



# The influence of bamboo culm water content on sap flux measurements with thermal dissipation probes: observations and modeling

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## Abstract

**Key message** Water content fluctuations in bamboo culms significantly influence sap flux measurements with thermal dissipation probes, as indicated and quantified by experimental, monitoring and model analyses.

**Abstract** Bamboos and other plants may substantially rely on stem water storage for transpiration. Fluctuations in wood water content ( $\theta_{\text{wood}}$ ) may lead to errors when estimating transpiration based on sap flux ( $J_s$ ) measurements with the widely used thermal dissipation probe (TDP) method. To test the effects of  $\theta_{\text{wood}}$  on  $J_s$ , we conducted a culm dehydration experiment, monitored bamboos with TDPs, and implemented a steady-state thermal model. Based on the model simulation, a mathematical correction method was built. Central to the calculation of  $J_s$ , and thus a major potential source of error, is the maximum temperature difference between probes ( $\Delta T_{\text{max}}$ ) which is often referred to as ‘zero flow’ conditions. In the culm dehydration experiment, we observed that  $\Delta T_{\text{max}}$  decreased when  $\theta_{\text{wood}}$  increased. In long-term field monitoring,  $\Delta T_{\text{max}}$  decreased when soil moisture content increased, potentially indicating changes in  $\theta_{\text{wood}}$  and a seasonal decrease in stem water storage. The steady-state model reproduced the  $\theta_{\text{wood}}$  to  $\Delta T_{\text{max}}$  relationship of the dehydration experiment and underlined a considerable sensitivity of  $J_s$  estimates to  $\theta_{\text{wood}}$ . Fluctuations in  $\theta_{\text{wood}}$  may lead to a substantial underestimation of  $J_s$ , and subsequently of transpiration, in commonly applied estimation schemes. However, our model results suggest that such underestimation can be quantified and subsequently corrected for with our correction equations when key wood properties are known. Our study gives insights into the relationship between  $\theta_{\text{wood}}$  and TDP-derived  $J_s$  and examines potential estimation biases.

**Keywords** Calibration · Culm water storage · Soil moisture content · Steady-state thermal model · Transpiration · Zero sap flow

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## Introduction

Plant stems are the pathways of soil water to the leaves for transpiration (Tyree and Sperry 1988). Measuring sap flow in stems and up-scaling it to plant transpiration can be conducted with several different sap flow methods such as the stem heat balance method, the heat pulse method or the thermal dissipation method (Smith and Allen 1996). Among

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these methods, the thermal dissipation probe (TDP) method (Granier 1985) is the most widely used one. Its advantages include its relatively low cost as well as relatively easy sensor construction and installation (Lu et al. 2004). The empirical TDP formula for the calculation of sap flux density ( $J_s$ ,  $\text{g m}^{-2} \text{s}^{-1}$ ) was first put forward by Granier (1985);  $J_s$  is expressed as a function of the temperature difference ( $\Delta T$ ) between a heating probe and a reference probe:  $J_s = 119 \times (\Delta T_{\text{max}}/\Delta T - 1)^{1.231}$ , where  $\Delta T_{\text{max}}$  is the  $\Delta T$  under zero flow condition, which is commonly substituted by the diurnal nighttime maximum  $\Delta T$  (Granier 1987).

As Granier's formula was derived from an empirical relationship of three tree species (*Pseudotsuga menziesii*, *Pinus nigra* and *Quercus pedunculata*; Granier 1985) rather than being based on wood physical properties (Wullschleger et al. 2011), the TDP method has been reported to substantially over- or underestimate  $J_s$  in various studies (Clearwater et al. 1999; Steppe et al. 2010; Bush et al. 2010). Potential reasons for observed divergences include non-uniform sap flow along the sensor (Clearwater et al. 1999), lacking compensation for the 'wound effect' (Wullschleger et al. 2011) and gradients in temperature along the stem (Do and Rocheteau 2002). Further, the effects of variations in wood water content ( $\theta_{\text{wood}}$ ) of the stem on the accuracy of TDP measurements have been the subject of investigation (Lu et al. 2004; Tatarinov et al. 2005; Vergeynst et al. 2014). Generally, the depletion and recharge of water storage in stems can lead to substantial fluctuations of  $\theta_{\text{wood}}$  (Nadler et al. 2008; Yang et al. 2015), which may influence wood thermal conductivity ( $K_{\text{wood}}$ ) and subsequently estimates of  $J_s$ . Based on theoretical analysis of the temperature– $\theta_{\text{wood}}$  relationship (Carslaw and Jaeger 1959) and a laboratory dehydration experiment on tree stem segments (Vergeynst et al. 2014), it was demonstrated that  $\theta_{\text{wood}}$  influenced  $K_{\text{wood}}$  around TDP probes and caused underestimations of daytime  $J_s$ . These underestimations were attributed to selecting one single  $\Delta T_{\text{max}}$  (usually at night) to calculate hourly  $J_s$  for the whole day (Granier 1987), while ignoring potentially differing  $K_{\text{wood}}$  between nighttime and daytime. Additionally, the influence of  $\theta_{\text{wood}}$  on  $\Delta T_{\text{max}}$  may differ with soil water conditions, as previous studies found that  $\theta_{\text{wood}}$  in trees and palms fluctuates with  $\theta_{\text{soil}}$  on the longer (i.e., monthly, seasonal) term (Constantz and Murphy 1990; Holbrook et al. 1992; Wullschleger et al. 1996). Further, on rainy days, trunk  $\theta_{\text{wood}}$  was reported to be significantly increased, and subsequently decreased during the following sunny days (Holbrook et al. 1992; Wullschleger et al. 1996; Hao et al. 2013), which may further influence  $K_{\text{wood}}$  around TDP probes, and thus  $\Delta T_{\text{max}}$ . Ignoring these influences could lead to a potential misinterpretation of the patterns or values of TDP-derived  $J_s$ .

In a previous study on bamboo water use, underestimated  $J_s$  by TDP was observed when using the original parameters of the calibration equation (Granier 1985), while newly

calibrated, species-specific equation parameters significantly improved the accuracy of the estimation (Mei et al. 2016). Among the potential reasons for the underestimation by the TDP approach on bamboos is the thus-far neglected influence of dynamics in  $\theta_{\text{wood}}$ . Bamboo culms have a large percentage of parenchyma (Liese and Köhl 2015), which provides a potential 'buffering' reservoir for transpiration. With the withdrawal from and refilling of water to this reservoir,  $\theta_{\text{wood}}$  may fluctuate accordingly, which can induce changes in culm circumference (Yang et al. 2015). Changes in  $\theta_{\text{wood}}$  in bamboo culms may at least partly be responsible for underestimations of  $J_s$  by influencing  $K_{\text{wood}}$  of the culm and consequently  $\Delta T_{\text{max}}$ .

However, the mentioned factors are rather difficult to assess under field conditions and are commonly ignored in TDP studies on bamboos and trees, which is mainly due to practical constraints and the difficulty of measuring the dynamics of temperature around the TDP sensors. One promising approach could be series of controlled numerical simulations of  $\theta_{\text{wood}}$  encompassing different scenarios. Such numerical simulations have previously been successfully applied to investigate the uncertainty of factors such as wood thermal conductivity, non-homogeneity of radial sap flow profiles or external temperature gradients on thermal-based methods including the TDP approach (Tatarinov et al. 2005) and to analyze the influence of wood and probe properties (Wullschleger et al. 2011) and of heat storage capacity (Hölttä et al. 2015) on the accuracy of TDP estimates.

