

# Seasonal patterns in depth of water uptake under contrasting annual and perennial systems in the Corn Belt Region of the Midwestern U.S.

H. Asbjornsen · G. Shepherd · M. Helmers ·  
G. Mora

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**Abstract** In agricultural landscapes, variation and ecological plasticity in depth of water uptake by annual and perennial plants is an important means by which vegetation controls hydrological balance. However, little is known about how annual and perennial plants growing in agriculturally dominated

landscapes in temperate humid regions vary in their water uptake dynamics. The primary objective of this study was to quantify the depth of water uptake by dominant plant species and functional groups growing in contrasting annual and perennial systems in an agricultural landscape in Central Iowa. We used stable oxygen isotope techniques to determine isotopic signatures of soil water and plant tissue to infer depth of water uptake at five sampling times over the course of an entire growing season. Our results suggest that herbaceous species (*Zea mays* L., *Glycine max* L. Merr., *Carex* sp., *Andropogon gerardii* Vitman.) utilized water predominantly from the upper 20 cm of the soil profile and exhibited a relatively low range of ecological plasticity for depth of water uptake. In contrast, the woody shrub (*Symphoricarpos orbiculatus* Moench.) and tree (*Quercus alba* L.) progressively increased their depth of water uptake during the growing season as water became less available, and showed a high degree of responsiveness of water uptake depth to changes in precipitation patterns. Co-existing shrubs and trees in the woodland and savanna sites extracted water from different depths in the soil profile, indicating complementarity in water uptake patterns. We suggest that deep water uptake by perennial plants growing in landscapes dominated by rowcrop agriculture can enhance hydrologic functioning. However, because the high degree of ecological plasticity allows some deep-rooted species to extract water from surface horizons when it is available, positive effects of deep water uptake may vary depend-

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H. Asbjornsen  
Department of Natural Resource Ecology and Management,  
Iowa State University,  
339 Science II,  
Ames, IA 50010, USA

G. Shepherd  
Bennett Agricultural Research Corp.,  
1109 Ivy Ave.,  
Richland, IA 52585, USA

M. Helmers  
Department of Agricultural and Biosystems Engineering,  
Iowa State University,  
209 Davidson Hall,  
Ames, IA 50010, USA

G. Mora  
Department of Geological and Atmospheric,  
Iowa State University,  
12 Science I,  
Ames, IA 50010, USA

H. Asbjornsen (✉)  
Iowa State University,  
234 Science II,  
Ames, IA 50010, USA  
e-mail: hasbjorn@iastate.edu

ing on species' growth patterns and water uptake dynamics. Knowledge about individual species' and plant communities' depth of water uptake patterns in relation to local climate conditions and landscape positions can provide valuable information for strategically incorporating perennial plants into agricultural landscapes to enhance hydrologic regulation.

**Keywords** Depth of water uptake · Grasslands · Prairie · Stable isotopes · Sustainable agriculture

## Introduction

Water is a major driver of plant productivity (Schulze and Zwolfer 1987; Gholz et al. 1990). Conversely, plants exert a strong influence on the local and regional hydrologic balance through their role in cycling water between the soil and atmosphere (Chahine 1992; Mahmood and Hubbard 2003). In the agricultural Corn Belt region of the Midwestern U.S., the replacement of deeply rooted native (pre-European settlement) perennial prairie and savanna ecosystems with more shallow-rooted, annual cropping systems has profoundly altered plant controls on ecosystem water balance. Increased overland flow, loss of nutrients and sediment into surface and groundwaters, and greater fluctuations in streamflow resulting in more frequent drought and flooding are just some of the environmental consequences attributed to intensive rowcrop agricultural production (Burkart and James 1999; Schilling and Libra 2000; Fohrer et al. 2001; Rabalais et al. 2002). Increasing evidence suggests that incorporation of perennial plant cover in landscapes dominated by rowcrop agriculture can enhance water balance functions (Tilman 1999; Tilman et al. 2002; Boody et al. 2005; Schulte et al. 2006). However, paucity of data on water uptake dynamics in contrasting annual and perennial plant communities currently hampers the development of both a theory and practice of using mixtures of annual-perennial vegetation to enhance hydrologic functioning in agricultural landscapes (Eckhardt et al. 2003).

One of the primary determinants of plant water uptake dynamics and, in turn, plant mediation of the hydrological balance, is the depth from which plants extract water from the soil (e.g., Qiu et al. 2001; Fu et al. 2003). Plants rarely take up water from a single

fixed depth throughout the growing season, and often shift their depth of water uptake in response to changing environmental conditions and soil moisture availability. Varying degrees of ecological plasticity (i.e., the capacity to adjust morphological and/or physiological characteristics in response to changing environmental conditions; Pigliucci 2001; Callaway et al. 2003) in rooting functions have been widely documented for plants growing in different ecosystems (Crick and Grime 1987; North and Nobel 1998; Liu et al. 2000; Callaway 1990; Ponton et al. 2002; Peek et al. 2005). However, relatively little attention has focused on assessing ecological plasticity of water uptake dynamics in crop species (Engels et al. 1994; Carmi et al. 1993; Dardanelli et al. 1997; Araki and Iijima 2005).

Depth of water uptake patterns by the vegetation directly affects the hydrological balance by influencing vertical and horizontal flowpaths of water. Water uptake by more deeply rooted vegetation reduces volumetric water content at greater depths relative to more shallow-rooted vegetation, thereby increasing total soil water storage capacity (Jofre and Rambal 1993; Randall et al. 1997; Brye et al. 2000; Fu et al. 2003; Fitzjohn et al. 1998; Huxman et al. 2005). In humid regions such as the Midwestern U.S., deep water uptake by plants can increase infiltration (Bharati et al. 2002) and reduce surface runoff and nutrient and sediment loss (Daniels and Gilliam 1996; Udawatta et al. 2002). Further, more deeply rooted plants are more likely to survive extended periods of drought by accessing more moist soil layers (Chaves et al. 2002). Drought-tolerance in plant communities is important for sustaining ecosystem processes related to nutrient, water, and carbon cycles and storage, all of which can have important implications for regulation of the hydrological balance (Baldocchi et al. 2004; Huxman et al. 2005).

Plant root distribution and plasticity in water uptake patterns is also, in part, a response to climate. On a global basis, plants growing in relatively wet climates tend to be more shallow-rooted compared to plants adapted to dry climates (Liu et al. 2000; Canadell et al. 1996; Collins and Bras 2007). In moderate or transitional climates like the Midwestern U.S., which although relatively humid may also experience extended periods of drought, ecological plasticity in root functions may enhance adaptation of native vegetation to high variability in water availability (Liu et al.

2000). For example, Knapp (1984) reported an exceptionally large range of osmotic adjustment in three tallgrass prairie species in Kansas in response to wet vs. dry years, and attributed this to the relatively frequent occurrence of drought in the tallgrass prairie biome. An even more extreme example is seen in desert ecosystems which experience pulses of rainfall, where plasticity of root production, growth and senescence in response to intermittent or heterogeneous water supply is critical to plant function (North and Nobel 1998).

The capacity of annual and perennial plant species to regulate the hydrological balance via their water uptake dynamics also varies markedly. Annual crops have a short active growing season, so that the ground is generally bare in early spring and late fall. In the Midwestern U.S., a large proportion of the annual precipitation occurs during this time period and precipitation generally exceeds evapotranspiration (Singh et al. 2007). Low plant water use combined with excess water leaves the soil vulnerable to surface runoff and/or leaching losses below the root zone. Further, >85% of the root biomass of corn and soybean roots is usually concentrated in the top 30 cm of the soil horizon, so that most water uptake may be restricted to shallow depths (Laboski et al. 1998; Benjamin and Nielsen 2006). Notwithstanding, a few studies report relatively deep roots for some crop species (e.g., 1.6 m for soybean, Mayaki et al. 1976; 2.3 m for soybean and 1.9 m for corn, Dardanelli et al. 1997), suggesting that water uptake by crops may extend to deeper horizons in some environments. However, because vertical distribution of root biomass in the soil profile and actual depth of plant water uptake are not necessarily correlated (Midwood et al. 1998; Yu et al. 2007), field data on water uptake patterns under varying environmental conditions are needed.

In contrast to annual cropping systems, many prairie species, especially  $C_3$  cool season forbs, initiate growth in early spring and remain active until late fall, thus providing continuous vegetative cover throughout the growing season. Although the majority of prairie root biomass (~ 80%) is also located in the upper 30 cm of the soil profile (Krucera and Dahlman 1968; Sims and Singh 1978), prairie roots commonly extend down to 2 m (Weaver 1958; Tufekcioglu et al. 1999), while oak tree roots in savanna ecosystems may reach 4.3 m in depth

(Canadell et al. 1996). Further, high species diversity in grassland and savanna ecosystems allows for greater vertical heterogeneity in rooting depth which can lead to niche partitioning and complementarity in water uptake patterns among species (Weltzin and McPherson 1997; Fargione and Tilman 2005). The co-existence of species having different structural and functional characteristics in perennial ecosystems can increase total resource uptake and ecosystem productivity (Ehleringer et al. 1991; Flanagan et al. 1992; Dodd et al. 1998; Nippert and Knapp 2007).

The primary objective of our study was to quantify the depth of water uptake by dominant plant species from different functional groups (herbaceous, shrub, tree) under contrasting annual (rowcrop corn and soybean) and perennial (reconstructed tallgrass prairie, restored oak savanna, encroached savanna-woodland) systems in an agricultural landscape in Central Iowa over the course of an entire growing season. We hypothesized that all plant species will take up water from relatively shallow soil depths during periods of high moisture availability (early and late growing season), but that the capacity of species to shift to deeper water supplies will vary among species due to differences in rooting functions and degree of ecological plasticity. Specifically, we predicted that more structurally and functionally diverse perennial plant communities (restored savanna, encroached savanna-woodland, reconstructed prairie) will extract water from greater depths in the soil profile relative to simplified annual cropping (corn, soybean) systems, and that woody functional groups (trees and shrubs) will exhibit greater ecological plasticity in response to changes in water availability compared to herbaceous species. This study provides insight into the underlying mechanisms by which annual and perennial vegetation regulate hydrological processes in intensively managed agricultural landscapes and the potential for enhancing these services through strategically maintaining or incorporating perennial plants.

