Non-convergent transpiration and stomatal conductance response of a dominant desert species in central Asia to climate drivers at leaf, branch and whole plant scales

Daxing Gu², Quan Wang³,† and Azim Mallik⁴,†

¹Graduate School of Science and Technology, Shizuoka University, Shizuoka 422-8529, Japan
²Faculty of Agriculture, Shizuoka University, Shizuoka 422-8529, Japan
³Department of Biology, Lakehead University, Thunder Bay, Ontario, P7B 5E1 Canada
⁴Guangxi Key Laboratory of Plant Conservation and Restoration Ecology in Karst Terrain, Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guilin 541006, China

Abstract

Desert ecosystems exposed to extreme droughts are vulnerable to climate change. Multi-scale mechanism of hydrological adaptation of desert plants to drought are not fully understood, creating uncertainty in risk assessment of desert ecosystems to climate change by ecological modelling. In this study, we investigated multi-scale water use strategies of *Haloxylon ammodendron*, a dominant desert shrub across central Asia. We found that whole plant water use of *H. ammodendron* was significantly reduced during most of the daytime period (ca. 79%). At low light water use was controlled by photosynthetic photon flux density (PPFD) and at high vapour pressure deficit (VPD) it was further conserved by stomatal closure. It appears that water conservation in *H. ammodendron* at leaf-scale may behave differently with that at whole plant scale. High stomatal sensitivity to VPD at whole plant scale means more conservative water use strategy at plant scale than branch- and leaf-scale. Response of transpiration and stomata to climate drivers were non-convergent among leaf, branch and whole plant scales for this desert shrub. Therefore, one must be cautious in up scaling leaf-scale data to infer canopy scale water conservation to avoid overestimation of plant response to climate drivers. Nonetheless, our results enrich the database of multi-scale water use response of desert plants to climate drivers, which is critical for ecological modelling aiming to predict arid land vulnerability to climate change.

Key words: Desert shrub, Organism scale, Stomatal sensitivity, Water use

1. Introduction

Water use of vegetation directly relates to ecosystem carbon assimilation and energy partitioning, which is influenced by climate drivers (Schlesinger, 1997; Allen et al., 2010). Stomata are the primary channels for H₂O and CO₂ exchange between plant and atmosphere. Therefore, stomatal conductance is a key parameter regulating plant water use and its response to climate drivers (de Arellano et al., 2012; Huntingford et al., 2015). A clear understanding of stomatal response to climate drivers is critical for accurate estimation of ecosystem water, carbon and energy fluxes.

Arid and semi-arid lands cover nearly 40% of terrestrial surface of the earth, which are expanding and intensifying globally due to climate change (Schlesinger, 1997). Previous studies on plant water use and stomatal response to climate drivers largely focused on trees in mesic environment while similar studies in arid ecosystems particularly in central Asia are very few (Xu and Li, 2006; Xu et al., 2007; Zheng and Wang, 2014, 2015). As a typical arid ecosystem in central Asia, desert has simple vegetation structure and is highly vulnerable to climate change and prone to severe degeneration (Lioubimtseva and Henebry, 2009). Shrub is the dominant vegetation in central Asian desert and existing limited studies on desert shrubs mainly dealt with water use estimation (Sala et al., 1996; Zheng and Wang, 2014), transpiration response to climate drivers, rain pulse events and elevated CO₂ (Pataki et al., 2000; Xu and Li, 2006; Yang et al., 2014; Zheng and Wang, 2014) and quantifying water use sources (Mooney et al., 1980; Ehleringer et al., 1991). The paucity of data from desert ecosystems creates large uncertainty in risk assessment of these ecosystems to global climate change (Yohe et al., 2006).

It is generally agreed that desert vegetation exhibits higher tolerance to water shortage through various strategies (Nobel, 1996; Kozlowski and Pallardy, 1997). However, water use strategies of desert plants vary widely depending on species and scales of measurement (Xu and Li, 2006; Du et al., 2011). For example, *Tamarix ramosissima* sustained stable water use at different surface soil water conditions while that of *Reaumuria soongorica* and *Haloxylon ammodendron* varied significantly under contrasting surface soil water conditions (Xu and Li, 2006), indicating interspecific difference in available water source among the three co-occurring shrubs. Zheng and Wang (2014) found that whole plant scale water use of *H. ammodendron* was saturated under high vapour pressure deficit (VPD) while such phenomena did not occur at branch scale, suggesting plant water use was scale dependent, too. These results are helpful in understanding water use strategies at seasonal and whole plant scale. However, stomatal conductance and its regulation on transpiration are thought
to be more sensitive to climate drivers at diurnal and leaf scale than at seasonal and canopy scale. Unfortunately, such data are currently unavailable.

