

Hydraulic redistribution by two semi-arid shrub species: Implications for Sahelian agro-ecosystems

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ABSTRACT

Hydraulic redistribution is the process of passive water movement from deeper moist soil to shallower dry soil layers using plant roots as conduits. Results from this study indicate that this phenomenon exists among two shrub species (*Guiera senegalensis* and *Piliostigma reticulatum*) that co-exist with annual food crops in Sahelian agro-ecosystems. Real-time measurements were conducted for soil water content, soil water potential and microclimate variables notably; air temperature, relative humidity, wind speed, precipitation and solar irradiance. Additionally, sap flow measurements were conducted in shrub roots using the thermal dissipation technique on intact and coppiced shrubs. Monthly predawn leaf water potential was measured using a portable pressure chamber. Soil water potential (Ψ_s) at the 20 cm depth declined significantly during the dry season with diel changes in Ψ_s of -0.6 to -1.1 MPa. These variations were attributed to passive water release from shrub roots resulting in overnight rewetting of drier upper soil layers. Sap flow measurements on tap and lateral shrub roots indicated daily reversals in the direction of flow. During the peak of the dry season, both positive (toward shrub) and negative (toward soil) flows were observed in lateral shrub roots with sap flow in the lateral roots frequently negative at night and rapidly becoming positive soon after sunrise. The negative sap flow at night in superficial lateral roots and the periodic positive flow in the descending tap roots were indicative of hydraulic redistribution. Hydraulic redistribution may be an important mechanism for drought stress avoidance while maintaining plant physiological functions in both shrubs and neighboring annuals in water-limited environments.

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1. Introduction

The productivity of arid and semi-arid ecosystems is controlled primarily by water dynamics. The relatively recent discovery of hydraulic redistribution (HR) has important implications for understanding ecosystem functioning in these dry environments (Caldwell et al., 1998). Hydraulic redistribution (HR) is the process of passive water movement from relatively moist to drier regions of soil using plant roots as a conduit (Caldwell, 1990; Dawson, 1995; Richards and Caldwell, 1987; Xu and Bland, 1993). It is driven by soil

matric potential gradients and modulated by resistance to reverse flow through roots and by rhizosphere resistance to transfer of water from roots to soil. Hydraulic redistribution usually occurs at night when transpiration has diminished sufficiently to allow the water potential in roots to exceed that in the drier upper portions of the soil profile (Scholz et al., 2002). Although movement of water via HR is usually upward from deep, moist soil layers to shallow, dry layers, both downward (Burgess et al., 2001; Smith et al., 1999) and lateral (Bleby et al., 2010; Brooks et al., 2002, 2006) HR have been documented. Downward HR may play an important role in deep soil moisture recharge in arid regions (Leffler et al., 2005; Ryel et al., 2003). Associated benefits of HR for the plants involved may include delaying loss of root xylem conductivity in shallow roots

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(Domec et al., 2004, 2006) and prolonging their nutrient uptake (Caldwell et al., 1998) during dry periods.

Now that more than 60 cases of HR have been reported in woody and herbaceous plants (Jackson et al., 2000), there is reason to expect that its existence is widespread wherever conditions are conducive to its occurrence. Evidence for HR consists largely of time fluctuations of soil water potential showing partial overnight recovery in drier soil layers (Millikin Ishiikawa and Bledsoe, 2000; Richards and Caldwell, 1987), movement of deuterated water as a tracer from roots to soil and neighboring plants (Brooks et al., 2002, 2006; Moreira et al., 2003), and reverse sap flow in roots (Burgess et al., 1998; Scholz et al., 2002; Smith et al., 1999).

Verification of HR requires close observation of other bio-physical processes that could account for altered soil moisture regime in the upper soil layers in the presence of woody shrubs. For instance, near-surface thermal variability can affect water movement within the vadose zone in liquid and vapor phases (Cahill and Parlange, 1998; Milly, 1996; Parlange et al., 1998; Philip and de Vries, 1957). These studies have demonstrated that the presence of temperature gradients in unsaturated soils may also induce water fluxes in gas and liquid phases that can significantly contribute to the water and energy transport processes. However, in a modeling study Ryel et al. (2002) concluded that during summer drought, the amount of water moved by unsaturated flow was typically negligible compared to that moved by HR in an *Artemisia tridentata* stand.

Transfer of water from plants conducting HR to surrounding plants has been documented (Brooks et al., 2006; Caldwell and Richards, 1989; Moreira et al., 2003), but the potential facilitating effects of HR on neighboring plants remain to be evaluated. Although recent studies in the East African savanna indicated that the deeply rooted tree *Acacia tortilis* conducts HR, the facilitative effects of hydraulically lifted water taken up by surrounding grasses were uncertain because soil water potential was consistently lower under the tree crowns than outside the crowns (Ludwig et al., 2003). Lufafa et al. (2009) have shown that two semi-arid shrub species (*Guiera senegalensis* and *Piliostigma reticulatum*) co-exist within row crops and are widely distributed in Senegal. Previous work (Kizito et al., 2006, 2007) has demonstrated that during the dry season, the soil surrounding the shrub shallow roots is substantially moister than soil distant from the shrubs, but these shrubs have not been investigated for their potential to perform HR. The existence of HR among these shrubs could alter hydrological processes enough to significantly impact water balances and improve or stabilize crop productivity by reducing drought stress. We therefore hypothesized the presence of a unique interaction and exchange of water pulses between the semi-arid shrubs and co-occurring annual row crops. Our objectives in this study were to: 1) evaluate the existence and magnitude of hydraulic redistribution by *G. senegalensis* and *P. reticulatum*; and 2) quantify the magnitude of other bio-physical processes potentially responsible for soil water transport during the dry season.

2. Materials and methods

2.1. Study sites

The study was conducted in two different agro-ecological zones in the Peanut Basin of Senegal, West Africa. The region is characterized by temporally and spatially variable unimodal rainfall with episodic droughts and frequent crop failures (Centre de Suivi Ecologique, 2000). The rainy season lasts from July to September, generally as scattered, high intensity, short-duration showers. Air temperature exhibits high diurnal and annual variability. The main annual crops are millet (*Pennisetum glaucum* (L.) R. Br.), groundnuts

(*Arachis hypogaea* L.), sorghum (*Sorghum bicolor* (L.) Moench), cowpeas (*Vigna unguiculata* (L.) Walp.) and corn (*Zea mays*) in the southern part of the Peanut Basin. The planting density for peanut is about 130,000 plants ha⁻¹ha (sown as one seed per hole) while that of corn is about 5000 plants ha⁻¹.

