Sapflow characteristics and climatic responses in three forest species in the semiarid Loess Plateau region of China

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ABSTRACT

In the semiarid Loess Plateau region of China, ecosystems are frequently affected by water shortages. Late spring and early summer are periods when forest communities tend to suffer from soil drought. To clarify the water-use strategies of the main species in this area, the xylem sap flow of trees from three species in the field was monitored for three successive periods in summer using Granier-type thermal dissipation probes. Vapor pressure deficit (VPD), solar radiation (R_s) and soil moisture had varying influences on sap flux density (F_d) in the species. Normalized F_d values could be fitted to VPD using an exponential saturation function, but the fit was better with a derived variable of transpiration (VT), an integrated index calculated from VPD and R_s. From differences in model coefficients, the species were roughly divided into two types with contrasting drought sensitivity. The exotic *Robinia pseudoacacia* was defined as drought-sensitive type. It showed higher sapflow increases in response to rainfall, suggesting a high water demand and high influence of soil water conditions on transpiration. This species showed relatively late stomatal response to increasing VPD. The wide-peak pattern of diurnal sapflow course also suggests relatively low stomatal regulation in this species. The drought-insensitive type consisted of the naturally dominant *Quercus liaotungensis* and an indigenous concomitant species, *Armeniaca sibirica*, in the forest. The sap flow of these species was not very sensitive to changes in soil water conditions. The results suggest that typical indigenous species can manage the water consumption conservatively under both drought and wet conditions. Variations in water use strategies within indigenous species are also detected.

1. Introduction

It is commonly accepted that climatic conditions control the ecological distribution of vegetation types. Precipitation is among the most important factors determining the occurrence and diversity of species (Archibold, 1995; Wu, 1980). In arid and semiarid regions, species have to cope with dry years or seasons. The semiarid Loess Plateau region in China is an area having high atmospheric evaporative demand and low rainfall. Compared with other environmental variables such as soil types and edaphic factors, climate is of primary significance affecting the distribution of forest species in the region (Fang et al., 2010). Annual total precipitation is about 500 mm and the area is defined ecologically as a forest-grassland transitional zone, naturally dominated by drought-resistant species of trees and shrubs (Cheng and Wan, 2002; Tian et al., 2003; Wu and Yang, 1998). Conservation of natural forest resources and reforestation of degraded land are particularly important because of severe soil erosion that has taken place during past decades (Tian et al., 2003). To encourage proper reforestation practices, common species need to be investigated to understand their water use strategies under different weather conditions and to determine if they are suitable for developing stable forest ecosystems.

Drought tolerance is frequently addressed when evaluating appropriate species for reforestation in arid areas. Tree species confronted with a dry climate and soil moisture stress will undergo structural or physiological adjustment in order to maintain the integrity of their hydraulic systems and to enable carbon assimila-

tion (Bréda et al., 2006). Several characteristics have been studied as being potentially responsible for the adaptability of tree species to dryland environments. These characteristics include the xerophytic structure of leaves, developed root systems, stems with high hydraulic conductivity and low cavitation risk, endurance of extremely low water potentials, stomatal control of transpiration, osmotic adjustment, activation of anti-oxidative enzymes, and possession of stiff cell walls (Kozlowski, 1976; Kozlowski and Pallardy, 1997; Larcher, 2003). Several investigations of forest species growing in the central Loess Plateau have documented responses of photosynthesis and water relations to drought stress (Hara et al., 2008; Yamanaka et al., 2006; Yan et al., 2010), the effects of plantations on soil properties (Cao et al., 2007), under-forest micrometeorology and soil development (Otsuki et al., 2005; Tateno et al., 2007), and growth in relation to climatic conditions (Du et al., 2007). However, there is limited information about water use characteristics for individual large trees in relation to atmospheric and soil moisture conditions within a forest stand.

Sap flow in co-existing tree species often shows species-specific responses to variation in microclimatic and edaphic parameters (Granier et al., 1996; Oren and Pataki, 2001; Pataki and Oren, 2003; Pataki et al., 2000). In areas subjected to predictable and recurring drought, sap flow measurements are particularly suitable for investigations into the different strategies that species use to cope with limited soil water availability (Pataki et al., 2000). An investigation in evergreen tropical trees reported that seasonal soil drought caused a reduction of sap flux density, and that the impact was more significant in shallow-rooted smaller trees than in larger trees with deep roots (Kume et al., 2007). During and following a drought period in south eastern Australia, sub-dominant eucalyptus species were observed to be more responsive to rainfall than the dominant species (Eberbach and Burrows, 2006). Obviously, there is a species-specific regime of sapflow characteristics in response to different water conditions.

Transpiration and sapflow characteristics vary not only with species and growth status, but also with meteorological environments and edaphic features. In areas with insufficient water, soil water conditions can restrict many physiological processes. Temporal recharge of soil water by rainfall causes sapflow acceleration due to a release of xylem hydraulic conductance (Eberbach and Burrows, 2006; Oren et al., 1996). However, sapflow dynamics in response to changes in atmospheric and soil moisture conditions should be different due to species-specific effects, such as the stomatal regulation of transpiration. Species assumed to differ in drought sensitivity and regulation of water use should show different behavior in response to different soil moisture conditions (Hölscher et al., 2005; Köcher et al., 2009).

The present study is focused on species differences in sapflow characteristics in response to environmental factors, i.e. differences in drought sensitivity. We investigated the sap flows of three forest species very common to the semiarid Loess Plateau region from two adjacent stands. *Robinia pseudoacacia* is an exotic fast-growing species with many plantations all over the region. *Quercus liaotungensis* and *Armeniaca sibirica* are indigenous to the region and co-occur in the natural forests dominated by *Q. liaotungensis*. Specifically, we aimed (1) to compare the difference in sap flux density in each species in conditions of different soil moisture separated by rainfall events, so that information about drought sensitivity of each species could be obtained; and (2) to compare the relationships among sapflow dynamics, solar radiation (R_s), vapor pressure deficit (VPD), and soil moisture conditions so that species water use strategies could be analyzed. The results are expected to contribute not only to the understanding of differences in water use strategies among typical species, but also to further researches on

stand-level hydrological properties and the choice of reforestation species in the region.

