Stem sap flow of Haloxylon ammodendron at different ages and its response to physical factors in the Minqin oasis-desert transition zone, China postprint

Authors: QIANG Yuquan

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Abstract

Haloxylon ammodendron, with its tolerance of drought, high temperature, and saline-alkaline conditions, is one of the main sand-fixing plant species in the oasis-desert transition zone in China. This study used TDP30 thermal dissipation probes to measure hourly and daily variations in stem sap flow velocity of H. ammodendron at three age classes (10, 15, and 20 years old, denoted as H10, H15, and H20, respectively) in the Minqin oasis-desert transition zone from May through October 2020. By simultaneously monitoring temperature, relative humidity, photosynthetically active radiation, wind speed, net radiation, rainfall, and soil moisture, we comprehensively investigated the stem sap flow velocity of different-aged H. ammodendron plants and revealed its response to physical factors. The results showed that on sunny days, the hourly variation curves of stem sap flow velocity for all three age classes were primarily unimodal. Additionally, stem sap flow velocity decreased significantly from September to October, which also delayed its peak time. On rainy days, stem sap flow velocity was multimodal and significantly lower than on sunny days.

Full Text

Preamble

Stem Sap Flow of Haloxylon ammodendron at Different Ages and Its Response to Physical Factors in the Minqin Oasis-Desert Transition Zone, China

Qiang Yuquan[1,2,3], Zhang Jinchun[1,2,3*], Xu Xianying[1,2,3], Liu Hujun[1,2], Duan Xiaofeng[1,2]

[1]College of Forestry, Gansu Agricultural University, Lanzhou 730000, China
[2]Key Laboratory of Forest Ecology and Environment of Gansu Province, Lanzhou 730000, China
[3]Minqin Desert Control Research Station, Gansu Agricultural University, Minqin 733300, China

Abstract: Haloxylon ammodendron, with its tolerance of drought, high temperature, and saline-alkaline conditions, is one of the main sand-fixing plant species in the oasis-desert transition zone in China. This study used TDP30 thermal dissipation probes to measure hourly and daily variations in stem sap flow velocity of H. ammodendron at three age classes (10, 15, and 20 years old, denoted as H10, H15, and H20, respectively) in the Minqin oasis-desert transition zone from May through October 2020. By simultaneously monitoring temperature, relative humidity, photosynthetically active radiation, wind speed, net radiation, rainfall, and soil moisture, we comprehensively investigated the stem sap flow velocity of different-aged H. ammodendron plants and revealed its response to physical factors. The results showed that on sunny days, the hourly variation curves of stem sap flow velocity for all three age classes were primarily unimodal. Additionally, stem sap flow velocity decreased significantly from September to October, which also delayed its peak time. On rainy days, stem sap flow velocity was multimodal and significantly lower than on sunny days.

Average daily water consumption of H. ammodendron plants at H10, H15, and H20 was 1.98, 2.82, and 1.91 kg/d, respectively. Temperature was the key factor affecting stem sap flow velocity at all age classes. Net radiation was the critical factor influencing stem sap flow velocity at H10 and H15; however, for H20, vapor pressure deficit was most important. Stem sap flow velocity was highly significantly correlated with soil moisture at depths of 50 and 100 cm, and this correlation strengthened with increasing stand age. Altogether, our results reveal the dynamic changes of stem sap flow velocity in different-aged H. ammodendron forest stands and its response mechanisms to local physical factors, providing a theoretical basis for the construction of new protective forests as well as the restoration and protection of existing ones in this region and other similar arid regions worldwide.

Keywords: Haloxylon ammodendron; stem sap flow; stand age; soil moisture; water consumption; Minqin oasis-desert transition zone

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*Corresponding author: Zhang Jinchun (E-mail: junchunzhang@163.com)

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1 Introduction

The oasis-desert transition zone represents the most intensive and prominent area of inter-conversion activities between oasis and desert ecosystems, making it extremely fragile and sensitive to human activities and quite difficult to restore once degraded or destroyed. Moreover, this zone serves as the interface where material cycling, energy flow, and information exchange occur most frequently between oasis and desert ecosystems.

