

Differences in soil water use by annual broomweed and grasses

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Abstract

The use of water in the upper 1 m of the soil profile by 3 common herbaceous species of the southern Great Plains was examined by labeling soil water with $^2\text{H}_2\text{O}$ and H_2^{18}O . Uptake of labeled water from the 15 cm depth was approximately equal for all species. However, water uptake from the 75 cm depth was significantly greater by annual broomweed [*Amphiachyris dracunculoides* (DC.) Nutt] than either sideoats grama [*Bouteloua curtipendula* (Michx.) Torr] or curlymesquite [*Hilaria belangeri* (Steud.) Nash]. Although both grasses had greater root length density than annual broomweed at the 75 cm depth, annual broomweed's rate of water extraction from the 75 cm depth was nearly twice that of sideoats grama or curlymesquite. Greater access to and more rapid utilization of deeper soil water by annual broomweed relative to the grass species may partially explain annual broomweed's success at invading grasslands and reducing grass production in semi-arid rangelands.

Key Words: sideoats grama, curlymesquite, stable isotopes, lysimeters, Great Plains

Annual broomweed [*Amphiachyris dracunculoides* (DC.) Nutt] is a single-stemmed annual forb native to the southern Great Plains. The distribution of this species is expanding, most notably on lowland rangelands of northern Mexico and xeric limestone sites in the southern United States (Gordon 1982). Annual broomweed is highly competitive with other types of herbaceous vegetation, resulting in a reduction of grass production and live-stock/wildlife carrying capacity (Haas 1976, Rittenhouse et al. 1977, Gordon 1982, Boyd et al. 1983).

Annual broomweed is most successful in dominating rangeland during years with abundant rainfall during the cool season (Boyd et al. 1983, Heitschmidt 1979). Beck and Sosebee (1975) speculated that annual broomweed reduced grass production through rapid utilization of soil moisture in early spring, thereby reducing soil moisture available to warm season grass species. However, no significant difference in water content in the upper 60 cm of

Resumen

Para 3 especies herbáceas comunes en la región sur de las Great Plains (USA), se estudió el uso de agua en el metro superior del perfil del suelo utilizando $^2\text{H}_2\text{O}$ y H_2^{18}O para marcar el agua contenida en éste. En los primeros 15 cm de profundidad, la absorción de agua marcada fue aproximadamente igual para las tres especies. Sin embargo, a 75 cm de profundidad la absorción fue significativamente mayor para "annual broomweed" [*Amphiachyris dracunculoides* (DC.) Nutt] que para "sideoats grama" [*Bouteloua curtipendula* (Michx.) Torr] o "curlymesquite" [*Hilaria belangeri* (Steud.) Nash]. Aunque ambas gramíneas tienen mayor densidad de la longitud de raíces a 75 cm de profundidad que el "annual broomweed," la tasa de extracción de agua de esta especie fue casi el doble de la observada en "sideoats grama" o "curlymesquite" a esa profundidad. Mayor acceso a agua en suelo más profundo y una más rápida utilización de ésta en relación a las especies gramíneas podrían explicar parcialmente el éxito de "annual broomweed" para invadir pastizales y reducir la producción de pasto en pastizal natural semiárido.

soil throughout the growing season was reported between plots where annual broomweed was controlled and plots that were heavily infested (Boyd et al 1983). No data have been published on annual broomweed's ability to utilize water from deeper soil depths, nor has the rate of water extraction by annual broomweed relative to grass species been investigated.

Both rate of water extraction (Eissenstat and Caldwell 1988) and water use from deep soil depths (Wan et al. 1994) have been linked to competitive abilities of rangeland species. The objective of this research was to determine if there are differences in the pattern and rate of water use throughout the soil profile that could confer a competitive advantage on annual broomweed relative to native perennial grasses. To achieve this objective, water labeled with deuterium (^2H) and oxygen-18 (^{18}O) was injected into the soil profile at 2 different depths to compare patterns of soil water uptake between annual broomweed, sideoats grama [*Bouteloua curtipendula* (Michx.) Torr] and curlymesquite [*Hilaria belangeri* (Steud.) Nash].

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Methods

Study Area

Field research was conducted at the Wagon Creek Spade Research Ranch in Throckmorton County located approximately 22 km north of Throckmorton, Tex. (33° 20'N, 99° 14'W). Elevation of the study site is 450 m. Climate is semi-arid continental, with average maximum/minimum daily temperatures of 13.1/−2.6°C in January and 36.1/21.1°C in July. The average frost free period is 220 days. Annual precipitation (1950–1993 mean and median = 646 mm) is bimodal, with peaks occurring in May and September.

