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Water use strategies of a young *Eucalyptus urophylla* forest in response to seasonal change of climatic factors in South China

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Abstract

To depict the wet (April with a soil water content, SWC, of 37 %) and dry (October with a SWC of 24.8 %) seasonal changes in the water use and physiological response of a *Eucalyptus urophylla* plantation in subtropical South China characterized by monsoon climate, the whole-year (June 2012 to May 2013) transpiration of *E. urophylla* was monitored using the TDP method. Daily transpiration (E_T) in October averaged $5.7 \pm 2.9\,\mathrm{kg\,d^{-1}}$ and was 58.0 % higher than that in April ($3.6 \pm 2.3\,\mathrm{kg\,d^{-1}}$). The difference is consistent with that of the radiation and evaporative demand of the two months, while the nocturnal transpiration ($E_{\text{T-NOC}}$) in the wet season ($0.18 \pm 0.021\,\mathrm{kg\,d^{-1}}$) was almost twice that in the dry season ($0.11 \pm 0.01\,\mathrm{kg\,d^{-1}}$). Trees displayed a higher stomatal conductance (G_S) (53.4–144.5 $\mathrm{mmol\,m^{-2}\,s^{-1}}$) in the wet season and a lower G_S (45.7–89.5 $\mathrm{mmol\,m^{-2}\,s^{-1}}$) in the dry season. The leaf-soil water potentials (Ψ_L) of the two months (April and October) were -0.62 ± 0.66 and -1.22 ± 0.10 MPa, respectively. A boundary line analysis demonstrated that the slight improvement in the G_S by SWC in wet season was offset by a significant decrease in D, and the slope of G_S sensitivity to D ($\mathrm{d}G_S/\mathrm{dln}D$) in response to $G_{S_{\mathrm{ref}}}$ (references G_S at $D = 1$ kPa) was affected by the variance of radiation instead of SWC. Specific hydraulic conductivity (k_s) of trees of different sizes decreased by 45.3–65.6 % from the wet to the dry season. Combining the decreased maximum reference G_S at $D = 1$ kPa ($G_{\text{Sref-max}}$) by 22.4 % with the constant max G_S (G_{Smax}) when $\Psi_L < -1.2$ MPa, we shed some light on the mechanism underlying the high water-use efficiency (WUE) of this *Eucalyptus* specie. With a slight change in $G_{\text{Sref-max}}$ and high sensitivity of k_s to decreasing Ψ_L, large trees used water more efficiently than small ones did. In addition, the $-m$ in the dry season (0.53 ± 0.007) was lower than that in the wet season (0.58 ± 0.01) due to the difference in the ratio of G_S to the boundary layer conductance (g_b) in the two months. The negative relationship between $-m$ (except when light is limited) and Q proved to be a plastic response to environmental changes for *E. urophylla* but did not change with decreased k_s as expected.

1 Introduction

Climate change resulting from global warming is gradually threatening tropical and subtropical forest communities in a variety of ways, one of which is the increasing frequency of severe droughts that are caused by changes in the precipitation pattern according to the IPCC's report (Davidson et al., 2012). Over the past 50 years, China has experienced significant changes in annual and seasonal precipitation (Zhai et al., 2005). Zhou et al. (2011) noted that with increasing air temperatures in southern China since 1980, rainfall patterns have shifted to more severe storms during the wet season, more rain-free days and fewer days of light rain, even though the total rainfall did not change significantly. The direct effect of decreased rain events is the increased vapor pressure deficit, which further induces more transpiration and soil evaporation. As a result, the soil moisture during the dry season has shown a significant decrease.

Tropical forests may not be resilient against climate change in the long term, primarily due to predicted reductions in rainfall, drought-induced excessive water loss and ecosystem disturbances (Zhou et al., 2013), thus decreasing forest productivity, increasing tree mortality, and decreasing forest biomass carbon sinks (Chaves et al., 2002). In planted forests, trees are more vulnerable under severe environmental stress because of their weaker ecological resilience (Bleby et al., 2012). *Eucalyptus* is the most planted tree genus in the world (Teketay et al., 2000) and has become a major economic resource in the southern provinces of China. The coverage of this species is expanding rapidly and has doubled in the past decade (Shi et al., 2012).

As reported, phenotypically "plastic" exotic species such as *Eucalyptus* are likely to develop traits that are hydraulically compatible with their soil environment from a young age and not likely to remain fixed as environmental conditions change (Bleby et al., 2012). These species respond to environmental feedback on hydraulic development such that older and taller trees may have substantially different hydraulic and physiological traits compared to their younger and smaller counterparts. This type of "transformation" plays an important role in tree robustness. Physiological regulations must also be considered with the changing and stressful environment, consisting of the resilience aspect at the single-tree level. Stomatal movement is the main physiological mechanism that controls gas exchange in terrestrial plants. Under light-saturating conditions and a high vapor pressure deficit (D), most plants reduce stomatal conductance (G_S) to avoid dehydrative damage by limiting the rate of water loss and the development of a potentially impairing low leaf water potential (Ψ_L) (Meinzer et al., 1993). The absence of stomatal regulation would cause excessive xylem cavitation and a failure of water transport (Cochard et al., 1996; Lu et al., 1996). However, stomatal regulation is typically coordinated with hydraulic conductance, which gradually decreases with aggravated water access limitation in the soil. Understanding the mechanistic responses of trees to low water availability and drought is essential to accurately incorporate these mechanisms into process-based ecophysiological models and global vegetation models (McDowell, 2011).

Trees of different sizes usually respond to soil drought-induced water stress in different ways due to the varied hydraulic structure (Forrester, 2015). To our knowledge, small trees have lower overall water loss rates at both the leaf and canopy levels and a greater sensitivity of water loss in response to water stress (increasing D or decreasing leaf water potential) than large trees (Dawson, 1996) and therefore have an advantage under drought conditions. Larger trees usually have a deeper root system for acquiring more available soil water, especially under drought conditions (Anderegg et al., 2012). In addition, the tree height, leaf area and sapwood area are in allometric relation with tree size in different ways, thereby changing the hydraulic properties when trees grow larger to adapt to the environment (Schäfer et al., 2000). This deviated physiological response had been intensely debated for many years and might be associated with species, ages, nutrient, climates, etc. (Binkley et al., 2013; Aranda et al., 2012). To shed light on the abovementioned effects, the impact of tree size needs to be considered when evaluating the effects of decreased water availability on tree growth (Feichtinger et al., 2014).

By reducing G_S to water vapor, plants minimize water loss and maintain the hydration of plant cells as D increases under conditions of low water availability. Thus, the magnitude of G_S reflects the drought intensity. For example, Medrano et al. (2002) observed a common response pattern that was species-and condition-dependent when G_S was light saturated. However, in addition to the regulation of stomatal aperture, the stomata must react rapidly to avoid excessive water loss in response to high transpiration demand under drought. The sensitivity of stomata to D has been accurately described using empirical relationships as the slope between G_S and ln (D) (Oren et al., 1999) and is closely related to the magnitude of G_S at $D = 1.0$ kPa (G_{Sref}). The stomatal sensitivity to D is linearly proportional to G_{Sref} (−0.6) for isotonic plants that are able to maintain a constant minimum leaf water potential (Ψ_{leaf}) (Pou et al., 2012). However, few studies have been conducted to explore the response of stomatal sensitivity to D in seasonal drought (Naithani et al., 2012). The hydraulic architecture of plants plays a vital role in the G_S response to changing leaf hydration (Sperry et al., 2002). In addition, because the decrease in G_S is usually accompanied by a change in hydraulic conductance, a better understanding of the coordination between hydraulic architecture and stomatal responses to changing D will provide insight into the diurnal and seasonal growth patterns of plants (Ocheltree et al., 2014).

Most of the research about *E. urophylla* in the subtropical monsoon climate of South China is related to the productivity (Du et al., 2012; Simpson et al., 2003), wood property (Jiang et al., 2004; Luo et al., 2012, 2013), and disease (Zhou et al., 2008) considering of the economic aspects, while the plasticity in physiological response and function of tree species remain poorly understood. Our interest is in determining how the young planted *Eucalyptus* forest in South China will function under enhanced drought stress and varied atmosphere conditions. We hypothesized that trees growing in the dry season would respond more sensitively to climatic factors (especially referred to D) and have less-efficient water-use traits (e.g., weak transpiration rates, small stomatal conductance) but greater sensitivity to soil–water deficits and high evaporative demand than in the wet season. More specifically, we seek to answer the following key questions: (1) will the soil drought alter the water use of *E. urophylla*? (2) How will the hydraulic and physiological traits of trees respond following a seasonal climate change? (3) Will the small and large trees respond differently to seasonal drought?

