MEASUREMENTS OF TROPICAL BAMBOO WATER USE

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Abstract

Bamboos are grasses (Poaceae) that are widespread in tropical and subtropical regions. As monocots, woody bamboos have thin-wall hollow culms with abundant parenchyma and the culms are connected by rhizomes. These properties may imply that bamboos have specific water use characteristics. For example, the abundant parenchyma in culms provides a water reservoir for internal water storage, which may influence the response of water use to environmental factors; the connected rhizome provides passages for water transfer between bamboo culms. However, only a few water-use related studies have been conducted with thermal dissipation probe (TDP) and deuterium (D_2O) tracing method until now. Therefore, in the present study, we aimed at exploring water use characteristics of four tropical bamboo species (*Bambusa vulgaris*, *Dendrocalamus asper*, *Gigantochloa atroviolacea* and *Gigantochloa apus*) with TDP and deuterium tracing method. At the meantime, to accurately measure bamboo water use, we also tested and calibrated TDP on the studied bamboo species, and assessed the influence of bamboo water content on TDP. Additionally, as a less used water use measurement method, potential error sources of deuterium tracing method were explored when applying it on bamboos to explore water use, storage and transfer.

As the first step, the TDP method was calibrated with the stem heat balance method (SHB) and gravimetric readings in *B. vulgaris* culms in a pot experiment. In this experiment, it was confirmed that the stem heat balance method is well suited for bamboos but that thermal dissipation probes need to be calibrated. In situ, TDP was further calibrated with SHB for the four bamboo species and species-specific parameters for such calibration formulas were derived. With the calibrated TDP, we monitored sap flux density (J_s) of the four bamboo species along with three tropical tree species (*Gmelina arborea*, *Shorea leprosula* and *Hevea brasiliensis*) during a dry and a wet period. During field monitoring, we found that some bamboo species reached high maximal J_s. Across bamboo species, maximal J_s increased with decreasing culm diameter. In the diurnal course, J_s in bamboos peaked much earlier than radiation and

vapor pressure deficit (VPD), and also much earlier than J_s in trees. There was a pronounced hysteresis between J_s and VPD in bamboos, which was less pronounced in trees. Three of the four bamboo species showed reduced J_s at high VPD values during the dry period, which was associated with a decrease in soil moisture content. Possible roles of internal water storage, root pressure and stomatal sensitivity are discussed.

Bamboos and other plants may substantially rely on stem water storage for transpiration. Fluctuations in wood water content (θ_{wood}) may lead to errors when estimating transpiration based on J_s measurements with the widely used TDP method. To test the effects of θ_{wood} on J_s, we conducted a culm dehydration experiment, monitored bamboos with TDP, and implemented a steady-state thermal model. Central to the calculation of J_s, and thus a major potential source of error, is the maximal temperature difference between probes (ΔT_{max}) which are usually assumed to happen under "zero sap flow" condition. In the culm dehydration experiment, θ_{wood} was found to be highly negatively correlated with ΔT_{max}. In the long-term field monitoring, soil moisture content was also negatively correlated with daily ΔT_{max}, indicating changes in θ_{wood} and a seasonal decrease in stem water storage. The steady-state model reproduced the θ_{wood} to ΔT_{max} relationship of the dehydration experiment and underlined a considerable sensitivity of J_s estimates to θ_{wood}. Fluctuations in θ_{wood} may lead to 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 when key wood properties are known. Our study gives insights into the relationship between θ_{wood} and TDP-derived J_s and examines potential estimation biases.

Deuterium tracing method was also applied on bamboos to explore water use, storage and transfer, and its potential error sources were explored. The deuterium-derived sap velocities correlated with the TDP-derived velocities in two of the three species. In all species, the deuterium residence time in bamboo culms was little influenced by the contribution of the culm water storage to transpiration as estimated by TDPs at different culm heights. Potential reasons include a small water storage volume in the culms, a low estimated contribution of the storage to transpiration and high sap flux densities. Daily culm water use rates estimated by the deuterium and the TDP approaches correlated linearly ($R^2 = 0.9$) but were by 70% in the deuterium estimates. After the experiment, culms were cut down and analyzed for residual deuterium, but concentrations were low which indicates that retention did not play a

major role in causing errors of the deuterium tracing approach. In culms neighboring the deuterium labeled culms of *B. vulgaris* and *G. apus*, elevated deuterium concentrations were detected indicating water transfer between culms. Based on the differences in daily water use on labeled culms and the enhanced deuterium concentrations in neighboring culms of these two species, we inferred that five neighboring culms might receive water from the labeled culms. On contrast, in culms neighboring labeled *D. asper* culms, only slightly elevated deuterium concentrations were observed which implies a limited role by water transfer. However, incomplete mixing as indicated by high variation among three TDP sensors at a given height may be of particular importance for deuterium tracing in *D. asper*. In conclusion, species-specific differences among big clumpy bamboos are indicated and the deuterium tracing points to water transfer among culms.

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Chapter 1

Introduction

1.1 The distribution and usage of bamboos

Bamboo is a generic term of Bambusoideae (Mathew, 1998), which is a subfamily of Poaceae (Liese and Köhl, 2015). The bamboos comprise more than 1400 species, and distribute over temperate and tropical regions (BPG, 2012). Until 2010, bamboos covered 31.5 million hectares in 31 countries mostly in South America and Asia (FAO, 2010). These areas are mainly characterized by relatively high air temperature and humidity levels, as such conditions promote the shoot emergence and the culm elongating of the newly sprouted bamboos during the culm elongating period (Liese and Köhl, 2015; Numata, 1987).

The bamboos provide important resources for people with many usages. Traditionally, the bamboos are used as food (bamboo shoot; e.g. *Dendrocalamus asper*, *Gigantochloa apus*), and for producing wine, medicine, tee, etc.; the harvested bamboos can be used for building, furniture and engineered bamboo products (Liese and Köhl, 2015). With the development of technologies, bamboos were frequently introduced into new areas, such as biofuel (Kremer et al., 2015), clean energy (Feng et al., 2015) etc. Some species (e.g. *Bambusa vulgaris*) can be even used for building high-quality "bamboo bicycle" (Liese and Köhl, 2015). At last, Bamboos are considered as valuable non-timber resources contributing to forest conservation and carbon bio-sequestration due to their great growth rate and potentially high yield (Parr et al., 2010; Song et al., 2013; Zhuang et al., 2015). For example, Moso bamboo (*Phyllostachys pubescens*) accounts for about 5% of total forest area in China and is an important carbon stock (35-85 Mg ha^{-1}) in subtropical regions (Wang et al., 2013).

1.2   The growing and anatomical characteristics of bamboos

Most of bamboos are woody bamboos, which have tree-like habits but differ from trees in many respects (BPG, 2012). One distinctive characteristic of the bamboos is their fast-growing property. Within one growth season, a newly sprouted bamboo culm can reach its full height with a growth rate of 10-80 cm per day (Liese and Köhl, 2015). For some species (e.g. *D. asper*), under favorable conditions daily growth can reach 120 cm (Durst et al., 1994). Secondly, as monocots, bamboos only have axial growth while without radial growth, which means the diameters of bamboos keep unchanged after the culms emerge from soil. Correspondingly, bamboo culms lack the radial transport of water across the culms (Liese and Köhl, 2015). Third, the bamboo culms (stems) are segmented by solid nodes and hollow internodes. Lacking secondary growth and the hollow culms require bamboos to keep the vascular bundles in the culms conducting over the whole life. Keeping conducting tissues working and avoiding embolism may probably rely on the powerful root pressure (Cao et al., 2012; Yang et al., 2015). Further, bamboos develop underground connections with rhizomes that have similar anatomical structure as culms (Ito et al., 2015), which was assumed as passage for water and nutrients transfer between mature and new sprouted culms (Song et al., 2016). The connected rhizomes make the culms relying to each other, losing one culm may influence the others (Liese and Köhl, 2015).

1.3   Water use characteristics of bamboos

The specific anatomy of bamboo may lead to special water use characteristics, while only a few studies focus on such topics thus far (Cao et al., 2012; Dierick et al., 2010; Ichihashi et al., 2015; Komatsu et al., 2010; Kume et al., 2010; Yang et al., 2015; Zhao et al., 2016). In these studies, except one study focusing on the role of root pressure (Cao et al., 2012), all of the others applied sap flow measurement to study the daily or seasonal dynamics of bamboo water use while had different emphasis.

1.3.1 Water use

One concerned question is whether the bamboos consume different water volumes than neighboring trees, on stand or individual scales. On stand scale, compared with the neighboring trees, the non-clump Moso bamboos in Japan transpired more water in both low- (Ichihashi et al., 2015) and high-density stands (Komatsu et al., 2010). On the individual scale, the maximal sap flux density (J_{s_max}) of Moso bamboos in low- and high-density stands was ca. four- and two-fold of that in the compared cedar trees (Ichihashi et al., 2015). The J_{s_max} of Moso bamboos in another study was about 20 g cm^{-2} h^{-1} (Kume et al., 2010), which was close to the values (22.6 and 20 g cm^{-2} h^{-1} in dry and wet seasons, respectively) of a clump species - *Bambusa vulgaris* in China (Yang et al., 2015). Similar results (on average 21 g cm^{-2} h^{-1}) were also earlier found on another clump species - *Bambusa blumeana* in the Philippines (Dierick et al., 2010), and such values lay in the range of that from the co-occurring trees in the Philippines (17.7-28.9 g cm^{-2} h^{-1}; Dierick and Hölscher, 2009).

The three bamboo species have similar sap flux densities measured with the widely used thermal dissipation probe method (TDP, Granier, 1985), but the TDP was installed at different positions with different sensor types (1 or 2.5 cm length) and calibrated with different methods. These factors may cause the results of the three studies incomparable. To avoid regular TDP sensor (2/2.5 cm length) from penetrating the thin culm-wall, TDP was installed at the base (0.35 m above ground) of the culm (Dierick et al., 2010) or at the breast height with self-made sensor with 1 cm length (Kume et al., 2010; Yang et al., 2015). However, as the different culm wall cross-section area along the culm may lead to large variation of sap flux density (J_s), J_s at the base of the culm was lower than that at the higher position (Dierick et al., 2010). Additionally, as Granier's formula was derived with empirical relationship (Granier, 1985) rather than based on the physical properties of the wood (Wullschleger et al., 2011), TDP was recommended calibrating on studied species (Lu et al., 2004; Vandegehuchte and Steppe, 2013; Wullschleger et al., 2011). On Moso bamboos, Kume et al. (2010) found TDP underestimate water use by 35% compared with gravimetric method, and on *B. blumeana* Dierick et al. (2010) found 13% underestimation with TDP compared with stem heat balance method (SHB, Sakuratani, 1981). However, Kume et al. (2010) calibrated TDP on cut down bamboo culms which may differ from standing culms on water physiology while Dierick et al. (2010) calibrated on standing

bamboos with SHB which was not further verified. Therefore, to accurately measure bamboo water use with TDP, calibrating TDP with reference method on standing bamboos of more bamboo species should be conducted.

1.3.2   Sap flow pattern and stem water content

In general, transpiration is driven by micrometeorological factors and limited by soil water availability (Bovard et al., 2005; Kume et al., 2007; O'Brien et al., 2004). When soil water availability cannot fulfill the high transpiration demand (e.g. at midday in the sunny day), transpiration can be maintained temporally by stem water storage (Carrasco et al., 2015; Goldstein et al., 1998; Waring and Running, 1978). For bamboos, the role of stem water storage may be influenced by two anatomical properties: relative small volume of culm (hollow center and thin culm-wall) and high percentage of parenchyma in the culm (50%, Liese and Köhl, 2015). The relative small volume of bamboo culm provides limited room for water storage, while the abundant parenchyma may offset the limitation. On *B. blumeana*, the sap flow at the base of the culms reached its maximal value before midday but the maximal value didn't last as long as that of trees (Dierick et al., 2010). Similar sap flow pattern was observed at the breast height on *B. vulgaris* (Yang et al., 2015). This was assumed due to limited soil water and low water storage in the part of the bamboo under the installed sensor. However, the near J_{s_max} at near the top of the culm persisted much longer than that at the breast height on *B. vulgaris* (Yang et al., 2015) which implied that the culm water storage may play an important role for bamboos. The depleted stored water may be refilled during night by root pressure (Cao et al., 2012).

The depletion and refilling of water storage causes fluctuation of wood water content (θ_{wood}, Nadler et al., 2008; Yang et al., 2015). On trees, with the daily fluctuation on transpiration, θ_{wood} showed a reverse fluctuation pattern. θ_{wood} reached to peak values during night when J_s was zero or minimal, and dropped to minimum during daytime (Hao et al., 2013; Sperling et al., 2015). On a bamboo species (*B. vulgaris*), similar pattern of bamboo culm circumference was observed (Yang et al., 2015). Although it's not the direct measurement on θ_{wood}, the daily dynamic of culm circumference should reflect at least part of change on θ_{wood} as assumed on trees (Köcher et al., 2013; Scholz et al., 2008).

The daily fluctuation of θ_{wood} may influence the wood thermal conductivity (K_{wood}) and thus influence estimating J_s with TDP method. According to a theoretical analysis based on a temperature-θ_{wood} function (Carslaw and Jaeger, 1959) and a dehydration experiment on tree stem segments in the lab, it was demonstrated that θ_{wood} influenced the K_{wood} around TDP probes and caused underestimation of daytime J_s (Vergeynst et al., 2014). Additionally, the influence of θ_{wood} on J_s may differ with soil water conditions. Previous studies found that θ_{soil} can strongly regulate the θ_{wood} in trees and palm (Constantz and Murphy, 1990; Holbrook et al., 1992; Wullschleger et al., 1996). During a long-term period (monthly or seasonally), the θ_{wood} in tree stems was found fluctuating with θ_{soil}. In rainy days, θ_{wood} in stems of trees or palms was significantly increased and subsequently decreased in the following sunny days (Hao et al., 2013; Holbrook et al., 1992; Wullschleger et al., 1996). Such dynamic θ_{wood} in stem may further influence the K_{wood} around TDP probes. If ignoring these influences, the patterns or values of TDP-derived J_s may be misinterpreted as eco-physiological phenomenon. Vergeynst et al. (2014) quantified the influence of θ_{wood} on J_s by setting possible temperature change that was assumed to relate to θ_{wood}. However, the direct relationship between θ_{wood} and errors on J_s remained unclear.

1.3.3 Water transfer among bamboo culms

Bamboo culms are connected with each other through underground rhizomes (Ito et al., 2015), which was assumed to provide passage for carbon, water and nutrients transfer between culms (Liese and Köhl, 2015; Song et al., 2016). Water transfer among bamboo culms was implied on *B. blumeana* by observing elevated deuterium concentrations in neighbor culms which closed to the deuterium labelled culms (Dierick et al., 2010). In a rhizome-cutting experiment on Moso bamboos, Zhao et al. (2016) cut the rhizome between juvenile culms and mature culms and found that the rhizome-cut juvenile culms transpired approx. 20% less of water compared with other still connected juvenile culms. The result thus implied water transfer among bamboo culms. The above two studies were conducted on mature or 1-year-old juvenile culms, which may rely less on the other culms than the freshly sprouted culms. These freshly sprouted culms may rely more on water transfer through rhizome due to less developed leaves and roots. The deuterium tracing method seems promising to trace the water transfer.

Deuterium tracing method was typically used to estimate tree daily water use, with injecting deuterated water at the base of the stem, tracing in water transpired from leaves over time and calculating water use with "total count" method (Calder et al., 1986). However, the method may produce errors when tracer was lost or unevenly mixed (Schwendenmann et al., 2010). On bamboos, the tracer loss may occur due to the existence of water transfer. However, if the tracer loss can be quantified, it will improve the application of deuterium tracing on estimating daily water use and probably also help to better understand the transfer dynamics.

1.4   Aims of the study

The study aims were:

(1) calibrating TDP on potted bamboos with gravimetric and SHB method and in situ on standing bamboos with SHB method;

(2) with the calibrated TDP, monitoring sap flux densities of bamboos and exploring their patterns and relationships with environmental factors;

(3) exploring the effects of wood water content on sap flux densities derived with TDP by conducting a culm dehydration experiment, monitoring bamboos with TDPs in situ, and implementing a steady-state thermal model; and

(4) detecting water transfer between bamboo culms with the deuterium tracing method, and exploring error sources of deuterium tracing method on bamboo water circulation.

1.5   Author contribution

The dissertation is substantiated by three manuscripts (Chapter 2-4) at various stages of the publication process (i.e. 'Advanced draft', 'Published'). The status as well as the contributions to each manuscript by the author of this dissertation (in the following simply refer to as 'the author') is indicated for each manuscript. Chapter 1 and 5 were solely compiled by the author.

Chapter 2: **Water use patterns of four tropical bamboo species assessed with sap flux measurements**

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The concept and research priorities for this bamboo and tree study in Bogor, Indonesia were developed by Dirk Hölscher. The author contributed to experimental design, field installation, maintenance of the installations, data collection, writing and revision for the manuscript, in close cooperation and coordination particularly with Dong-Ming Fang and Dirk Hölscher. Dong-Ming Fang worked through the field work and data analysis. Alexander Röll contributed to field installations and manuscript revisions. Fu-Rong Niu contributed to part of the field installations and plotting for the manuscript. Hendrayanto close cooperated in the project.

Chapter 3: **Assessing the influence of stem water content on TDP sap flux measurements by experimental, monitoring and modeling approaches**

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Manuscript status: Under review by **Trees**.

The concept and research priorities for this stem water content study in Bogor, Indonesia were developed by Dirk Hölscher. The author contributed to experimental design, field installation, maintenance of the installations, data collection, writing, plotting and revision for the manuscript, in close cooperation and coordination particularly with Dong-Ming Fang and Dirk Hölscher. Dong-Ming Fang contributed to model developing and data analysis. Alexander Röll contributed to the manuscript revisions.

Chapter 4: **Deuterium tracing on tropical bamboo water use**

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Manuscript status: Advanced draft.

The concept and research priorities for this deuterium tracing study in Bogor, Indonesia were developed by Dirk Hölscher. The author contributed to field installations, sample collections, plotting and revision for the manuscript, in close cooperation and coordination particularly with Dong-Ming Fang and Dirk Hölscher. Dong-Ming Fang contributed to the field installations, sample collections, data analysis and writing and revision for the manuscript. Alexander Röll contributed to the manuscript revisions.

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Chapter 2

Water use patterns of four tropical bamboo species assessed with sap flux measurements

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Running title: bamboo water use

Abstract

Bamboos are grasses (Poaceae) that are widespread in tropical and subtropical regions. We aimed at exploring water use patterns of four tropical bamboo species (*Bambusa vulgaris*, *Dendrocalamus asper*, *Gigantochloa atroviolacea* and *Gigantochloa apus*) with sap flux measurement techniques. Our approach included three experimental steps: (1) a pot experiment with a comparison of thermal dissipation probes, the stem heat balance method and gravimetric readings using potted *B. vulgaris* culms, (2) an in situ calibration of thermal dissipation probes with the stem heat balance method for the four bamboo species, and (3) field monitoring of sap flux of the four bamboo species along with three tropical tree species (*Gmelina arborea*, *Shorea leprosula* and *Hevea brasiliensis*) during a dry and a wet period. In the pot experiment, it was confirmed that the stem heat balance method is well suited for bamboos but that thermal dissipation probes need to be calibrated. In situ, species-specific parameters for such calibration formulas were derived. During field monitoring we found that some bamboo species reached high maximum sap flux densities. Across bamboo species, maximal sap flux density increased with decreasing culm diameter. In the diurnal course, sap flux densities in bamboos peaked much earlier than radiation and vapor pressure deficit (VPD), and also much earlier than sap flux densities in trees. There was a pronounced hysteresis between sap flux density and VPD in bamboos, which was less pronounced in trees. Three of the four bamboo species showed reduced sap flux densities at high VPD values during the dry period, which was associated with a decrease in soil moisture content. Possible roles of internal water storage, root pressure and stomatal sensitivity are discussed.

Keywords: calibration, environmental drivers, hysteresis, stem heat balance, thermal dissipation probes, trees, bamboos

2.1 Introduction

Bamboos (Poaceae, Bambuseae) are abundant in the natural vegetation of tropical and subtropical regions. They have been used by people for millennia and are still used as food and construction materials. In addition, a large variety of bamboo usages have been developed in recent decades, for example for pulp, paper or clothing production (INBAR, 2014). The increasing economic

exploitation of bamboos goes along with a considerable expansion of bamboo plantations in some regions (Chen et al., 2009; FAO, 2010), which may lead to changes in ecological processes such as water use patterns (Komatsu et al., 2010; Uchimura, 1994). Some bamboo stands were reported to evaporate more water than tree-dominated forests (Ichihashi et al., 2015; Komatsu et al., 2010), but studies focusing on water use patterns of bamboos are still rare thus far (Dierick et al., 2010; Ichihashi et al., 2015; Komatsu et al., 2010; Kume et al., 2010; Pereira and Hosegood, 1962).

Water use patterns of bamboos and trees differ in several aspects. In contrast to trees, bamboos are monocotyledonous species and lack secondary growth (Zimmermann and Tomlinson, 1972). Therefore, vascular conduits of bamboo xylem have to remain functional throughout the ontogeny of a bamboo culm. Bamboos consequently have great ability to avoid cavitation (Cao et al., 2012; Cochard et al., 1994; Petit et al., 2014); root pressure mechanisms may contribute to repairing embolized conduits at night (Cao et al., 2012). Such features and structural traits of bamboos may also lead to particular water use patterns.

In general, plant water use is driven by micrometeorological factors and can be limited by soil water availability (Bovard et al., 2005; Kume et al., 2007; O'Brien et al., 2004); it is regulated by stomata opening and closing (Jarvis, 1989) and can be influenced by internal water storage mechanisms (Carrasco et al., 2015; Goldstein et al., 1998; Waring and Running, 1978). Xylem sap flux reflects these multiple factors. For some tree species, for example, hysteresis in the diurnal sap flux response to radiation and vapor pressure deficit (VPD) of the air have been reported (Goldstein et al., 1998; O'Brien et al., 2004). Sap flux measurements thus appear suitable to study the water use patterns of bamboos as well as their controlling environmental factors.

Thermal dissipation probes (TDP) are widely used to measure sap flux density (J_s) in trees (Granier, 1985). Several studies suggest calibrating the method before studying new species (Lu et al., 2004; Vandegehuchte and Steppe, 2013; Wullschleger et al., 2011). To our knowledge, only two studies have applied the TDP method on bamboos so far. Both reported an underestimation of bamboo sap flux compared to stem heat balance (SHB) and reference gravimetric measurements (GM) when the TDP method was not calibrated (Dierick et al., 2010; Kume et al., 2010). In contrast, the SHB method (Sakuratani, 1981) was suggested to be well suited for sap flux measurements on bamboos (Dierick et al., 2010). Bamboo culms are hollow; hence heat loss in the form of heat

storage inside culms is marginal, so that steady thermal conditions as a main assumption of the method are met (Baker and Bavel, 1987).

The aim of this study was to analyze water use patterns of tropical bamboo species and particularly the response of J_s to the principal environmental drivers. First, we calibrated the SHB and the TDP method with reference GM in an experiment on potted culms of *Bambusa vulgaris*. We then measured J_s in the field in four bamboo species including *B. vulgaris* with both the TDP and SHB method, and calibrated the TDP method with the SHB method. Herein, three factors which may influence the quality of the calibration were tested: time step of the data, formula specificity and calibration formula type. After calibration of the TDP method, we applied it to monitor J_s in four bamboo and three tree species in a common garden in Bogor, Indonesia. Differences in the response of J_s to fluctuations in environmental conditions were assessed. The study intends to contribute to expanding the yet limited knowledge on the eco-hydrological functioning of bamboos.

2.2 Materials and methods

2.2.1 Study sites and species selection

The pot calibration experiment was conducted in Guangzhou, China (23°26'13" N, 113°12'33" E, 13 m asl). The field calibration experiment and monitoring campaign were carried out in a common garden in Bogor, Indonesia (6°33'40" S, 106°43'27" E, 182 m asl). Average annual temperature in Bogor is 25.6 °C and annual precipitation is 3978 mm.

Relatively dry conditions with consecutive rainless days can occur between June and September. During this dry period, monthly precipitation is on average 40% lower than during the wet period (230 vs. 383 mm), and the number of consecutive dry days (rainfall < 1 mm) is twice that of the wet period (8 vs. 4 days, 1989-2008, Van Den Besselaar et al., 2015). During our study period (July 2012 to January 2013), differences between dry and wet period were more pronounced, i.e. 155 vs. 489 mm monthly precipitation, 14 vs. 2 consecutive dry days, and 0.29 vs. 0.39 m^{-3} m^{-3} daily soil water content. In Bogor, four bamboo species (*Bambusa vulgaris*, *Dendrocalamus asper*, *Gigantochloa atroviolacea*, *Gigantochloa apus*) with five culms per species and three tree species (*Gmelina arborea*, *Shorea leprosula* and *Hevea brasiliensis*, Table 2.1) with five stems per species were selected and their J_s

were monitored with the TDP method for seven months.