Partially based on such series of numerical simulations, we hypothesized that the change of  $K_{\text{wood}}$ , responding to diurnal and seasonal fluctuations of  $\theta_{\text{wood}}$ , induces estimation biases in  $\Delta T_{\text{max}}$  and thus in TDP-derived daytime  $J_s$ ; this may (partly) be responsible for the mentioned underestimations of  $J_s$ . Therefore, the objectives of our study were (1) to test on bamboo segments in a laboratory dehydration experiment whether  $\Delta T_{\text{max}}$  is affected by decreasing  $\theta_{\text{wood}}$ , and to explore if  $\Delta T_{\text{max}}$  in bamboos is influenced by changes in  $\theta_{\text{soil}}$  under field conditions, and (2) to quantify and if necessary correct for potential deviations of  $J_s$  in bamboo culms with a steady-state thermal model. Our study is intended as a methodological baseline study to evaluate and improve the accuracy of TDP measurements on bamboos.

## Methods

### Culm $\theta_{\text{wood}}$ , $\theta_{\text{soil}}$ and $\Delta T_{\text{max}}$

To test if  $\Delta T_{\text{max}}$  is affected by changes in  $\theta_{\text{wood}}$  in bamboos, we applied three different approaches: (1) a dehydration experiment on freshly cut culm segments of *Gigantochloa apus*, (2) long-term field monitoring of  $\theta_{\text{soil}}$  and daily TDP-derived  $\Delta T_{\text{max}}$  on culms of three bamboo species (*Bambusa*

*vulgaris*, *Dendrocalamus asper*, *G. apus*), and (3) numerical simulation experiments with a steady-state thermal model based on the geometry and physical characteristics of a segment of *B. vulgaris*.

### Laboratory dehydration experiment

Similar to previously conducted dehydration experiments on tree segments (Vergeynst et al. 2014), we performed dehydration experiments on freshly cut culm segments of *G. apus*; our laboratory experiments took place in May 2013. Before the actual experiments, a freshly sprouted culm of *G. apus* (diameter 7.3 cm) was cut before sunrise in the common garden of Bogor Agriculture University, Bogor, Indonesia. From the cut culm, three segments (each 20 cm in length) were collected and immediately transported to the laboratory inside a sealed plastic bag to prevent water loss. In the laboratory, the segments were soaked in 40 mM of KCl solution for 24 h to ensure that they reached saturation moisture content. After that, water on the surface of the segments was removed with tissues, while the two ends of each segment were sealed with glue. This ensured that they subsequently only and uniformly dehydrated from the outer culm surfaces.

As a first step of the actual dehydration experiment, the fresh weight of each segment ( $w_{\text{fresh}}$ , g) was obtained with a balance with 0.01 g resolution (KB2400-2N, KERN & SOHN GmbH, Balingen, Germany). Each segment was then laid down horizontally and a pair of 1 cm-long TDP was installed in the culm wall (Mei et al. 2016). The heating and reference probes were placed 10 cm apart, at 5 cm distance to each end of the segment.

As a second step, cycles of 3-h probe powering and subsequent 2-h dehydration periods were conducted repeatedly over the duration of 5 days. During the powering phase, the heating probe of the TDP sensors was continuously powered with 0.1 W to obtain stable  $\Delta T_{\text{max}}$  readings. During this interval, room temperature was kept constant at about 20 °C and laboratory conditions prevailed (constant light, only little air circulation); the segments thus dehydrated only marginally during this time. During the following 2-h dehydration period, the power of the heating probe was turned off and the segments were placed under an electric fan to artificially accelerate the dehydration process. The segments were further continuously turned to ensure uniform dehydration. At the end of each 2-h period, TDP sensors were removed and the segments were weighted. By continuously repeating the powering-dehydration cycles, data pairs of  $w_{\text{fresh}}$  vs.  $\Delta T_{\text{max}}$  were produced and recorded.

After the end of the dehydration experiments, the segments were oven dried at 100 °C for 48 h to get their dry weight ( $w_{\text{dry}}$ , g). With the  $w_{\text{dry}}$  and  $w_{\text{fresh}}$  of each

powering-dehydration cycle, the  $\theta_{\text{wood}}$  ( $\text{kg kg}^{-1}$ ) was calculated as  $(w_{\text{fresh}} - w_{\text{dry}})/w_{\text{dry}}$ . Subsequently, the relationship between  $\theta_{\text{wood}}$  and  $\Delta T_{\text{max}}$  was examined.

### Field monitoring of $\theta_{\text{soil}}$ and $\Delta T_{\text{max}}$

To explore whether, and if so how,  $\Delta T_{\text{max}}$  in bamboo culms was influenced by the  $\theta_{\text{soil}}$  under field conditions, we monitored daily TDP-derived  $\Delta T_{\text{max}}$  on three culms each of *D. asper* and *G. apus* and on four culms of *B. vulgaris* for 7 months (July 2012–April 2013). Simultaneously,  $\theta_{\text{soil}}$  at 20 cm depth was monitored at the respective study sites with time-domain reflectometry sensors (TDR, CS616, Campbell, Logan, USA). For a detailed description of the installation process refer to Mei et al. (2016). Subsequently, the relationship between  $\Delta T_{\text{max}}$  and daily mean  $\theta_{\text{soil}}$  was examined.

### $\theta_{\text{wood}}$ and thermal conductivity for the numerical model

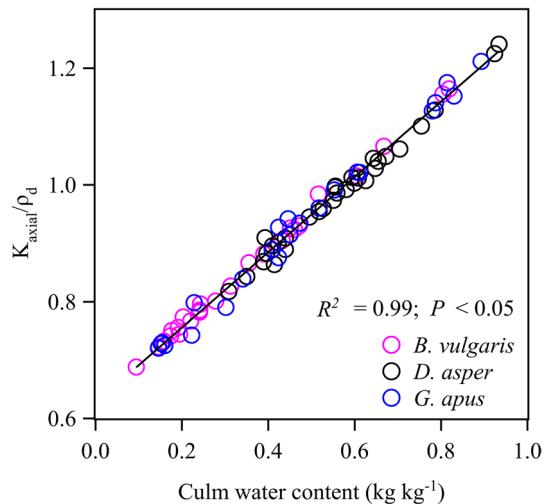
As the theoretical basis of the following numerical model, the relationship of thermal conductivity of wood ( $K_{\text{wood}}$ ) and  $\theta_{\text{wood}}$  was applied following Vandegheuchte and Steppe (2012a, b), who introduced a corrected thermal conductivity for axial directions ( $K_{\text{axial}}$ ,  $\text{W m}^{-1} \text{K}^{-1}$ ):

$$K_{\text{axial}} = K_w(\theta_{\text{wood}} - \theta_{\text{wood-FSP}}) \frac{\rho_{\text{dry}}}{\rho_w} + 0.04186 \times (21.0 - 20.0 \times F_{\text{v-FSP}}), \quad (1)$$

where  $K_w$  is thermal conductivity of water ( $0.6 \text{ W m}^{-1} \text{K}^{-1}$ ),  $\theta_{\text{wood-FSP}}$  is  $\theta_{\text{wood}}$  at the fiber saturation point (%),  $\rho_{\text{dry}}$  and  $\rho_w$  are the respective densities of dry wood and water ( $1000 \text{ kg m}^{-3}$ ) and  $F_{\text{v-FSP}}$  is the void fraction of wood at the fiber saturation point.  $\theta_{\text{wood-FSP}}$  and  $F_{\text{v-FSP}}$  were calculated with several different approaches, using  $\rho_{\text{dry}}$  and  $\rho_w$  (see details in Online Resource 1).