Soils are fine, silty, mixed, thermic Typic Calcicustolls (Nuvalde silty clay loam) that are deep, well-drained, slowly permeable and have a slope of 1–3% (SCS 1984). This silty clay loam surface is approximately 280 mm thick, and the silty clay loam subsoil is about 560 mm thick. The underlying parent material is calcitic silty clay.

Vegetation at this site is mixed-grass prairie dominated by the midgrasses sideoats grama, a warm-season perennial, and Texas wintergrass (*Stipa leucotricha* Trin. and Rupr.), a cool-season perennial. Subdominant grasses include curlymesquite and buffalo grass [*Buchloe dactyloides* (Nutt.) Engelm.], both stoloniferous, warm-season perennials. Annual broomweed and heath aster (*Aster ericoides* L.) are the most prevalent forbs (SCS 1984, Heitschmidt et al. 1985).

Isotope Labeling and Vegetation Collection

Nine weighing lysimeters (77 cm diameter, 120 cm deep) containing undisturbed, vegetated soil monoliths were installed in 1985 as part of a study to determine the role of grasses in rangeland water balance (Franklin 1987). Three lysimeters were covered by sideoats grama, 3 by curlymesquite, and 3 by annual broomweed.

On 29 July 1991, deuterated water (15 g of 99.9 atom % ²H₂O diluted to 200 ml with distilled water) and ¹⁸O-labeled water (83.3 g of 10 atom % H₂¹⁸O diluted to 200 ml with distilled water) were injected into the lysimeters to measure plant water uptake from 2 depths within each lysimeter simultaneously (isotopes were obtained from Icon Services, Inc., Summit, N.J.). H₂¹⁸O was injected at 15 cm and ²H₂O was injected at 75 cm in each of the 9 lysimeters. At each depth, the tracer was applied through the sides of the lysimeters as 4 horizontal, parallel, and equidistant bands (each 2 cm in diameter). The holes in the sides of the lysimeters were plugged and sealed after application of the tracers.

Vegetation samples (approximately 5 g fresh weight) were collected from each lysimeter before injection of the isotopes so that the background or baseline amount of isotope present prior to labeling could be determined. Following injection of the isotopes, vegetation samples were collected between 1000 and 1100 hours for 10 consecutive days. Samples were clipped from several points within the lysimeters to obtain a representative sample of the vegetation, placed immediately into 20 ml glass Vacutainers™ (Becton Dickinson & Co., Rutherford, N.J.) and sealed with rubber stoppers. The tops of the vacutainers were then overwrapped with parafilm to prevent evaporative water loss. Samples were stored on ice in a cooler until they could be frozen approximately 30 minutes later.

Leaf tissue was collected from sideoats grama and curlymesquite because there was insufficient stem tissue to support the extended sampling required by this study. Both leaf and stem tissue were collected for annual broomweed to test the hypothesis

Table 1. Precision and accuracy of ²H and ¹⁸O analyses of isotopic water standards (standard deviation in parentheses) from International Atomic Energy Agency (IAEA). Actual values for standards are taken from Parr and Clements (1991).

² H standards	measured	actual
	δ ² H _{VSMOW}	δ ² H _{VSMOW}
GISP	-188.2 (1.4)	-189.7 (0.9)
IAEA-302A	+504.4 (3.5)	+508.4 (4.1)
IAEA-302B	+989.6 (4.0)	+995.8 (12.1)
	measured	actual
¹⁸ O standards	δ ¹⁸ O _{VSMOW}	δ ¹⁸ O _{VSMOW}
IAEA-304A	+254.1 (2.1)	+251.7 (4.5)
IAEA-304B	+507.4 (1.9)	+502.5 (6.2)

that the isotopic composition of water from leaf and stem tissue of a given plant are strongly correlated.