The research was conducted at two sites. One study site, Keur Matar Arame (KMA), is located in the northern region (N14°46W 16°51'; 43 m above sea level, slope range 0–1%) of the Peanut Basin with a mean annual unimodal precipitation of 450 mm (Fig. 1). The water table at this site lies at 15 m. *G. senegalensis* is the dominant shrub, characteristically 1 m tall with a shrub canopy crown of about 2 m and a highly spreading shallow rooting system in the top 0.45 m and a narrow leading unbranched root to a depth greater than 2.5 m (Kizito et al., 2006). The site has a shrub stand density of 240 shrubs ha⁻¹. The minimum mean annual ambient temperature is 20 °C and a maximum mean annual ambient temperature of 33 °C. The area lies on a leached and disturbed ferruginous sand soil classified as a ferruginous Oxisol (FAO, 1998). The top horizon (0–0.7 m), is sandy with a friable continuous structure and no distinct horizonation with low clay contents of about 5% and scanty organic matter content of 0.5%.

The second study site is located at Nioro, in the southern region (N13°45 W 15°47'; 18 m above sea level, slope range of 0–2%) of the Peanut Basin, with a total mean annual unimodal precipitation of 750 mm (Fig. 1). *P. reticulatum* is the predominant shrub occurring at a density of 185 shrubs ha⁻¹ with a well developed and fairly deep rooting system (Diack et al., 2000; Kizito et al., 2006). The water table lies at about 12 m below the soil surface. This site has randomly scattered *Cordyla pinnata* and *Prosopis africana* trees in the landscape. The mean annual minimum ambient temperature is 20 °C and the mean annual maximum ambient temperature is

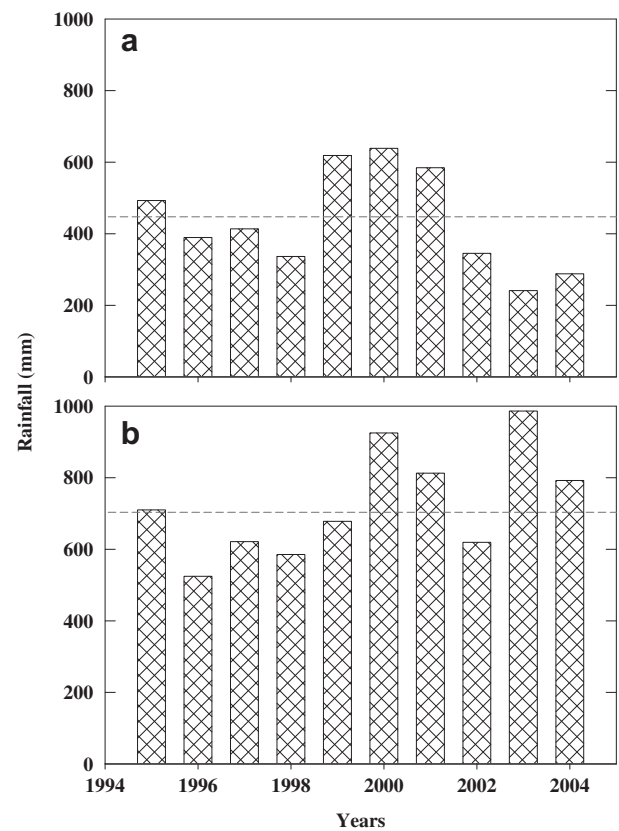


Fig. 1. Decadal cumulative annual rainfall for rain gauges 1995–2004 at (a) KMA and (b) Nioro. Dotted horizontal lines show the decadal average value (After Kizito et al., 2007).

36 °C. The area lies on a fine-sandy, mixed Haplic Ferric Lixisol, a leached ferrugeneous tropical Ultisol (Diack et al., 2000). It is characterized by a leached light brown ferrugeneous top horizon (0–0.6 m). This gradually blends into a red brown lateritic color (0.8–1.5 m) with ferric spots interspersed in the profile.

2.2. Field and laboratory methods

2.2.1. Experimental design and trial layout

The experimental area at both sites (KMA and Niore) was 64 m × 44 m. Each site had 18 plots with dimensions of 6 m × 8 m in a randomized block design with two treatments within three blocks replicated three times (Appendix 1, electronic version only). Treatment 1 served as the control: bare plots that had previously had an annual crop (peanut or millet). Treatment 2 was comprised of shrubs with one shrub monitored below shrub center; 50 cm away from shrub center (at the 20 cm depth); and 200 cm away from shrub center (at the 20 cm depth). For each treatment, soil water content and soil water potential measurements were conducted at 20, 40, 60, 80, 100 and 120 cm depths.

2.2.2. Soil water measurements

Volumetric soil water content (θ) was continuously monitored over a two-year period (2003–2004) below three replicate individuals of each species using dielectric soil water content sensors (ECH₂O Probe; Decagon Devices Inc, Pullman, WA, USA). These were calibrated gravimetrically in the field and were installed at 20, 40, 60, 80, 100 and 120 cm depths. Probe data were logged at hourly intervals with a data logger (CR10X; Campbell Scientific, Logan, UT, USA).

Soil water potential (Ψ_s) was measured using screen-cage soil psychrometers (PST-55, Wescor, Inc., Logan, UT, USA). These were individually calibrated using standard salt solutions following the procedures of Brown and Bartos (1982). Psychrometers were installed at depths of 20, 40, 60, 80, 100 and 120 cm. The psychrometers measured both soil water potential and soil temperature measurements on an hourly basis with a 30 s cooling time for the Peltier effect. Psychrometer data were logged and downloaded from a water potential data logger (PYSPRO; Wescor, Inc.). Soil psychrometers were installed in close proximity to the dielectric probes to permit concurrent comparison with soil water content measurements.