2.2.2   TDP construction and installation

To measure J_s in trees and bamboos, we used self-made TDP (1 cm and 2 cm length, respectively). In sensor design and construction, we followed Wang et al. (2012). Each TDP sensor was comprised of a heating (downstream) and a reference (upstream) probe made of steel hypodermic needles. The probes were placed 10 cm apart (vertically). For bamboos and trees, TDP installation depths in culms and stems were 1 and 2 cm, respectively. After installation, each TDP was supplied with a constant current of 120 mA; the respective power outputs of 1 cm and 2 cm length TDP were 0.1 and 0.2 W. TDP signals were sampled every 30 s and stored as 10-min averages for the pot calibration experiment and as 1-min averages for all other experiments by data loggers and multiplexers (CR1000, AM16/32, Campbell Scientific Inc., USA).

2.2.3   Calibration of the TDP method

Pot calibration experiment: TDP, SHB & GM

Five culms of *B. vulgaris* (diameter 5.3-7.3 cm, height 2.2-3.2 m) with trimmed canopies were transplanted into plastic bags (diameter 30 cm, height 25 cm) six months before the calibration experiment. One day before the experiment, the five bamboos were transplanted into bigger plastic pots (diameter 50 cm, height 65 cm). The pots were filled with cobblestones and water and were then fully sealed with plastic cover and aluminum foil to prevent evaporation of water from the pots (Figure 2.1.A). A scaled syringe tube was attached to each pot and connected into the pot through a U-type tube. At the beginning of the experiment, the water was added into the pot through the syringe tube to a fixed level (5 cm below the pot cover). Subsequently, water was added manually every 30 min to reach the pre-defined level. The weight of the added water was determined gravimetrically (GM). To measure J_s, each bamboo culm was equipped with 3 pairs of 1 cm length TDP which were evenly installed circumferentially, about 15 cm above the plastic cover. To minimize potential measurement errors induced by circumferential variations of J_s, the thermocouple wires of the three TDP were connected in paralFlel to get an average voltage signal for each bamboo culm (Lu et al., 2004). For a second J_s

Table 2.1 Structural characteristics of the studied bamboo and tree species (n=5 per species; mean±SD).

	Species	DBH (cm)	BCWT (cm)	Height (m)
Bamboo	*B. vulgaris*	7.0±0.3	1.3±0.1	17.9±0.8
	G. apus	8.6±0.4	1.2±0.2	16.2±2.7
	D. asper	11.9±1.9	2.4±0.2	21.1±0.9
	G. atroviolacea	8.9±0.6	1.6±0.1	17.0±1.0
Tree	*H. brasiliensis*	27.4±2.3	-	25.2±3.0
	G. arborea	26.3±7.7	-	26.5±2.3
	S. leprosula	20.7±4.8	-	19.2±2.5

Note: DBH (Diamter at Breast Height); BCWT (Bamboo Culm Wall Thickness)

estimate, a SHB gauge (SGB50 or SGA70, Dynagage Inc., USA) was installed about 1.5 m above the TDP. Both sensor types were protected by foil and the sensor signals were subsequently recorded as described in Section 2.2. For the comparison to reference gravimetric measurements (GM), 10-min TDP and SHB derived values were aggregated to half-hourly values.

To assess the performance of TDP and SHB in the pot experiments, J_s derived from TDP and SHB (J_{s_TDP} and J_{s_SHB}, respectively) on daily and 30-min scales were compared to GM derived J_s (J_{s_GM}) with paired t-tests. Additionally, the slopes of the respective linear fits between J_{s_TDP}, J_{s_SHB} and J_{s_GM} were tested for significant differences from 1 with the test of homogeneity of slopes. The same statistical analyses were applied again later when testing for significant differences between J_{s_TDP} and J_{s_SHB} in the field calibration experiments.

Field calibration experiment: TDP & SHB

Five culms per bamboo species (*B. vulgaris*, *D. asper*, *G. atroviolacea*, *G. apus*) were selected for TDP measurements (Table 2.1), three to four of which were additionally measured with SHB for a field calibration of the TDP method. TDP sensors were installed at 1.3 m height, and SHB gauges (SGB50, SGA70, Dynagage Inc., USA) were installed about 2.5 m above the TDP. Simultaneous TDP-SHB measurements were conducted for a minimum of five days per culm (Figure 2.1.B). Heat storage inside bamboo culms is assumed to be negligible, which was confirmed by installing thermocouple wires inside the measured segments of the respective bamboo culms to detect fluctuations in culm temper-
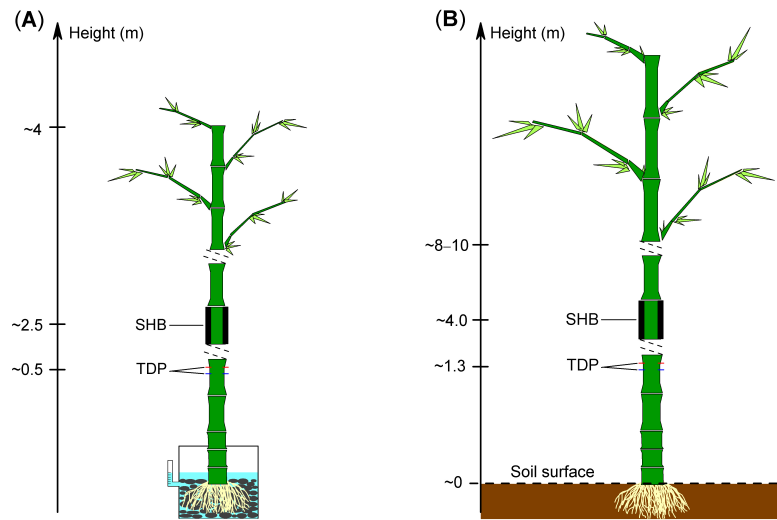
Fig. 2.1 Installation of thermal dissipation probe (TDP) and stem heat balance (SHB) sensors on bamboo culms for the calibration experiments on potted plants (A) and for field calibration (B).

ature (Dierick et al., 2010). The observed fluctuations were marginal, which meant stable thermal conditions as a requirement of the SHB method were met.

Parametrization for TDP calibration

We derived cross-sectional water conductive areas (A_TDP) from the culm wall thickness at the location of TDP sensor installation. In the pot calibration experiment, reference J_s were calculated by dividing water flow rates (g h^{-1}, GM-derived) by A_TDP. In the field calibration experiment, reference J_s were taken from the SHB measurements. The reference J_s could subsequently be used to calibrate J_{s_TDP}. Nighttime sap flux values were excluded in both calibration experiments.

In the field calibration, three factors were considered for obtaining a TDP calibration formula from reference (SHB) measurements: time step of the data, formula specificity and calibration formula type. To examine effects of varying time steps, the formulas were built and tested on data at varying intervals (1-, 10-, 30-, and 60-minute averages, respectively). The effects of formula specificity were examined by using common (i.e. all bamboo species pooled), species-specific and culm-specific formulas, respectively. Regarding the calibration formula type, two formulas were compared: one was nonlinear ($J_s = aK^b$) and generated by deriving new a and b parameters for the original

Granier formula (1985). The second was a linear formula ($J_{s\_SHB} = c \times J_{s\_TDP}$) which was calculated from the linear relationship between J_{s_TDP} and J_{s_SHB}.

To obtain stable calibration formulas, pooled data sets were randomly split in half for calibration and independent validation, respectively (Niu et al., 2015). First, for each time step (1-, 10-, 30-, and 60-minute, respectively), a data pool was built. Three culms of each bamboo species were randomly chosen, and for each, three days of data were randomly chosen from an initial common dataset. With these data pools, formula specificity was examined. For the common calibration, culms of all four species were selected for calibration. For species-specific and culm-specific calibration, only the data of the respective species or culms was selected. Next, the selected data was randomly split in half, for building the calibration formula and testing it, respectively. When testing the formula, the differences between J_{s_SHB} and calibrated J_{s_TDP} ($J_{s\_TDP\_cali}$, abnormal distribution, $P > 0.05$) were examined with the Wilcoxon Signed-Rank Test (no significant differences at $P > 0.05$). The process of randomly building and testing the formula was iterated 10,000 times. Final calibration formula parameters were derived by averaging the parameters of those iterations which passed the Wilcoxon Signed-Rank Test ($P > 0.05$).

For an evaluation of the performance of the different formulas and the influence of the three factors (time scale, formula specificity and calibration formula type), differences in normalized Root-Mean-Square Errors (nRMSE) were assessed for each culm, species and formula factor, respectively. First, the RMSE for each day was derived with the J_{s_SHB} and $J_{s\_TDP\_cali}$ values, and the nRMSE was calculated by normalizing the RMSE with the observed daily range of J_{s_SHB} (difference between maximum and minimum J_{s_SHB}). Then, the nRMSE were analyzed regarding the three formula factors (data time scale, formula specificity and calibration formula type) by ANOVA (Analysis of variance). Additionally, for each day, $J_{s\_TDP\_cali}$ with each formula type was tested for significant differences from J_{s_SHB} with the Wilcoxon Signed-Rank Test. The rates of passing the Wilcoxon Signed-Rank Test ($P > 0.05$ when no significant difference between TDP and SHB derived values) were assessed for each formula.

2.2.4   Field study

Monitoring bamboo and tree sap flux

Four calibrated bamboo species as well as three tree species (*G. arborea*, *S. leprosula* and *H. brasiliensis*) were monitored with the TDP method for seven months (July, 2012 to January, 2013). Five bamboo culms and five tree trunks per species were selected for the measurements. On bamboos, three pairs of TDP (10 mm in length) were installed evenly around each culm at 1.3 m height and connected in parallel (see Section 2.2 for details). On trees, two pairs of 20 mm TDP were installed in the trunk 1.3 m above the ground, in the North and South, respectively. J_s for the two sensors were separately derived with the original calibration formula (Granier, 1985) and subsequently averaged to obtain values for each tree. For bamboos, J_s derived with the original formula were calibrated with species-specific calibration parameters (from reference SHB field measurements) to obtain final J_s values.

Environmental measurements and analyses

A micrometeorological station was set up in an open area. It was about 100 and 600 m away from the closer measurement sites (*D. asper*, *G. arborea*, *G. atroviolacea*, *G. apus*, *S. leprosula*) and farthest sites (*B. vulgaris*, *H. brasiliensis*), respectively. Air temperature (T_a, °C) and air relative humidity (RH, %) were measured with a temperature and relative humidity probe (CS215, Campbell) installed in a radiation shield. VPD (kPa) was calculated from Ta and RH. Radiation (J m^{-2} s^{-1}) was measured with a pyranometer (CS300, Campbell). Data were recorded with the previously described data loggers every minute.

In addition to the mentioned micrometeorological variables, soil moisture (SM, m^{-3} m^{-3}) was measured with time domain reflectometry sensors (TDR, CS616, Campbell) at 0-20 cm depth. As the clump of *D. asper* and the stand of *G. arborea* were next to each other, one TDR was positioned between them to measure soil moisture. Likewise, one sensor was used for measurements of *G. atroviolacea* and *G. apus*. One TDR each were used for the remaining species (*S. leprosula*, *B. vulgaris*, *H. brasiliensis*). TDR measurements ran in parallel to the sap flux field campaign and data were recorded with the described data loggers every minute.

For the day-to-day analysis of influences of fluctuations in environmental conditions (VPD, radiation, SM) on J_s in the studied bamboo and tree species,

daily accumulated J_s (kg cm^{-2} d^{-1}) were normalized by setting the highest daily observation of each species to 1 and the lowest to 0. For a more isolated analysis of potentially limiting influences of soil moisture on J_s, we focused on 'dry period conditions' with consecutive rainless days, which occurred between June and September in the study area. During this period, monthly precipitation was only 32% of monthly wet period precipitation (155 vs. 489 mm), and the number of consecutive dry days (rainfall < 1 mm) was 7 times higher than during the wet period (14 vs. 2 days). Dry period conditions are also characterized by higher VPD (average daily VPD > 0.74 kPa on 92% of the days). 0.74 kPa was chosen as the threshold to distinguish between dry and wet period because it constituted the mean maximum ('turning point') in the fitted J_s response functions to VPD in three of the four studied bamboo species (except *D. asper*, see Figure 2.4.B).

For the diurnal analysis of influences of fluctuations in environmental conditions on J_s, time lags between J_s and micrometeorological drivers (radiation and VPD) were calculated as the time difference between the respective occurrences of maximal J_s (J_{s_max}) and maximal radiation and VPD. T-tests were used to test time lags for significant differences from 0 min. 30-min J_s values (average values of three selected sunny days) of each species were plotted against radiation and VPD to examine occurrences of hysteresis. The respective areas of hysteresis were compared between bamboos and trees with t-tests.

All data analyses were performed with SAS 9.3 (SAS Institute Inc., 2013).

2.3   Results

2.3.1   Calibration of the TDP method for bamboos

Pot calibration experiment: TDP, SHB & GM

In the pot calibration experiment with *B. vulgaris*, SHB yielded similar absolute values of J_s as GM on daily and 30-min scales ($P > 0.05$). The slope of the linear fit between SHB and GM on the 30-min scale was 0.98 ($R^2 = 0.93$, $P < 0.01$). It did not significantly differ from 1 ($P > 0.05$, Figure 2.2.A). In contrast to this, TDP estimates, with the original parameters of the calibration formula (Granier, 1985), differed substantially from GM values at both the daily (60% underestimation of accumulated J_s, $P < 0.01$) and 30-min scale
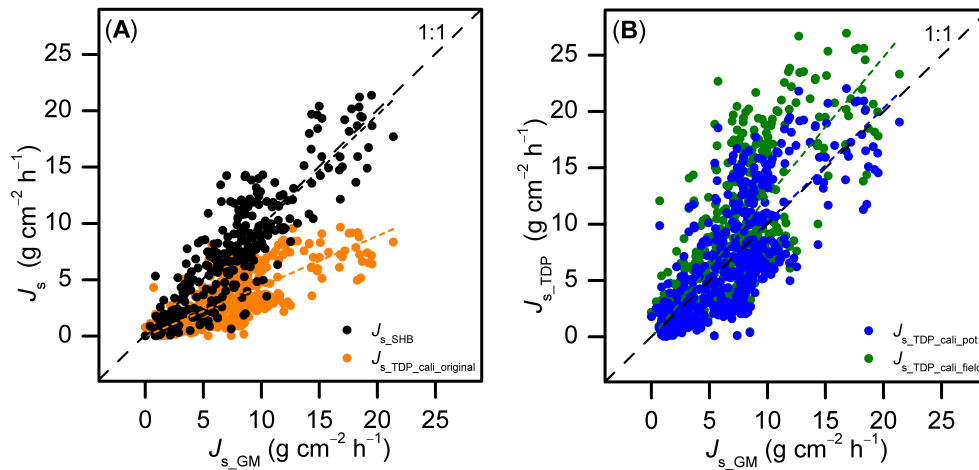
Fig. 2.2 Half-hourly sap flux density (J_s) measured with thermal dissipation probes (TDP) and stem heat balance (SHB) sensors on five potted *Bambusa vulgaris* culms plotted against GMderived reference sap flux densities (J_{s_GM}) before (A; $J_{s\_TDP\_cali\_original}$: $Y = 0.44X$, $R^2 = 0.84$, $P < 0.01$; J_{s_SHB}: $Y = 0.98X$, $R^2 = 0.93$, $P < 0.01$) and after (B; $J_{s\_TDP\_cali\_field}$: $Y = 1.24X$, $R^2 = 0.84$, $P < 0.01$; $J_{s\_TDP\_cali\_pot}$: $Y = 1.01X$, $R^2 = 0.84$, $P < 0.01$) species-specific calibration and field calibrations of the TDP method. Pooled data from 2 to 5 days of simultaneous TDP, SHB, and gravimetric measurements (GM).

(56% underestimation, $P < 0.01$). The slope of the linear fit between TDP and GM on the 30-min scale was 0.44 ($R^2 = 0.84$, $P < 0.01$). It was significantly different from 1 ($P < 0.01$, Figure 2.2.A).

After applying the TDP calibration parameter for *B. vulgaris* derived from the pot experiment ($c = 2.28$), the 30-min J_{s_TDP} were in line with those from GM. The slope was not significantly different from 1 ($P > 0.05$, Figure 2.2.B). When applying the calibration parameters derived for *B. vulgaris* from the SHB field calibration experiment ($c = 2.79$), J_{s_TDP} was 19% higher than J_{s_GM} ($P < 0.01$, Figure 2.2.B).

2.3.2 Field calibration experiment: TDP & SHB

Formula type and data time step had no significant influence on the performance of the calibration formula, but it mattered whether culm- or species-specific or a common calibration formula was used (Appendix Table 1; Appendix Table 2). Based on the nRMSE and the passing rate of the Wilcoxon test ($P > 0.05$) between calibrated J_{s_TDP} and J_{s_SHB}, culm-specific formulas performed better than species-specific and common formulas. In our study, there was no statistically significant difference between the species-specific

Table 2.2 Values of the parameter c of different bamboo calibrations (species-specific/common) for TDP sap flux estimates.

Formula specificity	Species	c	Formula nRMSE		P
			Species-specific	common	
Species	B. vulgaris	2.79 ± 0.13^{a}	0.10	0.11	0.07
	G. apus	3.32 ± 0.08^{b}	0.10	0.12	0.06
	D. asper	2.42 ± 0.06^{c}	0.18	0.18	0.97
	G. atroviolacea	2.53 ± 0.11^{d}	0.12	0.13	0.81
Common		2.74 ± 0.07^{e}			

Note: Significant differences between species-specific and common c estimates (Turkey's test, $P < 0.01$) are indicated by superscripted letters. $P < 0.05$ indicate significant differences between Normalized Root-Mean-Square Errors (nRMSE) of species-specific and common formula.

and the common calibration parameters (Table 2.2, $P > 0.05$). For two of the four studied bamboo species (*G. apus* and *B. vulgaris*), however, using species-specific formulas slightly improved the quality of predictions as compared to applying the common formula ($P = 0.06$ and 0.07, respectively, Table 2.2). These two bamboo species had lower nRMSE and higher passing rates than *D. asper* and *G. atroviolacea* (Appendix Table 2). The linear calibration parameters of the four bamboo species were significantly different from each other ($P < 0.01$). The linear calibration parameters, the slopes of J_{s_TDP} vs. J_{s_SHB}, were examined with the test of homogeneity of slopes and were found to differ significantly from each other ($t > 0.01$).

Before calibration, J_{s_TDP} was on average 66% and 63% lower than SHB-derived reference values on the daily and 30-min scales, respectively ($P < 0.01$). This deviation was reduced to 10% and 8% underestimations ($P < 0.01$) when using species-specific calibration parameters (Table 2.2). On average, for $77\pm6\%$ of the days that were included in the analysis, the species-specific post-calibration 30-min J_{s_TDP} values were not significantly different from the respective reference J_{s_SHB} (Wilcoxon Signed-Rank test, $P > 0.05$).
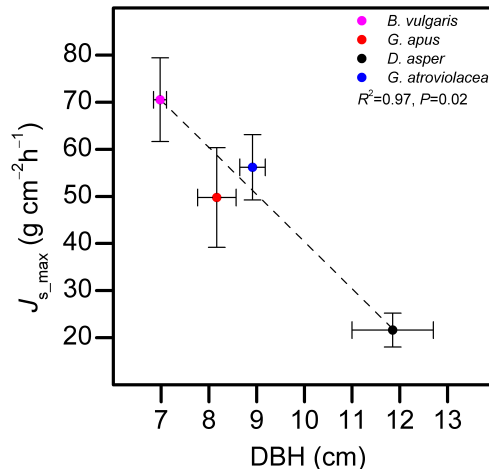
Fig. 2.3 Relationship between diameter at breast height (DBH) of bamboo culms and maximum observed sap flux density (J_{s_max}) in four bamboo species. Horizontal error bars indicate DBH standard errors, vertical bars standard errors of J_{s_max}. Data of five culms pooled per species, average of the highest 10% of daily J_{s_max} values of each culm used for the analysis.

2.3.3 Field study

Monitoring bamboo and tree sap flux

J_{s_max} in the studied bamboo species (averages from five individuals per species) were 70.5, 21.6, 49.7 and 56.2 g cm^{-2} h^{-1} for *B. vulgaris*, *D. asper*, *G. apus* and *G. atroviolacea*, respectively. In trees, corresponding values were 17.7, 10.5 and 23.3 g cm^{-2} h^{-1} for *H. brasiliensis*, *G. arborea* and *S. leprosula*, respectively. Across bamboo species, J_{s_max} decreased with increasing culm diameter ($R^2 = 0.97$, $P = 0.02$, Figure 2.3).

Environmental measurements and analyses

The normalized daily accumulated J_s of all studied species increased with increasing daily integrated radiation. This relationship did not fully hold up for accumulated J_s and average daily V*P*D. In several species, daily J_s increased with increasing VPD only to a certain VPD threshold (approx. 0.74 kPa, Figure 2.4); after this threshold, accumulated J_s decreased with further increasing VPD. Such conditions of high VPD were characteristic of the dry period. For days with VPD > 0.74 kPa, daily accumulated J_s of most studied species (except in *D. asper* and *G. arborea*) declined with decreasing soil moisture content ($R^2 = 0.39$, 0.44, 0.4 ,0.52 and 0.55 for *B. vulgaris*, *G.*
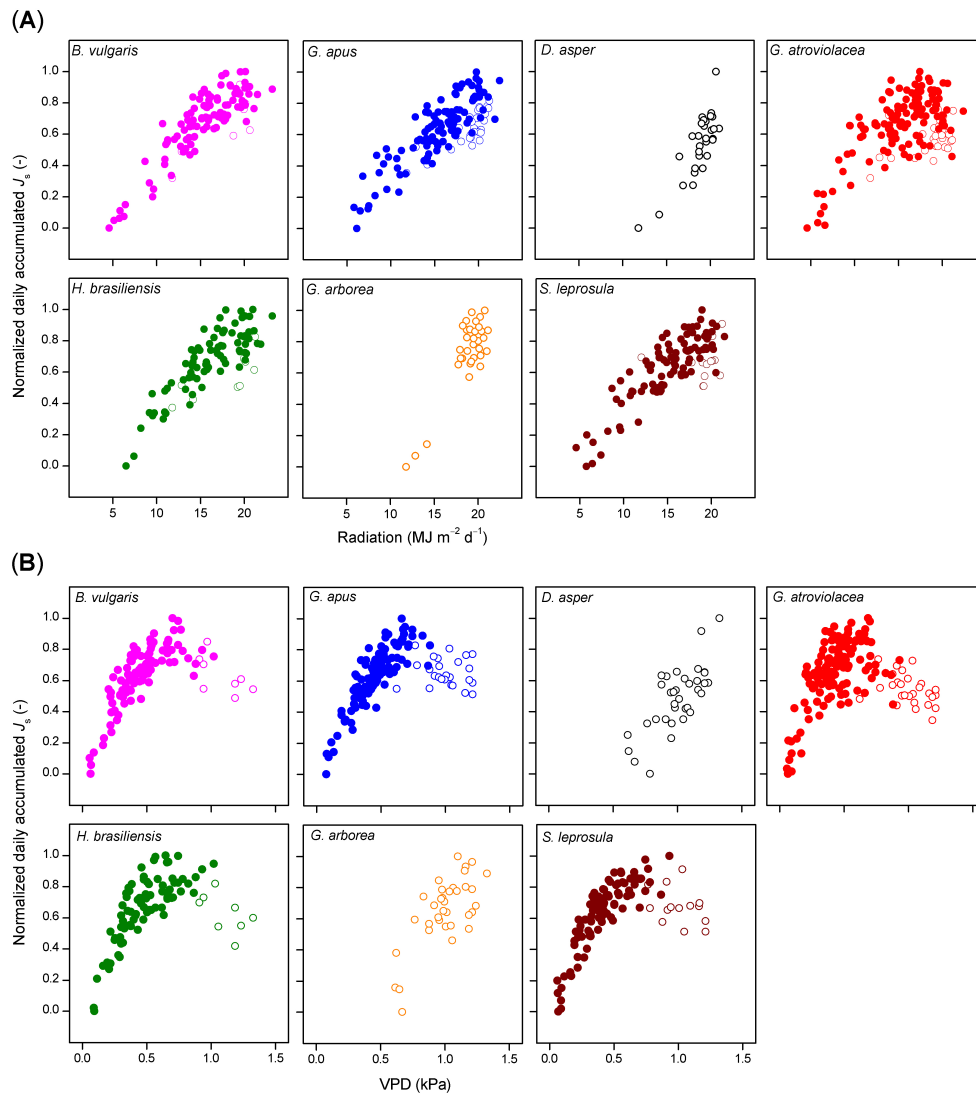
Fig. 2.4 Normallized daily accumulated sap flux density (J_s) plotted against absolute values of (A) intergrated daily radiation and (B) average daily vapor pressure deficit (VPD). Daily values of four bamboo (upper row) and three tree species (lower row); data from 7 months of measurements (July 2012-January 2013) encompassing both wet (filled circles) and dry (open circles) periods (except for *Dendrocalamus asper* and *Gmelina arborea*, mainly dry period). Daily averages derived from measurements of five culms per species.
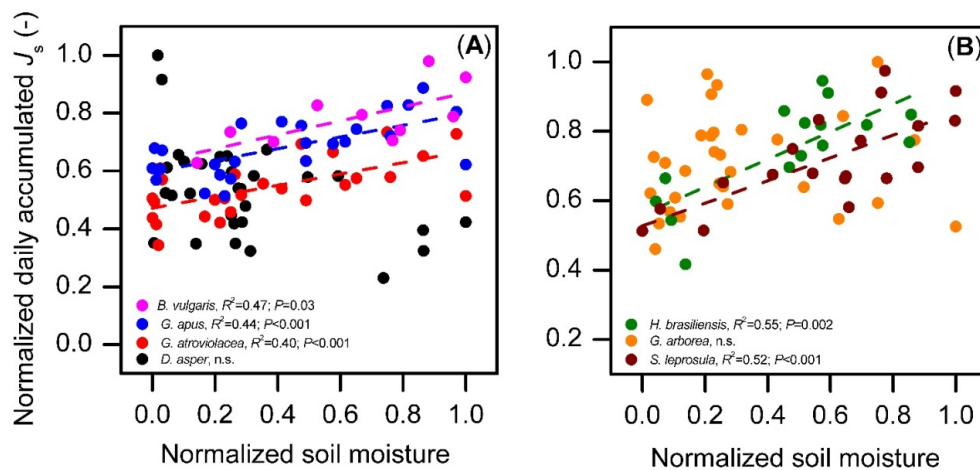
Fig. 2.5 Normalized daily accumulated sap flux density (J_s) of four bamboo species (A) and three tree species (B) in the 'dry period' (characterized with mean daily VPD > 0.74 kPa) plotted against normalized mean daily soil moisture content (SM). There was a significant linear relationship between J_s and SM ($P < 0.05$) for all species except *D. asper* and *G. arborea*. Normalized values do not reach 1.0 for all species in the figure as the normalization was performed by setting the maximum value of the full measurement period of each species (including wet period) to one, while the figure displays only values in dry period. Daily averages derived from measurements on five culms per species, data of at least 10 dry period days per species.

apus, *G. atroviolacea*, *S. leprosula* and *H. brasiliensis* respectively; $P < 0.05$, Figure 2.5.A and 2.5.B).

