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Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems

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Abstract Explanations for the occurrence of deep-rooted plants in arid and semi-arid ecosystems have traditionally emphasized the uptake of relatively deep soil water. However, recent hydrologic data from arid systems show that soil water potentials at depth fluctuate little over long time periods, suggesting this water may be rarely utilized or replenished. In this study, we examine the distributions of root biomass, soil moisture and nutrient contents to 10-m depths at five semi-arid and arid sites across southwestern USA. We couple these depth distributions with strontium (Sr) isotope data that show deep (>1 m) nutrient uptake is prevalent at four of the five sites. At all of the sites, the highest abundance of one or more of the measured nutrients occurred deep within the soil profile, particularly for P, Ca²⁺ and Mg²⁺. Phosphate contents were greater at depth than in the top meter of soil at three of five sites. At Jornada, for example, the 2–3 m depth increment had twice the extractable P as the top meter of soil, despite the highest concentrations of P occurring at

the surface. The prevalence of such deep resource pools, and our evidence for cation uptake from them, suggest nutrient uptake as a complementary explanation for the occurrence of deep-rooted plants in arid and semi-arid systems. We propose that hydraulic redistribution of shallow surface water to deep soil layers by roots may be the mechanism through which deep soil nutrients are mobilized and taken up by plants.

Keywords Cation uptake · Deep roots · Hydraulic redistribution · Nutrient uplift · Strontium isotopes

Introduction

Deep-rooted (>1 m) plants are ubiquitous in arid ecosystems (Weaver and Albertson 1943; Canadell et al. 1996; Schenk and Jackson 2002). Such deep-rooted individuals are thought to incur advantages over shallow-rooted plants by tapping into greater or more temporally reliable sources of water at depth (Noy-Meir 1973). According to this hypothesis, the construction and maintenance costs of deep roots are offset by increased photosynthesis and enhanced plant water status and survival during drought. Supporting this hypothesis, numerous studies in arid and semi-arid regions of USA, Chile, Africa, and Australia have shown that deep-rooted individuals are able to use relatively deep water stores during the growing season (Burgess et al. 1998; Caldwell et al. 1998; Jackson et al. 1999; Ludwig et al. 2003; Mooney et al. 1980).

Recent work suggests that hydraulic redistribution and soil water recharge represent a second possible water-relations benefit of deep roots in arid ecosystems (Burgess et al. 1998; Jackson et al. 2000; Richards and Caldwell 1987; Ryel et al. 2003; Smith et al. 1999). Such studies show that water moves passively through plant roots between deep and shallow soil layers along water potential gradients. This mechanism can result in water moving upwards or downwards within the soil profile, depending on environmental conditions. For example, when plant

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roots are in contact with groundwater, water can move upwards through roots into shallow, drier soil layers when plant water demand is low (Dawson 1993). In contrast, in arid ecosystems where deep roots exist within dry vadose zones, episodic rainfall events that wet the shallow layers of soil can result in a downward redistribution of moisture to deeper, drier soil layers (Burgess et al. 2001). Although hydraulic redistribution has been shown to occur in more than 50 species globally, the seasonal and stand-level benefits of the redistributed water are less clear (Hultine et al. 2003; Moreira et al. 2003). In fact, recent simulation results of an arid shrubland in Utah suggest that such water accounted for only a 3.5% increase in stand-level transpiration over a 100-day drying cycle (Ryel et al. 2002). Thus, while deep roots do appear to play a functional role in moving/storing water vertically within the soil profile, the plant carbon gain of this function may be small.

Long-term hydrologic data from arid ecosystems raise several unresolved questions about deep root functioning. Long-term (3–23 years) soil moisture and water potential datasets from Idaho, Texas, and Nevada suggest that soil moisture contents below 1–2 m depth show little variation (Andraski 1997; Scanlon et al. 1999; Seyfried et al. 2001). These results also suggest that deep soil water recharge (>1 m) rarely occurs in these systems. Current hydrological models also support observations that, in the absence of lateral or macropore flow, deep soil recharge is rare (Scanlon 1991; Seyfried et al. 2005; Walvoord et al. 2002). The temporally consistent soil moisture contents measured in boreholes suggest that if deep roots are extracting water during dry periods, the amount of water extracted may be too small to be detected in the borehole moisture measurements.

If deep-soil water recharge is rare and water uptake at depth is small, why do plants grow roots to such depths? In addition to the likely importance of macropore flow, one rarely explored mechanism is the coupling of water and nutrient uptake. Evidence such as high carbonic acid concentrations in forests (Richter and Markewitz 1995) and the presence of macro- and micro-fauna at depth in deserts (Freckman and Virginia 1989; Silva et al. 1989) suggest that processes important for nutrient availability occur deep in the soil profile, including decomposition and weathering (Richter and Markewitz 1995; Canadell et al. 1996; Jackson et al. 2000). Moreover, plants in arid and semi-arid systems have been shown to respond morphologically and physiologically to areas of high nutrient

availability within their rooting zones (Eissenstat and Caldwell 1988; Jackson et al. 1990). However, direct evidence of deep root nutrient uptake in arid and semi-arid systems is lacking. Here, we present deep root and soil resource profiles (nutrients and water) to 10 m depth for five sites in southwestern USA. We couple these nutrient profiles showing considerable cation and P availability at depth with evidence of cation uptake from 1 to 4 m depth using Strontium (Sr) isotopes. Based on the evidence presented, we suggest that deep roots play an important role in nutrient capture. We propose that the movement of small amounts of water from the soil surface to deeper layers through hydraulic redistribution may be one mechanism by which deeper nutrients are mobilized in arid and semi-arid ecosystems.

