1	Water use strategies of a young Eucalyptus urophylla forest
2	in response to seasonal change of Environmental factors in
3	South China
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18	Abstract
19	To depict the wet (April with a soil water content, SWC, of 37%) and dry (October
20	with a SWC of 24.8%) seasonal changes in the water use and physiological response
21	of a Eucalyptus urophylla plantation in subtropical South China characterized by
22	monsoon climate, the whole-year (June, 2012~May, 2013) transpiration of E.
23	urophylla was monitored using the TDP method. Daily transpiration ( $E_T$ ) in dry
24	season averaged 5.7 $\pm$ 2.9 kg d <sup>-1</sup> and was 58.0% higher than that in wet (3.6 $\pm$ 2.3 kg d <sup>-1</sup> ).
25	The difference is consistent with that of the radiation and evaporative demand of the
26	two months, while the nocturnal transpiration ( $E_{T-NOC}$ ) in the wet season (0.18±0.021
27	kg d <sup>-1</sup> ) was almost twice that in the dry season (0.11 $\pm$ 0.01 kg d <sup>-1</sup> ). Trees displayed a
28	higher stomatal conductance (G <sub>S</sub> ) (53.4~144.5 mmol $m^{-2} s^{-1}$ ) in the wet season and a
29	lower $G_S$ (45.7~89.5 mmol m <sup>-2</sup> s <sup>-1</sup> ) in the dry season. The leaf-soil water potentials

 $(\psi_{\rm L})$  of the wet and dry season were -0.62±0.66 and -1.22±0.10 MPa, respectively. A 1 boundary line analysis demonstrated that the slight improvement in the G<sub>S</sub> by SWC in 2 wet season was offset by a significant decrease in D, and the G<sub>S</sub> sensitivity to D (-m) 3 was affected by the variance of radiation instead of SWC. Specific hydraulic 4 conductivity ( $k_s$ ) of trees of different sizes decreased by 45.3 ~ 65.6% from the wet to 5 6 the dry season. Combining the decreased maximum reference  $G_S$  at D=1 kPa ( $G_{Sref-max}$ ) by 22.4% with the constant max  $G_S$  ( $G_{Smax}$ ) when  $\psi_L < -1.2$  MPa, we shed some light 7 8 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<sub>s</sub> to decreasing  $\psi_{L}$ , 9 large trees used water more efficiently than small ones did. In addition, the -m in the 10 dry season ( $0.53 \pm 0.007$ ) was lower than that in the wet season ( $0.58 \pm 0.01$ ) due to the 11 difference in the ratio of  $G_S$  to the boundary layer conductance  $(g_b)$  in the two months. 12 The negative relationship between -m (except when light is limited) and 13 photosynthetically active radiation  $(Q_0)$  proved to be a plastic response to 14 environmental changes for E. urophylla but did not change with decreased ks as 15 16 expected.

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### 18 **1. Introduction**

Climate change resulting from global warming is gradually threatening tropical and 19 subtropical forest communities in a variety of ways, one of which is the increasing 20 frequency of severe droughts that are caused by changes in the precipitation pattern 21 according to the IPCC's report (Davidson et al., 2012). Over the past 50 years, China 22 23 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 24 25 China since 1980, rainfall patterns have shifted to more rain-free days and fewer days of light rain in dry season (characterized with little rainfall and lower soil water 26 content), more severe storms during the wet season, even though the total rainfall did 27 not change significantly. The direct effect of decreased rain events is the decreased 28 soil water supply, which may further restrain transpiration especially for shallow root 29

plants. However, since vapour pressure deficit (D) increases exponentially with
increasing air temperatures and therefore warming is expected to have a larger
influence in future D, transpiration will be enhanced in drier atmosphere in the
absence of plant physiological regulation.

Tropical forests may not be resilient against climate change in the long term, 5 primarily due to predicted reductions in rainfall, drought-induced excessive water loss 6 and ecosystem disturbances (Zhou et al., 2013), thus decreasing forest productivity, 7 increasing tree mortality, and decreasing forest biomass carbon sinks (Chaves et al., 8 9 2002). While as reviewed by Lloret et al., (2012), many empirical evidences support 10 the existence of stabilizing processes minimizing and counteracting the effects of these extreme climate events, reinforcing community resilience. In planted forests, 11 trees are more vulnerable under severe environmental stress because of their weaker 12 13 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 14 southern provinces of China. The coverage of this species is expanding rapidly and 15 has doubled in the past decade (Shi et al., 2012). 16

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<sub>S</sub>) to avoid dehydrative damage by limiting the rate of water loss and the development of a potentially impairing low leaf

water potential ( $\Psi_{\rm L}$ ) (Meinzer et al., 1993). The absence of stomatal regulation would 1 cause excessive xylem cavitation and a failure of water transport (Cochard et al., 1996; 2 Lu et al., 1996). However, stomatal regulation is typically coordinated with hydraulic 3 conductance, which gradually decreases with aggravated water access limitation in 4 the soil. Understanding the mechanistic responses of trees to low water availability 5 6 and drought is essential to accurately incorporate these mechanisms into process-based ecophysiological models and global vegetation models (McDowell, 7 8 2011).