Diurnal peaks in J_s in the studied bamboo species occurred relatively early (on average at about 11 am), which was significantly earlier than the peaks of radiation and VPD (20-82 min and 131-206 min, respectively). In the studied tree species, maximal hourly J_s values were observed after the peak of radiation (3-97 min), but still before (51-108 min) VPD peaked. All time lags were significantly different from zero minutes ($P < 0.01$; Table 2.3), except for the time lag to radiation for the tree species *S. leprosula* ($P > 0.05$).

Diurnally, some of the studied species showed pronounced hysteresis of hourly J_s to radiation and VPD. Direction of rotation (i.e. order of observations) was counter-clockwise for radiation (Figure 2.6.A) and clockwise for VPD (Figure 2.6.B). The area of the hysteresis to VPD was on average 32% larger in bamboos than in trees, while the area of hysteresis to radiation was on average 50% smaller in bamboos ($P < 0.01$).
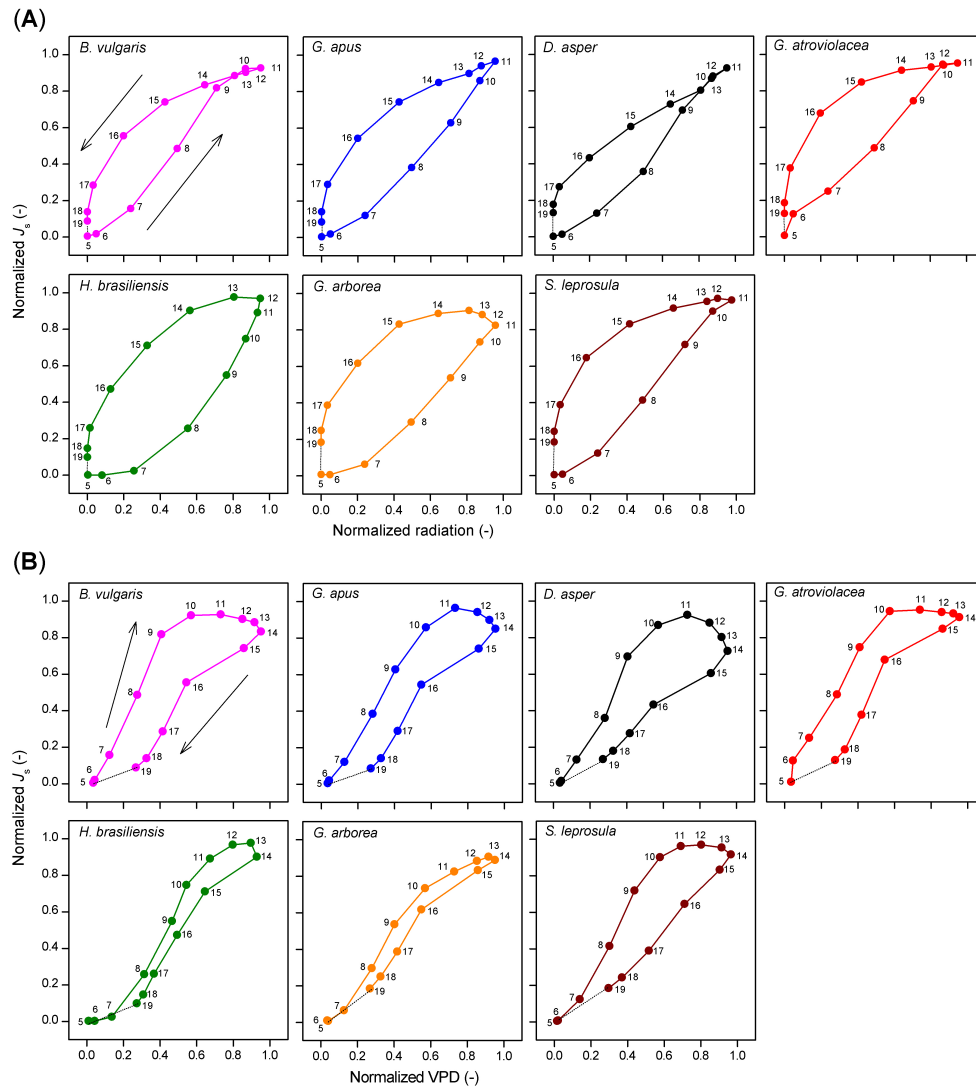
Fig. 2.6 Normalized hourly sap flux density (J_s) plotted against (A) normalized hourly radiation and (B) VPD. Data of four bamboo (upper row) and three tree species (lower row). Hourly averages derived from simultaneous measurements on five culms per species and by averaging the values of three sunny days to minimize influences of weather. The numbers in the sub-figures indicate the respective time of the day.

Table 2.3 Time lags between diurnal peaks of radiation and VPD and peaks of J_s in studied bamboos and trees.

Species	N	Time lag with radiation (min)	Time lag with VPD (min)
B. vulgaris	5	82±62	171±63
G. apus	5	41±57	206±57
D. asper	4	20±61	131±53
G. atroviolacea	5	64±30	170±35
Bamboo_mean	19	51[A]	169[A]
H. brasiliensis	5	-37±12[a]	51±9
G. arborea	5	-97±87[b]	67±87
S. leprosula	5	-3±25[a]	108±20
Tree_mean	15	-46[B]	75[B]

Note: Positive values indicate a peak of radiation/VPD after the peak of J_s, negative values indicate a peak before J_s; N, culms/trunks per species averaged (mean±SD). Significant differences in bamboo/tree mean time lags are indicated by different superscripted letters (Turkey's test, $P < 0.01$). Significant differences between species are indicated by capital letters ($P < 0.01$).

2.4 Discussion

2.4.1 Calibration experiments

In the pot calibration experiment, SHB yielded similar results as reference GM measurements. Bamboos seem well suited for the SHB method (Dierick et al., 2010) due to their round shape and smooth and barkless surface, which allows for tight contact with the gauges. Additionally, the hollow center and thin culm walls result in relatively low energy losses to heat storage so that the heat balance conditions required for the SHB method are met. "Zero sap flux" conditions to obtain the heat conductivity of the sheath (K_{sh}, Sakuratani, 1981) as a further requirement of the SHB method are difficult to determine in situ due to potential root pressure induced night time sap flux in bamboos (Cao et al., 2012); however, using K_{sh} derived from field conditions of very low night-time sap flux likely introduced only negligible errors into the calculation of daytime sap flux (Grime and Sinclair, 1999). As we observed very low sap flux over several hours during our experiments (e.g. about 1 g cm^{-2} h^{-1} during the pot experiment), our obtained K_{sh} were likely reliable.

In contrast to SHB, the TDP method was found to substantially underestimate J_s of bamboos in the pot and field calibration experiments. Underesti-

mations by TDP were also reported in two other bamboo species: respective average underestimations of 13% for *Bambusa blumeana* (Dierick et al., 2010) and 31% for *Phyllostachys pubescens* (Moso bamboo, Kume et al., 2010) were reported. Reasons for the observed underestimations could lie in the distinct hydraulic and physiological features of bamboos. Diurnal variations of stem water storage, for example, could affect the accuracy of TDP measurements (Vergeynst et al., 2014). Bamboos have approx. 50% parenchyma in culm walls (Dransfield and Widjaja, 1995), which potentially provides large water reservoirs. The depletion and refilling of the stem during the day and night, respectively, could cause diurnal fluctuations in culm thermal diffusivity. Higher water content during the night could lead to a lower maximum temperature difference (ΔT_{max}) between heated and reference probe under "zero sap flux" conditions. Likewise, lower water content during the day could lead to higher observed ΔT values. As $\Delta T_{max}/\Delta T$ constitutes the basis for calculations of daytime J_s, substantial underestimations of J_s could be introduced when using the original calibration parameters (Granier, 1985; Vergeynst et al., 2014). This hypothesis was assessed further by comparing the linear calibration parameters of *B. vulgaris* from the pot and the field calibration experiment ($c = 2.28$ and 2.79, respectively). In the pot experiment, the bamboos were always supplied with plenty of water, so that the variability of the culm water content was likely smaller than under field conditions. Effects of varying stem water content on $\Delta T_{max}/\Delta T$ are thus likely much smaller in the pot experiment, which may explain why pot and field calibration experiment yield different parameters for the linear calibration of the same species (*B. vulgaris*). Another potential factor for the divergence could be that the maximum observed J_s in the field (about 70 g cm^{-2} h^{-1}) was much larger than in the pot experiment (about 20 g cm^{-2} h^{-1}). Higher daytime sap flux (and thus transpiration) may cause a quicker depletion of the potential culm water storage, which consequently leads to a higher variability of culm water content between night and day.

We expected the calibration formula type (linear vs. nonlinear) and data time step to have an impact on the performance of TDP predictions. However, both were not as important as the factor formula specificity. Even though species-specific calibration formulas generally did not perform significantly better than the common formula, species-specific formulas tended to show slightly better performance (Table 2.1) for two of the studied species (*G. apus* and *B. vulgaris*). Also, the calibration parameters were significantly different among the four studied bamboo species (Table 2.2). Confronting this insight

with results from sap flux studies on other bamboo species (Dierick et al., 2010; Kume et al., 2010), differences among species become even more apparent. We thus used the derived species-specific formulas for further analysis. The observed differences among species may be indicative of highly heterogeneous wood anatomical properties among bamboo species. For example, size and shape of vascular bundles and parenchyma of 15 bamboo species were reported to be highly variable (de Agrasar and Rodríguez, 2003). For two further bamboo species (*Chusquea ramosissima* and *Merostachys claussenii*), it was suggested that differences in number of vascular bundles per unit area (1000 vs. 225 per cm^2) and vessel length ($\approx$ 1 m vs. 20 cm) could lead to differences in xylem hydraulic conductivity (Saha et al., 2009). Differences in wood anatomical properties may also lead to heterogeneous heat conductive properties, which potentially affects applicability and accuracy of sap flux measurements and particularly of the TDP method (Wullschleger et al., 2011).

In our study, culm-specific formulas performed better at predicting J_s than species-specific and common calibration formulas (Appendix Table 1 and 2). This result indicates heterogeneity in conductive properties among culms of the same species. Potential reasons could lie in the age and the ontogeny of individual culms. Even though we carefully selected culms of similar age (approx. two years old), the exact age of individual bamboo culms within a given clump is difficult to assess. As all monocot species, bamboos lack secondary growth (Zimmermann and Tomlinson, 1972), so culm diameters are not related to culm age. Additionally, over the ontogeny of a certain culm, events and processes such as conductive circuit failure (drought- or metabolism-related; Cochard et al., 1994; Liese and Weiner, 1996), lignification (Lin et al., 2002) or increasing hydraulic limitations with height (Cao et al., 2012; Renninger and Phillips, 2010) could result in overall reduced hydraulic conductivity and thus lower sap flux densities with increasing culm age. However, these processes remain difficult to assess from the outside of the culm; further studies linking the age and ontogeny of bamboos to (TDP-derived) sap flux and water use patterns are suggested.

2.4.2 Water use patterns of bamboos and trees

Half-hourly J_{s_max} in the four studied bamboo species ranged from 21.6 to 70.5 g cm^{-2} h^{-1} and were (on average) almost two times greater than in the studied tree species. The observed range for both bamboos and trees falls into

the range of J_{s_max} values reported for tropical tree species in a variety of sap flux studies (Meinzer et al., 2001; O'Brien et al., 2004). For *D. asper*, the J_{s_max} (21.6 g cm^{-2} h^{-1}) was similar to values reported for *Bambusa blumeana* culms (25.7 g cm^{-2} h^{-1}, Dierick et al., 2010) and Moso bamboos (approx. 20 g cm^{-2} h^{-1}, Kume et al., 2010) of similar size. Our four studied bamboo species showed significant differences in J_{s_max}, which were negatively correlated with species-specific differences in DBH (Figure 2.3). Consistent with this, in a study on 27 tropical tree species, the negative correlation between J_{s_max} and DBH was also observed (Meinzer et al., 2001). It was assumed to be related to a decline of the leaf area to sapwood area ratio with increasing DBH. This was also observed in a study on *Eucalyptus grandis* trees (Dye and Olbrich, 1993). In our study, we harvested leaves of three bamboo species (*B. vulgaris*, *D. asper*, and *G. apus*) and found that the leaf weight to sapwood area ratio was positively correlated with J_{s_max} ($R^2 = 0.45$, $P < 0.05$). However, studies connecting such anatomical and eco-hydrological properties of bamboos are yet scarce (Saha et al., 2009).

On the day-to-day level, accumulated J_s of both the studied bamboo and tree species were significantly correlated with radiation and VPD (Figure 2.4). During the long wet period, accumulated J_s linearly increased with higher integrated radiation and average daily VPD. Likewise, linear relationships in the day-to-day behavior of J_s to micrometeorological drivers have been reported for some tropical bamboo and several dicot tree species (Dierick and Hölscher, 2009; Köhler et al., 2009). During the dry period characterized by higher radiation and VPD (13% and 100% higher, respectively) than during the wet period, however, the observed linear relationship to VPD did not hold. Higher average daily VPD ("dry period conditions") led to decreases in accumulated J_s of several studied species (Figure 2.4.B). Similar decreases after a certain peak value have been reported for some previously studied tree species (Jung et al., 2011; Kubota et al., 2005), but in most species studied so far, higher average daily VPD leads to increases in accumulated J_s or water use (Hernández-Santana et al., 2008; Horna et al., 2011; Kume et al., 2007; Peters et al., 2010; Tang et al., 2006; Wullschleger and Norby, 2001). This was also reported for Moso bamboo (Komatsu et al., 2010). The observed decreasing accumulated J_s in bamboos under high VPD in our study were related to a reduction of soil moisture in the dry period (for three of the four bamboo and two of the three studied tree species). During the dry period, VPD was generally much higher than during the wet period. Soil moisture may become a limiting factor after several days without rainfall in the dry period.

Accumulated J_s decreased strongly and linearly with decreasing soil moisture under "dry period conditions" (i.e. VPD > 0.74 kPa) for all studied bamboo (except *D. asper*) and tree species (except *G. arborea*, Figure 2.5). Similarly, in a throughfall reduction experiment in Indonesia, declines of monthly J_s of Cacao and *Gliricidia sepium* were found to linearly correlate with reduced soil moisture (Köhler et al., 2010). Such sensitivity of daily J_s to fluctuating soil moisture may be related to a relatively shallow rooting depth (Kume et al., 2007).

Regarding the diurnal course of J_s, the studied bamboo species showed earlier peaks than radiation and VPD, and also earlier than the respective peaks of the studied tree species. In contrast to this, previous studies on tropical trees reported rather small time-lags between peaks of J_s and radiation and VPD, respectively (Dierick and Hölscher, 2009; Horna et al., 2011; Köhler et al., 2009). Pre-noon peaks of J_s have only been described for few species thus far, for example, *Acer rubrum* (Johnson et al., 2011) and oil palms (Niu et al., 2015). The early diurnal peaks of J_s result in substantial hysteresis of J_s particularly to VPD. For another monocot species, oil palm, it has been suggested that such pre-noon peaks of J_s and the resulting large hysteresis to VPD could be indicative of internal trunk water storage and/or root pressure mechanisms (Niu et al., 2015; Röll et al., 2015). Early peaks of J_s could be due to a pre-noon contribution of internal water storage to bamboo transpiration. Likewise, the decoupling of hourly J_s particularly from VPD in the afternoon, i.e. the drop in bamboo J_s (after an early peak) despite further rising VPD, could be connected to the reduced water availability for leaves after the depletion of internal water storage at a certain time of the day. The depletion of stored stem water may be compensated for during the night by root pressure mechanisms (Cao et al., 2012; Yang et al., 2012). Other potential reasons for the diurnally relatively early decline of bamboo J_s and the consequent decoupling of the sap flux response from micrometeorological drivers could be a decline in leaf hydraulic conductance in the afternoon hours, which could contribute to prevent stem water potential loss and subsequent xylem cavitation (Saha et al., 2009; Yang et al., 2012).

2.5   Conclusion

Adjusting and applying the TDP method for sap flux measurements on four
bamboo species pointed to substantial differences in water use patterns be-
tween the studied bamboos and three tree species studied. Bamboos had higher
J_s, and respective hourly maxima were reached earlier in the day than in tree
species. This resulted in strong diurnal hysteresis, particularly to VPD, and in
significant time lags between the peaks of J_s in bamboos and the respective
peaks of radiation and VPD. Both may point to a strong contribution of internal
water storage mechanisms to bamboo transpiration. We found substantial dif-
ferences in the day-to-day J_s response of most studied bamboo and tree species
to fluctuations in environmental conditions between the dry and the wet period.
Reduced J_s under conditions of high VPD in the dry period could largely
be explained by limiting soil moisture content. The regulation of bamboo
water use thus seems to involve mechanisms at the leaf-, culm- and root- level.
However, these mechanisms yet remain to be inter-connected convincingly.

Chapter 3

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

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Abstract

Bamboos and other plants may substantially rely on stem water storage for transpiration. Fluctuations in wood water content (θ_{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 θ_{wood} on J_s, we conducted a culm dehydration experiment, monitored bamboos with TDPs, and implemented a steady-state thermal model. Central to the calculation of J_s, and thus a major potential source of error, is the maximal temperature difference between probes (ΔT_{max}) which is often referred to as "zero sap flow" condition. In the culm dehydration experiment, we observed that ΔT_{max} decreased when θ_{wood} increased. In long-term field monitoring, ΔT_{max} decreased when soil moisture content increased, potentially indicating changes in θ_{wood} and a seasonal decrease in stem water storage. The steady-state model reproduced the θ_{wood} to ΔT_{max} relationship of the dehydration experiment and underlined a considerable sensitivity of J_s estimates to θ_{wood}. Fluctuations in θ_{wood} may lead to 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 when key wood properties are known. Our study gives insights into the relationship between θ_{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

3.1   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 these methods, the thermal dissipation probe (TDP) method (Granier, 1985) is most widely used. 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, g m^{-2} s^{-1}) was first put forward by (Granier, 1985); J_s is

expressed as a function of the temperature difference (ΔT) between a heating probe and a reference probe: $J_s = 119 \times (\Delta T_{max}/\Delta T - 1)^{1.231}$, where ΔT_{max} is the ΔT under zero flow condition, which is commonly substituted by the daily, nighttime maximum ΔT (Granier, 1987).

As the Granier's formula was derived from an empirical relationship (Granier, 1985) rather than 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 (Bush et al., 2010; Clearwater et al., 1999; Steppe et al., 2010). Potential reasons for the 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 (θ_{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 θ_{wood} (Nadler et al., 2008; Yang et al., 2015), which may influence wood thermal conductivity (K_{wood}) and subsequently estimates of J_s. Based on theoretical analysis of a temperature-θ_{wood} function (Carslaw and Jaeger, 1959) and a laboratory dehydration experiment on tree stem segments (Vergeynst et al., 2014), it was demonstrated that θ_{wood} influenced K_{wood} around TDP probes and caused underestimation of daytime J_s. The underestimation was attributed to selecting one single ΔT_{max} (usually at night) to calculate hourly J_s for the whole day (Granier, 1987) while ignoring the different K_{wood} between nighttime and daytime. Additionally, the influence of θ_{wood} on ΔT_{max} may differ with soil water conditions, as previous studies found that θ_{wood} in trees and palms fluctuates with θ_{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 θ_{wood} was reported to be significantly increased, and subsequently decreased during the following sunny days (Constantz and Murphy, 1990; Holbrook et al., 1992; Wullschleger et al., 1996), which may further influence K_{wood} around TDP probes, and thus ΔT_{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 θ_{wood}. Bamboo culms have a large percentage of parenchyma ($\approx 50\%$, Liese and Köhl, 2015), which provides a potential "buffering" reservoir for transpiration. With the withdrawal from and refilling of water to this reservoir, θ_{wood} may fluctuate accordingly, which can induce changes in culm circumference (Yang et al., 2015). Changes in θ_{wood} in bamboo culms may at least partly be responsible for underestimations of J_s by influencing K_{wood} of the culm and consequently ΔT_{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 θ_{wood} encompassing different scenarios. Such numerical simulations have been previously applied successfully to investigate the uncertainty of factors (wood thermal conductivity, non-homogeneity of sap flow radial profiles and of 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, the objectives of our study were 1) to test on bamboo segments in a laboratory dehydration experiment if ΔT_{max} is affected by decreasing θ_{wood}, and to explore if ΔT_{max} in bamboos is influenced by changes in θ_{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.

3.2 Methods

3.2.1 Culm θ_{wood} and θ_{soil} and ΔT_{max}

To test if ΔT_{max} is affected by changes in θ_{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 θ_{soil} and daily TDP-derived ΔT_{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 KCl solution for 24 hours 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 superficies.

At a first step of the actual dehydration experiment, the fresh weight of each segment (w_{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 three-hour probe powering and subsequent two-hour dehydration periods were conducted repeatedly over the duration of five days. During the powering phase, the heating probe of the TDP sensors was continuously powered with 0.1 W in order to obtain stable ΔT_{max} readings. During this interval, room temperature was kept constant at about 20 °C and laboratory conditions prevailed (constant light, only a little air circulation); the segments thus dehydrated only marginally during this time. During the following two-hour 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 two-hour period, TDP sensors were removed and the segments were weighted. By continuously

repeating the powering-dehydration cycles, data pairs of w_{fresh} vs. ΔT_{max} were produced and recorded.

After the end of the dehydration experiments, the segments were oven dried at 100 °C for 48 hours to get their dry weight (w_{dry}, g). With the w_{dry} and w_{fresh} of each powering-dehydration cycle, the θ_{wood} (kg kg^{-1}) was calculated as (w_{fresh} - w_{dry})/ w_{dry}. Subsequently, the relationship between θ_{wood} and ΔT_{max} was examined.

Field monitoring of θ_{soil} and ΔT_{max}

To explore whether, and if so how, ΔT_{max} in bamboo culms was influenced by the θ_{soil} under field conditions, we monitored daily TDP-derived ΔT_{max} on three culms each of *D. asper* and *G. apus* and on four culms of *B. vulgaris* for seven months (July 2012 to April 2013). Simultaneously, θ_{soil} at 20 cm depth was monitored at the respective study sites with time domain reflectometry sensors (TDR, CS616, Campbell). Detailed information of the installations refers to Mei et al. (2016). Subsequently, the relationship between ΔT_{max} and daily mean θ_{soil} was examined.