The role of HR in shrub–crop interaction was investigated by measuring Ψ_s at 20 cm and 40 cm depths for three distances from the shrub center: directly below the shrub, 50 cm away from shrub center and 200 cm away from shrub center outside canopy periphery. The Ψ_s were conducted to investigate the effect of partial soil profile rewetting. Total daily water use (mm day⁻¹) was calculated as soil moisture changes measured by the dielectric probes located at depths of 20 and 40 cm. This was the difference between the daily maximum and minimum moisture content values. The instruments located at the 20 cm and 40 cm depths were assumed to represent soil moisture conditions over a control volume that spanned approximately 10–50 cm depth. Based on field observations, it was estimated that the 10–50 cm depth would encompass the near-surface rooting zone for both annual crops and native shrubs. Hydraulic redistribution was calculated as the difference between the daytime minimum soil water storage and the following day's maximum, which represents overnight recovery of soil water storage (Brooks et al., 2002).

In order to derive the net effect of HR, moisture increases between the maxima of consecutive days, at the 20 and 40 cm depth were considered to be a dual contribution of HR and vapor

Table 1

Mean predawn water potential (soil water potential before sunrise) (MPa) for the 20 cm depth during peak of dry season (May–June).

Microsite	<i>Guiera senegalensis</i>		<i>Ptilostigma reticulatum</i>	
	Keur Matar Arame		Niore	
	2003	2004	2003	2004
Beneath shrub center	–2.84(0.02) ^a	–3.32(0.12) ^a	–1.99(0.11) ^a	–2.03(0.08) ^a
50 cm from shrub center	–2.92(0.06) ^{ab}	–3.46(0.08) ^{ab}	–2.45(0.14) ^{ab}	–2.47(0.02) ^{ab}
200 cm from shrub center	–3.26(0.18) ^c	–4.31(0.26) ^c	–2.92(0.01) ^{bc}	–2.93(0.04) ^{bc}
Bare soil site	–5.41(0.12) ^d	–5.25(0.09) ^d	–3.71(0.05) ^d	–3.74(0.03) ^d
Leaf water potential	–0.54(0.04)	–0.71(0.16)	–0.50(0.08)	–0.86(0.13)

*Numbers in parenthesis represent standard errors while letters in superscript represent Fisher's protected least significant difference (LSD) test where differences were considered statistically significant at $P < 0.05$.

flux deposition. The moisture increase was thus termed “apparent HR” (Table 2). The net HR was calculated as the difference between apparent HR and estimated vapor flux deposition. Cumulative apparent HR was calculated as the minimum soil water content for one day subtracted from the maximum soil water content at the commencement of the following day.

2.2.3. Environmental measurements

Microclimate variables monitored included air temperature, relative humidity, wind speed, precipitation and solar irradiance. Air temperature and relative humidity were measured with a combined probe (Vaisala HMP 45C, Campbell Scientific). This was placed in one of the study plots at two-thirds of the mean canopy height of the shrub stand. Wind speed and direction were monitored using a wind sensor (RM Young 05103-L, Campbell Scientific, Logan, UT, USA) placed 2 m above the soil surface. Solar irradiance was measured with a silicon diode pyranometer (LI-COR LI200X, Lincoln, NE, USA). A tipping bucket rain gauge (TE525-L, Texas Electronics, Dallas, TX, USA), with tips at 0.01” increments (about 0.254 mm of rainfall per tip) was used to monitor precipitation. All the above parameters were recorded every 15 min and data subsequently averaged at hourly intervals with a data logger (CR10X; Campbell Scientific).

Table 2

Seasonal variations at 20 cm depth of soil water status, vapor flux and HR (Values in brackets represent standard error of the mean).

Variable	<i>Guiera senegalensis</i>		<i>Ptilostigma reticulatum</i>	
	Keur Matar Arame		Niore	
	2003	2004	2003	2004
Soil water content (m ³ m ⁻³)				
Start of dry season	0.018(0.01) ^a	0.016(0.02) ^a	0.064(0.04) ^a	0.082(0.01) ^a
End of dry season	0.026(0.01) ^b	0.021(0.01) ^b	0.096(0.03) ^b	0.114(0.01) ^b
Soil water potential (MPa)				
Start of dry season	–5.60(0.05) ^a	–4.98(0.03) ^a	–4.32(0.07) ^a	–4.11(0.05) ^a
End of dry season	–4.89(0.03) ^b	–4.20(0.04) ^b	–4.19(0.06) ^{ab}	–3.92(0.02) ^{ab}
Vapor flux (mm)	1(0.01)	0.8(0.02)	0.12(0.02)	0.2(0.01)
Apparent HR (mm)	36(0.02)	48(0.01)	21(0.01)	18(0.01)
Net HR (mm)	35(0.01)	47.2(0.02)	20.88(0.01)	17.8(0.02)

*Numbers in parenthesis represent standard errors while letters in superscript represent Fisher's protected least significant difference (LSD) test where differences were considered statistically significant at $P < 0.05$.

2.2.4. Vapor transport dynamics

Vapor flux was deduced from soil temperature and Ψ_s measurements taken along the profile. Atmospheric measurements were used to compute the vapor pressure deficit, a component used in vapor transport derivation under field conditions (Milly, 1996). The rate of diffusion of water vapor is directly proportional to the gradient of vapor pressure or vapor density (Hillel, 1998). The density of water vapor in soil under saturation is a function of temperature as expressed by (Ahrens, 1994):

$$P_{\text{sat}} = 5.018 + 0.32321T_c + 8.1847 \times 10^{-3}T_c^2 + 3.1243 \times 10^{-4}T_c^3 \quad (1)$$

Where, P_{sat} is the saturated water vapor density in soil under saturation (gm m^{-3}) and T_c is the temperature ($^{\circ}\text{C}$). Since soil temperature fluctuates with depth diurnally, the amount of vapor that can be held in air changes. Decreasing temperature will therefore cause vapor to condense, this condition was assumed to apply at the range of water potential values exhibited at our study sites. The shape and depth of the soil thermal profile will be influenced by the thermal conductivity and heat capacity, which depend on soil moisture, organic and mineral content (Hillel, 1998). Movement of the thermal signal down the soil profile will determine the value of the saturated vapor density, and therefore the relative humidity impacting condensation, evaporation and vapor flux processes through the soil profile (Ahrens, 1994).

Fick's Law is generally used for steady state diffusion of vapor in soil air

$$J_g = -D_s \frac{\partial v_{\text{vapor}}}{\partial z} = -D_s \frac{v_l - v_u}{z_l - z_u} \quad (2)$$

Where, J_g is the diffusive flux of a gas ($\text{g m}^{-2} \text{s}^{-1}$), D is the diffusion coefficient (generally having dimensions of area per unit time), $\partial v_{\text{vapor}}$ is the change in vapor pressure and ∂z is the change in depth. Assuming that the relative humidity is 100% all the time for any particular soil layer, J_g can be calculated in the final equation where, v_l is the lower depth vapor pressure, v_u is the upper depth vapor pressure, z_l is the depth of the lower layer from the soil surface, z_u is the depth of the upper layer from the soil surface.