## Materials and methods

### Description of the study site and research design

This study was conducted at the Neal Smith National Wildlife Refuge (NSNWR) in Jasper County, central

Iowa (41°33'N, 93°17'W). The Refuge, administered by the National Fish and Wildlife Service, was established in 1991 under the mission of converting over 3,400 ha of an agriculturally dominated landscape to pre-European settlement tallgrass prairie and oak savanna ecosystems. Presently, the Refuge consists of a mosaic of reconstructions and agricultural land uses with approximately 1,200 ha planted to tallgrass prairie through annually successive plantings. Based on a long-term weather station near Des Moines, IA (41°32'N/93°39'W), this region has a mean annual precipitation (1971–2000 average) of 88.2 cm and a mean annual temperature of 9.6°C (National Climate Data Center, NCDC 2007a). In 2005, annual precipitation was approximately 64.2 cm and average monthly temperature was 10.8°C, ranging from –3.0°C in February to 24.8°C in July (NCDC 2007b). Dominant plant species growing in five different vegetative cover types were selected for determination of depth of water uptake, as follows: (1) encroached savanna woodland<sup>1</sup> (“woodland” hereafter): *Quercus alba* L. (tree), *Symphoricarpos orbiculatus* Moench. (shrub), and *Carex* sp. (sedge); (2) oak savanna restoration (“savanna” hereafter): *Q. alba*, *S. orbiculatus*, and *Carex* sp.; (3) 4-yr old reconstructed prairie (“prairie” hereafter): *Andropogon gerardii* Vitman (grass); (4) cornfield: *Zea mays* L. (corn); (5) soybean field: *Glycine max* L. Merr. (soybean). These five study areas were located within 1.6 km of each other under similar topographical conditions at approximately 256 to 277 m a.s.l. and NW aspect. Soils across the study sites are predominantly mesic Mollic Hapludalfs, Typic Argiudolls, and Typic Hapludolls characterized by a loam to silt clay loam texture (Otley silty clay loam, Ladoga silt loam, Nira silty clay loam, and Gara loam) (Soil Conservation Service 1979). Meteorological data (rainfall, solar radiation, humidity, and wind speed) were collected during the study period with an Intelimet<sup>TM</sup> Weather Station (Dynamax, Inc.) located in an open clearing adjacent to the study sites.

#### Analysis of oxygen isotope ratios of soil water and plant xylem tissue

We applied stable isotope techniques as natural tracers to infer the predominant depth of water uptake in our study species over time. This approach is based on the natural formation of isotopic gradients in soil water

with depth in the soil profile due to evaporative fractionation of the lighter isotope, and the retention of the isotopic signature of the soil water by the non-evaporating plant tissue, such that the approximate depth of water uptake can be directly inferred (e.g., Allison and Hughes 1983, Ehleringer and Dawson 1992), assuming that most water uptake occurs from within a small depth range (see Phillips and Gregg 2003 and Asbjornsen et al. 2007 for discussion of assumptions and limitations of this approach).

We collected plant and soil water samples for determination of oxygen isotope ratios monthly from May through September of 2005. The sampling date was near the beginning of each month (May 2, June 2, July 2, August 2, and September 1, 2005). For soil water, a single sample was collected from 0–5, 5–10, 10–20, 20–40, 40–60, 60–80, 80–100 and 100–150 cm depth increments within each treatment area using a 7.5 cm diameter telescoping bucket auger (AMS Forestry Suppliers). Concomitantly, non-photosynthetic tissue samples (e.g., plant stems) of all study species were collected from two to five individuals (in accordance with their size) growing near the soil sampling sites at least two hours after sunrise to ensure the establishment of isotopic steady-state conditions. Groundwater wells were installed at each site to a depth of approximately 8 m and groundwater samples collected on each sampling date to assess the oxygen isotope ratio of the groundwater source. Although weather conditions may have varied across sampling dates, continuous monitoring of climatic variables (above) allowed us to take such differences into account when interpreting the results. Depth to groundwater was measured on each sampling date. Upon collection, soil and plant tissue samples were immediately placed in 20 mL scintillation vials, tightly closed with Teflon-sealed caps, wrapped in Parafilm to prevent evaporative fractionation, and kept at approximately 3°C prior to the isotopic analysis.

Oxygen isotope ratios were determined on duplicate samples for each soil and plant water sample via equilibration with CO<sub>2</sub> using a Finnigan Gas-Bench II fitted to a Finnigan Delta Plus XL isotope mass-spectrometer, following the protocols outlined by Asbjornsen et al. (2007). Briefly, aliquots of soil and plant tissue sample were placed in 12 mL exetainer<sup>TM</sup> vials (Labco Limited, UK) that were flushed with a mixture of 0.5% CO<sub>2</sub> in helium of known isotopic composition. Samples were allowed to equilibrate at

25°C for 24 hours for the soil samples and for 72 hours for the plant tissues. The isotopic composition of the equilibrated CO<sub>2</sub> was then determined, and corrected for the varying amounts of soil and plant tissue water (derived gravimetrically). Isotope values were normalized to the V-SMOW/SLAP scale, using two lab water standards, and reported in the standard per mil (‰) notation relative to VSMOW. Analytical precision for individual measurements was better than 0.05‰ and accuracy was better than 0.1‰ as determined by the repeated measurements of water standards.

We used the direct inference approach (Brunel et al. 1995; Jackson et al. 1996; Mora and Jähren 2003) to determine the predominant soil depth from which each study species was extracting water throughout the growing season. According to this approach, the stable hydrogen (D and H) or oxygen (<sup>18</sup>O and <sup>16</sup>O) isotopic signature of plant stem water is compared with the isotopic signature of water at varying depths in the soil profile to determine at which depth the two values correspond to each other, which is interpreted as the depth from the plant extracted most of its water during the preceding time period. This approach assumes that there are no other possible water sources other than soil water and that the roots preferentially take soil water from a single depth zone during any given period of time (Asbjørnsen et al. 2007). An important limitation to this approach occurs when the isotopic gradient is not asymptotic and irregularities in the isotopic gradient in the soil profile occur. In these cases, different soil depth intervals may exhibit identical isotopic values for soil water, which would result in more than one possible depth of water uptake if plant tissue isotope values overlapped with those of soil water from these different depths. Whenever these situations occurred in our data (e.g., most frequently for *Q. alba*), we consistently selected the more conservative (i.e., shallower) soil depth. Further, we focus our discussion of major conclusions on those isotopic records having relatively uniform gradients.

#### Statistical analysis

Soil water  $\delta^{18}\text{O}$  values were analyzed using analysis of variance to assess the effect of site at each depth within the soil profile ( $\alpha=0.05$ ). Analysis of variance was also used to assess temporal patterns in soil water  $\delta^{18}\text{O}$  values by analyzing each site individually across

the sampling periods at each soil depth. If the results show no site effect on the soil water  $\delta^{18}\text{O}$  with depth (i.e., isotopic soil profiles are similar among sites), then plant water  $\delta^{18}\text{O}$  can also be compared using analysis of variance to evaluate the effect of plant species and vegetative cover type on isotopic composition. Similarly, if no temporal effect is detected on the soil water  $\delta^{18}\text{O}$ , then plant water  $\delta^{18}\text{O}$  can be compared across the different sampling periods. Least significant difference modeling was used to test for significant differences among mean values.

#### Results

Seasonal patterns in atmospheric conditions, precipitation data, and groundwater level

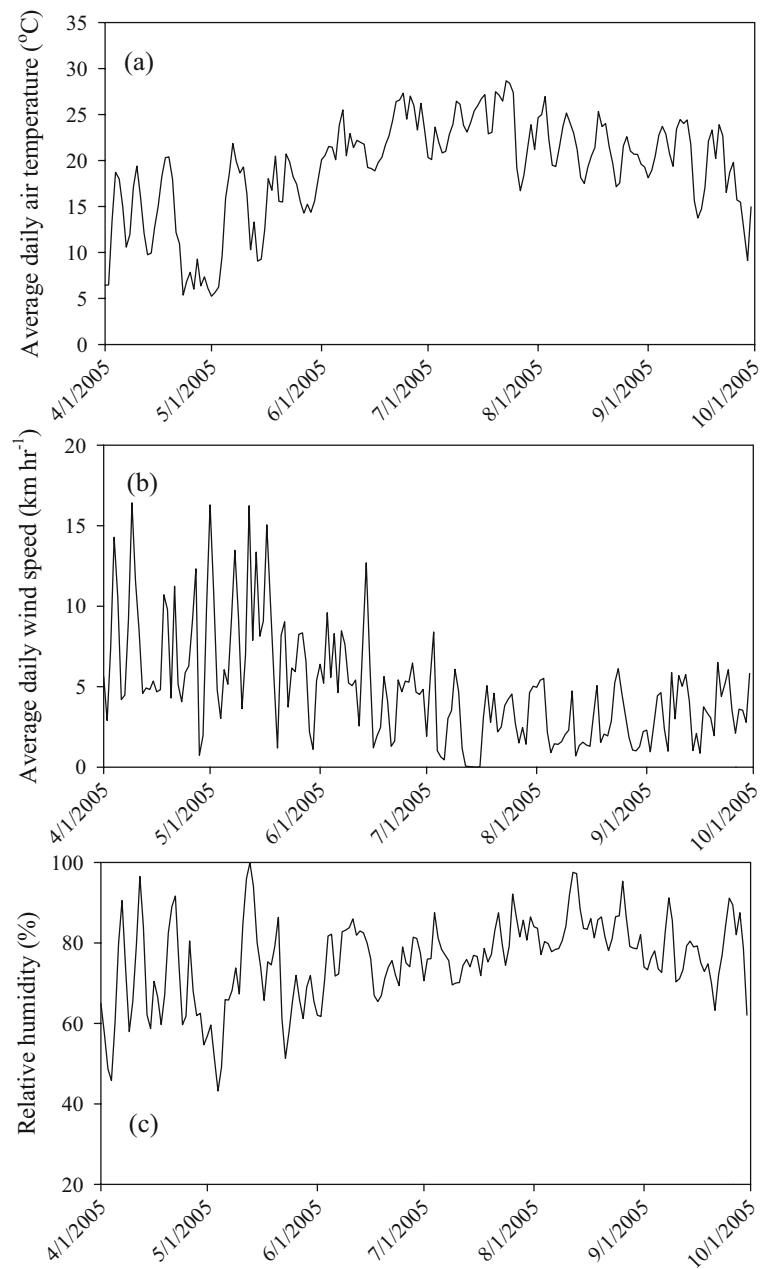
During the study period the average air temperature ranged from 5°C to 29°C (Fig. 1a), the average daily wind speed ranged from 0 km hr<sup>-1</sup> to 16 km hr<sup>-1</sup> (Fig. 1b), and the average daily relative humidity ranged from 43% to 100% (Fig. 1c). The total rainfall from April 1, 2005 through September 30, 2005 was 521 mm, which is 15% lower than the 30-yr average rainfall for this period (616 mm; Fig. 2a). The maximum daily precipitation was 55.6 mm on May 12, 2005; while four dry periods of greater than 9 consecutive days without any rainfall were observed in 2005 (April 27 to May 5, June 14 to June 24, July 5 to July 17, and August 27 to September 7; Fig. 2b). The amount of rainfall in the two week period preceding each sampling event varied from a minimum of 8.6 mm (June 2) to a maximum of 87.4 mm (August 27; Fig. 2c). Groundwater levels generally declined throughout the sampling period (Fig. 3). For the July through September sampling periods the water table was below the deepest depth for soil water sampling at all sites except for the soybean site at the July sampling.