Sample Preparation and Mass Spectrometry

Water was removed from the vegetation samples by azeotropic distillation with dry toluene (Revesz and Woods 1990). The ²H and ¹⁸O content of the water samples was then determined by gas isotope ratio mass spectrometry. Water samples were prepared for hydrogen isotopic analysis by conversion of water to hydrogen gas (H₂) by reduction over zinc (Coleman et al. 1982, Kendall and Coplen 1985, Wong et al. 1987) as modified by Hayes and Johnson (1987). The ¹⁸O content of the plant water was determined by equilibration of water with CO₂ (Midwood et al. 1992). All δ²H and δ¹⁸O values are expressed using conventional notation:

$$\delta^2\text{H}_{\text{VSMOW}} \text{ or } \delta^{18}\text{O}_{\text{VSMOW}} = (R_{\text{sample}}/R_{\text{VSMOW}} - 1) \times 1,000$$

where R_{sample} and R_{VSMOW} are the isotopic ratios (²H/¹H or ¹⁸O/¹⁶O) of the sample and the international standard VSMOW (Vienna Standard Mean Ocean Water), respectively. Precision and accuracy of ²H and ¹⁸O analyses were evaluated using reference materials distributed by the International Atomic Energy Agency (Table 1). The δ-values were converted to parts per million (ppm) by calculating fractional abundance (F) using the procedures outlined by Hayes (1983):

$$^2\text{H: } F = R_{\text{sample}}/(R_{\text{sample}} + 1)$$

$$^{18}\text{O: } F = R_{\text{sample}}/(R_{\text{sample}} + 1 + R_{17})$$

where $R_{17} = (1 + \delta^{18}\text{O})^{0.5} + R_{17\text{-VSMOW}}$; where $\delta^{18}\text{O} = ((R_{\text{sample}}/R_{\text{VSMOW}}) - 1) \times 1000$ and $R_{17\text{-VSMOW}} = 0.000373$ and $R_{\text{VSMOW}} = 0.0020052$.

$$\text{ppm} = (F) \times 10^6$$

Calculation of Tracer Uptake/Loss by Plants

The percent dose transpired values were calculated according to the following steps:

- 1.) ppm excess = ppm postdose - ppm background
where ppm postdose is the isotopic composition of plant tissue water at a point in time after labeling, and ppm background is the isotopic composition of the plant tissue water the day before labeling.
- 2.) Daily H₂O loss (kg) from the lysimeter is converted to molecules H₂O lost:

$$\text{Moles H}_2\text{O lost} = \frac{(\text{kg H}_2\text{O lost}) \times (1,000 \text{ g/kg})}{18.0152}$$

where 18.0152 is the molecular weight of H₂O, and molecules of H₂O is moles H₂O lost × (6.023 × 10²³ molecules/mole).

$$3.) \text{ Molecules of dose lost} = \frac{\text{molecules H}_2\text{O lost}}{1,000,000} \times \text{ppm excess}$$

where dose is the isotope: oxygen-18 (H₂¹⁸O) or deuterium (²H₂O).

$$4.) \text{ Moles of dose lost} = \frac{\text{molecules dose lost}}{6.023 \times 10^{23} \text{ molecules/mole}}$$

$$5.) \text{ Grams of dose lost} = \text{moles of dose lost} \times \text{molecular weight of dose}$$

where the molecular weight of ²H₂O is 20.00274, and the molecular weight of H₂¹⁸O is 20.0151.

$$6.) \text{ Percent dose transpired} = \frac{(\text{grams of dose lost})/(\text{atom \% of dose applied})}{\text{grams of dose applied}} \times 100$$

where the atom % of ²H₂O applied is 99.9; the atom % of H₂¹⁸O applied is 10.0; grams of ²H₂O applied is 15.0; and grams of H₂¹⁸O applied is 83.3.

Measurement of Soil Water Loss

Soil moisture was monitored daily in each lysimeter at the 15 cm and 75 cm depths with a Troxler 3300 Series moisture depth gauge (Troxler Electronics Inc., Research Triangle Park, N.C.) that had been calibrated for the site. Total daily water loss from each lysimeter was estimated by determining weight loss using a load cell (Campbell Scientific, Logan, Utah) and a pulley attached to an A-frame.

Soil Characteristics and Root Distribution Patterns

Soil profiles were characterized for each lysimeter (Franklin 1987). A soil core was collected when a neutron probe access tube was installed in the center of each lysimeter. These samples were analyzed at the following depth increments: 0–28 cm, 28–45 cm, 45–65 cm, 65–86 cm and 86–104 cm. Soil texture was determined by the particle size distribution method (Bouyoucos 1962), bulk density by the core method (Blake 1965), water retention at 0.1, 0.3, 1, 3, 5 and 15 mPa by the pressure plate method (Klute 1965a), hydraulic conductivity by the steady-state head control method for undisturbed and ground samples (Klute 1965b), soil organic matter content by the Walkley-Black method (Nelson and Sommers 1982), and soil aggregate stability by the wet-sieve method (Kemper 1965).

