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Juniperus virginiana and *Pinus ponderosa* and two dominant C₄
grasses in a semiarid grassland**

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Eggemeyer, Kathleen D.; Awada, Tala; Harvey, F. Edwin; Wedin, David A.; Zhou, Xinhua; and Zanner, C. William, "Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C₄ grasses in a semiarid grassland" (2009). *Papers in Natural Resources*. 202.

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Submitted February 8, 2008; accepted September 25, 2008.

Seasonal changes in depth of water uptake for encroaching trees *Juniperus virginiana* and *Pinus ponderosa* and two dominant C₄ grasses in a semiarid grassland

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Abstract

We used the natural abundance of stable isotopic ratios of hydrogen and oxygen in soil (0.05–3 m depth), plant xylem and precipitation to determine the seasonal changes in sources of soil water uptake by two native encroaching woody species (*Pinus ponderosa* P. & C. Lawson, *Juniperus virginiana* L.), and two C₄ grasses (*Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L.), in the semiarid Sandhills grasslands of Nebraska. Grass species extracted most of their water from the upper soil profile (0.05–0.5 m). Soil water uptake from below 0.5 m depth increased under drought, but appeared to be minimal in relation to the total water use of these species. The grasses senesced in late August in response to drought conditions. In contrast to grasses, *P. ponderosa* and *J. virginiana* trees exhibited significant plasticity in sources of water uptake. In winter, tree species extracted a large fraction of their soil water from below 0.9 m depth. In spring when shallow soil water was available, tree species used water from the upper soil profile (0.05–0.5 m) and relied little on water from below 0.5 m depth. During the growing season (May–August) significant differences between the patterns of tree species water uptake emerged. *Pinus ponderosa* acquired a large fraction of its water from the 0.05–0.5 and 0.5–0.9 m soil profiles. Compared with *P. ponderosa*, *J. virginiana* acquired water from the 0.05–0.5 m profile during the early growing season but the amount extracted from this profile progressively declined between May and August and was mirrored by a progressive increase in the fraction taken up from 0.5–0.9 m depth, showing plasticity in tracking the general increase in soil water content within the 0.5–0.9 m profile, and being less responsive to growing season precipitation events. In September, soil water content declined to its minimum, and both tree species shifted soil water uptake to below 0.9 m. Tree transpiration rates (*E*) and water potentials (Ψ) indicated that deep water sources did not maintain

E which sharply declined in September, but played an important role in the recovery of tree Ψ . Differences in sources of water uptake among these species and their ecological implications on tree–grass dynamics and soil water in semiarid environments are discussed.

Keywords: Great Plains, Nebraska Sandhills, *Panicum virgatum*, *Schizachyrium scoparium*, stable isotopes, water potential

Introduction

The distribution of soil water over time and with depth is a key determinate of vegetation structure, including the balance of grasses and woody species in semiarid and arid landscapes (Huxman et al. 2005, Darrouzet-Nardi et al. 2006). At 50,000 km², the Nebraska Sandhills are the largest stabilized sand dune formation in the Western Hemisphere. Although the Sandhills are almost entirely stabilized by grasses, tree encroachment into these semiarid grasslands is increasing. Ponderosa pine (*Pinus ponderosa* P. & C. Lawson), a major forest type in the USA (Sala et al. 2005), has expanded into grasslands from historic grassland–woodland ecotones (Steinauer and Bragg 1987), and eastern red cedar (*Juniperus virginiana* L.) is spreading throughout the Sandhills and the Great Plains (Schmidt and Stubbendieck 1993, Willson et al. 2008). These land cover changes reflect shifts from open grasslands and savannas to more closed-canopy woodlands in semiarid landscapes worldwide (Scholes and Archer 1997, Bond et al. 2005). Although decreased fire frequency is certainly a driver of these changes (Bond et al. 2005), over-grazing,

climate change, elevated atmospheric CO₂ concentration, atmospheric nitrogen deposition and human-enhanced dispersal may also favor woody species over native C₄ grasses such as those that dominate the Sandhills (reviewed by Scholes and Archer 1997). Regardless of the mechanisms behind woody plant expansion into semiarid grasslands, this transition has potentially large biogeochemical, hydrologic and ecologic impacts (Archer et al. 2001, Jackson et al. 2002, Huxman et al. 2005).

Root distributions and soil water dynamics play a key role in an ecosystem's water balance, as evidenced by the emphasis placed in recent ecohydrology theory and modeling (e.g., Huxman et al. 2005, Rodríguez-Iturbe and Porporato 2005). Ecohydrology models make assumptions about the rooting zone, i.e., the depth to which roots effectively deplete soil water. For native grasslands, various modelers have used rooting zones ranging from 0.3 to 1.5 m depth. The classic studies of Weaver (1958 and references therein) remain the "benchmark for studies of root morphology and distribution" in the Great Plains (Schenk and Jackson 2002). For the Sandhills, Weaver (1958) concluded that the 'Sandhills grasses are characterized by moderately fine roots which spread widely in the surface, usually 1.5–3.0 ft (0.45–0.91 m), and penetrate deeply, mostly 4–7 ft (1.2–2.15 m)', with a maximum rooting depth of 2.4 m. However, Weaver (1958) also clearly stated that most grass roots are shallow (> 75% in top 0.1 m). Measurements on our site indicated that 75–80% and 85–90% of cumulative grass root biomass and length, respectively, were found in the top 0.3 m (Wedin unpublished data, Wang et al. 2008). Trees and shrubs clearly have the potential for deeper roots than grasses (Schenk and Jackson 2002), but estimates of the depth to which soil water depletion occurs vary widely among species and ecosystems (Asbjornsen et al. 2008), making determination of source of water uptake for individual species important within functional groups and ecosystems (Goldstein et al. 2008).

Due to the general difference between tree and grass rooting depths, the partitioning of soil water as a resource into shallow and deep layers is often cited as a mechanism for the stable coexistence of trees and grasses in semiarid landscapes (Walter 1979, Hesla et al. 1985, Schulze et al. 1996, Darrrouzet-Nardi et al. 2006). Several semiarid woodland findings support the niche partitioning hypotheses: woody species predominantly use deep soil water and grasses predominantly use soil water from the upper soil profile (Sala et al. 1989), although other studies have shown significant competition for soil water between woody species and grasses (Le Roux et al. 1995, Scholes and Archer 1997). Studies that compared the depth of water uptake by co-occurring woody species report both patterns: some species use only deep soil water, while others tap both shallow and deep layers (Dodd et al. 1998, Williams and Ehleringer 2000, West et al. 2007, Goldstein et al. 2008). When trees and grasses use overlapping regions of the soil profile, grasses are assumed to have a competitive advantage for water in the upper soil profile (Belsky 1994), whereas trees alone

have access to deeper soil layers where water is available to them during drought periods (Walker and Noy-Meir 1982), contributing to their success in semiarid environments. Daly et al. (2000) modeled tree-grass interactions in water-limited landscapes and concluded that, when trees are more deeply rooted than grasses, trees inevitably become the dominant life form in the absence of fire. Conversely, when trees and grasses share the same rooting zone, grass dominance or co-dominance is predicted.

