Water Transfer Between Bamboo Culms in the Period of Sprouting

Dongming Fang1,2*, Tingting Mei1,2, Alexander Röll2 and Dirk Hölscher2

1 State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, Lin’an, China, 2 Tropical Silviculture and Forest Ecology, University of Göttingen, Göttingen, Germany

Bamboo culms are connected to neighboring culms via rhizomes, which enable resource exchange between culms. We assessed water transfer between established and neighboring, freshly sprouted culms by thermal dissipation probes (TDP) inserted into culms and the connecting rhizome. During the early phase of sprouting, highest sap flux densities in freshly sprouted culms were observed at night, whereas neighboring established culms had high sap flux densities during daytime. After leaf flushing on freshly sprouted culms, the nighttime peaks disappeared and culms switched to the diurnal sap flux patterns with daytime maxima as observed in established culms. TDP in rhizomes indicated water flowing from the established to the freshly sprouted culms. When the established culms of a clump were cut, freshly sprouted culms without leaves reduced sap flux densities rates by 79%. Our findings thus suggest that bamboos exchange water via rhizomes and that nighttime fluxes are highly important for the support of freshly sprouted culms. The (water) resource support may facilitate the very fast growth of the bamboo shoots, and enable the colonizing of new places.

Keywords: bamboo shoots, nighttime flux, rhizome, sap flux, water exchange

INTRODUCTION

Plants with connected roots or rhizomes have the possibility to share resources with each other directly (Baret and DesRochers, 2011). Resource exchange among connected individuals, referred to as “physiological integration” (Lau and Young, 1988; Caraco and Kelly, 1991; Kroon et al., 1996), has been intensively studied and seems to be relatively widespread in herbaceous species (Alpert and Mooney, 1986; Lau and Young, 1988; Chapman et al., 1992; Kroon et al., 1996; Stueffler et al., 1996). In tree species such as lodgepole pine (Fraser et al., 2006), aspen (Baret and DesRochers, 2011), and poplar (Adonsou et al., 2016) resource exchange via connected roots was also observed. The direction of transfer and the transferred amounts depended on the status of the connected plants; e.g., plants that suffered drought received water from watered neighbors, in which the amount of transferred water was related to the leaf water potential or leaf area of the connected plants (Kroon et al., 1996; Adonsou et al., 2016). Such resource integration was shown to be of critical importance for new ramets grown from the parental root systems of aspen (Populus tremuloides) (Baret and DesRochers, 2011).

As rhizomatous monocot species, bamboos are well known for their fast expansion via their underground rhizome system as well as the rapid growth of freshly sprouted culms (Liese and Köhl, 2015). After emerging from the soil, bamboo culms can attain their full heights within 1 or 2 months, with maximum growth rates up to 10–80 cm per day (Liese and Köhl, 2015;
Song et al., 2016). Some species may even grow up to 1 m per
day during the fast growing phase (Ueda, 1960). This leads to
the question of where developing culms, with no leaves and
only few roots, get the resources to sustain such growth rates.
Important mechanisms include nutrient storage in the rhizome as
well as resource translocation from connected mature culms (Li
et al., 1998a,b; Liese and Köhl, 2015). A study on Moso bamboo
(Phyllostachys pubescens) revealed that the content of non-
structural carbohydrates in mature culms declined substantially
during the “explosive growth” period of neighboring, young
bamboo shoots due to the translocation of carbohydrates from
mature to young culms via the underground rhizomes (Song
et al., 2016). Applying deuterium tracing on culms in a clump of
Bambusa blumeana, Dierick et al. (2010) found higher deuterium
concentration than the background values in neighboring culms
close to the labeled culms. This elevated deuterium concentration
was thought to imply water transfer among the culms via the
rhizomes. In another study on Moso bamboo all rhizomes of
several culms were cut and the culms thus disconnected from
the clump’s rhizome network. The culms with cut rhizomes
subsequently consumed 20% less water than neighboring culms
with intact rhizomes (Zhao et al., 2016).