θ_{wood} and thermal conductivity

The thermal conductivity of each sample segment was calculated following Vandegehuchte and Steppe (2012), who introduced a corrected thermal conductivity for axial directions (K_{a}, W m^{-1} K^{-1}; Eq. 1):

$$K_a = K_w(\theta_{wood} - \theta_{wood-FSP})\frac{\rho_{dry}}{\rho_w} + 0.04186 \times (21.0 - 20.0 \times F_{v-FSP})$$

Where K_{w} is thermal conductivity of water (0.6 W m^{-1} K^{-1}), $\theta_{\text{wood-FSP}}$ is θ_{wood} at the fiber saturation point (%), ρ_{dry} and ρ_{w} are the respective densities of dry wood and water (1000 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 ρ_{dry} and ρ_{w} (see details in Appendix).

To obtain ρ_{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 two meters on the respective culms. The segments were immediately transported to the laboratory in sealed plastic bags. The fresh volumes (v_{fresh}, cm^3) of the segments were derived by measuring

lengths and inner and outer radiuses of the cylindrical segments; additionally, the w_{fresh} of each segment was established. After that, the segments were dried in an oven at 100 °C for 48 hours to get their w_{dry}. Subsequently, ρ_{d} could be calculated as $w_{\text{dry}}/v_{\text{fresh}}$.

With the mentioned variables (ρ_{dry}, ρ_{w}, $\theta_{\text{wood-FSP}}$ and $F_{\text{v-FSP}}$), we calculated series of K_{a} with θ_{wood} ranging from 0.1 to 1 kg kg^{-1} (in incremental 0.1 kg kg^{-1} steps); the thermal conductivity in the transverse direction (K_{t}) was set to half the value of the K_{a} (Wullschleger et al., 2011). At last, using the same variables as above (ρ_{dry}, ρ_{w}, $\theta_{\text{wood-FSP}}$ and $F_{\text{v-FSP}}$) and varying K_{a} and K_{t} with varying θ_{wood} (Eq. 2), we derived a series of temperatures at thermal steady state with zero sap flow. Thus, ΔT_{max} between the heating probe and unheated reference probe was calculated.

Steady-state thermal model

To test if ΔT_{max} decreased with increasing θ_{wood} in bamboos, numerical simulations of temperature distributions were performed with a steady-state thermal model (Academic version, CFX 17.0, ANSYS Inc., Pennsylvania, USA). The simulations were conducted on a 3D anisotropic grid by numerically solving the steady-state energy balance equation (Eq. 2):

$$-\lambda \nabla^2 T + c_w Q_w \nabla T = q$$

Where q is the heat input of a grid (W m^{-3}), T is the temperature of a grid (K), λ is matrix of thermal conductivity (W $^{-1}$ K^{-1}), ∇ is vector differential operator, c_{w} is the specific heat of water (J kg^{-1} K^{-1}) and Q_{w} is the sap flow vector (kg m^{-2} s^{-1}). To explore the relationship between θ_{wood} and ΔT_{max}, Q_{w} was set to zero sap flow when aiming to simulate ΔT_{max} (See detailed parameters in Table 3.1).

In order 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 axial and radial direction of

Table 3.1 Parameters for the ANSYS numerical simulation

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

the heating probe, the temperature was assumed to be fairly uniform (following Wullschleger et al., 2011), and wood physical properties along the probe were also assumed to be uniform. Therefore, the steady state simulations were thus simplified on the front and back surfaces of the segment. Generally, a 2 mm (quadratic) mesh was used for the thermal steady state model. However, mesh type was set to quad/tri around the heating probe, because the contact area between the heating probe and the surrounding wood was irregular.

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^{-2} (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.

3.2.2   The influence of θ_{wood} on J_s

To simulate the influence of varying θ_{wood} on TDP-derived J_s in bamboo culms, we simulated the ΔT between probes in a series of numerical simulations of J_s and θ_{wood}. We incrementally increased J_s from 0 to 30 g cm^{-2} h^{-1} in 5 g cm^{-2} h^{-1} steps, and θ_{wood} from 0.1 to 1 kg kg^{-1} in 0.1 kg kg^{-1} steps. The ΔT of each possible combination at zero J_s was used as ΔT$_{max}$. The settings of geometry, meshing and change of K_a against θ_{wood} followed the previously described model description (see 2.1.3).

Two scenarios were simulated: 1) relative to a fixed nighttime θ_{wood} (e.g. 1 kg kg^{-1}), the daytime θ_{wood} was reduced in 0.1 kg kg^{-1} steps (for clarity, some of the figures only show reductions of 0.1, 0.3, 0.7 and 0.9 kg kg^{-1}); 2) based on different nighttime θ_{wood} (0.3, 0.6 and 0.9 kg kg^{-1}), the daytime θ_{wood} was reduced by half compared to nighttime θ_{wood}. The first scenario was simulated to explore the influence of changes in θ_{wood} between daytime and nighttime ($\Delta\theta_{wood}$) on daytime J_s in a day. The second scenario compared the varying influence of $\Delta\theta_{wood}$ on daytime J_s among the days with different nighttime θ_{wood}, which likely occurs e.g. between different seasons (dry vs. wet season) or among days with different weather conditions (sunny vs. rainy days).

For a set θ_{wood} (e.g. θ_{wood} = 1 kg kg^{-1}), the derived ΔT were used to calculate J_s in two ways: (1), J_s was calculated with ΔT_{max} and ΔT for the same θ_{wood}; (2), $J_{s\text{-mis}}$ was calculated with ΔT_{max} and ΔT for a lower θ_{wood} (e.g. $\theta_{wood\text{-mis}}$ = 0.9 kg kg^{-1}). The respective relative changes of J_s and $\Delta\theta_{wood}$ were calculated as (J_s - $J_{s\text{-mis}}$)/J_s and (θ_{wood} - $\theta_{wood\text{-mis}}$)/θ_{wood}. Relative changes of J_s were analyzed with the $\Delta\theta_{wood}$ between nighttime and daytime. The relationship between the relative changes of J_s and $\Delta\theta_{wood}$, respectively, was then applied to the J_s of *B. vulgaris* on a sunny day, to determine the degree of influence on daily water use.

All data analysis and figures were performed with SAS 9.3 (SAS Institute Inc., Cary, NC, USA, 2013).

3.3   Results

3.3.1 ΔT_{max} and θ_{wood}/θ_{soil}

In the laboratory dehydration experiment, the three freshly sprouted bamboo segments of *G. apus* showed differences in θ_{wood} vs. ΔT_{max} patterns. Nonetheless, when pooled, all three segments showed significant negative linear correlations between ΔT_{max} and θ_{wood} (R^2 = 0.61, $P < 0.05$; Fig. 3.1).

In the field monitoring, daily mean θ_{soil} was found to have a significant negative linear relationship ($P < 0.05$) with daily ΔT_{max} on all three bamboo species (*D. asper*, *G. apus*, *B. vulgaris*; Fig. 3.2). The slope of the ΔT_{max}-θ_{soil} regression line was larger on *B. vulgaris* (-3.55) than on *D. asper* (-1.91) and *G. apus* (-2.14).
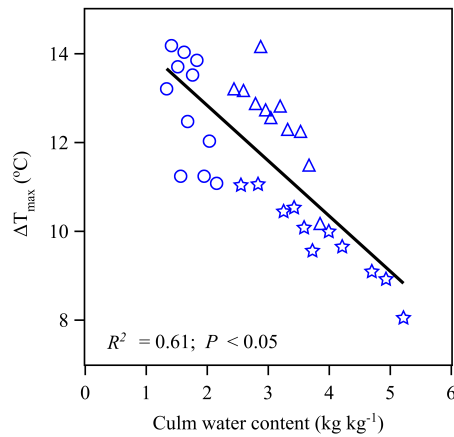
Fig. 3.1 The maximum temperature difference between the probes of TDP (ΔT_{max}) in relation to the water content in culm segments of freshly sprouted *G. apus* in a dehydration experiment. Different symbols indicate different segments. The unit of culm water content (kg kg^{-1}) indicates kg water in the culm per kg dry weight.
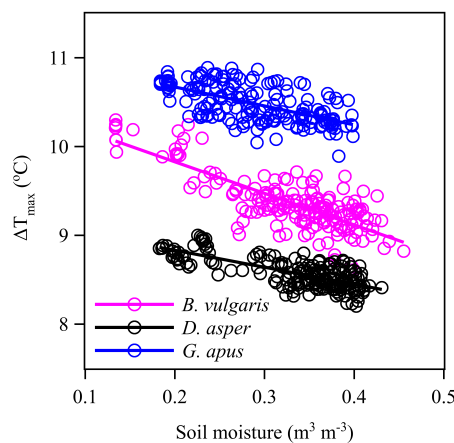
Fig. 3.2 The daily maximum temperature difference between the probes of TDP (ΔT_{max}) in relation to daily mean soil moisture for three bamboo species (*B. vulgaris*: $Y = -3.55X + 10.54$, $R^2 = 0.63$, $P < 0.01$; *D. asper*: $Y = -1.91X + 9.21$, $R^2 = 0.54$, $P < 0.01$; *G. apus*: $Y = -2.14X + 11.10$, $R^2 = 0.37$, $P < 0.01$).
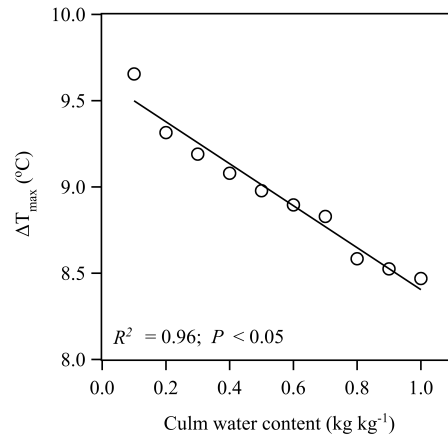
Fig. 3.3 The simulated maximum temperature difference between the probes of TDP (ΔT_{max}) with the ANSYS model in relation to culm water content. The unit of culm water content ($kg\ kg^{-1}$) indicates kg water in the culm per kg dry weight.

Using a steady-state thermal model (ANSYS), the heat field around TDP sensors was simulated for different θ_{wood} when J_s was zero ("zero sap flow" condition). With increasing θ_{wood}, the heat field area became smaller, and temperatures became lower (Appendix Fig. 1). A significant negative linear relationship between ΔT_{max} and θ_{wood} was found with data provided by the steady-state thermal model ($R^2 = 0.97$, $P < 0.05$; Fig. 3.3). This negative correlation could potentially be attributed to changes of culm K_a (Eq. 1) with changing θ_{wood} around the heating probe. To test for this, we calculated K_a using the ρ_{dry} and θ_{wood} of 82 segments from a total of 10 culms from the three bamboo species. The normalized ratio of culm K_a to ρ_{dry} of all segments was significantly linearly correlated to θ_{wood} ($R^2 = 0.99$, $P < 0.05$; Fig. 3.4).

3.3.2   The influence of θ_{wood} on J_s

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

Using the ANSYS model for series of numerical simulations of θ_{wood} and J_s, we found that TDP underestimated daytime J_s calculated with nighttime ΔT_{max} when θ_{wood} was lower during the day than during the night. For a given nighttime θ_{wood} (e.g. 1 $kg\ kg^{-1}$), lower daytime θ_{wood} (e.g. -0.9 $kg\ kg^{-1}$) led
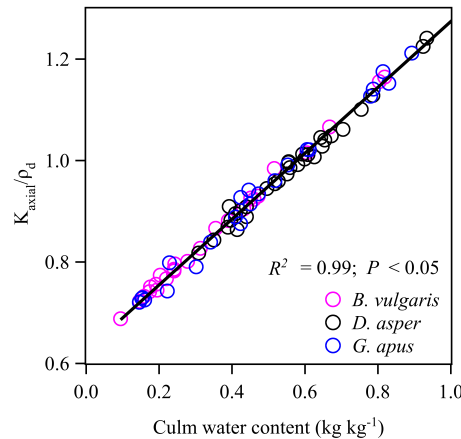
Fig. 3.4 The relationship between the ratio of thermal conductivity in the axial direction to culm dry density and the culm water content.

to larger underestimation of J_s of up to 44% (Fig. 3.5). Numerical simulations with the ANSYS model for reductions of daytime θ_{wood} by 0.1, 0.3, 0.7 and 0.9 kg kg^{-1} from a 1 kg kg^{-1} nighttime θ_{wood} result in underestimation of daily accumulated J_s by 2%, 10%, 19% and 28%, respectively (Fig. 3.6).

The relative error of 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 relative error was 18.6% at 5 g cm^{-2} h^{-1} while only 9.4% at 30 g cm^{-2} h^{-1} when θ_{wood} was decreased by 0.3 kg kg^{-1} in the daytime from 1 kg kg^{-1} in nighttime (Fig. 3.7). Even though relative errors were smaller at higher daytime J_s, they were responsible for most of the underestimation of daily water use. For example, the relative errors caused by the sap flux over 30 g cm^{-2} h^{-1} constituted as much as 64% of the total underestimation of daily water use when θ_{wood} was decreased by 0.3 kg kg^{-1} in the daytime from 1 kg kg^{-1} in nighttime (Fig. 3.6).

For hypothetical reductions of nighttime θ_{wood} (0.3, 0.6, 0.9 kg kg^{-1}) to half of their respective values in the daytime (i.e. 0.15, 0.3 and 0.45 kg kg^{-1}), the highest (> 25%) underestimation of daytime J_s were simulated for scenarios with high nighttime θ_{wood} (i.e. 0.9 kg kg^{-1}) under conditions of low sap flux density (e.g. 5 g cm^{-2} h^{-1}). With increasing J_s, the underestimation became smaller (e.g. < 15% at 30 g cm^{-2} h^{-1}), particularly for lower (i.e. 0.3, 0.6) nighttime θ_{wood} (< 10% at 30 g cm^{-2} h^{-1}, Fig. 3.7).
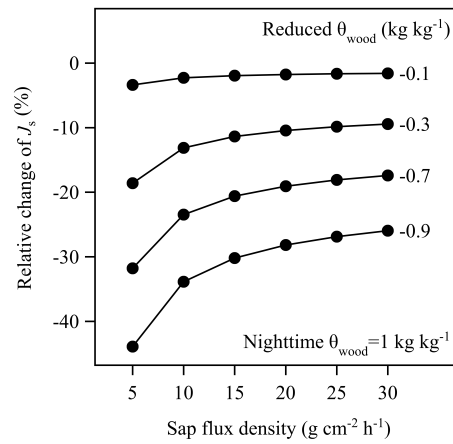
Fig. 3.5 The simulated relative change of daytime sap flux density (J_s) in percentage (%) at different absolute J_s (g cm^{-2} h^{-1}). Relationships are provided for different reductions of stem water content in daytime (-0.1, -0.3, -0.7 and -0.9 kg kg^{-1}) from 1 kg kg^{-1} in the nighttime, which results in different degrees of change of stem thermal conductivity. Provided data based on numerical simulations with the ANSYS model.
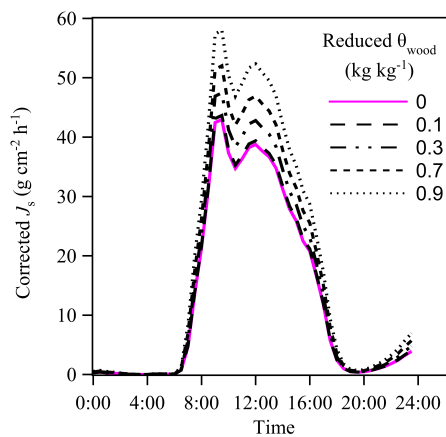
Fig. 3.6 The corrected sap flux density (J_s) for different levels of θ_{wood} reduction (%) during the daytime. Simulations based on field monitoring data of a *B. vulgaris* on 17 September 2012. Numerical simulations with the ANSYS model for reductions of daytime θ_{wood} by 0.1, 0.3, 0.7 and 0.9 kg kg^{-1} from a 1 kg kg^{-1} nighttime θ_{wood} result in underestimation of daily accumulated J_s by 2%, 10%, 19% and 28%, respectively.
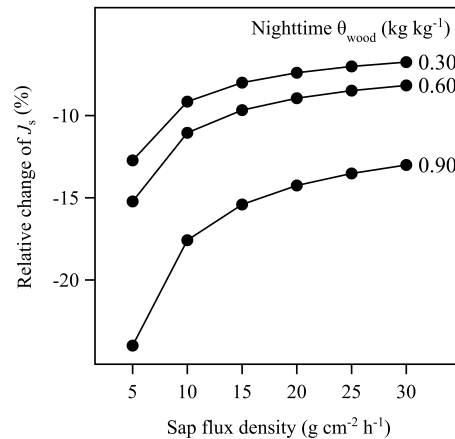
Fig. 3.7 The simulated relative change of daytime sap flux density (J_s) in % at different absolute J_s (g cm^{-2} h^{-1}). Relationships are provided for different nighttime stem water contents (θ_{wood}, 0.3, 0.6 and 0.9 kg kg^{-1}), assuming a constant reduction (i.e. by half) in the ratio between nighttime and daytime θ_{wood}. Provided data based on numerical simulations with the ANSYS model.

3.4   Discussion

3.4.1 ΔT_{max} and $\theta_{wood}/\theta_{soil}$

The Granier's formula is based on one assumption that the wood thermal property keeps constant during the whole day, and this constant wood thermal property corresponds to one daily ΔT_{max} (Granier, 1987). However, ΔT_{max} would change accordingly when the wood thermal property fluctuated during one day, and one common daily ΔT_{max} would not reflect such change and would cause errors if still insisting on calculating J_s with this common daily ΔT_{max} (Vergeynst et al., 2014). In our study, a dehydration experiment was conducted on segments of freshly sprouted bamboo culms. The results showed that decreasing culm θ_{wood} led to increasing ΔT_{max} (Fig. 3.1). Similar results were found in a dehydration experiment on tree segments (Vergeynst et al., 2014). In trees, contrasting the daily fluctuation pattern of transpiration, θ_{wood} showed an opposite fluctuation pattern. θ_{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 this study did not include direct measurements of θ_{wood}, the daily dynamics of culm circumference can be expected to at least partly reflect changes in θ_{wood} (Köcher et al., 2013; Scholz et al., 2008). According

to our findings, such fluctuations of θ_{wood} between nighttime and daytime go along with corresponding fluctuations of ΔT_{max}. In the bamboo culms in our study, ΔT_{max} significantly decreased with increasing θ_{soil} (Fig. 3.2). This may be attributed to corresponding changes of θ_{wood} caused by the dynamics in θ_{soil}. For trees, close coupling of the θ_{wood}-θ_{soil} relationship was reported for rainy days and sunny days and for different seasons; on rainy days or after irrigation, θ_{wood} was significantly increased and subsequently decreased during following sunny days (Hao et al., 2013; Holbrook et al., 1992; Wullschleger et al., 1996). Similarly to θ_{wood} and being an important indicator of θ_{wood}, stem circumference changed substantially between dry soil conditions and fully watered conditions (Köcher et al., 2013). Over the course of a growing season, variation in θ_{wood} was reported to be 39% in red maple; they were most produced between the dry and the wet season (Wullschleger et al., 1996). It has been put forward that dynamics in θ_{wood} may reflect changes in stem water storage (Sperling et al., 2015). Stem water storage mechanisms were shown to alleviate water shortage due to high transpiration demand during the daytime, with the assumption that depleted reservoirs can be fully recharged within one day, i.e. during the nighttime (Čermák et al., 2007; Goldstein et al., 1998; Köcher et al., 2013). However, this assumption may lead to errors in calculating stem water storage when the water storage depleted during the day-time is not fully refilled every day. Such incomplete refilling could be implied by a continuous decrease or increase of θ_{wood} on a day-to-day basis (Sperling et al., 2015; Wullschleger et al., 1996), e.g. due to changes in θ_{soil}. Dynamics in stem water storage may thus be derived by changes in θ_{wood} between days, when θ_{wood} is derived from the ΔT_{max}-θ_{wood} relationship and dry weight or volume of the tree stems or bamboo culms are known.

The model-derived ΔT_{max}-θ_{wood} relationship was based on an ideal assumption that the nighttime zero sap flow existed and lasted long enough to establish a one-to-one correspondence between ΔT_{max} and maximum θ_{wood}. However, this ideal assumption may not always be met during 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 the 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 the wet season (approx. April to May), we observed guttation from midnight to approx. 6:00 in the morning on bamboos growing close to a river. During this time, or even in general, zero nighttime sap flux conditions might thus not have been met, which would consequently affect the derived ΔT_{max}. In our study, ΔT_{max} thus could have potentially been affected (i.e. lowered) by water fluxes occurring for different reasons. Therefore, both changes in θ_{wood} and nighttime sap flow are likely to influence ΔT_{max} in the same direction. As to which proportion they contributed in our study can thus far not be disentangled. This will require further, more in-depths ecophysiological studies.

3.4.2   The influence of θ_{wood} on J_s

In our study, we numerically simulated the influence of θ_{wood} on TDP-derived J_s. The results pointed to a direct and quantifiable relationship between θ_{wood} and changes in J_s, and thus potential errors in previous studies assuming a static θ_{wood} (Vergeynst et al., 2014; Wullschleger et al., 2011). Wullschleger et al. (2011) simulated scenarios examining the impact of wood thermal conductivity on the relationship between J_s and k (= $\Delta T_{max}/\Delta T$-1). They found a negative relationship between ΔT and thermal conductivity and pointed out that the J_s-k relationship might be influenced by several factors including θ_{wood}, wood density, and thermal conductivity. Vergeynst et al. (2014) quantified the influence of θ_{wood} on J_s by simulating possible temperature changes that were assumed to relate to θ_{wood}. However, they did not find a direct relationship between θ_{wood} and errors in J_s. Our results supplement previous TDP error analyses and point to a direct and quantifiable relationship between θ_{wood} and errors on J_s, which could potentially be corrected for e.g. with the mentioned model.

Using numerical simulations, we found increasing underestimation of J_s with the larger decrease of θ_{wood} from nighttime to daytime, e.g. due to depleted stem water storage (Fig. 3.5, 3.6). In previous studies on bamboos (Yang et al., 2015) and palms (Sperling et al., 2015), gradual decreases of θ_{wood} from sunrise to sunset were reported. θ_{wood} in the afternoon and especially at dusk was likely the lowest, which could introduce substantial bias into according estimates of J_s (Fig. 3.5). Our results indicate that the magnitude of the 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. 3.5). TDP-derived J_s is thus influenced more profoundly by changing θ_{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 the plants with generally high J_s or at peak times of J_s (e.g. around noon), the influence of changes in θ_{wood} would be smaller. Despite the relatively smaller errors at higher daytime J_s, they were responsible for causing most of the underestimation of daily water use (Fig. 3.6).

Additional to varying with different J_s, the influence of θ_{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 indicated that, when θ_{wood} was reduced by the same ratio (e.g. half) from nighttime to daytime, higher nighttime θ_{wood} caused larger underestimation of J_s (Fig. 3.7). High nighttime θ_{wood} 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. As such, it was reported that even after calibrating the method with a full month of data encompassing parallel measurements of a reference method, the daily J_s of bamboos was still on average 10% lower when derived by TDP than by the stem heat balance method (Mei et al., 2016). Consequently, calibration approaches conducted over short periods of time may not reflect medium- or long-term dynamics in θ_{wood}. Similarly, one-time laboratory calibration experiments on tree or bamboo segments may also be prone to error due to potentially varying (or unknown) θ_{wood}, e.g. as a result of varying soil water conditions. We therefore strongly recommend multiple calibration experiments encompassing different seasons and soil water conditions, particularly if the TDP approach is applied for long-term monitoring; alternatively, the model applied in our study could potentially be used to correct for errors due to changing θ_{wood} if some basic wood properties are known.

For TDP and other heat-based methods, influences or biases due to changes in θ_{wood} cannot fully be avoided (Vergeynst et al., 2014). Additional to calibration-based approaches to correct for such errors, other possible solutions may include new types of sensors, which already account for dynamic changes of θ_{wood} when estimating J_s (Trcala and Čermák, 2016; Vandegehuchte and Steppe, 2013). Decreasing the sensitivity of the heat domain by increasing the power supply (Tatarinov et al., 2005) may be a further option. However, this may lead to possible damages to the wood structure; including dynamic change of θ_{wood} into estimating J_s thus seems to be a more promising

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approach. The model applied in our study to simulate the influence of changes
in θ_{wood} on J_s may be a first step to developing such a dynamic solution. In
our study, the model was built under steady-state conditions, under which each
simulation result was derived from the assumption of constant sap flow. These
steady-state conditions may not (always) be met under field conditions, where
sap flow is prone to external influences and may thus change frequently and
not always predictably. For future studies, the application of the model in situ
for simultaneous assessments of θ_{wood} and sap flow would be an interesting
next step.