At the end of the study, root distribution patterns were determined in each lysimeter (Yoder et al. 1995). A soil core, 4.13 cm in diameter, was sampled from near the center of each lysimeter at 7.6 cm increments to a depth of 104 cm. Roots were gently washed through a 0.06 mm sieve. Once separated from the soil, root length was measured using an electro-optical imager that determines space and shape parameters in any given pattern by a laser scanning technique (Bohm 1979). Root length was also determined by manually measuring random samples of roots from each depth to confirm that there was no difference in estimates between the 2 techniques.

Statistical Analysis

Data were analyzed using analysis of variance procedures with species as the main effect (SAS 1988). Dependent variables were: root length (m/m³), volumetric water content (%), ppm tracer in excess of background, and percent dose transpired. The indepen-

dent variables were species and depth. Means were separated using the Duncan's New Multiple Range Test (Snedecor and Cochran 1980).

Linear regression was conducted in order to determine the degree of correlation between the isotopic composition of water in stem tissue versus leaf tissue of annual broomweed using the model: LEAF WATER ¹⁸O or ²H (ppm) = STEM WATER ¹⁸O or ²H (ppm). Significance levels were determined at P ≤ 0.05.

Results and Discussion

The percent of isotopically labeled water transpired is a direct measure of the amount of labeled water taken up by plants from a specific depth. The percent dose transpired represents a maximum estimate because the values are based, in part, on total daily water loss from lysimeters that includes both evaporation and transpiration. Plant tracer concentrations (ppm in excess of background) were not influenced by evaporative water loss. However, tracer concentrations reflect only the instantaneous isotopic concentration of plant water at the time of sampling and do not reflect the total amount of water passing through the plant each day. Therefore, we believe that the most accurate comparisons of water use patterns between plant species is made by considering percent dose transpired and plant tracer concentrations concurrently. Percent dose transpired and plant tracer concentration data are supported further by neutron probe measurements of soil moisture content at the treated depths.

Comparison of Isotopic Composition of Leaf and Stem Water

Due to insufficient stem tissue it was necessary to use the more abundant leaf tissue for our isotopic analysis. We hypothesized that the isotopic composition of water from both leaf and stem tissue of a given plant reflect the pattern of labeled water uptake. To test this supposition, water from leaf and stem tissue of annual broomweed was analyzed for ²H and ¹⁸O content.

The isotopic composition of water in stem tissue was nearly twice that in leaf tissue following injection of labeled water into the soil profile (Fig. 1). Greater enrichment of stem water relative to leaf water was not expected because under natural abundance conditions leaf water is more enriched than stem water due to equilibrium and kinetic effects (Gonfiantini et al. 1965, Wershaw et al. 1970, Allison et al. 1985). The extent of enrichment depends on the leaf-air water vapor pressure gradient (Flanagan and Ehleringer 1991). Analysis of vegetation sampled the day prior to labeling yielded the expected result of leaf water being more enriched than stem water by approximately 4 and 30 ppm for ²H and ¹⁸O, respectively (Table 2). However, after injection of labeled water into the lysimeters, all samples of water collected from annual broomweed stems had greater concentrations of tracers than water collected from annual broomweed leaves. Lower

Table 2. Mean natural abundance concentrations of leaf and stem water of annual broomweed (standard deviation in parentheses; n=3).

leaf ² H (ppm)	Leaf vs. Stem		stem ¹⁸ O (ppm)
	stem ² H (ppm)	leaf ¹⁸ O (ppm)	
157.5 (0.85)	153.73 (0.93)	20037.37 (4.05)	20007.57 (2.03)