2. Material and methods

2.1. Study site

The study was performed at Mount Gonglushan located in the southern suburb of Yan'an city of Shaanxi Province in the central part of the Chinese Loess Plateau (36°25.40′N, 109°31.53′E). We chose two adjacent stands for the experiment, a secondary natural forest dominated by *Q. liaotungensis* Koidz and an artificial plantation of introduced *R. pseudoacacia* L., at an elevation of 1350 m a.s.l. The area has the typical topographical characteristics of loess hills and gullies. The mean annual precipitation and air temperature during the past 20 years (1988–2007) were 498 mm and 10.6 °C, respectively, according to data from the city meteorological station. Most of the rainfall occurs from July to September, and spring and early summer are usually characterized as a dry season. The growing season for usual deciduous species ranges from April to October in this region. The parent material of the soil is loess with a depth of 50–200 m depending on topography. The loess in this area usually has a texture of more than 50% silt (0.002–0.05 mm) and less than 20% clay (<0.002 mm), with a porosity of about 50%. The gravimetric field capacity and wilting percentage of soil water are 20–24% and 3–6%, respectively (Yang and Shao, 2000; Zhu et al., 1983). Average soil water content in the top 0–1.0 m horizons ranged from 7.2% to 12.5% for the months of this study which is very low for tree growth (Fig. 1, measurement description in Section 2.3). Details of the study site have also been documented by Du et al. (2007) and Tateno et al. (2007).

There was a permanent research plot in each of the two deciduous forest stands. The *Robinia* stand was an approximately 30-year-old plantation on an east-facing slope. Artificial *Robinia* stands in this region generally show rapid growth in their early years and a decline in growth around this age. Dieback phenomena are frequently observed. The *Quercus* stand was around 50 years old and was on a northeast-facing slope. Besides *Q. liaotungensis*, other species present included *A. sibirica* L., *Acer stenolobum* Rehd., *Platycladus orientalis* (L.) Franco (an evergreen conifer), *Ulmus macrocarpa* Hance, *Euonymus bungeanus* Maxim., and several other species of small trees and shrubs. General characteristics of the two study plots and investigated individuals in this study were presented in Table 1.

2.2. Sap flow measurements

Xylem sap flow was measured in 15 individuals with diameters at and above mean tree diameter belonging to 3 species, i.e. *R. pseudoacacia, Q. liaotungensis* and *A. sibirica*, for three successive periods during the summer months of 2008. There were not sufficient replicates of other species large enough for such measurement. Sap flux densities were measured using Granier-type thermal dissipation probes (TDP) constructed after Granier (1985, 1987). Each sensor consisted of a pair of probes 10 mm long and 2 mm in diameter and a copper-constantan thermocouple was placed in each probe. After peeling off two pieces of bark (ca. 15 mm × 15 mm), the probes were inserted into the sapwood about 0.15 m vertically apart at breast height. The upper probe included a heater that was supplied with a constant power of 0.15 W and the lower probe was unheated for reference (James et al., 2002). The temperature difference between the upper heated probe and the lower reference probe was measured every 30 s, and 30 min averages were recorded on a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA) with
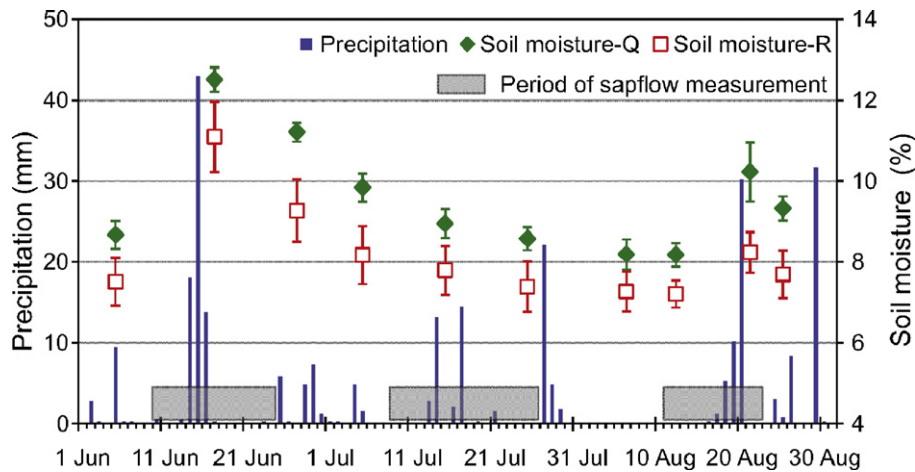
Fig. 1. Precipitation and soil volumetric moisture content in the field during the summer months (June–August) of 2008. Soil moisture data were averages (with standard errors) of 3 rods each containing 5 measurement depths for the top 1 m of soil (0.2, 0.4, 0.6, 0.8, and 1.0 m). Soil water condition in the *Quercus* plot (soil moisture: *Q*) was consistently better than the *Robinia* plot (soil moisture: *R*), but showed the same pattern of changes during the months. Sap flows were monitored for three periods each being broken by several rainy days.

a multiplexer (AM16/32A, Campbell Scientific). The sensor was mounted with waterproof silicone and covered with an aluminum box-cover to avoid physical damage and thermal influences from radiation.

According to the empirical relationship between sap flux density and the temperature difference between probes established by Grainer and revalidated by other researchers (Clearwater et al., 1999; Granier, 1987), standard uncalibrated sap flux density was calculated as:

$$F_d = 119 \left(\frac{\Delta T_m - \Delta T}{\Delta T} \right)^{1.231} \tag{1}$$

where F_d is sap flux density (ml m^{-2} s^{-1} or μm s^{-1}), ΔT is the temperature difference between the two probes, and ΔT_m is the maximum value of ΔT recorded at the no-transpiration state when F_d is near zero.

There has been concern about the validity of the empirical equation when the sensor design deviates from the original (Lu et al., 2004). In addition, there has also been recommendation that species-specific calibration be applied to the Granier-type probes data (e.g. Lu et al., 2004; Smith and Allen, 1996). Moreover, a recent report suggests that sap flux density is significantly underestimated by heat techniques, particularly with thermal dissipation method (Steppe et al., 2010). In the present study, with the forgoing considerations, we calculated sap flux densities by the original calibration

of Granier and data-normalized as explained in Section 2.5 for analyses of their responses to environmental factors.