#### Isotopic profiles of soil water across the study sites

In general,  $\delta^{18}\text{O}$  values of soil water increased from May through August and then declined in September (Fig. 4). Across all sites and sampling events, the highest  $\delta^{18}\text{O}$  values occurred in the top 5 cm of the soil profile (Fig. 4). Values typically declined with depth, with high inter-site variability occurring in the



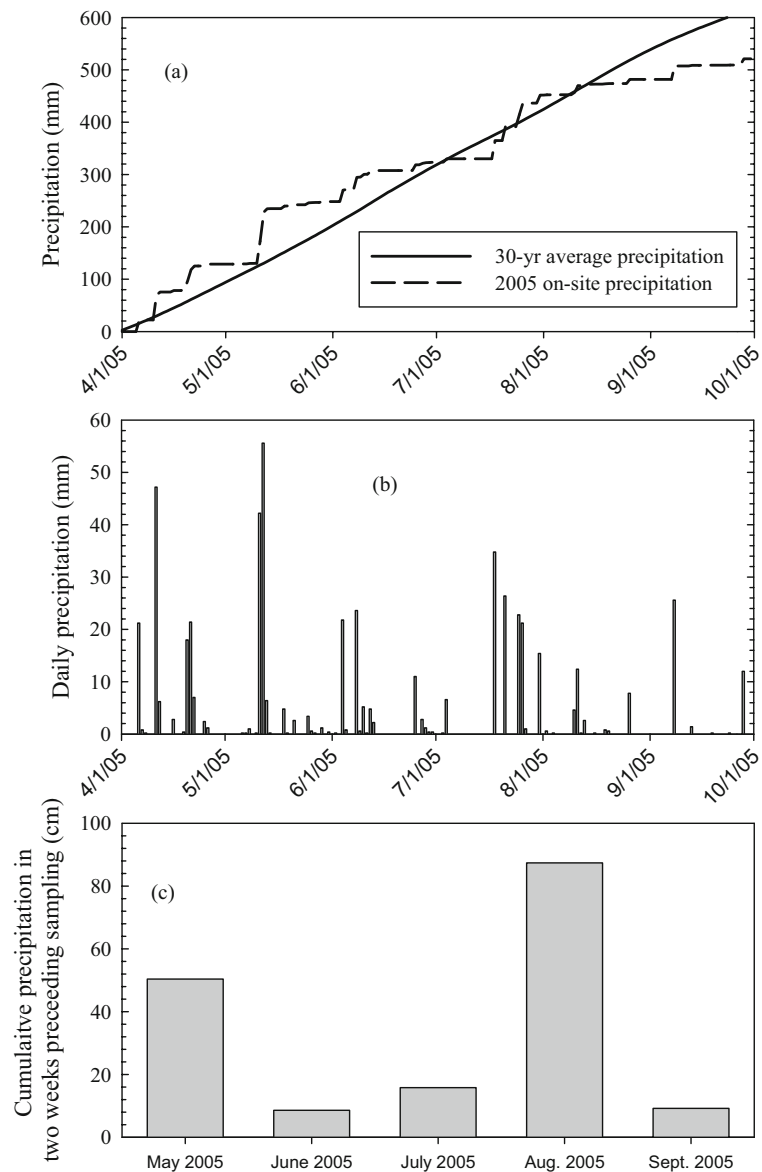
**Fig. 1** On-site average (a) air temperature, (b) average wind speed, and (c) relative humidity



rate of decline. Early in the season (May), a discrete minimum in  $\delta^{18}\text{O}$  values along the isotopic soil profile gradient occurred at most sites; the depth at which this minimum occurred was greater for the savanna site (40–60 cm) and shallower in the prairie, soybean, and cornfield sites (10–30 cm) (Fig. 4a). This discrete minimum became less pronounced or disappeared altogether as the season progressed.

Isotopic soil profiles under the different vegetative cover types were highly variable, as indicated by the significant differences in  $\delta^{18}\text{O}$  values when comparing the same depth and sampling event across study sites (Table 1 and Fig. 5). Notwithstanding these differences, the isotopic gradients became increasingly similar among the sites as the season progressed, particularly in August and September. Soil water  $\delta^{18}\text{O}$

**Fig. 2** On-site precipitation: (a) cumulative precipitation from April 1, 2005 through September 30, 2005 and the 30-yr average precipitation, (b) daily precipitation, and (c) cumulative precipitation in two week period preceding sampling



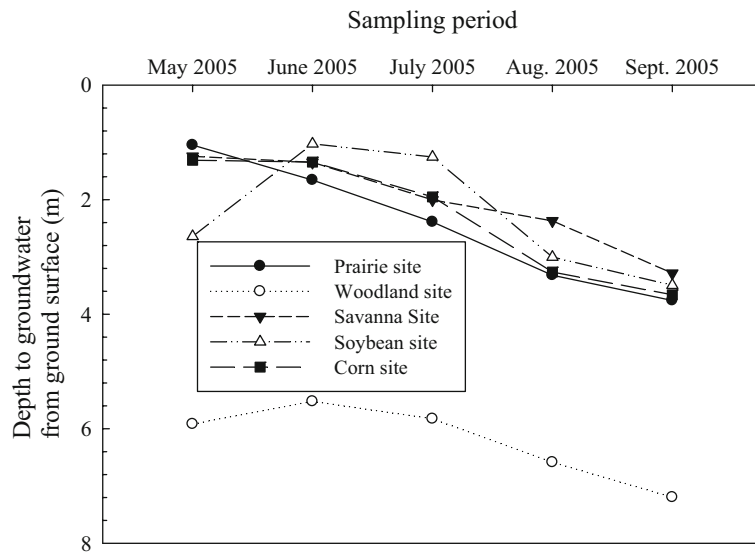
values at depths below 100 cm were fairly constant within each site for the August and September sampling periods (Table 1).

#### Isotopic composition of plant xylem tissue across species

We observed a consistent trend in  $\delta^{18}\text{O}$  values across species, with *Q. alba* and *S. orbiculatus* growing in the savanna and woodland sites having the lowest  $\delta^{18}\text{O}$  values ( $-8.97$  to  $-5.06\text{‰}$ ), and *Carex* sp. (savanna and

woodland) displaying the highest  $\delta^{18}\text{O}$  values ( $-4.58$  to  $1.13\text{‰}$ ; Fig. 6). *Zea mays* and *G. max*  $\delta^{18}\text{O}$  values were intermediate and ranged from  $-6.37$  to  $-2.88\text{‰}$ . Intra-specific variation in  $\delta^{18}\text{O}$  values of plant water for each of the nine species between sampling events was typically less than  $2.79\text{‰}$ , with the exception of higher variability (up to  $4.90\text{‰}$ ) in  $\delta^{18}\text{O}$  values recorded for *Carex* sp. and *S. orbiculatus* (Fig. 6). Among the studied species, *A. gerardii* had the smallest range of isotopic variability (less than  $1.38\text{‰}$ ). Positive  $\delta^{18}\text{O}$  values were obtained for *Carex*

**Fig. 3** Depth to groundwater at the five sampling periods



sp. in July and September, reaching a maximum of 1.13‰ in July at the savanna site.

The high degree of variability in the isotopic soil profiles across the study sites precludes direct comparison of isotopic signatures of plant xylem tissue among species growing in different vegetative cover types since determining whether measured differences in plant  $\delta^{18}\text{O}$  values are due to actual differences in depth of water uptake or merely an artifact of the differences in soil water isotope profiles is not possible. Thus, we only apply statistical analysis to test for within site differences in the isotopic signatures of co-existing plant species. For the woodland and savanna sites, *Carex* sp. had significantly higher  $\delta^{18}\text{O}$  values than either the *Q. alba* or *S. orbiculatus* (Table 2). Later in the growing season (August and September sampling events), *S. orbiculatus* has significantly greater  $\delta^{18}\text{O}$  values compared to *Q. alba*. Comparisons of depth of water uptake across sites and sampling times was limited to assessments of general trends based on the water uptake ranges derived from the stable  $\delta^{18}\text{O}$  values for each study species.

#### Inferred depth of plant water uptake

Although the isotopic gradients for soils at all of the sites were irregular,  $\delta^{18}\text{O}$  values for plant water and soil water overlapped at a single depth range for most sampling events, enabling relatively accurate inferences of depth of water uptake for each species (Figs. 7, 8, 9 and 10). Prior to crop emergence (May 2

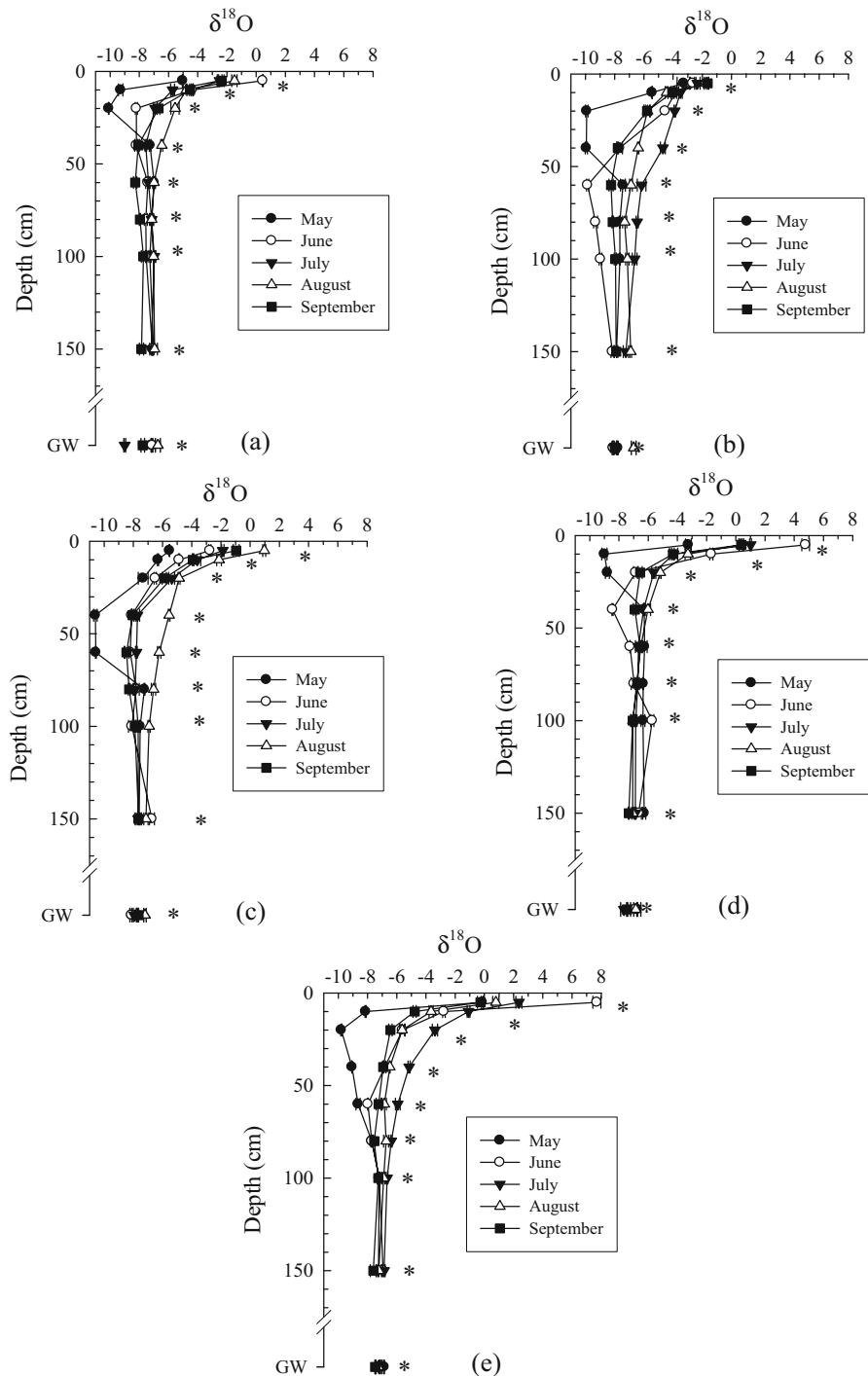
sampling event, relatively high rainfall during preceding 2 weeks: 50.4 mm), *A. gerardii* extracted water from the upper 0–5 cm. *Carex* sp. in the woodland and savanna site exhibited  $\delta^{18}\text{O}$  values more positive than those of the soil water from the uppermost soil horizon (Figs. 7, 9, 10, and 11). The savanna and woodland *Q. alba* trees and *S. orbiculatus* shrubs also extracted water from relatively shallow soil depths on May 2, though slightly deeper than the herbaceous plants (20–40 cm).