Materials and methods

Site descriptions

Five field sites were located along a ~600 mm mean annual precipitation (MAP) gradient in southwestern USA (Table 1). Each of the five sites contained a paired native grassland and adjacent former grassland invaded by woody vegetation 30–100 years ago (Jackson et al. 2002). Soil cores were taken from adjacent communities at each site. The 200,000-ha Waggoner Ranch is the long-term research site for the Vernon, Tex. Experimental Research Station of Texas A&M University. The Riesel site has been maintained by the USDA-ARS for >50 years. The three other sites, Jornada, Sevilleta, and the Central Plains Experimental Range (CPER), are part of the international Long Term Ecological Research (LTER) network. Based on aerial photographs and additional records, the youngest age of the woody stands was 30–40 years (Sevilleta and Vernon).

Pre-settlement vegetation consisted of desert grassland at Jornada and Sevilleta, shortgrass steppe at CPER, southern mixed grass prairie at Vernon, and tallgrass prairie at Riesel (see Table 1). Over the past century, woody plant abundance has increased across this region, most likely because of the combined effects of domestic livestock grazing, fire suppression, and climate change (Van Auken 2000). See Jackson et al. (2002) for further details about the sites, vegetation history, and experimental design.

Table 1 Site characteristics. The three driest sites (Jornada, Sevilleta, and CPER) are part of the international LTER network. The Vernon site is located on the 200,000 ha Waggoner ranch near Vernon, Texas and is part of the Texas Agricultural Experiment

Station network associated with Texas A&M University. Riesel is a long-term blackland prairie research station in Riesel, Texas operated by the United States Department of Agriculture's Agricultural Research Service

Site	MAP (mm)	Soil taxonomy	Dominant grass species	Dominant woody species
1. Jornada, N.M.	230	Calcic Petrocalcid	<i>Bouteloua eriopoda</i>	<i>Prosopis glandulosa</i>
2. Sevilleta, N.M.	277	Typic Calciargid	<i>Bouteloua eriopoda</i>	<i>Larrea tridentata</i>
3. CPER, Colo.	322	Fluventic Ustochrept	<i>Bouteloua gracilis</i>	<i>Atriplex canescens</i>
4. Vernon, Tex.	660	Vertic Natrustoll	<i>Stipa</i> spp.	<i>Prosopis glandulosa</i>
5. Riesel, Tex.	840	Udic Chromustert	<i>Schizachyrium scoparium</i>	<i>Prosopis glandulosa</i>

Soil sampling and processing

At each site during the summer of 1997, 6-cm diameter soil cores from 7.5 to 10 m deep were extracted in 61-cm increments with an environmental drilling rig ($n=2-8$ cores in each grassland and also in adjacent woody systems; the lowest replicate numbers were for some of the deepest sampling depths, where extracting cores was most difficult). To increase spatial resolution at shallow depths, soil pits (25 cm diameter and 50 cm deep) were dug randomly in both vegetation types at each site. Soil cores and pits were sampled by depth for gravimetric soil moisture, air-dried, and sieved (2 mm) to remove rocks and root material. Roots were oven dried (55°C) and weighed for root biomass. The 95% rooting depth was calculated as the depth where 95% of the root biomass for the entire core was achieved. Volumetric soil moisture values were calculated using soil bulk density values and the gravimetric data.

Air-dried soil samples were analyzed for extractable P and exchangeable Ca^{2+} , Mg^{2+} , K^{+} , Na^{+} and Cl^{-} at the Utah State University Analytical Laboratory using standard soil protocols. These included 0.5 M NaHCO_3 ,

extraction for P (Olsen and Sommers 1982), 1 N $\text{CH}_3\text{-COONH}_4$ extraction for exchangeable Ca^{2+} , Mg^{2+} , K^{+} , and Na^{+} (Thomas 1982), and a 1:5 soil-to-water extract for Cl^{-} (Rhoades 1982). Extractable P and Cl^{-} concentrations were determined colorimetrically on a Spectronic 20 Genesys and a Lachat Quickchem FIA+8000, respectively. Concentrations of Ca^{2+} , Mg^{2+} , K^{+} , and Na^{+} were measured using a Thermo Iris Advantage ICP. Nutrient concentrations were converted to a soil surface-area basis for a given depth increment using the appropriate data values and soil bulk density data. Values for specific depth intervals were interpolated from the sampled depth increments.