2.3. Atmospheric and soil moisture measurements

Several meteorological instruments were placed in an open area outside the stands. Environmental data measured included solar radiation (R_s) measured by a pyranometer (Li-200, Li-Cor Inc., Lincoln, NE, USA) connected to a CR10X data logger (Campbell Scientific), air temperature and relative humidity measured by a thermo recorder (TR-72U, T&D Corp., Japan), and precipitation measured by a tipping-bucket rain gauge (Model 7852, Davis Instruments, USA) connected to a CR10X data logger. In addition, soil moisture contents were measured 3–4 times per month at depths of up to 3 m below the forest floor in each plot using a time-domain reflectometry (TDR) moisture measurement system (TRIME, IMKO Micromodultechnik, Germany). Three Tecanat® plastic tubes of 3 m long and 42 mm in internal diameter were permanently placed in each plot for repetitive TDR measurements. The measured data were calibrated into volumetric water contents by an equation established in the study site with gravimetric water contents from drilled soil cores (conventional oven-drying method) and soil bulk density along profiles. The data along vertical profiles indicated that short-term changes of soil moisture below a depth of 1 m were small and subject to little influence from rainfall during

Table 1
Characteristics of study plots and sample trees.

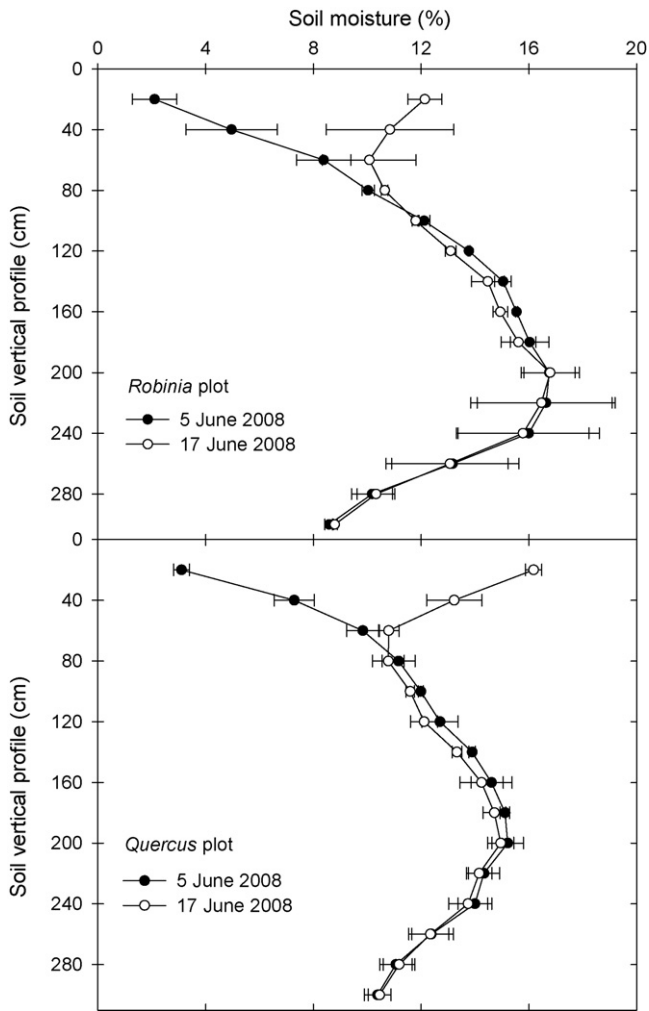| Species and plot	R. pseudoacacia (Robinia plot)	Q. liaotungensis (Quercus plot)		A. sibirica (Quercus plot)
Basal area (BA, m^2 ha^{-1})				
Species	23.3 (n = 124)	10.3 (n = 27)		4.9 (n = 16)
Plot	23.3 (n = 124)		17.6 (n = 54)	
Tree height (H, m)				
Species	8.6	7.0		6.2
Sample trees	8.8–13.5	6.9–9.4		5.4–9.1
Diameter at breast height (DBH, cm)				
Species	9.3	12.8		11.7
Sample trees	9.7–16.6	12.2–20.4		10.1–22.8
Conducting wood anatomy	Ring porous	Ring porous		Ring porous
Sapwood width (cm)	0.72–0.92	1.85–2.62		0.99–1.21
Plot leaf area index (LAI, m^2 m^{-2})				
June	2.89		3.08	
July	2.83		3.10	
August	2.51		2.81	

Fig. 2. Soil volumetric moisture content along vertical profiles in the two plots measured on June 5 and 17, representing pre- and post-rainfall conditions, respectively. They indicated that rainfall-induced short-term changes in soil moisture mainly occurred in the top 0–1 m horizons.

