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Hydraulic lift: Substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots

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Summary. Diel soil water potential fluctuations reflected daytime depletion and nocturnal resupply of water in upper soil layers. Transpiration suppression experiments demonstrated that water absorption by roots caused the daytime depletion. The soil water potential data and experimental results suggest that at night water absorbed from moist soil by deeper roots is transported to and lost from roots into drier upper soil layers. The deeper roots appear to absorb and transport water both day and night. Implications for the efficiency of deep roots and water storage, nutrient uptake and water parasitism in upper soil layers are discussed.

Key words: Root water efflux – Roots – Soil water potential – Plant water relations – Desert shrubs

Roots commonly pass through dry soil layers to layers that contain more moisture. In the drier soil layers, the soil water potential, Ψ_s, is often more negative than the root water potential, Ψ_r. If water is lost from roots to drier soil, the root system can form a bridge for water transport between soil layers. Simulation models indicate that movement of water by such a bridge would be much more rapid than either liquid- or vapor-phase movement of water in the soil itself (van Bavel and Ahmed 1976; Rowse et al. 1978; Landsberg and Fowkes 1978; van Bavel et al. 1984; Campbell 1985). Such water transport by roots has been hypothesized to occur under certain circumstances in the field (Schippers et al. 1967; Hansen and Dickson 1979; Mooney et al. 1980; van Bavel et al. 1984). However, there is little direct evidence as to the presence or magnitude of this transport under field conditions.

The magnitude of water transport between soil layers depends strongly on root radial conductance for water efflux. Several laboratory studies indicate that roots may exhibit hysteresis in radial conductance such that, with the same Ψ gradient, water flows into roots more readily than it flows in the reverse direction (Molz and Peterson 1976; Nobel and Sanderson 1984; Dirksen and Raats 1985). How general and how pronounced these rectifier-like properties are for roots under field conditions is not clear. Other laboratory studies have shown that roots may leak water into dry soils if another portion of the root system is in moist soil (Jensen et al. 1961; Schippers et al. 1967; Hansen and Dickson 1979; Shone and Flood 1980; Corak et al. 1987). Recently, van Bavel and Baker (1985) showed that stolon-connected *Cynodon dactylon* plants in separate moist- and dry-soil compartments transferred considerable quantities of water from one compartment to the other. All of the water transpired by the plants in the dry compartment was transferred through the stolons from the plants in the moist soil. Approximately half of this transfer occurred at night when water was delivered to the soil of the dry compartment by root efflux.

We report Ψ_s measurements that suggest water transport and loss to dry soil layers can be of considerable magnitude under field conditions. Several implications of this transport for plants with root systems penetrating dry soil layers are discussed.

Methods

Soil water potentials were measured during drying cycles in the midsummer of 1985 and 1986 in field plots of interspersed sagebrush (*Artemisia tridentata* ssp. *vaseyana* (Rydb.) Beetle) and tussock grasses (*Agropyron desertorum* and *Agropyron spicatum*). As the grasses were essentially quiescent in midsummer, this study only concerns the shrub. The field plots were established near Logan, Utah from transplants in 1978 and have been described previously (Caldwell et al. 1981).

The soils at the study site are loamy-skeletal, carbonatic, mesic Typic Haploxerolls formed in alluvial fan deposits composed of dolomitic limestone fragments (Southard et al. 1978). The surface horizons of these soils extend to 40 cm depth, have gravelly loam texture, contain <20% coarse fragments and have available water capacity (water content at -0.03 MPa minus that at -1.5 MPa) >22%. At depths >40 cm, the soils have very gravelly fine sandy loam texture with coarse fragments constituting 40–70% of the volume. Available water capacity ranges from 19% at 40 cm to 14% at depths >1 m. Root density of *Artemisia tridentata*, based on roots washed from soil cores, is $\sim 1\ \mathrm{cm \cdot cm^{-3}}$ and is reasonably uniform from 20 cm to >1 m (Caldwell and Richards unpublished work; see also Fig. 2).

Individually calibrated screen-cage thermocouple psychrometers (J.R.D. Merrill Specialty Equip., Logan, Utah) were installed in 1984 beneath shrubs at three locations in the plots. Each location was surrounded by at least four rows of plants (50 cm spacing along and between rows). To provide a measurement standard and to control for potential errors in the data logger and measurement proce-

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dure, additional psychrometers were enclosed in stainless steel chambers lined with saturated filter paper (0.5 or 1.0 M KCl solutions). These chambers were located in a thermally insulated box on the soil surface at the field site.