9 Trees of different sizes usually respond to soil drought-induced water stress in 10 different ways due to the varied hydraulic structure (Forrester 2015). Tree height, leaf area and sapwood area are in allometric relation with tree size in different ways, 11 thereby changing the hydraulic properties when trees grow larger to adapt to the 12 13 environment (Schäfer et al., 2000). The different physiological response of juvenile and full-grown trees had been intensely debated for many years and might be 14 associated with species, ages, nutrient, climates, etc. (Binkley et al., 2013; Aranda et 15 al., 2012). To our knowledge, small trees have lower overall water loss rates at both 16 the leaf and canopy levels and a greater sensitivity of water loss in response to water 17 stress (increasing D or decreasing leaf water potential) than large trees (Dawson 1996) 18 and therefore have an advantage under drought conditions. While larger trees usually 19 have a deeper root system for acquiring more available soil water, especially under 20 drought conditions (Anderegg et al., 2012). As proposed by Cavender-Bares and 21 Bazzaz (2000), juvenile trees are more affected by drought than mature trees, due both 22 to their shallower rooting as well as their inability to fix C at low leaf water potential. 23 They resist drought by closing stomata early in the day at the expense of C uptake. 24 Mature trees avoid drought conditions by accessing deeper water reserves and 25 26 adjusting WUE, sacrificing C gain only marginally. To shed light on the physiological response strategies of E. urophylla, the impact of tree size needs to be considered 27 when evaluating the effects of decreased water availability on tree growth 28 (Feichtinger et al., 2014). 29

By reducing G<sub>s</sub>, plants minimize water loss and maintain the hydration of plant 1 cells as D increases under conditions of low water availability. Thus, the magnitude of 2 G<sub>S</sub> reflects the drought intensity. For example, Medrano et al. (2002) observed a 3 common response pattern that was species-and condition-dependent when G<sub>S</sub> was 4 light saturated. However, in addition to the regulation of stomatal aperture, the 5 stomata must react rapidly to avoid excessive water loss in response to high 6 transpiration demand under drought, i.e., the sensitivity. Sensitivity of stomata to D 7 8 has been accurately described using empirical relationships as the slope between G<sub>S</sub> and ln (D) (Oren et al., 1999) and is closely related to the magnitude of  $G_S$  at D=1.0 9 kPa (G\_{Sref}). The stomatal sensitivity to D is linearly proportional to  $G_{Sref}\left(\text{-0.6}\right)$  for 10 isohydric plants that are able to maintain a constant minimum leaf water potential 11  $(\psi_{\text{leaf}})$  (Pou et al., 2012). The hydraulic architecture of plants plays a vital role in the 12 G<sub>s</sub> response to changing leaf hydration (Sperry et al., 2002). In addition, because the 13 decrease in G<sub>S</sub> is usually followed by a change in hydraulic conductance 14 (Mart nez-Vilalta et al., 2014), a better understanding of the coordination between 15 16 hydraulic architecture and stomatal responses to changing D will provide insight into the diurnal and seasonal growth patterns of plants (Ocheltree et al., 2014). 17

Most of the research about E. urophylla in the subtropical monsoon climate of 18 South China is related to the productivity (Du et al., 2012; Simpson et al., 2003), 19 wood property (Jiang et al., 2004; Luo et al., 2012; Luo et al., 2013), and disease 20 (Zhou et al., 2008) considering of the economic aspects, while the plasticity in 21 physiological response and function of tree species remain poorly understood. Our 22 interest is in determining how the young planted Eucalyptus forest in South China 23 will function under enhanced drought stress and varied atmosphere conditions. We 24 hypothesized that trees growing in the dry season would respond more sensitively to 25 26 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-27 water deficits and high evaporative demand than in the wet season. More specifically, 28 we seek to answer the following key questions: (1) Will the water use of E. urophylla 29

will be limited in dry season? (2) How the hydraulic and physiological traits of trees
respond following a seasonal climate change? (3) How differently will the small and
large trees respond to seasonal drought?

4

# 5 2. Materials and Methods

# 6 2.1 Study site and plant material

This study was conducted at the Huangmian state forest farm (24 %6'N, 109 %7'E) 7 approximately 60 km southwest of Guilin city in South China. This farm is planted 8 9 with Eucalyptus urophylla for lumber and pulp production. The plantation area was 32000 ha in 2010. All of the reported measurements took place in an E. urophylla 10 stand 3~5 years old on a hill with an inclination of approximately 30° facing 11 southwest. The forest density was 1375 trees ha<sup>-1</sup>. The soil of this forest is 12 characterized with heavy loam. This area is characterized by a low subtropical 13 monsoon climate with an annual precipitation ranging from 1750 to 2000 mm and an 14 average annual temperature of 19°C. Although the rainfall is abundant, it is unevenly 15 distributed through the year, producing wet (March to September) and dry (October to 16 February of the next year) seasons. The measurement was carried out from June 2012 17 18 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 19 observation tower 23 m high was erected within the plantation providing access to the 20 canopy of the *E. urophylla* stand. 21

### 22 2.2 Sap flux and environmental variable measurements

The sap flow density ( $F_d$ , g m<sup>-2</sup> s<sup>-1</sup>) 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 scaling up of sap flow density 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 8 photosynthetic photon flux density ( $Q_0$ , µmol m<sup>-2</sup> s<sup>-1</sup>), temperature (T, °C), relative 9 humidity (RH, %), and wind speed (u, m s<sup>-1</sup>) were measured simultaneously with the 10 sap flow measurement (Zhu et al., 2015). The rainfall data during the study period of 11 Guilin were obtained from the China Metrological Data Sharing Service System 12 (http://cdc.cma.gov.cn/home.do). The soil water content (SWC, m<sup>3</sup> m<sup>-3</sup>) was 13 monitored with three soil water probes (SM300, UK) that were buried 30 cm under 14 the ground surface. 15

# 16 **2.3 Tree morphological features and stand transpiration**

17 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 18 harvested 7 sample trees that were grown close to the experimental plot for biomass 19 determination. The DBH was measured with diameter tape. The tree height (h) was 20 measured with the tape draped from the top of the tower, and crown of sampled trees 21 for sap flow measurements were aligned with tape to obtain the reading of the tree 22 height. The total leaf area (AL) was measured with a portable leaf area meter 23 (Licor-3000, USA). Five small subsamples of each tree were scanned and weighted 24 25 (fresh weight), the ratio of leaf area/ fresh weight was estimated. Then the whole tree leaves were then collected for the estimation of A<sub>L</sub>. We take cores with a growth 26 increment on trees around the stand (n=27). The sapwood depth was visually 27 distinguished from heartwood by changed color at the boundary of the two parts on 28 the cores before the sapwood area was estimated  $(A_S)$ . Because the DBH of the 29

harvested trees ranged from 6.6 to 11.1 cm, while those for sap flow measurements 1 ranged from 8.5 to 16.06 cm, we referred to Zhou et al.'s study (2004) to obtain 2 3 biomass information of E. urophylla trees with a DBH greater than 11.1 cm. As of the sample trees was estimated base on the relationship of DBH and As. We used the 4 fitted relationship between DBH and As and the AL from the harvested trees together 5 6 with Zhou et al.'s study (2004) to scale up whole tree transpiration ( $E_T$ ) by multiple  $F_d$ of each tree. The nocturnal transpiration ( $E_{T-NOC}$ ) was defined as  $E_T$  when  $Q_0=0$ . 7 8 Because Eucalyptus leaves are characteristically thick, tough and long lived and are 9 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 10 dynamics in leaf area. 11