To obtain  $\rho_{\text{dry}}$  of bamboo culms, all culms of the three species that were monitored in our study were harvested at 6:00 am on 15, 16 and 28 April 2013. Segments were obtained every 2 m on the respective culms. The segments were immediately transported to the laboratory in sealed plastic bags. The fresh volumes ( $v_{\text{fresh}}$ ,  $\text{cm}^3$ ) of the segments were derived by measuring lengths and inner and outer radii of the cylindrical segments; additionally, the  $w_{\text{fresh}}$  of each segment was established. After that, the segments were dried in an oven at 100 °C for 48 h to get their  $w_{\text{dry}}$ . Subsequently,  $\rho_{\text{d}}$  could be calculated as  $w_{\text{dry}}/v_{\text{fresh}}$ .

With the mentioned variables ( $\rho_{\text{dry}}$ ,  $\rho_w$ ,  $\theta_{\text{wood-FSP}}$  and  $F_{\text{v-FSP}}$ ), we calculated series of  $K_{\text{axial}}$  with  $\theta_{\text{wood}}$  ranging from 0.1 to 1  $\text{kg kg}^{-1}$  (in incremental 0.1  $\text{kg kg}^{-1}$  steps); the thermal conductivity in the transverse direction ( $K_t$ ) was set to half the value of the  $K_{\text{axial}}$  (Wullschlegel et al. 2011). The linear relationship between the  $K_{\text{axial}}$  and  $\theta_{\text{wood}}$  of the



**Fig. 1** The relationship between the ratio of thermal conductivity in the axial direction ( $K_{\text{axial}}$ ) to culm dry density ( $\rho_d$ ) and culm water content. The relationship was derived by Eq. 1

**Table 1** The parameters for the ANSYS numerical simulation

Parameters	Values	Reference
Specific heat capacity of fresh wood	1644 J kg <sup>-1</sup> K <sup>-1</sup>	Measured
Dry wood density	956 kg m <sup>-3</sup>	Measured
Heating probe power	1444 W m <sup>-2</sup>	Measured
Probe length	1 cm	Measured
Ambient temperature	300 K/26.85 °C	Set

bamboo culms was derived (Fig. 1), and this relationship was applied in the following numerical steady-state thermal model to set the corresponding parameters.

### Steady-state thermal model

To test if  $\Delta T_{\text{max}}$  decreased with increasing  $\theta_{\text{wood}}$  in bamboos, numerical simulations of temperature distributions were performed with a steady-state thermal model (Academic version, CFX 17.0, ANSYS Inc., PA, USA). The simulations were conducted on a 3D anisotropic grid by numerically solving the steady-state energy balance equation:

$$-\lambda \nabla^2 T + c_w Q_w \nabla T = q, \quad (2)$$

where  $q$  is the heat input of a grid (W m<sup>-3</sup>),  $T$  is the temperature of a grid (K),  $\lambda$  is matrix of thermal conductivity (W m<sup>-1</sup> K<sup>-1</sup>),  $\nabla$  is vector differential operator,  $c_w$  is the specific heat of water (J kg<sup>-1</sup> K<sup>-1</sup>) and  $Q_w$  is the sap flow vector (kg m<sup>-2</sup> s<sup>-1</sup>). To explore the relationship between  $\theta_{\text{wood}}$  and

$\Delta T_{\text{max}}$ ,  $Q_w$  was set to zero sap flow when aiming to simulate  $\Delta T_{\text{max}}$  (see detailed parameters in Table 1).

To simplify the simulation, the geometry of the model was based on a simplified 3D bamboo segment, i.e., a cuboid with 20 cm height, 6.65 cm width, and 1 cm depth, ignoring the curvature of the stem surface. The heating probe of the TDP sensor was modeled as an aluminum tube with its actual dimensions, i.e., 0.235 cm in diameter and 1 cm in length (Mei et al. 2016); it was inserted through into the 1-cm-wide simulated culm wall of the cuboid, in the center of the segment (Wullschleger et al. 2011). Resembling the (actual) field methodology, the unheated reference probe was positioned 10 cm upstream from the heating probe. Along the length of the heating probe, the temperature was assumed to be fairly uniform (Wullschleger et al. 2011), and wood physical properties along the probe were also assumed to be uniform. The steady-state simulations were thus simplified for both the front and back surfaces of the segment. Generally, a 2 mm (quadratic) mesh was used for the thermal steady-state model. To better fit the round shape of the heating probe, mesh type was set to quad/tri for the contact area between the heating probe and the surrounding wood.

The boundary conditions of the segment surfaces included inlet, outlet, probe, symmetric surfaces (front and back) and wall. The inlet surface was located on the upstream side and the water came into the segment from the inlet. The outlet surface was located on the downstream side and the pressure was set to 0 Pa. The heating probe was located in the center of the bamboo segment and was powered with 1444 W m<sup>-2</sup> (the input power divided by the surface area of the aluminum tube). The front and back surfaces of the wood domain were set as symmetric, which means any plane between the front and back surfaces has same physical and thermal properties. The left and right sides of the bamboo segment were defined as walls with no water flowing out of the segment. The initial temperatures on all segment surfaces and of sap water were set to 300 K (26.85 °C) by default in the ANSYS model.

### The influence of $\theta_{\text{wood}}$ on $J_s$ simulated in ANSYS model

To simulate the influence of varying  $\theta_{\text{wood}}$  on TDP-derived  $J_s$  in bamboo culms, we simulated the  $\Delta T$  between probes in a series of numerical simulations of  $J_s$  and  $\theta_{\text{wood}}$ . We incrementally increased  $J_s$  from 0 to 30 g cm<sup>-2</sup> h<sup>-1</sup> in 5 g cm<sup>-2</sup> h<sup>-1</sup> steps and  $\theta_{\text{wood}}$  from 0.1 to 1 kg kg<sup>-1</sup> in 0.1 kg kg<sup>-1</sup> steps, and thus got a series of  $\Delta T$  under each combination of  $J_s$  and  $\theta_{\text{wood}}$ . The  $\Delta T$  of each possible combination at zero  $J_s$  was used as  $\Delta T_{\text{max}}$ . The settings of geometry, meshing and change of  $K_a$  against  $\theta_{\text{wood}}$  followed the previously described model description (see “ $\theta_{\text{wood}}$  and thermal conductivity for the numerical model”).