Although sap flow at branch and whole plant scales have been reported for selected central Asian desert shrubs (Gong et al., 2006; Zheng and Wang, 2014), such studies are rather limited and it is desirable to obtain additional data, which is urgently needed for ecological modelling for reliable risk assessment of desert communities to climate change. In this study, we examined water use strategies of H. ammodendron, a dominant desert plant of central Asia, from both water use and stomatal conductance perspectives in response to climate drivers at leaf (assimilating shoot), branch and whole plant scales.

2. Materials and Method

2.1 Site description

We conducted this study in an experiment plot near the southern edge of Gurbantünggüt desert in central Asia (44°25'54"N, 87°54'9"E, 600 m a.s.l.). The site is characterized by a continental arid climate with dry hot summer and cold winter. Annual mean temperature is 7.5°C with large seasonal range from < -30°C to > 45°C (Zheng and Wang, 2015). Annual pan evaporation is approximate 2000 mm while annual precipitation is 160 mm, most of which falls as snow in winter, leaving prolonged drought in summer and autumn (Luo et al., 2003). The study site is dominated by a C₃ type desert shrub H. ammodendron, with few companion shrubs (e.g. Tamarix ramosissima) and short-lived grasses (e.g. Ceratocarpus arenarius, Limonium bicolor) during springtime (Pyankov et al., 1999). Mean height and basal diameter (DBH) of H. ammodendron in the study plot was 2.0 m and 6.4 cm respectively with a canopy projection area 3.26 m². Stem density, total sapwood area and canopy cover of H. ammodendron were 584 stems ha⁻¹, 0.77 m² ha⁻¹, and 16%, respectively (Zheng and Wang, 2014, 2015).

2.2 Measurement of meteorological parameters

We used an automated weather station (Vantage Pro²™, Davis Instruments, USA) to record meteorological parameters such as air temperature (Taq), relative humidity (RH), wind speed and precipitation. We measured photosynthetic photon flux density (PPFD) above H. ammodendron canopy using a quantum sensor (Li900SB, Campbell Scientific, Inc., Logan, USA). Air pressure values were obtained from a nearby eddy covariance system (LI-7500, LI-COR, USA) installed at an 11 m tower.

2.3 Measurement of leaf scale transpiration

Terminal shoots of H. ammodendron are modified to green succulent cylindrical structures with stomata, which carry out the main photosynthetic function of the plant (Kazantsev et al., 2012; Huang et al., 2003). These needle-like shoots (assimilating shoots) are the basic organs of carbon assimilation. However, to be consistent with the scaling terminology in gas exchange literature (leaf, branch and whole plant scale) we called this basic photosynthetic unit ‘leaf’ as in previous studies (Gong et al., 2006; Xu and Li, 2006). The canopy of H. ammodendron is rather open and sparse, most of leaves receive sunlight at the same time. As such, the leaves in top canopy were selected to represent leaf-scale behaviors. We measured diurnal variations of leaf-scale transpiration and stomatal conductance at an interval of 1 to 1.5 hours from sunrise to sunset using a portable gas exchange system (GFS-3000, Heinz Walz GmbH, Germany) from June 15 to July 12, 2016. All measurements were taken on clear days with minimum cloud in five healthy H. ammodendron plants representing the diameter and height distribution of the entire plot. For each measurement we used two sunlit mature leaves (assimilating shoots) in each of the five sample plants (n = 10). The leaves were clamped in the chamber parallel to each other to avoid overlapping. Because the assimilating shoots of H. ammodendron are almost cylindrical and covered with stomata equally on the surface (Xu and Li, 2006), we assumed that all leaf surface area in the chamber contributed equally to gas exchange. The recorded gas exchange and stomatal conductance were calibrated using the surface area of cylinder calculated from diameter and length of the shoot samples in the chamber.

2.4 Sap flow measurement at branch and whole plant scales

Branch-scale sap flow was measured using the stem heat balance (SHB) method (Sakuratani, 1981). The Sakuratani sensors were heated at a constant power (0.1 W) and covered tightly around the branch with two layers of bubble wrap to protect the sensors from outside heat, and one layer of plastic foil to protect the sensors from rain. In total we measured nine branches at the top canopy of five sample plants (one branch in each of four sample plants and five branches at different directions in one central sample plant). All branches were < 20 mm in diameter. All cross sectional areas were calculated as sapwood.

Water use at whole plant scale was measured by using thermal dissipation probes (Granier, 1987). Five Granier sensors were installed on north side stem of each of the five sample plants. Data recorded at one-minute interval from which mean values at 10 min interval were computed and recorded in a data logger (DT80, Thermo Fisher Scientific Australia Pty Ltd, Australia). Branch and stem sap flow were monitored continuously form June 1 to July 31, 2016, representing the pick growing season of H. ammodendron. Sap flow density was calculated according to Sakuratani (1981) or Granier, (1987). Transpiration was scaled up based on cross sectional area of branch or sapwood area of stem. Stem sapwood area was assessed according to empirical relation between stem diameter (D, cm) and sapwood area (Aₛ, cm²) according to Zheng and Wang (2014) as follows:

\[ Aₛ = 0.39 \times D^{1.39} \]  \hspace{1cm} (1)

To be comparable with result at leaf scale, transpiration at branch and whole plant scales were normalized based on leaf area (E₁). The leaf area of a sample branch (Aₛ, cm²) was estimated using allometric equation based on branch diameter (D, cm) as per Li et al. (2013) as follows:

\[ Aₛ = 740.16 \times D^{1.3} \]  \hspace{1cm} (2)

Leaf area of a sample plant was assessed by dividing the product between LAI and canopy projected area by canopy coverage.

