Effective Water Use and Growth of a Prostrate Lifeform Shrub, *Juniperus Sabina*, in Semiarid Areas of China

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Abstract: *Juniperus sabina* L. is an evergreen shrub with prostrate life form that may effectively stabilize sand dunes and moving sand. Therefore, it serves as an important woody species for revegetation in semiarid areas of China. The main root system of *J. sabina* can reach deep into soil while adventitious roots mostly extend into surface soil. To evaluate water movement between different soil-layers these root systems that is associated with rainfall-induced vertical heterogeneity in soil moisture, we measured changes in sap flow and soil moisture content as well as atmospheric temperature and humidity. The patch radius of twenty-four patches was also measured for 7 years to monitor changes in growth rate. Nighttime sap flow between the main root system and adventitious roots during periods of no rainfall was measured; nighttime sap flow decreased or disappeared after rainfall. The annual growth rate of the patch radius was significantly correlated with the annual deposition rate of sand and the amount of annual precipitation. It was suggested that water movement occurs from the deeper moist soil layer to dry surface soil layer via the main root system and adventitious roots by hydraulic redistribution (HR). This movement increased with the progression of drought in the surface soil layer after a rain event. *J. sabina* can effectively use both subsoil water during periods of drought and rainwater in surface soil layer after an occasional rain event through the HR. This allows the plant to survive and continuously grow under water-limited conditions and in a mobile sand environment in semiarid areas.

Key Words: Adventitious roots, Decumbent stem, Hydraulic redistribution, Vertical heterogeneity in soil moisture, Water acquisition.

1. Introduction

The effects of global warming are expected to result in a reduction of future rainfall in arid regions (Treysdte et al., 2006). The ecosystems of arid regions have been established based on receiving low amounts of annual rainfall; therefore, recovery of this type of ecosystem is very difficult and slow if the ecosystem is disrupted. After this type of disturbance, measures to counteract ecosystem degradation, such as the conservation of native plants and revegetation using native plants, become more important as a part of efforts to slow or stop the progress of desertification.

The Mu Us Sandy Land in Inner Mongolia Autonomous Region, China is a semiarid area (UNEP, 1997; Zha and Gao, 1997) where desertification is currently in progress (Zha and Gao, 1997; Wang et al., 2010). Recent mean annual precipitation (1997-2011) in this area was 303 mm (Yang et al., 2014). However, underground water resources are relatively plentiful. The spatial heterogeneity of soil moisture in the deeper and surface soil layer is believed to be caused by the presence or absence of rain events.

Hydraulic redistribution (HR) is the passive movement of water from relatively moist to dry portions of a soil profile via root systems driven by water potential gradients (Burgess et al., 1998; Caldwell et al., 1998). HR often occurs in arid regions, which have heterogeneous moisture conditions in different soil layers (Caldwell et al., 1998). Loik (2007) has pointed out the importance of the efficient use of water by HR for plants growing in arid regions with limited water availability.

*J. sabina* L. (synonym: *Sabina vulgaris* Antoine), an evergreen shrub with a prostrate life form, can effectively prevent sand movement making it an important woody species for revegetation. The root system of *J. sabina* is divided into a main root system penetrating into deeper soil layers along with adventitious roots mostly extending into surface soil (Zhang et al., 1999). HR is believed to occur between the deeper and surface soil via the main and adventitious roots in relation to the vertically heterogeneous water availability in the different soil layers, allowing *J. sabina* to use water efficiently.

In *J. sabina*, our previous studies have suggested the existence of HR based on the results of sap flow rate measurements (Yang et al., 2014). In this study, we verified the existence of HR associated with a rainfall event using quantitative analysis based on measurements of the soil moisture conditions in addition to the sap flow rate, and discussed water use characteristics of *J. sabina* growing in a semiarid environment by also measuring the growth of individual patches.