enrichment of leaf water relative to stem water may be due to

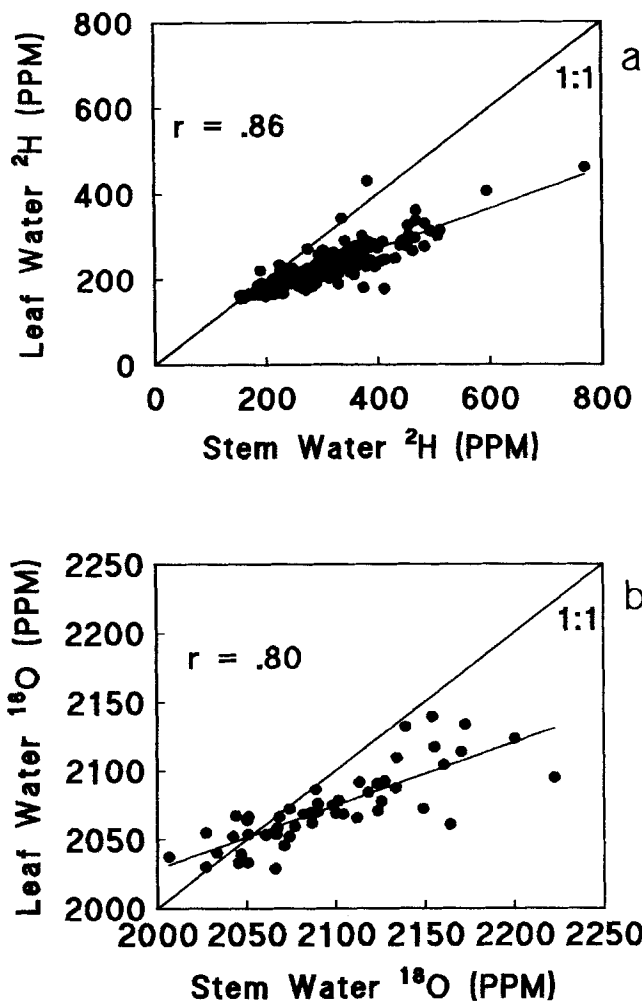


Fig. 1. Correlation between the isotopic composition of leaf and stem water of annual broomweed.

vapor exchange with the atmosphere. Couchat et al. (1983) showed that 84% of total leaf water was exchanged with tritiated atmospheric water vapor in sunflowers. Regardless of this effect, however, the strong correlation between the isotopic composition of water in the leaves and stems of annual broomweed (Fig. 1) indicate that water from either type of tissue can be used to compare patterns of labeled water uptake.

Soil and Root Characteristics

Mean soil characteristics were not significantly different among lysimeters or between depths within lysimeters (Franklin 1987). Because soil moisture retention was not significantly different between soil samples collected from each lysimeter, or between depths within a given lysimeter, the amount of soil water present was considered equally available between species and depths.

Sideoats grama had significantly greater root length at both depths than either annual broomweed or curlymesquite (Table 3). Curlymesquite had significantly greater root length than annual broomweed at the 15 cm depth but not at the 75 cm depth. Differences in root distribution between the study species reflect differences in root system geometry. Annual broomweed has a long central tap root with lateral roots that extend in a fairly uni-

Table 3. Root length density at the 15 cm and 75 cm soil depths (standard deviation in parentheses; n=3).

Soil Depth	Root Length		
	Broomweed	Sideoats grama	Curlymesquite
	----- (m/m ³) -----		
15 cm	7,712 (1,368)	52,974 (2,367)	38,595 (7,679)
75 cm	4,085 (324)	14,886 (760)	7,614 (4,002)

form manner throughout the soil profile, whereas the grasses have fibrous root systems with the greatest concentration of roots in the upper soil profile (Yoder et al. 1995).

Tracer and Neutron Probe Data

The volumetric soil water content on the day of labeling was significantly different at the 15 cm depth for all species (Table 4). Annual broomweed had the lowest soil water content, and sideoats grama had a lower soil water content than curlymesquite. There were no significant differences in soil water content between species at the 75 cm depth.

Table 4. Volumetric soil water content at the 15 cm and 75 cm soil depths on the day of soil water labeling (standard deviation in parentheses; n=3).

Soil Depth	Soil Water Content		
	Broomweed	Sideoats grama	Curlymesquite
	----- (Vol. %) -----		
15 cm	32.80 (0.83)	36.93 (0.77)	39.47 (1.07)
75 cm	37.03 (2.56)	37.30 (0.22)	36.53 (1.25)

Different water contents at the 15 cm depth may have resulted in different concentrations of labeled water at that depth (due to dilution). Specifically, labeled soil water at 15 cm in the annual broomweed lysimeters may have been more concentrated than labeled soil water in sideoats grama and curlymesquite lysimeters, respectively. Despite the possible greater concentration of labeled water in the annual broomweed lysimeters, water from annual broomweed leaf tissue had consistently lower concentrations of the 15 cm depth tracer than leaf water from sideoats grama and curlymesquite (Fig. 2a). Also, the percent dose transpired at the 15 cm depth was approximately equal for all species (Fig. 3a). Therefore, annual broomweed did not utilize significantly more water from shallow soil layers than the grasses. Neutron probe data support this conclusion (Table 5). These findings concur with Boyd et al. (1983) who documented no difference in soil moisture in the top 60 cm of soil between plots infested with annual broomweed and plots where broomweed was controlled by herbicide.