2.5 Stomatal conductance

Apparent noise and incorrect data caused by power failure or
other equipment errors were excluded from analysis. We used sap flow data to calculate stomatal conductance \( g_s \). Stomatal conductance (m/s) at branch and whole plant scales were estimated by inverting Penman-Monteith (P-M) equation according to Granier et al. (1996):

\[
g_s = \frac{\gamma \lambda}{\rho_a c_p (e_s - e_a)}
\]

where \( \lambda \) is latent heat of vaporization (energy required per unit mass of water vaporized (J g\(^{-1}\) K\(^{-1}\)), \( C_p \) is specific heat capacity of air (J kg\(^{-1}\) K\(^{-1}\)), \( \rho_a \) is dry air density (kg m\(^{-3}\)).

Stomatal conductance was converted to mol conductance (mmol m\(^{-2}\) s\(^{-1}\)) according to ideal gas law (Lide, 2009):

\[
g_{\text{mol}} = \frac{g_v V_m T_w P_{\text{air}}}{T_{\text{air}} P_{\text{air}}}
\]

Where \( g_{\text{mol}} \) is molar leaf stomatal conductance (mmol m\(^{-2}\) s\(^{-1}\)), \( g_{\text{ref}} \) is leaf stomatal conductance derived from the Penman-Monteith equation (mm s\(^{-1}\)) and \( V_m \) is molar volume of air (44.6 mol m\(^{-3}\)) at standard air temperature \( (T_{\text{air}} = 273.15 \text{ K}) \) and pressure \( (P_{\text{air}} = 101.3 \text{ kPa}) \). The correlations among transpiration, stomatal conductance and meteorological factors were determined by Pearson’s correlation analysis, 2-segment-linear piecewise function was employed to describe hourly \( E_i \) and \( g_s \) response to climate drivers except between \( g_s \) and \( VPD \). Difference among the three scales (leaf, branch and whole plant) were analyzed with one-way ANOVA followed by Tukey test.

3. Results

3.1 Diurnal multi-scale transpiration of \textit{H. ammodendron} and climate drivers

During the study period, daily average \( E_i \) of \textit{H. ammodendron} at branch scale varied from 0.20 to 0.51 mmol m\(^{-2}\) s\(^{-1}\) and averaged 0.33 mmol m\(^{-2}\) s\(^{-1}\) (Fig.1a), while that at whole plant varied from 0.20 to 0.35 mmol m\(^{-2}\) s\(^{-1}\) and averaged 0.26 mmol m\(^{-2}\) s\(^{-1}\) (Fig.1b). Daily PPFD and VPD were relatively stable varying from 504 to 893 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) and 1.4 to 5.8 kPa, respectively (Fig.1c, d).

In four clear days, the maximum \( E_i \) at leaf-scale ranged from 1.00 to 2.00 mmol m\(^{-2}\) s\(^{-1}\), significantly \( (P < 0.05) \) higher than that at branch and whole plant scales (around 0.50 mmol m\(^{-2}\) s\(^{-1}\) (Fig.2a)). Although diurnal maximum \( E_i \) values between branch and whole plant scales did not vary significantly, their difference in diurnal patterns were apparent. Whole plant scale \( E_i \) peaked

---

Fig. 1. Daily average transpiration rate per leaf area \( E_i \) of \textit{H. ammodendron} at branch (a) and tree scale (b), photosynthetic photon flux density (PPFD, c) and vapour pressure deficit (VPD, d) during daytime. The red arrow point to the day when the diurnal data showed in Fig.2.
at mid-morning, followed by a decrease and finally disappearing just before sunset (Fig. 2a). Branch-scale $E_i$ showed consistently wider picks (plateau) followed by a decline, which lasted till sunrise (Fig. 2a). Diurnal PPFD showed stable maximum around 1400 $\mu$mol m$^{-2}$ s$^{-1}$, usually occurring at midday (Fig. 2b). However, diurnal VPD generally picked before the sunset varying from 3 to 6 kPa. After sunset the VPD value decreased to 0 and remained so till sun rise (Fig. 2b).