The diffusion coefficient for a soil can be calculated from the diffusion coefficient in free-air (Penman, 1940):

$$D_s = D_o 0.66 f_a \quad (3)$$

Where, D_o is the diffusion coefficient of water vapor in air, 0.66 is the tortuosity coefficient, and f_a is the air-filled porosity. Air-filled porosity (f_a) was derived from hourly measured field water content

$$f_a = \left(1 - \frac{\rho_b}{\rho_s}\right) - \theta \quad (4)$$

Where θ is the measured field moisture content, ρ_b is the site specific soil bulk density (g cm^{-3}), ρ_s is the particle density (g cm^{-3}).

Vapor movement in the 20–40 cm depth includes fluxes deposited in this layer across the boundary between layers. In order to account for the vapor flux within the 20–40 cm layer, the flux was calculated for each depth and was subsequently summed for both depths over the season.

2.2.5. Sap flow measurements and coppicing treatments

Sap flow measurements were performed simultaneously on the shrub tap and lateral roots to ascertain the relative contribution of each of these roots to the HR process. Root sap flow was measured using the thermal dissipation technique (Granier, 1987), which was modified to permit the direction of flow to be detected (Brooks

et al., 2002, 2006). As shown (in Appendix 2, electronic version only), the schematic portrays the modification to the probe that permitted determination of sap flow direction. In its original form, this technique relies on a probe that indicates the magnitude of flux by measuring the difference between a heated temperature sensor and a single unheated reference temperature sensor. It was insensitive to the direction of flow and unsuitable for monitoring reversal of flow in roots associated with hydraulic redistribution (Burgess et al., 2000). However, an additional directional probe was installed where two thermocouples were placed up and downstream with the differential between these two thermocouples indicating the direction of flow. As shown in Appendix 2, electronic version only, the sensor has a symmetrical design centering on the heater probe, with one sensor upstream and one sensor downstream reference probe (placed 10 cm axially from the heater) as well as one upstream and one downstream fine-wire thermocouples (7 mm away from the heater). Together, this assembly generated three different temperature measurements recorded in mV with which to calculate root xylem water flux ($\text{g m}^{-2} \text{s}^{-1}$). Data from the sap flow sensors were sampled at 10-s intervals with means logged hourly. The sensors were connected to a data logger (CR10X, Campbell Scientific) via a 32-channel multiplexer, with both the heater source and data logger being powered by a 12-V battery.

Sap flow sensors were installed on one superficial lateral root and a larger descending tap root on three shrubs per site. For each root monitored, a flux and a directional probe were installed. The probes were inserted at about 15 cm soil depth on each of the roots (tap and lateral). The mean root sapwood areas for the instrumented shrubs in KMA site were 8.4 cm^2 for the lateral roots and 11.5 cm^2 for the tap root. The mean root sapwood areas for the instrumented shrubs in Niore site were 10 cm^2 for the lateral roots and 16.5 cm^2 for the tap roots. For both shrub species, it was assumed that wood in the root was predominantly sapwood.

Baseline sap flow data was collected from intact shrubs before conducting the coppicing treatments (only conducted in 2004). On day 198, shrubs were partially coppiced by removal of a portion of their above ground biomass which was about 80% of the canopy including shoot tips. For each of the coppicing treatments, real-time sap flux data were monitored for about 13 days at both shrub sites. On day 202, complete removal of the above ground biomass was conducted leaving only the shrub base close to the soil surface. Sap flow data was collected before, during and after coppicing treatments.

2.2.6. Leaf water potential measurements

Predawn leaf water potential was measured on a monthly basis using a portable pressure chamber (PMS 600, PMS Instruments, Corvallis, OR, USA). In addition to predawn water potential, measurements were performed at several additional times to determine shrub diurnal trends up to just before midnight when the shrubs were assumed to have recuperated to their predawn values. For all sampling dates, measurements were performed on the same shrubs to minimize errors (Turner, 1988). These measurements spanned over three consecutive seasons, two dry seasons and the transition into the wet cropping season. Measurements were conducted on the third rank of a fully opened well-exposed upper canopy leafy twig. These were excised with sharp blades and immediately transferred to the pressure chamber for measurement. Real-time monitoring of soil water potentials (as described in Section 2.2.2) permitted close comparison with leaf water potential measurements. In addition, for each season, three replicates of leaf water potential of neighboring annual weeds *Amaranthus* species (pig weed) in close proximity to the shrubs were measured.

2.3. Data analysis

Since sampling was conducted on the same shrubs over time, sap flow and leaf water potential data were analyzed using a repeated measures model (Lindsey, 1993). Pre-planned comparisons between treatment (shrub areas) and control (bare soil) means were made using Fisher's protected least significant difference (LSD) test and differences were considered statistically significant at $P < 0.05$. Differences in field measurements between shrub areas and bare soil areas were determined using a one-way ANOVA and to assess the difference at each date, a two-way ANOVA with one repeated measure factor was made for soil water content. All statistical procedures were conducted with Statistical Analysis Systems software, SAS V8 (2001).

3. Results

3.1. Soil water status

The Ψ_s observed at all three distances from the shrub center to 200 cm away was consistently higher and significantly different than those in the bare soil plots (Table 1). Soil water potential values before dawn were slightly higher directly beneath the shrub than further away (Table 1) though this was not consistent over the entire dry season. Predawn leaf water potentials were higher than soil water potentials before dawn indicating the water potential gradient was from the plant to the soil.

The minimum for each day was mainly between 1300 h and 1400 h (1 p.m.–2 p.m) while the maximum was between 2400 h and 100 h (midnight and 1 a.m). The KMA site depicted considerably higher net HR values compared to the Nioro site (Table 2). Results from Table 2 depicted significant differences for both soil water content and soil water potential between the start and end of the dry seasons for both sites.