Two scenarios were simulated: (1) relative to a fixed nighttime  $\theta_{\text{wood}}$  ( $\theta_{\text{wood\_night}}$ , e.g. 1 kg kg<sup>-1</sup>), where the daytime  $\theta_{\text{wood}}$  ( $\theta_{\text{wood\_daytime}}$ ) was reduced in 0.1 kg kg<sup>-1</sup> steps until its minimum 0.1 kg kg<sup>-1</sup>; in total, 45 pairs of  $\theta_{\text{wood\_night}}$  and  $\theta_{\text{wood\_daytime}}$  were simulated; (2) based on different  $\theta_{\text{wood\_night}}$  (0.3, 0.6 and 0.9 kg kg<sup>-1</sup>), where  $\theta_{\text{wood\_daytime}}$  was reduced by a constant ratio (i.e., half of  $\theta_{\text{wood\_night}}$ ). The first scenario was simulated to explore the influence of changes in  $\theta_{\text{wood}}$  between daytime and nighttime ( $\Delta\theta_{\text{wood}}$ ) on diurnal (daytime)  $J_s$ . The second scenario compared the varying influence of  $\Delta\theta_{\text{wood}}$  on daytime  $J_s$  among days with different  $\theta_{\text{wood\_night}}$  but with the same relative reduction during the daytime. The second scenario likely occurs, e.g. between different seasons (dry vs. wet season) or among days with different weather conditions (e.g. sunny vs. rainy days).

For a set  $\theta_{\text{wood\_daytime}}$  (e.g.  $\theta_{\text{wood\_daytime}} = 0.1$  kg kg<sup>-1</sup>), the derived  $\Delta T$  were used to calculate  $J_s$  in two ways: (1),  $J_s$  was calculated with  $\Delta T_{\text{max}}$  derived from  $\theta_{\text{wood\_night}}$  values equal to the set  $\theta_{\text{wood\_daytime}}$ ; (2), a biased  $J_s$  ( $J_{s\_bias}$ ) was calculated with a  $\Delta T_{\text{max}}$  derived from a  $\theta_{\text{wood\_night}}$  that was higher than the set  $\theta_{\text{wood\_daytime}}$  (e.g.  $\theta_{\text{wood\_night}} = 0.9$  kg kg<sup>-1</sup>). The respective relative changes of  $J_s$  ( $\Delta J_s$ ) were calculated as  $\Delta J_s = (J_{s\_bias} - J_s)/J_s$ . To determine the influence of using different (e.g. biased vs. un-biased)  $\Delta T_{\text{max}}$  on daily accumulated  $J_s$ , the relationship between  $\Delta J_s$  and  $\Delta\theta_{\text{wood}}$  was then applied to one culm of *B. vulgaris* on a sunny day as a case study.

### Correcting $J_{s\_bias}$

To correct the  $J_{s\_bias}$ , in a first step, we compared  $\Delta J_s$  to  $J_{s\_bias}$  for each combination of  $\theta_{\text{wood\_daytime}}$  and the mismatched  $\theta_{\text{wood\_night}}$  by applying a continuous logistic equation with three variables ( $\Delta J_{s\_max}$ ,  $\Delta J_{s\_0}$ ,  $r$ ):

$$\Delta J_s = \Delta J_{s\_max} / \left( 1 + \left( \frac{\Delta J_{s\_max}}{\Delta J_{s\_0}} - 1 \right) \times e^{-r \times J_{s\_bias}} \right), \quad (3)$$

where  $\Delta J_{s\_max}$  is the maximum  $\Delta J_s$ ; note that as  $\Delta J_s$  is negative value,  $\Delta J_{s\_max}$  is the value closest to 0 and means the least relative change between  $J_{s\_bias}$  and  $J_s$ ;  $\Delta J_{s\_0}$  is the  $\Delta J_s$  when  $J_{s\_bias}$  is 0;  $r$  is the maximum increasing rate of  $\Delta J_s$ , for each  $\Delta J_s$  and per unit of increase in  $J_{s\_bias}$  ((g cm<sup>-2</sup> h<sup>-1</sup>)<sup>-1</sup>), in analogy to the maximum rate of population increasing per capita per year in logistic regression of population growth (Balakrishnan 1991, vlab.amrita.edu 2011).

As a second step, the three parameters of Eq. 3 ( $\Delta J_{s\_max}$ ,  $\Delta J_{s\_0}$ ,  $r$ ), for all combinations that passed the logistic regression, were fitted with  $\theta_{\text{wood\_daytime}}$  and the mismatched  $\theta_{\text{wood\_night}}$  by linear regressions. Then, we replaced the three parameters in Eq. 3 with  $\theta_{\text{wood\_daytime}}$  and the mismatched  $\theta_{\text{wood\_night}}$ , so that the  $\Delta J_s$  was instead represented

as a function of  $\theta_{\text{wood\_daytime}}$ , the mismatched  $\theta_{\text{wood\_night}}$  and  $J_{s\_bias}$ . The thus derived  $\Delta J_s$  was subsequently used to correct  $J_{s\_bias}$ :

$$J_{s\_corrected} = J_{s\_bias} / (1 + \Delta J_s) \\ = J_{s\_bias} / \left( 1 + \Delta J_{s\_max} / \left( 1 + \left( \frac{\Delta J_{s\_max}}{\Delta J_{s\_0}} - 1 \right) \times e^{-r \times J_{s\_bias}} \right) \right). \quad (4)$$

For all data analysis and plotting presented in our study, we used SAS 9.3 (SAS Institute Inc., Cary, NC, USA).

## Results

### $\Delta T_{\text{max}}$ and $\theta_{\text{wood}}/\theta_{\text{soil}}$

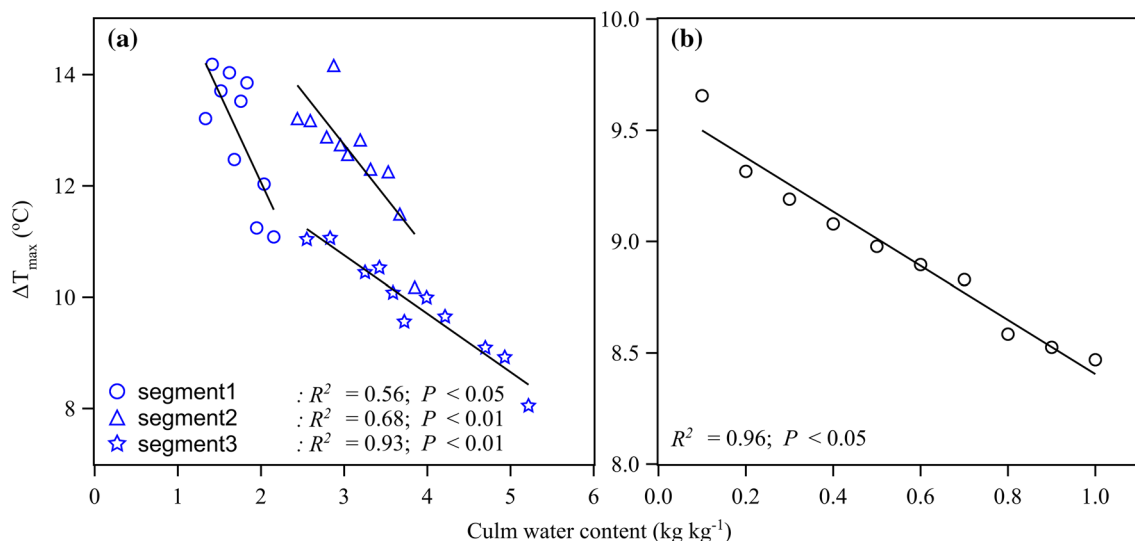
In the laboratory dehydration experiment, the three freshly sprouted bamboo segments of *G. apus* showed differences in  $\theta_{\text{wood}}$  vs.  $\Delta T_{\text{max}}$  patterns. Nonetheless, all three segments showed significant negative linear correlations between  $\Delta T_{\text{max}}$  and  $\theta_{\text{wood}}$  ( $R^2 = 0.56, 0.68$  and  $0.93$  for the segment 1, 2 and 3, respectively;  $P < 0.05$ ; Fig. 2a). The negative linear relationship was also observed for simulated  $\theta_{\text{wood}}$  and  $\Delta T_{\text{max}}$  derived from the ANSYS model ( $R^2 = 0.96, P < 0.05$ ; Fig. 2b).