Determining species' source of water uptake and role in an ecosystem's water balance is critical for accurately modeling and predicting species dynamics and the effects of climate change on ecosystem processes (West et al. 2007). Our primary objective was to determine the seasonality and depth of water uptake by two native encroaching woody species (*P. ponderosa* and *J. virginiana*) and two C₄ grasses (*Schizachyrium scoparium* (Michx.) Nash and *Panicum virgatum* L.). The selected grasses dominate the Sandhills of Nebraska and are a major vegetation component of the Great Plains. We used the natural abundance of stable isotopic ratios of hydrogen (δ D) and oxygen (δ^{18} O) to differentiate the source of soil water uptake (Ehleringer and Dawson 1992, Williams and Ehleringer 2000, Phillips et al. 2005, West et al. 2007). We hypothesized that: (1) during periods of high soil water content, grasses and trees use water from overlapping soil profiles, whereas when water is unavailable in the upper soil profile, because of drought or freezing temperatures, tree species acquire water from deeper soil profile, giving them a competitive advantage over grasses and (2) tree species differ in patterns of water uptake that might influence their future distributions.

Materials and methods

Site description

The study was conducted at the Nebraska National Forest (NNF) at Halsey, NE, USA (825 m altitude, 41°51'45" N and 100°22'06" W). The NNF is an experimental forest established in the semiarid Sandhills grasslands of Nebraska in 1902 and planted with coniferous species, predominantly *P. ponderosa*. Most of the forest was planted in the 1930s and in the 1940s. In 2005, pine stands in the study area were 60–65 years old. The documented site history and relatively uniform stand age and soils at the NNF make it uniquely suited to investigate the ecosystem effects of tree encroachment in the Great Plains.

The climate is semiarid continental, with a mean annual precipitation of 573 mm of which 77% falls during the growing season (April–September). Mean annual temperature is 8.4 °C. The mean minimum temperature in January is –13.8 °C, and the mean maximum temperature in July is 31.3 °C. Soils are Valentine fine sand (mixed, mesic Typic Ustipsamments) with deep loose sandy well-drained soils (Sherfey et al. 1965). The vegetation of the study area consists of scattered *P. ponderosa* and *J. virginiana* and a pe-

rennial grassland dominated by little bluestem (*S. scoparium*), switchgrass (*P. virgatum*), sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray), Kentucky bluegrass (*Poa pratensis* L.), and white sage (*Artemisia ludoviciana* Nutt.). Tree basal area of the study site is 5.6 m² ha⁻¹ with a density of 123 trees ha⁻¹. Four native species were selected for study: two woody species (*J. virginiana* and *P. ponderosa*) and two dominant C₄ grass species (*S. scoparium* and *P. virgatum*). The selected *P. ponderosa* trees averaged 0.44 m in diameter at breast height (DBH; range 0.35–0.52 m). *Juniperus virginiana* trees were 20–30 years old and averaged 0.18 m DBH (range 0.11–0.24 m).

Isotope measurements

Precipitation and groundwater – Precipitation in the study area was measured continuously with a tipping bucket rain gauge (TE525, Campbell Scientific, Logan, UT) connected to a Campbell Scientific data logger (CR10X). Precipitation samples for isotopic analyses were collected monthly from May 2003 to April 2004 using light mineral oil in the collector apparatus to prevent evaporation between sampling events. The collected samples were stored at -10 °C until isotopic analyses. Groundwater (~7 m deep, Harvey unpublished data) was sampled monthly from three wells within 2.5 km of the study site between May 2003 and April 2004. The groundwater samples were placed in 8-ml polypropylene vials and stored at -10 °C until isotopic analyses.

Plant and soil sampling – Stems were collected monthly between May 2003 and April 2004 from eight trees per species (*P. ponderosa* and *J. virginiana*). Stems were > 0.02 m in diameter and were 0.15 m long. Twenty thick fleshy root crowns were harvested on a monthly basis during the growing season (May–August 2003), from *S. scoparium* and *P. virgatum* individuals. In several herbaceous species, root crowns have been shown to be the least variable plant tissues to sample for the assessment of plant source water by isotope techniques (Barnard et al. 2006). Samples were put immediately in glass vials following the method of Dawson and Ehleringer (1998), and placed in plastic bags and stored at -10 °C until isotopic analyses.

Soil profiles were sampled with a truck-mounted hydraulic corer (Giddings Machine Co., Fort Collins, CO) with a barrel (0.0625 × 1.22 m) containing an inert PETG plastic liner. The liner was sealed with plastic caps to prevent drying or evaporation. Two soil cores (up to 3 m each) were collected monthly between May 2003 and April 2004 from two locations at the site. The soil cores were cut into 0.1 m increments from 0 to 0.2 m and 0.2 m increments from 0.2–3 m. Samples were placed in plastic bags and stored at -10 °C until isotopic analyses. Soil samples were not collected in December because winter conditions prevented site access. Similarly, winter conditions prevented access to Location 2 in February and so soil isotope values, although presented, were not included in the

plant source of water analysis because the soil core was taken from the site edge and therefore might not be fully representative of Location 2.

Isotopic analyses – Isotopic analyses were performed at the Water Science Laboratory, University of Nebraska–Lincoln. Water was extracted from plant and soil samples by azeotropic distillation in dry toluene (Revesz and Woods 1990). This method has been shown to extract only hydrologically active water. The extracted water and meteoric water (precipitation) samples were analyzed for δD (deuterium) by an online chromium reduction technique (Morrison et al. 2001) on a continuous flow isotope ratio mass spectrometer (EuroPyrOH-3110, Isoprime with Eurovector Pyrolysis Furnace, GV Instruments, Manchester, UK). Water samples were analyzed for δ¹⁸O with an automated CO₂ equilibration technique (Midwood et al. 1992) connected to an isotope ratio mass spectrometer (GV2003 with an IsoprepB Equilibration System, GV Instruments). The δD and δ¹⁸O values were expressed in parts per thousand (‰) relative to the V-SMOW standard (Gonfiantini 1978)

$$\delta D \text{ or } \delta^{18}O = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

where $R = {}^2\text{H}/{}^1\text{H}$ for deuterium, or $R = {}^{18}\text{O}/{}^{16}\text{O}$ for oxygen. Instruments were calibrated daily, with calibration checks interspersed throughout a run. Samples were analyzed in triplicates, averaged and reanalyzed if the standard deviation exceeded the measurement precision (0.2‰ for δ¹⁸O and 2‰ for δD).

Annual weighted means of δD and δ¹⁸O for precipitation (δ_{PWT}) were calculated as

$$\delta_{\text{PWT}} = \sum_{x=1}^n \delta x_i f x_i \quad (2)$$

where δ_{PWT} is the weighted mean δD and δ¹⁸O for rainfall, δ_x is isotopic composition of the *i*th month, *f_x* is the fraction contribution of the *i*th month to the yearly rainfall total, and *n* is the number of months (*i* = 1–12).