We estimated the depth of cation uptake using stable isotope ratios of Sr, an element geochemically similar to Ca that is taken up and transported within plants similarly to Ca and that undergoes negligible biological fractionation (Capo et al. 1998; Vitousek et al. 1999). Comparing the $^{87}\text{Sr}/^{86}\text{Sr}$ isotope signature of a plant with the isotopic signatures in the soil profile yields an estimate of the depth of Sr uptake. This approach has been commonly used for estimating the depth of N (^{15}N) and water (^2H , ^{18}O) uptake from the soil (Rundel et al. 1989; Garten 1993; Schulze et

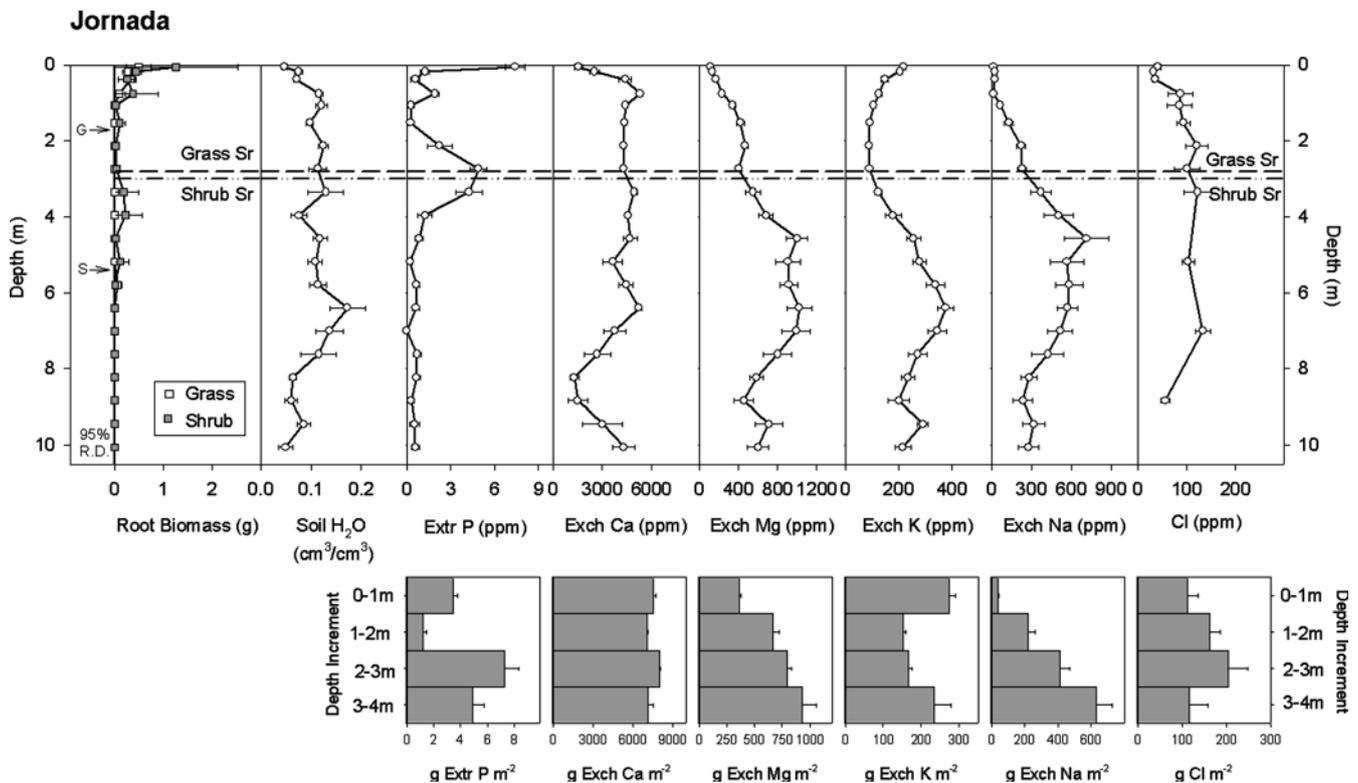


Fig. 1 Depth distributions at Jornada of root biomass, volumetric soil moisture, and concentrations of extractable P and exchangeable Ca^{2+} , Mg^{2+} , K^{+} , Na^{+} and Cl^{-} (mean \pm SE, $n = 2-8$; replication was lowest at the deepest depths). Root biomass data is presented for both the grassland and shrubland vegetation types at each site, with the 95% rooting depth for each vegetation type indicated by the arrows at the far left of the upper panels (G grassland, S shrubland). For the other panels, the points represent the average soil moisture and nutrient concentrations (ppm is equivalent to $\mu\text{g g soil}^{-1}$). The reference lines [Grass Sr (dashed line); Shrub Sr (dash-dot line)]

indicate the mean depth of Sr uptake for both vegetation types as inferred from Sr isotopes (see Materials and methods and Supplementary figure). Actual Sr uptake likely comes from depths both below and above these lines. The bottom panels indicate the nutrient availability (P, Ca^{2+} , Mg^{2+} , K^{+} , Na^{+} and Cl^{-}) on a volumetric basis (g m^{-2} ; mean \pm SE) for the top 4 m of soil in 1 m depth increments. Average bulk density values for each depth increment were used in this calculation; thus, the standard errors reflect only the variation in nutrient concentrations across cores

al. 1996) but has only recently been applied to Sr (Jackson et al. 2002; Poszwa et al. 2002). Thus, the depth at which the Sr isotope ratio of the plant material and the soil profile overlap is representative of the integrated depth of Sr uptake; however, actual Sr uptake likely occurs from depths both below and above this “integrated” value in a combination that provides the observed plant ratio.