3.5 Conclusions

In our study encompassing laboratory dehydration experiments, field monitor-
ing and model simulations, ΔT_{max}, the core variable in calculating J_s with the
TDP method, was found to correlate negatively with both θ_{wood} in bamboo
culms and with θ_{soil}. By numerically simulating this negative ΔT_{max}-θ_{wood}
relationship for different scenarios of daily and seasonal changes in θ_{wood}, the
corresponding underestimation of J_s was quantified. Keeping other control-
ling variables constant, large underestimation became apparent 1) for large
decreases of θ_{wood} from nighttime to daytime, 2) at relatively low J_s, and 3) for
relatively larger nighttime θ_{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 θ_{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).
Our study further suggests that ΔT_{max} derived by TDP could be a proxy for
the stem water status and could thus potentially help to further understand
the dynamics of stem water storage when coupled with steady-state thermal
models. Interesting approaches for future studies include testing the here
applied model in situ by simultaneously assessing dynamics in θ_{wood} and J_s,
as well as further improving and developing heat-based methods to include the
assumption of non-stable θ_{wood} at different temporal scales.

Chapter 4

Deuterium tracing for assessing water circulation in bamboos

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Abstract

Bamboos are woody monocots with a hollow culm and connected rhizomes. We assessed bamboo water circulation in three big clumpy bamboo species by deuterium tracing along with formerly calibrated thermal dissipation probes (TDP) in a common garden in Indonesia. The deuterium-derived sap velocities correlated with the TDP-derived velocities in two of three species. In all species, the deuterium residence time in bamboo culms was little influenced by the contribution of the culm water storage to transpiration as estimated by TDPs at different culm heights. Potential reasons include a small water storage volume in the culms, a low estimated contribution of the storage to transpiration and high sap flux densities. Daily culm water use rates estimated by the deuterium and the TDP approaches correlated linearly ($R^2 = 0.9$) but were by 70% in the deuterium estimates. After the experiment, culms were cut down and analyzed for residual deuterium, but concentrations were low which indicates that retention did not play a major role in causing errors of the deuterium tracing approach. In culms neighboring the deuterium labeled culms of *Bambusa vulgaris* and *Gigantochloa apus*, elevated deuterium concentrations were detected indicating water transfer between culms. Based on the differences in daily water use on labeled culms and the enhanced deuterium concentrations in neighboring culms of these two species, we inferred that five neighboring culms might receive water from the labeled culms. On contrast, in culms neighboring labeled *Dendrocalamus asper* culms, only slightly elevated deuterium concentrations were observed which implies a limited role by water transfer. However, incomplete mixing as indicated by high variation among three TDP sensors at a given height may be of particular importance for deuterium tracing in *D. asper*. In conclusion, species-specific differences among big clumpy bamboos are indicated and the deuterium tracing points to water transfer among culms.

Keywords: error analysis, sap velocity, water residence time, water storage, water transfer, water use

4.1   Introduction

Unidirectional water transport from the soil through plants to air was thought to be the general framework when studying plant water use (Goldsmith, 2013;

Philip, 1966). However, this framework has been enlarged gradually by the new findings, such as foliage water uptake from air into leaves (Goldsmith et al., 2013; Studer et al., 2015) and inverse flow from the leaves to soil (Eller et al., 2013; Goldsmith, 2013), soil water translocation by roots (Burgess et al., 2001b; Sakuratani et al., 1999; Smith et al., 1999), and water transfer among interconnected plants through roots or rhizomes (Adonsou et al., 2016; Zhao et al., 2016). Such these water use characteristics, in combination with the frequently studied internal water storage (James et al., 2003; Meinzer et al., 2006; Yang et al., 2015) and the most studied transpiration, seem to constitute a more complicated water circulation within and among the plants. Within the plants, the internal water circulation can be formed by water transport (sap flow) to canopy or soil, and by water exchange between conduits and storage compartments for water storage (James et al., 2003). Between the plants and the environment (air and soil) and among the plants, the outer water circulation can be composed by water uptake from soil or foliage, water translocation, and water transfer. These water circulations were important to stimulate and maintain some physiological processes, e.g. regulating stomatal closure by transporting the root-produced abscisic acid to leaves (Hartung et al., 2002), maintaining high transpiration rates with the temporally stored water in stems (Goldstein et al., 1998; James et al., 2003), or relieving water shortage by water redistribution among interconnected plants (Adonsou et al., 2016; Zhao et al., 2016). Therefore, exploring and monitoring these water circulations would deepen our understanding of plant physiology.

Bamboos, as fast growing monocots, may have unique characteristics of water circulation. Compared with trees, comparable (Dierick et al., 2010; Kume et al., 2010) or higher (Ichihashi et al., 2015; Mei et al., 2016) maximum sap flux densities were found on bamboo species in previous studies. High sap flux densities may be attributed to the large culm hydraulic conductivity and low sapwood capacitance, as sap velocity on trees was found positively correlated with stem hydraulic conductivity and negatively with sapwood capacitance (Meinzer et al., 2006). If such correlations applied to bamboos, it may mean that bamboos had low sapwood capacitance which could be implied by the short residence time of water in the stem (Meinzer et al., 2006). However, longer residence time on one bamboo species (*Bambusa blumeana*) than on the reference trees was found (Schwendenmann et al., 2010). The contradictory findings may be case-specific or common for bamboos, and therefore, the corresponding investigation needs to be done on more bamboo species. Another distinctive characteristic of water circulation on

bamboos is the water transfer among culms, due to the rhizomes which possibly provide passages for transporting water among culms (Stapleton, 1998). Water transfer among culms has been implied on *B. blumeana* by observing elevated deuterium (D_2O) concentrations on the leaves of the neighbor culms which were in the same clump of the D_2O labeled culms (Dierick et al., 2010). Another investigation on Moso bamboo (*Phyllostachys pubescens*) also implied water transfer by finding 20% less water use on the rhizome-cut culms than on the regular culms (Zhao et al., 2016). These findings need to be further tested on more species with the directly connected culms and with no destructive operation.

Deuterium tracing method, due to its traceability, has been applied for measuring sap velocity and water residence time in the stems of trees (Gaines et al., 2016; James et al., 2003; Meinzer et al., 2006), and for estimating daily water use rates (Calder, 1991; Dierick et al., 2010; Dye et al., 1992; Schwendenmann et al., 2010). In these studies, the D_2O was first injected into the base stem of trees/bamboos (this operation is usually called labeling) and then the water transpired from leaves in the labeled trees/bamboos was periodically sampled to trace the D_2O movement (Calder, 1991). Subsequently, the D_2O concentration in the samples was used to estimate sap velocity, water residence time and daily water use rates (See details in Calder (1991) or Meinzer et al. (2006)). However, deuterium-derived water use rates were thought to be less reliable when two assumptions proposed by Calder (1991) for estimating the water use rates were violated (Schwendenmann et al., 2010). The two assumptions were: First, all the D2O injected into the base stem is taken up and transpired out from leaves without tracer loss in other forms; Second, the D_2O is thoroughly mixed in the transpiration stream before water flowed into different regions of the crown (Calder, 1991). Compared with the other methods (e.g. thermal dissipation probe, TDP), both overestimation (Kalma et al., 1998; Marc and Robinson, 2004; Schwendenmann et al., 2010) and underestimation (Dye et al., 1992) on water use rates from deuterium tracing method were observed. On one bamboo species (*B. blumeana*), water use rates were found eight times higher with deuterium tracing method than with TDP method (Schwendenmann et al., 2010). The discrepancies could be attributed to several potential interference sources which may break the two assumptions, such as tracer loss due to retention of tracer in plants and water transfer among plants (Schwendenmann et al., 2010). Nevertheless, the discrepancies caused by the interference sources can also be estimated to explore the corresponding water circulation characteristics (e.g. water transfer). This process could be

realized by monitoring tracer dynamics on leaves, stem and the interconnected plants to address the difference in water use rates simultaneously derived with deuterium tracing method and a reference method.

Our objectives were applying D_2O: (1) to explore the water circulation characteristics of the bamboos, including sap velocities, water residence time, water use rates, and water transfer between culms, (2) and to evaluate the potential interference sources in D_2O-based daily water use estimates with referring to TDP method, such as D_2O retention and transfer. To achieve the aims, we applied deuterium tracing method simultaneously with measurements of calibrated TDP sensors (Mei et al., 2016) on three tropical clumpy bamboo species in a common garden.

4.2   Materials and methods

4.2.1   Study site and species

The study was conducted in a common garden in Bogor, Indonesia (6°33'40" S, 106°43'27" E, 182 m asl). Bogor is a city with moderate temperature (average annual temperature 25.6 °C) and plenty of rainfall (annual precipitation 3978 mm) but has apparent wet and dry season (Van Den Besselaar et al., 2015). Three bamboo species (*Bambusa vulgaris*, *Gigantochloa apus* and *Dendrocalamus asper*) were selected for D_2O labeling. For each species, the selected bamboo culms for D_2O labeling were in one clump and located at the edge of the clump. The clump base areas were 18, 20 and 6 m^2, and the canopy areas were 346, 427 and 63 m^2 for *B. vulgaris*, *G. apus* and *D. asper*.

4.2.2   Deuterium tracing

Three to four culms per species were labeled (Table 4.1). The labeled culms were injected with D_2O (99.90% D, euroiso-top, Gif sur Yvette, France) during 6:00-7:00 on 8th March 2013 (Fig. 4.1). The operation of injecting D_2O into the studied bamboos followed Dierick et al. (2010). First, plastic tubes were fixed with an angle of 45° to the bamboo culms at the height of 50 cm above the ground. Four to six tubes (four tubes for *B. vulgaris* and *G. apus*; six tubes for *D. asper*) were fixed eventually around each labeled culm. The tubes were then filled with 40 mM KCl solution and holes were drilled under water. After
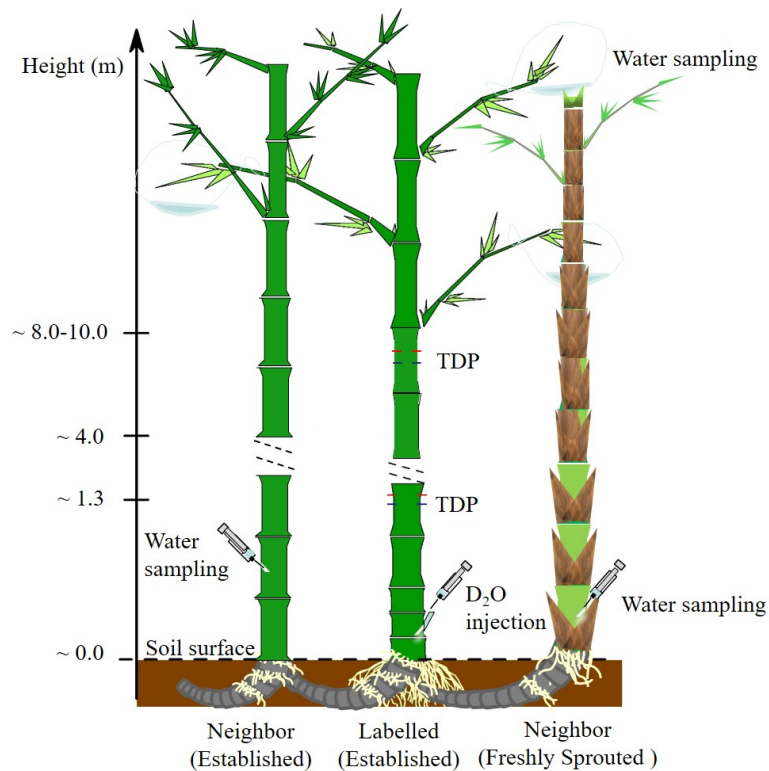
Fig. 4.1 Scheme of applying deuterium tracing and TDP methods.

that, holes were washed by injecting more solution and the remaining solution in the holes were extracted by a syringe and replaced with 1.5-3 g D_2O in each hole. The D_2O was taken up by transpiration stream and KCl solution was added into holes for several times afterward to make the residual D_2O in the tubes/holes being taken up as much as possible. After sunset, water remained in the tubes and holes was collected and weighed, and then 1.5 ml of them was stored at 4 °C in the refrigerator and used for isotope analysis to measure the amount of remained D_2O.

Following the approach of Calder (1991), the D_2O samples were collected from leaf condensate water by installing transparent bags. On each sampling day between 7:00 and 8:00, ten self-sealing transparent bags were installed on five different sun-exposed regions on each bamboo canopy (sealing 5-6 leaves per bag) and the bags were collected at the same time in the next day. All the ten condensate samples for a culm were totally combined to a mixed sample, and 1.5 ml of the mixed sample was transferred into a glass vial and stored as same as mentioned above. Sampling was conducted every day in the first ten days and 4-6 days' interval in the next three weeks.

Table 4.1 The information of studied bamboos and trees (3 culms per species but 4 culms of *B. vulgaris* used). The adjusted WU_{D_2O} was WU_{D_2O} adjusted with deuterium transfer on bamboos. The values were represented as the means(SD) which were in parenthesis.

Species	Height (m)	DBH (cm)	D_2O injected	$T_{arrival}$	$T_{residence}$
B. vulgaris	17.9(0.8)	7.0(0.4)	5.8(1.6)	1.5(1.0)	5.5(1.3)
D. asper	21.1(0.9)	10.7(0.9)	8.0(1.1)	1.0(0.0)	5.0(1.7)
G. apus	16.2(2.7)	7.9(1.1)	5.7(0.1)	1.0(0.0)	6.3(0.6)

To detect if there was D_2O retention in the bamboos, on 16th, 17th or 20th April 2013, all the D_2O labeled bamboos were harvested in early mornings (from 5:00-7:00). On each culm, three water samples (1.5 ml) were extracted from leaves, branches and rhizomes, and one sample was obtained from each culm segment every 2 m height. The sampling organs were sealed in the transparent plastic bags and left under the sunshine to make water transpired out, and water samples (1.5 ml) were collected in glass vials. Outside diameter, wall thickness and height of the segment were measured to calculate the fresh volume (v_f, cm^3). Samples collected from each organ were weighted (w_f, g) and dried with 100 °C in the oven for 24/48 hours (24 hours for leaves/branches, 48 hours for rhizomes and culms) to get dry weight (w_d, g) in the lab. The water content of each segment was then derived as (w_f - w_d)/ w_d.

To test for D_2O transfer among bamboo culms, three established and three freshly sprouted neighbor culms, which were 30-50 cm distant to the D_2O labeled culms, were sampled in 3-5 days' interval. The established culms were similar to the labeled ones. The young culms popped up 4-5 months before the tracer study began and had already reached a height of around 10 m or higher, but they still hold some brown sheaths attached to the culms and were not fully leafing. In approximately 6:00, small holes were drilled in the bamboo wall at around 1 m height, and water samples (1.5 ml) were collected directly from the holes (Fig. 4.1).

The D_2O concentrations in the culm segments of the cut-down labeled culms were used as background values for correcting the D_2O concentrations in the samples in the labeled and neighboring culms.

4.2.3   Deuterium analysis in the lab

The isotope analysis was carried out in the Center for Stable Isotope Research and Analysis (KOSI) at the University of Göttingen, Germany. The samples

were measured in a Delta V Plus isotope ratio mass spectrometer (Thermo-Electron Cooperation, Bremen, Germany) coupled with a high-temperature conversion/elemental analyzer (TC/EA, Thermo Quest Finnigan, Bremen, Germany). The results with 2‰ measurement precision are expressed in delta notation in units of per mil (δD, ‰) as D/H of the sample (R_{sample}) relative to that of Vienna Standard Mean Ocean Water (R_{VSMOW}).

4.2.4   Deuterium arrival time, velocity and residence time

Three variables were used to describe the behavior of the D_2O reflecting the water uptake and storage characteristics (Meinzer et al., 2006; Schwendenmann et al., 2010). First, arrival time (T_{arrival}, days) was defined as the time of leaf D_2O concentration passing over 10% of the maximum D_2O concentration for the first time. Second, tracer velocity (V_{D_2O}, m day^{-1}) was derived as the distance between sampling and injecting points over the arrival time. At last, tracer residence time ($T_{\text{residence}}$, days) was estimated as the time course when D_2O concentration was above 10% of the maximum D_2O concentration.

To calculate water use estimated by deuterium tracing method, the notation of D_2O (δD) values were converted to give a mass concentration of the tracer (Calder, 1991). The mean daily water use (WU_{D_2O}) over the experiment was calculated with the equation as below:

$$WU_{D_2O} = \frac{M}{\sum_{i=1}^{T} C_i \Delta t_i} \tag{4.1}$$

Where C_i is the mass concentration (g kg^{-1}) in the ith time increment, Δ_{ti} is the duration of the ith time increment (days) and T is the last time increment. This function is usually used under two assumed conditions as described in the introduction part (Calder et al., 1992).

4.2.5   Sap flow measurement and water use estimation by TDP method

On each labeled bamboo culm (three culms per species but four culms of *B. vulgaris* used), sap flux density (J_s, g cm^{-2} h^{-1}) was measured by self-made 1 cm length TDP. The sensors were inserted into the bamboo culm at breast height (Mei et al., 2016) and below the lowest branches at around 7 m height.

Three pairs of 1 cm length TDP were installed evenly apart from each other. From 8th March to 6th April 2013, the three TDP signal wires were connected in parallel to get an averaged voltage value. From 7th April 2013, to detect the circumferential variation of J_s, the three TDP sensors were installed separately to measure J_s in three directions for at least one week. The TDP signals were sampled every 30 seconds and stored as 1-minute averages in data loggers and multiplexers (CR1000, AM16/32, Campbell Scientific Inc., USA). J_s was calculated with species-specific calibrated formulas for these bamboos (Mei et al., 2016).

To compare with tracer velocity (V_{D_2O}, m day^{-1}), daily accumulated J_s (J_{s-d}, kg cm^{-2} day^{-1}) derived from TDP method was converted into sap velocity (V_{TDP}, m day^{-1}) by the unit change. Water use (WU$_{TDP}$) of each bamboo was derived by multiplying J_s with the culm wall cross-sectional area. Because WU$_{D_2O}$ was not arithmetic mean of daily water use during the experiment, mean TDP-derived WU and WU$_{D_2O}$ cannot be directly compared (Calder, 1991). Therefore, a weighted WU was introduced with the following equation:

$$WU_{TDP} = \frac{\sum_1^T WU_i C_i}{\sum_1^T C_i} \tag{4.2}$$

Where WU$_i$ is the daily water use (kg d^{-1}) in the ith time period (day) and C_i is the mean mass concentration of D$_2$O in condensate water in the ith time period.

To assess the influence of stem water storage on WU$_{D_2O}$, the relative contribution of stem water storage to transpiration (C_{WS}) was calculated following the procedure by Goldstein et al. (1998). The underlying assumption is that the daily water use measured at the lower (near breast height) and upper stems (under the crown) were equal in one day. First, adjusted half-hourly water use at the upper stem was derived by multiplying half-hourly water use at the upper stem with the ratio between the daily water use at the lower stem and at the upper stem. Second, the difference between the half-hourly water use at the lower stem and the upper stem was calculated, and the positive difference in one day was integrated as water storage that contributed to daily transpiration. At last, water storage was divided by daily transpiration to get the C_{WS}.

4.2.6   Data analysis and statistics

Linear regressions were done on exploring relationships between V_{D_2O} and V_{TDP}, between $T_{residence}$ and V_{D_2O}, V_{TDP} or C_{WS}, and between WU_{D_2O} and WU_{TDP}. The relative differences between WU_{D_2O} and WU_{TDP} (Dif_{WU}, %) was first calculated as the ratio of the difference between WU_{D_2O} without considering any D_2O loss and WU_{TDP} to WU_{TDP}. In the following step, two interference sources relating D_2O losses for bamboo WU_{D_2O} were quantitatively assessed in our study: D_2O retention in the labeled culms and D_2O transfer to the neighbor culms. For each interference source (retention or transfer), the corresponding D_2O losses were included into the Calder's equation (Calder, 1991) for calculating corrected WU_{D_2O}. Subsequently, the corresponding relative differences between the corrected WU_{D_2O} and WU_{TDP} were calculated. When assessing the influence of D_2O transfer, the maximum amount of culms that may receive the transferred D_2O from each labeled culm (N_{max}) was calculated under the assumption that the Dif_{WU} was caused solely by D_2O transfer. The distribution of the N_{max} of all the labeled culms was subsequently plotted with histogram and kernel density distribution, from which a mode was derived. Thereafter, a corrected WU_{D_2O} and a corresponding Dif_{WU} were calculated with assumptions that water was transferred from each labeled culm to neighbor culms and that the amount of the receiving culms equaled to the mode value of the N_{max} distribution. The newly derived Dif_{WU} was further plotted with CV_{J_s} with linear regression to assess the influence of incomplete mixing on WU_{D_2O} estimation. All data analysis and figures were performed with SAS 9.3 (SAS Institute Inc., 2013).

4.3   Results

4.3.1   Tracer movement and sap velocity

On most of the studied bamboo culms, the D_2O concentrations showed a two-peak pattern during the experiment, with a drop in the second day after labeling, which was a rainy day (Fig. 4.2). $T_{arrival}$ from stem base to the crown was one day on most of the labeled bamboos, except 3 days on one culm of *B. vulgaris* (Table 4.1). The maximal D_2O concentrations on the labeled culms appeared in 1-3 days and varied between 0.09 and 0.79 g kg^{-1} for the three bamboo species (Fig. 4.2). Sap velocities derived from deuterium tracing
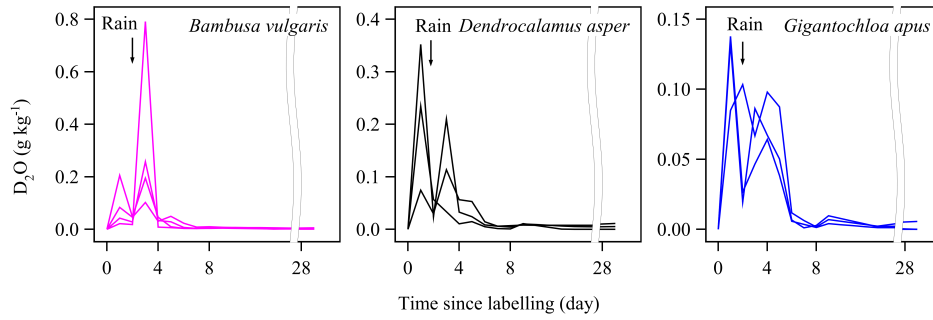
Fig. 4.2 Deuterium concentration (D_2O g kg^{-1} above background level) in transpired water of *B. vulgaris*, *G. apus* and *D. asper* over the course of the experiment. Day 0 is the day of deuterium injection.
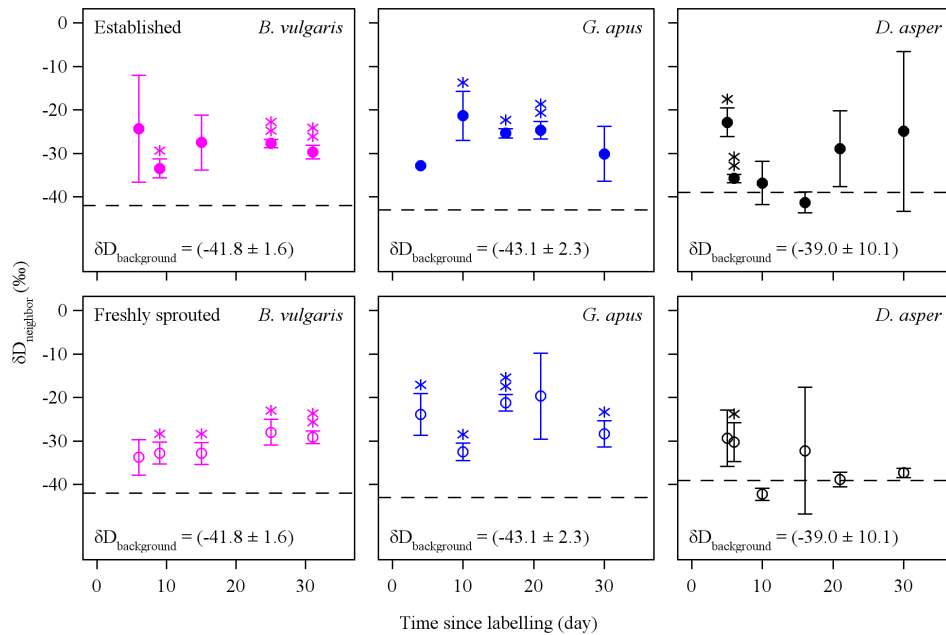
Table 4.2 Deuterium signature (δD, ‰) in different bamboo organs (leaf, branch, stem at 0, 2, 6, 10 m height and rhizome) of the labelled bamboos (4 culms of *B. vulgaris* and 3 culms of *D. asper* and *G. apus*) which was harvested after about 40 days since labelling. The values were represented as the means (standard deviation).