the research period (Fig. 2). Consequently, averages of data for within the top 1 m were used in this study. Rainfall events and soil moisture conditions during the present study periods are shown in Fig. 1.
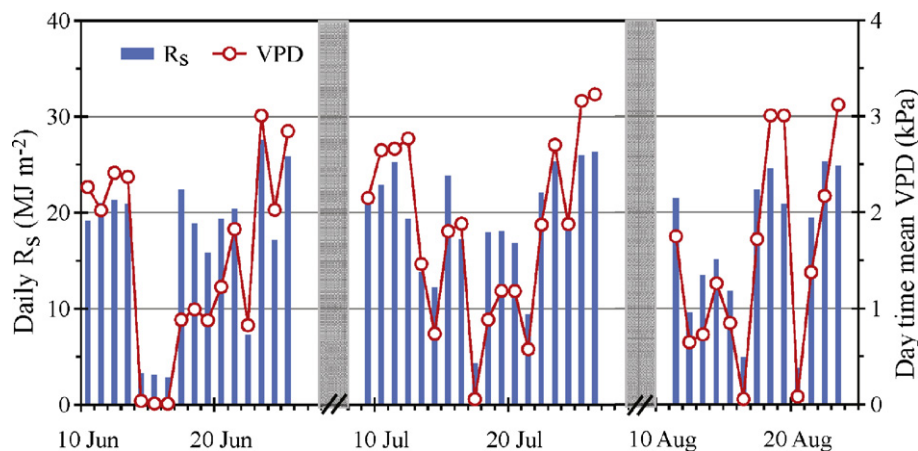
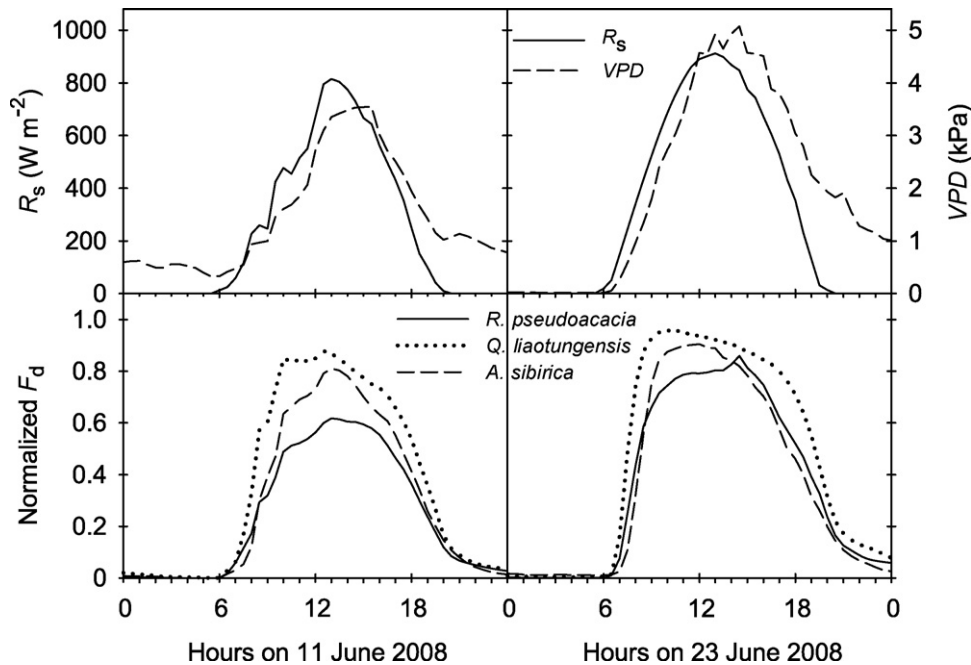### 2.4. Measurement of leaf stomatal conductance

For further understanding the transpiration characteristics of the species, daytime temporal change patterns of canopy and leaf conductance were also investigated. Crown conductance changes were estimated using sapflow data as presented below. Leaf stomatal conductance and CO_2/H_2O gas exchanges were measured in situ for canopy intact leaves. A large tower was temporally constructed in each plot for access to top-of-the-canopy leaves. On June 23 and 25, 2008, diurnal course of stomatal conductance and gas exchanges was measured for *Q. liaotungensis* and *R. pseudoacacia*, respectively. Three sample trees were successfully accessed on each tower and three well-expanded leaves were selected from each sample tree. Measurements were carried out at 1 h intervals from early morning till late afternoon with a portable photosynthesis system (LI-6400, Li-Cor Inc., Lincoln, NE, USA) under approximately natural conditions. The light intensity inside the leaf chamber was controlled according to the in situ-measured photosynthetic active radiation (PAR) just before each hourly-measurement started. Temperature and CO_2 concentration were not controlled. In each 1 h interval, three leaves were measured in each of the three replicate trees.

2.5. Data analyses and estimation of several parameters

This study emphasized the comparison of transpiration characteristics among species and before and after rainfall. Whole-tree transpiration is usually calculated by scaling up (multiplying) mean F_d and conducting sapwood area. Hence, F_d values were used as an index to evaluate variations in transpiration and water use. This method was considered to be useful when transpiration characteristics rather than absolute amounts of water use were discussed, as F_d values are correlated with whole-tree water use (e.g. Hirose et al., 2005; Kume et al., 2007). Furthermore, normalized F_d data were used in this study so that differences among replicated trees were minimized. This was determined by dividing all F_d data for each replicate tree by the maximum throughout the present three months. Consequently, each replicate individual has a maximum normalized F_d of 1.0 and averages can be reasonably calculated for replicates within species.

To investigate the response of sap flow to microclimate, an integrated index named variable of transpiration (VT) was used in addition to R_s and VPD. VPD was calculated using 30 min averages of temperature and relative humidity as described by Campbell and Norman (1998). VT was calculated as a simplified combination of

Fig. 3. Daily sum of solar radiation (R_s) and daytime mean vapor pressure deficit (VPD) in the sapflow measurement periods. This figure in addition to Fig. 1 gives information for rainfall events and days of wet canopy with low VPD.

Fig. 4. Diurnal courses of R_s, VPD, and normalized sap flux densities (F_d) for the three species on two typical bright days, i.e. a pre-rainfall day of 11 June and a post-rainfall day of 23 June (refer to Figs. 1 and 2). The monitoring was sampled as half-hourly mean values and F_d data were normalized within each sample tree before averaging the five individuals. For clear viewing of the diurnal patterns, error bars were omitted in these graphs.

VPD and R_s (Iida et al., 2006; Kakubari and Hosokawa, 1992).

$$VT = VPD \times R_s^{1/2} \tag{2}$$

This is because VPD usually contributes more than two-thirds of the total transpiration, making it the dominant environmental variable, with the remainder coming from the radiation component (Green, 1993; Zhang et al., 1997).

Using normalize F_d, relative crown conductance was also estimated. Total crown conductance of individual trees is usually estimated from the ratio of whole-tree F_d and VPD with an unit conversion coefficient (Kostner et al., 1992) as:

$$G_t = k \times \frac{E}{VPD} \tag{3}$$

where G_t is total crown conductance ($\mu m\, s^{-1}$), E is whole-tree F_d ($\mu m\, s^{-1}$), k is an unit conversion coefficient (kPa) calculated from water density, gas constant for water vapor, and air temperature. As we used normalized F_d in this paper, we calculated a simplified relative crown conductance from the ratio of normalized F_d and VPD to compare the diurnal patterns among species. Aerodynamic conductance in relation to canopy surface micrometeorology (e.g. wind speed) was not calculated in this case.

Statistical analyses were applied to several data sets to investigate the significance of difference and responses of normalized F_d values to environmental variables. SigmaPlot 10.0 software for Windows (Systat Software Inc., USA) and SPSS 13.0 software for Windows (SPSS Inc., USA) was used for the analyses.