Early in the crop growing season (June 2 sampling event, low rainfall during preceding 2 weeks: 8.6 mm), all herbaceous species obtained their water from the upper 20 cm, with the corn, soybean, and prairie species extracting water from slightly more shallow depths (5–10 cm) compared to *Carex* sp. (20 cm; Figs. 8 and 12). *Symphoricarpos orbiculatus* obtained its water from a depth of approximately 30 cm when growing in both the savanna and woodland sites. Depth of water uptake for *Q. alba* reached 40 cm for both the woodland and savanna trees.

As the season progressed and rainfall declined, depth of plant water uptake shifted to deeper levels in the soil profile for all species. During the peak growing season (e.g., July 2 sampling date, relatively low rainfall during previous 2 weeks: 15.8 mm), the corn, soybean, and prairie species extended their depth of water uptake down to 20 cm (Figs. 9 and 12). *Symphoricarpos orbiculatus* obtained water from approximately 60 cm depth when growing in either the savanna or woodland site. Savanna *Q. alba* trees



**Fig. 4** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water for the five sample periods at the five sites: (a) Prairie, (b) Woodland, (c) Savanna, (d) Soybean, and (e) Corn (\*beside a depth interval indicates statistically significant difference at  $\alpha=0.05$ )



obtained water from an interval of 40–150 cm for the July 2 sampling date, whereas woodland *Q. alba* trees likely obtained water from depths greater than 150 cm (e.g., its  $\delta^{18}\text{O}$  values were more negative than isotopic signatures within the entire soil profile down to

150 cm). The *Carex* sp. once again had  $\delta^{18}\text{O}$  values generally more positive than the  $\delta^{18}\text{O}$  values obtained for the soil profile (a pattern that continued through the August and September sampling events), suggesting extraction of water from very near the soil surface,

**Table 1** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water at the five sites for the five sample collection periods: (a) May 2005, (b) June 2005, (c) July 2005, (d) August 2005, and (e) September 2005

Depth	Treatment				
	Prairie	Woodland	Savanna*	Soybean	Corn
(a) May					
5	-5.03(0.022)cA	-3.27(0.955)bA	-5.53(0.013)c	-3.25(0.192)bA	-0.14(0.063)aA
10	-9.27(0.151)dE	-5.44(0.003)aB	-6.31(0.041)b	-9.00(0.181)dD	-8.14(0.035)cE
20	-10.09(0.023)cF	-9.91(0.085)cD	-7.33(0.333)a	-8.80(0.135)bD	-9.79(0.038)cH
40	-7.26(0.060)bD	-9.94(0.078)dD	-10.60(0.125)e	-6.27(0.013)aB	-9.07(0.002)cG
60	-6.99(0.097)bB	-7.44(0.165)cC	-10.57(0.026)e	-6.24(0.171)aB	-8.65(0.139)dF
80	-7.15(0.078)bBCD	-7.65(0.009)cC	-7.24(0.033)b	-6.34(0.006)aB	-7.71(0.033)cD
100	-7.28(0.068)bD	-7.65(0.026)cC	-7.54(0.004)c	-6.36(0.132)aB	-7.20(0.005)bC
150	-7.03(0.010)bBC	-7.87(0.009)eC	-7.60(0.030)d	-6.27(0.101)aB	-7.25(0.002)cC
GW <sup>a</sup>	-7.17(0.024)CD	-7.80(0.026)C	-7.76	-6.75(0.027)C	-6.87(0.010)B
(b) June					
5	0.45(0.037)cA	-2.66(0.221)d	-2.76(0.078)dA	4.78(0.261)bA	7.70(0.275)aA
10	-4.39(0.052)dB	-3.84(0.083)c	-4.87(0.038)eB	-1.68(0.113)aB	-2.77(0.089)bB
20 <sup>b</sup>	-8.20(0.076)E	-4.54	-6.51(0.078)C	-6.86(0.139)D	-5.61(0.183)C
40	-8.20(0.115)cdE	-7.67(0.198)b	-8.11(0.013)cD	-8.44(0.040)dF	-6.83(0.090)aD
60	-7.41(0.150)aD	-9.85(0.081)c	-8.21(0.361)bD	-7.24(0.008)aE	-7.97(0.012)bF
80	-7.55(0.100)bD	-9.31(0.138)c	-7.81(0.214)bD	-6.96(0.206)aDE	-7.71(0.072)bF
100	-7.53(0.030)cD	-8.97(0.091)e	-8.10(0.231)dD	-5.72(0.110)aC	-7.20(0.073)bE
150	-7.10(0.001)bC	-8.15(0.104)c	-6.73(0.174)aC	-6.65(0.188)aD	-6.93(0.098)abDE
GW	-7.12(0.050)bC	-8.11(0.062)c	-8.12(0.120)cD	-6.88(0.110)aD	-7.18(0.042)bE
(c) July					
5	-2.51(0.161)dA	-2.34(0.192)dA	-1.88(0.087)cA	1.01(0.065)bA	2.36(0.210)aA
10	-5.72(0.129)dB	-3.50(0.118)bB	-3.62(0.239)bB	-4.26(0.285)cB	-1.09(0.095)aB
20	-6.92(0.141)dC	-3.89(0.049)bC	-5.37(0.205)cC	-5.62(0.145)cC	-3.39(0.182)aC
40	-7.56(0.049)dF	-4.70(0.164)aD	-7.72(0.141)dD	-6.32(0.002)cD	-5.16(0.070)bD
60	-7.38(0.035)cEF	-6.16(0.292)aE	-7.78(0.042)cD	-6.66(0.208)bE	-5.93(0.163)aE
80	-7.15(0.072)cDE	-6.47(0.075)aEF	-7.89(0.070)dD	-6.71(0.035)bE	-6.38(0.054)aF
100	-6.98(0.052)bCD	-6.63(0.164)aF	-7.67(0.074)cD	-6.85(0.084)abE	-6.66(0.058)aFG
150	-7.18(0.109)aDE	-7.23(0.180)aG	-7.67(0.218)bD	-6.88(0.052)aE	-6.87(0.074)aG
GW	-9.00(0.065)cG	-7.98(0.099)bH	-7.94(0.165)bD	-7.66(0.235)abF	-7.23(0.225)aH
(d) August					
5	-1.49(0.185)cA	-1.74(0.133)cA	0.96(0.100)aA	0.35(0.100)bA	0.78(0.211)aA
10	-4.79(0.235)cB	-4.45(0.094)cB	-2.13(0.163)aB	-3.28(0.191)bB	-3.65(0.145)bB
20	-5.56(0.281)bcC	-5.75(0.151)cC	-4.87(0.069)aC	-5.17(0.050)abC	-5.63(0.168)cC
40	-6.46(0.066)cD	-6.39(0.047)cD	-5.55(0.056)aD	-6.02(0.178)bD	-6.47(0.021)cD
60	-6.99(0.071)bEF	-6.88(0.093)bEF	-6.23(0.116)bE	-6.51(0.122)aE	-6.86(0.151)aE
80	-7.15(0.142)bF	-7.32(0.143)bG	-6.62(0.144)aF	-6.79(0.091)aEF	-6.73(0.169)aDE
100	-7.04(0.163)aEF	-7.13(0.115)aFG	-6.92(0.086)aG	-7.05(0.146)aF	-6.90(0.103)aEF
150	-6.96(0.206)aEF	-6.90(0.060)aEF	-7.14(0.141)aGH	-7.06(0.066)aF	-7.24(0.189)aFG
GW	-6.73(0.170)aDE	-6.70(0.168)aE	-7.20(0.089)abH	-6.85(0.350)abEF	-7.27(0.153)bG
(e) September					
5	-2.38(0.185)eA	-1.64(0.080)dA	-0.96(0.207)cA	0.37(0.164)aA	-0.27(0.204)bA
10	-4.52(0.226)cdB	-4.06(0.088)abB	-3.92(0.045)aB	-4.31(0.083)bcB	-4.77(0.108)dB
20	-6.69(0.093)bcC	-5.78(0.216)aC	-5.88(0.141)aC	-6.55(0.131)bcC	-6.43(0.114)bcC
40	-8.07(0.080)cEF	-7.79(0.050)bD	-8.05(0.073)cEF	-6.91(0.098)aDE	-6.93(0.051)aD
60	-8.28(0.118)cF	-8.25(0.141)cF	-8.47(0.162)cG	-6.56(0.016)aC	-7.24(0.171)bE
80	-7.96(0.039)cDE	-8.14(0.057)cdEF	-8.28(0.060)dFG	-6.75(0.146)aCD	-7.54(0.064)bFG
100	-7.72(0.141)bD	-7.95(0.080)bDE	-7.90(0.070)bDE	-7.06(0.107)aE	-7.26(0.083)aEF

**Table 1** (continued)

Depth	Treatment Prairie	Woodland	Savanna*	Soybean	Corn
150	−7.85(0.141)bDE	−7.90(0.117)bDE	−7.64(0.163)abD	−7.33(0.041)aF	−7.60(0.212)abG
GW	−7.76(0.126)cbDE	−7.98(0.144)cDE	−7.65(0.014)abD	−7.45(0.030)aF	−7.48(0.023)aEFG

Mean values at each depth (i.e. row) with the same lower case letter are not significantly different at  $\alpha=0.05$ . Mean values for the same treatment (i.e. column) with the same upper case letter are not significantly different at  $\alpha=0.05$ .

<sup>a</sup>No LSD or standard deviation since only one replicate for Savanna at GW depth

<sup>b</sup>No LSD or standard deviation since only one replicate for Woodland at 20 cm depth

or an artifact of isotopic fractionation occurring during evapotranspiration by its extremely thin vascular tissue (see [Discussion](#) section).