Haloxylon ammodendron is a deciduous shrub or small tree in the family Amaranthaceae, being a C4 plant species native to Central Asian desert habitats. It is a key functional species for establishing windbreak and sand-fixation forests in the Minqin oasis-desert transition zone. However, due to climate change and human activities, both groundwater levels and soil moisture in this transition zone are declining. Nearly 60% of the existing 44,600 hm^2 of H. ammodendron shelterbelt has suffered from poor growth or degradation, which greatly impairs its windbreak and sand-fixation functions. This ongoing degradation threatens the survival and development of the Minqin oasis.

Water consumed via plant transpiration is a fundamental component of the water cycle and energy balance in forest ecosystems, serving as a crucial indicator of plant water status and a key factor affecting regional and even global climate dynamics. Poyatos et al. (2021) summarized existing research on the relationship between stem sap flow and transpiration, concluding that under normal circumstances, stem sap flow can accurately reflect the transpiration efficiency and water use status of individual plants across time periods. Accordingly, studying how stem sap flow in different-aged H. ammodendron plants responds to physical factors is essential for understanding age-related changes in water consumption. Previous research on H. ammodendron in the Minqin oasis-desert transition zone has focused on leaf photosynthesis, transpiration, and water use efficiency, drought tolerance, and root morphological characteristics. However, a systematic investigation of whole-growing-season water consumption per plant and its relationship with external meteorological factors and soil moisture for different-aged H. ammodendron remains unreported. Analyzing dynamic changes in stem sap flow across different ages can help us grasp the water consumption patterns of H. ammodendron during its growth process and reveal its response mechanisms under self-thinning when adapting to local arid environmental changes, thereby informing effective protection and restoration efforts.

This study continuously measured stem sap flow in different-aged H. ammodendron plants throughout the entire growing season in the Minqin oasis-desert transition zone. External physical factors were simultaneously monitored to analyze changes in stem sap flow and its correlation with physical factors, thereby understanding age-dependent characteristics of water consumption and responses to abiotic factors. These findings provide a theoretical basis for restoring and protecting degraded H. ammodendron plants and establishing new shelterbelts.

2.1 Study Area

The study area (Minqin oasis-desert transition zone; 39°08$‘56’‘–39°09’02’‘N, 103°36’54’‘–103°38’01”E; [Figure
seeoriginalpaper])islocatedneartheMinqinDesertControlResearchStationatthesoutheasternedgeoftheBada
freeperiodlasts168days, with3181hoursofsunshineperyearand630kJ/cm^{2}$
of solar radiation. The prevailing northwest wind has an annual average speed of 4.1 m/s. Soils are predominantly sandy with poor nutrients and serious wind erosion. The landform consists mostly of semi-fixed sandy land interspersed with 3–10 m sand dunes. From 2019 to 2022, groundwater depth in the study area ranged between 22.95 and 23.41 m. Vegetation is dominated by xerophytic shrubs, semi-shrubs, and annual and perennial herbs, including the shrubs H. ammodendron, Nitraria tangutorum, and Artemisia arenaria, and the herbs Phragmites australis, Kali collinum, Halogeton glomeratus, and Agriophyllum squarrosum.