3. Results and discussion

### 3.1. Climate and soil water conditions during the study period

Precipitation and soil moisture conditions during the measurement periods are shown in Fig. 1. Soil moisture in the *Robinia* plot was consistently lower than that in the *Quercus* plot, but the trend of changes was identical throughout the three months. There was a 75 mm rainfall event during 13–16 June, resulting in pronounced increases in soil moisture contents in both stands. Total rainfall

between 13 and 17 July was 32 mm and was intermittent, broken by a bright day on 15 July. Thus soil water might not be recharged much by this rainfall event. Pronounced increases in soil moisture were also observed after a 46 mm rainfall event from 18 to 20 August. Fig. 3 shows daily R_s and daytime mean VPD, the main climatic factors driving plant transpiration, for the sapflow measurement days.

3.2. Variations in the diurnal courses of sap flow

Fig. 4 shows the diurnal courses of R_s, VPD, and normalized F_d for the three species on two bright days (11 and 23 June) representing pre- and post-rainfall days, respectively. There was a pronounced diurnal hysteresis between VPD and R_s (2–3 h between the peaks). Dynamics of normalized F_d reflected R_s and VPD values, but they were not necessarily synchronized. Normalized F_d was approximately zero between 0:00 and 6:00 h, and increased shortly after sunrise. It reduced to a very low level towards sunset and gradually reached the minimum after midnight. There were some differences in diurnal courses between the two days presented. The peak time of normalized F_d for *Q. liaotungensis* and *A. sibirica* appeared slightly later on 11 June than on 23 June, which might be related to difference in absorption of soil water. Normalized F_d in all species are generally higher on 23 June than on 11 June. However, considering the differences in R_s and VPD between the two days, it is difficult to conclude an effect of rainfall on the diurnal patterns.

Typical daytime F_d patterns of for these species may represent different types of water-use strategies. Normalized F_d in *R. pseudoacacia* steadily rose in the morning and reached peak relatively late, roughly coinciding with the VPD course. However, *Q. liaotungensis* showed an early-peak at around 9 h followed by a continuous decrease throughout the remainder of the day. *A. sibirica* peaked later than *Q. liaotungensis* and roughly matched the course of R_s, showing an intermediate pattern between the former two species. These characteristics may be important as an early-peak type of diurnal pattern implies stomatal regulation of transpiration in response to increasing VPD.
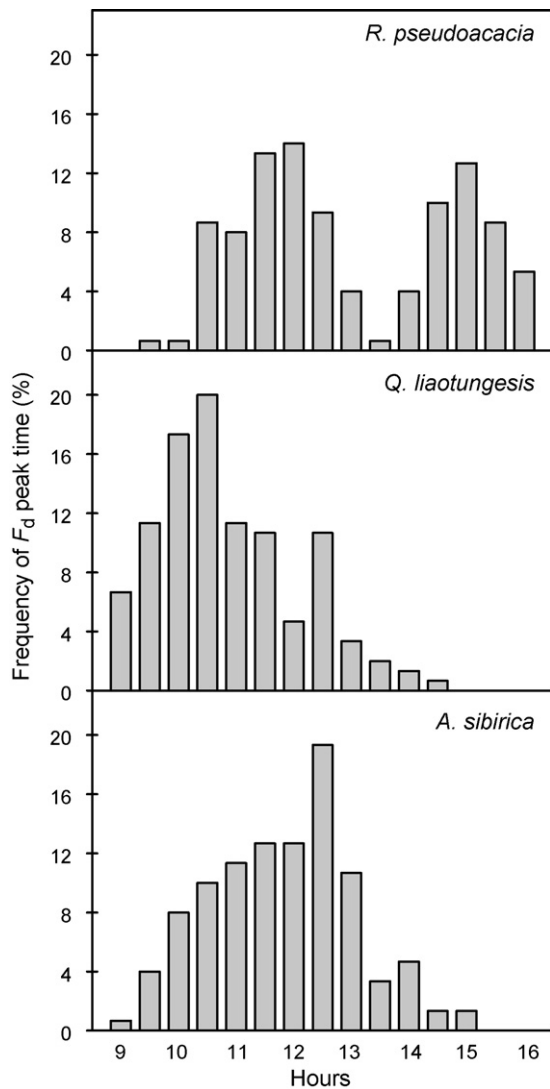
Fig. 5. Frequency of times when normalized F_d peaked referring diurnal patterns. The data sets cover 30 days with daytime mean VPD > 1.0 kPa for the five individuals of each species.

To further clarify these differences among species, we calculated the frequency of F_d peak time over 30 days with daytime mean VPD > 1.0 kPa for representatives throughout all study periods (refer to Fig. 3). The results are presented in Fig. 5. It suggests that *R. pseudoacacia* has a very wide band of peak time distribution. A little more than 1/3 peaks appeared around 12 h (11:30–12:30) and about 1/3 peaks appeared around 15 h (14:30–15:30). This kind of diurnal pattern is accordingly referred to as a wide-peak type which implies active sap flow till late afternoon. In *Q. liaotungensis* the peaks concentrated at around 10:30, with more than 50% being at 9:30–11:00. *A. sibirica* showed relatively late peaks at around 12:30 with more than 50% appearing at 11:30–13:00. Therefore, the sensitivity of stomatal response to ambient air humidity can be sorted in an order of *R. pseudoacacia* < *A. sibirica* < *Q. liaotungensis*.

3.3. Variations in the diurnal courses of crown and leaf conductance

Fig. 6 shows diurnal courses of estimated relative crown conductance for the three species and measured leaf stomatal conductance for two species (*A. sibirica* was not measured for several reasons).

All the three species showed rapid rising and declining of crown conductance in morning hours and then kept low levels in the afternoon. This suggests that all the species regulate their conductance in response to high VPD. However, *Q. liaotungensis* reached its maximum earlier than the other two species and was followed by a steep decline. By midday time the crown conductance in this species had reduced to a level lower than that at early morning (e.g. at 6:30). The other two species showed gradual declines after peaks and maintained their conductance at or above the levels at early morning.

Measurements of intact canopy leaves yielded information approximately identical to the abovementioned results. *R. pseudoacacia* peaked its stomatal conductance at 8:30 and was followed by gradual declines. In contrast, *Q. liaotungensis* showed its highest stomatal conductance at 6:30 and reduced to low levels by 8:30. Midday depression of stomatal conductance was clearly shown in *Q. liaotungensis*. These characteristics support the suggestion for higher sensitivity of stomatal response to VPD in *Q. liaotungensis* than in the other two species.