Later in the growing season (August 27 sampling date, high rainfall amount during previous 2 weeks: 87.4 mm), depth of water uptake for corn, soybean, and prairie remained fairly constant at approximately 20 cm (Figs. 10 and 12). This pattern continued for these species through the September 1 sampling event (Figs. 11 and 12), despite the substantially lower rainfall during the previous 2 weeks (9.0 mm). *Symphoricarpos orbiculatus* had a slightly deeper depth of water uptake when growing in the woodland (20 cm) compared to the savanna (10 cm) in August, which extended down to 30 cm and 20 cm, respectively, in September. Depth of water uptake for *Q. alba* was not possible to determine conclusively for either the August or September sampling dates due to overlapping isotopic concentrations of the soil water and plant xylem water. However, we can infer potential ranges of water uptake for the woodland and savanna oaks of 60 cm to groundwater and 150 cm to groundwater, respectively, for August, and 40 cm to groundwater for both oak sites for September. Thus, the oaks continued to extract water from deeper levels in the soil profile relative to the other studied species later in the season.

## Discussion

Spatial and temporal patterns in water use for contrasting vegetative cover types

In this study, we used stable isotope techniques to infer depth of water uptake among contrasting annual and perennial plant communities across an entire

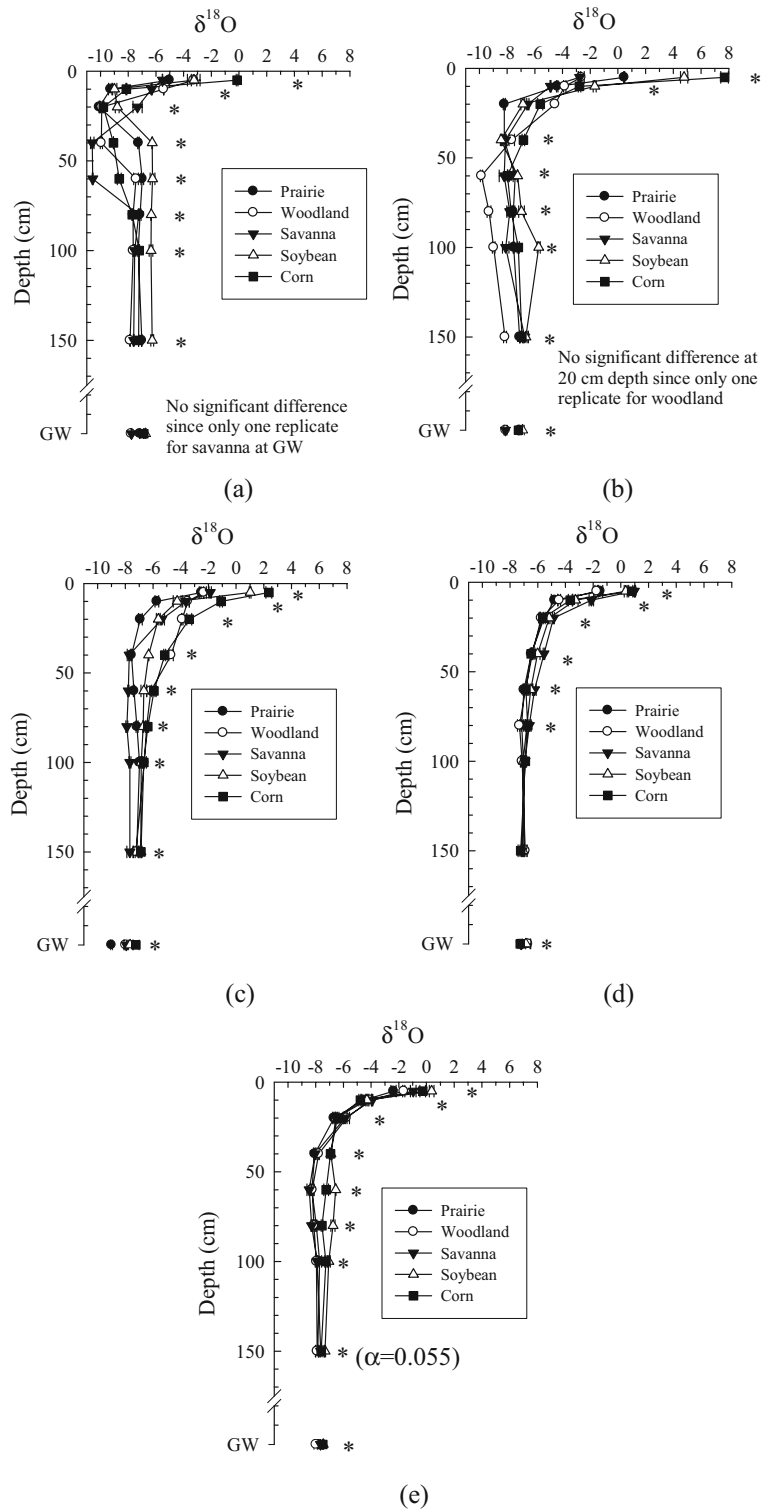
growing season in Central Iowa. Although stable isotopes have been applied broadly to assess depth of water uptake patterns in grassland and savanna ecosystems (e.g., Weltzin and McPherson 1997; Midwood et al. 1998, Durand et al. 2007; Nippert and Knapp 2007), only a few such studies have been conducted for annual crops (Grieu et al. 2001; Araki and Iijima 2005). We are aware of no studies that have explicitly compared water uptake dynamics in perennial plant communities with co-occurring annual cropping systems.

Our findings demonstrated that annual crops, herbaceous perennial plants, and woody shrubs and trees all initially extracted most of their water from the upper soil horizon (5–40 cm) in early spring when water was plentiful, and increased their depth of water uptake as rainfall declined and water became less available into the mid- and late summer months. Maximum depth of water uptake ranged from 20 cm for the herbaceous species (*Z. mays*, *G. max*, *A. gerardii*) to 55 cm for the shrub species *S. orbiculatus*, to below 150 cm for *Q. alba* trees. These patterns support previous work documenting that plants can adjust their active zone of water uptake in response to changing environmental conditions (e.g., Chaves et al. 2002).

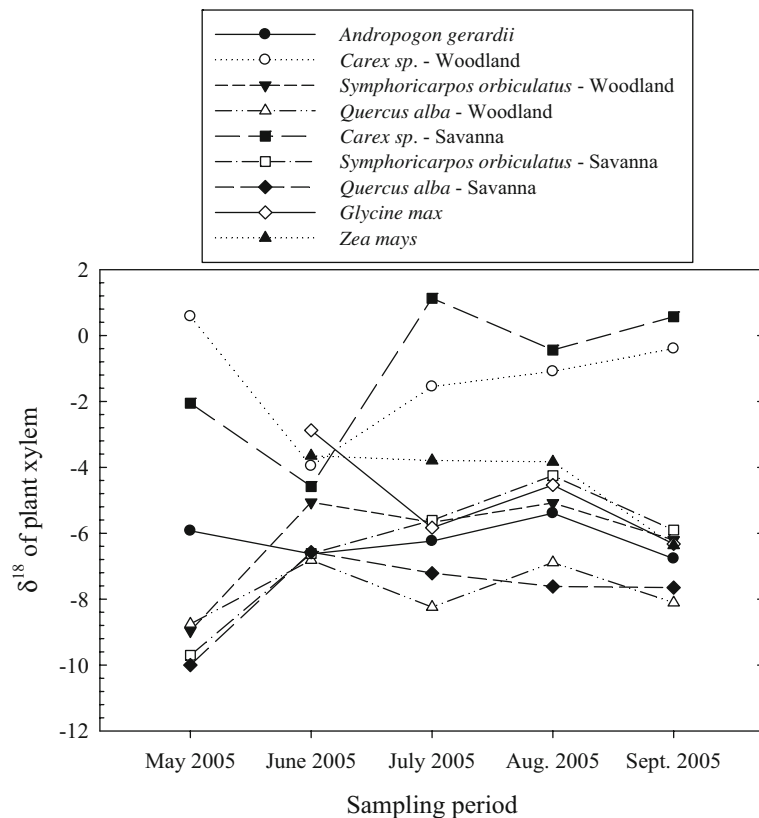
## Annual cropping systems

The two annual crops, *Z. mays* and *G. max*, increased their depth of water uptake from 5 cm to 20 cm during the course of the growing season. Their relatively narrow range (15 cm) of soil depth from which water was extracted throughout the growing season, suggests a low degree of ecological plasticity in water uptake functions. These results are consistent with the findings of Benjamin and Nielsen (2006), who also reported that water deficit did not affect soybean root

**Fig. 5** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water at the five sites for the five sample collection periods: (a) May 2005, (b) June 2005, (c) July 2005, (d) August 2005, and (e) September 2005 (\*beside a depth interval indicates statistically significant difference at  $\alpha=0.05$ )



**Fig. 6** Mean  $\delta^{18}\text{O}$  values for plant xylem for the five sampling periods (corn and soybean plant xylem not available for May sampling period since plants had not emerged)



distribution, and that approximately 97% of the total soybean roots occurred in the surface 0.23 m, irrespective of sampling time or water regime. Similarly, Pandey et al. (1984) found that soybean had relatively low capacity to increase its rooting depth in response to drought stress. Our findings apparently contrast those of Engels et al. (1994), who demonstrated that *Z. mays* adjusted its root growth in the topsoil (0–40 cm) and subsoil (80–120 cm) in response to drying and rewetting by locally increasing root growth in soil layers with the most favorable conditions.

Nevertheless, the above studies only measured root distribution and not actual depth of water uptake, which makes direct comparisons with our results problematic. Application of isotopic techniques has demonstrated that some crop species can exhibit substantial ecological plasticity. For example, Araki and Iijima (2005) showed that upland rice (*Oryza sativa* L.) shifts its water uptake to deeper and moister soil layers in response to topsoil desiccation. Grieu et al. (2001) used artificially manipulated irrigation

solutions with different deuterium concentrations to show that mixtures of white clover and ryegrass extracted water from different depths of the soil profile in response to soil moisture deficit. Dardanelli et al. (1997), using soil water depletion curves to estimate apparent rooting depth, found that *Z. mays* and *G. max* exhibited a high degree of plasticity in rooting depth, extracting water from depths as great as 190 and 230 cm, respectively, as water availability declined.