12 Stand water use per ground area (E, mm) was estimated as the product of plot 13  $(20\times20 \text{ m})$  sapwood area (derived from the DBH versus A<sub>S</sub> relationship above for each tree in the plot) and hourly mean of  $F_d$  of the monitored trees (since no 14 significant relationship between F<sub>d</sub> and DBH was observed, p=0.45), and divided by 15 the ground area of the plot. The total water use during the experimental period was 16 summed by the hourly mean of E. However, because of the power down and 17 equipment failure, there were missing data during the experiment. We fitted the 18 relationship between  $Q_0$  and daily sum of E to fill the gap. 19

# 20 **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:

23 
$$G_{Sref} \propto E_L = k_s (\Delta \psi - 0.01h) \frac{A_s}{A_L h}$$
(1)

where the transpirational demand is proportional to the  $G_S$  times the vapor pressure deficit (D).  $k_S$  is The sap wood specific hydraulic conductivity (whole-plant conductance per unit sapwood).  $\Delta \Psi$  responds to the water potential gradient between root and leaf. On this base, percentage loss of conductivity (PLC) is estimated as 100 1  $\times$  (1- k<sub>s</sub>/k<sub>m</sub>), where k<sub>m</sub> is the max k<sub>s</sub>.

To estimate the wet-dry seasonal variation in  $\Delta \Psi$ , the leaf water potentials at 2 pre-dawn ( $\Psi_{pre-dawn}$ ) and midday ( $\Psi_{midday}$ ) were measured with a portable plants 3 pressure chamber (PMS 1000, Corvallis, OR, USA) for sunny days in wet (5 days) 4 and dry (4 days) season. Five trees were selected for the experiment. The 5 measurements were averaged from three replicate shoots that were sampled from the 6 mid-crown (most of the leaves were fully expanded) per tree. We assumed  $\Psi_{pre-dawn}$  to 7 be a substitute for the water potential in the soil ( $\Psi_{s}$ ) (Kim et al., 2008; Bleby et al., 8 9 2012) because soil moisture remain unchanged throughout the whole sunny day. Therefore, the  $\Delta \Psi$  was calculated as the difference between  $\Psi_{S}$  and  $\Psi_{midday}$ . 10

# 11 **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 & Jarvis (1981) assuming that the  $F_d$ scaled by  $A_S/A_L$  is equal to the transpiration rate per unit of leaf area ( $E_L$ ). The mean stomatal conductance for individual trees,  $G_S$ , can be calculated as:

$$17 \qquad G_S = (G_V T_A \boldsymbol{\rho} \ E_L) / D \tag{2}$$

18 where  $E_L$  is whole-tree transpiration per unit leaf area (g m<sup>-2</sup> s<sup>-1</sup>), G<sub>V</sub> is the universal 19 gas constant adjusted for water vapor (0.462 m<sup>3</sup> kPa K<sup>-1</sup> kg<sup>-1</sup>), T<sub>a</sub> is the air 20 temperature (K),  $\rho$  is the density of water (998 kg m<sup>-3</sup>), and D is in kPa. G<sub>Si</sub> is in units 21 of mmol m<sup>-2</sup> s<sup>-1</sup> (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 & Loustau 1994). The forest had an LAI of 1.68  $\pm 0.28$  m<sup>2</sup> m<sup>-2</sup> and did not show significant seasonal changes (p=0.78) (Zhu et al., 2015). Therefore, G<sub>Si</sub> calculation is not subjected to errors that are caused by leaf area dynamics. Thus, G<sub>Si</sub> 1 was estimated after (1) performing a cross-correlation analysis between D and  $F_d$ , and 2 using the time lag to infer a time-corrected  $F_d$  and (2) filtering out data for D<0.6 kPa 3 in the hours of early morning and late afternoon (Oren et al., 1998).

### 4 2.6 Stomatal sensitivity to vapor pressure deficit

5 Many non-linear functions and models have been used to analyze the effect of 6 environmental variables on  $G_S$  (Monteith 1995; Dang et al., 1997; Martin et al., 1997). 7 Granier et al. (1996) proposed that stomatal sensitivity is proportional to the 8 magnitude of  $G_S$  at low D (D=1 kPa) when soil moisture is not limiting, which was 9 expressed as:

10

$$11 \qquad G_S = G_{Sref} - m \ln D \tag{3}$$

12

where  $G_{Sref}$  is the intercept (i.e., the value of  $G_S$  at D=1 kPa in a log-linear relationship), and -m is the slope of the regression fit representing stomatal sensitivity to D (i.e.,  $dG_S/dln$  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.

19 A boundary line analysis of the relationship between D and G<sub>S</sub> was performed in 20 the dry and wet seasons. The datasets of G<sub>S</sub> for each tree were classified by radiation (9 levels). The data at night ( $Q_0=0$ ) were excluded because the plant physiological 21 22 response in the night was much more complicated than that in the daytime (Oren et al., 23 2001). The relationship between the lnD and G<sub>S</sub> of each small subset was linearly fitted, and the intercept and slope corresponded to the G<sub>sref</sub> (G<sub>S</sub> at D=1 kPa) and 24 sensitivity in response to D (dG<sub>S</sub>/dlnD, mmol m<sup>-2</sup> s<sup>-1</sup> kPa<sup>-1</sup>), respectively (Oren et al., 25 1999). Then, the relationship between  $G_{Sref}$  and  $-dlnd/dG_S$  for the two months was 26 27 fitted.