2 Materials and methods

2.1 Study site and plant material

This study was conducted at the Huangmian state forest farm (24°66′ N, 109°87′ E) approximately 60 km southwest of Guilin city in South China. This farm is planted with *Eucalyptus urophylla* for lumber and pulp production. The plantation area was 32 000 ha in 2010. All of the reported measurements took place in an *E. urophylla* stand 3–5 years old on a hill with an inclination of approximately 30° facing southwest. The forest density was 1375 trees ha^{-1}. The soil of this forest is characterized with heavy loam. This area is characterized by a low subtropical monsoon climate with an annual precipitation ranging from 1750 to 2000 mm and an average annual temperature of 19 °C. Although the rainfall is abundant, it is unevenly distributed through the year, producing wet (March to September) and dry (October to February of the next year) seasons. The measurement was carried out from June 2012 to May 2013. Fifteen trees of *E. urophylla* with an average height of 11.5 m and a mean diameter at breast height (DBH) of 10.1 cm were chosen for our study. An observation tower 23 m high was erected within the plantation providing access to the canopy of the *E. urophylla* stand.

2.2 Sap flux and environmental variable measurements

The sap flow density (F_d, $g\,m^{-2}\,s^{-1}$) of the 15 sample trees was monitored with Granier-type sensors (e.g., Granier, 1987). Details about the sensors and installation can be found in Zhu et al. (2015). The F_d of *E. urophylla* is assumed to be isotropic in terms of the dependence of leaf transpiration on crown illuminance (Burgess and

Dawson, 2008). An implicit assumption for sap flow measurement is that the variability in xylem flux within a tree is smaller than that among trees. If not, F_d may be used to estimate transpiration only after it is converted to a spatially weighted mean flux. Zhou et al. (2002) conducted a survey of the radial variation in the sap flow density for 3–4 year-old *E. urophylla* using the heat pulse method. The variation in sapwood depth from the outmost surface of the stem can be expressed as $y = ax^3 + bx^2 + cx + d$, where x is the ratio of the sensor depth to the radial sapwood thickness. We integrated the results of two plots in their study and obtained the equation $y = 4.33x^3 - 8.31x^2 + 4.07x + 0.52$.

A meteorological station was equipped on the top of the tower. The photosynthetic photon flux density (Q_0, $\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$), temperature ($T$, °C), relative humidity (RH, %), and wind speed (u, $\text{m}\,\text{s}^{-1}$) were measured simultaneously with the sap flow measurement (Zhu et al., 2015). The rainfall data during the study period of Guilin were obtained from the China Metrological Data Sharing Service System (http://www.escience.gov.cn/metdata/page/index.html). The soil water content (SWC, $\text{m}^3\,\text{m}^{-3}$) was monitored with three soil water probes (SM300, UK) that were buried 30 cm under the ground surface.

2.3 Tree morphological features

Allometry in plants has been conceptualized as a proportional- or ratio-driven process ("partitioning") (Weiner, 2004). To obtain the allocation information, the sap wood depth (d_s) was measured from trees that were lumbered for wood pulp during the period of rotation cutting. We harvested 7 sample trees that were grown close to the experimental plot for biomass determination. The DBH was measured with diameter tape. The tree height (h) was measured with the tape draped from the top of the tower, and crown of sampled trees for sap flow measurements were aligned with tape to obtain the reading of the tree height. The total leaf area (A_L) was measured with a portable leaf area meter (Licor-3000, USA). The sapwood depth was visually distinguished from heartwood by changed color at the boundary of the two parts on the cores before the sapwood area was estimated (A_S). Because the DBH of the harvested trees ranged from 6.6 to 11.1 cm, while those for sap flow measurements ranged from 8.5 to 16.06 cm, we referred to Zhou et al.'s study (2004) to obtain biomass information of *E. urophylla* trees with a DBH greater than 11.1 cm. We used the fitted relationship between DBH and A_S and the A_L from the harvested trees together with Zhou et al.'s study (2004) to scale up transpiration based on sap flow measurement. Because *Eucalyptus* leaves are characteristically thick, tough and long lived and are generally retained throughout a growing season and often longer (Reich et al., 1999; Ashton, 1975; Cannell, 1989), these relationships do not account for the seasonal dynamics in leaf area.

2.4 Hydraulic properties of the stem xylem

The physical limitations on water flow through sapwood xylem influence stomatal behavior and transpiration in trees, which can be expressed based on Darcy's law as:

$$G_\mathrm{Sref} \propto E_\mathrm{L} = k_\mathrm{s}(\Delta\Psi - 0.01h)\frac{A_\mathrm{S}}{A_\mathrm{L}h} = k_\mathrm{s}H_\mathrm{p} \tag{1}$$

where the transpirational demand is proportional to the G_S times the vapor pressure deficit (D). The hydraulic conductivity (k_S) of sapwood as a function of water potential differences between soil and leaf ($\Delta\Psi$) and the hydraulic properties of trees (H_p) represent the interaction effect of the $\Delta\Psi$, h and Huber values.

To estimate the wet-dry seasonal variation in $\Delta\Psi$, the leaf water potentials at pre-dawn ($\Psi_\text{pre-dawn}$) and midday (Ψ_midday) were measured for sunny days in April (5 days) and October (4 days). Five trees were selected for the experiment. The measurements were averaged from three replicate shoots that were sampled from the mid-crown (most of the leaves were fully expanded) per tree. We assumed $\Psi_\text{pre-dawn}$ to be a substitute for the water potential in the soil (Ψ_S) (Kim et al., 2008; Bleby et al., 2012) because soil moisture remain unchanged throughout the whole sunny day. Therefore, the $\Delta\Psi$ was calculated as the difference between Ψ_S and Ψ_midday.

2.5 Canopy stomatal conductance

In the forests where transpiration is well-coupled with atmosphere conditions, the mean stomatal conductance can be calculated based on a simplified equation (Köstner et al., 1992) that is derived from Whitehead and Jarvis (1981) assuming that the F_d scaled by $A_\mathrm{S}/A_\mathrm{L}$ is equal to the transpiration rate per unit of leaf area (E_L). The mean stomatal conductance for individual trees, G_Si, can be calculated as:

$$G_\mathrm{Si} = (G_\mathrm{V} T_\mathrm{a} \rho E_\mathrm{L})/D \qquad (2)$$

where E_L is whole-tree transpiration per unit leaf area ($\mathrm{g\,m^{-2}\,s^{-1}}$), G_V is the universal gas constant adjusted for water vapor ($0.462\,\mathrm{m^3\,kPa\,K^{-1}\,kg^{-1}}$), T_a is the air temperature (K), ρ is the density of water ($998\,\mathrm{kg\,m^{-3}}$), and D is in kPa. G_Si is in units of $\mathrm{mmol\,m^{-2}\,s^{-1}}$ (Monteith and Unsworth, 2013).

This approach is based on the assumption that the contribution of water that is stored in the trees above the sensors to transpiration is negligible or explicitly accounted for. If the contribution is not negligible, it can be accounted for by determining the time lags between water uptake and an appropriate driving variable (Köstner et al., 1992; Granier and Loustau, 1994). The forest had an LAI of $1.68 \pm 0.28\,\mathrm{m^2\,m^{-2}}$ and did not show significant seasonal changes ($p = 0.78$) (Zhu et al., 2015). Therefore, G_Si calculation is not subjected to errors that are caused by leaf area dynamics. Thus, G_Si was estimated after (1) performing a cross-correlation analysis between D and F_d, and using the time lag to infer a time-corrected F_d and (2) filtering out data for $D < 0.6\,\mathrm{kPa}$ in the hours of early morning and late afternoon (Oren et al., 1998).

Many non-linear functions and models have been used to analyze the effect of environmental variables on G_S (Monteith, 1995; Dang et al., 1997; Martin et al., 1997). Granier et al. (1996) proposed that stomatal sensitivity is proportional to the magnitude of G_S at low D ($D = 1\,\mathrm{kPa}$) when soil moisture is not limiting, which was expressed as:

$$G_\mathrm{S} = G_\mathrm{Sref} - m \ln D \qquad (3)$$

where G_{Sref} is the intercept (i.e., the value of G_{S} at $D = 1\,\mathrm{kPa}$ in a log-linear relationship), and $-m$ is the slope of the regression fit representing stomatal sensitivity to D (i.e., $\mathrm{d}G_{\mathrm{S}} / \mathrm{d}\ln D$). Oren et al. (1999) demonstrated that m is approximately 0.6 by analyzing data from a variety of sources that were acquired with both porometric and sap flux estimates of G_{S}. In this study, the $-m$ and G_{Sref} for *E. urophylla* in the wet and dry seasons will be estimated to determine the response of G_{S} to drought.