The psychrometers were read every hour with an automatic microprocessor-controlled data logger (CR 7X, Campbell Scientific, Inc., Logan, Utah). The measurement protocol followed Brown and Bartos (1982). This included determination of the "zero offset" which provides a measure of thermal gradients that may exist in the psychrometers. Such gradients can cause large errors in the Ψ_s determinations (Wiebe et al. 1977). The measurements reported here are for depths (35, 50 and 80 cm) where diel temperature fluctuations were very weak and temperature gradients in the psychrometers were small enough to be adequately corrected by the calibration model (Brown and Bartos 1982). With these precautions and procedures, we feel the reported data are free of artifact.

To test the influence of transpiration on the behavior and magnitude of root water transport and loss, the shrubs surrounding a psychrometer location were covered with opaque plastic bags for 3-day periods. These bags were covered with moist cheese cloth and shaded to prevent overheating of the shrubs. The soil surface in the interspaces between the shrubs was not covered so that normal thermal exchanges would continue. At the time the measurements reported here were taken, the soil surface was very dry and thus little direct evaporation would have occurred (Campbell 1985). These transpiration-suppression experiments were repeated at two different locations at two different times during a two-month drying cycle in 1986.

Root distributions of the shrubs were determined in adjacent plots by profile wall mapping (Böhm 1979; Caldwell and Richards 1986).

Results

Pronounced diel fluctuations in Ψ_s occurred at all locations during midsummer of 1985 and 1986 when the upper portions of the soil profile were relatively dry (Fig. 1). These disappeared following heavy rains that moistened the upper soil layers. The fluctuations were not sinusoidal, but instead exhibited sharp peaks and troughs which occurred at approximately the same time of day in all three layers. During clear weather, for example during the first three days shown in Fig. 1, there was a rapid, nearly linear decrease in Ψ_s when the plants were transpiring rapidly during the day. With darkness and subsequent stomatal closure of the shrubs, root water uptake from the 35–80-cm soil layers quickly ceased and water efflux began as indicated by increasing Ψ_s. Daily maximum and minimum Ψ_s gradually decreased over this three-day period. During a subsequent cloudy period, the fluctuations were still evident, but the decrease of Ψ_s began later in the day and was much less than the increases during preceeding or following nights. When transpiration of the shrubs was suppressed during 3 days of clear weather, Ψ_s in all three layers increased steadily both night and day. When transpiration resumed, so did the daytime declines in Ψ_s. At this time, the daytime decreases of Ψ_s exceeded the nocturnal increases.

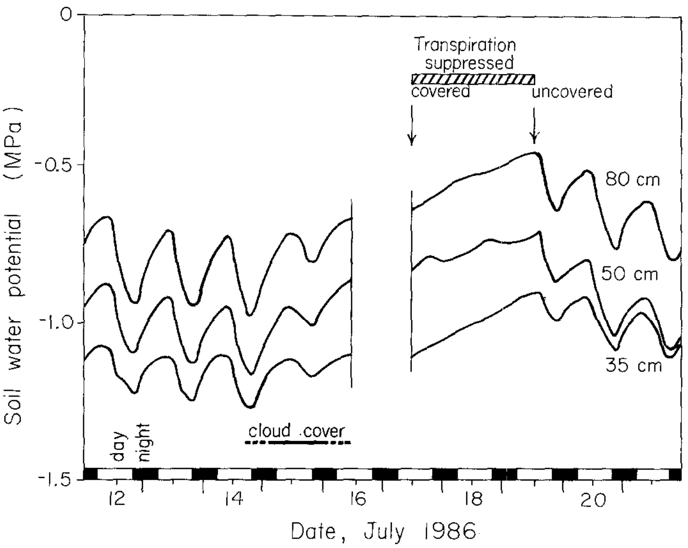

Fig. 1. Time course of Ψ_s at three soil depths during a drying cycle and a transpiration-suppression experiment in July, 1986. Periods of cloud cover and transpiration suppression are indicated. Missing data on July 16–17 are the result of power failure