In the field monitoring, daily mean  $\theta_{\text{soil}}$  was found to have a significant negative linear relationship ( $P < 0.05$ ) with daily  $\Delta T_{\text{max}}$  for all three bamboo species (*D. asper*, *G. apus*, *B. vulgaris*; Fig. 3). The slope of the  $\Delta T_{\text{max}} - \theta_{\text{soil}}$  regression line was larger for *B. vulgaris* ( $-3.55$ ) than for *D. asper* ( $-1.91$ ) and *G. apus* ( $-2.14$ ).

### The influence of $\theta_{\text{wood}}$ on $J_s$

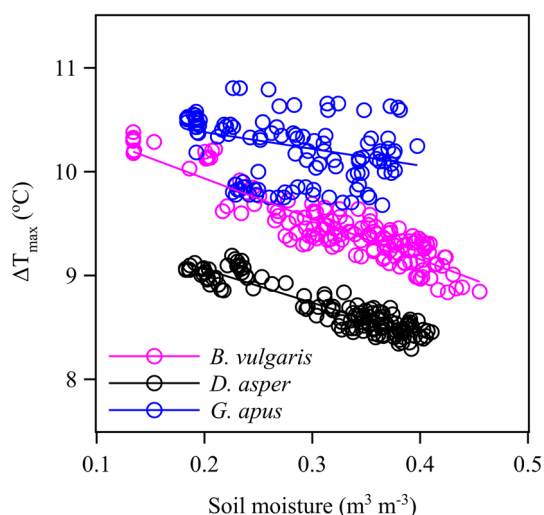
Keeping other controlling variables constant in the ANSYS model, large relative underestimation became apparent (1) for large decreases of  $\theta_{\text{wood}}$  from nighttime to daytime, (2) at relatively low  $J_s$ , and (3) for relatively larger nighttime  $\theta_{\text{wood}}$  when the ratio of decrease from daytime  $\theta_{\text{wood}}$  was kept constant (e.g. by half).

Using the ANSYS model for series of numerical simulations of  $\theta_{\text{wood}}$  and  $J_s$ , we found that TDP underestimated daytime  $J_s$  calculated with nighttime  $\Delta T_{\text{max}}$  when  $\theta_{\text{wood}}$  was lower during the day than during the night. For a given nighttime  $\theta_{\text{wood}}$  (e.g. 1 kg kg<sup>-1</sup>), lower daytime  $\theta_{\text{wood}}$  (e.g. 0.1 kg kg<sup>-1</sup>) led to large underestimation of  $J_s$  of up to 44% (Fig. 4). The  $\Delta J_s$  (%) was larger at lower  $J_s$ , and it gradually became smaller and approached to a stable value with increasing  $J_s$ . For example, the  $\Delta J_s$  was 18.6% at 5 g cm<sup>-2</sup> h<sup>-1</sup>, while being only 9.4% at 30 g cm<sup>-2</sup> h<sup>-1</sup>, when  $\theta_{\text{wood}}$  was decreased from 1 kg kg<sup>-1</sup> (nighttime) by 0.3 kg kg<sup>-1</sup> in the daytime (Fig. 4). Even though relative



**Fig. 2** The maximum temperature difference between the probes of TDP ( $\Delta T_{\max}$ ) in relation to the water content in culm segments of a freshly sprouted *G. apus* in **a** the dehydration experiment and **b** the

ANSYS simulation experiment. Different symbols indicate different segments. The unit of culm water content ( $\text{kg kg}^{-1}$ ) indicates kg water in the culm per kg dry weight



**Fig. 3** The daily maximum temperature difference between the probes of TDP ( $\Delta T_{\max}$ ) in relation to daily mean soil moisture for three bamboo species (*B. vulgaris*:  $Y = -3.55X + 10.54, R^2 = 0.63, P < 0.01$ ; *D. asper*:  $Y = -1.91X + 9.21, R^2 = 0.54, P < 0.01$ ; *G. apus*:  $Y = -2.14X + 11.10, R^2 = 0.37, P < 0.01$ )

errors were smaller at higher daytime  $J_s$ , they were responsible for most of the underestimation of daily accumulated  $J_s$ . Numerical simulations with the ANSYS model for reductions of  $\theta_{\text{wood\_daytime}}$  by 0.1 and 0.7  $\text{kg kg}^{-1}$  (corresponding to 0.9 and 0.3  $\text{kg kg}^{-1} \theta_{\text{wood\_daytime}}$ ) from 1  $\text{kg kg}^{-1} \theta_{\text{wood\_night}}$  resulted in underestimations of daily accumulated  $J_s$  by 2 and 19%, respectively (Fig. 5). For example, the relative

errors caused at  $J_s$  over 30  $\text{g cm}^{-2} \text{h}^{-1}$  constituted as much as 64% of the total underestimation of daily water use (Fig. 5).

For hypothetical reductions of  $\theta_{\text{wood\_night}}$  (0.3, 0.6, 0.9  $\text{kg kg}^{-1}$ ) to half of their respective values in the daytime (i.e., 0.15, 0.3 and 0.45  $\text{kg kg}^{-1}$ ), the highest (>25%) underestimation of daytime  $J_s$  were simulated for scenarios with high  $\theta_{\text{wood\_night}}$  (i.e., 0.9  $\text{kg kg}^{-1}$ ) under conditions of low  $J_s$  (e.g. 5  $\text{g cm}^{-2} \text{h}^{-1}$ ). With increasing  $J_s$ , the underestimation became smaller (e.g. <15% at 30  $\text{g cm}^{-2} \text{h}^{-1}$ ), particularly for lower (i.e., 0.3, 0.6  $\text{kg kg}^{-1}$ )  $\theta_{\text{wood\_night}}$  (e.g. <10% at 30  $\text{g cm}^{-2} \text{h}^{-1}$ , Fig. 6).