### 3.4. Effects of rainfall on the environmental response pattern of sap flow

To further elucidate the response patterns of F_d to atmospheric factors for each species under different soil water conditions, data sets of normalized F_d vs. R_s, VPD, and VT were analyzed for the pre- and post-rainfall periods in June, respectively (Fig. 7). To prevent the influence of hysteresis between F_d and the environmental factors, only data sets collected in the morning hours were used in each analysis, with those after the daily peak of each environmental factor being excluded. Generally, the results reflected the positive correlations between normalized F_d and each atmospheric factor during the first half of daytime (refer to Fig. 4). Linear correlations between normalized F_d and R_s were obtained at levels of $R^2 > 0.88$ in *R. pseudoacacia* and *A. sibirica*, reflecting low hysteresis between the two indices and relatively late appearance of F_d peak time in these species (Fig. 7, graphs on the left, curves not shown). The normalized F_d–R_s data sets for *Q. liaotungensis* and normalized F_d–VPD data sets for all the species showed saturation at high R_s and VPD. Previous researchers tended to analyze the relationship between sap flux and VPD by using the following exponential saturation function (e.g. Ewers et al., 2002; Ewers et al., 2007; Kumagai et al., 2008):

$$Y = a(1 - \exp(-bX)) \tag{4}$$

where a and b are fitting parameters, and Y and X are corresponding variables. In this study, we found the normalized F_d–VT data sets more significantly fitted such curves (Fig. 7, only normalized F_d–VT curves were shown). In addition, it was also shown that the data sets for *R. pseudoacacia* clearly separated into pre- and post-rainfall groups, suggesting a high sensitivity of this species to soil water changes.

While rainfall resulted in accelerated increases in normalized F_d in response to rising VT, variations among species were revealed from the regression curves. Table 2 summarized analysis reports for the normalized F_d–VT regression fitting and related significance tests. Large difference in each coefficient (parameters a or b) between pre- and post-rainfall periods in *R. pseudoacacia* suggests that the transpiration process is sensitive to soil moisture conditions. In contrast, the other two species showed less difference in the regression parameters between pre- and post-rainfall regression curves, suggesting less amplitude in the response of transpiration to soil drought.

According to Oren et al. (1996), the hydraulic conductance from soil to atmosphere can be estimated from the slope of the F_d–VPD relationship through the origin. A steep slope in the relationship
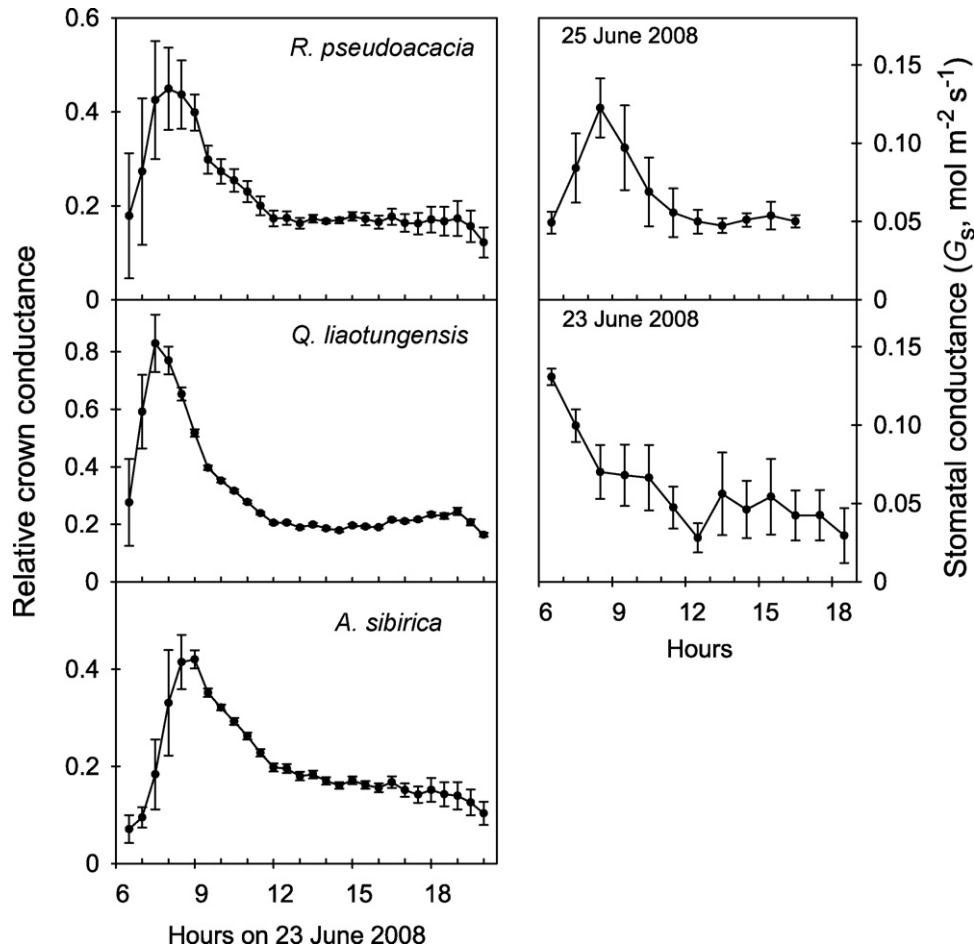
Fig. 6. Daytime courses of relative crown conductance and stomatal conductance (G_s). Relative crown conductance (left graphs) was estimated by dividing normalized F_d by VPD and was presented as mean ± SE for five replicate trees. G_s (right graphs) was measured data (mean ± SE) from three sample trees in each of the two species. G_s measurements for *R. pseudoacacia* were conducted on 25 June and stopped at 16:30 when the sky clouded over.

indicates a high conductance. This is consistent with what has been revealed by the model coefficient (parameter *b*). The characteristic of relatively high values for parameter *b* in *Q. liaotungensis* suggests that F_d values tend to reach their saturation level early at low VT values resulting from early stomatal closure. Relatively large difference in parameter *b* in *R. pseudoacacia* implies larger change of hydraulic conductance between pre- and post-rainfall periods.