A consistent diel partial rewetting of portions of the profile occurred below and around the shrub root zone during the dry season observed as overnight increases in soil Ψ_s at the 20 and 40 cm depths (Fig. 2a, b). The 60 cm depth also exhibited a gradual increase but with differing diurnal trends to the 20 cm and 40 cm depths (Fig. 2a, b). The Ψ_s below and around shrubs at the 20 cm depth ranged from -3.5 to -6.3 MPa at KMA and from about -1.8 to -4.2 MPa in Nioro, resulting in similar diel amplitude of about 2.5 MPa at both sites. In contrast, Ψ_s at the 20 cm depth bare soil remained low with small diel fluctuations of about 0.2 MPa occurring during the day around noon.

The magnitude of HR seemed to peak at both sites between April–May and declined in the subsequent two months (Fig. 3). For the 0–20 cm depth range, averaged over the entire 2003 dry season, the average daily HR in KMA was about 0.13 mm day^{-1} , replenishing 30% of the daily depletion and for the 2004 dry season, the average daily HR in KMA was about 0.17 mm day^{-1} , replenishing 42% of the daily depletion. For the 0–20 cm depth range, averaged over the entire 2003 dry season, the average daily HR in Nioro was about 0.07 mm day^{-1} , replenishing 15% of the daily depletion and for the 2004 dry season, the average daily HR in Nioro was again 0.06 mm day^{-1} , replenishing 22% of the daily depletion.

There were notable differences in the magnitudes of HR and the above results show that HR peaked a month earlier in 2004 at both study sites and in 2003, replenishment of soil water through HR was lower than in 2004 at both study sites. Replenishment of soil water through HR was also lower at the Nioro site than at the KMA site. Based on the rainfall data, for KMA, there was less rainfall in 2003 than 2004 (Fig. 1) and the HR peak magnitude was higher in 2003 than

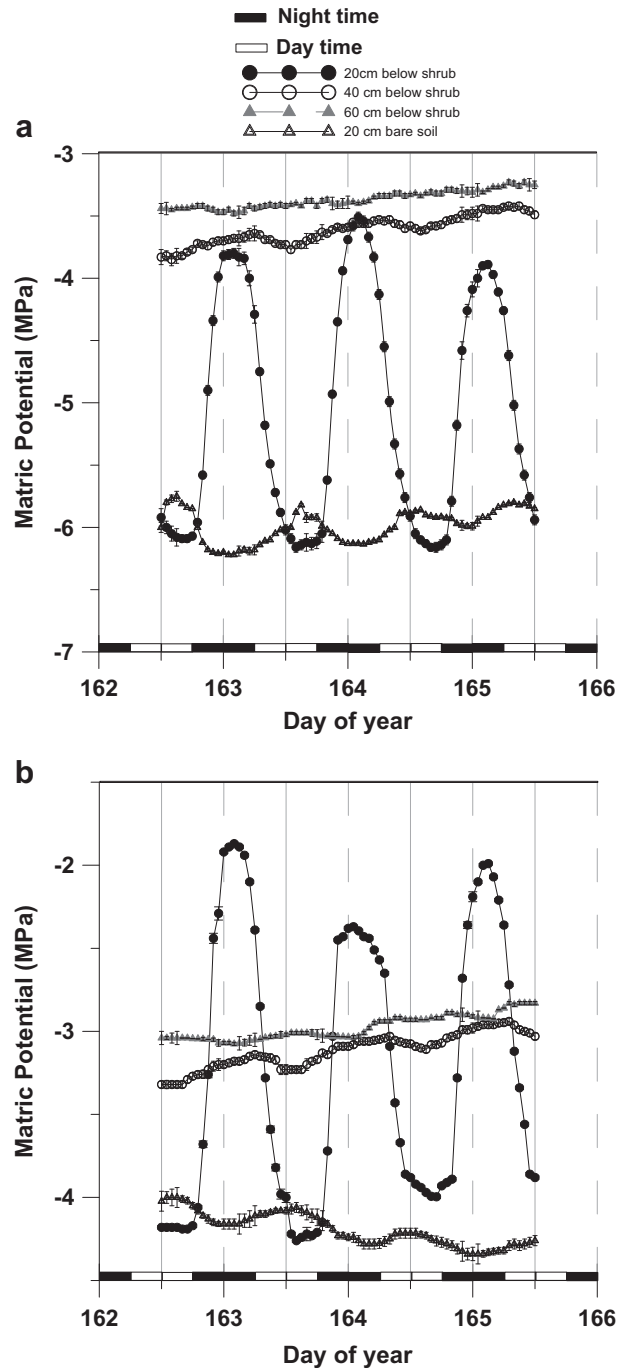


Fig. 2. Daily soil matric potential (MPa) variation with day of year, 2004 below shrubs for the 20–60 cm depths and at bare soil plots for the 20 cm depth for both sites (a) KMA; (b) Nioro. Standard error bars are computed from mean values of three shrub replicates per measurement.

2004 (Fig. 3). In Nioro, there was less rainfall in 2004 than 2003 (Fig. 1) and the HR peak magnitude was higher in 2004 than 2003 (Fig. 3).

3.2. Vapor flux dynamics

Soil vapor flux entering or exiting the control volumes was computed for the 20 and 40 cm depths and showed substantial diurnal variation with the greatest magnitudes occurring between 1000 h and 1200 h at both study sites (Appendix 3, electronic version only). This may be indicative of the peaks observed in

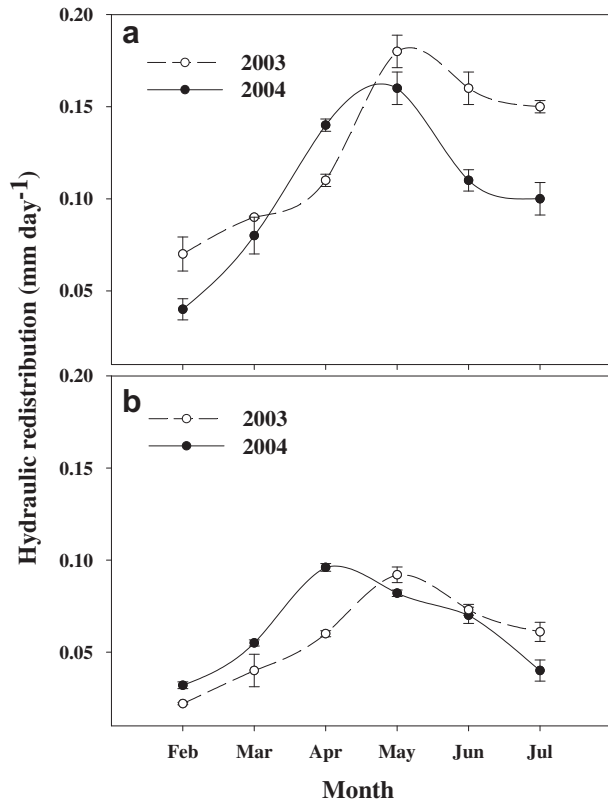


Fig. 3. Net hydraulic redistribution during dry seasons of 2003 and 2004 for the 20–40 cm depths with: (a) *Gueira senegalensis* at the KMA site; (b) *Ptilostigma reticulatum* at the Nioro site (Standard error bars are means for HR from three shrub replicates as shown on each curve).