To determine the fractional contribution of water sources to studied species, the IsoSource program was used: <http://www.epa.gov/wed/pages/models/stable-isotopes/isosource/isosource.htm> (Phillips et al. 2005). IsoSource finds all feasible solutions of source contributions based on linear mixing models (Phillips and Gregg 2003, Phillips et al. 2005, West et al. 2007), and because the two studied isotopes were highly correlated ($r = 0.94$), it was not possible to use other traditional mixing models (West et al. 2007). At first, source endpoints were derived from means of the 0.05–0.3, 0.3–0.5, 0.5–0.7, 0.7–0.9 and 0.9–3 m soil depths. However, these sources were too many to allow for feasible solutions; therefore, we combined the data into three layers (0.05–0.5, 0.5–0.9 and 0.9–3 m) post hoc following Phillips et al. (2005).

Soil water content

Soil water content at depths of 0.2, 0.4, 0.6 and 1 m was measured at two locations by time domain reflectometry technology (ThetaProbe ML2 probes, Dynamax Inc., Houston, TX). Data were recorded every 30 min and stored on a Campbell Scientific data logger. Mean values for replicate sensors at the same depth are presented. Sensors were calibrated (High Plains Regional Climate Center, University of Nebraska–Lincoln) for sandy soils and values were compared with other sites equipped with similar sensors at the NNF. Additionally, gravimetric soil water content was determined in subsamples from the two cores collected for soil isotope measurements.

Plant water potential and transpiration

Predawn (Ψ_{pre} MPa; 1–1.5 h before sunrise) and midday (Ψ_{mid} MPa; 1300 h during winter and 1230 h during summer months) water potentials were measured to assess plant water relations. Measurements were followed once a month between May 2003 and April 2004 for the trees and over the growing season (June–August 2003) for the grasses. Water potential was determined with a pressure chamber (PMS Instrument Co., Albany, OR) on tree twigs and grass leaves collected from the same individuals that were used for stable isotope measurements. Foliar transpiration rates (E ; $\text{mmol m}^{-2} \text{s}^{-1}$) were determined at light saturation, concurrently with midday water potential measurements with an infrared gas analyzer (LI-6400, Li-Cor, Lincoln, NE). Detailed measurement conditions for gas exchange measurements have been described by Eggemeier et al. (2006).

Statistical analyses

Data were analyzed with SAS statistical software (SAS 1996, SAS Institute, Cary, NC) using the mixed models procedure. Orthogonal contrasts were used to examine species differences in seasonal dynamics. Means were separated by the pairwise mean comparison in SAS.

Results

Environmental parameters

Air temperature was consistent with the 30-year mean (High Plains Regional Climate Center, University of Nebraska–Lincoln) reaching a maximum in July and August and a minimum in January and February (Figure 1). Total precipitation for the study period was 370 mm, well below the long-term mean of 573 mm (Figures 1 and 2). The climate diagram (Figure 1) indicates that drought on site started in mid-July and ended in October. Volumetric soil water content (Figure 2) was highest in spring, and fell to a minimum in September. Soil water content was highly variable at 0.2 m depth, reflecting recent precipitation events. Soil water fluctuations were smaller with increasing

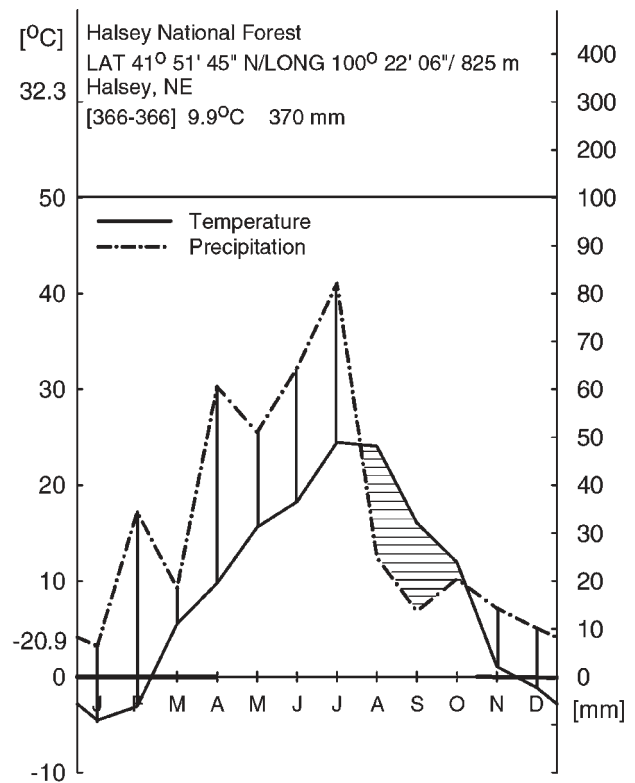


Figure 1. Climate diagram of mean monthly temperature and precipitation data during the study period (May 2003 to April 2004). Horizontal and vertical lines indicate relative drought and humid periods, respectively. Bold dates (on x-axis) indicate frost periods (Eggemeier et al. 2006).

depth (0.6 and 1 m), and exhibited a steady decline after May, before stabilizing by late August (Figure 2). For much of August and September, soil water content at 1 m was higher than in the upper soil profile. Although comparable continuous measurements of volumetric soil water below 1 m were not made, the gravimetric soil water content of the soil cores used for isotopic analysis averaged between 4% and 7.5% for the 0.9–3 m soil profile during the drought period.

Seasonal isotopic variations in precipitation, soil water and groundwater

The $\delta^{18}\text{O}$ and δD values of precipitation were consistent with regional monthly means (Harvey and Welker 2000), varying seasonally as a function of temperature and ranging from -4.6‰ to -21‰ for $\delta^{18}\text{O}$, and from -25‰ to 138‰ for δD (Figures 3 and 4). Soil water $\delta^{18}\text{O}$ and δD differed significantly between months ($P < 0.0001$) and depths ($P < 0.0001$) (Figures 3 and 4). Isotopic values in the 0.05–0.3 m soil profile reflected the seasonal variation in local precipitation and were generally less negative than precipitation during the hottest part of the summer (July–September), because of enrichment associated with evaporation (Figures 3 and 4). Values of $\delta^{18}\text{O}$ and δD remained constant deeper in the soil profile, approaching values comparable

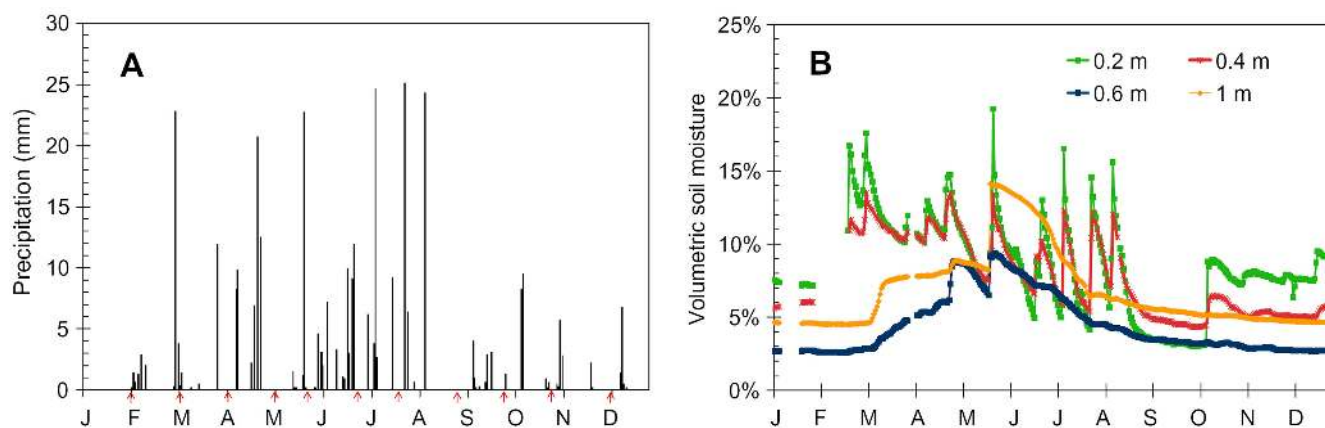


Figure 2. Seasonal dynamics in (A) precipitation (mm), and (B) volumetric soil water content (%) at 0.2, 0.4, 0.6 and 1 m depths, at the site during the study period (May 2003 to April 2004). Arrows indicate sampling dates.