We determined ⁸⁷Sr/⁸⁶Sr isotope ratios on soil samples throughout the soil profile (see Supplementary Fig. 1) and on leaves collected from the dominant plants at each site. Leaf samples were ground, ashed at 500–800°C, and dissolved in concentrated HNO₃. Exchangeable soil Sr was extracted by leaching ~4 g of soil for 20 min with 10 ml of 0.5 M CH₃COONH₄ adjusted to a pH 8 (Suarez 1996). Both plant and exchangeable soil ⁸⁷Sr/⁸⁶Sr isotope ratios were measured using a Finnigan-MAT 261 thermal ionization mass spectrometer in automated, dynamic multi-collection mode (for more details on the Sr isotope analyses see Jackson et al. 2002).

Results

At all sites, availability of one or more nutrients was greatest deep within the soil profile (Figs. 1, 2, 3, 4, 5, upper panels). This was particularly true for exchangeable Ca²⁺ and Mg²⁺, where the highest concentrations occurred at depths >1 m for all sites, in some cases values three times the concentrations found at the soil surface. The Jornada and CPER sites also showed strong secondary

peaks in extractable P concentrations at depths >1 m and had their highest exchangeable K⁺ concentrations below 1 m depth (Figs. 1, 3). Soil water contents also had their largest values below 1 m depth for all sites except Vernon (Figs. 1, 2, 3, 4, 5).

On an ecosystem or soil surface area basis (g m⁻²), the nutrient contents in the deeper soil layers were even larger compared to the surface layers than the concentration data suggest (Figs. 1, 2, 3, 4, 5, lower panels). Although the highest concentration of P occurred in the top 10 cm of soil at Jornada, the 2–3 and 3–4 m depth increments had twice the amount of extractable P as the top meter of soil (Fig. 1). Soil exchangeable K⁺ contents tended to be more shallowly distributed than P contents; however, layers below the top meter of soil contained more K⁺ than the top meter of soil at both CPER and Riesel. Similarly, the deeper soil layers (2–3 and 3–4 m) at Jornada, Sevilleta, CPER, and Riesel all contained more exchangeable Mg²⁺ than the 0–1 m depth increment (Figs. 1, 2, 3, 5). In general, Ca²⁺ availability was at least as great at depths below 1 m as in the top meter of soil, especially at Sevilleta, where deeper layers had 2 or 3 times the exchangeable Ca²⁺ as the upper meter (Fig. 2). While these data indicate that deep soils contain significant pools of a number of nutrients, P is the nutrient we examined that is most likely to limit growth in arid and semi-arid ecosystems.

Thus, at all sites except Vernon, the deeper depth increments had greater nutrient availability (P, Ca²⁺, K⁺, or Mg²⁺) than the top meter of soil; similarly, at every site but