		Stem					
Species	Rhizome	0 m	2 m	6 m	10 m	Branch	Leaf
B. vulgaris	-32.9(5.6)	-40.9(1.7)	-42.8(1.5)	-43.3(1.7)	-43.7(4.5)	-41.7(2.8)	-33.8(1.5)
G. apus	-38.5(0.8)	-42.4(2.5)	-44.3(3.0)	-43.1(2.3)	-41.7(3.0)	-38.4(3.0)	-30.2(1.1)
D. asper	-44.9(2.2)	-32.5(25.1)	-38.0(9.0)	-40.9(5.0)	-42.4(3.3)	-39.0(11.6)	-52.3(13.1)

method (V_{D_2O}) were on average 5.6 times higher than from the TDP method (V_{TDP}; 12.5 vs. 3.6, 13.3 vs. 3.2 and 16.1 vs. 1.3 m day^{-1} on *B. vulgaris*, *G. apus* and *D. asper*, respectively). V_{D_2O} was significantly correlated with V_{TDP} among culms of *B. vulgaris* and *D. asper* ($R^2 = 0.78$; $P < 0.01$) but not in *G. apus* (Fig. 4.3).

4.3.2 Residence time and stem water storage

$T_{residence}$ varied between 5.5 and 6.3 days on average for the three studied bamboo species (Table 4.1). $T_{residence}$ seemed to decrease with increasing V_{TDP} and did not significantly correlate with culm water storage (C_{WS}; Fig. 4.4). During the experiment, C_{WS} were 15%, 9% and 9% on average for *B. vulgaris*, *G. apus* and *D. asper*, respectively.
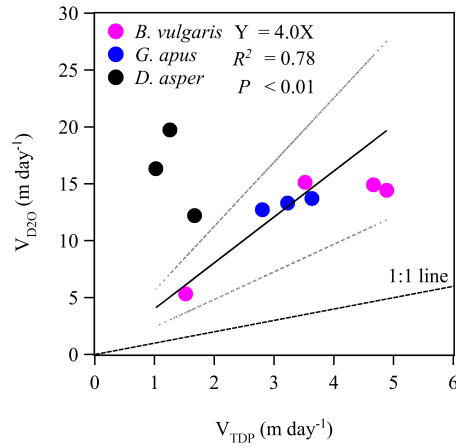
Fig. 4.3 Sap velocities (m day^{-1}) derived from deuterium tracing method (V_{D_2O}) in relation to the sap velocities obtained from TDP method (V_{TDP}). The two grey dot lines represent 95% confidence limits for the expected values. The black line accounts for a regression line.
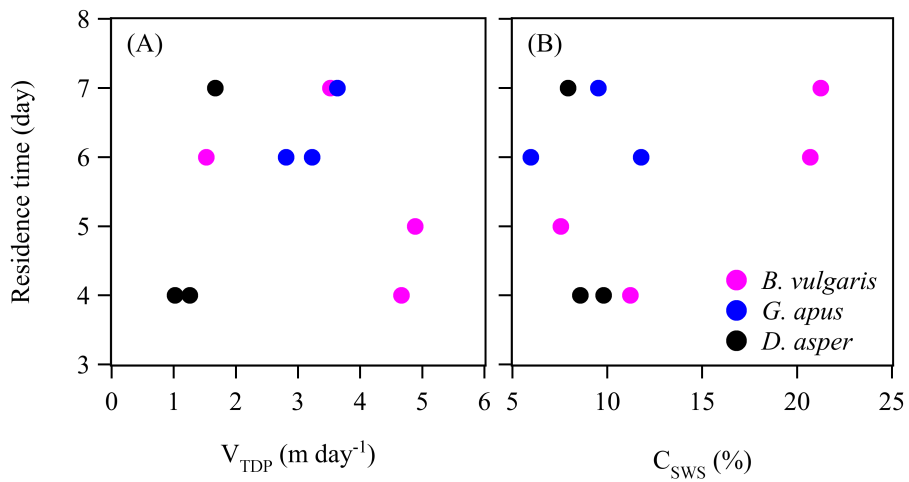
Fig. 4.4 Residence time in relation to (A) the sap velocity derived from thermal dissipation probe (V_{TDP}, m day^{-1}) and (B) the contribution of culm water storage to daily water use (C_{WS}, %).
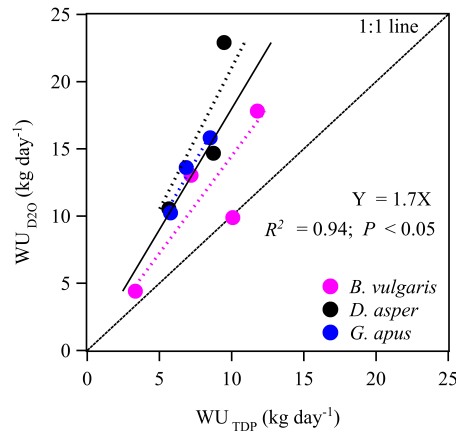
Fig. 4.5 Water use estimated by the TDP method (WU_{TDP}, kg day^{-1}) versus water use determined by deuterium tracing (WU_{D_2O}, kg day^{-1}) on bamboos. The solid line represents regression of all values of the three bamboo species. The dash lines represent species-specific regressions: *B. vulgaris*: $Y = 1.4X$, $R^2 = 0.95$, $P < 0.01$; *D. asper*: $Y = 2.0X$, $R^2 = 0.97$, $P < 0.01$; *G. apus*: $Y = 1.9X$, $R^2 = 0.99$, $P < 0.01$.

4.3.3   Water use

There was a significant correlation between WU_{D_2O} and WU_{TDP} estimates ($R^2 = 0.94$, $P < 0.05$; Fig. 4.5). However, the deuterium tracing method gave 70% on average higher values than the TDP method. WU_{D_2O} and WU_{TDP} were 11.3 vs. 8.1, 13.2 vs. 7.0 and 16.0 vs. 8.0 kg day^{-1} for *B. vulgaris*, *G. apus* and *D. asper*, respectively

4.3.4   D$_2$O retention, transfer, incomplete mixing and their influence on deuterium derived water use rate

In the cut-down bamboo tissues, the D$_2$O concentration (δD, ‰) showed an increasing trend from stem base to leaves and root in *B. vulgaris* and *G. apus*, while not in *D. asper* (Table 4.2). In *B. vulgaris* and *G. apus*, the δD values were significantly higher on leaves than on stems ($P < 0.05$ with a t-test). The remained D$_2$O in each whole bamboo (including leaves, branches, culm and rhizome) varied between 0.005 to 0.075 g, which was negligible to the injected mass (Table 4.1) and produced only 1% on average higher values on WU_{D_2O} referring to WU_{TDP}.

Fig. 4.6 Deuterium values (δD, ‰) in different bamboo organs (leaf, branch, stem at 0, 2, 6, 10 m height and rhizome) of the labeled bamboos which was harvested after about 40 days since labeling. Each dot (mean±SD) stands for the mean values from 4 culms of *B. vulgaris* and 3 culms of *D. asper* and *G. apus*.
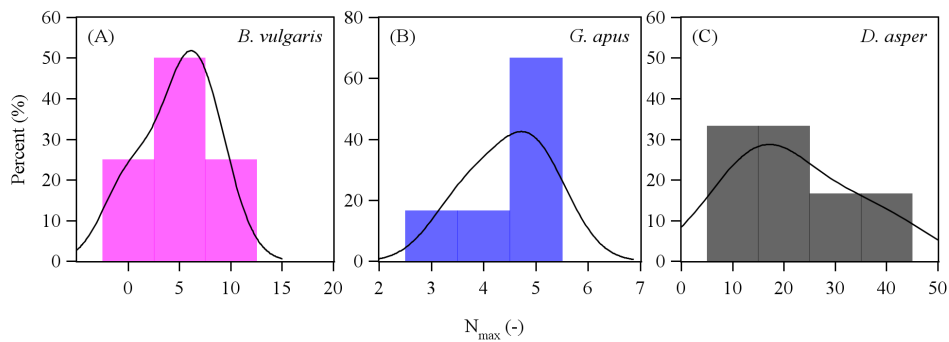
Fig. 4.7 The distribution of the maximal amount of neighboring culms (N_{max}) which may receive transferred water from the labeled culms (*B. vulgaris*, *G. apus* and *D. asper*). For each species, data of 3 established and 3 freshly sprouted culms were used. The black line represented fitted kernel distribution. The mode (at the most frequency) of the N_{max} was 5.1, 4.5 and 22.0 on *B. vulgaris*, *G. apus* and *D. asper*, and the mode was 6.7 when pooling the three species together.

Compared with the background δD values, significant higher δD values were found in the transpiration stream of neighbor established and freshly sprouted bamboos almost over the 30 days on *B. vulgaris* and *G. apus*, while only in the first 6 days on *D. asper* ($P < 0.05$ with t-test; Fig. 4.6). Such elevated δD values may be related to water transfer through rhizomes between the labelled bamboos and neighbor ones. Based on the assumption that the water transfer existed continuously during the experiment, the total transferred D_2O on one neighbor culm varied between 0.36 to 0.93 g, which accounted for 1.7-11.7% of the injected D_2O. As the D_2O retention was negligible, the difference between WU_{D_2O} and WU_{TDP} was assumed mainly relating to tracer loss by water transfer among culms. Under such assumption, the amount of culms that may receive D_2O transfer from the labeled culms ranged from 0 to 41 culms with the mode of 6 culms (Fig. 4.7).

We assumed the incomplete mix of D_2O in sap flow was another interference source of WU_{D_2O} estimation, which may be indicated by the different sap flux densities in different directions. Among the culms of each species, the averaged coefficients of variation of daily sap flux densities at breast height in three directions (CV_{J_s}) were 23%, 52% and 14% for *B. vulgaris*, *D. asper* and *G. apus* respectively. With the assumption that a labeled culm transferred D_2O to 6 neighboring culms (Fig. 4.7), the calculated differences between the corrected WU_{D_2O} and WU_{TDP} was found significantly correlated with CV_{J_s} (Fig. 4.8; $R^2 = 0.44$, $P < 0.05$).

4.4 Discussion

4.4.1 Sap velocity

Compared to *B. blumeana* in Philippine (Dierick et al., 2010; Schwendenmann et al., 2010), the three bamboo species (*B. vulgaris*, *G. apus* and *D. asper*; Table 4.1) in our study showed much smaller $T_{arrival}$ (1.5, 1.0, 1.0 vs. 3.1 days) and T_{max} (2.5, 1.3, 1.7 vs. 4.8 days) while larger V_{D_2O} (12.5, 13.3, 16.1 vs. 8.5 m day^{-1}) and V_{TDP} (3.6, 3.2, 1.3 vs. 0.9 m day^{-1}). Such differences among the bamboo species in the two studies may be attributed to the species-specific anatomical structures, different sampling methods or various environmental conditions in these sites. Bamboos had highly variable size and shape of vascular bundles among species (de Agrasar and Rodríguez, 2003) which may lead to different water transport velocities. Despite this, different sampling

methods applied in our study and the study in Philippine might also contribute to the differences. In the Philippine study, leaves were collected twice a day (interval sampling) while we installed transparent bags on the branches to gather water for a whole day (Calder et al., 1986). The interval sampling may cause missing of the peak value that was used to derive the $T_{arrival}$ and V_{D_2O}.

The averaged V_{D_2O} of the three bamboo species was 5.6 times higher than V_{TDP}. Such large differences between V_{D_2O} and V_{TDP} were also found in other studies (Dierick et al., 2010; James et al., 2003; Meinzer et al., 2006). Compared with V_{TDP}, higher V_{D_2O} was found on one bamboo species (*Bambusa blumeana*) and five tropical tree species (Schwendenmann et al., 2010), and on temperate conifers (Meinzer et al., 2006). Meinzer et al. (2006) explained that sap velocity derived from sap flux density by the unit change were not the right sap velocity transported in the conduits and the fraction of the conduit area to the whole cross sectional area may influence the calculation. In an early study, Tatarinov et al. (2005) described sap flux density as the product of sap velocity, wood porosity, and water density. Therefore, following the work of Vandegehuchte and Steppe (2012), we calculated wood porosity from easily obtained factors such as dry wood density and fresh wood volume of a sample and got new V_{TDP}, which reduced the relative deviation of V_{D_2O} to V_{TDP} from 5.6 times to 0.86 times higher. Despite the new V_{TDP} calculated in such way may also introduce errors, it did reduce the differences and may be improved with the more accurate calculation on porosity. The different measurement scales of the two methodologies could be another reason for the difference between V_{D_2O} and V_{TDP}. V_{TDP} only stand for the velocity between the installation heights of the TDPs while V_{D_2O} is a mean value along the hydraulic path from stem base to the crown until water left the leaves.

Despite V_{D_2O} was higher in our study and also the other previous studies, V_{D_2O} could even be larger when D_2O sampling was done at a higher frequency. The arrival time ($T_{arrival}$, 1 day for all but one) could be shorter if the tracer arrived at the crown within one day and strong water uptake occurred in daytime. The one-day sampling interval in the present study may be too coarse for a precise estimation of the arrival time. Therefore, $T_{arrival}$ was the maximal D_2O transit time from base stem to canopy, and thus V_{D_2O} derived with $T_{arrival}$ and the transport pathway was minimum estimates of maximum sap velocity (James et al., 2003; Meinzer et al., 2006). In future studies, one should probably sample water from leaves with shorter intervals, such as 4 hours over the initial days.

4.4.2   D$_2$O residence time and water storage

$T_{\text{residence}}$ varied between 5.5 and 6.3 days on average for the three studied bamboo species (Table 4.1), while 11.5 days on another bamboo species - *B. blumeana* and 4.7 days on the five reference tree species (Schwendenmann et al., 2010). However, $T_{\text{residence}}$ on these bamboo species was shorter than the $\approx$ 20 days of two tropical tree species in Panama (James et al., 2003) and much shorter than the 36-79 days on two coniferous species in North America (Meinzer et al., 2006). $T_{\text{residence}}$ on trees was found positively correlating with the normalized maximum crown-base sap flow which implies the relative reliance of transpiration on water storage (James et al., 2003), and with sapwood capacitance which reflects the water exchange capacity between transporting lumens and surrounding tissues (Meinzer et al., 2006). Therefore, It was assumed that $T_{\text{residence}}$ could be an indicator of the relative reliance of transpiration on water storage (James et al., 2003). However, on the three studied bamboo species in our study, $T_{\text{residence}}$ was found not significantly related to the normalized maximum crown-base sap flow (data not show) nor with the daily C_{WS} (Fig. 4.4.A). Such finding may be attributed to the limited support of the water storage to the relatively high daily transpiration, as the bamboo culms have much fewer volumes to store water than tree stems due to the thin culm wall and the hollow center. In the present study, during the experiment from 8th March to 6th April 2013, daily C_{WS} were 15%, 9% and 9% on average for *B. vulgaris*, *D. asper* and *G. apus*, respectively. On contrast, on trees or palms, 10-50% of daily transpiration can be contributed by stem water storage (Carrasco et al., 2015; Goldstein et al., 1998; Holbrook et al., 1992; Scholz et al., 2008; Waring and Running, 1978). However, although $T_{\text{residence}}$ was not correlated with C_{WS}, it appeared to negatively correlate with $V_{\text{D}_2\text{O}}$ (Fig. 4.4.A). It may indicate that high axial water transport efficiency reduced the time of water staying in the bamboo culms. These findings seemed to verify the hypothesis that the trade-off of water transport efficiency and water storage capacity could contribute to a safe water status in the crown (Gleason et al., 2016; James et al., 2003). On bamboos, culm water storage may be less important than the relatively high water transport efficiency on maintaining leaf water status, which could be indicated by the higher maximum sap flux densities on bamboo species than on the neighbored trees (Ichihashi et al., 2015; Mei et al., 2016).

4.4.3   Water use derived with deuterium tracing method

On most of the studied culms (90%) in our study, water use was higher by deuterium tracing method compared to calibrated TDP method. On average, the deuterium tracing method gave 41±35%, 99±38% and 87±11% higher values on *B. vulgaris*, *D. asper* and *G. apus* respectively. Higher values (11-43%) by D_2O method was found on *Eucalyptus grandis* compared with Heat Pulse Method (Kalma et al., 1998), while lower values (7-26%) was also found in the same species with the same reference method by Dye et al. (1992). On the only studied bamboo species (*B. blumeana*) applied with D_2O method (Schwendenmann et al., 2010), on average 813% higher water use was found compared with TDP. The discrepancy between D_2O method and the reference methods were supposed to come from both of the methods (Kalma et al., 1998; Schwendenmann et al., 2010). Errors could be raised if the reference method was used violating its application conditions (Lu et al., 2004; Smith and Allen, 1996). Lower estimation (by 66% on average on 4 bamboo species) by uncalibrated TDP was found in situ when compared with stem heat balance method (Mei et al., 2016). Considering the errors associated with D_2O method, two primary sources presumed mostly related to D_2O method were tracer loss (retention in labeled plants or redistribution to soil or neighbor plants) and incomplete mixing of D_2O in the stem before flowing to different branches or crown levels. Both of them could break the underlying assumptions of applying the D_2O method (Kalma et al., 1998; Kline et al., 1970; Schwendenmann et al., 2010).

4.4.4   Deuterium retention and its influence on WU_{D_2O}

Residual D_2O were found in the labeled bamboos after 40 days since D_2O injection, but it was insignificant to affect the water use estimation. The total remaining D_2O in each bamboo culm was merely 1% on average of the injected D_2O, which could correspondingly lead to 1% higher estimate of the WU_{D_2O}. It was thought that the plants would retain too little tracer to change the water use rates estimate after sampling for enough long time (James et al., 2003; Kline et al., 1970; Schwendenmann et al., 2010). James et al. (2003) found prominent tracers from all portions of the *Cordia alliodora* tree after eight days of D_2O labeling and Schwendenmann et al. (2010) found the absent of D_2O in branches after three weeks of labeling. Therefore, to exclude the influence from retention of D_2O, the sampling period should be long enough, and the time may differ from different species.

Although the remaining D_2O was too little to influence water use estimated by D_2O method, they showed arresting distribution within the labeled bamboos after the experiment. On *B. vulgaris* and *G. apus*, the remaining D_2O were obviously more in leaves and roots than in stems, with smallest values appearing in 2 m height (Table1 4.2). This D_2O distribution on the organs may indicate that the injected D_2O was relocated upward and downward from the injected points. On leaves, the enrichment of D_2O may be partly attributed to the element fractionation, which makes more D_2O than hydrogen left in the leaves when water was transpired rapidly to the air during daytime (Roden and Ehleringer, 1999). While in roots, D_2O could be transferred from injected points via phloem according to Münch flow-pressure theory (Münch, 1927). Inverse water flow through phloem was considered as a possible way to take tracers downwards (Choi and Aronoff, 1966; Dierick et al., 2010; Schwendenmann et al., 2010). On *Eucalyptus saligna* trees, D_2O was observed exchanging between phloem and xylem through ray parenchyma (Pfautsch et al., 2015a,b). On bamboos, we assumed that the water exchange between phloem and xylem were much easier than trees, as the phloem and xylem stay closely to each other in vascular bundles (Grosser and Liese, 1971). Additionally, the inverse water flow may be more active when leaves were wet due to rain, fog or dew, as in this situation water potential gradient could be formed from leaves to roots (Goldsmith, 2013; Goldsmith et al., 2013). In our study, when rain occurred on the second day after D_2O labeling, a clear drop of the D_2O concentration was observed in most of the labeled bamboos (Fig. 4.2). The drop may also be possibly induced by the foliage water uptake that diluted D_2O in the crown and stem.

4.4.5 D_2O transfer between culms and its influence on WU_{D_2O}

The water transported by inverse water flow may be released to soil from roots, or transferred to other trees or bamboo culms if the plants had connected rhizomes (Dierick et al., 2010; Kline et al., 1970; Marc and Robinson, 2004; Zhao et al., 2016). In this case, loss of D_2O occurred and led to an overestimation of the water upward to the leaves. In the present study, water transfer was implied obviously on *B. vulgaris* and *G. apus* but slightly on *D. asper* by the elevated D_2O concentration in the neighbor freshly sprouted and established bamboos (Fig. 4.6), and the water transfer may probably happen among five culms on *B. vulgaris* and *G. apus* (Fig. 4.7). These findings indicated the bamboo
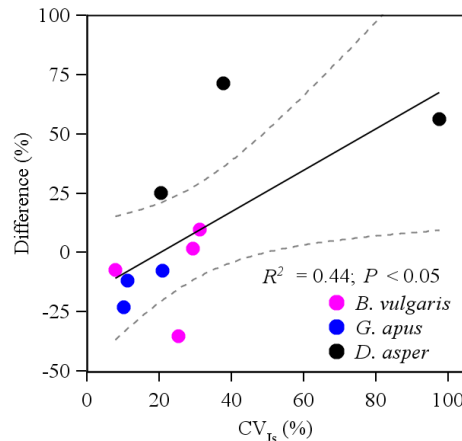
Fig. 4.8 The relative differences between the corrected WU_{D_2O} and WU_{TDP}, in relation to coefficients of variation of daily sap flux densities at breast height (CV_{J_s}). The corrected WU_{D_2O} was calculated based on the assumption that D_2O transfer between one labeled culm and six neighboring culms, and the assumption was based on the mode of the distribution of the maximal amount of neighboring culms when pooling the three species together.

culms might transport water downward to the underground rhizome system, and further redistribute this water to the other culms in a clump. However, even among big clumpy bamboo species, water transfer might be different on different species. Additionally, the quantity of the transferred water was unclear. In another recent study on a running bamboo species (*P. pubescens*), the rhizome-cutting culms consumed $\approx 20\%$ less water use than the intact culms and such difference was thought relating to water transfer through rhizomes from other culms or roots (Zhao et al., 2016). Furthermore, the reliance on the water transfer may differ upon the age of the culms. For example, freshly sprouted culms were thought more relied on rhizomes of mother culms than older ones (Liese and Köhl, 2015; Zhao et al., 2016). However, in our study on both freshly sprouted and established neighbor culms of the three studied bamboo species, significant higher δD values were observed ($P < 0.05$ with t-test; Fig. 4.6). This finding indicated that water transfer might be a typical water use characteristic at clump edges of bamboo culms regardless of their ages. The actual impact of water transfer from rhizomes may be more complex than our understanding due to the sophisticated rhizome system of bamboos (Stapleton, 1998).

4.4.6 Variability of sap flux and incomplete mixing of D_2O

Besides the tracer loss due to retention and transfer, incomplete mixing of D_2O may become another interference source to WU_{D_2O}. Unlike the direct influence on water use estimation from tracer loss, influence from incomplete mixing of D_2O was harder to detect and quantify. The injected D_2O at the base of the culms could be transported axially and radially (James et al., 2003). Therefore, the D_2O concentration in the leaves could be influenced by the speeds of the axial water transport and the radial water exchange between the xylem vessels and the surrounding tissues. In the present study, the $T_{\text{residence}}$ of the D_2O appeared to correlate with V_{D_2O} negatively. Such relationship may mean that if the water transport efficiency was different in the different directions, the $T_{\text{residence}}$ of the D_2O injected in the different directions may vary accordingly and furtherly the mixing extent of the D_2O was different. In our study, the averaged CV_{J_s} at breast height were 14-52% on the three bamboo species, which may indicate incomplete D_2O mixing according to the assumption mentioned above. Excluding the influence of water transfer on WU_{D_2O} with assuming six culms receiving transferred D_2O (Fig. 4.7), the differences between WU_{D_2O} and WU_{TDP} were correlated with the CV_{J_s} significantly (Fig. 4.8). These findings indicated that except avoiding D_2O loss in any form, we should also try to eliminate the influence of incomplete D_2O mixing when estimating water use rates with deuterium tracing method. Uniform sampling over the entire canopy could be a seemingly reasonable way. Additionally, drilling more holes around the culms for injecting D_2O could be another way to reduce errors from incomplete mixing.

4.5 Conclusions

The deuterium tracing method was applied to three tropical bamboo species. Contrast to TDP method, deuterium tracing method showed its advantages on revealing water transfer among bamboo culms and estimating sap velocity. Water use estimated with deuterium tracing method was obviously influenced by water transfer and incomplete mixing indicated by the circumferential sap flux variety. Deuterium retention can be ignored if enough long time was satisfied to collect the D_2O samples. Conclusively, the deuterium tracing is a good method to estimate sap velocity with short enough sampling intervals, but it is not so suitable to estimate quantitate water use of species that have

strong water redistribution. However, the deuterium tracing has its obvious advantage on tracing water movement or transfer within or among bamboo culms, and such advantage makes the method to be a powerful way to explore water redistribution or exchange on plants.