with groundwater (-11% and -77% for $\delta^{18}\text{O}$ and δD , respectively). Although we did not sample the groundwater (~ 7 m deep), minimal isotopic variation was expected below 3 m because a steady state value was likely reached (Zimmerman et al. 1967). Soil water $\delta^{18}\text{O}$ and δD also indicated one or more pulses moving down the soil profile between January and April. Pulses were also evident in the May and June profiles, but not in late summer profiles. These pulses may indicate water percolating through the soil profile by piston flow movement of a precipitation event, or they may represent diffusion of a larger seasonal pulse. There was a significant interaction between month and depth ($P < 0.003$) indicating that the $\delta^{18}\text{O}$ and δD of soil water were changing with depth throughout the year.

The isotopic composition of groundwater from nearby wells was relatively constant over the year averaging $-11\% \pm 0.063\%$ for $\delta^{18}\text{O}$ and $-77\% \pm 0.31\%$ for δD (Figures 3 and 4). The weighted mean isotopic composition of precipitation over the year was similar to the groundwater yearly mean from the three wells, implying direct local recharge (Gat and Matsui 1971).

Seasonal variations in plant xylem isotopic composition and water uptake

The $\delta^{18}\text{O}$ and δD of xylem water did not differ among grass species (*S. scoparium* and *P. virgatum*, $P > 0.05$) (Figures 3–6). Grass xylem water $\delta^{18}\text{O}$ and δD ranged from -4% to -6.5% , and -28% to -50% , respectively. Values generally tracked recent precipitation and soil water in the upper soil profile. The $\delta^{18}\text{O}$ of grasses was slightly less negative than those of precipitation and soil water on a few sampling dates. The $\delta^{18}\text{O}$ and δD of grass xylem water were significantly less negative than those of *P. ponderosa* and *J. virginiana* ($P < 0.01$; Figures 3–6), indicating that grasses and trees might be obtaining water from different depths within the soil profile. The $\delta^{18}\text{O}$ values differed significantly between tree species (*P. ponderosa* and *J. virginiana*, $P = 0.04$), and together with the difference in δD between dates ($P < 0.001$) indicate that, in

one or more months, *P. ponderosa* and *J. virginiana* were obtaining water from different depths within the soil profile.

Species were plotted on a δD - $\delta^{18}\text{O}$ graph to evaluate fractionation processes (Figure 5). Results showed that grass species plotted along and slightly to the right of the meteoric water line (MWL), whereas tree species plotted on the MWL, indicating that grasses obtained shallow surface waters at or near the ground surface that had been enriched slightly by evaporation and that the trees used deeper water unaffected by evaporation.

A three-source mixing model was used to determine the fraction of water acquired by plants from three ranges of soil depths (0.05–0.5, 0.5–0.9 and 0.9–3 m in Figure 6). The model (Figure 7) predicted that grasses extracted most of their water ($\sim 100\%$) from the 0.05–0.5 m soil profile when water was available (May and June), and as the season progressed and soil water declined in this profile, *S. scoparium* and *P. virgatum* slightly increased their uptake of deeper water sources ($\sim 20\%$ of water acquired from below 0.5 m). In August, *S. scoparium* reverted to obtaining its water almost exclusively from the upper soil profile (0.05–0.5 m). In contrast, *P. ponderosa* and *J. virginiana* showed plasticity in their patterns of water uptake. In November, January and February, when below zero air and soil temperatures were recorded, *P. ponderosa* and to a lesser extent *J. virginiana* extracted most soil water from below 0.9 m depth. In March, soil $\delta^{18}\text{O}$ and δD values were irregular and isotopic values of the tree species overlapped with several soil depths, resulting in less accurate model estimations (large range of model solutions) for the 0.05–0.5 and 0.9–3 m soil profiles. However, with snow melt in March and increases in precipitation, temperature and soil water content in the upper soil profile, and the initiation of fine root production, we infer that water might have been predominately acquired from that source. The upper soil profile (0.05–0.5 m) was also the main source of water in April for *P. ponderosa* and in April and May for *J. virginiana*. From May to August, *P. ponderosa* extracted a sizeable fraction of its water from the 0.05–0.5 and 0.5–0.9 m soil profiles. This was not