In order to depict the radiation control on stomatal conductance of different season,
 the G<sub>Sref</sub> under different light conditions was normalized by the value at the maximum
 Q<sub>0</sub> of each tree in both seasons, and the relationship between the G<sub>Sref</sub> and mean Q<sub>0</sub> at
 that level for all of the trees was fitted with an exponential function expressed as:

5 
$$G_{Sref} = a \times (1 - exp(-b \times Q_0))$$
 (4)

6 where *a* refers to the maximum dependent variable, i.e., the max  $G_{Sref}$  ( $G_{Sref-max}$ ).

Since soil water content is vital for stomatal regulation, the boundary analysis
performed above was applied at different soil moisture conditions to depict the
maximal potential water use of *E. urophylla*. SWC was evenly divided into five
intervals from 20% to 45%.

### 11 **2.7 Data analysis**

Boundary-line analysis was conducted in Excel (version 2010, Microsoft Office Excel) 12 13 to set up the relationship between environmental conditions and maximal canopy stomatal conductance or F<sub>d</sub>. The upper boundary line was derived by: (1) partitioning 14 15 data of independent variables (V<sub>I</sub>) into a specific intervals, (2) calculating the mean and standard deviation of dependent variables (V<sub>d</sub>) in each interval, (3) removing 16 outliers (P < 0.05; Dixon's test), (4) selecting the data falling above the mean plus one 17 standard deviation, and (5) averaging the selected data for each V<sub>I</sub> interval with  $n \ge 5$ 18 remaining V<sub>d</sub> values. Excluding intervals with n<5 was done to prevent V<sub>I</sub> intervals 19 with too little information from affecting the relationship. 20

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. Origin pro (version 8.6, Origin Lab, USA) was used to draw all of the graphs in this paper.

### 27 **3. Results**

## 1 **3.1** Water and atmospheric conditions

The precipitation (P) in the research site (Huangmian) totaled 2167.6 mm from June 2 2012 to May 2013, and varied from the minimum of 26.2 mm in January to the 3 maximum of 487 mm in June. The water input was mainly contributed by 4 precipitation in late spring and early summer (i.e., from April to June), which 5 accounted for 55.4% of the whole year, while that from October to February was 16% 6 and is typically defined as the dry season in South China. The nonlinear curve fit 7 between SWC and P indicated that SWC linearly increases with P when P<200 mm 8 and holds a constant value of  $0.38 \text{ m}^3 \text{ m}^{-3}$  when P>200 mm (Fig. S1), meaning that the 9 10 soil was not saturated throughout most of the year except for the period from April to July. The SWC in dry decreased 32.6% from wet season, revealing a significant 11 difference in the soil water conditions between the wet and dry seasons. The monthly 12 average  $Q_0$  showed an inverse pattern with SWC, which was 154.2±109.4 µmol m<sup>-2</sup> s<sup>-1</sup> 13 in wet season and 283.7 $\pm$ 108.6 µmol m<sup>-2</sup> s<sup>-1</sup> in dry season. D was higher in dry 14 (1.07±0.39 kPa) than in wet (0.32±0.28 kPa) season. The differences in the three 15 environmental factors between the two seasons were significant (p<0.01). 16

### 17 **3.2 Tree water use in different seasons**

A boundary line analysis of the relationship between  $F_d$  and  $Q_0$  was conducted, and the maximal  $F_d$  was derived from the exponential relationship. The  $F_d$  of the 15 trees was  $41.03\pm7.97$  g m<sup>-2</sup> s<sup>-1</sup> and  $38.82\pm13.16$  g m<sup>-2</sup> s<sup>-1</sup> 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<sup>2</sup>=0.19, p=0.06) was observed.

The annual stand  $E_T$  was 462.42 mm, and the  $E_T$  in dry and wet season 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±0.7 kg d<sup>-1</sup> (2.49±0.16 kg d<sup>-1</sup>) and 9.52±0.97 kg d<sup>-1</sup> (2.2±0.3 kg d<sup>-1</sup>), respectively. The daily transpiration ( $E_T$ ) in dry season averaged 5.7±2.9 kg d<sup>-1</sup> and was 58.0% higher than that in wet season (3.6±2.3 kg d<sup>-1</sup>) 1 (Fig. 2a, p<0.01). The greatest variance was observed for the tree of DBH=8.5 cm, 2 whose  $E_T$  in dry increased by 185.1% from wet season. In contrast, the  $E_T$  of the 3 largest tree (DBH=16.1 cm) increased by 48.5%, lower than the mean value. The 4 wet/dry ratio varied from 0.4 to 0.8 and slightly increased with the tree size (R<sup>2</sup>=0.03), 5 implying that the  $E_T$  of the larger trees was less sensitive to seasonal changes in 6 environmental factors.

7 In our stand, the nocturnal transpiration (E<sub>T-NOC</sub>) was 0.18±0.021 kg in wet and 0.11±0.01 kg in dry season, indicating its decrease with decreasing water supply (Fig. 8 9 2b, p=0.047). This transpiration accounted for a proportion of daily  $E_T$  by 1.82±0.45% 10 and 4.51±1.34% in dry and wet season, respectively. However, the variances in E<sub>T-NOC</sub> among individuals were much higher in wet than in dry season, which 11 mirrored a different sensitivity of trees responding to environmental changes at 12 13 nighttime. The nocturnal sap flow (E<sub>T-NOC</sub>) also followed a linear relationship with tree size, but larger trees were much more sensitive to the environmental changes in 14 15 wet than in dry season.