2.2 Experimental Design

Based on time since planting, we selected three artificial H. ammodendron forest stands with afforestation ages of 10, 15, and 20 years (hereafter H10, H15, and H20) in the Minqin oasis-desert transition zone. Four representative, healthy H. ammodendron individuals were chosen at each age class (). Plant height was measured with a tower ruler, crown width and inter-plant distances with a tape measure, and stem ground diameter with a vernier caliper. Using TDP30 thermal dissipation probes (Rainroot Scientific Limited, Beijing, China), we measured stem sap flow velocity for each individual from May 1 to October 30, 2020. The TDP30 was installed on a smooth spot on the east side of the stem, 40 cm aboveground. The installation spot was sanded with sandpaper, then the probe was drilled and inserted using a matching drill needle. Once installed, the probe was wrapped with special plastic fixing sponge, then covered with silver radiation-proof aluminum foil; thermal insulation cotton was placed around the probe on the ground to reduce temperature influence. A CR1000 data logger (Campbell Scientific Inc., Logan, UT, USA) connected to the probe collected data every 1 minute throughout the observation period.

2.3 Determination of Stem Sap Flow and Water Consumption

Stem sap flux density (i.e., stem sap flow velocity) was calculated using the empirical formula from Granier (1987):

$$F_d = 0.000119 \times \left(\frac{\Delta T_{max} - \Delta T}{\Delta T}\right)^{1.231}$$

where F_d is stem sap flux density ($\mathrm{cm}^3/(\mathrm{cm}^2 \cdot \mathrm{h})$), ΔT_{max} is the maximum temperature difference between the two probes when there was no stem sap flow (°C), and ΔT is the temperature difference when stem sap flow existed (°C). The measurement time without stem sap flow was set to 00:00–01:00 (LST) in May, July, August, September, and October, and to 03:00–04:00 in June.

Daily transpiration of a single individual was calculated as:

$$Q = \int_0^T F_d \times A_s \, dt$$

where Q is daily transpiration (cm^3), A_s is sapwood area (cm^2), and T is 24 h. Sapwood area was calculated using the exponential function from Zhang et al. (2017):

$$A_s = 0.699e^{0.966x}$$

where x is H. ammodendron diameter (cm). Finally, water consumption was calculated using $m = \rho \times V/1000$, where m is water consumption (kg), ρ is water density ($\mathrm{g/cm}^3$, taken as 1 $\mathrm{g/cm}^3$), and V is daily transpiration (cm^3), equivalent to Q.

2.4 Determination of Meteorological Factors

Three portable weather stations were deployed at the sampled forest stands to monitor meteorological factors. These stations recorded daily average temperature (°C), relative humidity (RH; %), photosynthetically active radiation (PAR; mol/($\mathrm{s} \cdot \mathrm{m}^2$)), surface net radiation (R_n; $\mathrm{W/m}^2$), daily average wind speed at 2 m height (m/s), and rainfall (mm) every 10 minutes from May through October 2020. Vapor pressure deficit (VPD) was calculated following Zheng and Wang (2015) and Zhang et al. (2016).

2.5 Determination of Soil Moisture

EC-5 soil moisture sensors (Ecotek Technology Limited, Beijing, China) were installed at depths of 5, 20, 50, 100, and 150 cm at each H. ammodendron stand and connected to EM50 data loggers (Ecotek Technology Limited, Beijing, China). Data were downloaded using ECH2O Utility software. After installation, soil bulk density was measured and actual soil moisture was determined near each sensor to calibrate probe error. The measurement period spanned April to November 2020 with a 1-hour data interval.

2.6 Data Processing and Calculations

Under sunny conditions, we selected representative days with stable changes from consecutive days showing similar trends each month to characterize monthly stem sap flow variations for each age class (H10, H15, H20). Under rainy conditions, we selected days with high rainfall and significant sap flow changes for analysis. The average of four individuals per age class expressed age-specific trends. Hourly and daily sap flow velocity data were aggregated from 10-minute monitoring intervals. SPSS 16.0 and Microsoft Excel 2019 were used for statistical analysis.