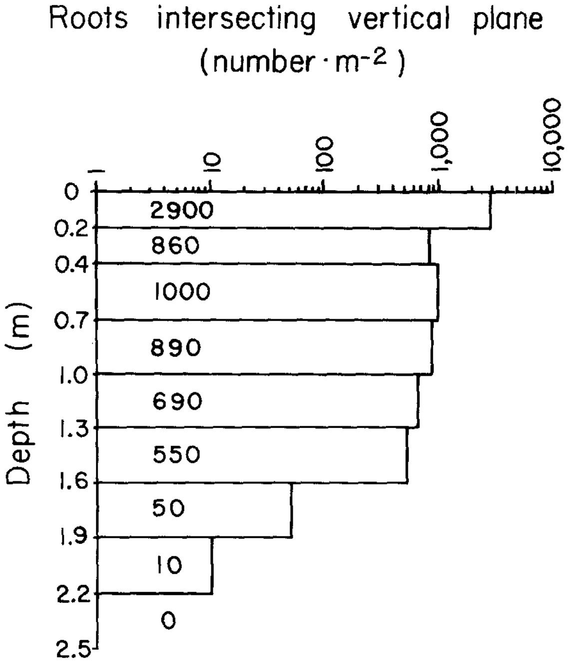

Fig. 2. Root density distribution of *Artemisia tridentata* roots with depth, based on profile wall mapping. The number of roots intersecting the mapping plane generally does not include the very fine roots (< ~0.3 mm dia.)

The transpiration-suppression experiments clearly demonstrated that the daily declines in Ψ_s resulted from root water uptake driven by transpirational demand. The increase of Ψ_s at night simultaneously in all three layers represents a flux of water into these layers that is much greater than can be supplied by water movement in the soil itself. The quantity of water delivered to these layers, that corresponds to the increase of Ψ_s in one night (e.g., July 12–13), is approximately $1\,\mathrm{l \cdot m^{-2}}$ ground area. This is a sizeable fraction of the total daily transpiration of the shrubs at this time of year (Caldwell and Richards, unpublished). Combined diffusivity of soil water in liquid and vapor phase is commonly 1 to $2\,\mathrm{cm^2 \cdot d^{-1}}$ for soils of a broad range of texture when Ψ_s is within the range -0.5 to -2.0 MPa (Rose 1968, Passioura 1985). It is in this range where we observed diel variations in Ψ_s (see Fig. 1). Following Passioura (1985) a time constant that describes the rate of water movement into dry soil from saturated soil was calculated with a conservative assumption that the depth of saturated soil was 1 m. This time constant was 2500–5000 d. This result indicates that water movement in soil alone is several orders of magnitude too slow to account for the diel changes in Ψ_s that we observed. We infer that the nocturnal increase in Ψ_s results from water efflux from roots in the 35–80 cm soil layers. This water must come from absorption by deeper roots. In our plots, roots of the shrubs penetrate to 2.2 m (Fig. 2) where moist soil would have been present at the time of our measurements.

Discussion

In midsummer there is typically a monotonic increase of Ψ_s with depth on sagebrush-dominated sites (Branson et al. 1976; Sturges 1977; Campbell and Harris 1977; Caldwell 1985). The deeper moisture is in part a result of subsurface water movement (Eakin et al. 1967). The deep roots of sagebrush should absorb and transport water both night and day, in accordance with prevailing Ψ_s and Ψ_r gradients. During the day when stomata are open, deep roots, as well as roots in the upper soil layers, should continue to absorb water and supply the transpiration stream. At night, when stomata are closed, water should flow from the deeper roots into the upper layers as a function of Ψ_s, rooting density, root radial conductance and root-soil conductance in the respective layers. We label this phenomenon hydraulic lift.

Diel plant xylem water potential fluctuations for *Artemisia tridentata* (DePuit and Caldwell 1975) are consistent with this explanation. Furthermore, the rates of change of plant Ψ after dusk and after dawn are sufficiently rapid to account for the rapid changes in direction of water movement between roots and the upper soil layers as shown in Fig. 1.

Two factors might preclude substantial efflux of water from roots. First, it has been suggested that either low root-soil or low soil hydraulic conductivities may limit efflux (Molz and Peterson 1976; Dirksen and Raats 1985; Baker and van Bavel 1986). Second, high root radial resistance to water efflux could limit the flux of water from the roots. When water readily flows into roots during the day, however, a very high nocturnal resistance seems unlikely. In laboratory studies, Baker and van Bavel (1986) have shown that roots of *Cynodon dactylon* have resistances to water loss only slightly greater than their resistance to water uptake. A very large and rapid increase in radial resistance has been demonstrated for two desert succulents, when the roots were subjected to drastic drying (roots exposed to air at 20 C with a vapor pressure deficit of 1.2 kPa, or water potential of -93.6 MPa) (Nobel and Sanderson 1984). However, without large changes in the Ψ_s of the root environment, we have not found cases in the literature where radial resistance for efflux was high enough to strongly curtail water loss.