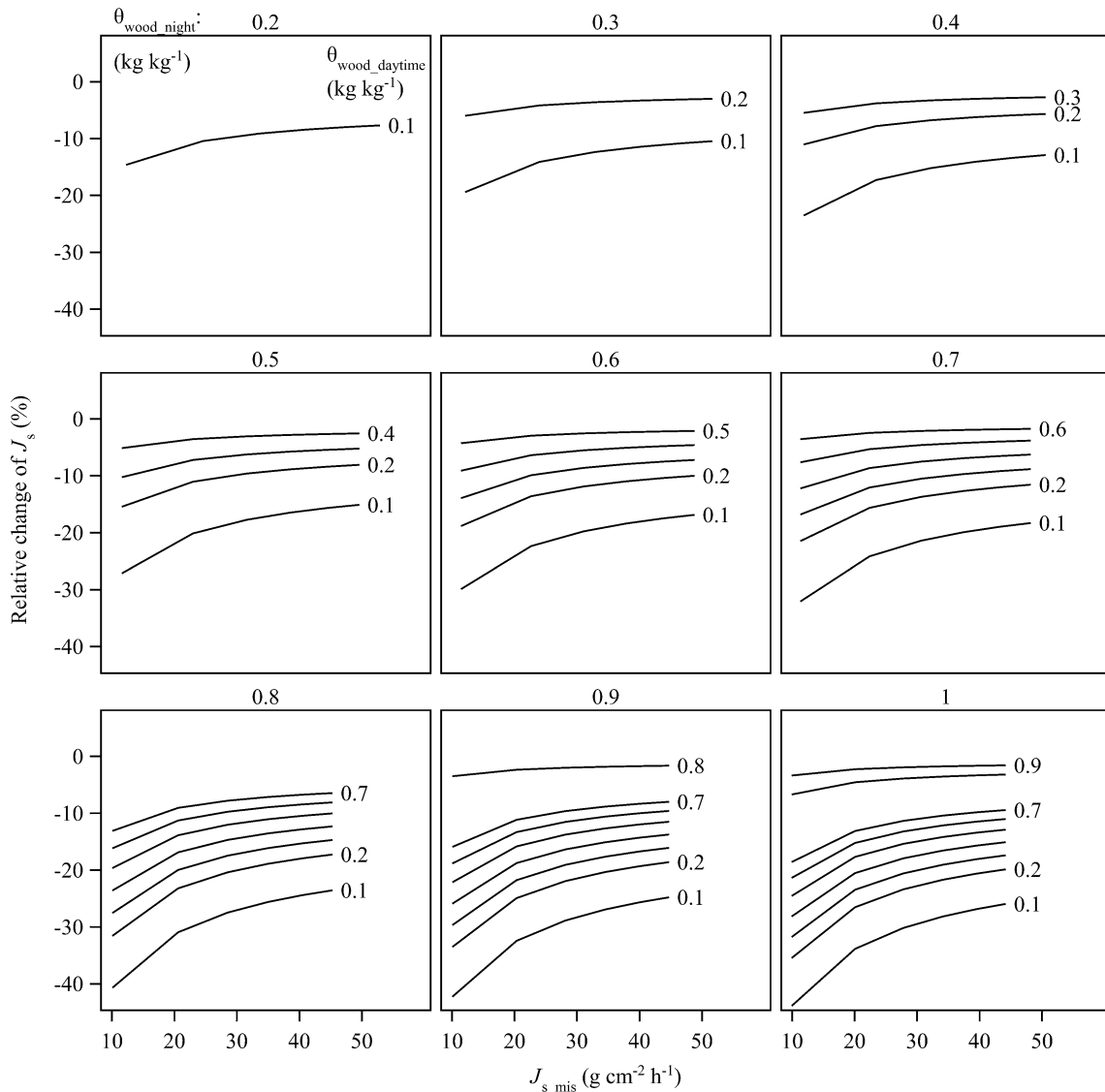
### Correcting $J_{s\_bias}$

Among the 45 combinations of  $\theta_{\text{wood\_night}}$  and  $\theta_{\text{wood\_daytime}}$  (Fig. 4), there are 21 whose  $\Delta J_s$  (negative percentage) and  $J_{s\_bias}$  converged when applying a logistic regression. Two of the three parameters ( $\Delta J_{s\_max}$  and  $\Delta J_{s\_0}$ ) derived in these 21 logistic regressions were linearly related with both  $\theta_{\text{wood\_night}}$  and  $\theta_{\text{wood\_daytime}}$  (Eqs. 5, 6), while  $r$  was correlated with  $\theta_{\text{wood\_night}}$  (Eq. 7), as shown below:

$$\Delta J_{s\_max} = -3.19\% - 0.20\% \times \theta_{\text{wood\_night}} + 0.25\% \times \theta_{\text{wood\_daytime}} \quad (R^2 = 0.94; P < 0.01) \quad (5)$$

$$\Delta J_{s\_0} = -24.93\% - 0.62\% \times \theta_{\text{wood\_night}} + 0.84\% \times \theta_{\text{wood\_daytime}} \quad (R^2 = 0.91; P < 0.01) \quad (6)$$

$$r = 0.03\% - 0.00005\% \times \theta_{\text{wood\_night}} \quad (R^2 = 0.96; P < 0.01) \quad (7)$$



**Fig. 4** The simulated relative change of daytime sap flux density ( $J_s$ ) in percentage (%) at different absolute  $J_s$  calculated with the mismatched  $\Delta T_{max}$  ( $J_{s\_bias}$ ,  $g\ cm^{-2}\ h^{-1}$ ). The value on the top of each sub-figure is the night water content ( $\theta_{wood\_night}$ ,  $kg\ kg^{-1}$ ), and the val-

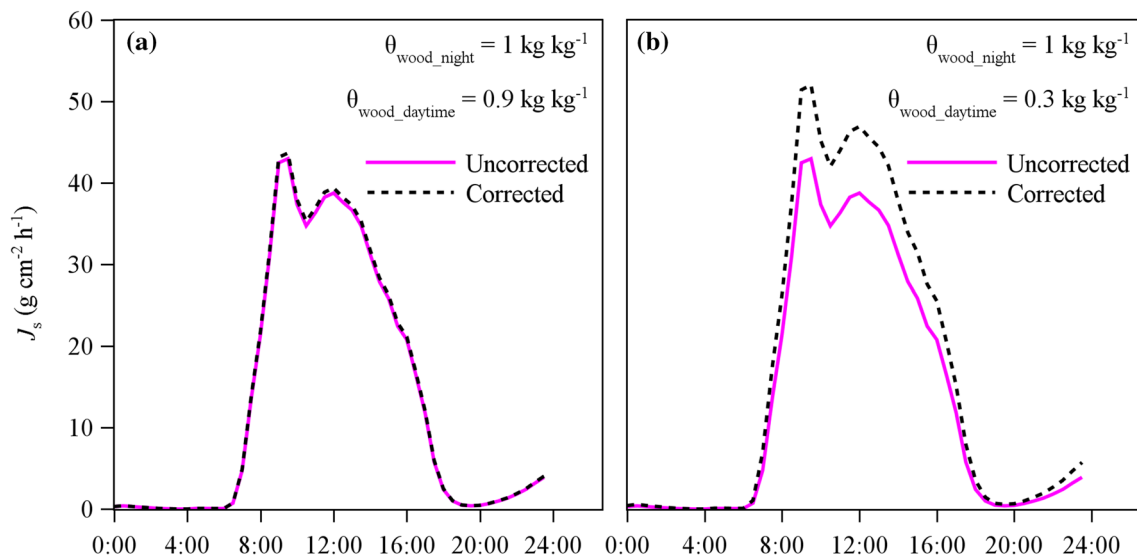
ues at the ends of the lines are daytime water content ( $\theta_{wood\_daytime}$ ,  $kg\ kg^{-1}$ ). The provided data based on numerical simulations with the ANSYS model

By inserting Eqs. 5–7 into Eq. 4, we derived an equation for correcting the previously discussed estimation biases. With this ‘correction equation’, we thus corrected  $J_{s\_bias}$  of the remaining 24 combinations of  $\theta_{wood\_night}$  and  $\theta_{wood\_daytime}$ , for which the logistic regression had not worked. Before correction,  $J_{s\_bias}$  was about 10% smaller than  $J_s$  ( $J_{s\_bias} = 0.90 \times J_s - 0.82$ ;  $R^2 = 0.98$ ;  $P < 0.01$ ; Online Resource 2 Fig. 2), while corrected  $J_{s\_bias}$  ( $J_{s\_corrected}$ ) was much closer to actual  $J_s$  ( $J_{s\_corrected} = 1.01 \times J_s - 0.64$ ;  $R^2 = 0.99$ ;  $P < 0.01$ ; Online Resource 2 Fig. 2).