2.7 Response of Stem Sap Flow to Physical Factors

A structural equation model (SEM) determined the relative response of stem sap flow in different-aged H. ammodendron to meteorological factors and their weightings. Model building involved five steps: constructing a theoretical model, formulating hypotheses, testing reliability and validity, assessing model fit, and adjusting as needed. Daily sap flow velocity values for H10, H15, and H20 served as the criterion layer, while temperature, RH, R_n, wind speed, and VPD served as the indicator layer, assuming all factors could drive sap flow. MPLUS 8.0 software tested discriminant validity. Data reliability was assessed using Cronbach's alpha and Kaiser-Meyer-Olkin (KMO) tests. Model fit was evaluated using chi-square/df ratio, comparative fit index (CFI), Tucker-Lewis index (TLI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR). Based on path coefficients, the Analytic Hierarchy Process (AHP) obtained weighted results for each meteorological factor. Correlation analysis between soil moisture and sap flow velocity used SPSS 16.0.

3.1 Dynamics of Meteorological Factors

Meteorological factor variations during the growing season (May 1–October 31, 2020) are presented in [Figure 2: see original paper]. Temperature peaked at 30.8°C in early July and reached a minimum of -4.5°C in October. Relative humidity fluctuated between 10% and 97% from May to July, and between 26% and 91% from August to October. Photosynthetically active radiation increased then decreased, peaking at 940 $\mathrm{mol/(s \cdot m^2)}$ in June. Wind speed reached a maximum daily average of 3.7 m/s in May and minimum of 0.3 m/s in May, with frequency increasing from August to September and considerable daily fluctuation. Vapor pressure deficit increased then decreased, peaking at 2.6 kPa in June. Total rainfall during the growing season was 55.5 mm, with the highest daily rainfall of 7.1 mm on September 30. Net radiation showed multiple peaks: 172.9 $\mathrm{W/m^2}$ in June, 179.2 $\mathrm{W/m^2}$ in July, and 175.0 $\mathrm{W/m^2}$ in September.

3.2 Dynamics of Stem Sap Flow Velocity in H. ammodendron at Different Ages

3.2.1 Hourly Dynamics on Sunny Days

Hourly dynamics on six typical sunny days (May 20, June 17, July 15, August 20, September 16, and October 21) revealed variation characteristics across ages ([Figure 3: see original paper]). In June, H10 and H15 peaked between 08:50–09:00, while H20 peaked later at 14:10. In July, H10 and H15 started at 05:40–06:00 and peaked at 08:50–09:20, whereas H20 started at 08:00 and peaked at 11:20. In August, all age classes started between 07:00–07:30; H15 and H20 peaked at 11:40–12:00, while H10 peaked later at 13:30. In September, H10 and H15 started at 02:30 and peaked at 13:20–13:30, while H20 started later at 07:30 but peaked earlier at 11:10. In October, H10 and H15 started at 02:10–02:30 and H20 at 07:40, with peaks at 15:50, 10:40, and 12:30, respectively.

3.2.2 Hourly Dynamics on Rainy Days

Four typical high-rainfall days (May 26, June 20, July 10, and August 24) were selected to analyze rainfall effects ([Figure 4: see original paper]). Sap flow velocity on rainy days was significantly lower than on sunny days, with a consistent ~1-hour time lag in response across all age classes. However, response magnitude differed among ages, ranking as H15 > H10 > H20.

3.3 Daily Dynamics in Stem Sap Flow Velocity

Daily dynamics during the growing season (May 1–October 31) differed among age classes ([Figure 5: see original paper]). H10 showed an overall trend of initial increase then decrease, peaking at 112.28 $\mathrm{cm^3/(cm^2 \cdot d)}$ on August 28 before declining sharply in October. H15 exhibited a multi-peak pattern with peaks on June 17 (227.11 $\mathrm{cm^3/(cm^2 \cdot d)}$), July 19 (188.70 $\mathrm{cm^3/(cm^2 \cdot d)}$), and September 18 (288.79 $\mathrm{cm^3/(cm^2 \cdot d)}$). H20 fluctuated considerably in May, with an overall increasing then decreasing trend, peaking at 119.01 $\mathrm{cm^3/(cm^2 \cdot d)}$ on August 11 before declining sharply in September.