Our study was implemented on three clumpy bamboo species
during the phase of vegetative sprouting of fresh culms. The
aim was to assess water transfer among established culms and
sprouting culms with thermal dissipation probes (TDP) and a
cutting experiment.

**MATERIALS AND METHODS**

**Study Site and Bamboos**

The study was conducted in a bamboo garden in Bogor, Indonesia
(6°33′40″ S, 106°43′27″ E, 182 m asl). Rainfall in Bogor is
3978 mm per year and the mean annual temperature is 25.6°C
(Van Den Besselaar et al., 2014). The months between October
and May are particularly wet. During this wet period, new
shoots of bamboos sprout from the soil and grow to their full
height. This study was conducted in clumps of B. vulgaris and
Gigantochloa apus; culm heights were 17.9 ± 0.8 m (mean ± SD)
and 16.2 ± 2.7 m and culm diameters at breast height were
7.0 ± 0.4 cm and 7.9 ± 1.1 cm, respectively. In the clumps,
established culms and freshly sprouted culms were connected
via rhizomes of 30 to 50 cm length. Unlike the hollow culms of
the bamboos, the rhizomes are solid. During the nearly 4-month
experimental period from December 2012 to March 2013, fresh
culms sprouted and grew to their full height. Culm growth was
slowed down during the period of leaf development.

**Sap Flux in Culms and the Rhizome, and Measurements of Radiation**

For B. vulgaris, three pairs of established and attached freshly
sprouted culms were selected at the culm edge (Figures 1A,B).
The connection between established and freshly sprouted culms
was verified by partially removing the topsoil and directly
observing the rhizomes. Sap flux densities ($J_s$, g cm⁻² h⁻¹) in
bamboo culms were monitored with TDP (Granier, 1985). Each
TDP consists of two probes – a heated probe and a reference one,
and a thermal couple is built into each probe to detect thermal
dynamic. The temperature around the heated probe is negatively
correlated with $J_s$. The temperature differential between heated
and reference probe were used for monitoring and calculating
$J_s$ (Lu et al., 2004). On each studied bamboo culm, three pairs
of TDP with 1 cm sensor length were inserted into the culm
walls at breast height (Figure 1A and Appendix Figure S1A).
The heated probe, powered by 120 mA, was installed 10 cm
above the reference probe. Voltage signals were recorded every
30 s and averaged every 10 min (CR1000 data loggers and
AM16/32 multiplexer, Campbell Scientific Inc., United States). $J_s$
of established culms was first calculated based on Granier’s
equation (Granier, 1985), and $J_s$ was further corrected by
multiplying it with species-specific calibration parameters (SSCP;
2.79 for B. vulgaris; 3.32 for G. apus; Mei et al., 2016).

$$J_s = 119 \times \left( \frac{T_{max} - \Delta T}{\Delta T} \right)^{1.231} \times 0.36 \times SSCP$$

Where $\Delta T$ is the temperature difference between the heated
and reference probe and $T_{max}$ is the maximal $\Delta T$ within a
given day; $T_{max}$ usually occurs during the night and is used to
set zero-flux conditions ($J_s = 0$). The model parameters 119 and
1.231 were empirically derived by Granier (1985). These original
parameters were found to substantially underestimate $J_s$ in
the bamboo species B. vulgaris and G. apus (Mei et al., 2016),
which is why the mentioned SSCP were applied.