### 3.2 Correlations among hourly $E_i$ and $g_s$ and climate drivers

Hourly $E_i$ of *H. ammodendron* showed significant positive correlations with $T_{air}$, PPFD and VPD at leaf, branch and whole plant scales ($P < 0.001$), except VPD at whole plant scale ($P > 0.5$, Table 1). In contrast, $E_i$ showed significant negative correlations with RH at all three scales ($P < 0.001$, Table 1). Stomatal conductance ($g_s$) had the highest negative correlation with VPD among all climate drivers ($P < 0.001$). Stomatal conductance ($g_s$) showed significant correlation with $T_{air}$ and RH at branch scale and with RH and PPFD at whole plant scale ($P < 0.001$).

### 3.3 Response patterns of hourly and daily $E_i$ to climate drivers

Response patterns of hourly $E_i$ to PPFD at the three scales were similar, with $E_i$ increasing linearly with increasing PPFD until saturation (Fig. 3a-c). Hourly $E_i$ tended to saturate when PPFD approached 371, 761 and 624 $\mu$mol m$^{-2}$ s$^{-1}$ at leaf, branch and whole plant scales respectively. The saturation points of $E_i$ also varied with scales ($P < 0.05$) with mean hourly $E_i$ saturation values 0.86, 0.39 and 0.32 mmol m$^{-2}$ s$^{-1}$ at leaf, branch and whole plant scales, respectively.

We found no significant correlation between hourly $E_i$ and VPD at whole plant scale ($P > 0.05$), but their peak patterns were distinct (Fig. 3d). Daytime (PPFD $> 50$ $\mu$mol m$^{-2}$ s$^{-1}$) $E_i$ of *H. ammodendron* increased linearly at low VPD until reaching inflection points when VPD values were 1.6, 2.1 and 2.0 kPa.
for leaf, branch and whole plant scales, respectively (Fig. 3d-f). After inflection points, hourly $E_i$ showed different response patterns to increasing VPD at different scales, with nearly saturated response at leaf and branch scales and negative linear response at whole plant scale.

Response of daily $E_i$ to PPFD and VPD are shown in Fig. 4. Being different from hourly $E_i$ response pattern, the daily $E_i$ stayed relative stable under various daily PPFD and VPD at both branch and whole plant scales, except $E_i$ response to VPD at whole plant scale, where daily $E_i$ decreased with increasing daily VPD (Fig. 4d).

3.4 Response patterns of $g_s$ to climate drivers

Stomatal conductance ($g_s$) declined sharply with increasing VPD under strong irradiation (PPFD > 600 μmol m$^{-2}$ s$^{-1}$) at all scales (Fig. 5 a-c). However, stomata level, sensitivity and the reference stomatal conductance ($g_{sref}$, when VPD = 1 kPa) differed among the three scales. Mean $g_s$ at leaf scale was 20.23 mmol m$^{-2}$ s$^{-1}$, which was significantly higher than that at branch and whole plant scales ($P < 0.01$). On the other hand, the mean $g_s$ values were nearly identical to both branch and whole plant scales (Fig. 5 b, c). Stomatal sensitivity to VPD (m/ g$_{sref}$) was 0.35, 0.45 and 0.52 at leaf, branch and whole plant scale, respectively (Fig. 5). Under low light conditions (PPFD < 600 μmol m$^{-2}$ s$^{-1}$) we found little response of $g_s$ to VPD at branch and whole plant scales (insets of Fig. 5 b, c).

4. Discussion

4.1 Water use of $H$. ammodendron and its control by climate drivers

We found much lower mean diurnal maximum $E_i$ of $H$. ammodendron (0.40–1.50 mmol m$^{-2}$ s$^{-1}$ depending on organismic scales) than that reported by Xu and Li (2006) at branch scale (~ 2 mmol m$^{-2}$ s$^{-1}$) and Gong et al. (2006) at leaf scale (~ 6 mmol m$^{-2}$ s$^{-1}$) for the same species. Whole plant scale mean daily $E_i$ (0.26 mmol m$^{-2}$ s$^{-1}$) was also much lower than other shrub species reported from other arid regions (~5 mmol m$^{-2}$ s$^{-1}$, Naithani et al., 2012). The different results compared to previous studies might be related to different soil water contents, climate drivers and/or plant functional traits (C$_3$/C$_4$). The lower water use in our study seem to suggest an adaptive response of $H$. ammodendron to extreme drought and more conservative water use of C$_4$ plants.

Fig. 3. Relationships between hourly transpiration rate per leaf area ($E_i$) of $H$. ammodendron during daytime at leaf (a, d), branch (b, e) and tree (c, f) scales in relation to photosynthetic photon flux density (PPFD) and saturate vapour pressure deficit (VPD). Solid lines represent fits according to 2-segment-linear piecewise function.
Fig. 4. Relationship between daily transpiration per leaf area ($E_L$) of *H. ammodendron* during day time at branch (a, b) and tree scale (c, d) in relation to photosynthetic photon flux density (PPFD) and saturate vapour pressure deficit (VPD).