3.4 Variation in Water Consumption at Different Ages

Average daily and total water consumption during the 2020 growing season are shown in [Figure 6: see original paper]. Average daily water consumption was highest in May for all age classes, reaching 5.6, 5.2, and 3.6 kg/d for H10, H15, and H20, respectively. Across the entire growing season, H15 showed significantly different average daily water consumption (2.8 kg/d) compared to

H10 and H20 (both 1.9 kg/d). Total growing season water consumption was 357.3 kg for H10, 509.1 kg for H15, and 344.3 kg for H20.

3.5 Correlations Between Stem Sap Flow Velocity and Physical Factors

3.5.1 Relationships with Meteorological Factors

Daily variation data from four consecutive days each month (May 19–22, June 16–19, July 14–17, August 19–22, September 14–17, and October 19–22) were used to fit SEMs. Cronbach's alpha and KMO coefficients for H10, H15, and H20 exceeded minimum acceptable values, indicating reliable correlations (). Second-order confirmatory factor analysis showed good model fit: ^{2}/df = 1.202, RMSEA = 0.049, SRMR = 0.073, CFI = 0.984, and TLI = 0.927, satisfying all critical value requirements.

Meteorological factors clearly correlated with sap flow velocity across ages ([Figure 7: see original paper]). Temperature had the largest weighting, making it the key factor affecting sap flow (). Factor effects ranked as temperature > R_n > VPD > wind speed > RH for H10 and H15, and temperature > VPD > R_n > wind speed > RH for H20.

Correlations varied under different weather conditions (), being significantly greater on sunny than rainy days. Under sunny conditions, VPD was the main influencing factor. Correlations changed across months and shifted among ages. Rainfall showed very significant correlation with sap flow velocity ($P < 0.01$), ranking H15 > H20 > H10.

3.5.2 Relationships with Soil Moisture

On sunny days, sap flow velocity at each age class showed very significant correlations with soil moisture at 50 and 100 cm depths (). Correlations were negative in the upper soil layer and positive in the deeper layer, with coefficients ranking H10 > H15 > H20. On rainy days, correlations were weaker and non-significant.

4.1 Variation in Stem Sap Flow Velocity at Different Ages

In May, H15 showed larger sap flow velocity and longer daily duration compared to H10 and H20, likely due to its relatively large crown diameter (), suitable temperatures ([Figure 2: see original paper]), and frequent winds that reduced leaf humidity and increased VPD. These favorable conditions resulted in greater sap flow velocity for H15. Xia et al. (2019) reported single-peak "Z"-shaped patterns in apple trees with higher daytime values, similar to our finding of primarily unimodal curves with weak nocturnal flow and significant diurnal differences under sunny conditions, a pattern also observed in Elaeagnus angustifolia (Liu et al., 2021).

In May, H20 started late, ended early, peaked later, and showed significantly lower velocity than H10 and H15 during new branch germination. This likely resulted from low rainfall and soil moisture, plus branch dieback, rodent damage, pests, and diseases in this water-scarce environment (Luo et al., 2017; Ma et al., 2012), leading to smaller crown diameter, decreased surface accumulation, poor water-holding capacity, and groundwater dependence.

In October, sharp temperature drops slowed metabolism and reduced soil moisture absorption and transpiration, creating stark differences among age classes. On sunny days, hourly curves remained unimodal with weak nocturnal flow and significant day-night differences. On rainy days, velocity was significantly lower than on sunny days, ranking H15 > H10 > H20, because larger crowns absorb more water directly during rainfall, consistent with findings from the Gurbantunggut Desert (Xia et al., 2014; Yue et al., 2020).