2. Materials and Methods

2.1. Study Site and Plant Materials

The present study was conducted under natural conditions
in the semiarid environment of the Mu Us Sandy Land (UNEP, 1997; Zha and Gao, 1997), located in the center of the Ordos Plateau of China. The mean annual temperature and precipitation (1997-2011) were 7.4°C and 303 mm, respectively, at Wushenzhao Meteorological Station 18 km west of the study site (Yang et al., 2014). Windborne sand movement occurs frequently in this environment. *J. sabina*, one of the most dominant shrubs in this area, has decumbent stems with plentiful adventitious roots and forms dense patches (Zhang et al., 1997; Dong and Zhang, 2000). We studied two individuals of *J. sabina* in an experimental field of the Mu Us Sandy Land Developmental Research Center (38°59'N, 109°09'E, ca. 1300 m a.s.l.) for sap flow measurements (Table 1) and 24 patches of *J. sabina* (minimum and maximum initial radii of these patches were 254 cm and 1124 cm, respectively) on a fixed sand dune for growth of the patch size.

### 2.2. Sap Flow Measurement

Sap flow was measured using the Heat Ratio Method (Burgess et al., 2001). Sap flow measurements were collected with probe sets (each consisting of one heater and two sensor probes) and data logger (HRM-30 and SL5 Smart Logger, ICT International, Armidale, NSW, Australia). Three probe sets per individual were installed. On each studied individual, two probe sets were inserted in the axis (Axis) and base of a decumbent stem (DS-base), which was located between the main root system and adventitious roots, and one probe set was in a tip of the decumbent stem (DS-tip) (Fig. 1). The radial depths of measurement were 3.2 mm to 16.7 mm depending on diameter of the axis or decumbent stem. To prevent the influence of changes in ambient temperature, the spaces between the probes were stuffed with cotton and the probe sets were covered with aluminum foil. Measurements were conducted at 1 h intervals in 2012 for individual No. 1 and in 2013 for individual No. 2. Heat pulse velocity (HPV, cm h⁻¹) was calculated based on Burgess et al. (2001). The heater and sensor probes were spaced 5 mm apart. Thermal diffusivity of wet (fresh) wood (k) was assigned a value of 2.43 × 10⁻³ cm² s⁻¹ calculated according to Burgess et al. (2001). In this study, we evaluated the sap flow rate using the HPV. To correct for small errors associated with inaccurate probe spacing, a reference velocity (i.e., HPV = 0) was established based on 1-4 days of nighttime sap flow data after substantial rainfall and under conditions when nighttime relative humidity was higher than 99.9%, according to a non-destructive method (Burgess and Bleby, 2006).

### 2.3. Meteorological Data

Daily precipitation data were obtained from the Wushenzhao Meteorological Station. Air temperature and relative humidity were monitored during the 2012 and 2013 experimental periods at canopy height of *J. sabina* (approximately 50 cm) at 1 h intervals by a thermo recorder (TR-77Ui, T&D Corp. Matsumoto, Nagano, Japan). Vapor pressure deficit (VPD) was calculated from air temperature and relative humidity using Tentens’s equation (Buck, 1981).

Soil volumetric water content was measured during the experimental period of 2012 at depths of 20, 35, 65, 100 and 170 cm at 1-h intervals by a soil moisture sensor and logger (ECH2-TE and Em50, Decagon Devices Inc., Pullman, WA, USA). To calculate the soil water potential (Ψₛₚₑₑ), the relationship between the soil volumetric water content and the pF value was measured in the laboratory using the centrifuging method (data not shown).

### 2.4. Growth of Patch Size

To evaluate the growth rate of the patch radius (crown radius of the patch), we measured the radial sizes for the four cardinal directions of the 24 patches. The mean annual growth rate of patch radius was determined by averaging the growth rate of the four directions during each year. In addition, we place a stake in the four cardinal directions of each patch, and measured the height of the ground surface. Then, we determined the mean annual sand deposition rate for each patch by averaging the change of the ground surface level of the four directions during each year. Both measurements were conducted during August–September on each year. The radial sizes of each patch were measured from 1996 to 2003, and the height of the ground surface was measured from 1996 to 2002. The relative height of the main trunk of each patch was measured in 2008. To calculate the distance to the water table for each patch based on the relative height, the distance from the water table to the ground surface was measured by digging a hole at one point in the study site. Annual

### Table 1. Size data for the two sample individuals used for sap flow measurements.

<table>
<thead>
<tr>
<th>Individual</th>
<th>Cross-diameter in main direction (cm)</th>
<th>Axis diameter (cm)</th>
<th>Decumbent stem measured</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. 1</td>
<td>680, 610</td>
<td>5.5</td>
<td>2.4</td>
</tr>
<tr>
<td>No. 2</td>
<td>580, 620</td>
<td>5.9</td>
<td>2.4</td>
</tr>
</tbody>
</table>

Fig. 1. Installation position of probe sets for sap flow measurement in studied individuals showing probe locations in the axis of the main stem (Axis) as well as in the base (DS-base) and tip (DS-tip) of a decumbent stem.
precipitation was evaluated from October 1 of the previous year to September 30 of the current year, to correspond to the measurement of patch size growth. The mean patch growth rates represented the mean values for 6 years (1996-2002) (Table 3) and the mean values for all patches (n = 24) in growth rate for each year (Fig. 5), respectively.