The interaction between $\Delta\Psi$, G_{S} and A_{L} in response to D at steady state (and infinite boundary layer conductance, g_{bl}) can be described by the following function (modified from Sperry, 1995):

$$k_{\Psi} = G_{\mathrm{S}} \times D \times \frac{A_{\mathrm{L}}}{\Delta\Psi} \tag{4}$$

where k_{Ψ} is the whole-tree hydraulic conductance.

2.6 Data analysis

Statistical analyses were performed using SAS (version 9.2, SAS Institute, Cary, NC). A multiple regression analysis was conducted to determine the hydraulic architecture effect on tree water use in the wet and dry seasons. A paired *t* test with SAS was used to compare the differences in environmental and plant physiological changes between wet and dry seasons. A boundary-line analysis was conducted in Excel (version 2010, Microsoft Office Excel) to set up the relationship between environmental conditions and maximal canopy stomatal conductance, and Origin pro (version 8.6, Origin Lab, USA) was used to draw all of the graphs in this paper.

3 Results

3.1 Water and atmospheric conditions

The precipitation (P) in the research site (Huangmian) totaled 2167.6 mm from June 2012 to May 2013, which was slightly higher than the annual mean (1900–2000 mm). There was a significant monthly variation from the minimum of 26.2 mm in January to the maximum of 487 mm in June. The water input was mainly contributed by precipitation in late spring and early summer (i.e., from April to June), which accounted for 55.4 % of the whole year, while that from October to February was 16 % and is typically defined as the dry season in South China. As a whole, the rainfall in Huangmian followed a typical pattern in South China (much more water input in Spring and Summer, relatively drier in autumn and winter). The seasonal change in the soil water content (SWC, $m^3\,m^{-3}$) in the forest was well correlated with that of rainfall (Fig. 1). The nonlinear curve fit between SWC and P indicated that SWC linearly increases with P when $P < 200$ mm and holds a constant value of 0.38 $m^3\,m^{-3}$ when $P > 200$ mm (Supplement Fig. S1), meaning that the soil was not saturated throughout most of the year except for the period from April to July.

The radiation (Q), evaporative demand (D) and soil water content (SWC) significantly changed from April to October. The SWC in October decreased 32.6 % from April, revealing a significant difference in the soil water conditions between the wet and dry seasons. Variations in the two months were contributed by rain pulse four times in April and one time in October. The monthly average Q showed an inverse pattern with SWC, which was $154.2 \pm 109.4\ \mu mol\,m^{-2}\,s^{-1}$ in April and $283.7 \pm 108.6\ \mu mol\,m^{-2}\,s^{-1}$ in October. D was higher in October (1.07 ± 0.39 kPa) than in April (0.32 ± 0.28 kPa). The differences in the three environmental factors between the two seasons were significant ($p < 0.01$).

3.2 Tree water use in different seasons

A boundary line analysis of the relationship between F_d and Q was conducted, and the maximal F_d was derived from the exponential relationship (Fig. S2). The F_d of the 15 trees was $41.03 \pm 7.97\,\mathrm{g\,m^{-2}\,s^{-1}}$ and $38.82 \pm 13.16\,\mathrm{g\,m^{-2}\,s^{-1}}$ in the dry and wet seasons, respectively, implying a similar ability to transport water to the canopy. The tree size did not have any effect on F_d even though a weak negative relationship between DBH and F_d in the dry season ($R^2 = 0.19$, $p = 0.06$) was observed.

The annual stand E_T was 462.42 mm, and the E_T in October and April accounted for 12.24 and 6.57 %, respectively. The maximal (minimal) daily E_T of individual trees in the dry and wet seasons was $14.1 \pm 0.7\,\mathrm{kg\,d^{-1}}$ ($2.49 \pm 0.16\,\mathrm{kg\,d^{-1}}$) and $9.52 \pm 0.97\,\mathrm{kg\,d^{-1}}$ ($2.2 \pm 0.3\,\mathrm{kg\,d^{-1}}$), respectively. The daily transpiration (E_T) in October averaged $5.7 \pm 2.9\,\mathrm{kg\,d^{-1}}$ and was 58.0 % higher than that in April ($3.6 \pm 2.3\,\mathrm{kg\,d^{-1}}$) (Fig. 2a, $p < 0.01$). The greatest variance was observed for the tree of DBH = 8.5 cm, whose E_T in October increased by 185.1 % from April. In contrast, the E_T of the largest tree (DBH = 16.1 cm) increased by 48.5 %, lower than the mean value. The wet / dry ratio varied from 0.4 to 0.8 and slightly increased with the tree size ($R^2 = 0.03$), implying that the E_T of the larger trees was less sensitive to seasonal changes in environmental factors.

In our stand, the nocturnal transpiration ($E_\mathrm{T\text{-}NOC}$) was 0.18 ± 0.021 kg in April and 0.11 ± 0.01 kg in October, indicating its decrease with decreasing water supply (Fig. 2b, $p = 0.047$). This transpiration accounted for a proportion of daily E_T by 1.82 ± 0.45 % and 4.51 ± 1.34 % in October and April, respectively. However, the variances in $E_\mathrm{T\text{-}NOC}$ among individuals were much higher in April than in October, which mirrored a different sensitivity of trees responding to environmental changes at nighttime. The nocturnal sap flow ($E_\mathrm{T\text{-}NOC}$) also followed a linear relationship with tree size, but larger trees were much more sensitive to the environmental changes in April than in October. The ratio of $E_\mathrm{T\text{-}NOC}$ between the wet and dry seasons for different trees ranged from 0.6 to 2.7 and was positively related to the tree size ($R^2 = 0.39$), which was consistent with that of E_T.

The water potential at pre-dawn ($\Psi_{\text{pre-dawn}}$) was -0.24 ± 0.04 MPa and -0.21 ± 0.03 MPa in the dry and wet seasons ($p = 0.23$), respectively, and at pre-night ($\Psi_{\text{pre-night}}$) was -0.29 ± 0.02 and -0.31 ± 0.05 MPa. The water potential at noon (Ψ_{noon}) was -7.51 ± 2.32 and -14.55 ± 2.31 MPa in April and October ($p < 0.01$), respectively. None of the above values were significantly different among the 5 trees ($p > 0.05$). The water potential gradients at midday ($\Delta\Psi$) averaged -0.62 ± 0.66 (April) and -1.22 ± 0.10 MPa (October). Similar to the leaf water potential, $\Delta\Psi$ showed no significant variance among the five trees (ANOVA, $p = 0.14$ in April and $p = 0.25$ in October) or between the two months ($p = 0.33$). $\Delta\Psi$ was much higher in April than in October ($p < 0.01$), which was consistent with the seasonal pattern of E_T.

3.3 G_S and its sensitivity in response to vapor pressure deficit under different light conditions

A boundary line analysis of the relationship between D and G_S was performed in the dry (October) and wet (April) seasons. The datasets of G_S for each tree were classified by radiation (9 levels). The data at night ($Q_0 = 0$) were excluded because the plant physiological response in the night was much more complicated than that in the daytime (Oren et al., 2001). The relationship between the lnD and G_S of each small subset was linearly fitted, and the intercept and slope corresponded to the G_{sref} (G_S at $D = 1$ kPa) and sensitivity in response to D ($\mathrm{d}G_S / \mathrm{d}\ln D$, $\text{mmol}\,\text{m}^{-2}\,\text{s}^{-1}\,\text{kPa}^{-1}$), respectively (Oren et al., 1999). Then, the relationship between G_{Sref} and $-\mathrm{d}\ln D / \mathrm{d}G_S$ for the two months was fitted.