The relatively humid and high rainfall climate of the Midwestern U.S. may contribute to the low plasticity in rooting functions in corn and soybean observed in our study. On the other hand, the lack of responsiveness of water uptake patterns to lower rainfall later in the season was surprising, but could in part be explained by the inability of annual crops to modify their rooting functions once grain filling has been initiated (Dardanelli et al. 1997). Thus, maximum rooting depth in these annual crops may be largely determined by moisture availability early in the season, thereby limiting root function plasticity in

**Table 2** Mean  $\delta^{18}\text{O}$  values of plant xylem values for the five sample collection periods for (a) woodland site and (b) savanna site

Species	Month				
	May	June	July	August	September
(a) Woodland site <sup>a</sup>					
<i>Carex</i> sp.	0.58a	−3.96	−1.55a	−1.09a	−0.40a
<i>Symphoricarpos orbiculatus</i>	−8.75b	−5.06	−5.67b	−5.08b	−6.21b
<i>Quercus alba</i>	−8.97b	−6.82	−8.24c	−6.89c	−8.11c
(b) Savanna site <sup>b</sup>					
<i>Carex</i> sp.	−2.06a	−4.58	1.13	−0.44a	0.57a
<i>Symphoricarpos orbiculatus</i>	−9.71b	−6.62	−5.61	−4.26b	−5.91b
<i>Quercus alba</i>	−10.00b	−6.58	−7.21	−7.62c	−7.65c

<sup>a</sup>No LSD in June since only one replicate for one of the plant species

<sup>b</sup>No LSD in June and July since only one replicate for one of the plant species

Mean values at each sampling period (i.e. column) within the same site with the same letter are not significantly different at  $\alpha=0.05$ .

response to within-season rainfall fluctuations. Merrill et al. (2002) showed that soybean exhibited greatest total root length during a drier-than-average year compared to average or wet years, supporting the idea that root growth is primarily mediated by early season water availability. Another potential limitation to deep water uptake is that subsoil compaction and subsequent increases in bulk density and limited water infiltration common in agricultural lands may prevent root extension (Araki and Iijima 2005; Collins and Bras 2007).

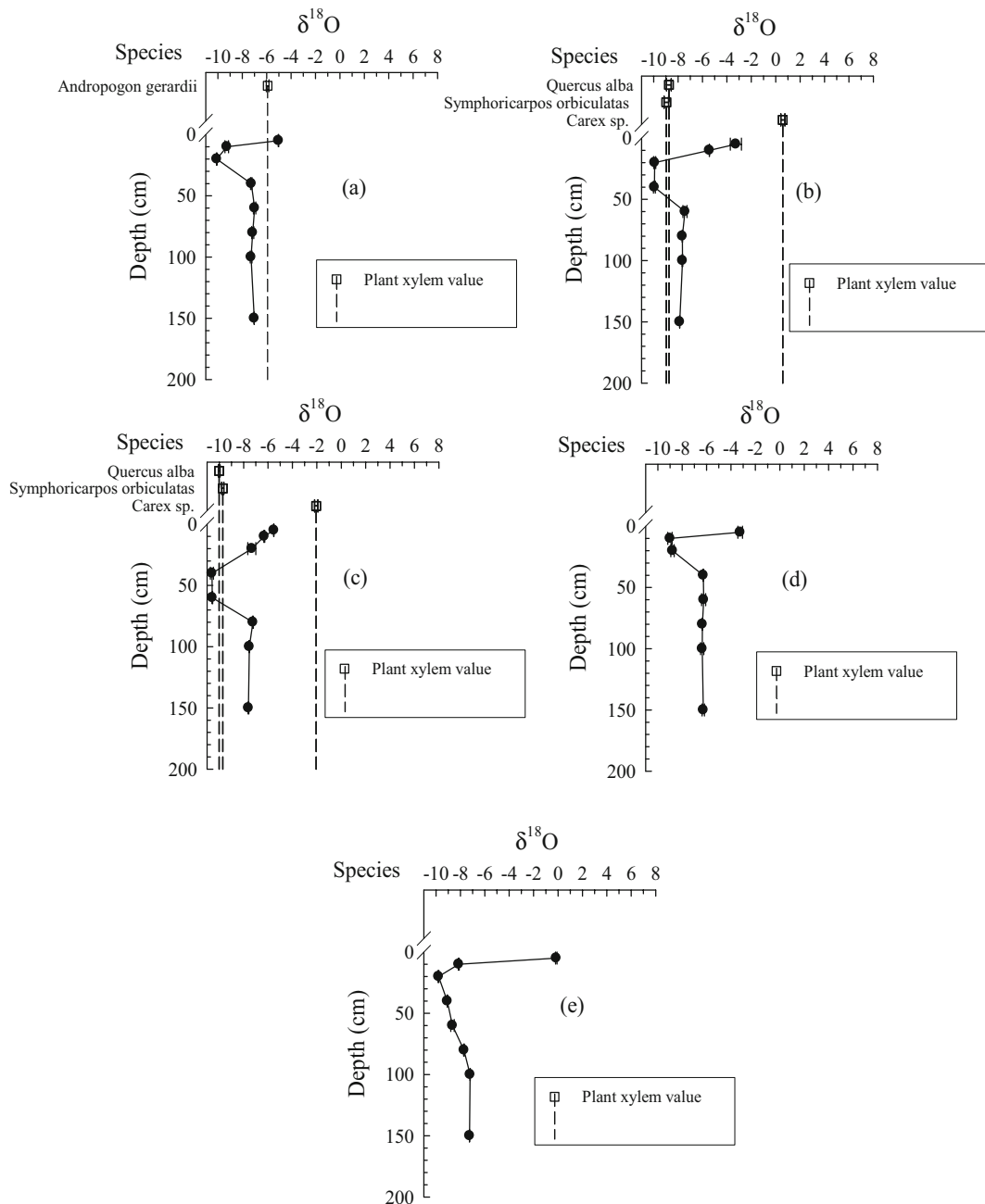
### Restored prairie ecosystem

*Andropogon gerardii* is a dominant  $C_4$  species of the North American tallgrass prairie ecosystem (Risser et al. 1981) and is considered to be particularly sensitive to competition during the early establishment stage (Foster 1999; Suding and Goldberg 1999). Similar to the annual crop species, *A. gerardii* plants also exhibited a maximum range of 15 cm for depth of water uptake in response to changing environmental conditions, withdrawing water from the upper 5 cm early in May and from 10–15 cm from June through July as precipitation levels declined. The restricted water uptake from the upper soil horizon by *A. gerardii* agrees with findings by Nippert and Knapp (2007) for four co-existing  $C_3$  forbs and three co-existing  $C_4$  grasses (including *A. gerardii*). In this study, the  $C_4$  grasses consistently depended on shallow water, whereas  $C_3$  species extracted water from deeper soil layers as water

availability declined and inter-specific competition increased. However, since stable isotope composition was only determined for leaf tissue and not for soil water with depth in this study, depth of water uptake patterns could not be determined conclusively. Root excavation studies also confirm that *A. gerardii* typically concentrate a high proportion of roots in the upper soil horizon (Sims et al. 1978; Weaver 1968), yet maximum rooting depth may extend down to > 2 m (Weaver 1958). Under conditions of extensive drought conditions or stressors, such as defoliation, *A. gerardii* has the capacity to increase the depth from which it extracts water (Hayes and Seastedt 1987; Mousel et al. 2005).

The lack of significant differences in water uptake patterns observed for *A. gerardii* relative to corn and soybean in our study may be attributed to the relatively young age of the prairie reconstruction (4 yr) and inadequate time for vertical development of the root system. Thus, we might expect that greater inter- and intra-specific competition for limited water resources in the reconstructed prairie with increasing age of development may lead to deeper water uptake (e.g., Grieu et al. 2001; Gustafson et al. 2004). Alternatively, drought conditions during our study period may not have been extreme enough to elicit significant competition for scarce water resources and the need to extract water from deeper depths. Moreover, *A. gerardii* may have other adaptive mechanisms for tolerating drought not directly related to plasticity of depth of water uptake functions, such as greater carbon allocation to roots,

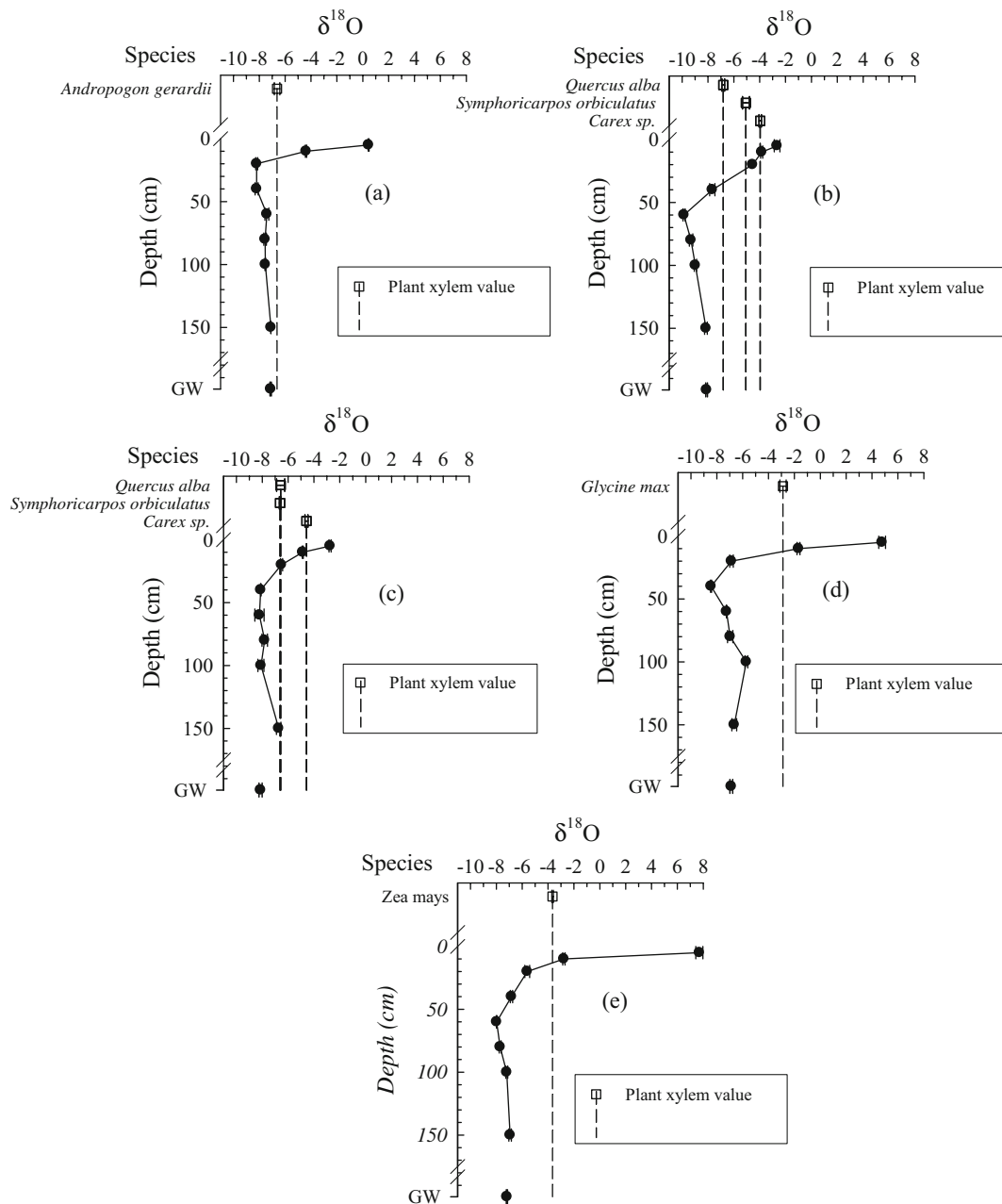




**Fig. 7** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water and plant xylem at the five sites for the May 2005 sampling: (a) Prairie, (b) Woodland, (c) Savanna, (d) Soybeans, and (e) Corn

reduced allocation to flowering, more rapid leaf turnover, and more rapid recovery of photosynthesis after wilting (Swemmer et al. 2006). Lack of plasticity in depth of water uptake in response to changing environmental conditions does not necessarily indicate lower competitiveness, as it may reflect high tolerance for low resource environments

(Monaco et al. 2005), greater importance of the  $\text{C}_4$  species' photosynthesis pathway in maintaining high productivity under low moisture conditions (Knapp et al. 2001), or the reliance on rapid fine root turnover (dieback and regrowth) in the upper soil horizon in response to water pulses and shortages (Hayes and Seastedt 1987).