2.5. Statistical Analyses

A generalized linear mixed model with a Gaussian error distribution and no link function was used in this analysis. Specifically, these were used to determine the response of sap flow rates of each position in nighttime (1:00-6:00) to the VPD as well as the difference in soil water potential (ΔΨ\text{soil}) obtained by subtracting the surface (20 cm) from deeper (170 cm) soil layers which contain adventitious roots and main root system, respectively. Normalized values of VPD and ΔΨ\text{soil} were used as predictor variables. Analysis was performed related to individual No. 1 using data collected during June and July, 2012, when nighttime sap flow was observed.

The response of the annual growth rate (measured as final patch radius minus the initial radius) to the initial radius size, water table depth below ground level and the rate of sand deposition for each patch were tested using a generalized linear model with a gamma error distribution and log-link function.

Akaike’s information criterion (AIC; Akaike, 1973) was used to identify optimal parameterization of the models. The R package (R64 3.2.0, http://www.r-project.org/index.html) was used to fit the generalized linear mixed model and generalized linear model.

3. Results

Figure 2 shows the changes of rainfall and Ψ\text{soil} during May-August in 2012. The Ψ\text{soil} at a depth of 20 cm increased rapidly after rainfall; then, it tended to decrease gradually. Although Ψ\text{soil} had the same tendency at the depths of 35 cm and 50 cm, it tended to increase rapidly after a substantial amount of rainfall was received. Meanwhile, Ψ\text{soil} remained stable at a high value at depths of 65, 100 and 170 cm without being much affected rainfall when compared with values in the surface soil layer. The value of Ψ\text{soil} was vertically very heterogeneous in relation to a rainfall event.

Nighttime sap flow in the Axis and DS-base appeared during periods without rainfall and it decreased or disappeared after a rainfall event (Figs. 3bc). Nighttime sap flow was remarkable from June to July. However, nighttime sap flow was not observed in the DS-tip even during dry soil conditions (Figs. 3d). In daytime, sap flow rates at any position (Axis, DS-base, DS-tip) in the studied individual decreased during periods without rain and increased immediately after a rainfall event (Fig. 3bcd). These trends were also noticeable from June to July, when remarkable nighttime sap flow was observed.

The sap flow rate increased after dawn, but was stable till predawn from a few hours after sundown (Fig. 4).
Table 2. Coefficients of fixed effects (±SE) and intercepts estimated using a generalized linear mixed model approach to sap flow rate on each position. Symbols/abbreviations: VPD, vapor water pressure deficit (hPa); \(\Delta\Psi_{soil}\), difference of soil water potential calculated as the deeper (170 cm) soil layer minus the surface (20 cm) soil layer (MPa).

<table>
<thead>
<tr>
<th>Position</th>
<th>VPD</th>
<th>VPD</th>
<th>Intercept</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Axis</td>
<td>0.623 ± 0.047</td>
<td>0.632 ± 0.059</td>
<td>4.510 ± 0.073</td>
<td>127.5</td>
</tr>
<tr>
<td>DS-base</td>
<td>0.862 ± 0.050</td>
<td>0.633 ± 0.077</td>
<td>5.142 ± 0.057</td>
<td>138.2</td>
</tr>
<tr>
<td>DS-tip</td>
<td>0.218 ± 0.019</td>
<td>Not selected</td>
<td>0.073 ± 0.040</td>
<td>49.6</td>
</tr>
</tbody>
</table>

Not selected indicates that the explanatory variable was excluded from the best model with minimum AIC.

Table 3. Coefficients of fixed effects (±SE) and intercepts estimated using a generalized linear mixed model approach to mean annual growth rate of patch radius. Symbols/abbreviations: IR, initial radius of each patch (cm); WT, water table depth below ground level in each patch (cm); DS, mean annual deposition rate of the sand in each patch (cm).