To measure $J_s$ and detect directions of sap flow in the rhizome
between established and freshly sprouted culms, we built self-
made, modified TDP sensors with three probes instead of two.
The modified TDP consisted of one central heating and two
unheated reference probes. The heating probe was installed
at the mid-point of the rhizome between the culms, and the
two reference probes were installed at 5 cm distance from the
heated probe, one on each side (Figure 1C and Appendix
Figure S1B). The temperature differences between each reference
probe and the heating probe were recorded, stored and used to
calculate rhizome $J_s$ in the same way as described above
for the “standard” TDP sensors. The directions of sap flow
in rhizome were determined by comparing the two derived
voltage signals, and the reference probe with the lower signal
value was assigned the downstream position of sap flow. This
was based on the assumption that sap flow brought the heat
energy to the downstream sensor and that this heat would
increase the temperature of the downstream sensor and thus
a smaller temperature difference between the heating and the
downstream reference probe than that between the heating and
the upstream reference probe. In this case, the signal value
from the downstream sensor was smaller than that from the
upstream sensor. To test this assumption, we simulated the
heat field around the heating and the two reference sensors
under different sap flow densities with the ANSYS model (CFX
17.0, ANSYS Inc., Pennsylvania, United States; Mei et al., 2017),
and the simulated results confirmed our initial assumption
(Appendix Figures S2–S4).
Within 600 meters of the *B. vulgaris* site, we set up a micrometeorological station. A pyranometer (CS300, Campbell Scientific Inc., United States) was installed to measure radiation. The data was stored on a CR1000 data logger with the same recording intervals as described for the TDP measurements.

**Cutting Experiment**

Additionally to directly monitoring the water transfer via rhizome with modified TDP, a cutting experiment was implemented to explore the influence of established culms on the water status of freshly sprouted culms. Two clumps of *G. apus* in a bamboo garden were selected, one for the cutting experiment and the other as a control. Both clumps had a similar density of culms (∼18 culms m$^{-2}$). All established culms in the cutting experiment clump were removed, so that only freshly sprouted culms remained. In the control clump, no culms were cut.

From 29 Dec 2012 to 10 Feb 2013, $J_s$ of five freshly sprouted culms in the cutting experiment clump was monitored by TDP as described in section 2.2. The culms had a height of around 2 m at the beginning of the experiment and had no leaves. The monitoring stopped after about 40 days, when the culms were collapsing. Until then, the culms had reached approx. 5 – 8 m in height without any leaf development. In the control clump, we monitored $J_s$ of five established culms but not freshly sprouted ones. To estimate the $J_s$ of freshly sprouted culms in the *G. apus* control clump, we used an indirect assessment involving a nearby long-term monitoring *B. vulgaris* clump. There, we measured $J_s$ of both established and freshly sprouted culms. We found a significant linear relationship (slope = 0.63, with no intercept) between $J_s$ of established culms in the *B. vulgaris* and *G. apus* control clumps ($R^2 = 0.9; P < 0.01$; Appendix Figure S5). We assume that the freshly sprouted culms of the two species have the same relationship as established culms and estimated $J_s$ of freshly sprouted culms in the control *G. apus* clump by multiplying the observed values of freshly sprouted *B. vulgaris* by 0.63 (Appendix Figure S5).

**Statistics**

To compare the patterns of $J_s$ among the rhizome, established and freshly sprouted culms, we normalized the half-hourly $J_s$ of each day (by fitting them to a range from 0 to 1) and plotted average hourly values of six sunny days (Figure 2). To further explore the relative change between established and freshly sprouted culms, we further plotted the normalized $J_s$ values of newly sprouted culms directly versus the normalized $J_s$ of established culms (Figure 3).

To explore the contribution of nighttime to whole-day sap flow, we calculated the ratio between nighttime (18:00 to 6:00 in next morning) and whole-day accumulated sap flow (24 h) of established and freshly sprouted culms and of the rhizomes connecting them (Figure 4). To compare the patterns of $J_s$ between the cutting and control freshly sprouted culms in the cutting experiment, we averaged...
half-hourly $J_s$ of 5 culms in each clump, and normalized the pooled data of both clumps by selecting one common hourly maximum (set to one) and minimum (set to zero) within three consecutive days of measurements (Figure 5).

All data analyses and plotting were performed with SAS 9.4 (SAS Institute Inc., Cary, NC, United States).

**RESULTS**

**Diurnal Patterns of Sap Flux Densities in Culms and Rhizome**

In established culms, sap flux density ($J_s$) showed a typical diurnal pattern corresponding approximately to the diurnal patterns of radiation. With rising radiation in the morning, $J_s$ started to increase until reaching its peak values at around midday, gradually decreased in the afternoon and remained close to zero during the night (Figure 2).