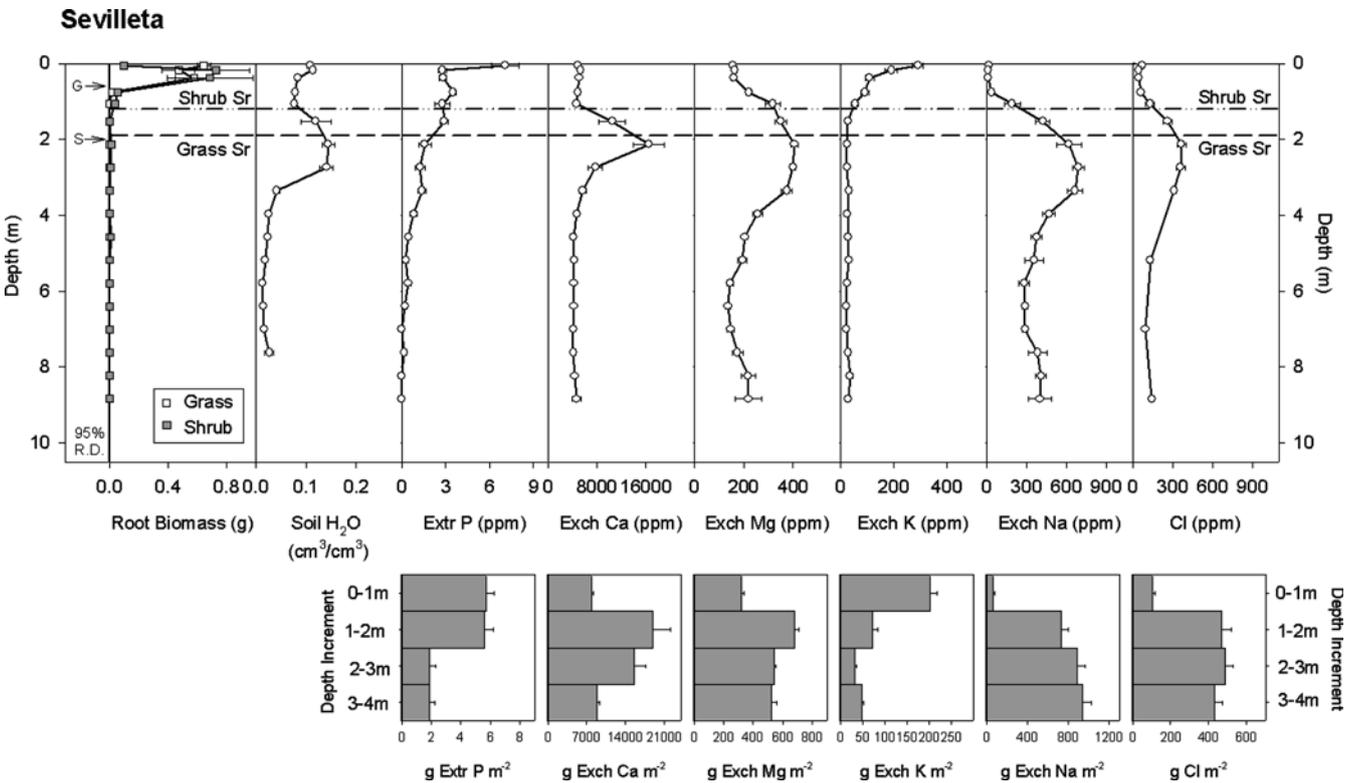


Fig. 2 Depth distributions of root biomass, volumetric soil moisture, and concentrations of extractable P and exchangeable Ca²⁺, Mg²⁺, K⁺, Na⁺ and Cl⁻ (mean ± SE, n = 2–8) at Sevilleta. For further details, refer to legend of Fig. 1

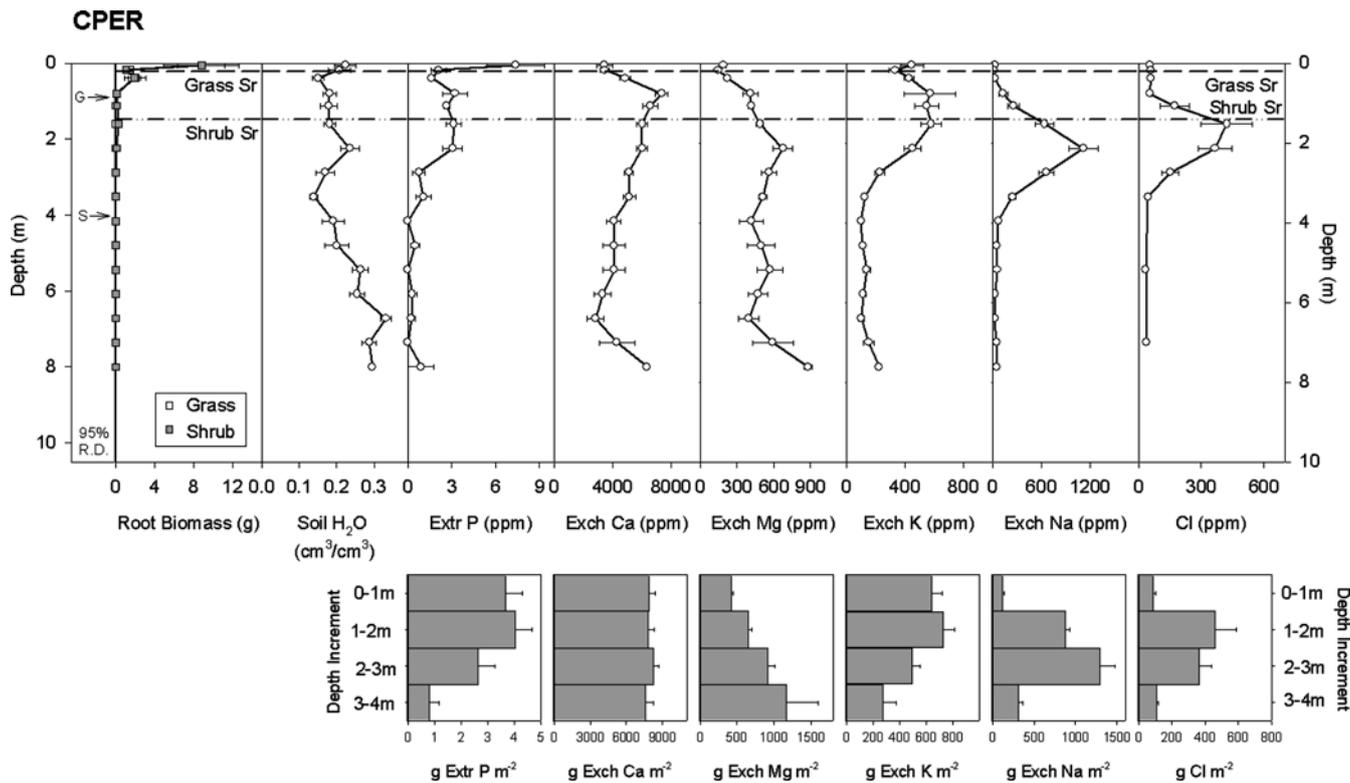


Fig. 3 Depth distributions of root biomass, volumetric soil moisture, and concentrations of extractable P and exchangeable Ca^{2+} , Mg^{2+} , K^+ , Na^+ and Cl^- (mean \pm SE, $n = 2-8$) at CPER. For further details, refer to legend of Fig. 1