Table 5. Total water loss (mm) from the 15 cm and 75 cm soil depths (standard deviation in parentheses; n=3).

Soil Depth	Total Water Loss		
	Broomweed	Sideoats Grama	Curlymesquite
	----- (mm) -----		
15 cm	10.23 (0.58)	8.03 (0.41)	8.53 (3.03)
75 cm	4.83 (0.39)	2.10 (0.36)	0.87 (0.24)

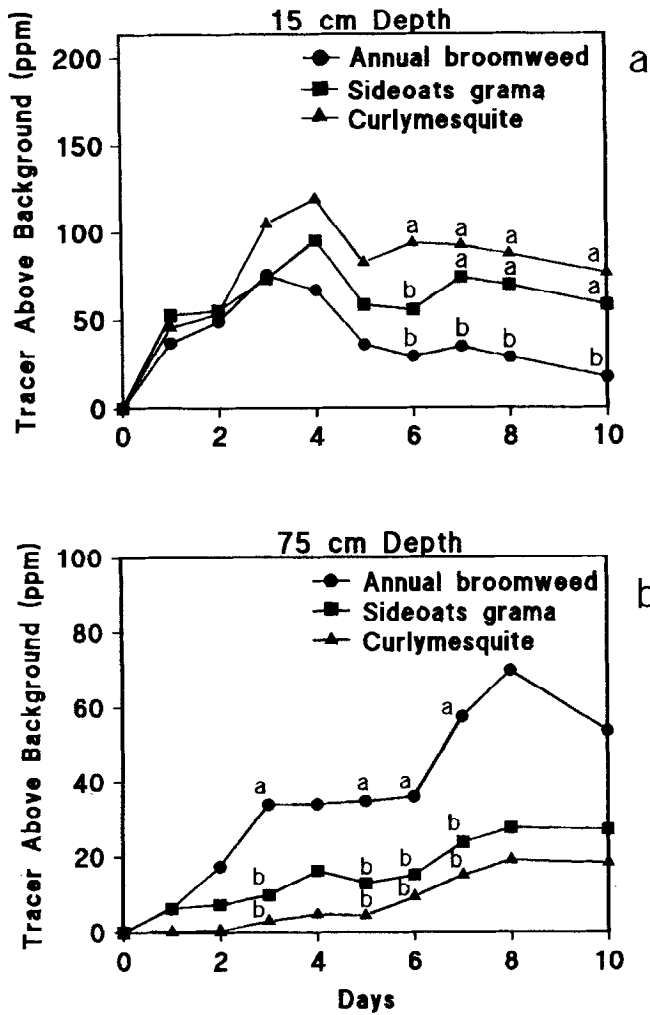


Fig. 2. Two day running average of tracer concentrations (ppm in excess of background). Different letters represent significant differences between species ($p < 0.05$).

The percent dose transpired from the 75 cm depth was more than double for annual broomweed than for sideoats grama or curlymesquite (Fig. 3a). Tracer concentrations (Fig. 2b) and neutron probe measurements (Table 5) also indicate that annual broomweed extracted more water from the 75 cm depth than the grasses. These data imply that annual broomweed utilizes deep soil water more effectively than the grass species. Greater water uptake from deep soil layers has been reported for a variety of species (Taylor and Klepper 1973, Proffitt et al. 1985, Sharp and Davies 1985, Sheffer et al. 1987, Wan et al. 1993) and may be partially attributed to the younger age of deep roots. Lopez and Nobel (1991) reported that hydraulic resistance increases with root age. Also, Wan et al. (1994) concluded that deep roots of broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britt and Rusby] absorb water more readily than the shallow laterals, probably due to suberization of shallow roots. Although we did not measure directly the hydraulic conductivity of annual broomweed roots in this study, greater use of water from the 75 cm depth relative to the 15 cm depth by annual broomweed suggests greater hydraulic conductivity of deep roots.