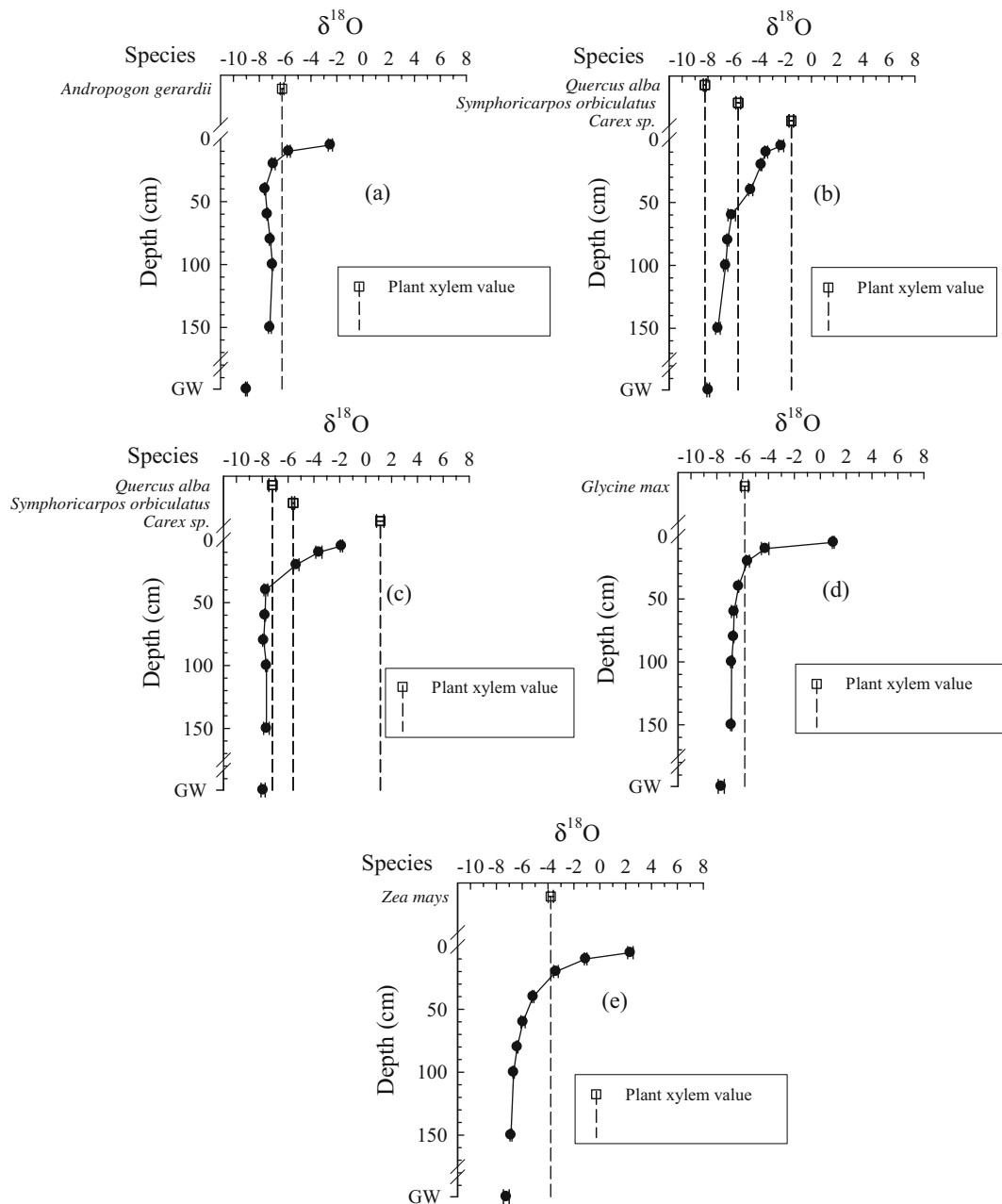


**Fig. 8** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water and plant xylem at the five sites for the June 2005 sampling: (a) Prairie, (b) Woodland, (c) Savanna, (d) Soybeans, and (e) Corn

Encroached savanna woodland and reconstructed savanna ecosystems

Herbaceous and woody plant species growing in the savanna and woodland sites varied widely in their patterns of water uptake. Throughout the growing season, *Carex* sp. had extremely high  $\delta^{18}\text{O}$  values

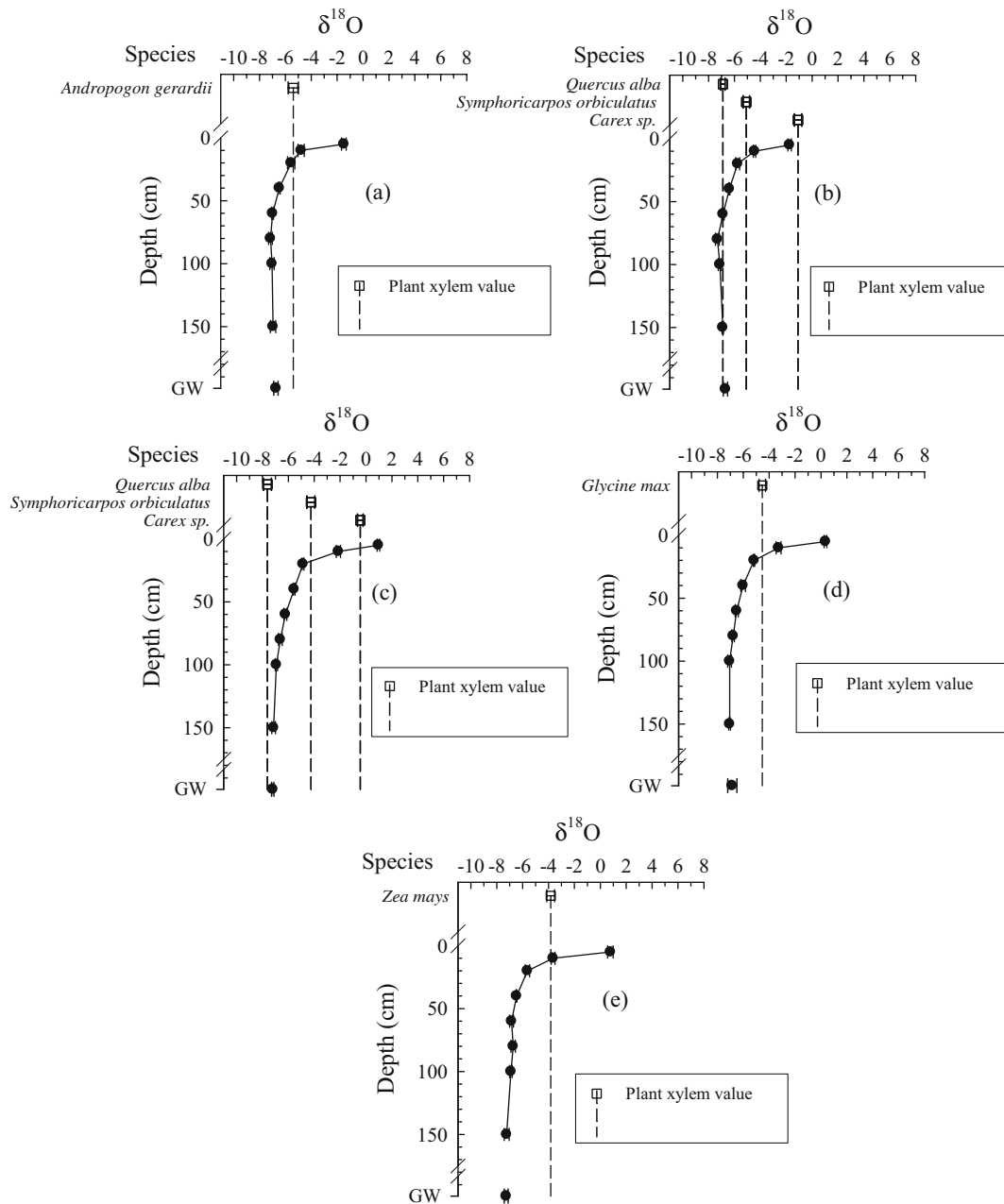
reflective of a probable water uptake depth from the uppermost portion of the soil profile or the ground surface (as inferred from xylem isotopic values being more positive than for soil water). Furthermore, while no isotope fractionation occurs during water uptake by plants, fractionation does occur in leaf tissue during transpiration (Flanagan and Ehleringer 1991). As



**Fig. 9** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water and plant xylem at the five sites for the July 2005 sampling: (a) Prairie, (b) Woodland, (c) Savanna, (d) Soybeans, and (e) Corn

*Carex* sp. consists largely of leaf tissue, an alternate explanation may be its greater susceptibility to isotopic fractionation during evapotranspiration (Dongmann et al. 1974). The resultant enrichment of the heavier isotopes in the leaf tissue could erroneously be interpreted as water uptake depths that are shallower than true depths. The lack of a strong temporal pattern