Appendix 3 for the 20 cm bare soil that were occurring around 1200 h (noon). Positive values of vapor flux signify movement of vapor into each control volume, with negative numbers implying vapor flux leaving the control volume. Seasonal vapor flux in the *G. senegalensis* dominated site at KMA over the two years averaged about 0.9 mm while in the *P. reticulatum* dominated site at Nioro averaged about 0.16 mm. Cumulative seasonal vapor deposition was roughly an order of magnitude less than the observed seasonal increases in soil moisture within the 20–40 cm layer attributable to HR at both study sites (Table 2).

3.3. Sap flow measurements

Reversals in the direction of sap flow were detected in the instrumented roots of both shrub species (Fig. 4a, b). During the peak of the dry season, when shrubs were still intact (uncoppiced) both positive (toward shrub) and negative (toward soil) flows were observed in the lateral shrub roots. Sap flow in the lateral root was frequently negative (toward soil) at night and rapidly became positive (toward shrub) soon after sunrise, with the larger descending tap root remaining positive at this time and with consistently more flow than the lateral (Fig. 4a, b). For the KMA site, uncoppiced mean seasonal root sap velocity for the lateral at night time (1900 h–600 h) and volumetric sap flux were about -2 cm h^{-1} and $0.9 \text{ gm}^{-2} \text{ s}^{-1}$, respectively while for Nioro these were about -5 cm h^{-1} and $1 \text{ gm}^{-2} \text{ s}^{-1}$ (Negative sap flow velocity indicates that flow reversals toward soil). There was slightly higher sap flow at Nioro though it had a lower replenishment through HR than KMA. Sap flow sensors showed consistent and fairly similar results among the different coppicing regimes hence the small barely visible standard error bars.

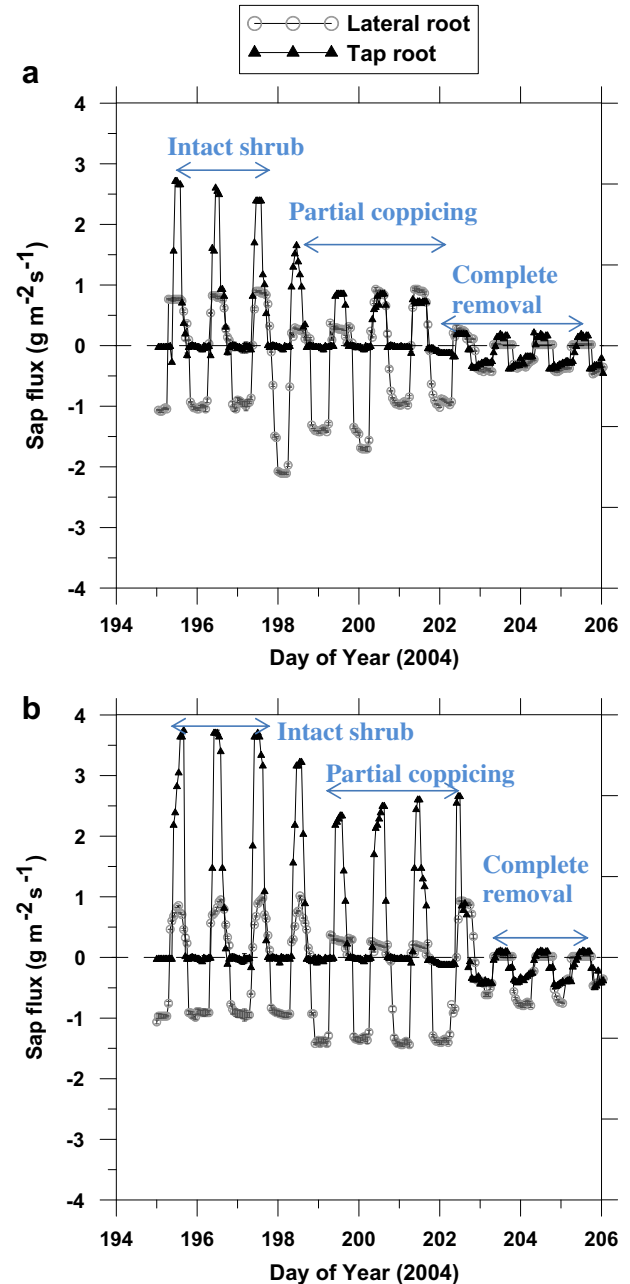


Fig. 4. Sapflow dynamics mimicking traditional management at study sites (a) KMA; (b) Nioro. Standard error bars are computed from mean values of three shrub replicates per measurement.

With partial coppicing (Fig. 4a, b), there were pronounced changes for both tap and lateral root flow. Daytime sap flow in the lateral roots toward the plant remained constant however, a significant increase in nighttime sap flow toward the soil was observed soon after partial coppicing, with an apparent return to normal values after three days. Tap roots continued to show minimal downward reversal at night, but as expected, reduced the amount of upward flux during the day. Lateral flow remained negative (toward soil) at night with an increase in reverse flow magnitude and a decrease in positive flow (toward shrub) during the day. Tap root flow remained positive (toward shrub) but with a 48% decrease in flow for the KMA site and a 30% decrease at Nioro compared to the flow before coppicing.

After complete canopy removal (Fig. 4a, b), tap roots exhibited trends of negative flow (toward soil) hence redistribution at night but mainly remaining positive (toward shrub) during the day though with very low magnitudes (Fig. 4a, b). Lateral root flow variations indicated that complete coppicing halted positive flow (toward shrub) at both sites during the day, but at night both species exhibited negative flow (toward soil) and hence continued to redistribute during this time but with lower magnitudes than when shrubs were either intact or partially coppiced. Night time reverse flow in the tap root was not significantly different from zero in the coppiced shrub.