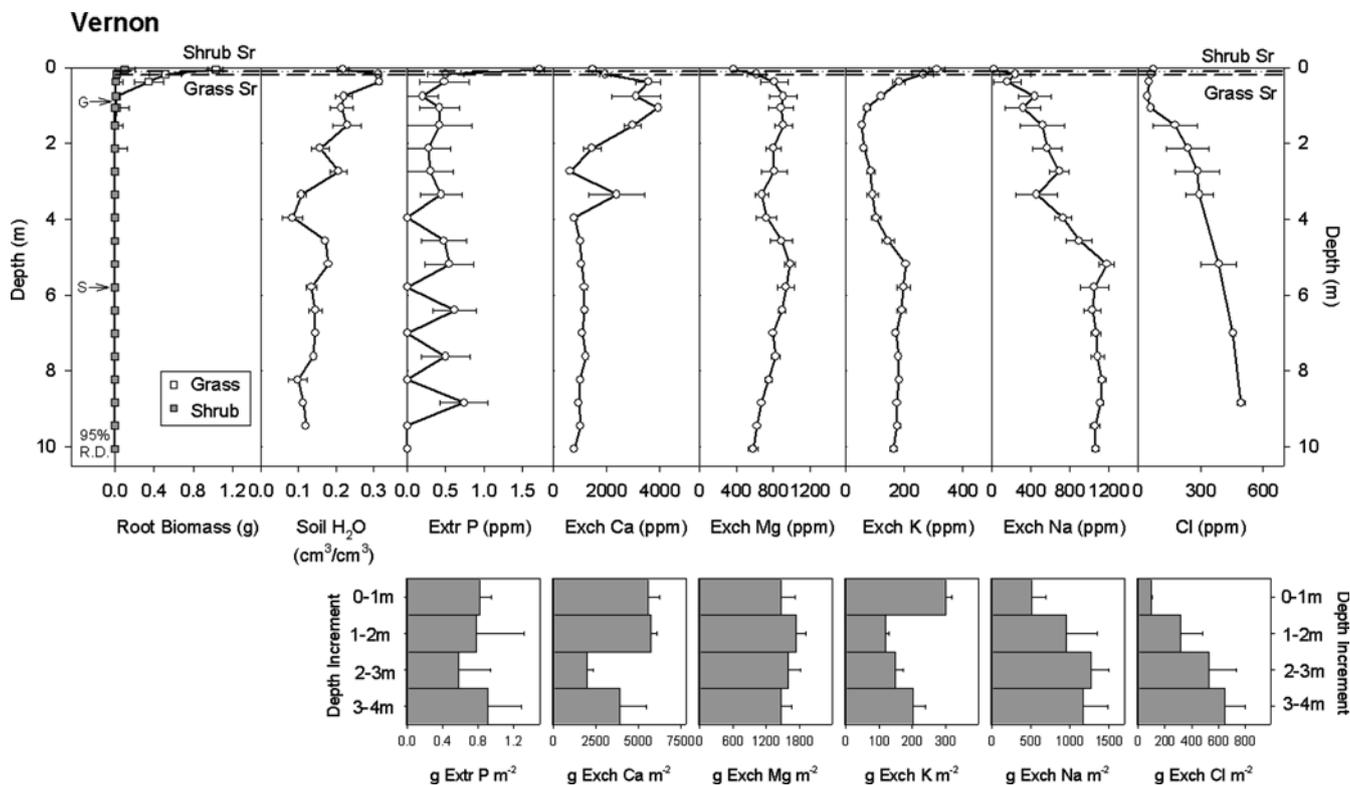


Fig. 4 Depth distributions of root biomass, volumetric soil moisture, and concentrations of extractable P and exchangeable Ca^{2+} , Mg^{2+} , K^+ , Na^+ and Cl^- (mean \pm SE, $n = 2-8$) at Vernon. For further details, refer to legend of Fig. 1