Fig. 5. Relationship between hourly stomatal conductance of *H. ammodendron* per leaf area ($g_s$) and saturate vapour pressure deficit (VPD) at leaf (a), branch (b) and tree (c) scales during study period at PPFD > 600 μmol m$^{-2}$ s$^{-1}$. The solid lines represent fits according to exponential function. The inset figure denotes the relationship between $g_s$ and VPD at PPFD < 600 μmol m$^{-2}$ s$^{-1}$. PPFD data at < 600 μmol m$^{-2}$ s$^{-1}$ at leaf scale were not enough to produce an inset figure.
In diurnal cycle, peak water use at whole plant scale occurred ~ 9 h earlier than that of VPD. Similar result was reported by Zheng and Wang (2014) for the same species. This happened much earlier than other semiarid species (0 ~ 2 h, Du et al., 2011; Naithani et al., 2012) and rain-forest species (1 ~ 4 h, Motzer et al., 2005), indicating stronger water deficit and larger stomatal regulation on water use of *H. ammodendron*. Compared to peak water use at midday commonly found in other species in mesic and semiarid regions (Oren and Pataki, 2001; Tang et al., 2006, Du et al., 2011), the whole plant water use of *H. ammodendron* during mid and past midday time was largely depressed, which was related to stomatal closure induced by decreased leaf water potential and whole plant hydraulic conductance under high atmospheric drought (Tyree, 2003; Xu et al., 2011; Zhao, 2011). Diurnal water use pattern of *H. ammodendron* in our study reflects response of hourly water use and stomatal conductance to climate drivers as explained below.

During daytime, hourly water use of *H. ammodendron* was consistently controlled by both PPFD and VPD across the three scales, even though the evaporation patterns were different. Hourly water use responded similar to PPFD at the three scales, linearly increasing at low PPFD but saturated under high PPFD, similar to those of semiarid tree species (*Quercus liaotungensis, Robinia pseudoacacia*) reported by Du et al. (2011) but different from plants of wet tropical forests (*Cecropia insignis, Pentaclethra macroloba*) in which water use increase linearly even under high radiation (O’Brien et al., 2004). This might be explained by different canopy structures (generally open and sparse canopies of shrubs in arid and semiarid regions vs. closed and dense canopies in mesic tropical region) and soil moisture conditions between arid and mesic region. We found water use of *H. ammodendron* to be saturated at all three scales when PPFD was > 800 μmol m⁻² s⁻¹. Similar values were reported from semiarid region by Du et al. (2011). This indicates that solar radiation was usually not a limiting factor for arid and semiarid regions. During saturation period of water use under high PPFD, hourly water use was controlled by VPD, variation of which lagged behind the diurnal PPFD.

Hourly water use of *H. ammodendron* linearly increased with VPD when VPD was < 2 kPa regardless of scale, indicating that water use was mainly controlled by transpirational pull resulting from VPD following stomatal opening. Under VPD > 2 kPa, which usually occurred during midday and afternoon, leaf- and branch-scale water uses were nearly saturated but at whole plant scale it was decreased with increasing VPD, indicating that water use at this scale was limited by partially closed stomata. Whole plant scale hourly water use response to VPD in this study was different from those in semiarid and mesic regions where plant water use remained highest under high VPD (O’Brien et al., 2004; Du et al., 2011). This might be due to different VPD ranges (0 ~ 1.5 kPa in mesic region, 0 ~ 6 kPa in semiarid region and 0 ~ 8 kPa in this study), species-specific functional types or thresholds of safe hydraulic between this and previous studies. According to diurnal variation of VPD, the duration when VPD above 2 kPa accounted for approximately 50% of the diurnal cycle or 79% of daytime. So water use of this desert plant was greatly reduced due to atmospheric drought during most of the daytime, leaving the most favorable water use in mid-morning.

### 4.2 Non-convergent water use and stomatal conductance among multi-scales

The increasing stomatal sensitivity to VPD (μmol g⁻¹) from leaf to whole plant scale indicate that whole plant-scale average stomatal conductance declined faster than that at smaller scales under high VPD, showing the strong stomatal regulation on hydraulic safety and more conservative water use strategy at whole plant scale than leaf and branch scales. The different stomatal sensitivity also induced inconsistent patterns of diurnal water use and its response to main climate drivers at multiple scales. Similar results have been reported by Zheng and Wang (2014) at branch and whole plant scales.