The G_{Sref} linearly increased with sensitivity in both the dry and wet seasons (Fig. 3). The $-m$ from the relationship was significantly different among the different light levels, ranging from 0.46–0.69 (dry season) and 0.48–0.82 (wet season). We also qualified the tree size effect on $-m$ in both seasons; the $-m$ at different light levels did not change significantly with the tree size. The G_{Sref} under different light conditions was normalized by the value at the maximum Q_0 of each tree in both seasons, and the relationship between the G_{Sref} and mean Q_0 at that level for all of the trees was fitted with an exponential function expressed as:

$$G_{\mathrm{Sref}} = a \times (1 - \exp(-b \times Q_0)) \tag{5}$$

where a refers to the maximum dependent variable. As a result, the normalized G_{Sref} of all of the trees increased rapidly when Q_0 was low and gradually saturated at the maximum (Fig. 4a). The normalized G_{Sref} reached 90 % of the maximum (G_{S90}) when Q_0 was 287.8 and 167.1 $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$ in the dry and wet seasons, respectively, indicating that the G_{Sref} in the wet season was more sensitive to light, resulting in a lower saturation point than that in the dry season ($p < 0.01$). The effect of Q_0 on $-m$ was also qualified in both seasons (Fig. 4b). When light was limited, $-m$ gradually increased and then decreased when Q_0 became strong enough (ANOVA, Duncan, $p < 0.01$). Of note, the $-m$ in the wet season (0.58 ± 0.01) was higher than that in the dry season (0.53 ± 0.007) ($p = 0.038$) when all of the data were considered, but it was not significant when the data from the low-light conditions (first two light levels) were removed.

The max G_{S} ($G_{\mathrm{Sref\text{-}max}}$) of each tree was obtained from the exponential function (Eq. 5, corresponding to a) before being normalized. The $G_{\mathrm{Sref\text{-}max}}$ was fitted to the tree size (Fig. 5). The $G_{\mathrm{Sref\text{-}max}}$ of small trees (< 9 cm) in the wet season increased rapidly with DBH, then decreased before approaching a constant value, while no clear relationship between the $G_{\mathrm{sref\text{-}max}}$ and tree size was observed in the dry season. The $G_{\mathrm{Sref\text{-}max}}$ averaged $68.8 \pm 14.4\ \mathrm{mmol\,m^{-2}\,s^{-1}}$ and $88.6 \pm 25.1\ \mathrm{mmol\,m^{-2}\,s^{-1}}$ in the dry and wet seasons, respectively, and the latter was significantly higher ($p < 0.01$). The $G_{\mathrm{Sref\text{-}max}}$ ratio of dry to wet ranged from 0.58 to 1.26 (0.81 on average), decreased rapidly when DBH < 9 cm and stabilized after DBH > 9 cm (Fig. 5).

To depict the maximal potential water use of *E. urophylla* under a given soil moisture, the boundary analysis that was performed above for the dry and wet seasons was applied at different light levels (Fig. S3). All of the data during the monitoring period (June 2012 to May 2013) were considered in the analysis. SWC was evenly divided into five intervals from 20 to 45 % and then classified by Q_0 as above. The slope for the five soil moisture levels ranging from 0.50 to 0.59 was weakly improved by SWC

($p = 0.15$). The $G_{\mathrm{Sref\text{-}max}}$ of each tree also slightly improved by SWC but was not significant ($p > 0.05$), as some of these values were significantly improved or suppressed by SWC when each tree was fitted, while the others were weakly related. The relationship between $-m$ and mean Q_0 was also fitted and still independent from SWC ($p > 0.05$).

3.4 Hydraulic architectures and sap wood conductivity

To determine the effect of the tree hydraulic structure on the plant physiological response, the integrative effects of Huber value, tree height and leaf water potential of the 15 trees on G_s were described using Eq. (1). The Huber value linearly increased with DBH (Fig. 6), while the decrease in the other components ($\Delta\Psi - 0.1h$, $1/h$) counteracted the positive effect and led to weakly changed hydraulic properties ($\mathrm{H_p}$). $\Delta\Psi - 0.1h$ and $1/h$ are known as the "voltage" and "conductance", respectively, between the root and leaf. However, the extent of compensation depends on the change in $\Delta\Psi$. The mean H_p in the dry season was significant higher than that in the wet season ($p = 0.002$, Paired t test, $n = 15$), and both were independent from tree size ($p > 0.05$).

Equation (1) was applied when $D = 1\,\mathrm{kPa}$ to evaluate the seasonal change in k_s (Fig. 7b). As a result, the k_s of both seasons was linearly fitted. The k_s in the wet season ($29.1 \pm 13.1\,\mathrm{mmol\,m^{-1}\,MPa^{-1}}$) was much higher than that in the dry season ($9.4 \pm 3.2\,\mathrm{mmol\,m^{-1}\,MPa^{-1}}$). In addition, large trees had a much higher seasonal variation in k_s ($p < 0.01$). As shown in Fig. 7b, the dry to wet ratio of k_s decreased rapidly with tree growth and maintained constant when $\mathrm{DBH} > 10\,\mathrm{cm}$.

4 Discussion

4.1 Water use of *E. urophylla*

From June 2012 to May 2013, the transpiration accumulated 462.42 mm ($1.26\,\mathrm{mm\,d^{-1}}$), accounting for 21.3 % of the total rainfall. This value was much lower as a young forest than that in other areas of the world. Transpiration rates in *Eucalyptus* forests range from 0.5 to 6.0 $\mathrm{mm\,d^{-1}}$, mostly from 2.0 to 4.0 $\mathrm{mm\,d^{-1}}$ (Cunningham et al., 2009; Yunusa et al., 2010; Mitchell et al., 2009; Benyon et al., 2006). Even the same species, *E. urophylla*, in a savanna in Venezuela transpired more water than in our study (2.3 $\mathrm{mm\,d^{-1}}$) (Herrera et al., 2012). In general, transpiration may reach maximum values when the canopy is completely closed (Shi et al., 2012). The relatively low LAI (1.68 ± 0.28) revealed a high-opening forest canopy in our study and might be the reason for low transpiration.

E_T was promoted during the drought period compared to that during the wet season. Meanwhile, a significant decrease in the soil water content (by 27.3 %) was observed from September to October. A boundary analysis with the partitioning of the multiple effects of D, Q_0 and SWC on stomatal conductance demonstrated that $G_\mathrm{Sref\text{-}max}$ was enhanced by weakly increased SWC for some trees but depressed for the other, and $-m$ was also maintained constant along soil moisture gradients under different light conditions (Fig. 4b). In agreement with our results, the reported higher transpiration for a *Eucalyptus miniata* in Australian savannas in the dry season also suggests that soil water availability is not limited during the extended dry season (O'Grady et al., 1999). A deep root system may explain the enhanced water during periods of decreased soil water content. *Eucalyptus* species have a high photosynthetic capacity and WUE (Whitehead and Beadle, 2004), which are attributed to the high growing speed of the root system under the ground. For example, fine roots have been observed down to a depth of 6 m in 1 year-old Brazilian eucalypt plantations (Christina et al., 2013). This observation implies that during a prolonged dry season, trees would obtain more water from the ground water with deep roots. Jarvis (1993) believed that trees in aerodynamically rough forests that are well coupled to the atmosphere continue their transpiration at the rate that is imposed by D under unlimited soil water availability. The promoted E_T in the dry season in our study can be explained by a low decoupling coefficient (0.10 ± 0.03, unpublished data) and an obvious increase in D by 234.4 % from April to October. However, this trend is not always the case under some other conditions. Zhou et al. (2004) reported a significantly decreased daily sap flux with decreased available soil water of *E. urophylla* plantation in the Nandu River watershed on the Leizhou Peninsula, Guangdong Province, China, where the atmospheric conditions are very similar to those in our study. These authors believed that the soil type produces uncertainty in this relationship.

Despite the unlimited transpiration in the dry season, the rapidly decreased SWC in our research site revealed the weak ability of soil to hold water. With a low LAI for *Eucalyptus* (Whitehead and Beadle, 2004), many studies demonstrated that plants under *Eucalyptus* trees are sparsely distributed in some small swales, resulting in a high evaporation of the surface ground (Campinhos Jr., 1999). Similar low species diversity was also observed in our stand. In addition, some litter on the ground enhanced the surface exposure. Combined with the prolonged transpiration, the indirect impact of *E. urophylla* on the regional water balance should not be ignored, especially in drought areas. To address the effect of transpiration on water balance, the water table level of *Eucalyptus grandis* hybrid plantations in Brazil was observed and found to decrease gradually before clear cutting 6 years after seeding and recover to the normal level 1–2 years after replanting (Almeida et al., 2007).