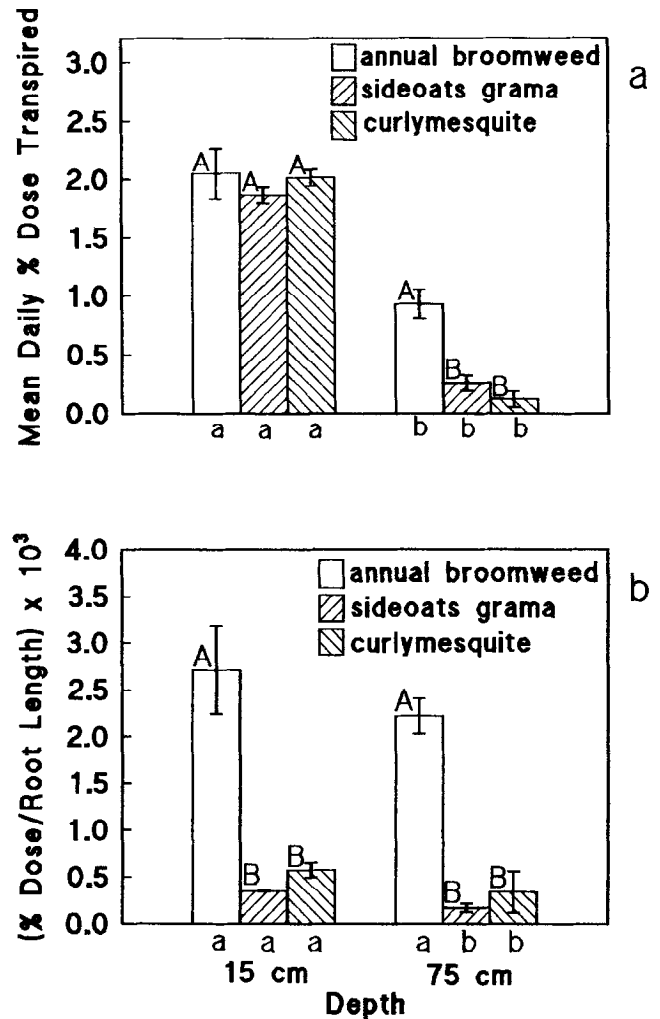


Fig. 3. Mean percent dose transpired and percent dose transpired normalized for differences in root length density. Different capital letters for a given depth indicate a significant difference ($p < 0.05$) between species. Different lower case letters indicate differences ($p < 0.05$) between depths for a given species. Error bars represent standard error of the mean.

Annual broomweed also extracted significantly more water per unit of root length (Fig. 3b) and had greater rates of water uptake (Fig. 4) from both depths than either sideoats grama or curlymesquite, implying greater hydraulic conductivity of annual broomweed roots relative to the grasses. Greater hydraulic conductivity of annual broomweed roots may result from low axial resistance to water flow in the xylem of dicots (Passioura 1988). High rates of water uptake may confer a competitive advantage to annual broomweed over the grasses. Eissenstat and Caldwell (1988) reported that *Agropyron desertorum* [(Fisch. ex Link) Shult.] has a competitive advantage relative to *Pseudoroegneria spicata* [(Pursh) Löve] due to *A. desertorum's* ability to deplete the water resource more rapidly than *P. spicata*.

On average during the sample period annual broomweed did not extract significantly more water from the 15 cm depth than the grasses. However, annual broomweed's rate of water extraction from the 15 cm depth was greater than that of the grasses. Hence, annual broomweed's more rapid water uptake from the 15 cm depth early in the sample period was balanced by lower rates