The water potential at pre-dawn ( $\Psi_{pre-dawn}$ ) was -0.24±0.04 MPa and -0.21±0.03 16 MPa in the dry and wet seasons (p=0.23), respectively, and at pre-night ( $\Psi_{pre-night}$ ) was 17 -0.29  $\pm$ 0.02 and -0.31  $\pm$ 0.05 MPa. The water potential at noon ( $\Psi_{noon}$ ) was -7.51  $\pm$ 2.32 18 19 and -14.55 ±2.31 MPa in wet and dry season (p<0.01), respectively. None of the above values were significantly different among the 5 trees (p>0.05). The water potential 20 gradients at midday ( $\Delta\Psi$ ) averaged -0.62±0.66 (wet) and -1.22±0.10 MPa (dry). 21 Similar to the leaf water potential,  $\Delta \Psi$  showed no significant variance among the five 22 23 trees (ANOVA, p=0.14 in wet and p=0.25 in drr) or between the two months (p=0.33).  $\Delta \Psi$  was much higher in wet than in dry season(p<0.01), which was consistent with 24 the seasonal pattern of E<sub>T</sub>. 25

# 3.3 G<sub>s</sub> and its sensitivity in response to vapor pressure deficit under different light conditions

 $G_{Sref}$  linearly increased with sensitivity in both the dry and wet seasons (Fig. 3). The

normalized G<sub>Sref</sub> of all of the trees increased rapidly when Q<sub>0</sub> was low and gradually 1 saturated at the maximum (Fig. 4a). It reached 90% of the maximum (G<sub>S90</sub>) when Q<sub>0</sub> 2 was 287.8 and 167.1  $\mu$ mol m<sup>-2</sup> s<sup>-1</sup> in the dry and wet seasons, respectively, indicating 3 that the G<sub>Sref</sub> in the wet season was more sensitive to light, resulting in a lower 4 saturation point than that in the dry season (p<0.01). We also qualified the tree size 5 effect on -m in both seasons; the -m at different light levels did not change 6 significantly with the tree size (p=0.33). The effect of Q<sub>0</sub> on -m was also qualified in 7 8 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), i.e., the 9 sensitivity was not maintained constant even within a single day when the light 10 intensity varied substantially. Oren et al. (1999) suggested that low light may be 11 expected to cause deviations in -m from the predicted slope (0.6). As the low-light 12 data were removed ( $Q_0 < 200 \ \mu mol \ m^{-2} \ s^{-1}$ ), a linear decrease in -m that ranged from 13 0.32 to 0.83 (dry season) and 0.22 to 1.10 (wet season) with radiation for the 15 trees 14 was observed (Fig. 4b). The fact that -m increases rapidly under low light conditions 15 16 may be due to the closed stomas in the morning. Mean of -m was substantially higher in the wet season  $(0.58 \pm 0.01)$  than that in the dry season  $(0.53 \pm 0.007)$  (p=0.038). 17

Oren et al. (1999) reported that as long as stomata regulate the leaf potential near 18 a constant value, a slope near 0.6 is expected. This variation depended on the D range, 19 boundary layer conductance (gbl), and changes in hydraulic conductance associated 20 with D. To determine the effect of the D range, we selected the data shown in Fig. 3 21 by the criterion that D ranged from 1 to 2 kPa for each light level to perform a 22 23 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 24 and Q<sub>0</sub> in the wet and dry seasons was not significantly different from that analyzed 25 above (p=0.43 and 0.14, respectively, ANOVA). Characterized by narrow leaves, the 26  $g_{b1}$  of the *E. urophylla* stand in wet and dry season was 930.1 and 1149.8 mmol m<sup>-2</sup>s<sup>-1</sup>, 27 (unpublished data) respectively, which led to a ratio of gbl/Gs of more than 2 in dry 28 season. Oren et al. (1999) argued that the -m is negatively related to the  $g_{bl}/G_S$  and 29

equals 0.55 when the  $g_{bl}/G_S$  is 10, which is the case of our study. As a result, the changes in hydraulic conductance might be responsible for the -m variation.

The max  $G_S$  ( $G_{Sref-max}$ ) of each tree was obtained from the exponential function 3 (eq. 4, corresponding to a) before being normalized. The  $G_{Sref-max}$  was fitted to the tree 4 size (Fig. 5). The G<sub>Sref-max</sub> of small trees (<9 cm) in the wet season increased rapidly 5 with DBH, then changed little after DBH>9 cm, while no clear relationship between 6 the  $G_{sref-max}$  and tree size was observed in the dry season. The  $G_{Sref-max}$  averaged 68.8 7 and 88.6 mmol  $m^{-2} s^{-1}$  in the dry and wet seasons, respectively, and the latter was 8 significantly higher (p<0.01). The G<sub>Sref-max</sub> ratio of dry to wet ranged from 0.58 to 9 10 1.26 (0.81 on average), decreased rapidly when DBH<9 cm and stabilized after DBH>9 cm (Fig. 5). 11

The slope of  $G_{Sref}$  versus -m (Figure S3) for the five soil moisture levels ranging from 0.50 to 0.59 was weakly improved by SWC (p=0.15). The  $G_{Sref-max}$  of each tree also slightly improved by SWC but was not significant (p>0.05), as some of these values were positive or negative related to 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).

To understand the role of  $\psi_L$  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 April 19, 2013) of 15 trees (Fig. 7a).  $G_{Smax}$ was positively related to  $\psi_L$  when light was limited. According to the cell turgor theory, the change in  $\psi_L$  is derived from the G<sub>S</sub>-promoted water loss on the leaf (Dow & Bergmann, 2014). However, this value peaked and was maintained from -0.6 to -0.9 MPa for a while before a gradual decrease.

### 25 **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). Eq. (1) was applied when D=1 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±13.1 mmol m<sup>-1</sup> MPa<sup>-1</sup>) was much higher than that in the dry season (9.4±3.2 mmol m<sup>-1</sup> MPa<sup>-1</sup>). 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 DBH>10 cm.