3.4. Leaf water potential

Mean monthly leaf water potential at the peak of the dry season showed that shrubs at both sites had higher predawn water potential values than either annual herbs in association with shrubs or those that were far away from shrubs (Fig. 5). However, minimum leaf water potential of annual herbs was consistently more negative than that attained by their shrub counterparts. Leaf water potential of shrubs reached its minimum between May and June with gradual rewetting in the transition into the rainy season.

4. Discussion

With reference to the study objective, it was hypothesized that a unique interaction of hydraulic redistribution existed between shrubs and annual crops. Study results support this hypothesis as indicated by pronounced diel fluctuations in Ψ_s and sap flow measurements. During the study period at both sites, increases in Ψ_s over the dry season indicate that the soil water content at 20 and 40 cm depths had also increased. Since there was no rain during this period, the increases indicate upward HR from lower layers with greater Ψ_s . To the best of our knowledge, this is the first report of HR by roots of *G. senegalensis* and *P. reticulatum*. Support for this interpretation is provided by the lack of diel changes in Ψ_s in the bare plot sites at the same depth, consistent with diel fluctuations in Ψ_s in the vicinity of both shrub species being the result of uptake of water by deep roots and exudation of water from shallow roots to the surrounding dry soil.

Peaks in HR were observed in the mid-dry season which could be attributed to Ψ_s before dawn having fallen sufficiently below predawn leaf water potential to allow the upper dry soil layers to effectively compete with the above ground portion of the plant for water taken up by deep roots. This is consistent with observations reported for Douglas-fir and ponderosa pine (Brooks et al., 2006; Domec et al., 2004) in the Pacific Northwest, U.S.A. and for Brazilian savanna trees (Scholz et al., 2002).

Results from the study enabled the quantification of the magnitude of other bio-physical processes potentially responsible for water transport. Soil moisture variability within the profile is the result of HR, vapor transport and plant uptake. In comparison with bare plot results at the same sites as shrubs, the increases in Ψ_s at the 20 and 40 cm depths in shrub areas seem not to be solely from hydraulic redistribution through root systems. Estimates from our data are consistent with the presence of vapor transport and deposition at both study sites which confounds estimation of net HR magnitudes. Vapor transport processes operate slowly and are principally driven by extreme temperature gradients (Marshall et al., 1996; Hillel, 1998) as those prevalent at our study sites temperature data (Kizito et al., 2006, 2007). The slight diurnal increases in Ψ_s in bare soil areas, at both sites, during the day suggest vapor transport and deposition in the upper soil layers. Though the existence of vapor transport has been refuted in mesic regions (Leffler et al., 2005), our results indicate that the process is

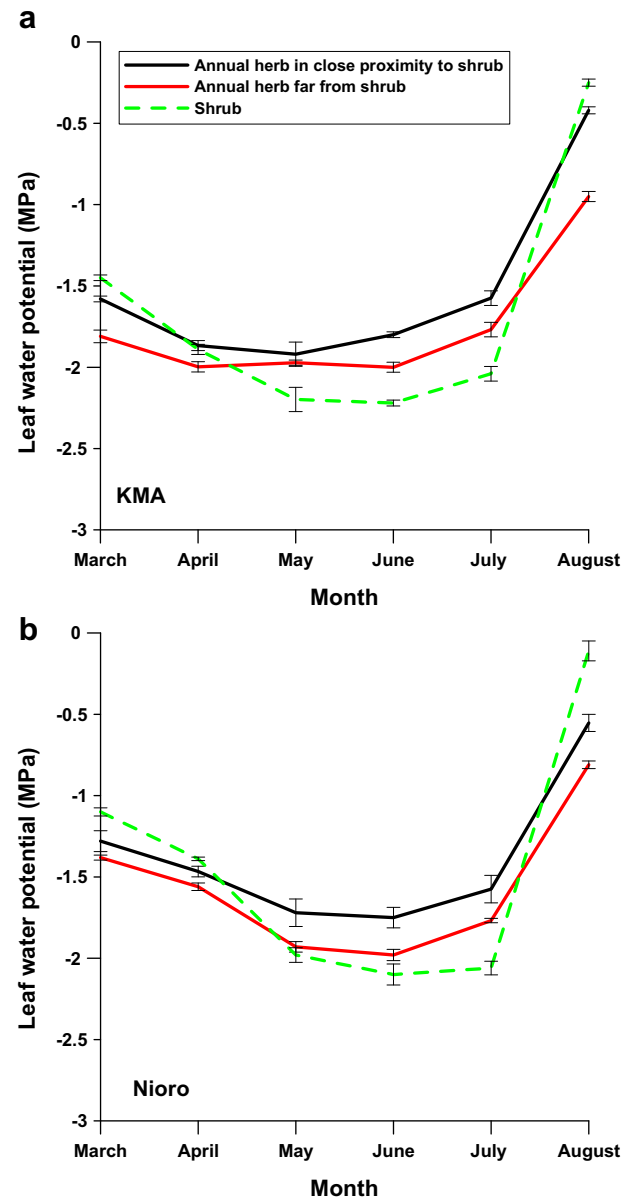


Fig. 5. Monthly variations in leaf water potential (MPa) of shrub, annual herb close to shrub and annual herb away from shrub for both study sites (a) KMA; (b) Nioro. Standard error bars are computed from mean values of three shrub and annual replicates per measurement.

existent though at small magnitudes and was more pronounced in the upper soil layers. This is consistent with findings elsewhere in arid ecosystems (Scanlon and Milly, 1994; Milly, 1996). Though small, vapor transport and deposition fractionally contributed to replenishing the depleted soil moisture pool in the upper soil layers.

Previous work by Kizito et al. (2006) noted facilitative interactions where soil below shrubs was associated with lower soil temperature extremes than adjacent bare soil which was attributed to shade provision by shrub canopies. This has an effect of reducing both air and soil temperatures giving a shrub-imparted alteration in microclimate and lower soil evaporation below shrub canopies than bare soil which in turn alters water potential trends below shrubs compared to bare soil areas. The vapor flux trends and the aforementioned facilitative effects of shrubs indicate potential contribution of other factors and is not solely HR driven.