## Discussion

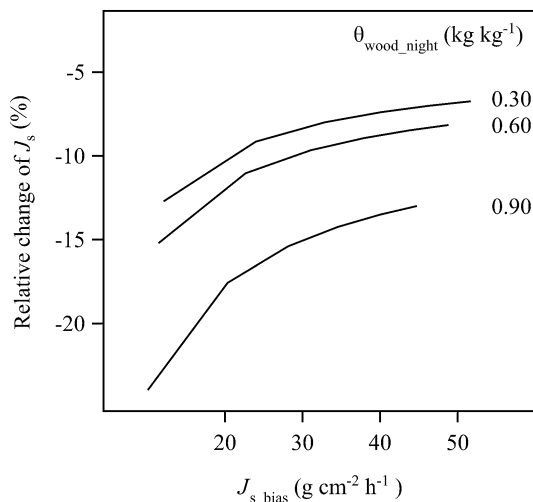
### $\Delta T_{max}$ and $\theta_{wood}/\theta_{soil}$

Granier’s formula for estimating  $J_s$  with TDP method is based on the assumption that wood thermal properties are constant throughout the day, which results in one constant diurnal  $\Delta T_{max}$  (Granier 1987). However,  $\Delta T_{max}$  actually changes as wood thermal properties fluctuate diurnally, which is not reflected when using a common  $\Delta T_{max}$ . This introduces estimation errors when calculating  $J_s$  based on a common daily  $\Delta T_{max}$  (Vergeynst et al. 2014). In our study,



**Fig. 5** The corrected sap flux density ( $J_s$ ) for different daytime culm wood water content ( $\theta_{\text{wood}}$ ,  $\text{kg kg}^{-1}$ ), **a**  $\theta_{\text{wood}}=0.9$  and **b**  $\theta_{\text{wood}}=0.3$ . Simulations based on field monitoring data of a *B. vulgaris* on 17 September 2012. Numerical simulations with the ANSYS model for

daytime  $\theta_{\text{wood}}$  of 0.9, 0.3  $\text{kg kg}^{-1}$  reduced from a 1  $\text{kg kg}^{-1}$  nighttime  $\theta_{\text{wood}}$  result in underestimation of daily accumulated  $J_s$  by 2, 19%, respectively



**Fig. 6** The simulated relative change of daytime sap flux density ( $J_s$ ) in percentage (%) at different absolute  $J_s$  calculated with the mismatched  $\Delta T_{\text{max}}$  ( $J_{s,\text{bias}}$ ,  $\text{g cm}^{-2} \text{h}^{-1}$ ). Relationships are provided for different nighttime stem water contents ( $\theta_{\text{wood,night}}$ , 0.3, 0.6 and 0.9  $\text{kg kg}^{-1}$ ), assuming a constant reduction (i.e., by half) in the ratio between nighttime and daytime  $\theta_{\text{wood}}$ . The provided data based on numerical simulations with the ANSYS model

a dehydration experiment was conducted on segments of freshly sprouted bamboo culms. The results show that decreasing culm  $\theta_{\text{wood}}$  led to increasing  $\Delta T_{\text{max}}$  (Fig. 2a). Similar results were found in a dehydration experiment on tree segments (Vergeynst et al. 2014). In trees, the fluctuation pattern of  $\theta_{\text{wood}}$  contrasted the daily fluctuation pattern

of transpiration.  $\theta_{\text{wood}}$  reached peak values during the night, when  $J_s$  was zero or marginal, and dropped to a minimum during the daytime (Hao et al. 2013; Sperling et al. 2015). On culms of the bamboo species *B. vulgaris*, a similar pattern of culm circumference was observed (Yang et al. 2015). Although Yang et al. (2015) did not perform direct measurements of  $\theta_{\text{wood}}$ , the daily dynamics of culm circumference can be expected to at least partly reflect changes in  $\theta_{\text{wood}}$  (Scholz et al. 2008; Köcher et al. 2013). Based on our findings, such fluctuations of  $\theta_{\text{wood}}$  between nighttime and daytime go along with corresponding fluctuations in  $\Delta T_{\text{max}}$  (Fig. 2). In the bamboo culms used in our study,  $\Delta T_{\text{max}}$  significantly decreased with increasing  $\theta_{\text{soil}}$  (Fig. 3), which may be attributed to the corresponding changes of  $\theta_{\text{wood}}$  caused by the dynamics of  $\theta_{\text{soil}}$ . For trees, close coupling of the  $\theta_{\text{wood}}-\theta_{\text{soil}}$  relationship was reported for rainy days and sunny days and for different seasons; on rainy days or after irrigation,  $\theta_{\text{wood}}$  was significantly increased and subsequently decreased during following sunny days (Holbrook et al. 1992; Wullschleger et al. 1996; Hao et al. 2013). Over the course of a growing season, variation in  $\theta_{\text{wood}}$  of red maple was reported to be 39% between the dry and the wet season (Wullschleger et al. 1996). It has been put forward that dynamics in  $\theta_{\text{wood}}$  may reflect changes in stem water storage (Sperling et al. 2015). Dynamics in stem water storage may thus be derived from changes in  $\theta_{\text{wood}}$  among days, given that  $\theta_{\text{wood}}$  is derived from the  $\Delta T_{\text{max}}-\theta_{\text{wood}}$  relationship and dry weight or volume of the tree stems or bamboo culms are known.



## The influence of $\theta_{\text{wood}}$ on $J_s$

Using numerical simulations, we found increasing relative underestimations of  $J_s$  for larger decreases of  $\theta_{\text{wood}}$  from nighttime to daytime (Fig. 4), which may be due to depleted stem water storage. In previous studies on bamboos (Yang et al. 2015) and palms (Sperling et al. 2015), gradual decreases of  $\theta_{\text{wood}}$  from sunrise to sunset were reported. Thus,  $\theta_{\text{wood}}$  in the afternoon and especially at dusk was likely the lowest, which could introduce substantial bias into according estimates of  $J_s$  (Fig. 4). Our results indicate that the magnitude of the relative underestimation of  $J_s$  substantially differed with varying  $J_s$ : the relative error of  $J_s$  (%) was largest at low  $J_s$  and gradually became smaller, eventually approaching a stable value with increasing  $J_s$  (Fig. 4). TDP-derived  $J_s$  is thus influenced more profoundly by changing  $\theta_{\text{wood}}$  in plants with generally low  $J_s$  or when  $J_s$  tends to be low (e.g. early morning, late afternoon). In contrast, for plants with generally high  $J_s$  or at peak times of  $J_s$  (e.g. around noon), the influence of changes in  $\theta_{\text{wood}}$  would be smaller. Nevertheless, despite the relatively smaller errors at higher daytime  $J_s$ , they were responsible for causing most of the absolute underestimations of daily water use (Fig. 5).

