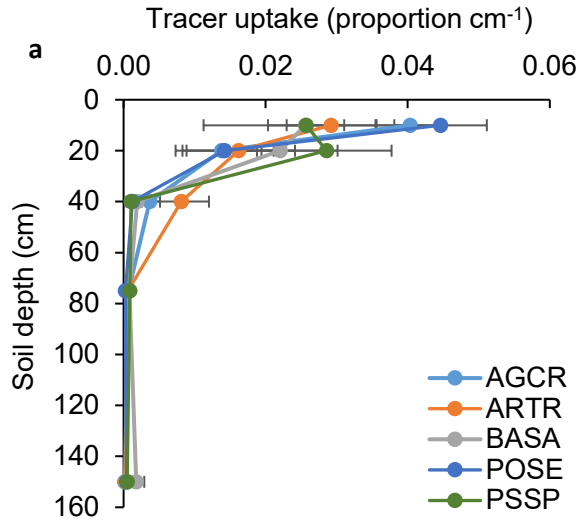
Fig. 2. *Species-level tracer uptake (a, c, e) and simulated water uptake (b, d, f) by depth during early- (a, b), mid- (c, d) and late- (e, f) season samplings. The sum of water uptake across the profile (0-188 cm) indicates the total amount a soil water a root profile absorbed in simulations. The color-filled areas in the water-use panels show the amount of water one species was able to extract in excess of any other species (i.e., unique hydrological niches).*

Within sampling periods, the 50% of tracer uptake value was deepest for *B. sagittata* in the early- (21 cm) and mid- (32 cm) season and for *A. tripartita* at the end of the season (64 cm; Fig. 2). The 50% of simulated water uptake value was deepest for *A. tripartita's* rooting distribution in the early- (32 cm) and late-season (102 cm) and for *B. sagittata's* rooting distribution in the mid-season (69 cm).

The sum of water a rooting distribution could extract (i.e., potential water uptake) differed as a function of each species' tracer uptake distribution: *A. tripartita* (11.3 cm) > *B. sagittata* (10.7 cm) > *P. spicata* (10.0 cm) > *A. cristatum* (9.0 cm) > *P. secunda* (6.1 cm; Fig. 2). There was a strong, non-linear relationship between species cover on the landscape and potential water uptake (Fig. 3c).