Shallow distribution of root systems may also be a reason for sensitive responses to soil moisture recovery (Kume et al., 2007). However, a preliminary survey of fine root distribution along soil profiles in the present site showed that both *Q. liaotungensis* and *R. pseudoacacia* tend to concentrate their fine roots in the upper 50 cm horizon, though the fine root mass from *Q. liaotungensis* trees was more than that from *R. pseudoacacia* trees (Shi et al., unpublished data). Extensive investigation of the root systems is needed to clarify their difference and possible contribution to water use strategies among these species.

3.5. Sapflow changes over the three months and in response to temporary water recharge from rainfall

As F_d reaches a relatively static level at high VPD (Fig. 7), the mean normalized F_d values covering the data sets at VPD ≥ 2.0 kPa were calculated for each of the six phases over the three months (Fig. 8). This was expected to show the average maximum level of normalized F_d at a given phenological stage and soil moisture condition. Overall, F_d decreased throughout the three measure-

ment periods from June to August, corresponding to decreasing soil moisture conditions.

The general reduction of F_d may also come from the growth status of a species. For example, the fruits of *A. sibirica* should have been a carbon sink and related to active photosynthesis and transpiration during June and early July. Leaf loss was observed for *R. pseudoacacia* in late July and August, probably as a result of soil drought. This might be one of the strategies to reduce water consumption for that species. Investigations with seedlings also revealed that *R. pseudoacacia* tends to drop leaves in response to soil moisture stress (Hara et al., 2008).

There was a general increase in maximum normalized F_d in response to the rainfall events in each month, though the difference observed in July was not significant for most of the species, probably because of the small quantity of rainfall. Large increases were observed in *R. pseudoacacia* after the June and August rainfalls. The result was consistent with the suggestion of a high sensitivity of this species to soil moisture conditions.

In a comparative study on natural and planted forests in South America, it was found that the daily peak of sap flow in native species occurred much earlier than in exotic species, and native species showed saturation responses of F_d at lower VPD values (Fernández et al., 2009). These authors characterized the exotic Douglas fir as having higher water use with lower sensitivity to VPD (Fernández et al., 2009; Gyenge et al., 2008). Similar studies in Europe revealed that more adaptive birch trees maintained their common daily pattern of sap flow better than less adap-
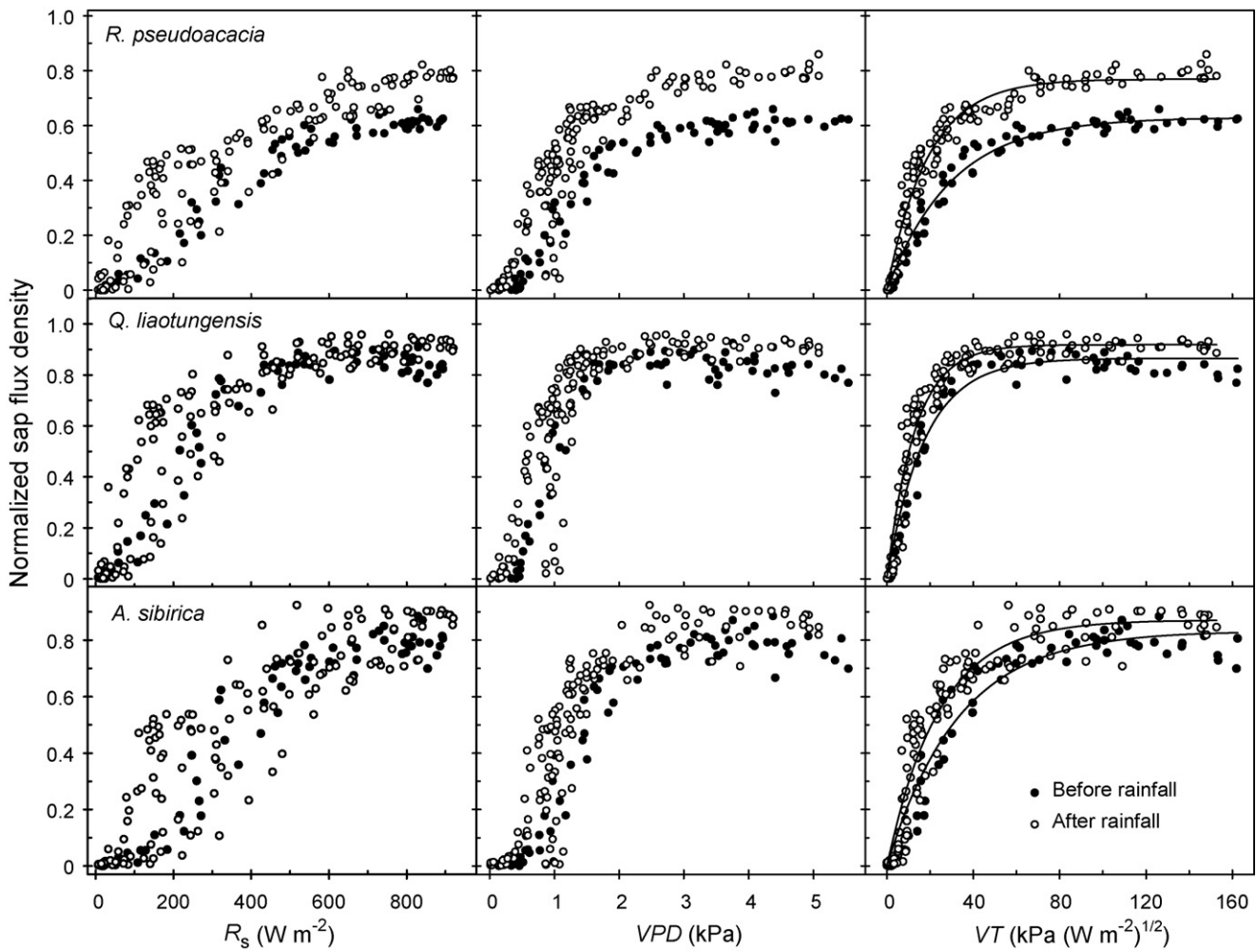
Fig. 7. Normalized F_d in relation to R_s (left column), VPD (middle column), and variable of transpiration (VT, right column) in the morning hours of pre- and post-rainfall days in June, respectively. Exponential saturation curves were well fitted to all normalized F_d–VT data sets (refer to Table 2).

tive spruce trees in an extreme drought summer (Gartner et al., 2009), and less drought-sensitive species of ash, hornbeam and little-leaf linden showed a lower reduction in F_d with decreasing soil water content and higher sensitivity to VPD than species sensitive to soil drought (Köcher et al., 2009). Only Hölscher et al. (2005) failed to confirm a correlation between drought sensitivity and the relative reduction in sap flow in dry periods. Our results agreed that indigenous species are less sensitive to tempo-

rally changes in soil water conditions than the fast-growing exotic species.