The observations of slightly higher sap flow at Nioro than KMA yet with lower replenishment through HR than KMA may be attributed to the varying rainfall regimes at both study sites. Nioro has higher rainfall and the soils have higher clay content than those in KMA (sandier soils) with lower rainfall. The matric potential gradients between the drier sandy soil and plant roots would subsequently be greater in KMA than those in Nioro hence the lower HR levels in Nioro. Complete removal of shrubs seemed to have a lower effect on reverse sap flow than partial coppicing. It could be that the completely coppiced plants experience reduced transpiration during the day with little or no depletion of soil water in the shallow layers to create a sufficient gradient necessary for HR.

The differences in HR magnitude in the different years (2003–2004) as well as differences in HR peaking a month earlier in 2004 at both study sites are also likely due to differences in rainfall patterns and soil types as explained previously. When the soil profile is drier due to lower rainfall, this induces a greater gradient between the drier soil and plant roots hence the shrub roots compensate for the diminished water reserves in the upper soil profile by extracting water from deeper moist layers and in turn perform the HR process. Hence HR magnitudes were higher for each of the years with lower rainfall at the study sites.

Monthly changes in plant water potential revealed that the soils were driest between April and July which resulted in higher matric potential gradients between the dry soil and shrub roots. This may explain the observed peaks in HR during these months. Additionally, at both study sites, plant water potential of annual herbs in close proximity to the shrubs tended to recover to values closer to the shrub water potential than the annual herbs that were far from the shrubs (Appendix 4, electronic version only). This indicates that shrubs rewetted the upper profile and the annual herbs tapped some of those water pulses. Other shrub facilitative benefits beyond leaf water potentials for shrub-annual crop interactions have been demonstrated where shrub leaf and stem amendments improved carbon, nitrogen and phosphorus mineralization (Dossa et al., 2009).

Initially, sap flux was positive (toward shrub) during the day in the tap roots and negative (toward soil) at night in the lateral roots, which is consistent with redistribution of water from tap to lateral roots. After partial canopy removal, with increased soil drying during the day (less shrub shade, higher soil moisture evaporative losses) and a decreased transpiration gradient due to a reduced canopy volume (same root volume), shrub roots may have attained higher turgor pressures. Hence, root water potential would greatly exceed that of the surrounding desiccated soil, which might explain the greater HR observed at night soon after coppicing.

The negative sap flow at night (toward soil) in the surface lateral root and the periodic positive flow (toward root) in the taproot at night are indicative of hydraulic lifting of water from the lower to the upper soil layers which are drier. With complete canopy removal, there was slight positive tap root flow (toward shrub) suggesting there could have been some leaking stems or uncoppiced twigs that contributed to the transpiration gradient. The lower tap root sap flow values for day 198 at Nioro were due to cloud cover which greatly reduced the vapor pressure deficit hence the lower sap fluxes. There was some unexplained behavior by the tap roots in this study as it would be expected that the tap roots should have shown a small amount of positive flow at night when the laterals are showing reverse flow. The flow from the tap roots was not sufficiently positive but hovered slightly above zero. This suggests that the water for reverse flow may not be coming entirely from tap roots but from some lateral sinker roots. Previous studies conducted by Kizito et al. (2006) on root architecture for both shrub

species indicated that lateral roots have numerous sinker roots branching from them some of which extend to depths beyond 5 m.

The data suggest that partial coppicing may trigger slight increases in HR. However, a longer period of partial coppicing is needed before this suggestion can be tested conclusively. Results indicate that the HR process provides a mechanism for partial recharge of the upper soil profile in the absence of new precipitation, and since recharge is driven by gradients in Ψ_s , HR may significantly retard the rate of soil drying in the upper profile and reduce the number of severe drought stress days for the shrub or any opportunistic neighboring annuals. This may also be related to other factors such as shade, temperature, lower soil water evaporation under the shrub canopy as noted by facilitative effects reported by Kizito et al. (2007) and Callaway, 2007. Based on personal field observations, the recovery of sap flow rates in the lateral roots at KMA to pre-coppicing values on days 201 and 202 may have been a response to production of new, rapidly transpiring shoots.

Coppicing as a management practice could have significant implications on shrub physiological behavior with particular reference to HR. The current study suggests that intercropping of annual crops with shrub stands may provide benefits to agricultural productivity since the roots of annual food crops overlap with the wetting zone provided by the shrub's HR process. Work conducted by Kizito et al. (2006) on shrub root systems in the study area indicates that the shrubs exploit the first 40 cm where most of the rewetting is and this is the same zone where shallow rooting annual herbs thrive. Recent findings show that deeper-rooted 'nurse plants' if subjected to complete shoot removal capture water that is out of reach of other crops in a 'water safety-net' role and maximize hydraulic redistribution (Burgess, 2011).

We suggest that as opposed to complete shrub removal, partial coppicing may be a feasible management regime in these semi-arid environments. Partial coppicing reduces overall shrub water consumption and transpiration which in turn dampens the recovery of the redistributed water by the shrubs during daytime transpiration to the benefit of annual crops. Partial coppicing also reduces the shrub canopy size hence increasing available acreage for annual row food crops, yet preserves the shrub-imparted benefits that provide a favorable microclimate for agricultural productivity under harsh semi-arid conditions. However, farmers prefer complete canopy removal and sometimes uproot the entire shrub cluster to increase agricultural acreage on their farm plots. While this might seem appealing in the short term for the farmers, other ramifications such as reduced profile recharge, increased raindrop impact and run-off, higher surface soil temperatures and increased soil evaporation (Kizito et al., 2006) which could culminate in long-term detrimental impacts to agricultural productivity.

5. Conclusion

This study demonstrated that HR was a beneficial component in Sahelian crop-shrub agro-ecosystems with *G. senegalensis* and *P. reticulatum*. Results indicate that the HR process was highest during the prolonged dry seasons in both study years. The process was strongly governed by Ψ_s gradients and consumptive water use by shrub species. The quantities of water moved by HR in this study were relatively small. However, these amounts can have significant benefits to the plant lifting the water and to neighboring annual plants to the shrubs. The HR process provided prolonged stored water for annual herbs survival in the dry season with a potential of preventing or delaying loss of water transport capacity in shallow roots.

Hydraulic redistribution of water by plant roots has important implications for both local and regional hydrological cycles and

functioning of ecosystems. The process may play a significant role in the ratio of ecosystem evaporation and transpiration on both diurnal and seasonal scales. This process could alter soil water and groundwater distributions at levels that may significantly impact regional water balances and improve crop productivity in water-scarce environments through shrub-imparted facilitative effects.

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Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jaridenv.2012.03.010.

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