Although differences in tracer uptake profiles were detected with GAMMs, all species generally had large tracer uptake near the surface, which resulted in very large niche overlap values calculated using the Pianka index (0.83, 0.89, 0.86 for the early-, mid-, and late-season, respectively). These observed niche overlap values were greater than would be expected by chance ($P < 0.01$) for all three sampling periods. Niche overlap was also large for water uptake in each of the three sampling periods (0.95, 0.87, 0.83, respectively) and again, greater than would be expected by chance in the early- and late- season ($P = 0.00$ and 0.01, respectively), but not for the mid-season ($P = 0.12$).
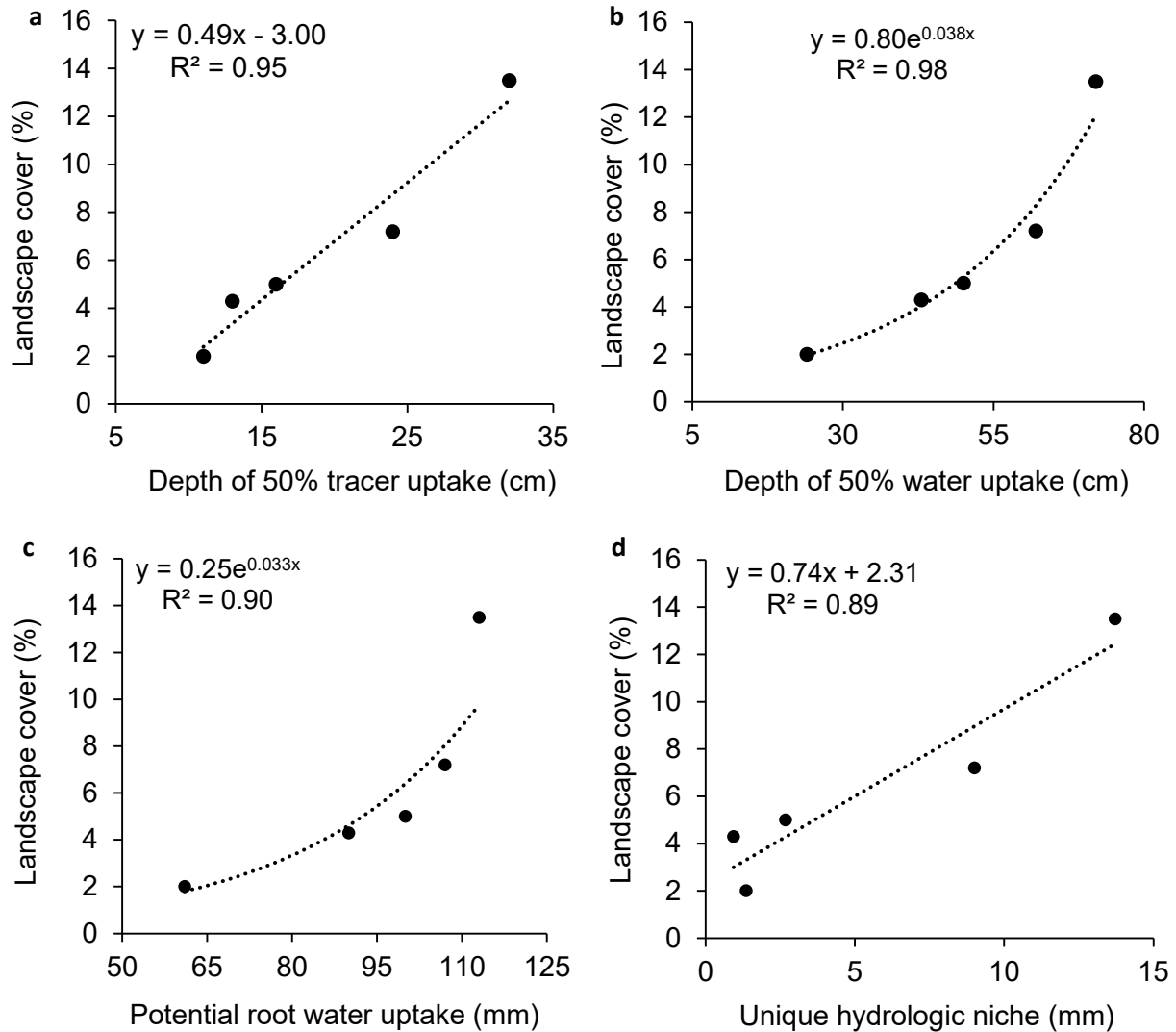
Fig. 3. *Plant abundance (Landscape cover) was positively correlated with hydrologic traits associated with plant rooting distributions. The depth at which 50% of tracer uptake occurred (a), the depth at which 50% of simulated water uptake occurred (b), the total amount of water a rooting distribution was estimated to be able to extract (potential root water uptake; c), and the amount of water that each species could extract in excess of any other species (unique hydrologic niche; d) were all well correlated with plant landscape abundance.*

Despite large niche overlap values calculated with the Pianka index, each species was able to extract more water from some soil depths at some times than all other species, indicating

that each species had a unique hydrological niche (Fig. 2b, d, and f). Unique hydrological niche

size varied among species: *A. tripartita* (13.7 mm) > *B. sagittata* (9.0 mm) > *P. spicata* (2.7 mm)

> *P. secunda* (1.4 mm) > *A. cristatum* (0.9 mm). There was a strong correlation between unique

niche size and species landscape abundance (Fig. 3d).

Discussion

Niche partitioning has long been assumed to allow species coexistence (Ward et al. 2013;

Silvertown et al. 2015), but empirical data demonstrating the mechanisms and consequences of

niche partitioning have remained elusive (Adler et al. 2010; Guderle et al. 2018; Ellner et al.

2019). Here, we used depth-specific tracer uptake data in a soil water movement model to

provide an unusually clear example of how niche partitioning can determine plant growth and

coexistence. Similar to root biomass data from around the world, we found that most tracer

uptake occurred in shallow (0-30 cm) soils (Jackson *et al*. 1996). As a result, tracer uptake

distributions of different species appeared quite similar and produced large niche overlap values

(as measured by a standard index). However, small differences in deep tracer uptake produced

large differences in the depth of 50% of tracer uptake (11 to 32 cm) and the depth of 50% of

simulated water uptake (24 to 72 cm). These differences appeared to be biologically important

because they were strongly and positively correlated with plant landscape abundance ($R^2 > 0.89$).

In other words, the more water a rooting distribution was estimated to extract, the more abundant

the species with that distribution was on the landscape. Perhaps more importantly, we also found

that trade-offs among rooting strategies provided each species with unique hydrological niches, and the sizes of these niches was also strongly correlated with species landscape abundance (R^2 = 0.89). In short, regardless of any other factors, we demonstrated that deeper rooting distributions accessed 1) more soil water and 2) more unique soil water and were associated with the most abundant plants on the landscape. We suggest that potential water uptake imposes a limit on plant growth in monoculture (or very weak competition) and unique hydrologic niche size imposes a limit on plant growth in competition.