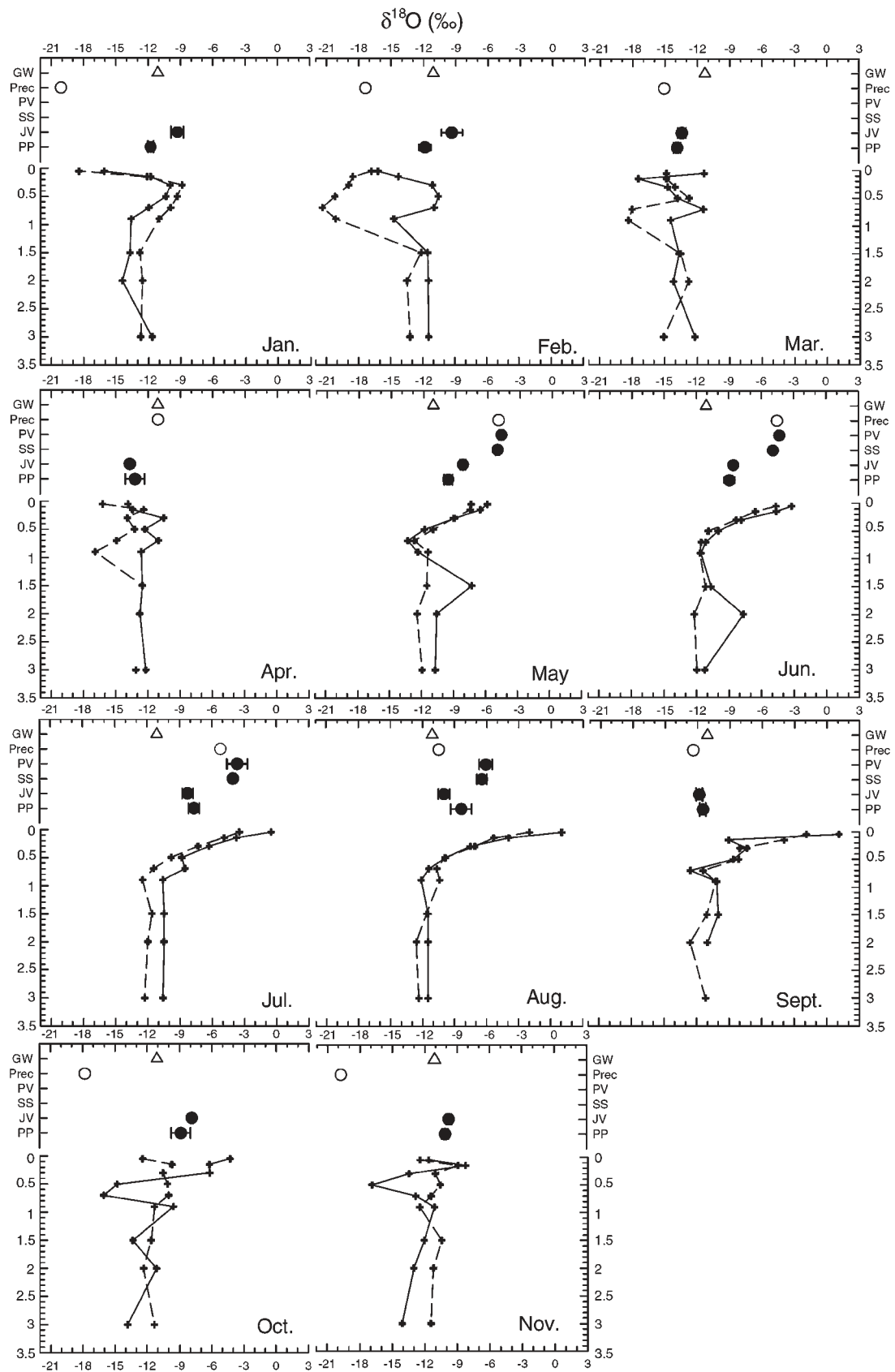


Figure 3. Monthly (May 2003 to April 2004) dynamics in $\delta^{18}\text{O}$ (‰) in soil water at Location 1 (solid line) and Location 2 (dotted lines), groundwater (GW), precipitation (Prec), *P. virgatum* (PV), *S. scoparium* (SS), *J. virginiana* (JV) and *P. ponderosa* (PP) at the study site in the Nebraska Sandhills.

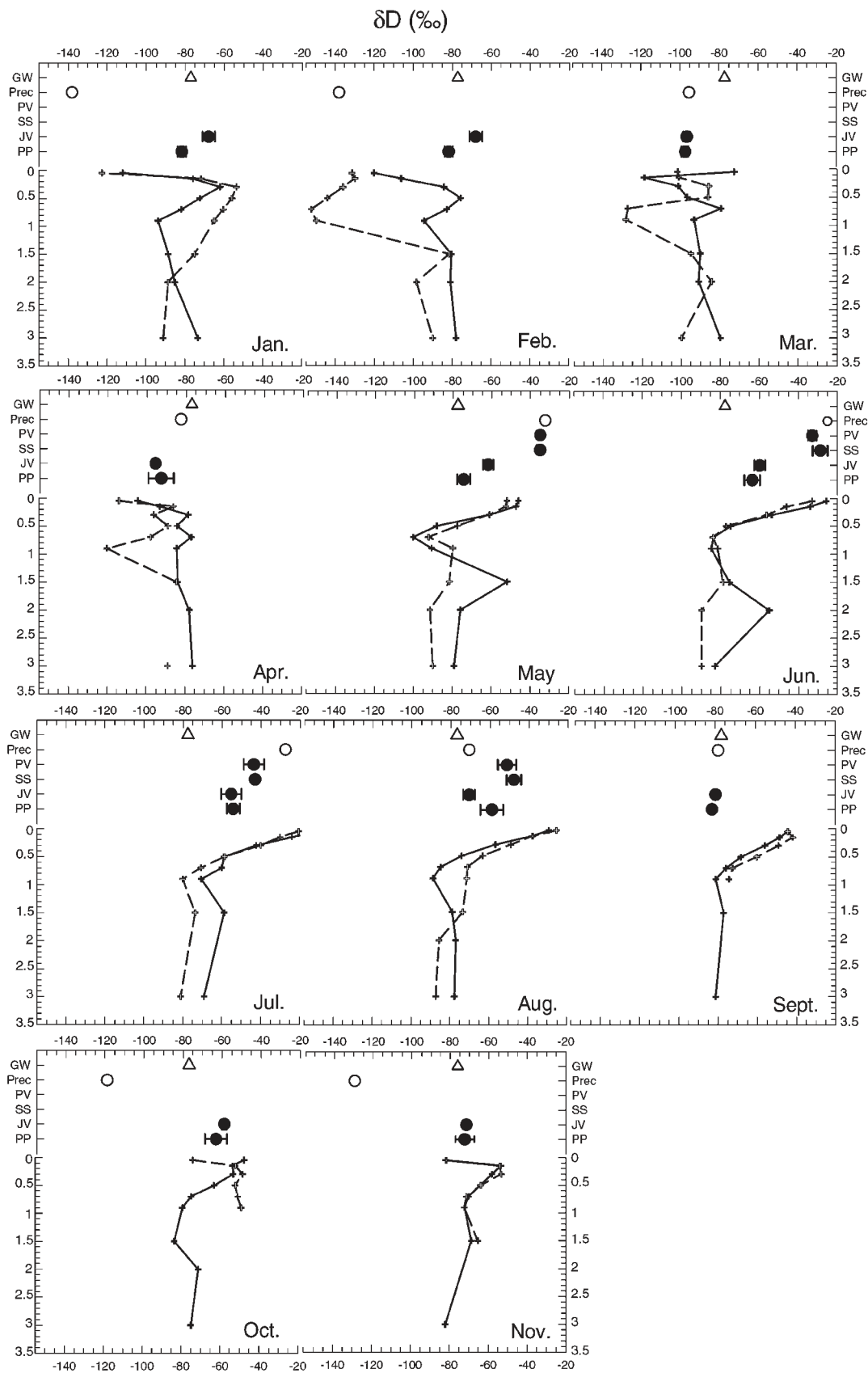


Figure 4. Monthly (May 2003 to April 2004) dynamics in δD (‰) in soil water at Location 1 (solid line) and Location 2 (dotted lines), groundwater (GW), precipitation (Prec), *P. virgatum* (PV), *S. scoparium* (SS), *J. virginiana* (JV) and *P. ponderosa* (PP) at the study site in the Nebraska Sandhills.