<table>
<thead>
<tr>
<th>IR</th>
<th>DS</th>
<th>Intercept</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not selected</td>
<td>Not selected</td>
<td>0.457 ± 0.141</td>
<td>2.187 ± 0.121</td>
</tr>
</tbody>
</table>

Not selected indicates that the explanatory variable was excluded from the best model with minimum AIC.

Fig. 5. Annual precipitation and mean annual growth rate of patch radius (mean ± SE, n = 24) (a) and the correlation between annual precipitation and mean annual growth rate of patch radius (b).

4. Discussion

Sap flow occurred at night between main root system and the adventitious roots (Axis and DS-base) during periods without rain; however, it decreased or disappeared after a rain event (Figs. 3bc). In contrast, sap did not flow in tips of decumbent stems (DS-tip) at night irrespective of rain events (Fig. 3d). In a few hours after sunset, sap flows to recharge water capacitance or to rehydrate water deficit of plant organs caused by transpiration (Dawson et al., 2007; Yang et al., 2014). Positive nighttime sap flow was still observed even after the sap flow rate stabilized from late after sundown to the predawn hours (Fig. 4). These results show that nighttime sap flow was observed even after recharge of water capacitance or the rehydration of a water deficit within plant organs caused by transpiration.

Nighttime sap flow (1:00-6:00) increased with an increase in the VPD at any position (Table 2). Nighttime transpiration, which driven by the VPD (Dawson et al., 2007; Buckley et al., 2011), may occur because the stomata of the leaves do not fully close at night. The \(\Delta\Psi_{soil}\) had a positive effect on nighttime sap flow only at the position located the main root system and the adventitious roots. The \(\Delta\Psi_{soil}\) indicates the difference of \(\Psi_{soil}\) calculated as the deeper (170 cm) soil layer minus the surface (20 cm) soil layer which contain main root system and the adventitious roots, respectively (Zhang et al., 1999). HR is the process of passive water movement from relatively moist to dry soil layers using plant root systems and is driven by gradients of water potential (Burgess et al., 1998; Caldwell et al., 1998). Therefore, it was suggested that the nighttime sap flow observed in this study could be HR and could occur as the soil dries after rain. In addition, the nighttime sap flow could be hydraulic lift that has been described as the passive movement of water in an upward direction (Caldwell et al., 1989), one type of HR.

Most rainfall in semiarid areas occurs as small pulses of rain (Sala and Lauenroth, 1982) and therefore, often results in soil moisture that has vertical heterogeneity (Fig. 2). During periods without rain, hydraulic lift at night partially recharges the upper layer of the soil profile and delays the drying of the soil surface (Brooks et al., 2002). As a result, fine roots in the dry surface soil can survive and retain their function (Williams et al., 1993; Bauerle et al., 2008). When rainfall occurred during dry conditions, such as when nighttime sap flow was observed, daytime sap flow recovered quickly (Fig. 3). Therefore, effective absorption of the rain pulse is believed to have occurred in the adventitious roots. The annual growth rate of patch radius increased with an increase in the annual sap flow data from 1:00-6:00 to represent nighttime sap flow because the value remained substantially constant at that time.

Model selection based on the AIC differed between positions (Axis, DS-base, DS-tip; Table 2). The model using VPD and \(\Delta\Psi_{soil}\) as predictor variables was selected for nighttime sap flow rates in Axis and DS-base installed between the main root system and the adventitious roots; however, the model using only VPD was selected for nighttime sap flow rates in the DS-tip.

Only the mean annual deposition rate for sand was included in the best model used for predicting the mean annual growth rate of patch radius (Table 3). In addition, the mean annual growth rate of patch radius was significantly correlated with the amount of annual precipitation (Fig. 5).
deposition rate of sand (Table 3) and an increase in the amount of annual precipitation received (Fig. 5). Some species growing in an environment with sand movement have been reported to produce adventitious roots that become buried in sand (Teraminami et al., 2010, 2013; Miyazaki et al., 2014). J. sabina would generate adventitious roots by the deposition of sand, and would have grown by effectively acquiring rainfall. These results suggest that J. sabina can effectively use both subsoil water during periods of drought and rainwater in surface soil layers after an occasional rain event through HR, allowing the species to survive and continuously increase their size under water-limited conditions and a mobile sand environment in a semiarid area.

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