Describing hydrological niches

Tracer uptake patterns (Fig. 2) and Pianka's index suggested that species had very similar water-use niches (i.e., niche overlap was large). More specifically, all species relied on shallow water but also accessed some deep water (Schenk 2008). With one exception, 50% of tracer uptake for each species in each month of the study occurred in the top 35 cm. At the same time, all species absorbed some deep water (i.e., 75 -150 cm). The results appear typical for many semi-arid systems. Around the world, most plants roots are found in the top 30 cm (Jackson *et al*. 1996; Rodriguez et al. 2007) even though many plants including annuals and saplings can produce roots below 100 cm in a growing season (Peek *et al*. 2005; Kulmatiski & Beard 2013).

Although niche overlap values were large, small differences in deep (i.e., 35 – 150 cm) root activity resulted in large differences in potential water uptake because deep soils held more water. For example, in the middle of the growing season, 50% of *P. secunda* tracer uptake occurred in the top 10 cm while 50% of *B. sagittata* tracer uptake occurred in the top 32 cm. A

deeper rooting distribution afforded *B. sagittata* nearly three times as much soil water as *P. secunda* largely because very shallow soils (0-10 cm) provided little plant available water in the middle of the growing season.

In addition to growing deep roots, the dominant species, *A. tripartita,* also demonstrated a dynamic rooting pattern that 'followed' soil water availability (Guderle et al. 2018). In the middle of the growing season, 50% of *A. tripartita* tracer uptake occurred in the top 13 cm of soil. A few weeks later, as shallow soils dried, 50% of *A. tripartita* tracer uptake occurred in the top 64 cm of soil. Dynamic foraging may be a common and important strategy for woody relative to herbaceous plant roots (Dodd *et al*. 1998; Ogle & Reynolds 2004; Wang *et al*. 2017; Dubbert and Werner 2019).

Each of the dominant species also demonstrated a unique hydrological niche. For example, while *P. secunda* had the smallest potential root water uptake and *A. tripartita* had the largest potential root water uptake, *P. secunda* was estimated to extract 50% more water from the top 20 cm of soil than *A. tripartita* early in the season (Fig. 2b). Similarly, *B. sagittata* was estimated to extract 71% more water from 40-100 cm depths than *A. tripartita* in the middle of the season. These unique hydrological niches afforded species between 1 and 14 mm of soil water that was not available to any other common species. In other words, our results suggested that each species was able to extract some soil water regardless of the presence of competitors and as a result, each species should be able to grow even when rare (Adler et al. 2010; Ellner et al. 2019).

Hydrological niches and species abundances

Rooting distributions that could extract more water were more abundant on the landscape. Post-hoc analyses suggested that these results were robust. In addition to correlations with plant ground cover, plant biomass was also well correlated with potential water uptake ($R^2 = 0.49$; Fig. S3). Further, when a separate Hydrus 1D simulation was performed using climate data from the more typical (i.e., wetter) 2014 growing season, potential water uptake and unique hydrological niche size were observed to vary among species and were again well correlated with plant landscape cover ($R^2 = 0.69$; Fig. S4).

Our results provide only correlations between niche size and plant abundance, but the physiological mechanism that relates water uptake to plant growth is well understood and therefore can be used to test whether or not our water-use estimates can predict landscape cover. CO_2 fixation is tightly correlated with transpiration because water loss and CO_2 uptake occur simultaneously through stomata. Assuming a rain-use efficiency of 0.4 g biomass m^{-2} mm^{-1} of precipitation (Huxman *et al*. 2004; Knapp *et al*. 2017), and a specific leaf area of 2.5% g^{-1} biomass (Shipley 2006), total potential water uptake values of 6 to 11 cm can be expected to produce 60 to 110% leaf area and unique hydrological niches of 1 to 14 mm would produce ca. 1 to 14% leaf area. The rain-use efficiency value is likely to underestimate ground cover from our root water uptake values because rain-use efficiency includes water that is lost to evaporation. At the same time, the specific leaf area value is likely to overestimate ground cover because it does not include biomass allocation to stems or roots. These estimates, therefore, are certainly very imprecise, but they demonstrate that our estimates of potential water uptake and unique hydrological niche size certainly are in the correct order of magnitude to estimate observed total plant cover (39% ground cover) and subdominant species plant cover (1 to 9% ground cover). In

short, our estimates of potential water uptake and unique hydrological niche size were not only correlated with landscape abundance but were also reasonable from a physiological perspective.