Additional to varying for different  $J_s$ , the influence of  $\theta_{\text{wood}}$  on TDP-derived  $J_s$  may also differ with different water conditions of the soil due to different weather or management conditions, e.g. between rainy or sunny days or after irrigation. The applied model simulation indicated that, when  $\theta_{\text{wood}}$  was reduced by the same ratio (e.g. half) from nighttime to daytime, higher nighttime  $\theta_{\text{wood}}$  caused larger relative underestimation of  $J_s$  (Fig. 6). High  $\theta_{\text{wood\_night}}$  may occur during the wet season or during the growing period of a plant. This could potentially lead to estimation errors when calibrating the TDP method with other methods in situ. Consequently, calibration approaches conducted over short periods may not reflect medium- or long-term dynamics in  $\theta_{\text{wood}}$ . Similarly, one-time laboratory calibration experiments on tree or bamboo segments may also be prone to error due to potentially varying (or unknown)  $\theta_{\text{wood}}$ , e.g. because of varying soil water conditions at the time of stem harvest.

## Correcting $J_{s\_bias}$

In our study, we numerically simulated the influence of  $\theta_{\text{wood}}$  on TDP-derived  $J_s$ . The results point to a direct and quantifiable relationship between  $\theta_{\text{wood}}$  and relative changes in  $J_s$ , and thus potential errors in previous studies when assuming a static  $\theta_{\text{wood}}$  (Wullschleger et al. 2011; Vergeynst et al. 2014). Wullschleger et al. (2011) simulated scenarios examining the impact of  $K_{\text{wood}}$  on the relationship between  $J_s$  and  $k$  ( $= \Delta T_{\text{max}} / \Delta T^{-1}$ ), and they pointed out that the  $J_s$ - $k$  relationship might be influenced by several factors including  $\theta_{\text{wood}}$ , wood density, and  $K_{\text{wood}}$ . Vergeynst et al. (2014)

quantified the influence of  $\theta_{\text{wood}}$  on  $J_s$  by simulating possible temperature changes that were assumed to relate to  $\theta_{\text{wood}}$ . Our results supplement these previous TDP error analyses by building a direct and quantifiable relationship between  $\theta_{\text{wood}}$  and  $J_{s\_bias}$  with a numerical model. In our study,  $J_{s\_bias}$  successfully corrected with our derived ‘correction equations’ (Eqs. 4–7). The four equations (Eqs. 4–7), which built upon 21 of the 45 sets of the simulated data, yielded satisfactory corrections of  $J_{s\_bias}$  when applying them to the remaining 24 (Online Resource 2 Fig. 2). Nonetheless, our correction approach still needs further improvements for future applicability.

First, in our study, the model was built under steady-state conditions, under which each simulation result was derived from the assumption of constant  $J_s$ . These steady-state conditions may not (always) be met under field conditions, where  $J_s$  is prone to external influences and may thus change frequently and not always predictably. For future studies, a non-steady-state with varying  $J_s$  should be considered, and an application of the model in situ for simultaneous assessments of  $\theta_{\text{wood}}$  and  $J_s$  would be needed. Additionally, the simulation in our study was mainly based on Eq. 1, derived by applying density and porosity of the bamboo species *B. vulgaris*. For other (bamboo) species, the parameters in the equations may thus differ. Further correction attempts could for e.g. directly include the density and porosity of wood into the correction equations as further variables, making it more universally applicable. In addition, it has to be considered that nighttime sap flow may occur in some species and that ‘zero sap flow’ conditions might thus not always be met. Our model-derived  $\Delta T_{\text{max}} - \theta_{\text{wood}}$  relationship was based on the assumption that the nighttime zero sap flow existed and lasted long enough to establish a one-to-one correspondence between  $\Delta T_{\text{max}}$  and maximum  $\theta_{\text{wood}}$ . This ideal assumption may not always be met during field experiments (Regalado and Ritter 2007). As such, several studies have reported nighttime sap flow in different species, which was presumably related to atmospheric evaporative demand (Forster 2014). Further, during dry periods, the commonly high daytime transpiration in combination with relatively low soil–water availability could potentially lead to more nighttime sap flow in the form of refilling depleted stem water reservoirs (Wang et al. 2012). In some cases, this might mean that zero flow conditions are not met at all, not even during the night. Even when the stem is fully recharged and reaches its maximum water content, nighttime sap flow could still occur, e.g. in the form of guttation. In this case, the  $\Delta T_{\text{max}}$  might be derived under a non-zero sap flux conditions and might lead to underestimation of  $J_s$ . Therefore, both changes in  $\theta_{\text{wood}}$  and nighttime sap flow are likely to influence  $\Delta T_{\text{max}}$  in the same direction. It will require further, more in-depth ecophysiological studies to evaluate and correct the impact

of nighttime sap flow as well as the coupled effects of both changes in  $\theta_{\text{wood}}$  and nighttime sap flow on TDP-derived  $J_s$ .

For TDP and other heat-based methods, influences or biases due to changes in  $\theta_{\text{wood}}$  cannot fully be avoided (Vergynst et al. 2014). Decreasing the sensitivity of the heat domain by increasing the power supply (Tatarinov et al. 2005) may be an option. However, such operation may lead to possible damages to the wood structure. Additionally to calibration-based and mathematical approaches to correct for such errors due to changes in  $\theta_{\text{wood}}$ , other possible solutions, as previously explored by Vandegehuchte and Steppe (2012b) and Trcala and Čermák (2016), may include new types of sensors that already account for dynamic changes of  $\theta_{\text{wood}}$  when estimating  $J_s$ . The model applied in our study to simulate the influence of changes in  $\theta_{\text{wood}}$  on  $J_s$  may be a possible reference for future studies to develop new models and for testing and further improving such new types of sensors.

## Conclusions

In our study encompassing laboratory dehydration experiments and field monitoring,  $\Delta T_{\text{max}}$ , a core variable in calculating  $J_s$  with the TDP method, was found to correlate negatively with both  $\theta_{\text{wood}}$  in bamboo culms and with  $\theta_{\text{soil}}$ . By numerically simulating this negative  $\Delta T_{\text{max}}-\theta_{\text{wood}}$  relationship for different scenarios of daily and seasonal changes in  $\theta_{\text{wood}}$ , the corresponding relative underestimation of  $J_s$  was quantified. Keeping other controlling variables constant, large relative underestimation became apparent (1) for large decreases of  $\theta_{\text{wood}}$  from nighttime to daytime, (2) at relatively low  $J_s$ , and (3) for relatively larger nighttime  $\theta_{\text{wood}}$  when the ratio of decrease to the daytime (e.g. by half) was kept constant. Our findings indicate that TDP measurements can be profoundly influenced by diurnal changes in  $\theta_{\text{wood}}$ , particularly in species with low water consumption, in species with large diurnal changes in stem water storage (between nighttime and daytime), and between periods with strongly alternating soil–water conditions (e.g. between sunny and rainy days). A mathematical correction equation was built with the simulated data by the steady-state numerical model, and it yielded acceptable corrected  $J_s$ . Interesting approaches for future studies include testing the here applied model in situ by simultaneously assessing dynamics in  $\theta_{\text{wood}}$  and  $J_s$ , as well as further improving and developing heat-based methods to include the assumption of non-stable  $\theta_{\text{wood}}$  at different temporal scales.

**Author contribution statement** TM designed the experiment; TM, DF, AR performed measurements; DF developed the model and analyzed the data; TM, DF, DH and AR wrote and revised the paper.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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