7 **4.** Discussion

# 8 4.1 Water use of *E. urophylla*

9 From June 2012 to May 2013, the transpiration accumulated 462.42 mm (1.26 mm d<sup>-1</sup>), accounting for 21.3% of the total rainfall. This value was much lower as a young 10 forest than that in other areas of the world (Cunningham et al., 2009; Yunusa et al., 11 2010; Mitchell et al., 2009; Benyon et al., 2006). Even the same species, E. urophylla, 12 in a savanna in Venezuela transpired more water than in our study (2.3 mm d<sup>-1</sup>) 13 (Herrera et al., 2012). In general, transpiration may reach maximum values when the 14 canopy is completely closed (Shi et al., 2012). The relatively low LAI (1.68±0.28) 15 revealed a high-opening forest canopy in our study and might be the reason for low 16 transpiration. 17

18 E<sub>T</sub> 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 19 observed from September to October. A boundary analysis with the partitioning of the 20 multiple effects of D, Q<sub>0</sub> and SWC on stomatal conductance demonstrated that 21 G<sub>Sref-max</sub> was enhanced by weakly increased SWC for some trees but depressed for the 22 other, and -m was also maintained constant along soil moisture gradients under 23 different light conditions (Fig. 4b). In agreement with our results, the reported higher 24 transpiration for a *Eucalyptus miniata* in Australian savannas in the dry season also 25 26 suggests that soil water availability is not limited during the extended dry season 27 (O'Grady et al., 1999). Jarvis (1993) believed that trees in aerodynamically rough forests that are well coupled to the atmosphere continue their transpiration at the rate 28

that is imposed by D under unlimited soil water availability. The promoted  $E_{T}$  in the 1 dry season in our study can be explained by a low decoupling coefficient  $(0.10\pm0.03,$ 2 unpublished data) and an obvious increase in D by 234.4% from wet to dry season. 3 However, this trend is not always the case under some other conditions. Zhou et al. 4 (2004) reported a significantly decreased daily sap flux with decreased available soil 5 water of E. urophylla plantation in the Nandu River watershed on the Leizhou 6 Peninsula, Guangdong Province, China, where the atmospheric conditions are very 7 8 similar to those in our study. These authors believed that the soil type produces 9 uncertainty in this relationship.

10 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). 11 The similar  $\Psi_{pre-night}$  and  $\Psi_{pre-dawn}$  in the dry and wet seasons revealed the same 12 demands for water replenishment in the night. However, nocturnal sap flux  $(E_{T-NOC})$ 13 in the wet season  $(0.18\pm0.021 \text{ kg d}^{-1})$  was almost twice that in the dry season 14 (0.11±0.01 kg d<sup>-1</sup>). The difference in  $E_{T-NOC}$  was inferred to be caused by leaf 15 transpiration at nighttime. In fact, evidence was found by simultaneous leaf level gas 16 exchange measurement and water potential measurement, demonstrating that stomatal 17 conductance in wet and dry season was  $63.1\pm31.0$  and  $33.6\pm5.0$  mmol m<sup>-2</sup> s<sup>-1</sup>, 18 respectively, when Q<sub>0</sub>=0 after pre-night and before the pre-dawn. A new finding was 19 reported that a subsequent increase in transpiration in the night 6 h after dusk was 20 caused by the wood circadian clock regulation of Gs and Fd for Eucalyptus grandis 21 (Resco de Dios et al., 2013). The authors concluded that the endogenous regulation of 22 G<sub>S</sub> is an important driver of nighttime water flux under natural environmental 23 24 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 25 26 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 27 mechanism (Dawson et al., 2007). 28

# **4.2 Stomatal regulation in response to the leaf water potential**

One of the views on the mechanisms of stomatal closure is usually treated as direct 1 response to the change in leaf water potential as related closely to cell turgor 2 (Martorell et al., 2014). A significant decrease (by 22.4%, Fig. 5) in G<sub>S</sub> was observed 3 accompanying a two-fold increase in  $\Delta \psi$  in the dry season. According to eq. (2), if G<sub>S</sub> 4 is constant, a 234.4% increase in D will lead to the same proportional enhancement of 5  $E_L$  and  $E_T$  because the difference in  $T_a$  and  $A_L$  between the two months was not 6 significant (p>0.05). Thus, a 22.4% decrease in G<sub>S</sub> eventually led to a less increase in 7  $E_{T}$  and  $E_{L}$  by 159.5%. Stomatal closure also played a significant role to suppress 8 9 excessive transpiration in our study.

10 The change in  $G_S$  is a response to altered  $\psi_L$  (Höltt ä & Sperry, 2014).  $G_S$  peaked and was maintained from -0.6 to -0.9 MPa for a while before a gradual decrease 11 (Figure 6a). This trend is consistent with the relationship between  $\psi_L$  and  $G_S$  across 70 12 trees species (Klein, 2014). Of note, the stomata did not fully close when  $\psi_L$  reached 13 the minimum value when  $\psi_L$ =-1.6 MPa. In addition, G<sub>S</sub> of Eucalyptus pauciflora 14 gradually decreased with  $\psi_L$  when  $\psi_L > 1.0$  MPa (Martorell et al., 2014), while a 15 stomatal closure of 25% of the maximum remained when  $\psi_L$ =-1.6 MPa according to 16 the fitting line. This value was lower than our result (50~60%, Fig. 7a). Another 17 example presented by Mielke et al. (2000) showed that G<sub>S</sub> of Eucalyptus grandis 18 maintained ~40% of the maximum when  $\psi_L$ <-2.45 MPa until the minimum  $\psi_L$  was 19 reached (-2.8 MPa). G<sub>S</sub> was also found to stabilized at ~37.5% of the maxmim after 20 predawn  $\psi_L$ <-2.37 MPa until the minimum predawn  $\psi_L$  (-3.37 MPa) when three 21 allopatric Eucalyptus (E. camaldulensis Dehnh, E. leucoxylon F. Muell and E. 22 *platypus* Hook) were investigated together (White et al., 2000). even the minimum  $\psi_L$  of 23 -4.8 MPa was observed, t a value of ~65 mmol  $m^{-2} s^{-1}$  still occurred in their study Even the 24 minimum of midday  $\psi_L$  was observed (-4.8MPa), a value of ~65 mmol m  $^{-2}$  s  $^{-1}$  for  $G_8$ 25 still occurred in their study. Klein et al. (2014) reported that the minimum (maximum) 26 value of  $\psi_L$  can reach -2.2 MPa (-1.0 MPa) when G<sub>S</sub> decreased to 50% of the max for 27 most tree species. Franks et al. (2007) argued that Eucalyptus (Eucalyptus 28 gomphocephala) does not regulate  $\Psi_L$  at or above any particular value as groundwater, 29