Water efflux from roots into soil might be viewed as an undesirable process. Nevertheless, there are several features of hydraulic lift that would benefit the shrubs. If moisture is available only in the soil penetrated by the deepest roots, the small number of roots at these depths (Fig. 2) might not be able to support the maximum daytime transpiration rates of these shrubs without hydraulic lift. With hydraulic lift, additional moisture would be stored in upper soil layers where it would then be available to support daytime transpiration. By absorbing and transporting water both night and day, the deep roots would have a high efficiency of water uptake with respect to the investment required to produce and maintain them.

With hydraulic lift, the upper soil layers not only provide diel water storage, but can also serve as a buffer for several days. The potential magnitude of the water storage buffer, as indicated in the transpiration-suppression experiments (Fig. 1), is much larger than the normal diel storage. During periods of cloudy weather when transpiration is reduced, nocturnal storage can exceed the diurnal use of water (Fig. 1). During midsummer in the North American Great Basin, heavy precipitation events are comparatively rare, but alternating periods of cloudy and sunny weather are common. Following cloudy periods, even without precipitation, the shrubs will have more water available than following several days of clear warm weather.

During extended drying cycles, hydraulic lift should prolong the activity of roots and associated organisms, such as mycorrhizae, in the upper soil layers. On our study plots, as in most soils, available nutrients and root biomass (Fig. 2) are concentrated in the upper soil horizons. Nutrient uptake from dry soil when part of the root system has access to moisture has been clearly demonstrated (Nambiar 1976, 1977). The implications for nutrient uptake in dry seasons and for nutrient cycling need not be elaborated.

Diel variation in Ψ_s and coupled Ψ_r in the soil layers containing the majority of root biomass may have important consequences for the modulation of abscisic acid production by roots (see Lachno and Baker 1986). Hydraulic lift also has implications for the calculation of total plant hydraulic resistance (see Küppers et al. (1987) for discussion of calculation procedures). Unless the diel variation in Ψ_s is taken into account, large errors in this resistance could arise.

Coexisting plant species with different root depth distributions are commonly considered to partition belowground resources and largely avoid competition (e.g., Cody 1986; Davis and Mooney 1986). While this may be generally true, hydraulic lift by deep-rooted species and parasitism of water lost to the soil by shallow-rooted species can result in greater resource competition than root distributions would indicate.

There are also implications of hydraulic lift and water parasitism on an hydrological scale. In many arid and semi-arid regions, dry soils are often underlain by moist soils or aquifers. In the Great Basin abundant aquifers underlie most of the valleys between the numerous mountain ranges. As the Great Basin is a closed system with internal drainage, these aquifers discharge in springs or playas in the lowest parts of the valleys where the water eventually evaporates (Eakin et al. 1967). The depth of the soil moisture associated with the aquifers varies with location in the valleys and this depth often determines vegetation distribution. Conversely, the vegetation composition will determine how much of the subsurface moisture is tapped before it reaches the playas. While it is obvious that more deeply rooted plants will tap this moisture, hydraulic lift and water parasitism may increase the effectiveness of water uptake from subsurface moisture.

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References

Baker JM, van Bavel CHM (1986) Resistance of plant roots to water loss. Agronomy J 78:641–644

Böhm W (1979) Methods of studying root systems. Springer, Berlin, p 188

Branson FA, Miller RF, McQueen IS (1976) Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. Ecology 57:1104–1124

Brown RW, Bartos DL (1982) A calibration model for screen-caged Peltier thermocouple psychrometers. USDA Forest Service Research Paper INT-293, Ogden, p 155

Caldwell MM (1985) Cold desert. In: Chabot BF, Mooney HA (eds) Physiological ecology of North American plant communities. Chapman and Hall, New York. pp 198–212

Caldwell MM, Richards JH (1986) Competing root systems: Morphology and models of absorption. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge. pp 251–273

Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS (1981) Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. Oecologia (Berlin) 50:14–24