The nighttime sap flow is regarded as water recharge in the trunk and is vital for the plant water-use strategy, especially in a drought landscape (Fisher et al., 2007). The similar $\Psi_{\text{pre-night}}$ and $\Psi_{\text{pre-dawn}}$ in the dry and wet seasons revealed the same demands for water replenishment in the night. However, nocturnal sap flux ($E_{\text{T-NOC}}$) in the wet season ($0.18\pm0.021\,\text{kg}\,\text{d}^{-1}$) was almost twice that in the dry season ($0.11\pm0.01\,\text{kg}\,\text{d}^{-1}$). The fast growth of *E. urophylla* may contribute to this quantitative difference, as the stem capacitance increased from October 2012 to April 2013 (Bohrer et al., 2005; Phillips et al., 2009). However, few trees can double in size in half a year, especially for large trees. Thus, the difference in $E_{\text{T-NOC}}$ was inferred to be caused by leaf transpiration at nighttime. In fact, evidence was found by simultaneous leaf level gas exchange measurement and water potential measurement, demonstrating that stomatal conductance in April and October was 63.1 ± 31.0 and $33.6\pm5.0\,\text{mmol}\,\text{m}^{-2}\,\text{s}^{-1}$, respectively, when $Q_0 = 0$ after pre-night and before the pre-dawn. A new finding was reported that a subsequent increase in transpiration in the night 6 h after dusk was caused by the wood circadian clock regulation of G_S and F_d for *Eucalyptus grandis* (Resco de Dios et al., 2013). The authors concluded that the endogenous regulation of G_S is an important driver of nighttime water flux under natural environmental variability. We believe that *E. urophylla* tended to transpire water continually after sufficient water recharge, especially when water was available in the soil. The same conclusion was proposed across a diversity of ecosystems and woody plant species by various methods, and a variety of explanations were considered plausible for the mechanism (Dawson et al., 2007).

4.2 Stomatal regulation in response to the leaf water potential

Stomatal closure is usually treated as direct response to the change in leaf water potential as related closely to cell turgor (Martorell et al., 2014). A significant decrease (by 22.4 %, Fig. 5) in G_S was observed accompanying a two-fold increase in $\Delta\Psi$ in the dry season. According to Eq. (2), if G_S is constant, a 234.4 % increase in D will lead to the same proportional enhancement of E_L and E_T because the difference in T_a and A_L between the two months was not significant ($p > 0.05$). Thus, a 22.4 % decrease in G_S eventually led to a less increase in E_T and E_L by 159.5 %. The light-induced opening of stomata enhances leaf transpiration, which consequently decreases the leaf water potential and therefore transpires more water along the SPAC system (Whitehead, 1998; Lambers et al., 2008). Stomata are usually regarded as the key in the regulation of transpiration (Jarvis and McNaughton, 1986), while the role ofΨ_L has been less emphasized in most related studies (Aranda et al., 2005). In fact, the change in G_S is a response to altered Ψ_L (Hölttä and Sperry, 2014).

To understand the role of Ψ_L in the regulation of *E. urophylla* transpiration, we fitted the relationship between leaf water potential at noon and the corresponding G_{Smax} (normalized by the measurement on 19 April 2013) of 15 trees. G_{Smax} was positively related to Ψ_L when light was limited (Fig. 7a). According to the cell turgor theory, the change in

Ψ_L is derived from the G_S promoted water loss on the leaf (Dow and Bergmann, 2014). However, this value peaked and was maintained from −0.6 to −0.9 MPa for a while before a gradual decrease. This trend is consistent with the relationship between Ψ_L and G_S across 70 trees species (Klein, 2014). Of note, the stomata did not fully close when Ψ_L reached the minimum value when $\Psi_L = -1.6$ MPa. In addition, G_S of *Eucalyptus pauciflora* gradually decreased with Ψ_L when $\Psi_L > 1.0$ MPa (Martorell et al., 2014), while a stomatal closure of 25 % of the maximum remained when $\Psi_L = -1.6$ MPa according to the fitting line. This value was lower than our result (50–60 %, Fig. 7a). The twist of G_S from the max with decreasedΨ_L revealed the beginning of "plastic" adjustment to water loss, and the decreased slope of the fit curve indicated a less-sensitive G_S to Ψ_L. Klein et al. (2014) reported that the minimum (maximum) value of Ψ_L can reach −2.2 MPa (−1.0 MPa) when G_S decreased to 50 % of the max. This result implies lots of carbon assimilation for trees because less-sensitive stomata will take up more CO_2 and lose more water at the same time. The 50–60 % of G_{Smax} at −1.6 MPa indicates that *E. urophylla* was more likely to maintain a balance between gas exchange and water loss under a given leaf water potential.

4.3 Hydraulic conductivity and promoted water-use efficiency

A change in Ψ_L depends on the leaf water loss and water recharge by sap flow. Ψ_L decreases if water loss > water recharge. The stomata aperture showed less change when $\Psi_L < -1.2$ MPa. When Ψ_L decreased to −1.2 MPa in the dry season, k_s decreased by 45.3 to 65.6 % from the wet season along tree size ranks (Fig. 7a). The decreased Ψ_L indicated a failed water recharge by sap flow when G_S was maintained constant. Thus, k_s will continue to decrease when $\Psi_L < -1.2$ MPa to drive the change in Ψ_L. Such a water-use strategy may contribute to a high water-use efficiency for *E. urophylla*, especially under dry conditions because of a low water flux in the xylem and high gas exchange on the leaves. We found that G_S decreased by 22.4 % from the wet to dry seasons, while k_s decreased by 45.3 to 65.6 %, much higher than G_S. If the tree leaves in the wet and dry seasons have the same demand for CO_2, the WUE will also be higher in the dry season. This possibility had been demonstrated by some other studies, such that stable carbon isotopes in tree rings indicate an improved water-use efficiency and drought responses of a tropical dry forest tree species (Brienen et al., 2011). A large number of studies have demonstrated that moderate drought contributes to the high WUE of tree species of different ecosystems, including forest (Maseyk et al., 2011), farmland (Sharma et al., 2015), desert (Liu et al., 2012), etc. However, an increased water-use efficiency does not necessarily lead to enhanced tree growth under xeric and mesic conditions (Lévesque et al., 2014) because stomata may not react effectively under severe drought or limited soil water, resulting in the failure of hydraulic compensation and even death (Pita et al., 2003).

Here, we tried to determine the effect of tree size on plant physiology as proposed in the "Introduction". The ratio of dry / wet k_s decreases from 0.55 to 0.30 with increased tree size. Because Ψ_L tended to remain constant when $\Psi_\mathrm{L} < -1.2\,\mathrm{MPa}$, the greater depression of k_s for large trees indicated a higher WUE according to the above discussion. Otto et al. (2014) argued that dominant clonal *Eucalyptus grandis* × *urophylla* trees use water more efficiently; however, the underlying mechanisms that are responsible for higher WUE are unclear. We simulated the relationship between Ψ_L and percentage loss of hydraulic conductivity (PLC) for large and small trees, and a more sensitive k_s was observed for the dominant tree (Fig. 8). These results seem to shed some light on the mechanisms under the high WUE of the dominant trees.

It was also implied that large trees are more vulnerable in the face of drought stress. An increased Huber value as trees grew in our study revealed the demands for enhancing the ability of water transportation, while the fast-growing speeds in tree height counteracted this type of hydraulic compensation. For a planted forest where resourceful stress is limited, more investment will be allocated to tree height growth. The resource allocations of *E. urophylla* eventually maintained a constant H_p that was independent of tree size, which mirrored a maximum assimilation potential under unlimited resources. Under these conditions, a high resistance along the SPAC would lead to a rapid decrease in Ψ_L and k_s (Ambrose et al., 2009). Bleby et al. (2012) reported that trees of the same height in a natural *Eucalyptus marginata* take five times longer to grow compared to those growing on a restored site. Obviously, we concluded that the restored forest was more vulnerable with a high growing speed.

In addition to tree size and drought, other climatic factors among the climate changes (including nitrogen deposition and elevated CO_2, among others) were also reported to affect WUE (Vaidya et al., 2014; Cruz et al., 2014; Novriyanti et al., 2012). Ward et al. (2013) proposed that the decreased stomatal conductance under these conditions is attributed to the high WUE. However, concern regarding the change in k_s was less emphasized. Domec et al. (2010) argued that some species under elevated CO_2 altered the hydraulic pathway, most likely structurally, affecting the liquid phase transport and consequently reducing stomatal conductance. This argument contrasts with previous studies focusing on a direct stomatal response to CO_2. Thus, we proposed that hydraulic changes in sap wood contribute greatly to enhanced WUE under most conditions.