Chapter 5

Synthesis

5.1 Bamboo water use and methods testing

As monocots, woody bamboos have tree-like habits but differ from trees in many respects: relatively limited water conducting area due to the hollow culm, high parenchyma which provides a potential reservoir for water storage, and connected culms through rhizomes which may provide passages for water transfer (Liese and Köhl, 2015). These features may cause specific water use characteristics of bamboos and may influence sap flux measurement with the widely used thermal dissipation probe and water use estimation with deuterium tracing method. In our study, thermal dissipation probe (TDP) method was calibrated by comparing it to the stem heat balance (SHB) and gravimetric measurement on a bamboo species (*Bambusa vulgaris*). The calibrated TDP was thereafter applied in the field to monitor sap flow of four tropical bamboo species (*B. vulgaris*, *Dendrocalamus asper*, *Gigantochloa atroviolacea*, and *G. apus*) and three nearby tree species (Chapter 2). To explore the deviation of TDP measurement on bamboos due to the daily fluctuation of culm water content (θ_{wood}), we conducted a dehydration experiment on bamboo segments, a long-term monitoring of bamboo sap flux and soil moisture and a steady-state thermal model (Chapter 3). During long-term monitoring with TDP, deuterium tracing method was applied synchronously for about one month on the studied bamboos to explore sap velocity, water use rates and water transfer among culms (Chapter 4).

TDP was widely used to measure sap flux density (J_s) in trees (Granier, 1985), but the method should be calibrated before studying new species (Lu et al., 2004; Wullschleger et al., 2011). In three studies conducting TDP calibration on bamboos, J_s derived with Granier's formula, was lower than

that with reference gravimetric method on Moso bamboo (Kume et al., 2010; Zhao et al., 2016) and SHB method on *B. blumeana* (Dierick et al., 2010). In our study (Chapter 2), compared with SHB method, TDP underestimated J_s of the four bamboo species by on average 66 and 63% on the daily and 30-min scales respectively ($P < 0.01$). The calibration parameters of TDP against SHB differed upon species and culms of same species. Confronting this insight with results from sap flux studies on other bamboo species (Dierick et al., 2010; Kume et al., 2010), differences among species become even more apparent. The observed differences may be related to highly heterogeneous wood anatomical properties among bamboo species (de Agrasar and Rodríguez, 2003; Saha et al., 2009). Differences in wood anatomical properties may lead to heterogeneous heat conductive properties, which potentially affects applicability and accuracy of sap flux measurements of the TDP method (Wullschleger et al., 2011). The differences among culms of same species may be attributed to culm ages. Over the ontogeny of a certain culm, events and processes such as conductive circuit failure (drought- or metabolism-related; Cochard et al., 1994; Liese and Weiner, 1996) and lignification (Lin et al., 2002) could result in overall reduced hydraulic conductivity and further influence the heat conductivity of the wood.

The underestimation of J_s by TDP was assumed partly due to the diurnal fluctuation of θ_{wood}. On trees, θ_{wood} reached to peak values during the night when J_s was zero or minimum and dropped to minimum during daytime (Hao et al., 2013; Sperling et al., 2015). On a bamboo species (*B. vulgaris*), a similar pattern of bamboo culm circumference was observed (Yang et al., 2015). Although it's not the direct measurement on θ_{wood}, the daily dynamic of culm circumference should reflect at least part of change on θ_{wood} as assumed on trees (Köcher et al., 2013; Scholz et al., 2008). In our study (Chapter 2), the bamboos reached peak values of J_s earlier than trees and also earlier than vapor pressure deficit (VPD). Consistent with this, the hysteresis between sap flow and VPD on bamboos were larger than on trees, indicating the decouple of transpiration and VPD. The observed early peak of J_s and the larger hysteresis implied that bamboos had a quick depletion of water storage in the morning despite the high percentage of parenchyma (50%, Liese and Köhl, 2015). These findings and assumptions may mean that the water content in bamboo culms dropped to low values earlier than in trees. The large change of θ_{wood} between daytime and nighttime can change thermal conductivity of wood (K_{wood}) and the maximal temperature difference (ΔT_{max}) of TDP (Vergeynst et al., 2014; Wullschleger et al., 2011). ΔT_{max} is central to the calculation

of J_s, and it is measured at zero flow conditions usually at night (Granier, 1985, 1987). Underestimation of J_s happened if selecting one ΔT_{max} at night to calculate J_s in the whole day with ignoring the different K_{wood} between nighttime and daytime. Vergeynst et al. (2014) quantified the influence of θ_{wood} on J_s by setting possible temperature change that was assumed to relate to θ_{wood}. However, the direct relationship between θ_{wood} and errors on J_s remained unclear.

The previously found negative correlation between θ_{wood} and ΔT_{max} on trees (Vergeynst et al., 2014) was verified on bamboo segments in our study with a dehydration experiment and a steady-state thermal model in AN-SYS (Chapter 3). Based on the previous studies (Vergeynst et al., 2014; Wullschleger et al., 2011), we numerically simulated the influence of θ_{wood} on TDP-measured J_s and the results showed more direct and quantifiable relationship between θ_{wood} and errors on J_s. By the simulation in the model, we found at any J_s, more underestimation was introduced by larger decreasing of θ_{wood} from nighttime to daytime. Therefore, most significant underestimation of J_s would occur when θ_{wood} was lowest. According to the previous studies on bamboo (Yang et al., 2015) and palm (Sperling et al., 2015), θ_{wood} was decreasing gradually from sunrise until sunset. Therefore, in the afternoon especially at dusk, J_s may be influenced significantly by θ_{wood}. Additionally, the magnitude of underestimation differed with J_s. The relative error of J_s (%) was larger at lower J_s, and it gradually became smaller and approached to a stable value with increasing J_s. This finding may mean that on plants with low water consumption or when J_s was low, the TDP-measured J_s was influenced more obvious by the changing θ_{wood}. In contrast, for the plants with high J_s, the influence from θ_{wood} would be small. Despite relative small errors at higher daytime J_s, they were responsible for most of the underestimation on daily water use. For example, relative error was only 9.4% at 30 g cm^{-2} h^{-1} (in contrast, 18.6% at 5 g cm^{-2} h^{-1}), but it could lead to 64% of the underestimation on daily water use of a bamboo culm. Except varying with different J_s, the influence of θ_{wood} on TDP-measured J_s may also differ with different water conditions due to weather or management, e.g. rainy or sunny days or irrigation. In the model, when θ_{wood} was reduced with same ratio (half) from nighttime to daytime, higher nighttime θ_{wood} caused larger underestimation of J_s. High nighttime θ_{wood} may occur in a wet season. This may raise a problem when calibrating TDP with other methods in situ. It was reported that after calibrating with one-month data, about 10% of the TDP measurements still significantly differ from SHB measurements (Chapter 2). Therefore, the

calibration conducted in a short period may not be suitable for a long period with dynamic θ_{wood}. With the same concern, calibration on segments with fully water supply may be also not applicable to the field measurement due to the varying water conditions. Therefore, if applying TDP through obvious dry and wet seasons, we recommended calibration with different water conditions or use the model to correct the possible bias of TDP.

Except for the widely used thermal methods (e.g. TDP), deuterium tracing method is another way to investigate water use of trees or bamboos (Calder et al., 1986; Schwendenmann et al., 2010). In our present study (Chapter 4), with TDP as a reference method, we applied deuterium tracing method to estimate sap velocities. V_{TDP} was much lower than deuterium derived sap velocity (V_{D_2O}) on the three studied bamboo species. The V_{D_2O} was derived by dividing the tracing length ($\approx$ bamboo/tree height) with the transit time from deuterium injection to when deuterium concentration in the leaves first reach 10% of the maximal of the deuterium concentration (Meinzer et al., 2006). In such straightforward way, V_{D_2O} seemed more reliable. The further improvement on V_{D_2O} may be estimating the deuterium transit time more precisely with shorter sampling intervals. We think V_{D_2O} could even be larger when D_2O sampling is done at a higher frequency. Additionally, we found that V_{TDP} seem to have a negative relationship with D_2O residence time in labeled culms, i.e. the deuterium residence time in labeled culms was shorter under high sap velocity. However, the residence time was not correlated to the culm water storage (C_{WS}) as found in other studies on trees (James et al., 2003; Meinzer et al., 2006). The insignificant correlation may be attributed to the limited contribution of stem water storage as estimated based on the TDP method. During the experiment from 8th March to 6th April 2013, C_{WS} were 15%, 9% and 9% on average for *B. vulgaris*, *G. apus* and *D. asper*, respectively. On our study bamboos, it was implied that culm water storage was quickly depleted in the morning due to high J_s (Chapter 2). Half-hourly maximal J_s in the four studied bamboo species ranged from 21.6 to 70.5 g cm^{-2} h^{-1} and were (on average) almost two times greater than in the studied tree species (Chapter 2). When applying deuterium tracing method to estimate water use, we found deuterium derived water use was 70% ($R^2 = 0.9$) higher than that derived from TDP on three bamboo species. Such high overestimation cannot fully be explained by TDP underestimation ($\approx 10\%$, Chapter 2), and the overestimation was attributed to tracer loss (deuterium retention and transfer) and incomplete mixing of tracers. Among these error sources, water transfer between bamboo culms through rhizome was proved to be the main cause of tracer loss. With

deuterium tracing method, we found elevated deuterium concentration in the non-labeled culms near the deuterium labeled one. In conclusion, the deuterium tracing method is more suitable to trace water movement than to estimate water use in bamboos or other trees that characterized with water redistribution.

5.2   Outlook

In our study, we found the four studied bamboo species had higher and earlier maximal J_s than nearby tree species. However, the near maximal J_s cannot be maintained for a long time under increasing transpiration demand (e.g. larger VPD) in midday. These results implied the internal water storage supported transpiration in the morning but the contribution may be limited (c.a. 10%). However, in another study on *B. vulgaris* (Yang et al., 2015), the culm water storage showed more important role in the afternoon. These different findings suggested more work on exploring the mechanisms of bamboo water storage. Additionally, water transfer was implied by the deuterium tracing method in the present study, and more direct and quantifiable measurement should be done in the future work. As an important part of this study, method testing and calibration was conducted on widely used TDP method. The calibration results and the modeling on the influence of θ_{wood} on TDP can help further studying bamboo water use and understanding dynamic of water storage. The future work may emphasize on testing the present model in the field with simultaneous measurement of θ_{wood} and J_s by TDP, or on improving and developing heat-based methods with considering θ_{wood}. Regarding the deuterium tracing method, it was proved to be a good method to estimate sap velocity with short enough sampling intervals, but it is not so suitable to estimate quantitate water use of species that have strong water redistribution. However, the deuterium tracing has its obvious advantage on tracing water movement or transfer within or among bamboo culms, and such advantage makes the method to be a powerful way to explore water redistribution or exchange on plants.

Bibliography

Adonsou, K. E., DesRochers, A., and Tremblay, F. (2016). Physiological integration of connected balsam poplar ramets. *Tree Physiology*, 36(7):797–806.

Baker, J. and Bavel, C. v. (1987). Measurement of mass flow of water in the stems of herbaceous plants. *Plant, Cell & Environment*, 10(9):777–782.

Bovard, B., Curtis, P., Vogel, C., Su, H.-B., and Schmid, H. (2005). Environmental controls on sap flow in a northern hardwood forest. *Tree Physiology*, 25(1):31–38.

BPG (2012). An updated tribal and subtribal classification of the bamboos (poaceae: Bambusoideae). *The Journal of the American Bamboo Society*, 24(1):1–10.

Burgess, S. S., Adams, M. A., Turner, N. C., Beverly, C. R., Ong, C. K., Khan, A. A., and Bleby, T. M. (2001a). An improved heat pulse method to measure low and reverse rates of sap flow in woody plants. *Tree Physiology*, 21(9):589–598.

Burgess, S. S., Adams, M. A., Turner, N. C., White, D. A., and Ong, C. K. (2001b). Tree roots: conduits for deep recharge of soil water. *Oecologia*, 126(2):158–165.

Bush, S. E., Hultine, K. R., Sperry, J. S., and Ehleringer, J. R. (2010). Calibration of thermal dissipation sap flow probes for ring-and diffuse-porous trees. *Tree Physiology*, 30(12):1545–1554.

Calder, I., Narayanswamy, M., Srinivasalu, N., Darling, W., and Lardner, A. (1986). Investigation into the use of deuterium as a tracer for measuring transpiration from eucalypts. *Journal of Hydrology*, 84(3-4):345–351.

Calder, I. R. (1991). Implications and assumptions in using the 'total counts' and convection-dispersion equations for tracer flow measurements-with particular reference to transpiration measurements in trees. *Journal of Hydrology*, 125(1):149–158.

Calder, I. R., Kariyappa, G., Srinivasalu, N., and Murty, K. S. (1992). Deuterium tracing for the estimation of transpiration from trees part 1. field calibration. *Journal of Hydrology*, 130(1-4):17–25.

Cao, K.-F., Yang, S.-J., Zhang, Y.-J., and Brodribb, T. J. (2012). The maximum height of grasses is determined by roots. *Ecology Letters*, 15(7):666–672.

Carrasco, L. O., Bucci, S. J., Di Francescantonio, D., Lezcano, O. A., Campan-
ello, P. I., Scholz, F. G., Rodríguez, S., Madanes, N., Cristiano, P. M., Hao,
G.-Y., et al. (2015). Water storage dynamics in the main stem of subtropical
tree species differing in wood density, growth rate and life history traits.
Tree Physiology, 35(4):354–365.

Carslaw, H. S. and Jaeger, J. C. (1959). *Conduction of heat in solids*. Oxford:
Clarendon Press.

Čermák, J., Kučera, J., Bauerle, W. L., Phillips, N., and Hinckley, T. M.
(2007). Tree water storage and its diurnal dynamics related to sap flow and
changes in stem volume in old-growth douglas-fir trees. *Tree Physiology*,
27(2):181–198.

Chen, X., Zhang, X., Zhang, Y., Booth, T., and He, X. (2009). Changes of
carbon stocks in bamboo stands in china during 100 years. *Forest Ecology
and Management*, 258(7):1489–1496.

Choi, I. C. and Aronoff, S. (1966). Photosynthate transport using tritiated
water. *Plant Physiology*, 41(7):1119–1129.

Clearwater, M. J., Meinzer, F. C., Andrade, J. L., Goldstein, G., and Holbrook,
N. M. (1999). Potential errors in measurement of nonuniform sap flow using
heat dissipation probes. *Tree Physiology*, 19(10):681–687.

Cochard, H., Ewers, F., and Tyree, M. (1994). Water relations of a tropical vine-
like bamboo (*Rhipidocladum racemiflorum*): root pressures, vulnerability
to cavitation and seasonal changes in embolism. *Journal of Experimental
Botany*, 45(8):1085–1089.

Constantz, J. and Murphy, F. (1990). Monitoring moisture storage in trees
using time domain reflectometry. *Journal of Hydrology*, 119(1):31–42.

de Agrasar, Z. R. and Rodríguez, M. F. (2003). Culm anatomy of native woody
bamboos in argentina and neighboring areas: cross section. *Bamboo Science
and Culture: Journal of the American Bamboo Society*, 17:28–43.

Dierick, D. and Hölscher, D. (2009). Species-specific tree water use charac-
teristics in reforestation stands in the philippines. *Agricultural and Forest
Meteorology*, 149(8):1317–1326.

Dierick, D., Hölscher, D., and Schwendenmann, L. (2010). Water use char-
acteristics of a bamboo species (*Bambusa blumeana*) in the philippines.
Agricultural and Forest Meteorology, 150(12):1568–1578.

Do, F. and Rocheteau, A. (2002). Influence of natural temperature gradients
on measurements of xylem sap flow with thermal dissipation probes. 1. field
observations and possible remedies. *Tree Physiology*, 22(9):641–648.

Dransfield, S. and Widjaja, E. (1995). Bamboos-plant resources of southeast
asia, no. 7. *Prosea. Bogor, Indonesia*.

Durst, P. B., Ulrich, W., Kashio, M., Khan, S., Shi, K., Gupta, B., Silitonga, T., Yong, P. L., Khatri, D. B., and Iqbal Sial, M. (1994). *Non-wood forest products in Asia*. RAPA Publication (FAO).

Dye, P. and Olbrich, B. (1993). Estimating transpiration from 6-year-old *Eucalyptus grandis* trees: development of a canopy conductance model and comparison with independent sap flux measurements. *Plant, Cell & Environment*, 16(1):45–53.

Dye, P., Olbrich, B., and Calder, I. (1992). A comparison of the heat pulse method and deuterium tracing method for measuring transpiration from *Eucalyptus grandis* trees. *Journal of Experimental Botany*, 43(3):337–343.

Edwards, W. and Warwick, N. (1984). Transpiration from a kiwifruit vine as estimated by the heat pulse technique and the penman-monteith equation. *New Zealand Journal of Agricultural Research*, 27(4):537–543.

Eller, C. B., Lima, A. L., and Oliveira, R. S. (2013). Foliar uptake of fog water and transport belowground alleviates drought effects in the cloud forest tree species, drimys brasiliensis (winteraceae). *New Phytologist*, 199(1):151–162.

FAO (2010). Global forest resources assessment 2010: main report, fao forestry paper, 0258-6150; 163.

Feng, Y., Lin, H., Ho, S., Yan, J., Dong, J., Fang, S., and Huang, Y. (2015). Overview of wind power generation in china: status and development. *Renewable and Sustainable Energy Reviews*, 50:847–858.

Forster, M. A. (2014). How significant is nocturnal sap flow? *Tree Physiology*, 34(7):757–765.

Gaines, K. P., Meinzer, F. C., Duffy, C. J., Thomas, E. M., and Eissenstat, D. M. (2016). Rapid tree water transport and residence times in a pennsylvania catchment. *Ecohydrology*, 9(8):1554–1565.

Gleason, S. M., Westoby, M., Jansen, S., Choat, B., Hacke, U. G., Pratt, R. B., Bhaskar, R., Brodribb, T. J., Bucci, S. J., Cao, K.-F., et al. (2016). Weak tradeoff between xylem safety and xylem-specific hydraulic efficiency across the world's woody plant species. *New Phytologist*, 209(1):123–136.

Goldsmith, G. R. (2013). Changing directions: the atmosphere–plant–soil continuum. *New Phytologist*, 199(1):4–6.

Goldsmith, G. R., Matzke, N. J., and Dawson, T. E. (2013). The incidence and implications of clouds for cloud forest plant water relations. *Ecology Letters*, 16(3):307–314.

Goldstein, G., Andrade, J., Meinzer, F., Holbrook, N., Cavelier, J., Jackson, P., and Celis, A. (1998). Stem water storage and diurnal patterns of water use in tropical forest canopy trees. *Plant, Cell & Environment*, 21(4):397–406.

Granier, A. (1985). Une nouvelle méthode pour la mesure du flux de sève brute dans le tronc des arbres. *Annales des Sciences forestières*, 42(2):193–200.

Granier, A. (1987). Evaluation of transpiration in a douglas-fir stand by means of sap flow measurements. *Tree Physiology*, 3(4):309–320.

Grime, V. and Sinclair, F. (1999). Sources of error in stem heat balance sap flow measurements. *Agricultural and Forest Meteorology*, 94(2):103–121.

Grosser, D. and Liese, W. (1971). On the anatomy of asian bamboos, with special reference to their vascular bundles. *Wood Science and technology*, 5(4):290–312.

Hao, G.-Y., Wheeler, J. K., Holbrook, N. M., and Goldstein, G. (2013). Investigating xylem embolism formation, refilling and water storage in tree trunks using frequency domain reflectometry. *Journal of Experimental Botany*, 64(8):2321–2332.

Hartung, W., Sauter, A., and Hose, E. (2002). Abscisic acid in the xylem: where does it come from, where does it go to? *Journal of Experimental Botany*, 53(366):27–32.

Hernández-Santana, V., David, T., and Martínez-Fernández, J. (2008). Environmental and plant-based controls of water use in a mediterranean oak stand. *Forest Ecology and Management*, 255(11):3707–3715.

Holbrook, N. M., Burns, M., and Sinclair, T. (1992). Frequency and time-domain dielectric measurements of stem water content in the arborescent palm, sabal palmetto. *Journal of Experimental Botany*, 43(1):111–119.

Hölttä, T., Linkosalo, T., Riikonen, A., Sevanto, S., and Nikinmaa, E. (2015). An analysis of granier sap flow method, its sensitivity to heat storage and a new approach to improve its time dynamics. *Agricultural and Forest Meteorology*, 211-212:2–12.

Horna, V., Schuldt, B., Brix, S., and Leuschner, C. (2011). Environment and tree size controlling stem sap flux in a perhumid tropical forest of central sulawesi, indonesia. *Annals of forest science*, 68(5):1027–1038.

Ichihashi, R., Komatsu, H., Kume, T., Onozawa, Y., Shinohara, Y., Tsuruta, K., and Otsuki, K. (2015). Stand-scale transpiration of two moso bamboo stands with different culm densities. *Ecohydrology*, 8(3):450–459.

Inagaki, T., Ahmed, B., Hartley, I. D., Tsuchikawa, S., and Reid, M. (2014). Simultaneous prediction of density and moisture content of wood by terahertz time domain spectroscopy. *Journal of Infrared, Millimeter, and Terahertz Waves*, 35(11):949–961.

INBAR (2014). International trade in bamboo and rattan 2012. beijing: International network for bamboo and rattan.

Ito, R., Miyafuji, H., and Kasuya, N. (2015). Rhizome and root anatomy of moso bamboo (*Phyllostachys pubescens*) observed with scanning electron microscopy. *Journal of Wood Science*, 61(4):431–437.

James, S. A., Meinzer, F. C., Goldstein, G., Woodruff, D., Jones, T., Restom, T., Mejia, M., Clearwater, M., and Campanello, P. (2003). Axial and radial water transport and internal water storage in tropical forest canopy trees. *Oecologia*, 134(1):37–45.

Jarvis, N. (1989). A simple empirical model of root water uptake. *Journal of Hydrology*, 107(1-4):57–72.

Johnson, D., McCulloh, K., Meinzer, F., Woodruff, D., and Eissenstat, D. (2011). Hydraulic patterns and safety margins, from stem to stomata, in three eastern us tree species. *Tree Physiology*, 31(6):659–668.

Jung, E., Otieno, D., Lee, B., Lim, J., Kang, S., Schmidt, M., and Tenhunen, J. (2011). Up-scaling to stand transpiration of an asian temperate mixed-deciduous forest from single tree sapflow measurements. *Plant Ecology*, 212(3):383–395.

Kalma, S. J., Thorburn, P. J., and Dunn, G. M. (1998). A comparison of heat pulse and deuterium tracing techniques for estimating sap flow in *Eucalyptus grandis* trees. *Tree Physiology*, 18(10):697–705.

Kline, J., Martin, J., Jordan, C., and Koranda, J. (1970). Measurement of transpiration in tropical trees with tritiated water. *Ecology*, 51(6):1068–1073.

Köcher, P., Horna, V., and Leuschner, C. (2013). Stem water storage in five coexisting temperate broad-leaved tree species: significance, temporal dynamics and dependence on tree functional traits. *Tree Physiology*, 33(8):817–832.

Köhler, M., Dierick, D., Schwendenmann, L., and Hölscher, D. (2009). Water use characteristics of cacao and gliricidia trees in an agroforest in central sulawesi, indonesia. *Ecohydrology*, 2(4):520–529.

Köhler, M., Schwendenmann, L., and Hölscher, D. (2010). Throughfall reduction in a cacao agroforest: tree water use and soil water budgeting. *Agricultural and Forest Meteorology*, 150(7):1079–1089.

Kollman, F. F. and Côté, W. (1968). Principles of wood science and technology, vol i.

Komatsu, H., Onozawa, Y., Kume, T., Tsuruta, K., Kumagai, T., Shinohara, Y., and Otsuki, K. (2010). Stand-scale transpiration estimates in a moso bamboo forest: Ii. comparison with coniferous forests. *Forest Ecology and Managemen*, 260(8):1295–1302.

Kremer, T. A., LaSarre, B., Posto, A. L., and McKinlay, J. B. (2015). N2 gas is an effective fertilizer for bioethanol production by zymomonas mobilis. *Proceedings of the National Academy of Sciences*, 112(7):2222–2226.

Kubota, M., Tenhunen, J., Zimmermann, R., Schmidt, M., Adiku, S., and Kakubari, Y. (2005). Influences of environmental factors on the radial profile of sap flux density in fagus crenata growing at different elevations in the naeba mountains, japan. *Tree Physiology*, 25(5):545–556.

Kume, T., Onozawa, Y., Komatsu, H., Tsuruta, K., Shinohara, Y., Umebayashi, T., and Otsuki, K. (2010). Stand-scale transpiration estimates in a moso bamboo forest: (i) applicability of sap flux measurements. *Forest Ecology and Management*, 260(8):1287–1294.

Kume, T., Takizawa, H., Yoshifuji, N., Tanaka, K., Tantasirin, C., Tanaka, N., and Suzuki, M. (2007). Impact of soil drought on sap flow and water status of evergreen trees in a tropical monsoon forest in northern thailand. *Forest Ecology and Management*, 238(1):220–230.

Liese, W. and Köhl, M. (2015). *Bamboo: the plant and its uses*, volume 10. Springer.

Liese, W. and Weiner, G. (1996). Ageing of bamboo culms. a review. *Wood Science and Technology*, 30(2):77–89.