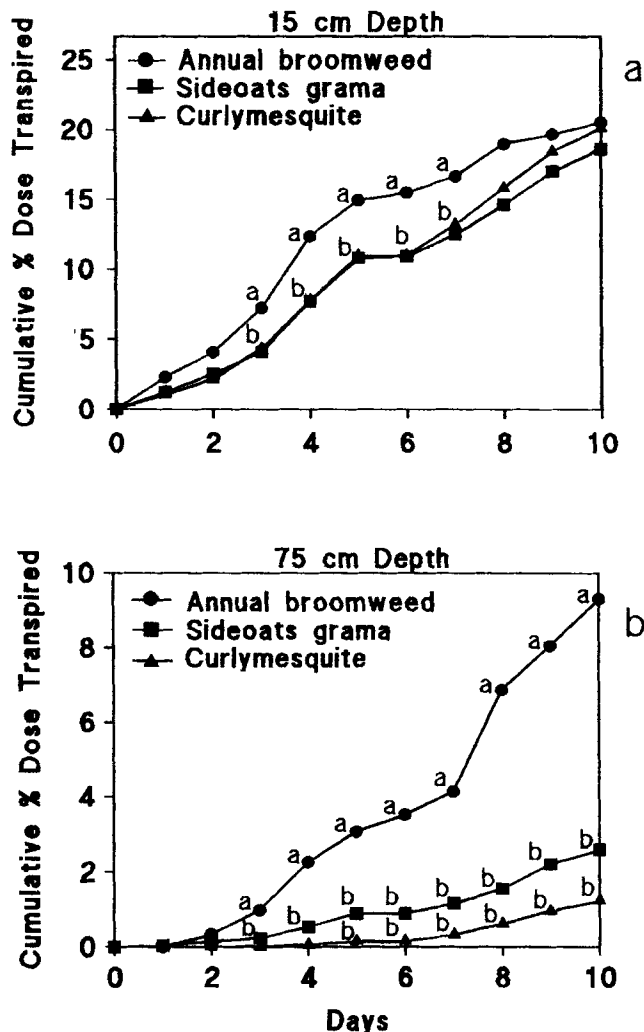


Fig. 4. Mean cumulative percent dose transpired from the 15 cm and 75 cm soil depths. Means with a different letter are significantly different ($p < 0.05$).

of water extraction from that depth when annual broomweed had depleted shallow soil water and was utilizing more deep soil water (Fig. 5). Similar patterns of water uptake by annual broomweed were observed the previous year following 2 rainfall events that recharged surface soils (Yoder 1993). This pattern concurs with observations of plant water use by Gardner (1983) who reported that, starting with a uniformly wet soil profile, water is extracted first from the region nearest the surface, with the zone of maximum extraction progressing downward through the soil profile as the surface dries. Reduced grass production in the presence of annual broomweed may be due, in part, to annual broomweed's ability to extract shallow soil moisture more rapidly than the grasses and then utilize deep soil water more effectively than the grasses.

Annual broomweed's effective utilization of deep soil water may also partially explain its cyclic dominance on rangelands. Annual broomweed is most successful in years with abundant winter rainfall (Heitschmidt 1979) which recharges deep soil water. In years with dry winters, annual broomweed must rely on shallow soil water and does not have the advantage of exploiting

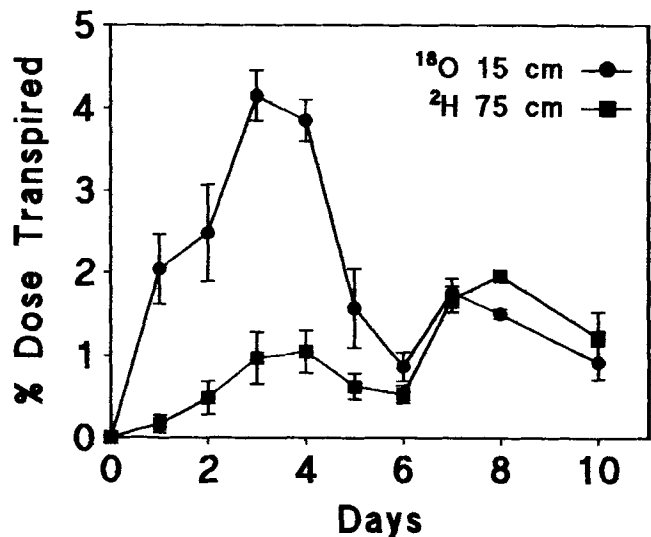


Fig. 5. Two-day running average of the percent isotope dose transpired by annual broomweed. Error bars represent standard error of the mean ($n=3$).

deep soil water that is largely unavailable to the grasses.

Leaf area indexes (LAI) were not significantly different between species (0.59, 0.60, and 0.56 for annual broomweed, sideoats grama, and curlymesquite, respectively). Therefore, differences in water use between species cannot be attributed to differences in LAI.

Summary

Knowledge of the physical distribution pattern of roots in the soil profile is not necessarily sufficient for understanding water uptake by roots because water uptake is more closely related to the activity of deep roots in some species (Flanagan et al. 1992). Tracer and neutron probe data from this study indicate that the activity of deep roots is important in determining water uptake by annual broomweed. Reduced grass production in the presence of annual broomweed has been attributed largely to competition for light (Gordon 1982, Boyd et al. 1983). The results of this study suggest that annual broomweed may also have a competitive advantage over native perennial grass species due to more rapid utilization of shallow soil water and effective utilization of deep soil water.

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