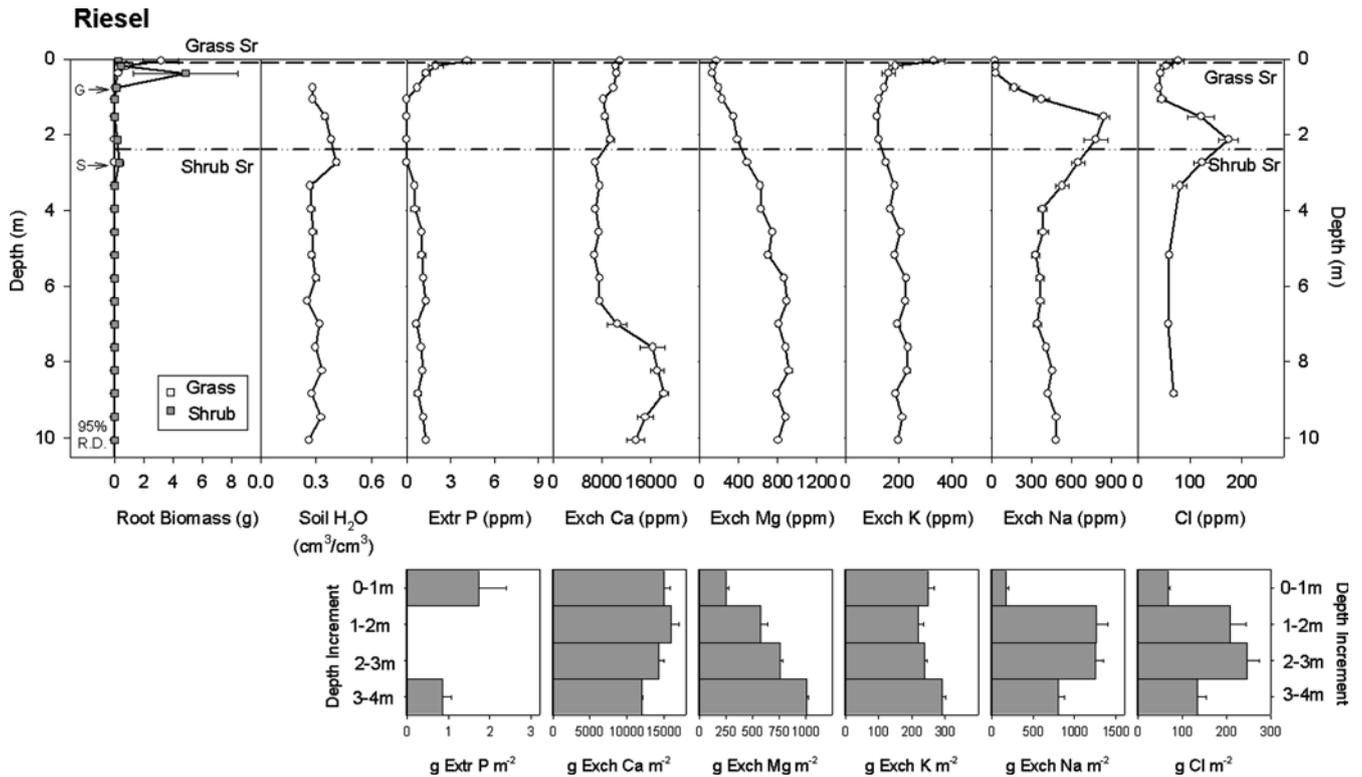


Fig. 5 Depth distributions of root biomass, volumetric soil moisture, and concentrations of extractable P and exchangeable Ca^{2+} , Mg^{2+} , K^+ , Na^+ and Cl^- (mean \pm SE, $n = 2-8$) at Riesel. For further details, refer to legend of Fig. 1

Vernon the depth of Sr uptake for at least one of the vegetation types was also relatively deep (>1 m; Figs. 1, 2, 3, 4, 5). There was also a close relationship between the depth of Sr uptake and peaks in various nutrient concentrations, particularly P at Jornada (Fig. 1) and Ca^{2+} at Sevilleta (Fig. 2). These results highlight the co-occurrence of greater abundance of nutrients at depth and evidence of nutrient uptake at similar depths through the Sr isotope data.

A link between deeper nutrient contents and root activity inferred from the Sr uptake data is supported by direct measures of root biomass with depth as well as some soil moisture values. Small but detectable peaks in root biomass occurred at many of the same depths associated with Sr uptake and greater nutrient contents (Figs. 1, 2, 3, 5). Roots were encountered deeper than the Sr uptake depths at all sites and vegetation types (data not shown). Furthermore, the 95% rooting depths showed relatively deep root distributions at all sites, particularly for shrublands (Figs. 1, 2, 3, 4, 5, compare arrows to left of upper panels). At two sites, Sevilleta and Riesel, there were also small peaks in volumetric soil moisture around 2 m depth coincident with the nutrient peaks and with the depths of Sr uptake for at least one of the vegetation types at each site (Figs. 2, 5; though without soil water potential data, such increases in volumetric moisture do not automatically mean more water available to plants). The steady increase in soil water content with depth at the CPER is due to the presence of groundwater there (Fig. 3).

Further support for the link between the depths of Sr uptake and nutrient distributions comes from the Cl^- and Na^+ depth distributions. At all sites except Vernon, soil Cl^- and Na^+ concentrations peaked between 2 and 4 m depth, suggesting that these are the maximum, long-term depths of water movement and uptake at each site (Figs. 1, 2, 3, 4, 5). These depths also coincided fairly closely with the observed depths of Sr uptake by at least one vegetation type at all sites except Vernon (Figs. 1, 2, 3, 4, 5). Chlorine is a relatively mobile element in the soil that undergoes little plant uptake (Yaalon 1965). As Cl^- percolates downward with water through the soil, its concentration increases as a result of water absorption and exclusion by roots. For this reason, the vertical distribution of Cl^- has been interpreted as an indication of water uptake patterns through the soil profile, and its peak used to shed light on the maximum depth of water uptake (Phillips 1994; Tyler and Walker 1994). Although Na^+ is a cation and can be adsorbed by the negatively charged exchange complexes in well-saturated soils, its relatively low binding affinity (Sposito 1989) and its exclusion by plant roots (Marschner 1995) result in vertical distributions similar to Cl^- (Jobbágy and Jackson 2001).