4.4 Elastic fluctuating isotonicity with radiation

The $-m$ averaged 0.58 ± 0.01 and 0.53 ± 0.007 (Fig. 3) in April and October, respectively. Oren et al. (1999) reported that as long as stomata regulate the leaf potential near a constant value, a slope near 0.6 is expected. This variation depended on the D range, boundary layer conductance (g_{bl}), and changes in hydraulic conductance associated with D. To determine the effect of the D range, we selected the data shown in Fig. 3 by the criterion that D ranged from 1 to 2 kPa for each light level to perform a boundary analysis. Then, $-m$ of the 15 trees at each light level was compared with the results that were derived from all of the data. As a result, the relationship between $-m$ and Q in the wet and dry seasons was not significantly different from that analyzed above ($p = 0.43$ and 0.14, respectively, ANOVA). Characterized by narrow leaves, the g_{bl} of the *E. urophylla* stand in April and October was 930.1 and 1149.8 $\mathrm{mmol\,m^{-2}\,s^{-1}}$, respectively, which led to a ratio of g_{bl} / G_S of more than 2 in October. Oren et al. (1999)

argued that the $-m$ is negatively related to the $g_{\mathrm{bl}}/G_{\mathrm{S}}$ and equals 0.55 when the $g_{\mathrm{bl}}/G_{\mathrm{S}}$ is 10, which is the case of our study.

Of note, G_{Sref} was negatively related to Q and ranged from 0.32 to 0.83 in the dry season and 0.22 to 1.10 in the wet season for the 15 trees (Fig. 4b), even though no SWC effect was found. An ANOVA analysis of $-m$ at different light levels indicated a significant seasonal difference in D ranging 1–2 kPa ($p < 0.01$). i.e., the sensitivity was not maintained constant even within a single day when the light intensity varied substantially. The fact that $-m$ increases rapidly under low light conditions may be due to the closed stomata in the morning. Oren et al. (1999) suggested that low light may be expected to cause deviations in $-m$ from the predicted slope (0.6) and that stomata continue to regulate the leaf water status even under non-saturating light. As the low-light data were removed ($Q < 200\,\mu\mathrm{mol\,m^{-2}\,s^{-1}}$), a linear decrease in $-m$ with radiation was observed (Fig. 4b). To qualify the effect of max radiation in different locations on the stomatal sensitivity, we analyzed the relationship between the max Q and mean $-m$ within that Q range (Fig. 9).

The average $-m$ of each light range linearly decreased with the increase in the max light condition. Schäfer et al. (2000) assessed the importance of the mechanism for sustaining gas exchange in tall trees by directly relating $-m$ to G_{Sref}, and these authors concluded that tall trees have lower G_{Sref} sensitivity than short trees. These authors argued that the lower stomatal sensitivity in tall trees ensures a more stable carbon uptake rate over the wide diurnal range of D and may serve to support carbon exchange. Combining the tree size effect as proposed above, it was hypothesized that less-sensitive stomata causing much more access to light on the leaves may be another strategy for plants to improve WUE. However, a lower G_{Sref} of large trees was not observed in our study, which may be the consequence of a highly opened canopy, as light was available to all of the trees. It is unfortunate that, to date, none of the previous studies associated with stomatal sensitivity considered light as an independent factor; therefore, we cannot assert whether the hypothesis is true or not. If the hypothesis is true, plants that grow near the equator will be predicted to be less sensitive to changes in D, and compared to dominant trees in the forest, plants growing under the canopy will be inversely more sensitive as light is more precious there (Fig. 9). However, there is no doubt that light plays a significant role in controlling the stomata response to D. Obviously, further studies are needed for revealing the mechanism within this relationship.

Giving the importance of G_{Sref} for trees to regulate water loss under severe drought, it was predictable that stomata should be more sensitive during the drought period to prevent excessive water loss, as k_{s} suffered a substantial decrease. Bourne et al. (2015) observed a linear relationship between the stomatal sensitivity to D and the aridity index for five *Eucalyptus* and concluded that the stomata are more sensitive to drought and play a selective role in constraining the water-use response among the five *Eucalyptus* species. However, our results, even though G_{S} decreased by 22.4 % from the wet to the dry season, did not support this result, as the seasonal difference was caused by the difference in $g_{\mathrm{bl}}/G_{\mathrm{S}}$. One of the possibilities may be the relatively high SWC at our research site. As presented by Martorell et al. (2014), the leaf water potential of *E. pauciflora* reached a minimum of −3.0 MPa. Because such an extreme drought stress was not found in our stand, we cannot verify this possibility under field conditions. Another reason may be related to the same demand for carbon assimilation because the light conditions were similar in both the dry and wet seasons (Schäfer et al., 2000).

5 Conclusions

a. The transpiration of *E. urophylla* was weakly enhanced by the increase in soil water content and eventually offset by the decrease in D during the wet season. Our results also revealed a water compensatory mechanism of *E. urophylla* when E_{T} was relatively lower in the wet season by nighttime transpiration, which partially compensated for the lower water use in the daytime by a proportion of 4.51 %.

b. The combined regulation of water use by decreased stomatal and hydraulic conductances kept the leaf water potential from hydraulic failure. However, more dramatically decreased k_s may shed some light on the mechanism of the high WUE of *Eucalyptus* when exposed to drought conditions.

c. Our results verified the hypothesis that trees of different sizes have different strategies to respond to climate factors (D, Q_0, and SWC). As a tree grows, k_s is more sensitive to water loss. Because large trees suffered more water loss than small trees did, the rapid response of k_s will potentially improve the WUE.

d. The decrease in stomatal sensitivity of G_{Sref} to D along the radiation gradient accounted for another aspect of "plastic characteristics" for *E. urophylla*. It is predicted that trees growing under high light conditions will ensure a more stable carbon uptake rate. However, the sensitivity did not decrease significantly with decreased k_s as expected.

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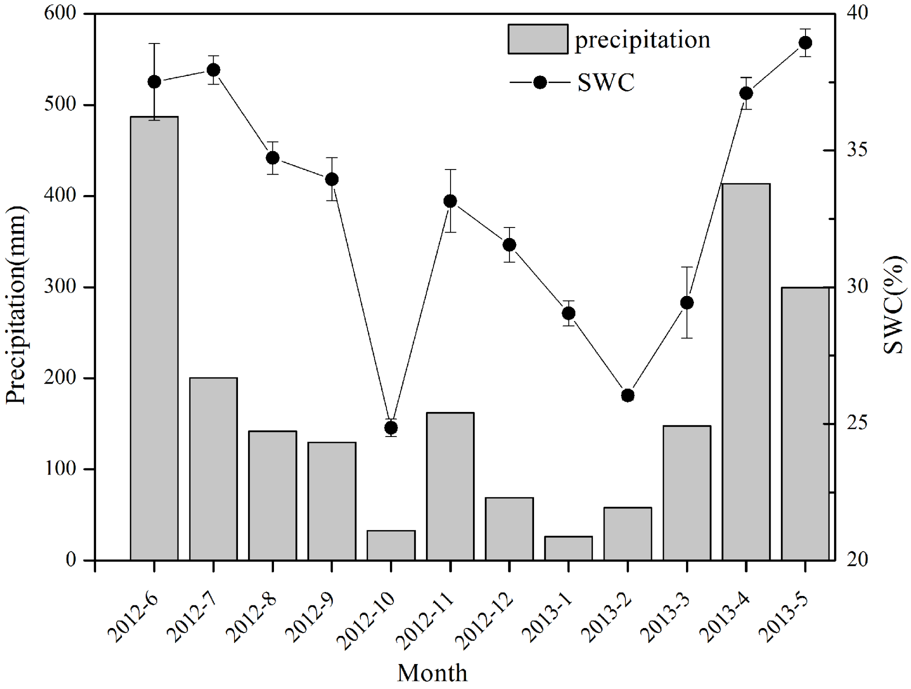

Figure 1. Precipitation (*P*) and soil water content (SWC) dynamics across the period of sap flow measurement, Data of SWC in the Figure are daily mean ± SE of that month, $n = 28$–31.