Whole plant water use could be approximated by integrating all leaves’ water use in canopy ignoring non-stomatal water loss, so diverse diurnal patterns and response patterns of water use and stomatal conductance to climate drivers among organismic scales would likely show that leaves in canopy behave unevenly and at least part of leaves and branches may behave differently compared to the whole plant. Such non-convergent behaviors of leaves in canopy has been attributed to high spatial heterogeneity of climate drivers in closed forest (Jarvis, 1995). Although the canopy of *H. ammodendron* is open, sparse and sunlit leaves account for most of leaves in canopy, uneven distribution of climate drivers (especially radiation) in canopy still exists and it may further contribute to the heterogeneity of leaf behaviors in canopy. In this study, we measured leaves that were well lighted in top canopy of the tree. The results indicated that water relations of sunlit leaves in top canopy may not represent the tree-scale behavior, even for desert species with open and sparse canopy. Therefore, one must be cautious in driving canopy gas exchange models based only on parameters from top sunlit leaves. For shrubs living in harsh desert environment, leaves in middle canopy or shaded leaves may behave more similar with that of tree scale, which need more comprehensive and abundant studies within canopy in future.

Another potential reason contributing to the non-convergent hourly water relations between branch and whole plant is hysteresis caused by water stored in trunk. However, we did not find remarkable difference in hysteresis between branch- and whole plant-scale sap flow during morning (Fig. 1a).

The different water use and stomatal sensitivity also exist between leaf- and branch-scale, both of which located in the top of canopy and receive nearly the same climate drivers. This showed that there were other factors affecting the heterogeneity of leaf behaviors within canopy besides climate drivers. The patchy stomatal behavior has been found among adjacent leaves and even in the same leaf (Terashima, 1992; Mott and Buckley, 2000; Kamakura et al., 2011), which is consistent with the different water use and stomatal pattern between leaf- and branch-scale found in this study. Many hypothesis including circadian rhythms (Doughty et al. 2006), chemical signal (Garcia-Mata and Lamattina, 2001) and hydraulic interactions (Mott and Buckley, 2000) have been proposed but the underlying mechanism is still unclear. Zhao (2011) attributed the non-convergent behaviors among scales to the measurement using portable gas exchange
system which changed boundary layer conductance around leaf in leaf chamber leading to overestimation of leaf-scale stomatal conductance. In our study site, *H. ammodendron* has typical needle-like assimilating shoots (described as leaf) and they are sparsely distributed with open canopy and large boundary layer conductance around canopy leaf is expected. Therefore, the effect of measurement methods should be limit and could hardly explain the significant variations in stomatal conductance and water use among various scales.

Heterogeneity of stomatal aperture and related water use in canopy is one strategy for plant to adapt to drought environment (Zheng and Wang, 2014). The heterogeneity of stomatal conductance in *H. ammodendron* canopy (also called canopy patchiness) induced higher stomatal sensitivity to VPD (m/gsw) and lower water use at whole plant scale than leaf scale. The more conservative water use strategy at whole plant than smaller scales is benefit to protect whole plant water homeostasis under drought. Canopy patchiness can reduce whole plant water loss and allow partial assimilation by part of leaves under drought, making a balance between total water loss and carbon acquisition at whole plant scale (Buckley et al., 1999; O’Grady et al., 2013). Hence, patchiness must be considered in ecohydrology models to avoid systematic error of overestimating vegetation response to climate change.

Data poverty limits a clear understanding of water use strategies of dominated shrubs in arid ecosystems, creating problem in accurate evaluation of vulnerability of arid ecosystem to climate changes. Although this study provides useful data revealing water use strategies of *H. ammodendron* at three scales during the main growing season, future study should consider a year round and multi-year assessment of water use strategies of desert shrubs in response to changes in climate drivers.

### 5. Conclusions

We found that water use of *H. ammodendron* was significantly reduced due to strong atmospheric drought during most of the daytime. Hourly water use was limited by PPFD at low light and it was further reduced by stomatal closure under high VPD. This indicates high tolerance of *H. ammodendron* to drought and strong stomatal regulation on water loss. *H. ammodendron* showed more conservative water use strategy at whole plant scale than smaller scales which resulted from the highest stomatal sensitivity to VPD at whole plant scale. This canopy patchiness in stomatal behavior is a critical strategy for desert shrubs to balance water loss and carbon assimilation at whole plant under extreme drought. It appears that water relations of sunlit leaves in top canopy of *H. ammodendron* behave differently even opposite to whole plant scale. Therefore, cautious should be paid on driving canopy gas exchange models based only on parameters from top sunlit leaves in order to avoid overestimation of plant response to climate drivers. Nonetheless, our results enrich the database of multi-scale water use response of desert plants to climate drivers. Such data are critical for ecological modelling aiming to predict arid land vulnerability to climate change.

### Acknowledgements

We thank Jia Jin, Lu Xu and Bin Liu for their valuable assistance during fieldwork. This study was partly supported by the JSPS project [Grant No. 25302001]. Azim Mallik was able to contribute in this paper during his tenure as a Distinguished Foreign Expert for the Guangxi Zhuangzuo Autonomous Region at the Guangxi Institute of Botany.

### References

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fengsham R, Zhang Z, Castro J, Demidova N, Limp JH, Allard G, Running SW, Semerci A, Cobb N, 2010: A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259, 660–684.