soil moisture and evaporative demand vary seasonally. Instead, water table depth, 1 predawn  $\Psi_L$ , midday  $\Psi_L$  and midday  $G_S$  co-vary with monthly rainfall in a manner 2 that is consistent with classical anisohydric behaviour. However, is this behaviour (i.e. 3 not complete stomatal closure under low leaf water potentials) general among all 4 Eucalpytus needs further studies. Though, The 50~60% of G<sub>Smax</sub> at -1.6 MPa indicates 5 6 that E. urophylla in our study was more likely to optimized carbon assimilation under stressed leaf water condition, and it is also anticipated to take more risks of hydraulic 7 8 failure in the meanwhile compared with those species who fully closed stomas.

# 9 4.3 Hydraulic conductivity of *E. urophylla*

A change in  $\psi_L$  depends on the leaf water loss and water recharge by sap flow.  $\psi_L$ 10 decreases if water loss>water recharge. The stomata aperture showed less change 11 when  $\psi_L < -1.2$  MPa. When  $\psi_L$  decreased to -1.2 MPa in the dry season, k<sub>s</sub> decreased 12 by 45.3 to 65.6% from the wet season along tree size ranks (Fig. 7a). The decreased 13  $\psi_L$  indicated a failed water recharge by sap flow when G<sub>S</sub> was maintained constant. 14 15 Thus,  $k_s$  will continue to decrease when  $\psi_L < -1.2$  MPa to drive the change in  $\psi_L$ . Cavitation avoidance was a likely physiological function associated with stomatal 16 regulation during water stress in our experiments as we discussed above. However, 17 the possibility still exists that the striking relations that were observed between 18 19 cavitation and stomatal function were only correlations and that the main physiological trait involved in the regulation was elsewhere (Cochard et al. 2002). 20 Evidently, differences in the behavior of isohydric and anisohydric plants are due to 21 differences in the sensitivity of their respective guard cells to a critical  $\psi_L$  threshold 22 23 (Sade et al., 2012), The apparent differences in stomatal control of isohydric and anisohydric plants are thought to be due to differences in the perception of abscisic 24 acid (ABA) (Tardieu & Simonneau, 1998), which is highly related with stomatal 25 closure (Schultz et al., 2003). The substantially decreased k<sub>s</sub> will slow down the 26 27 transfer of ABA from root to leaf, which may contributed to the unsynchronized response of decreased k<sub>s</sub> and approaching stabilized G<sub>S</sub> of *E. urophylla*. 28

29

Even we didn't measured the  $k_s$  of root, trunk, or shoots, however, it was inferred

that the hydraulic conductivity of shoots may be responsible for the significant 1 decrease of k<sub>s</sub>, since many results had proved the branch dieback in periods of 2 extended drought across a variety of species (Kursar et al., 2009; Urli et al., 2013; 3 Choat et al., 2012). However, it also can't rule out other possibility, such as roots, 4 since Domec et al. (2010) also reported that embolism in roots explained the loss of 5 6 whole-tree hydraulic conductance and therefore indirectly constituted a hydraulic signal involved in stomatal conductance reduction for Liquidambar styraciflua and 7 8 Cornus florida.

9 However, Such a water-use strategy may contribute to high water-use efficiency 10 for E. urophylla, especially under dry conditions because of more reduced water flux in the xylem compared with less changed G<sub>S</sub> on the leaves. We found that G<sub>S</sub> 11 decreased by 22.4% from the wet to dry seasons, while  $k_s$  decreased by 45.3 to 65.6%, 12 13 much higher than G<sub>S</sub>. If the tree leaves in the wet and dry seasons have the same demand for CO<sub>2</sub>, the WUE will also be higher in the dry season. This possibility had 14 15 been demonstrated by some other studies (Brienen et al., 2011; Maseyk et al., 2011; Sharma et al., 2015; Liu et al., 2012). 16

### 17 **4.4 Tree size effect**

Here, we tried to determine the effect of tree size on plant physiology as 18 proposed in the "Introduction". Even no water stress was occurred in dry season, the 19 20 highly increased transpiration demands will also lead to the significantly change of  $k_s$ from wet to dry season (Figure 6b). As a result, the ratio of dry/wet k<sub>s</sub> decreases from 21 0.55 to 0.30 with increased tree size. We simulated the relationship between  $\psi_L$  and 22 percentage loss of PLC for large and small trees. A more sensitive k<sub>s</sub> was observed for 23 24 the dominant tree (Fig. 8). It was implied that large trees are more vulnerable in the 25 face of drought stress. Under these conditions, a higher resistance for dominant trees would lead to a rapid decrease in  $\psi_{\rm L}$  (Ambrose et al., 2009). A striking result was that 26 there was no significant differences (p=0.14 in wet and p=0.25 in dry season) among 27 tree sizes in our research. Controversial results also existed in some other studies. 28 Bleby et al. (2012) reported that the  $\Delta \Psi$  of trees with DBH of ~8cm was significantly 29

1 higher than that of ~14cm and ~5cm in the restored forest of *Eucalyptus marginata*, but not significant between~14cm and ~5cm. While  $\Delta \Psi$  in their study for trees of 2 3 ~14cm (DBH) in a natural E. marginata was much higher than that of ~8cm and ~5cm. However, both of the two sites shared a same increase of Huber value by 49.2% 4 and 33.3% respectively to maintain the hydraulic homeostasis. They argued that the 5 6 similar G<sub>S</sub> for and increased Huber value for ~14cm and 8cm trees in the restored plot can explain the relationship of  $\Delta \Psi$  among tree size. While in the natural forest,  $G_S$  of 7 8 ~14cm was significantly higher than that of ~8cm and 4cm in addition to the less compensatory Huber value, leading to a more stressed condition for large trees. The 9 same increase of Huber value (~70%) was also observed from 8cm to 16cm in our 10 11 plot, and similarly, G<sub>Sref-max</sub> showed no differences among tree sizes in dry season and stabilized when DBH>10cm after a gradually increase in wet season for E. urophylla 12 13 in our study (Figure 5). As a conclusion, we proposed that large trees may not be more stressed even the higher sensitivity of k<sub>s</sub> (unless it reached a threshold leading to 14 hydraulic failure such like cavitation) because of the less increased G<sub>S</sub> and structural 15 compensation of Huber value. 16