Discussion

Our results suggest that deep soils in arid and semi-arid regions may be an unstudied source of nutrients to plants there. Across a rainfall gradient from ~ 250 to 850 mm

MAP, the total amounts and concentrations of nutrients were frequently as high or higher at depth than observed in the top meter of soil (Figs. 1, 2, 3, 4, 5), with Sr isotope data suggesting at least some plant activity and uptake occurring at many of those depths. Examining P as a nutrient that is typically concentrated in the topsoil (Jobbágy and Jackson 2001), we found that the concentration of extractable P was indeed highest in the topsoil at all sites (Figs. 1, 2, 3, 4, 5). However, when depths >1 m were considered, P and the other nutrients studied all had comparable if not larger plant available pools in deeper soil layers at some or all sites. This result, coupled with the Sr uptake data, suggests that deep soils in arid and semi-arid regions may be a more significant nutrient source than previously believed.

The Sr isotope data presented here provide evidence that plants take up some deep nutrients at all sites where nutrient availability was relatively large at depth (Figs. 1, 2, 3, 5). Although cation uptake is inferred from the Sr isotope data, the correspondence of the integrated depth of Sr uptake with peaks in availability of other nutrients, such as P at Jornada, Mg^{2+} at Sevilleta, and K^+ at CPER, suggests that deep roots may allow plants to exploit deep soil as a source of multiple nutrients. This hypothesis is also consistent with previous research that has shown roots of several arid plant species are able morphologically and physiologically to respond to zones of high nutrient availability within the soil profile (Eissenstat and Caldwell 1988; Jackson et al. 1990). The one site where this relationship did not hold was Vernon (Fig. 4). The Vernon site had neither large stores of nutrients at depth (a consequence in part of its old soils; Koos et al. 1962), nor a deep estimated depth of Sr uptake (<0.3 m for both vegetation types, Fig. 4).

Water is required to mobilize nutrients within the soil and to supply those nutrients to roots through mass flow or diffusion (Nye and Tinker 1977). In this study, Sevilleta and Riesel had small peaks in volumetric soil moisture around 2 m depth, and these peaks coincided with the depths of Sr uptake for at least one of the vegetation types at each site (Figs. 2, 5). Our water measurements provide no information on the dynamics of water availability, but we suggest the interesting possibility that hydraulic redistribution or preferential flow of water via root channels could occur at these sites. A more temporally complete soil moisture dataset is needed to explore this possibility; nonetheless, the growing body of evidence for hydraulic redistribution in arid environments suggests that passive movement of water after rainfall from surface to deeper soil layers through roots may be a widespread phenomenon, even during dormant periods (Caldwell et al. 1998; Hultine et al. 2004). We propose that hydraulic redistribution may have a second ecological function in these ecosystems—facilitating nutrient acquisition.

Although hydraulic redistribution has been shown to occur in a number of arid and semi-arid systems, the ecological and hydrological importance of hydraulic redistribution and deep-water percolation in arid environments remains uncertain. First, substantial hydraulic

redistribution occurs only when plant transpiration is low and a sharp gradient in water potential exists between soil layers; simulation models suggest that small additions of water to dry layers can be enough to eliminate the driving force of the gradient (Ryel et al. 2002, 2003). Furthermore, the amount of water being hydraulically redistributed is likely to vary depending on the seasonality and size of precipitation events occurring at the site. Secondly, soil texture, through its effects on hydraulic conductivity and water storage, also affects the depth of water infiltration and the importance of hydraulic redistribution at a site (Yoder and Nowak 1999; Burgess et al. 2000; Ryel et al. 2002). Thirdly, long-term data from borehole measurements suggest that water availability at depths >1–2 m varies little through time (Andraski 1997; Seyfried et al. 2001), calling in to question the frequency of water infiltration at depth and uptake of that water by roots.

Like assessments of root activity at depth, however, the borehole and soil matric potential techniques used to monitor soil moisture over long time-scales have uncertainties. Their installation results in considerable soil disturbance, though artifacts may be minimal in multi-year experiments (Scanlon et al. 1997). Replicates may also be too few in number to capture macropore flow and other process that occur irregularly in space and time, including the effects of hydraulic redistribution. Infrequent large storms occurring at decadal time scales may be important for the growth of perennial desert plants but may fall outside the time scales of most experiments. In addition, these soil moisture monitoring techniques may lack the sensitivity to accurately measure the small amount of water thought to be transported via hydraulic redistribution. While more hydrological measurements are needed in arid and semi-arid systems to resolve this issue, ecologists and hydrologists need to collaborate to reconcile disparate data on water infiltration and plant activity at depth. The recent report of a large, deep soil NO_3^- pool in deserts, and uncertainties surrounding these pools, also highlight this need (Walvoord et al. 2003; Jackson et al. 2004).

The data presented here suggest a potentially overlooked role of deep roots in nutrient uptake. For such nutrients to be available to plants, there must be sufficient water in the soil for diffusion or mass flow of the nutrients to occur. We propose that hydraulic redistribution may provide that water, potentially mobilizing nutrients at depth. This possible role for hydraulic redistribution may help reconcile discrepancies with borehole data showing minimal changes in soil moisture contents at depth; hydraulic redistribution would mobilize nutrients directly around roots where nutrient uptake occurs. Understanding the benefits of deep roots will require models and experiments that examine both water and nutrient uptake at depth. The additional measurements that are needed include borehole data with greater spatial resolution to capture water dynamics across a heterogeneous landscape, and tracer studies and other experiments to confirm the extent and occurrence of nutrient uptake at depth.

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