Bond WI, 2008: What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* 39, 641–659.

Bourne AE, Haigh AM, Ellsworth DS, 2015: Stomatal sensitivity to vapour pressure deficit relates to climate of origin in Eucalyptus species. *Tree Physiology* 35, 266–278.

Buckley TN, Farquhar GD, Mott KA, 1999: Carbon-water balance and patchy stomatal conductance. *Oecologia* 118, 132–143.

Dai Z, Edwards GE, Ku MSB, 1992: Control of photosynthesis and stomatal conductance in *Ricinus communis* L. (castor bean) by leaf to air vapor pressure deficit. *Plant Physiology* 99, 1426–1434.

de Arellano JVG, van Heerwaarden CC, Lelieveld J, 2012: Modelled suppression of boundary-layer clouds by plants in a CO2-rich atmosphere. *Nature Geoscience* 5, 701–704.

Doughty CE, Goulden ML, Miller SD, da Rocha HR, 2006: Circadian rhythms constrain leaf and canopy gas exchange in an Amazonian forest. *Geophysical Research Letters* 33, L15404.

Du S, Wang YL, Kume T, Zhang JG, Otsuki K, Yamanaka N, Liu GB, 2011: Sapflow characteristics and climatic responses in three forest species in the semiarid Loess Plateau region of China. *Agricultural Forest Meteorology* 151, 1–10.

Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR, 1991: Analyses of assumptions and errors in the calculation of stomatal conductance from sap flux measurements. *Tree Physiology* 10, 579–589.

García-Mata C, Lamattina L, 2001: Nitric oxide induces stomatal closure and enhances the adaptive plant responses against drought stress. *Plant Physiology* 126, 1196–1204.

Gong JR, Zhao AF, Huang YM, Zhang XS, Zhang CL, 2006: Water relations, gas exchange, photochemical efficiency, and peroxidative stress of four plant species in the Heihe drainage basin of northern China. *Photosynthetica* 44, 355–364.

Granier A, 1987: Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology* 30, 393–320.

Granier A, Huc R, Barigah ST, 1996: Transpiration of natural rain forest and its dependence on climatic factors. *Agricultural Forest Meteorology* 78, 19–29.

Huang ZY, Zhang XS, Zheng GH, Gutterman Y, 2003: Influence of light, temperature, salinity and storage on seed germination of *Haloxylon ammodendron*. *Journal of Arid Environments* 55, 453–464.
Huntingford C, Smith DM, Davies WJ, Davies WJ, Falk R, Sitch S, Mercado LM, 2015: Combining the [ABA] and net photosynthesis-based model equations of stomatal conductance. *Ecological Modelling* **300**, 81–88.

Janssens PG, 1995: Scaling processes and problems. *Plant, Cell and Environment* **18**, 1079–1089.

Kamakura M, Kosugi Y, Takanashi S, Matsumoto K, Okumura M, Philip E, 2011: Patchy stomatal behavior during mid-day depression of leaf CO₂ exchange in tropical trees. *Tree Physiology* **31**, 160–168.

Kazantzseva TI, Slemnev NN, Gunin PD, Tsooj S, 2012: Structure Exploration into the Biological Resources of Mongolia. Institut für Biologie der Martin-Luther-Universität Halle-Wittenberg, Paper 37. http://digitalcommons.unl.edu/biolmongol/37.

Kozlowski TT, Pallardy SG, 1997: Physiology of Woody Plants, 2nd edn. San Diego: Academic Press, pp. 411.

Li ZB, Li PH, Wang Q, Xu L, 2013: Allometric characteristics of terminal twigs of *Haloxylon ammodendron* and *Haloxylon ammodendron* genotypes. *Journal of Arid Environ* **33**, 274–281.

Liu DR, 2009: CRC Handbook of Chemistry and Physics, 90th Edition. CRC Press, Boca Raton, FL, pp. 2804.

Lioubintseva E, Henbrey GM, 2009: Climate and environmental change in arid Central Asia: Impacts, vulnerability, and adaptations. *Journal of Arid Environment* **73**, 963–977.

Luo GF, Chen X, Zhou KF, Ye MQ, 2003: Temporal and spatial variation and stability of the oasis in the Sangong River Watershed, Xinjiang, China. *Science China (Earth Sciences)* **46**, 62–73.

Mooney HA, Gulmon SL, Ehleringer J, Rundel PW, 1980: Atmospheric water uptake by an Atacama Desert shrub. *Science* **209**, 693–694.

Mott KA, Buckley TN, 2000: Patchy stomatal conductance: emergent collective behaviour of stomata. *Trends in Plant Science* **5**, 258–262.

Motzer T, Munz N, Küppers M, Schmitt D, Anhuf D, 2005: Stomatal conductance, transpiration and sap flow of tropical montane rain forest trees in the southern Ecuadorian Andes. *Tree Physiology* **25**, 1283–1293.