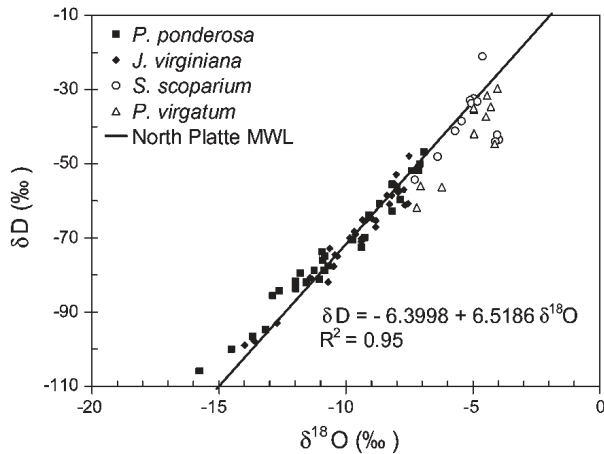


Figure 5. Values of δD (‰) as a function of $\delta^{18}O$ (‰) for plant xylem. Data were fitted against the North Platte (MWL, Harvey and Welker 2000).

the case for *J. virginiana*, where water uptake from the 0.05–0.5 m profile progressively declined from May to August, mirrored by an increase in the fraction of soil water uptake from the 0.5–0.9 m profile, more or less tracking the increase in soil water content within this depth range (Figure 7). *Juniperus virginiana* had negligible water uptake from below 0.9 m between April and July. In September, soil water content was at its lowest throughout the measured profile and we observed a switch in soil water uptake to sources below 0.9 m depth. The plasticity in patterns of soil water uptake in *P. ponderosa* and *J. virginiana* was observed again in October, where both species switched back to acquiring a sizeable fraction of soil water from the upper soil profile (0.05–0.5 m), with a negligible contribution from the driest 0.5–0.9 m soil profile.

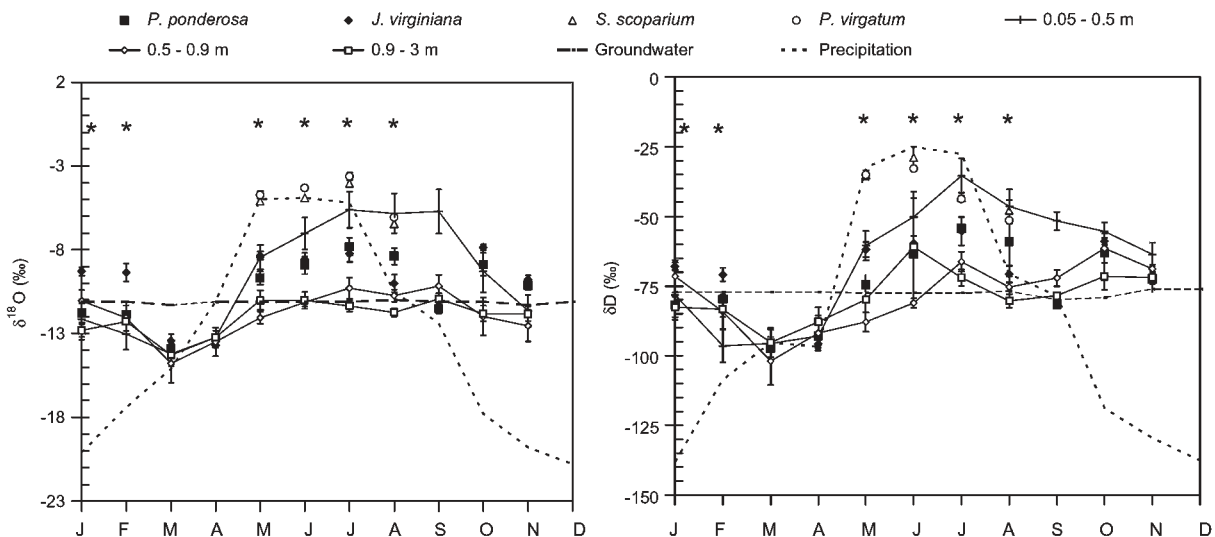


Figure 6. The $\delta^{18}O$ and δD seasonal dynamics in precipitation, soil water (0.05–0.5, 0.5–0.9 and 0.9–3 m), groundwater, trees (*P. ponderosa* and *J. virginiana*) and in grasses (*S. scoparium* and *P. virgatum*) with standard error bars, over a one-year period (May 2003 to April 2004). An asterisk (*) indicates significant differences between species within a sampling date ($P < 0.05$).

Seasonal variations in water potential and transpiration

Water potentials differed among species ($P < 0.01$) and displayed a significant seasonal variation ($P < 0.03$; Figure 8). The Ψ_{pre} that is an indication of soil and plant water status corresponded well with the observed seasonal variations in volumetric soil water content. *Pinus ponderosa* had the least negative Ψ_{pre} and Ψ_{mid} , followed sequentially by *J. virginiana* and finally the grass species. The most negative Ψ_{pre} and Ψ_{mid} occurred in August for all species. The most negative Ψ_{pre} (–1.0 MPa) and Ψ_{mid} (–2.5 MPa) were observed in grasses, followed by *J. virginiana* (Ψ_{pre} –0.95 and Ψ_{mid} –2.0 MPa) and *P. ponderosa* (Ψ_{pre} –0.8 and Ψ_{mid} –1.8 MPa). Grasses senesced in late August in response to drought conditions, whereas water potentials of the tree species increased in September (Figure 8).

Transpiration rates (E , Figure 9) increased in spring with the improvement in weather conditions in *P. ponderosa*, but remained low in *J. virginiana* before sharply increasing between May and June. Transpiration rates remained high in both tree species for the remainder of the summer before sharply declining in September, because of severe drought conditions. Grasses did not differ between each other, but exhibited significantly higher E than trees in June, before declining in July to similar rates as observed in the tree species.

Discussion

To use stable isotopes to identify the depth of soil water uptake by plants, the isotopic values of soil water must show a clear vertical gradient (Ehleringer and Dawson 1992, Dawson 1993, Brunel et al. 1995, Dawson and Ehleringer 1998). We observed such a vertical gradient in soil water $\delta^{18}O$ and