# 17 **4.5 Elastic fluctuating stomatal sensitivity to radiation**

18 The variation of -m seems significantly related with  $Q_0$  via two different phases (Figure 4b). When light was limited, the increase of  $Q_0$  will stimulate the opening of 19 stomas, as showed in Figure 4a, until the threshold was reached. Meanwhile, the 20 21 increased -m shared a same turning point of Q<sub>0</sub> with G<sub>Sref</sub> before gradually decreased. 22 In other words, the stomatal sensitivity was largely dependent on the photosynthetic 23 demands for light in this phase. Despite of the stabilized G<sub>Sref</sub>, the stomas tended to be 24 less and less sensitive to the increased D as  $Q_0$  was improved when light was abundant. However, the increase of  $Q_0$  was usually accompanied by the enhanced 25 transpiration rates (Oren et al., 2001), which will further reduce the  $\Psi_L$  if sap flow is 26 27 insufficient to the refill the water content in the leaf. As we discussed above, the decreased  $k_s$  didn't lead to a substantially closed stomas even  $\Psi_L$  was very low 28 (Figure 6a, b), which may contribute the less sensitive stomas under high light 29

1 condition. Evidence was found in the lower -m in dry season even though  $Q_0$  ranges 2 was higher in wet season (figure 4b).  $Q_0$  of  $G_{S90}$  in the dry (287.8 µmol m<sup>-2</sup> s<sup>-1</sup>) and 3 wet seasons (167.1 µmol m<sup>-2</sup> s<sup>-1</sup>) also support this hypothesis (Figure 4a).

It is unfortunate that, to date, none of the previous studies associated with 4 stomatal sensitivity considered light as an independent factor; therefore, we cannot 5 assert whether the hypothesis is true or not. If it was true, plants that grow near the 6 equator will be predicted to be less sensitive to changes in D, and compared to 7 dominant trees in the forest, plants growing under the canopy will be inversely more 8 9 sensitive as light is more precious there. Schäfer et al. (2000) assessed the importance 10 of the mechanism for sustaining gas exchange in tall trees by directly relating -m to  $G_{\text{Sref}}$  and concluded that tall trees have lower  $G_{\text{Sref}}$  sensitivity than short trees. They 11 argued that the lower stomatal sensitivity in tall trees ensures a more stable carbon 12 13 uptake rate over the wide diurnal range of D and may serve to support carbon exchange. However, there is no doubt that light plays a significant role in controlling 14 the stomata response to D. Obviously, further studies are needed for revealing the 15 mechanism within this relationship. 16

### 17 5. Conclusion

a) Transpiration was largely controlled by evaporative demand, with a weak effect of SWC. 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 conductance imposed restrictions on excessive evaporative demands, and the less changed  $G_S$  when  $\Psi_L <-1.6$  MPa mirrored a anisohydric behavior for *E. urophylla*, which may contribute the Higher WUE of *Eucalyptus* when the more decreased k<sub>s</sub> was compared.
- 28 c) Our results verified the hypothesis that trees of different sizes have different

strategies to respond to climate factors (D, Q<sub>0</sub>, and SWC). As a tree grows, k<sub>s</sub> is
 more sensitive to water loss. However, the stalblized G<sub>Sref-max</sub> (in dry season) and
 continually increased Huber value with DBH may compensate this effect, leading
 to insignificant deviated ΔΨ among trees.

d) The decrease in stomatal sensitivity of G<sub>Sref</sub> 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.

9

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28	Figure Legend



Figure 1. Precipitation (P), soil water content (SWC) and evaporative demands (D)
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. Relationship between DBH and (a) averaged daily transpiration ( $E_T$ ), (b) averaged total nocturnal water use ( $E_{T-NOC}$ ), Data are mean ±SE, all linear fittings are significant at the p<0.05 level. The insets in the figure represent the mean  $E_T$  (a) and  $E_{T-NOC}$  (b) of 15 trees in dry and wet season respectively, letters imply a significant difference between dry and wet season.





Figure 3. The sensitivity of average stomatal conductance of tree individuals at each light level in response to increasing vapour pressure deficit ( $-dG_{Si}/dlnD$ ) as a function of the canopy stomatal conductance at D=1 kPa ( $G_{Sref}$ ) in dry (open symbol) and wet season (solid symbol). Different symbols represent the different light levels of the 15 trees.

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- 8
- 9
- 10
- -0
- 11
- 12

- 14
- -+
- 15



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 dry (open symbols) and wet season (solid symbols). Lines are least-square fit through the entire data. Different symbols in the figure represent the 15 tree individuals. Light and dark lines respond to the least square fit in dry and wet season respectively.

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Figure 5. Relationship between DBH and max stomatal conductance at reference D
(=1kPa) (G<sub>Sref-max</sub>) deducted from Fig. 3. Lines represent least square fits for dry
(white circle) and wet (black circle) season respectively, data are mean ±SE.



Figure 6. (a) Limitation of leaf water potential (at noon, 12:00-13:00) 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 normalized by the data of each tree on April 19, 2013.

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Figure 7. Percentage loss of hydraulic conductivity (PLC) as a function of xylem water potential ( $\Psi_L$ ) for small (tree 1, DBH=8.1 cm) and large (tree 15, DBH=16.1cm) *E. urophylla* trees. The assumption here is PLC=0 when  $\Psi_L$ =0 and PLC=100% when  $\Psi_L$ =-3.0MPa for most species,  $\Psi_L$  in dry and wet seasons is used to simulate the curve.