Naithani KJ, Ewers BE, Pendall E, 2012: Sap flux-scaled transpiration and stomatal conductance response to soil and atmospheric drought in a semi-arid sagebrush ecosystem. *Journal of Hydrology* **464–465**, 176–185.

Nobel PS, 1996: Ecophysiology of roots of desert plants, with special emphasis on Agaves and Cactae. In Plant Roots: The Hidden Half. Eds. Y Waisel, A Eshel and U Katifki. New York: Marcel Dekker. pp.823–844.

O’Grady AP, Mitchell PJM, Pinkard EA, Tissue DT, 2013: Thirsty roots and hungry leaves: unravelling the roles of carbon and water dynamics in tree mortality. *New Phytologist* **200**, 294–297.

O’Brien JJ, Oberbauer SF, Clark DB, 2004: Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. *Plant, Cell and Environment* **27**, 551–567.

Oren R, Pataki DE, 2001: Transpiration in response to variation in microclimate and soil moisture in southeastern deciduous forests. *Oecologia* **127**, 549–559.

Oren R, Sperry JS, Katul GG, Pataki DE, Ewers BE, Phillips N, Schäfer KVR, 1999: Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment* **22**, 1515–1526.

Pataki DE, Huxman TE, Jordan DN, Zitzer SF, Coleman JS, Smith SD, Nowak RS, Seemann JR, 2000: Water use of two Mojave Desert shrubs under elevated CO₂. *Global Change Biology* **6**, 889–897.

Pyankov VI, Black CC, Artyusheva EG, Voznesenskaya EV, Xu MS, Edwards GE, 1999: Features of photosynthesis in *Haloxylon* species of Chenopodiaceae that are dominant plants in Central Asian deserts. *Plant and Cell physiology* **40**, 125–134.

Sakuratani T, 1981: A heat balance method for measuring water flux in the stem of intact plants. *Journal of Agricultural Meteorology* **37**, 9–17.

Sala A, Smith SD, Devitt DA, 1996: Water use by *Tamarix ramosissima* and associated phreatophytes in a Mojave Desert floodplain. *Ecological Applications* **6**, 888–898.

Schlesinger WH, 1997: Biogeochemistry: An Analysis of Global Change. Academic Press, UK, pp. 588.

Tang JW, Bolstad PV, Ewers BE, Desai AR, Davis KJ, Carey EV, 2006: Sap flux–upscaled canopy transpiration, stomatal conductance, and water use efficiency in an old growth forest in the Great Lakes region of the United States. *Journal of Geophysical Research* **11**, 1–12.

Terashima I, 1992: Anatomy of non-uniform leaf photosynthesis. *Photosynthesis Research* **31**, 195–212.

Tyree MT, 2003: Hydraulic limits on tree performance: transpiration, carbon gain and growth of trees. *Trees* **17**, 95–100.

Xu GQ, Li Y, Xu H, 2011: Seasonal variation in plant hydraulic traits of two co-occurring desert shrubs, *Tamarix ramosissima* and *Haloxylon ammodendron*, with different rooting patterns. *Ecological Research* **26**, 1071–1080.

Xu H, Li Y, 2006: Water-use strategy of three central Asian desert shrubs and their responses to rain pulse events. *Plant and Soil* **285**, 5–17.

Xu H, Li Y, Xu GQ, Zou T, 2007: Ecophysiological response and morphological adjustment of two Central Asian desert shrubs towards variation in summer precipitation. *Plant, Cell and Environment* **30**, 399–409.

Yang QY, Zhao WZ, Liu B, Liu H, 2014: Physiological responses of *Haloxylon ammodendron* to rainfall pulses in temperate desert regions, Northwestern China. *Trees* **28**, 709–722.

Yole G, Malone E, Brenkert A, Schlesinger M, Mei J, Xing X, 2006: Global Distributions of Vulnerability to Climate Change. *Integrated Assessments* **6**, 35–44.

Zhao P, 2011: On the coordinated regulation of forest transpiration by hydraulic conductance and canopy stomatal conductance. *Acta Ecologica Sinica* **31**, 1164–1173.

Zheng CL, Wang Q, 2014: Water-use response to climate factors at whole tree and branch scale for a dominant desert species in central Asia: *Haloxylon ammodendron*. *Ecohydrology* **7**, 56–63.

Zheng CL, Wang Q, 2015: Seasonal and annual variation in transpiration of a dominant desert species, *Haloxylon ammodendron*, in Central Asia up-scaled from sap flow measurement. *Ecohydrology* **8**, 948–960.

Zheng SX, Lan ZC, Li WH, Shao RX, Shan YM, Wan HW, Taube F, Bai YF, 2011: Differential responses of plant functional trait to grazing between two contrasting dominant C₃ and C₄ species in a typical steppe of Inner Mongolia, China. *Plant and Soil* **340**, 141–155.