4.2 Variation in Water Consumption at Different Ages

Maximum average daily water consumption occurred in May across all ages, likely because branches began sprouting in April, temperatures ranged 5.0–25.0°C, and May's windy weather increased transpiration. Combined with strong photosynthetically active radiation and frequent rainfall, these conditions facilitated rapid rhizome and branch development. Jia et al. (2020) similarly found maximum shrub water consumption in May due to rainy season timing and drought stress. However, Cao et al. (2013) and Zhang et al. (2016) reported July maxima for H. ammodendron, a discrepancy explained by different rainfall and temperature regimes. In our study, June and July had highest temperatures but scarce rainfall, promoting stomatal closure, reducing photosynthesis, and slowing metabolism, thereby decreasing water consumption. H15 consumed much more water than H10 or H20 during these months due to larger canopy diameter and strong transpiration at high temperatures.

September had the most rainfall but lowest water consumption across ages because decreasing temperatures, large diurnal temperature differences, diminished photosynthetically active radiation, and peak abscisic acid content (Ma et al., 2012) cued dormancy (Zhao et al., 2017; Gao et al., 2020), reducing water use.

Comparing regional water consumption (), H10 and H20 values were similar to native Gurbantunggut Desert plants, while H15 matched Badain Jaran Desert consumption rates. Previous research indicates H. ammodendron plantations undergo pronounced self-thinning after >10 years (Song et al., 2021; Zhao et al., 2023). At H10, decreasing plant numbers and disappearing shrub belt structure gradually reduced community water consumption (Song et al., 2021; Liu et al., 2022). At H15, few remaining plants achieved better water consumption balance. At H20, despite groundwater access, mortality remained high, suggesting that water consumption lowered groundwater levels insufficiently to maintain physiological activity.

4.3 Responses of Stem Sap Flow Velocity to Physical Factors

Temperature was the chief factor governing sap flow velocity. Within the effective range, rising temperatures accelerated growth; at light saturation, H. ammodendron reached maximum water consumption (Sun et al., 2010; Mahdavi et al., 2022), giving temperature high weight among meteorological factors. Net radiation influenced photosynthetic rate and, as a heat source, warmed/cooled the surface and atmosphere, with heat consumed by evapotranspiration (Dong, 2013), thus carrying high weight for H10 and H15. Vapor pressure deficit reflected atmospheric aridity and evaporative stress (Yang et al., 2018). Decreasing humidity increased VPD, causing stomatal closure that altered sap flow while indirectly improving photosynthetic performance, giving VPD high weight for H20. Wind speed and RH had lower weights despite some influence.

On sunny days, sap flow velocity showed strong significant correlation with soil moisture at 50 and 100 cm depths, with correlations strengthening in younger stands. The 0–100 cm soil layer consisted of sandy soil with poor water-holding capacity (Guo et al., 2016), while the layer below 100 cm had better water retention, and water-absorbing root depth increased with stand age (Zhang et al., 2016). Therefore, older stands showed better correlation with deep soil moisture. At 50 cm depth, sap flow velocity showed very significant negative correlation with soil moisture across all ages, likely because surface evaporation from sandy soils at high temperatures reduced water availability around roots, inhibiting consumption (Zhou et al., 2017). At 100 cm depth, significant positive correlation indicated that soil below this depth retained water and contained most water-absorbing roots (Xu et al., 2021).

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5 Conclusions

This study demonstrated that stem sap flow velocity curves show single peaks on sunny days and multiple peaks on rainy days, with significantly lower magnitude on rainy days. Temperature is the primary factor affecting sap flow velocity, with correlations more significant in younger stands. Older stands utilize soil moisture from deeper layers. Water consumption of H. ammodendron in the Minqin oasis-desert transition zone peaks at 15 years of age (H15) compared to H10 and H20. Although H20 plants can use groundwater, their water consumption is low and mortality likely high, possibly because their water consumption lowers groundwater levels insufficiently to maintain physiological activity. Therefore, initial stand density must be reasonably planned to mitigate future soil moisture consumption in arid regions, maintaining plantation stability and facilitating greater ecological benefits.

Conflict of Interest: The authors declare no known competing financial interests or personal relationships that could have influenced this work.

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Note: Figure translations are in progress. See original paper for figures.