Campbell GS (1985) Soil physics with Basic: Transport models for soil-plant systems. Elsevier, New York, p 150

Campbell GS, Harris GA (1977) Water relations and water use patterns for *Artemisia tridentata* Nutt. in wet and dry years. Ecology 58:652–659

Cody ML (1986) Structural niches in plant communities. In: Diamond J, Case TJ (eds) Community ecology. Harper & Row, New York. pp 381–405

Corak SJ, Blevins DG, Pallardy SG (1987) Water transfer in an alfalfa/maize association: Survival of maize during drought. Plant Physiol 84:582–586

Davis SD, Mooney HA (1986) Water use patterns of four co-occurring chaparral shrubs. Oecologia (Berlin) 70:172–177

DePuit EJ, Caldwell MM (1975) Gas exchange of three cool semi-desert species in relation to temperature and water stress. J Ecol 63:835–858

Dirksen C, Raats PAC (1985) Water uptake and release by alfalfa roots. Agronomy J 77:621–626

Eakin TE, Price D, Harrill JR (1967) Summary appraisals of the nation's ground-water resources-Great Basin Region. USGS Professional Paper 813 G, Washington, D.C., p G37

Hansen EA, Dickson RE (1979) Water and mineral nutrient transfer between root systems of juvenile *Populus*. Forest Sci 25:247–252

Jensen RD, Taylor SA, Wiebe HH (1961) Negative transport and resistance to water flow through plants. Plant Physiol 36:633–638

Küppers M, Neales TF, Küppers BIL, Swan AG, Myers BA (1987) Hydraulic flow characteristics in the lignotuberous mallee *Eucalyptus behriana* F. Muell. in the field. Plant Cell Env 10:27–37

Lachno DR, Baker DA (1986) Stress induction of abscisic acid in maize roots. Physiol Plant 68:215–221

Landsberg JJ, Fowkes ND (1978) Water movement through plant roots. Ann Bot 42:493–508

Molz FJ, Peterson CM (1976) Water transport from roots to soil. Agronomy J 68:901–904

Mooney HA, Gulmon SL, Rundel PW, Ehleringer J (1980) Further observations on the water relations of *Prosopis tamarugo* of the northern Atacama desert. Oecologia (Berlin) 44:177–180

Nambiar EKS (1976) Uptake of Zn^{65} from dry soil by plants. Plant and Soil 44:267–271

Nambiar EKS (1977) The effects of water content of the topsoil on micronutrient availability and uptake in a siliceous sandy soil. Plant and Soil 46:175–183

Nobel PS, Sanderson J (1984) Rectifier-like activities of roots of two desert succulents. J Exper Bot 35:727–737

Passioura JB (1985) Roots and water economy of wheat. In: Day W, Atkin RK (eds) Wheat growth and modelling. Plenum, New York. pp 185–198

Rose DA (1968) Water movement in porous materials. III. Evaporation of water from soil. Brit J Appl Phys (J Phys D) Ser 2 1:1779–1791

Rowse HR, Stone DA, Gerwitz A (1978) Simulation of the water distribution in soil. II. The model for cropped soil and its comparison with experiment. Plant and Soil 49:533–550

Schippers B, Schroth MN, Hildebrand DC (1967) Emanation of water from underground plant parts. Plant and Soil 27:81–91

Shone MGT, Flood AV (1980) Studies on uptake and loss of water by barley roots in relation to changes in root resistance. J Exper Bot 31:1147–1159

Southard AR, Wilson L, Erickson AJ (1978) Chemical and physical properties of soils of the Cache Valley area and the eastern portion of Box Elder County, Utah. Utah Agric Exper Sta Res Rep 31, p 112

Sturges DL (1977) Soil water withdrawal and root characteristics of big sagebrush. Am Midl Nat 98:257–274

Van Bavel CHM, Ahmed J (1976) Dynamic simulation of water depletion in the root zone. Ecol Modell 2:189–212

Van Bavel CHM, Baker JM (1985) Water transfer by plant roots from wet to dry soil. Naturwissenschaften 72:606–607

Van Bavel CHM, Lascano RJ, Stroosnijder L (1984) Test and analysis of a model of water use by sorghum. Soil Sci 137:443–456

Weibe HH, Brown RW, Barker J (1977) Temperature gradient effects on in situ hygrometer measurements of water potential. Agronomy J 69:933–939

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