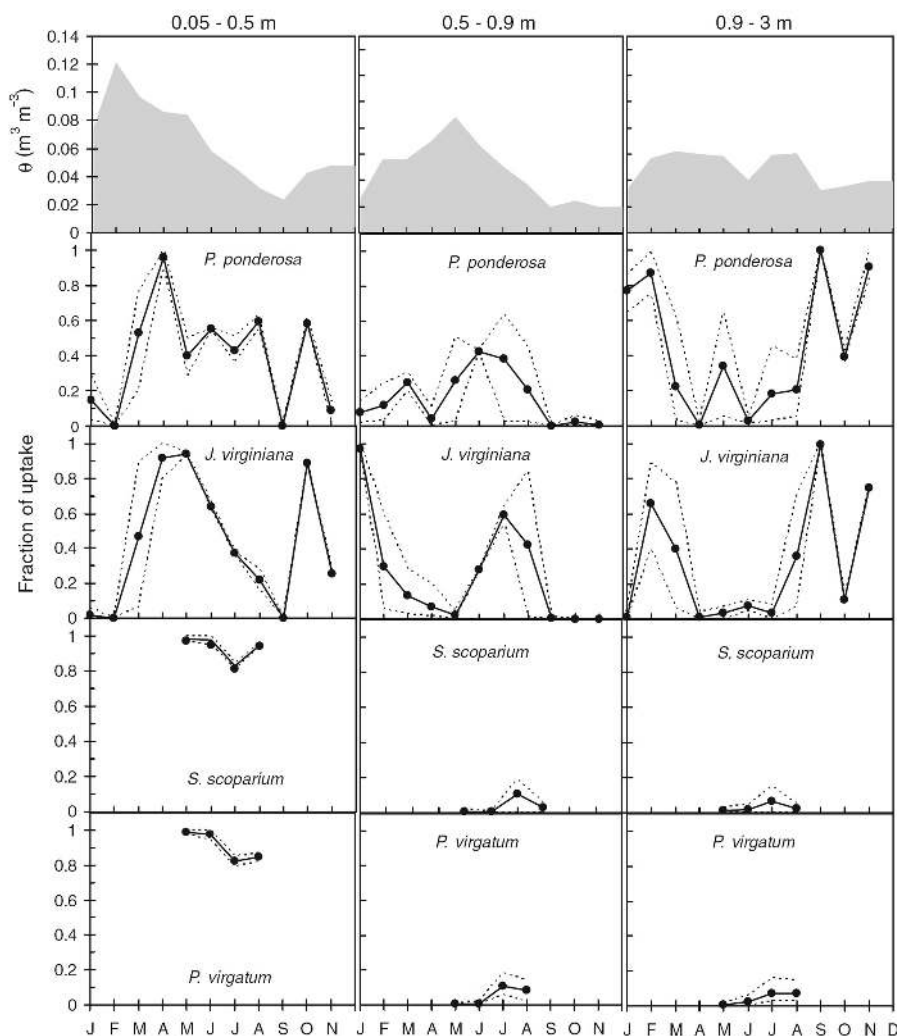


Figure 7. Seasonal dynamics in gravimetric soil water content (θ) and fraction of water uptake from 0.05–0.5, 0.5–0.9 and 0.9–3 m soil depths for trees (*P. ponderosa* and *J. virginiana*) and grasses (*S. scoparium* and *P. virgatum*) between May 2003 and April 2004. Solid and dashed lines represent the mean and the range of model solutions produced with the IsoSource program, respectively.

δD profiles taken over a year in an open savanna–grassland site in the Nebraska Sandhills. Generally, the $\delta^{18}O$ and δD values below 1–2 m depth, depending on the season, were uniform and comparable with the signature of deep groundwater taken from nearby wells. The exception to this was a pulse of $\delta^{18}O$ - and δD -enriched water observed at 1.5–2.5 m depth in May and June. In contrast, soil water between the surface and 1 m depth showed a clear $\delta^{18}O$ and δD profile that changed dramatically during the year. Isotopic ratios of soil water in the upper profile varied and reflected both the isotopic ratio of recent precipitation and evaporative fractionation. Thus, the isotopic soil water profile at the study site was useful in identifying the depth of plant water uptake.

Water sources did not differ between grass species (*S. scoparium* and *P. virgatum*) except for August. Isotopic values generally tracked recent precipitation, and the mixing model showed that water was extracted from the upper soil profile (0.05–0.5 m). Soil water uptake from below 0.5 m depth slightly increased during drought in *P. virgatum* and to a lesser extent in *S. scoparium*, yet uptake of soil water by deep grass roots appeared to be minimal in relation to the total water use of these species. The reliance on

water from the upper soil profile also contributed to the observed more negative Ψ in grasses compared with trees. Grasses of the shortgrass steppe of Colorado (Dodd et al. 1998), and the Corn Belt Region of Midwest (USA) (Asbjornsen et al. 2008), were also found to use shallow soil water predominantly. The use of shallow water in semiarid environments might reflect high tolerance to low resource environments and a reliance on rapid fine root turnover in response to water pulses and shortages (Asbjornsen et al. 2008). The fibrous roots of *S. scoparium* and *P. virgatum* are within 0.6–1.2 m of the surface, respectively (Stubben-dieck et al. 1985), with the majority being in the top 0.3 m (Wang et al. 2008). Although the deeper roots of *P. virgatum* relative to *S. scoparium* contributed to a small fraction of total water uptake, they may be an important survival mechanism in the Sandhills and might explain in part the high susceptibility of *S. scoparium* to prolonged periods of drought compared with *P. virgatum* and other C_4 grass species that dominate the Sandhills (Schacht et al. 2000, Awada et al. 2002). Values of grass $\delta^{18}O$ were less negative than both precipitation and uppermost soil profile values on a few sampling dates. This might reflect water uptake from very shallow soils that have been enriched by evaporation,

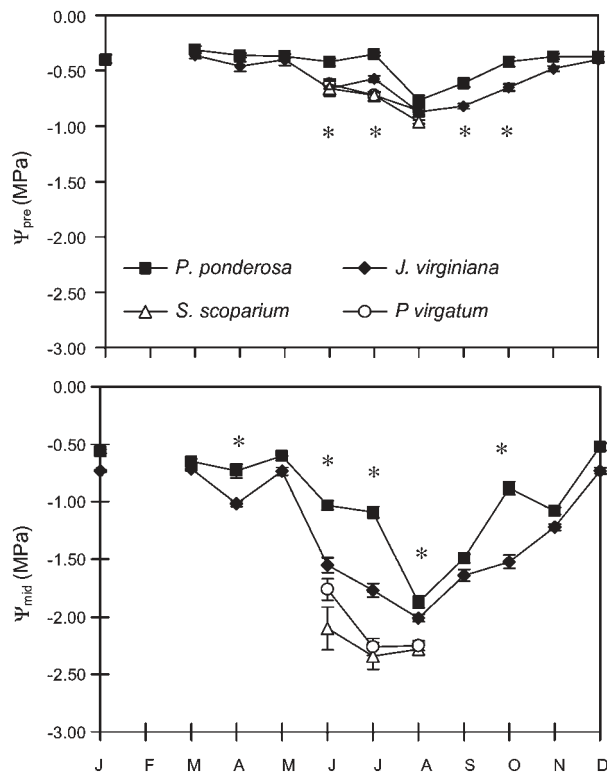


Figure 8. Seasonal dynamics in predawn (Ψ_{pre}) and midday (Ψ_{mid}) water potentials with standard error bars for trees (*P. ponderosa* and *J. virginiana*) and grasses (*P. virgatum* and *S. scoparium*) between May 2003 and April 2004. An asterisk (*) indicates significant differences between species within a sampling date at $P < 0.05$.

or species-specific physiologic and morphologic traits, or both (Wang et al. 1998, Barnard et al. 2006, Asbjornsen et al. 2008). Barnard et al. (2006) reported a general progressive enrichment of plant water ^{18}O from the root crown to leaves in several herbaceous species, concluding that root crowns showed the least variability and are the most suitable if not the best plant parts to sample for ^{18}O analysis in herbaceous species.