As an indigenous species, *A. sibirica* showed similar characteristics to *Q. liaotungensis* in their relative small amplitude in sap flow subjected to rainfall events, implying high adaptability to possible soil water deficiency. However, experiments with seedlings suggest that this species has some characteristics similar to *R. pseudoacacia*, such as high specific leaf area and large amount of water use with

Table 2
Results of regression analyses for normalized F_d vs. VT in Fig. 6.

Species	Before rainfall	After rainfall	Difference between coefficients
R. pseudoacacia	$a = 0.630$	$a = 0.770$	$P < 0.001$
	$b = 0.033$	$b = 0.053$	$P < 0.001$
	$R^2 = 0.9768$	$R^2 = 0.9597$	
	$P < 0.0001$	$P < 0.0001$	
Q. liaotungensis	$a = 0.865$	$a = 0.919$	$P < 0.05$
	$b = 0.057$	$b = 0.077$	$P < 0.01$
	$R^2 = 0.9601$	$R^2 = 0.9495$	
	$P < 0.0001$	$P < 0.0001$	
A. sibirica	$a = 0.833$	$a = 0.871$	Not significant
	$b = 0.030$	$b = 0.041$	$P < 0.01$
	$R^2 = 0.9484$	$R^2 = 0.9207$	
	$P < 0.0001$	$P < 0.0001$	

The data sets of normalized F_d and VT covered pre- and post-rainfall periods in June, respectively. Equation $Y = a(1 - \exp(-bX))$ was well fitted ($P < 0.0001$) to each data set. Significance for regression analyses and differences in coefficients between pre- and post-rainfall periods was checked using *t*-test.
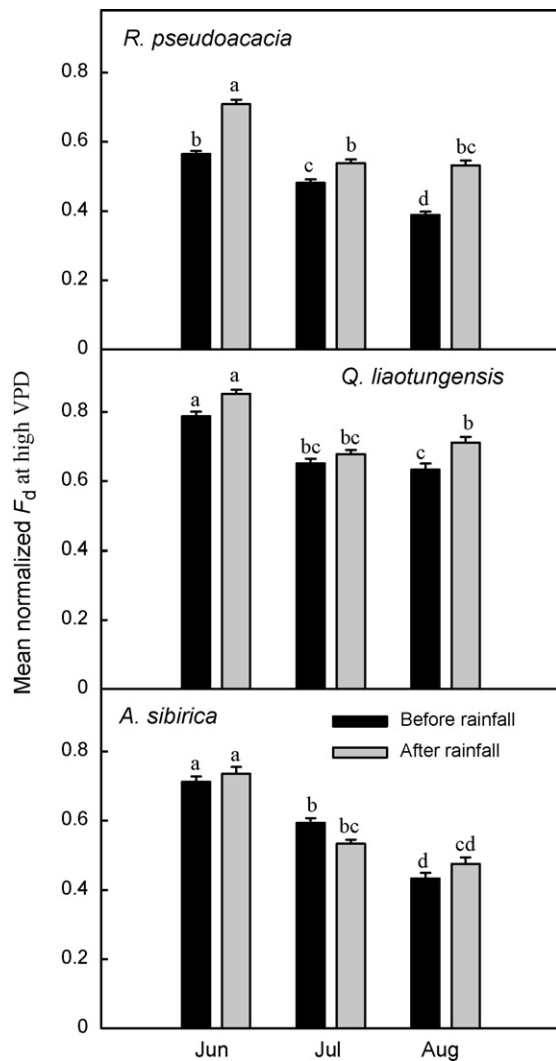
Fig. 8. Normalized F_d averaged for the data sets at VPD ≥ 2.0 kPa during each pre- and post-rainfall period over the three months, respectively. Error bars represent standard errors (n ranged 45–103). Means without common letters are significantly different at $P < 0.05$ according to Scheffe's test for multiple comparisons.

respect to total leaf area or biomass (Yan et al., 2010). These findings also support the results in the present study that *A. sibirica* has lower sensitivity of stomatal regulation in response to increasing VPD than *Q. liaotungensis*.

4. Conclusions

In semiarid regions with a dry atmosphere and frequent soil drought, each tree species needs to manage its water use to cope with the environmental stress. Species vary in water use strategy and thus contribute to different successional phases or structural and functional components of a forest stand. This study showed differences in sapflow characteristics, not only between exotic and native species but also between the two native species. VPD, R_s, and soil moisture had varying influences on F_d in these species. Generally, exponential saturation curves could be applied to each data set for normalized F_d and VPD. Decline of normalized F_d at high VPD values appeared in the instantaneous normalized F_d–VPD relationships (half-hourly means), suggesting a stomatal regulation of transpiration (Pataki et al., 2000). Normalized F_d was better explained by an exponential saturation with the integrated index VT.

From species differences in model coefficients, the three investigated species can be characterized as different types with contrasting drought sensitivity. The exotic species of *R. pseudoacacia* belongs to a drought-sensitive type as sap flow in this species is more affected by soil drought. The two indigenous species can be categorized into a drought-insensitive type as they manage the water supply under both drought and wet conditions. However, in contrast to *Q. liaotungensis* which showed early responses to VPD, *A. sibirica* showed less sensitivity to atmospheric conditions. *A. sibirica* should not be as conservative as *Q. liaotungensis* in water use in this semiarid region. Different patterns of diurnal normalized F_d change for the species reflected their different sensitivity to VPD.

All species showed acceleration in sap flow following rainfall. However, the drought-sensitive type of *R. pseudoacacia* showed higher sapflow increases in response to rainfall. The results revealed differences in water use strategy between indigenous and exotic species in the region. Furthermore, difference between the two indigenous species is also detected. *Q. liaotungensis* tends to use water more conservatively, whereas *R. pseudoacacia* may transpire water actively as long as it is supplied. The results may have implications for evaluating water use by different forest stands, creating regional hydrological models, and selecting sustainable reforestation species. Variations in water use and growth between wet and dry years and at different ages need further investigation to understand the long-term hydrological regime of these species.

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