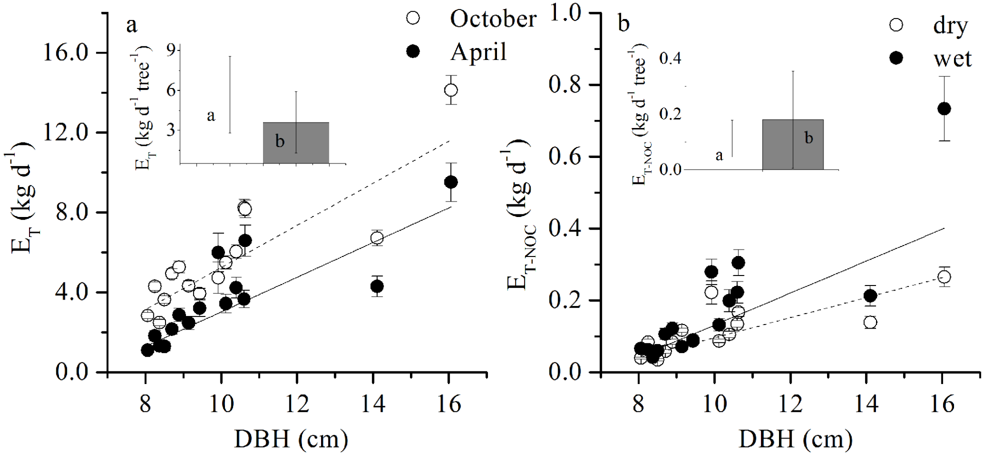

Figure 2. The insets in the figure represent the mean E_T **(a)** and $E_{T\text{-NOC}}$ **(b)** of 15 trees in dry and wet season respectively, letters implied a significant difference between dry and wet season

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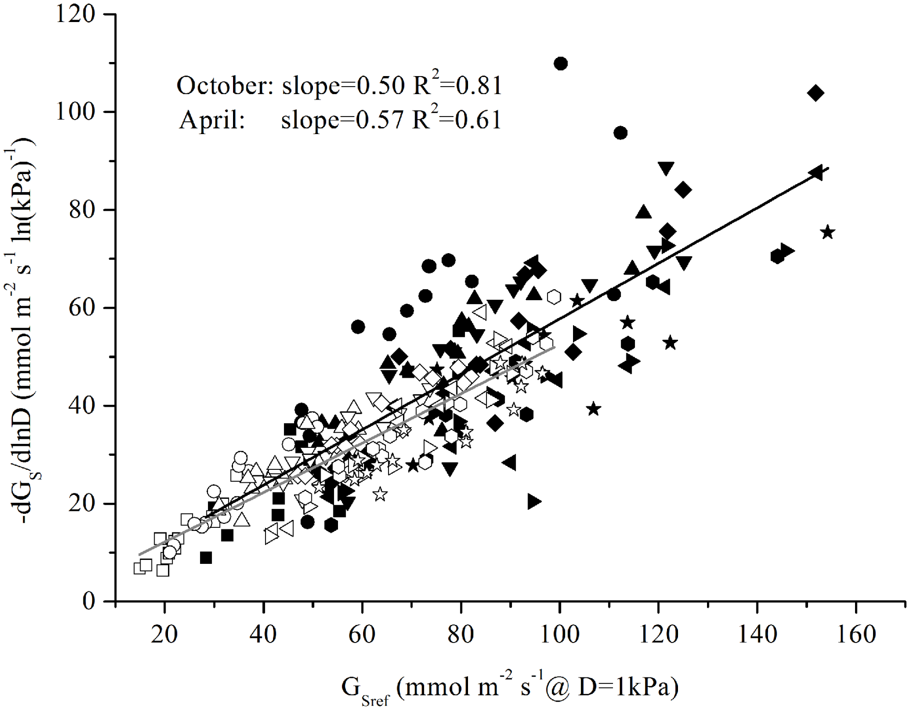

Figure 3. The sensitivity of average stomatal conductance of tree individuals at each light level in response to increasing vapour pressure deficit ($-\mathrm{d}G_{\mathrm{Si}}/\mathrm{d}\ln D$) as a function of the canopy stomatal conductance at $D = 1$ kPa (G_{Sref}) in dry (open symbol) and wet season (solid symbol).

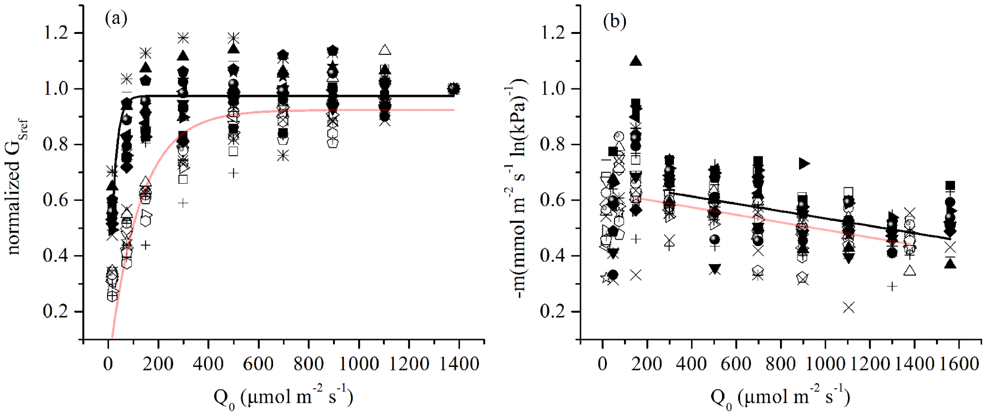

Figure 4. (a) G_{Sref} is G_{S} of each tree at D = 1 kPa and normalized based on the highest value in relation to mean photosynthetically active radiation (Q_0). **(b)** The stomatal sensitivity ($-m$) of each tree in relation to Q_0 in both seasons. Lines are least-square fit through the entire data.

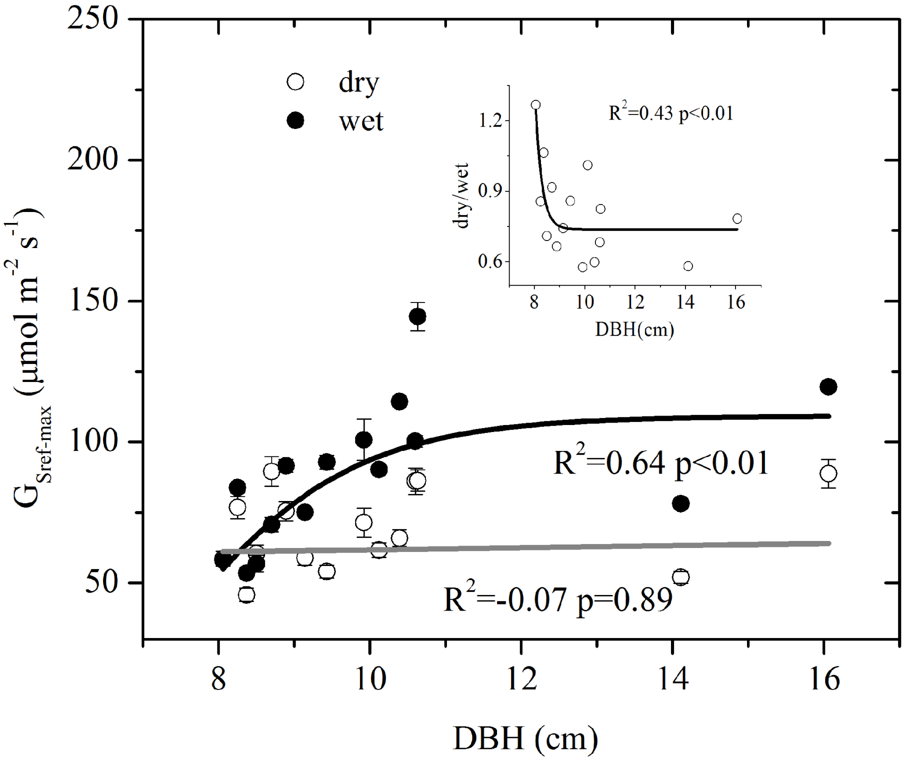

Figure 5. Relationship between DBH and max stomatal conductance at reference *D* (= 1 kPa) ($G_{\text{Sref-max}}$) deducted from Fig. 3. Lines represent least square fits for dry (white circle) and wet (black circle) season respectively, data are mean ± SE.