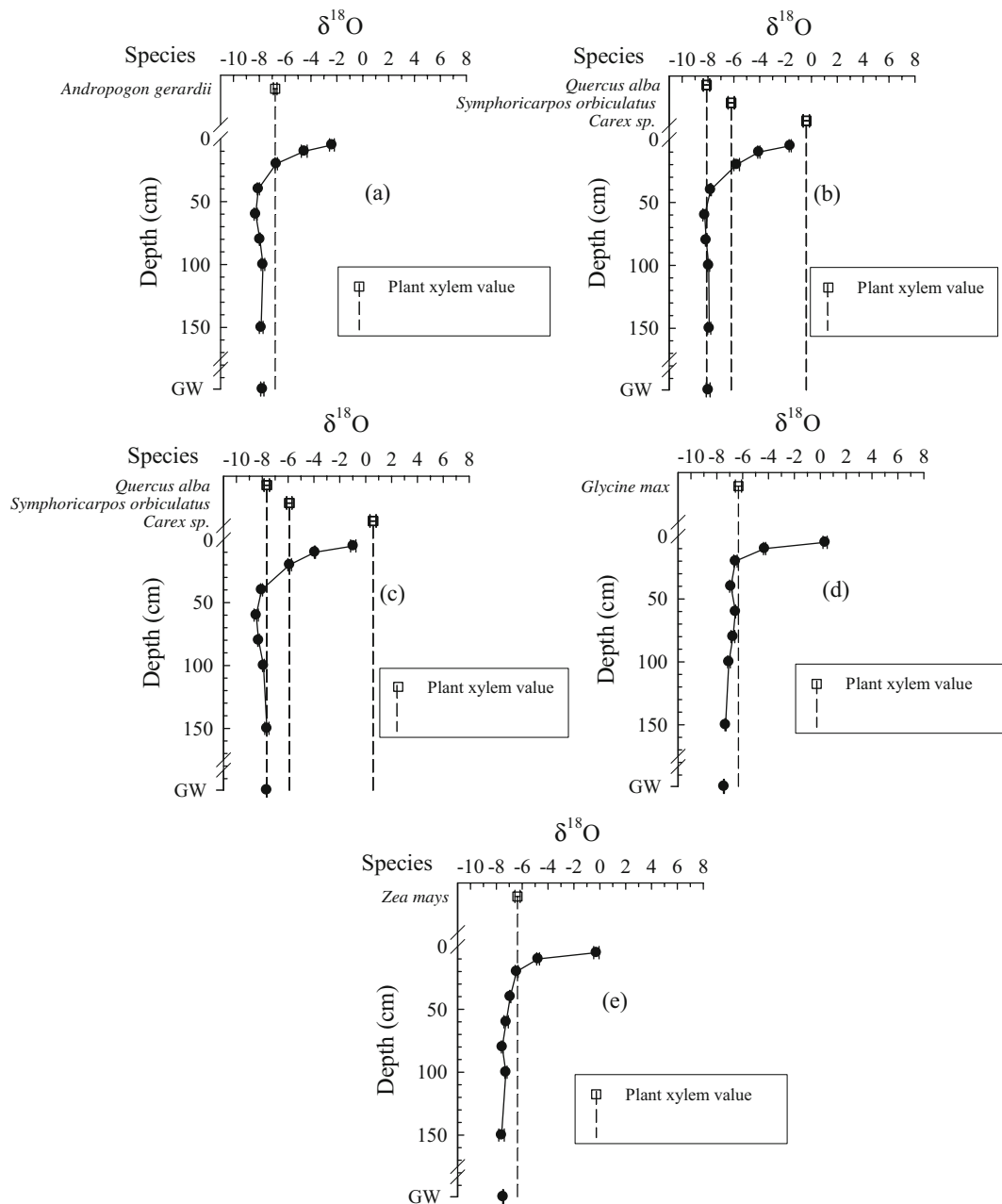
of depth of water uptake for *Carex* sp. in response to seasonal changes in water availability may also be an artifact of foliar isotopic enrichment in this species. Additional research is needed to conclusively establish the occurrence and magnitude of isotopic enrichment and its potential implications for interpreting depth of water uptake patterns in *Carex* sp.



**Fig. 10** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water and plant xylem at the five sites for the August 2005 sampling: (a) Prairie, (b) Woodland, (c) Savanna, (d) Soybeans, and (e) Corn

In contrast to *Carex* sp., depth of water uptake for the understory shrub *S. orbiculatus* showed a strong relationship with precipitation events when growing in both the savanna and woodland sites. This species withdrew water from relatively shallow (15 cm) depths in May, but as rainfall declined in June and July, it extracted water from depths as great as 30 cm

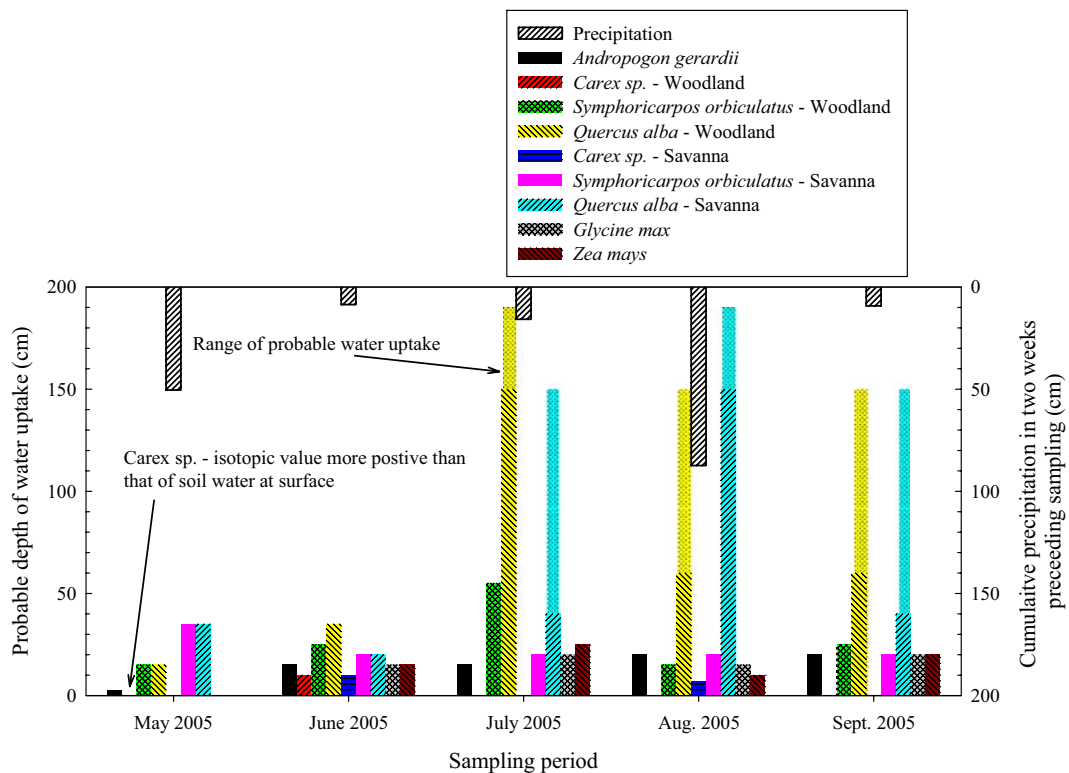
and 55 cm, respectively. Interestingly, by the August and September sampling events, when rainfall increased again, depth of water uptake for *S. orbiculatus* became substantially shallower (20–30 cm). The relatively large maximum range in water uptake depth (40 cm) combined with the apparent responsiveness to changing water availability suggests a high degree



**Fig. 11** Mean ( $\pm$ S.D.)  $\delta^{18}\text{O}$  values of soil water and plant xylem at the five sites for the September 2005 sampling: **(a)** Prairie, **(b)** Woodland, **(c)** Savanna, **(d)** Soybeans, and **(e)** Corn

of plasticity in rooting functions. Further, the similarity in water uptake depths by *S. orbiculatus* growing in the savanna and woodland sites suggests that these plants experienced similar degrees of competition for water, despite the significantly lower overstory stand density in the savanna site due to the restoration treatment (e.g., Karnitz and Asbjornsen 2005).

Not surprisingly, of all the study species, *Q. alba* exhibited the greatest plasticity in depth of water uptake patterns, ranging from 10–20 cm in early spring to greater than 1.5 m and possibly groundwater in mid- to late summer. This observed shift between shallow and deeper water sources for *Q. alba* is consistent with results of studies from different forest



**Fig. 12** Probable depth of water uptake for the nine species at the five sampling periods and the cumulative precipitation in two week period preceding sampling

ecosystems showing a high degree of ecological plasticity in water uptake functions by trees in response to water availability (Meinzer et al. 1999; Retzlaff et al. 2001). However, only a few studies have specifically assessed depth of water uptake by *Quercus* sp. over time, and have revealed inconsistent results. For example, Weltzin and McPherson (1997) reported that mature *Q. emoryi* trees in a temperate savanna predominantly used deep sources of water throughout the entire growing season, irrespective of rainfall patterns. Similarly, Phillips and Ehleringer (1995) showed that *Q. gambelii* in the Intermountain Western U.S. relied exclusively on deep-soil moisture sources derived from winter precipitation throughout the growing season. In contrast, Williams and Ehleringer (2000) observed that *Q. gambelii* growing on sites with exceptionally high average summer precipitation predominantly used water in upper soil layers following recent summer rain events, and thus apparently had the capacity to shift between deep and shallow water sources in response to changing water availability. Deep rooting habit is an important drought tolerant strategy common to the genus

*Quercus* (Abrams 1996), and maximum rooting depth may extend down to 4.3 m (Canadell et al. 1996).

In our study, even after a period of high rainfall in late July *Q. alba* continued to obtain its water from relatively deep depths within the soil profile (> 1.5 m, possibly groundwater), rather than shifting its water uptake to shallower depths as observed for *S. orbiculatus*. Thus, our findings suggest that *Q. alba* exhibits a high degree of plasticity in response to water depletion by progressively extracting water from deeper levels in the soil profile, but appears relatively unresponsive to pulses of increased shallow water availability due to rainfall events later in the season.

Variation in water uptake depths can lead to niche differentiation and complementary use of resources and, in turn, promote species coexistence and ecosystem function. This possibility was illustrated in our study in that *S. orbiculatus* and *Q. alba* had similar depths of water uptake in May and June (when water was plentiful and competition presumably low), whereas in the subsequent months, *S. orbiculatus* obtained water from 15–50 cm and *Q. alba* withdrew water



from deeper soil depths. Total stand transpiration may be greater in ecosystems supporting multiple rooting depths by coexisting species (Asbjornsen et al. 2007), thereby serving to regulate the hydrological balance by increasing infiltration and water storage capacity, and reducing overland flow (Fitzjohn et al. 1998).

## Conclusions

Depth of water uptake and degree of ecological plasticity in root function in response to seasonal changes in moisture availability varied among the annual and perennial plant communities examined in our study. Annual crops did not extract water from depths deeper than 20 cm, suggesting a poor capacity to regulate hydrological processes associated with plant water cycling, soil water storage, and flood control. The similarly shallow water uptake depths observed for the dominant *C<sub>4</sub>* prairie species, *A. gerardii*, may be due to the relatively young age of the prairie reconstruction. Notwithstanding, it is also possible that coexisting prairie plants, especially *C<sub>3</sub>* species, are taking up water from deeper depths (e.g., Nippert and Knapp 2007). Savanna and woodland ecosystems exhibited the most dynamic response in water uptake functions during the course of the growing season. Establishing or maintaining structurally complex and species diverse savanna and woodland ecosystems within agricultural landscapes in the Midwest may serve to enhance hydrological functions by recycling water from deeper depths in the soil profile back to the atmosphere and increasing soil water holding capacity. High degree of ecological plasticity may allow some deep-rooted species to extract water from surface horizons when it is available, such as observed for *Q. alba* early in the growing season in our study, and therefore deep water uptake processes may vary depending on species' growth patterns and water uptake dynamics. Although studies are beginning to document the positive effects of perennial vegetation within agricultural landscapes on hydrologic regulation and other ecosystem services (e.g., Dosskey et al. 2002; Vaché et al. 2002; Lee et al. 2003; Schulte et al. 2006), the mechanisms underlying these observed patterns—such as differences in plant species' depth of water uptake—have not been extensively examined. More research is needed to understand how differences in species

composition influence water cycling functions and on what spatial and temporal scales in order to determine how to better target the choice of species and their placement on the landscape for maximizing benefits within agricultural landscapes in the Corn Belt region.

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