Differences in potential water uptake provided a reasonable estimate of how much water each rooting distribution could be expected to absorb, and therefore, how much that plant could be expected to grow in monoculture. Total potential water uptake, however, cannot be expected to explain species coexistence because in a water-limited environment, the species that can extract the most soil water would be expected to outcompete other species. In contrast, unique hydrological niches provide sub-dominant species a water resource that can allow growth even when that species is rare or competitively inferior (Silvertown et al. 2015).

Despite strong correlations with plant abundance, there are several factors that were likely to affect our niche size estimates. We defined unique hydrological niches as the water that a species can extract in excess of all other species even though plants are most likely to be competing with the dominant species (Tuck *et al*. 2018). When unique hydrological niches were calculated as the amount of water each species could extract in excess of the dominant competitor (*A*. *tripartita*), unique hydrological niche sizes were larger, but maintained the same rank-order (data not shown, but can be derived from Fig. 2). Future, spatially-explicit modeling efforts should be able to account for these species-specific niche interactions.

There are also many plant growth traits that were not considered in this study that may affect estimates of water uptake. For example, trade-offs between fast water uptake, shallow roots and drought avoidance may allow grasses to coexist with more deeply-rooted species and change the relationship between water uptake and landscape abundance (Chesson *et al*. 2004; Moreno-Gomez *et al*. 2012; Fort *et al*. 2017). It is interesting to note that the two least abundant species studied were shallow-rooted grasses that both realized the greatest ground cover at the

beginning of the season. In contrast, the three remaining, more deeply-rooted and dominant species increased cover throughout the growing season. Other plant traits such as photosynthetic pathway, evaporative demand, carbon storage legacy effects, specific leaf area, herbivory, disease and fire can be expected to change the relationship between water uptake and plant abundance (Schwinning *et al* 2002; Staver *et al*. 2011). None of these factors were considered in this study. These other factors are likely to change the shape of the relationship between water use niches and plant abundance, and they are likely to be more important in some ecosystems than in others, but the strong correlation between our estimates of niche size and plant landscape abundance suggest that these other factors are of secondary importance in this system. It is important to note that this is a water-limited system. Similarly strong correlations between water use niches and plant abundance may not be apparent in other systems that are limited by, for example, temperature, fire, or nitrogen availability.

Our results are from five species at one site during a relatively dry growing season, but these species represented 87% of total plant cover and are common throughout the western USA. As a result, we expect that our results provide valuable insight for our study site and that our inference extends to a relatively large area. More generally, our results provide a resolution for the conflicting hypotheses that rooting distributions can explain species coexistence (Ward *et al*. 2013; Silvertown *et al*. 2015) and that niche overlap in rooting distributions is too large to allow coexistence (Hipondoka *et al*. 2003; Rodriguez et al. 2007; Mommer *et al*. 2010; Hoekstra *et al*. 2015; Jesch *et al*. 2018). Studies describing root biomass or tracer uptake without considering water flow have suggested that niche partitioning is too weak to explain species coexistence and diversity-productivity relationships (Mommer *et al*. 2010; vonFelton *et al*. 2012; Ravenek *et al*. 2014). However, after over 100 years of inferring root function from root biomass distributions,

our results provide a clear example of how tradeoffs associated with the depth and timing of root water uptake can determine species coexistence even when differences in root biomass distributions are small.

Acknowledgements

Author Contributions

AK conceived and executed the research, performed analyses and wrote the manuscript. PBA executed the research and wrote the manuscript. KMF performed isotope analyses and data management and wrote the manuscript.

Data availability

Data will be archived at the USU Digital Commons (https://digitalcommons.usu.edu/) where it will receive a DOI.

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Supplementary information

Table S1. Hydrus parameter definition

Table S2. Soil moisture data

Table S3. Root biomass and tracer uptake distributions

Table S4. Soil texture and bulk density

Table S5. Climate input data for Hydrus simulations.

Fig. S1. Observed and predicted soil moisture across the 2013 growing season at a) 10 cm, b) 20 cm, c) 45 cm, d) 75 cm, Dubois, ID, USA.

Fig. S2. An alternative simulation of water flow into roots in which a dual-porosity water flow model, critical stress index of 0.8, and leaf area index of 1.5 produced qualitatively similar results to those reported in Fig. 2.

Fig. S3. Plant biomass observed on the landscape in 2013 vs. total water uptake estimated for dominant species estimated using climate data from 2014, Dubois, ID, USA.

Fig. S4. Plant cover observed on the landscape in 2013 vs. total water uptake by species estimated using climate data from the 2014 growing season, Dubois, ID, USA.