Lin, J., He, X., Hu, Y., Kuang, T., and Ceulemans, R. (2002). Lignification and lignin heterogeneity for various age classes of bamboo (*Phyllostachys pubescens*) stems. *Physiologia Plantarum*, 114(2):296–302.

Lu, P., Urban, L., and Zhao, P. (2004). Granier's thermal dissipation probe (tdp) method for measuring sap flow in trees: theory and practice. *Acta Botanica Sinica-English Edition-*, 46(6):631–646.

Marc, V. and Robinson, M. (2004). Application of the deuterium tracing method for the estimation of tree sap flow and stand transpiration of a beech forest (*Fagus silvatica L.*) in a mountainous mediterranean region. *Journal of Hydrology*, 285(1):248–259.

Mathew, P. (1998). *The bamboo economy of Kerala, India: an analysis of the production-to-consumption systems*. Number 12. International Network for Bamboo and Rattan.

Mei, T.-T., Fang, D.-M., Röll, A., Niu, F.-R., Hendrayanto, and Hölscher, D. (2016). Water use patterns of four tropical bamboo species assessed with sap flux measurements. *Frontiers in plant science*, 6:1202.

Meinzer, F., Brooks, J., Domec, J.-C., Gartner, B., Warren, J., Woodruff, D., Bible, K., and Shaw, D. (2006). Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. *Plant, Cell & Environment*, 29(1):105–114.

Meinzer, F., Goldstein, G., and Andrade, J. (2001). Regulation of water flux through tropical forest canopy trees: do universal rules apply? *Tree Physiology*, 21(1):19–26.

Mohmod, A. L. and Mustafa, M. T. (1992). Variation in anatomical properties of three malaysian bamboos from natural stands. *Journal of Tropical Forest Science*, 5(1):90–96.

Münch, E. (1927). Versuche über den saftkreislauf. *Berichte der Deutschen Botanischen Gesellschaft*, 45(6):340–356.

Nadler, A., Raveh, E., Yermiyahu, U., Lado, M., Nasser, A., Barak, M., and Green, S. (2008). Detecting water stress in trees using stem electrical conductivity measurements. *Soil Science Society of America Journal*, 72(4):1014–1024.

Niu, F., Röll, A., Hardanto, A., Meijide, A., Köhler, M., Hölscher, D., et al. (2015). Oil palm water use: calibration of a sap flux method and a field measurement scheme. *Tree Physiology*, 35(5):563–573.

Numata, M. (1987). The ecology of bamboo forests-particularly on temperate bamboo forests. *Bamb J*, 4:118–131.

O'Brien, J. J., Oberbauer, S. F., and Clark, D. B. (2004). Whole tree xylem sap flow responses to multiple environmental variables in a wet tropical forest. *Plant, Cell & Environment*, 27(5):551–567.

Parr, J., Sullivan, L., Chen, B., Ye, G., and Zheng, W. (2010). Carbon biosequestration within the phytoliths of economic bamboo species. *Global Change Biology*, 16(10):2661–2667.

Pereira, H. and Hosegood, P. (1962). Comparative water-use of softwood plantations and bamboo forest. *Journal of Soil Science*, 13:299–313.

Peters, E. B., McFadden, J. P., and Montgomery, R. A. (2010). Biological and environmental controls on tree transpiration in a suburban landscape. *Journal of Geophysical Research: Biogeosciences*, 115(G4):2156–2202.

Petit, G., DeClerck, F. A., Carrer, M., and Anfodillo, T. (2014). Axial vessel widening in arborescent monocots. *Tree Physiology*, 34(2):137–145.

Pfautsch, S., Hölttä, T., and Mencuccini, M. (2015a). Hydraulic functioning of tree stems-fusing ray anatomy, radial transfer and capacitance. *Tree Physiology*, 35(7):706–722.

Pfautsch, S., Renard, J., Tjoelker, M. G., and Salih, A. (2015b). Phloem as capacitor: radial transfer of water into xylem of tree stems occurs via symplastic transport in ray parenchyma. *Plant Physiology*, 167(3):963–971.

Philip, J. R. (1966). Plant water relations: some physical aspects. *Annual Review of Plant Physiology*, 17(1):245–268.

Regalado, C. M. and Ritter, A. (2007). An alternative method to estimate zero flow temperature differences for granier's thermal dissipation technique. *Tree Physiology*, 27(8):1093–1102.

Renninger, H. J. and Phillips, N. (2010). Intrinsic and extrinsic hydraulic factors in varying sizes of two amazonian palm species (iriartea deltoidea and mauritia flexuosa) differing in development and growing environment. *American journal of botany*, 97(12):1926–1936.

Roden, J. S. and Ehleringer, J. R. (1999). Observations of hydrogen and oxygen isotopes in leaf water confirm the craig-gordon model under wide-ranging environmental conditions. *Plant Physiology*, 120(4):1165–1174.

Roderick, M. L. and Berry, S. L. (2001). Linking wood density with tree growth and environment: a theoretical analysis based on the motion of water. *New Phytologist*, 149(3):473–485.

Röll, A., Niu, F., Meijide, A., Hardanto, A., Knohl, A., Hölscher, D., et al. (2015). Transpiration in an oil palm landscape: effects of palm age. *Biogeosciences*, 12(19):5619–5633.

Saha, S., Holbrook, N. M., Montti, L., Goldstein, G., and Cardinot, G. K. (2009). Water relations of chusquea ramosissima and merostachys claussenii in iguazu national park, argentina. *Plant Physiology*, 149(4):1992–1999.

Sakuratani, T. (1981). A heat balance method for measuring water flux in the stem of intact plants. *Journal of Agricultural Meteorology*, 37(1):9–17.

Sakuratani, T., Aoe, T., and Higuchi, H. (1999). Reverse flow in roots of sesbania rostrata measured using the constant power heat balance method. *Plant, Cell & Environment*, 22(9):1153–1160.

Scholz, F. C., Bucci, S. J., Goldstein, G., Meinzer, F. C., Franco, A. C., and Miralles-Wilhelm, F. (2008). Temporal dynamics of stem expansion and contraction in savanna trees: withdrawal and recharge of stored water. *Tree Physiology*, 28(3):469–480.

Schwendenmann, L., Dierick, D., Köhler, M., and Hölscher, D. (2010). Can deuterium tracing be used for reliably estimating water use of tropical trees and bamboo? *Tree Physiology*, 30(7):886–900.

Smith, D. and Allen, S. (1996). Measurement of sap flow in plant stems. *Journal of Experimental Botany*, 47(12):1833–1844.

Smith, D., Jackson, N., Roberts, J., and Ong, C. (1999). Reverse flow of sap in tree roots and downward siphoning of water by *Grevillea robusta*. *Functional Ecology*, 13(2):256–264.

Song, X., Peng, C., Zhou, G., Gu, H., Li, Q., and Zhang, C. (2016). Dynamic allocation and transfer of non-structural carbohydrates, a possible mechanism for the explosive growth of moso bamboo (*Phyllostachys heterocycla*). *Scientific reports*, 6.

Song, Z., Liu, H., Li, B., and Yang, X. (2013). The production of phytolith-occluded carbon in china's forests: implications to biogeochemical carbon sequestration. *Global change biology*, 19(9):2907–2915.

Sperling, O., Shapira, O., Schwartz, A., and Lazarovitch, N. (2015). Direct in vivo evidence of immense stem water exploitation in irrigated date palms. *Journal of Experimental Botany*, 66(1):333–338.

Stapleton, C. (1998). Form and function in the bamboo rhizome. *Journal of American Bamboo Society*, 12(1):21–29.

Steppe, K., De Pauw, D. J., Doody, T. M., and Teskey, R. O. (2010). A comparison of sap flux density using thermal dissipation, heat pulse velocity and heat field deformation methods. *Agricultural and Forest Meteorology*, 150(7):1046–1056.

Studer, M., Siegwolf, R., Leuenberger, M., and Abiven, S. (2015). Multi-isotope labelling of organic matter by diffusion of ^{2}h/^{18}o-h$_2$o vapour and ^{13}c-co$_2$ into the leaves and its distribution within the plant. *Biogeosciences*, 12(6):1865–1879.

Tang, J., Bolstad, P. V., Ewers, B. E., Desai, A. R., Davis, K. J., and Carey, E. V. (2006). Sap flux–upscaled canopy transpiration, stomatal conductance, and water use efficiency in an old growth forest in the great lakes region of the united states. *Journal of Geophysical Research: Biogeosciences*, 111(G2).

Tatarinov, F. A., Kučera, J., and Cienciala, E. (2005). The analysis of physical background of tree sap flow measurement based on thermal methods. *Measurement Science and Technology*, 16(5):1157.

Trcala, M. and Čermák, J. (2016). A new heat balance equation for sap flow calculation during continuous linear heating in tree sapwood. *Applied Thermal Engineering*, 102:532–538.

Tyree, M. T. and Sperry, J. S. (1988). Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? answers from a model. *Plant Physiology*, 88(3):574–580.

Uchimura, E. (1994). Invitation to bamboos: Wonder of biology. *Tokyo, Kenseisha*, 188.

Van Den Besselaar, E. J., Klein Tank, A. M., Van Der Schrier, G., Abass, M. S., Baddour, O., Van Engelen, A. F., Freire, A., Hechler, P., Laksono, B. I., Jilderda, R., et al. (2015). International climate assessment & dataset: climate services across borders. *Bulletin of the American Meteorological Society*, 96(1):16–21.

Vandegehuchte, M. W. and Steppe, K. (2012). Improving sap flux density measurements by correctly determining thermal diffusivity, differentiating between bound and unbound water. *Tree Physiology*, 32(7):930–942.

Vandegehuchte, M. W. and Steppe, K. (2013). Corrigendum to: Sap-flux density measurement methods: working principles and applicability. *Functional Plant Biology*, 40(10):1088–1088.

Vergeynst, L. L., Vandegehuchte, M. W., McGuire, M. A., Teskey, R. O., and Steppe, K. (2014). Changes in stem water content influence sap flux density measurements with thermal dissipation probes. *Trees*, 28(3):949–955.

Wang, B., Wei, W., Liu, C., You, W., Niu, X., and Man, R. (2013). Biomass and carbon stock in moso bamboo forests in subtropical china: characteristics and implications. *Journal of Tropical Forest Science*, 25(1):137–148.

Wang, H., Zhao, P., Hölscher, D., Wang, Q., Lu, P., Cai, X. A., and Zeng, X. P. (2012). Nighttime sap flow of acacia mangium and its implications for nighttime transpiration and stem water storage. *Journal of Plant Ecology*, 5(3):294–304.

Waring, R. and Running, S. (1978). Sapwood water storage: its contribution to transpiration and effect upon water conductance through the stems of old-growth douglas-fir. *Plant, Cell & Environment*, 1(2):131–140.

Wullschleger, S. D., Childs, K. W., King, A. W., and Hanson, P. J. (2011). A model of heat transfer in sapwood and implications for sap flux density measurements using thermal dissipation probes. *Tree Physiology*, 31(6):669–679.

Wullschleger, S. D., Hanson, P. J., and Todd, D. E. (1996). Measuring stem water content in four deciduous hardwoods with a time-domain reflectometer. *Tree Physiology*, 16(10):809–815.

Wullschleger, S. D. and Norby, R. J. (2001). Sap velocity and canopy transpiration in a sweetgum stand exposed to free-air co2 enrichment (face). *New Phytologist*, 150(2):489–498.

Yang, S.-J., Zhang, Y.-J., Goldstein, G., Sun, M., Ma, R.-Y., and Cao, K.-F. (2015). Determinants of water circulation in a woody bamboo species: afternoon use and night-time recharge of culm water storage. *Tree Physiology*, 35(9):964–974.

Yang, S.-J., Zhang, Y.-J., Sun, M., Goldstein, G., and Cao, K.-F. (2012). Recovery of diurnal depression of leaf hydraulic conductance in a subtropical woody bamboo species: embolism refilling by nocturnal root pressure. *Tree Physiology*, 32(4):414–422.

Zhao, X.-H., Zhao, P., Zhang, Z.-Z., Zhu, L.-W., Niu, J.-F., Ni, G.-Y., Hu, Y.-T., and Ouyang, L. (2016). Sap flow-based transpiration in *Phyllostachys pubescens*: applicability of the tdp methodology, age effect and rhizome role. *Trees*, pages 1–15.

Zhuang, S., Ji, H., Zhang, H., and Sun, B. (2015). Carbon storage estimation of moso bamboo (*Phyllostachys pubescens*) forest stands in fujian, china. *Tropical Ecology*, 56(3):383–91.

Zimmermann, M. H. and Tomlinson, P. B. (1972). The vascular system of monocotyledonous stems. *Botanical Gazette*, 133(2):141–155.

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Appendix Chapter 3

Table 1 The influence of the three factors formula type, time step and formula specificity on the performance of the linear calibration model. Results of multi-ANOVA of the three factors against normalized Root-Mean-Square Error (nRMSE).

Source	DF	Type SS	Mean Square	F value	P
Formula type	1	0.0046	0.0046	0.68	0.4093
Time step	3	0.0046	0.0015	0.23	0.8777
Formula specificity	2	7.7675	3.8838	577.54	<0.0001

Note: nRMSE, calculated by normalizing the RMSE with the observed range of sap flux densities from stem heat balance (SHB) measurements; RMSE derived from SHB measurements vs. model-predicted values of each day. Data of 63 days were used. $P < 0.01$ indicates significant difference.

Table 2 Performance of culm-specific vs. species-specific vs. common linear formulas for a simple linear field calibration of the thermal dissipation probe (TDP) method with the stem heat balance (SHB) method on four bamboo species Normalized Root-Mean-Square Errors (nRMSE) and passing rates of the Wilcoxon Signed-Rank test for each species and formula specificity type.

Species	Formula specificity	nRMSE	Passing rate (%)
B. vulgaris	common	0.11^a	83^a
	culm	0.04^a	94^a
	species	0.10^a	84^a
G. apus	common	0.12^a	77^a
	culm	0.06^a	90^a
	species	0.10^a	81^a
D. asper	common	0.18^a	74^a
	culm	0.04^a	94^a
	species	0.18^a	70^a
G. atroviolacea	common	0.13^a	74^a
	culm	0.06^a	89^a
	species	0.12^a	74^a

Note: Superscripted letters indicate significant differences between nRMSEs and passing rates, respectively, within each species (Tukey's test, $P<0.05$).

Appendix Chapter 4

The thermal conductivity of the sample segments was calculated following the work of Vandegehuchte and Steppe (2013) who introduced a corrected thermal conductivity on the axial direction (K_a, W m^{-1} K^{-1}) as shown in the following equation (Eq. 1).

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

Where K_w is thermal conductivity of water (0.6 W m^{-1} K^{-1}), $\theta_{wood\text{-}FSP}$ is θ_{wood} at fiber saturation point, ρ_{dry} and ρ_w are the density of dry wood and water (1000 kg m^{-3}), $F_{v\text{-}FSP}$ is a void fraction of wood at fiber saturation point (Eq. 2) according to Vandegehuchte and Steppe (2013):

$$F_{v-FSP} = 1 - G_b(\rho_w\rho_{cw}^{-1} + \theta_{wood-FSP}) \quad (2)$$

Where $F_{v\text{-}FSP}$ is void fraction of the wood at fiber moisture saturation point, ρ_{cw} is the density of cell wall (1530 kg m^{-3}, Kollman and Côté, 1968; Vandegehuchte and Steppe, 2013), G_b is the basic specific gravity as the function of weight of dry mass per fresh volume divided by the density of water. $\theta_{wood\text{-}FSP}$ (Eq. 3) refers to (Roderick and Berry, 2001):

$$\theta_{wood-FSP} = 0.2(\rho_d\rho_w^{-1})^{-\frac{1}{2}} \quad (3)$$

Where ρ_{ovend} is the density of oven dried wood (Eq. 4) refers to (kg m^{-3}, Inagaki et al., 2014):

$$\rho_d = \rho_{air}(1 - F_{ovencw}) + \rho_{ovencw}F_{ovencw} \quad (4)$$

Where ρ_{air} is the density of air at 20 °C (1.2 kg m^{-3}), ρ_{ovencw} is the density of oven dried cell wall (1400 kg m^{-3}). F_{ovencw} is the volume fraction of the oven dried cell wall (Eq. 5).

$$F_{ovencw} = w_{ovencw}\rho_{ovencw}^{-1}v_{fresh}^{-1} \quad (5)$$

Where w_{ovencw} is the weight of oven-dried cell wall (kg). In this study, we assumed w_{ovencw} approximately equal to the weight of oven-dried wood. v_{fresh} is the volume of the fresh wood (m^3). The specific heat capacity of the fresh

wood was calculated following (Burgess et al., 2001a) as shown below (Eq. 6).

$$c = \frac{w_{dry}c_{dry} + c_w(w_{fresh} - w_{dry})}{w_{fresh}} \qquad (6)$$

Where c is heat capacity of fresh wood (J kg^{-1} K^{-1}). c_{dry} and c_w are heat capacity of dry wood (1200 J kg^{-1} K^{-1}) and water (4186 J kg^{-1} K^{-1}) at 20 °C (Edwards and Warwick, 1984), and w_{fresh} and w_{dry} are weights of fresh and dry wood. Because the wood domain contains wood matrix and sap (approximately equal to water in physical properties), heat transfer in such porous media directly depends on the contact surface between the two phases. Such heat transfer is characterized by interfacial area density (IFA, Eq. 7) which is defined as the surface area per unit volume (m^{-1}).

$$IFA = \frac{\sqrt{4\pi P F_{v-FSP}}}{100} \qquad (7)$$

Where P is the number of conduits in 1 cm^2 of the wood which is approximately 250 for bamboos according to Mohmod and Mustafa (1992).
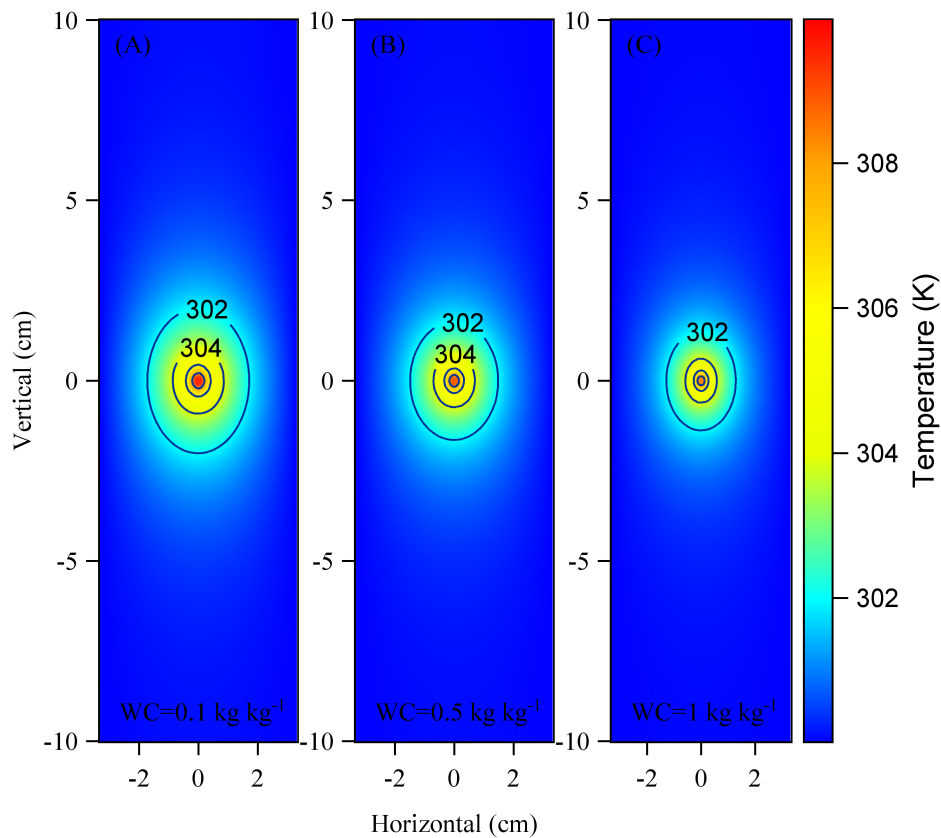
Fig. 1 The temperature contours around the heating probe under zero sap flow conditions. The simulated bamboo segments had different water contents of 0.1 (A), 0.5 (B) and 1 kg kg^{-1} (C), respectively. The ambient temperature in the model was set to 300 K. The legend shows the increase of temperature after reaching steady-state thermal conditions. The geometry and physical properties applied in the model were based on a mature culm segment of *B. vulgaris*, extracted from a culm at breast height.

Declaration

I hereby declare that I am the sole author of this dissertation entitled "MEA-SUREMENTS OF TROPICAL BAMBOO WATER USE". All the references and data sources that were used in this dissertation have been acknowledged. I further declare that this work has never been submitted in any forms as part of any other dissertation procedure.

Göttingen, January 2017 _____

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submitted by
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Ting-Ting Mei, Ping Zhao, Guang-Yan Ni, Quan Wang, Xiao-Ping Zeng, Cui-Ming Zhou, Xi-An Cai, Meng-Hao Yu, Qing-Ping Cao, 2012. Effect of

stem diameter at breast height on skewness of sap flow pattern and time lag. *Acta Ecologica Sinica* 32, 7018-7026. (In Chinese)

Ting-Ting Mei, Ping Zhao, Quan Wang, Xi-An Cai, Meng-Hao Yu, Li-Wei Zhu, Lv-Liu Zou, Xiao-Ping Zeng, 2010. Effects of tree diameter at breast height and soil moisture on transpiration of *Schima superba* based on sap flow pattern and normalization. *Chinese Journal of Applied Ecology* 21. (In Chinese)

Ting-Ting Mei, Chuan-Kuan Wang, Ping Zhao, Xi-An Cai, Xiao-Jing Liu, Quan-Zhi Zhang, 2010. Dynamics of trunk sap flux Density of *Schima superba*. *Scientia Silvae Sinicae* 40-47. (In Chinese)

Ping Zhao, **Ting-Ting Mei**, Li-Wei Zhu, Jun-Feng Niu, Guang-Yan Ni, 2014. Difference of measured sap flows of *Bambusa chungii* using thermal dissipation probes at different lengths and their in situ validation. *Chinese Journal of Ecology* 33, 1420-1428. (In Chinese)

Ping Zhao, **Ting-Ting Mei**, Guang-Yan Ni, Xiao-Ping Zeng, 2012. Application of thermal dissipation sap flow measuring system in investigating bamboo transpiration: Problems and solutions. *Chinese Journal of Ecology* 31, 187-193. (In Chinese)

Ping Zhao, **Ting-Ting Mei**, Guang-Yan Ni, Meng-Hao Yu, Xiao-Ping Zeng, 2012. Application of thermal dissipation probe in the study of *Bambusa chungii* sap flow. *Chinese Journal of Applied Ecology* 23, 979-984. (In Chinese)

Other publications

Xi-An Cai, Ping Zhao, Xiao-Ping Zeng, Li-Wei Zhu, Lv-Liu Zou, **Ting-Ting Mei**, Meng-Hao Yu, 2012. Dynamics of xylem sap flow of two Magnoliaceae tree species in relation to environmental factors. *Chinese Journal of Ecology* 31. (In Chinese)

Li-Wei Zhu, Ping Zhao, Xi-An Cai, Xiao-Ping Zeng, Guang-Yan Ni, Jun-Yan Zhang, Lv-Liu Zou, **Ting-Ting Mei**, Meng-Hao Yu, 2012. Effects of sap velocity on the daytime increase of stem CO2 efflux from stems of *Schima*

superba trees. *Trees* 26, 535-542.

Cui-Ming Zhou, Ping Zhao, Guang-Yan Ni, Li-Wei Zhu, Quan Wang, **Ting-Ting Mei**, Jun-Yan Zhang, Xi-An Cai, 2011. Whole-tree water use characteristics of *Schima superba* in wet and dry seasons based on sap flow and soil-leaf water potential gradient analysis. *Chinese Journal of Ecology* 30. (In Chinese)

Li-Wei Zhu, Ping Zhao, Guang-Yan Ni, Xi-An Cai, Xiao-Ping Zeng, Lv-Liu Zou, **Ting-Ting Mei**, Meng-Hao Yu, 2011. Differences of stem CO2 efflux among individual trees of *Schima superba* and effects of sap flow. *Chinese Journal of Applied Environmental Biology* 17, 447-452. (In Chinese)

Conference presentations

Ting-Ting Mei, Dong-Ming Fang, Michael Köhler, Hendrayanto, Dirk Hölscher: Water use of bamboos: methods test and first results. Poster presentation. *Annual Conference of the Society for Tropical Ecology (gtö)*. Freising, Germany, 25-28 February 2014.

Ting-Ting Mei, Dong-Ming Fang, Alexander Röll, Hendrayanto, Dirk Hölscher: Water transfer between bamboo culms indicated by deuterium tracing. Poster presentation. *46th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland (gfö)*. Marburg, Germany, 05-09 September 2016.

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