In contrast to grasses, *P. ponderosa* and *J. virginiana* exhibited significant plasticity in sources of water uptake. During winter, snow accumulated on site and both tree species extracted most of their soil water from below 0.9 m depth, with *P. ponderosa* possibly reaching deeper water sources than *J. virginiana*. Deep water uptake during winter could be attributed to low and more extreme soil temperatures in the upper soil profiles, reduced shoot demands, or changing root system function, or a combination thereof (Retzlaff et al. 2001). Winter measurements of E (Figure 9) and photosynthesis (Eggemeyer et al. 2006) showed that *P. ponderosa* and *J. virginiana* were physiologically active on warm winter days resulting in possible carbon gain (Awada et al. 2003) in trees while grasses are dormant. In spring, when shallow soil water became available, tree species extracted water from the upper soil profile (0.05–0.5 m) and relied lit-

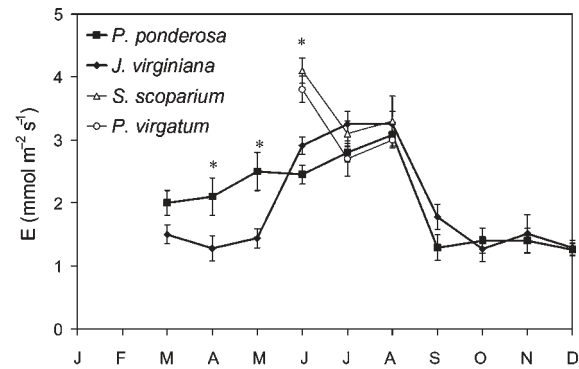


Figure 9. Seasonal dynamics in transpiration rates (E) with standard error bars for trees (*P. ponderosa* and *J. virginiana*) and grasses (*P. virgatum* and *S. scoparium*) between May 2003 and April 2004. An asterisk (*) indicates significant differences between species within a sampling date at $P < 0.05$.

tle on water from below 0.5 m depth. Water uptake from the upper soil profile in spring could be attributed to increases in fine root production, root system function as related to nutrient uptake (Retzlaff et al. 2001), and the ability of a species to switch its water uptake to soil profiles with highest water potentials (Plamboeck et al. 1999). During the growing season (May–August), *P. ponderosa* acquired a large fraction of its water from the 0.05–0.5 and 0.5–0.9 m soil profiles, whereas in *J. virginiana*, water uptake from the 0.05–0.5 m profile progressively declined between May and August, mirrored by an increase in the fraction of uptake from the 0.5–0.9 m profile, thus tracking the general increase in soil water within the 0.5–0.9 m profile, and being less responsive to growing season precipitation events. In September, soil water content declined to its minimum throughout the measured profile (0.05–3 m), and both tree species shifted their soil water uptake to below 0.9 m depth, and possibly groundwater (~7 m deep). We did not measure the rooting depth of tree species on site, but roots of *J. virginiana* and *P. ponderosa* are reported to penetrate up to 7.5 and 12 m deep, respectively (Burns and Honkala 1990). Root access to deep water sources and possibly groundwater did not seem to improve E , which significantly declined in September in response to severe drought, but might have played a role in the recovery of water potentials. This might be critical for plant survival during drought (West et al. 2007), especially for *P. ponderosa*, a species prone to xylem cavitation induced by water stress (Law et al. 2001, Martínez-Vilalta et al. 2004). However, *Juniperus* spp. are reported to be among the most resistant woody plants to drought-induced xylem cavitation (Willson et al. 2008). *Juniperus virginiana* has been found to maintain stomatal conductance, photosynthetic activity (Eggemeyer et al. 2006), and in this study E at significantly more negative water potentials compared with *P. ponderosa*. The latter species was reported to have strong stomatal control (Law et al. 2001), and high sapwood to leaf area ratios (Piñol and Sala 2000) to avoid xylem cavitation, rendering this species sensi-

tive to prolonged periods of drought. These differences in drought resistance strategies between the study tree species might explain the widespread encroachment by *J. virginiana* in water-limited grasslands relative to *P. ponderosa* (Schmidt and Stubbendieck 1993). In October, and with the increase in soil water availability in the upper soil profile, *J. virginiana* switched to extracting water from the 0.05–0.5 m profile, and *P. ponderosa* used a mixture of water derived from both the 0.05–0.5 and below 0.9 m depths. Depth of water uptake by woody plants in other studies has been shown to be species and ecosystem specific (e.g., Phillips and Ehleringer 1995, Williams and Ehleringer 2000, Weltzin and McPherson 1997, Asbjornsen et al. 2008, Goldstein et al. 2008), which illustrates the importance of studying individual species within ecosystems (Goldstein et al. 2008). For example, although our results are in agreement with what has been reported for the piñon-juniper woodland of southern Utah (West et al. 2007), *Pinus edulis* Englmn acquired water from both shallow and deep water sources, whereas *J. osteosperma* Torr. used shallow water when water was available in the spring and shifted to deeper sources for the remainder of the growing season. Furthermore, *Pinus taeda* L. was reported to use water predominantly from the upper soil profile (Retzlaff et al. 2001). Darrouzet-Nardi et al. (2006) found that the invading shrub *Artemisia rothrockii* A. Gray used deeper water than native herbaceous species.

The two encroaching tree species acquired water outside of the growing season, competed for shallow water with grasses during spring and early summer, and depended on water drawn from deeper in the soil profile during drought. This will have implications for tree–grass dynamics in semiarid grasslands. A shallow grass rooting zone may facilitate the co-existence of woody species and grasses (Le Roux et al. 1995, Weltzin and McPherson 1997), or give woody species a competitive advantage in the absence of fire, and projected climate change (Daly et al. 2000, Bond et al. 2005, Huxman et al. 2005). Thus, although grasses may outcompete trees for shallow soil water when their rooting zones overlap (Belsky 1994, Daly et al. 2000), trees use deep soil water unavailable to grasses and avoid grass competition for water during the six months each year when the C₄ grasses are dormant. *Pinus ponderosa* and *J. virginiana* appear to be suited for survival in a semiarid grassland, provided sufficient soil water exists in early spring, deep soil water persists during drought periods, and fire suppression continues to be a dominant policy (Eggemeier et al. 2006). This has important implications for regional hydrology. The Nebraska Sandhills are a major recharge zone for the High Plains (Ogallala) Aquifer (36% and 65% of the aquifer area and water, respectively, are located under Nebraska; Bleed and Flowerday 1998). Szilagyi et al. (2005) estimated that between 6% and 14% of annual precipitation falling across the entire Sandhills region enters the groundwater system (i.e., it is unused by plant roots). This is a surprisingly high groundwater recharge rate for a well-vegetated region where potential evapotranspiration well exceeds actual evapotranspiration on an annual

basis (Bleed and Flowerday 1998). However, if as our results suggest, grasses do not rely on water from deep in the soil profile, this high recharge rate is easier to explain. Our results indicate why high groundwater recharge rate may be affected with ongoing encroachment by native conifer tree species into grassland–savanna regions (Huxman et al. 2005). These results are also supported by soil water measurements (2005–2008, unpublished data) that have shown that soils (0.05–3 m depth) in dense sites of *J. virginiana* and of *P. ponderosa* are significantly drier than in open grasslands at NNF. The projected increase in the frequency and severity of droughts in semiarid ecosystems with climate change are predicted to further alter the competitive relationship between co-existing species and affect ecosystem processes. For the two studied tree species, prolonged summer drought would have greater effects on *P. ponderosa* than on *J. virginiana*, which might have further implications on the distributions of woody species in the semiarid grasslands of Nebraska.

Acknowledgments

This work was supported by the McIntire Stennis Forest Research Funds-USDA, and an Interdisciplinary Agriculture Research grant, ARD-University of Nebraska-Lincoln. K. Eggemeier would like to acknowledge a fellowship from the Center for Great Plain Studies. The authors appreciate the assistance of Dr. D. Snow (Water Sciences Laboratory, UNL), Kenneth Elgersma and J. Hellerick, and the cooperation of the US Forest Service. They would like thank the three anonymous reviewers for for *Tree Physiology* for their comments on this manuscript.

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