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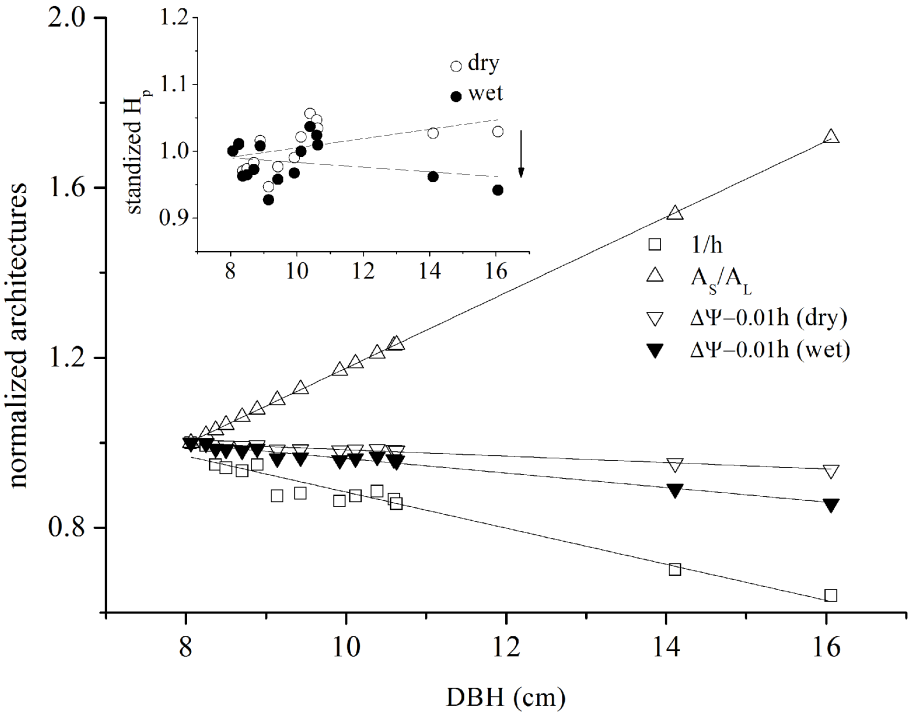

Figure 6. The normalized value of architectures including reciprocals of tree height ($1/h$), Huber value (A_S/A_L), the drivers of transpiration ($\Delta\Psi - 0.01h$) and the hydraulic properties (H_p) of 15 trees normalized by the smallest tree among them following with increased tree size (DBH) in dry and wet season.

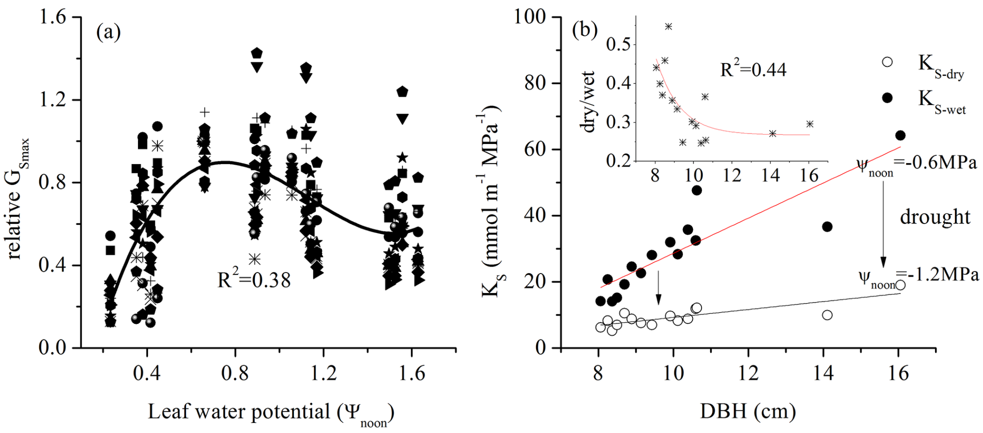

Figure 7. (a) Limitation of leaf water potential (at noon, 12:00–13:00 LT) on relative daily maximum G_S (G_{Smax}) and **(b)** relationship between tree size and specific hydraulic conductivity k_s of 15 trees for *E. urophylla* in dry and wet seasons. G_{Smax} estimated by the mean of G_S from 11:00 to 13:00 LT normalized by the data of each tree on 19 April 2013.

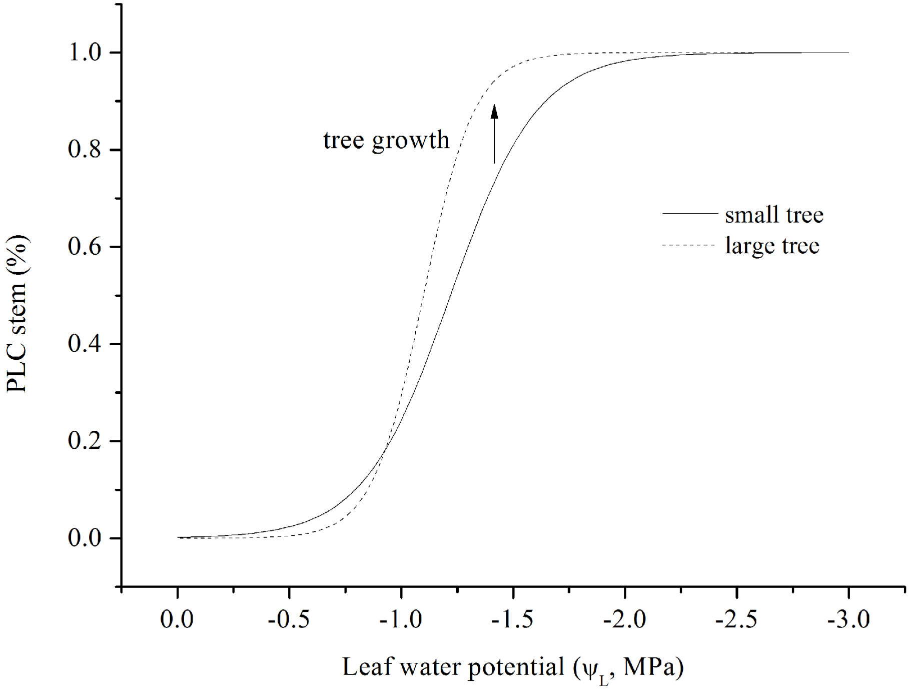

Figure 8. Percentage loss of hydraulic conductivity (PLC) as a function of xylem water potential (Ψ_L) for small (tree 1, DBH = 8.1 cm) and large (tree 15, DBH = 16.1 cm) *E. urophylla* trees. The assumption here is PLC = 0 when $\Psi_L = 0$ and PLC = 100 % when $\Psi_L = -3.0$ MPa for most species, Ψ_L in dry and wet seasons is used to simulate the curve.

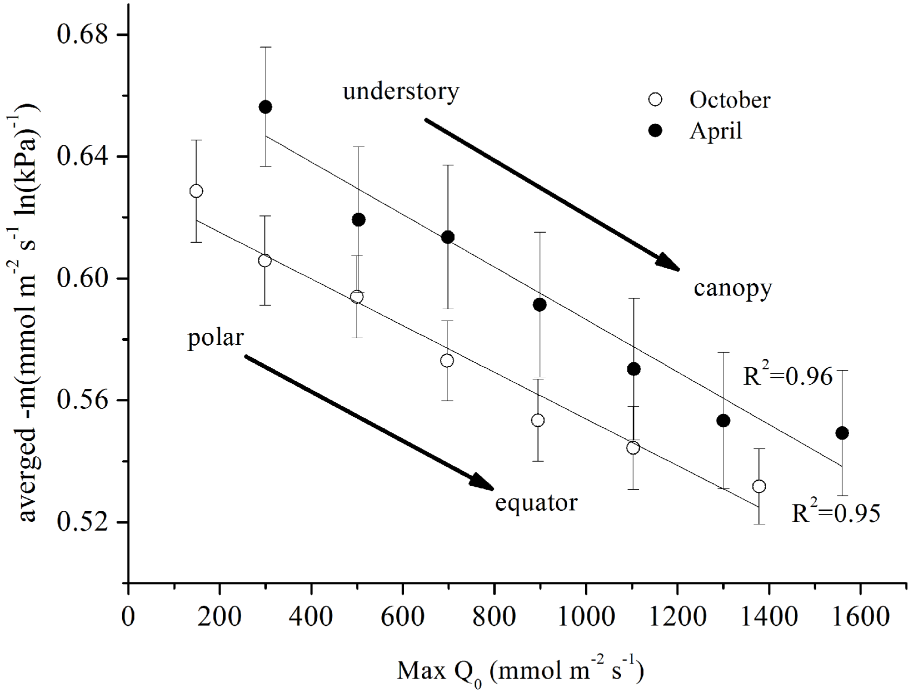

Figure 9. The max radiation determined stomatal sensitivity ($-m$) in dry and wet seasons. Data of each point are the mean ± SE ($n = 15$) of 15 trees averaged by $-m$ before (include) each light level showed in Fig. 4b (except for the first two light level of each month in order to remove the low light condition).