In freshly sprouted culms, $J_s$ switched from a day-night reversal mode through a transition mode to a similar diurnal pattern as that of established culms over the leafless, leafing, and well-leaved periods, respectively. In the leafless period, nighttime sap flux dominated. $J_s$ increased from near zero at sunset time to its peak around sunrise. The nighttime-dominated pattern switched gradually to the normal daytime-dominated pattern after leaves developed. In the well-leaved period, 3 months after sprouting, maximum $J_s$ was higher during the daytime than during the nighttime (Figure 2).

![FIGURE 2](image-url)
In rhizomes, there was substantial $J_s$ at night during times of high $J_s$ in freshly sprouted culms in the leafless period. During the daytime, the $J_s$ in rhizomes differed among the three culm pairs (Figure 2A), which may be attributed to different culm elongation stages. Once the leaves of young culms were well established (Figure 2B), $J_s$ patterns were more synchronized in rhizomes, established and young bamboo culms, usually with peaks between 9 am and midday. Based on observed temperature differences as measured with modified TDPs (Appendix Figure S2) and results from simulations (Appendix Figures S3, S4), we infer that the net sap flow in rhizomes was mainly from the established culms to the freshly sprouted culms in both the leafless and the well-leaved observation period. However, we cannot exclude the possibility of coexisting bidirectional sap flow in rhizomes.

**Comparison Between Freshly Sprouted Culms and Established Culms**

During the leafless period of freshly sprouted culms, they had near maximum rates of normalized hourly sap flux ($J_{s,max}$) from about 10 pm to 6 am, when $J_s$ of established culms was near its minimum (<10% of $J_{s,max}$) (Figure 3A). Sap flux in leafless young culms sharply decreased as soon as sap flux in established culms increased in the morning. $J_{s,max}$ in established culms coincided with near minimum values in freshly sprouted culms (9 am to 12 pm). $J_s$ in freshly sprouted culms increased back to 25% of its daily maximum as soon as $J_s$ in established culms dropped below 20% of $J_{s,max}$ (around 4 pm).

In freshly sprouted culms in the transition period (leafing), $J_{s,max}$ was also observed in the early morning hours, but the subsequent decline in $J_s$ was much slower; $J_s$ was still around 70% of $J_{s,max}$ at noon, when $J_s$ in established culms was at its highest (Figure 3B). Over the afternoon hours (12 to 6 pm), $J_s$ in leafing young culms declined to near zero. It subsequently gradually increased until the early morning hour maximum; during this time, $J_s$ of established culms remained below 10% of $J_{s,max}$.

In well-leaved freshly sprouted culms, substantial $J_s$ as well as $J_{s,max}$ were observed between 5 am and noon, thus coinciding with $J_{s,max}$ in established culms. In the afternoon, $J_s$ in the young culms gradually drops to near minimum (around 6 pm). However, in contrast to established culms (with marginal $J_s$ between 6 pm and 6 am), $J_s$ in well-leaved freshly sprouted culms starts to slowly and consistently rise again after sunset, reaching about 60% of $J_{s,max}$ until sunrise (Figure 3C).

**Contribution of Nighttime to Whole-Day Sap Flow**

Over the leafless, leafing, and well-leaved periods of newly sprouted culms, nighttime accumulated $J_s$ of neighboring established culms remained at 8 ± 1% of whole-day accumulated $J_s$ (Figure 4). In contrast, the contribution of nighttime to whole-day accumulated $J_s$ of freshly sprouted culms decreased from 69 ± 3% to 52 ± 6% to 35 ± 6% over the three periods (Figure 4). Nighttime accumulated $J_s$ in rhizomes accounted for 49 ± 5%, 32 ± 4%, and 23 ± 6% of whole-day accumulated $J_s$ over the three periods (Figure 4). Even though the nighttime contributions of rhizomes were thus consistently smaller than for freshly sprouted culms, they showed a similar decreasing trend over the three periods (Figure 4).

**Influence of Cutting Established Culms on Freshly Sprouted Culms**

After removing all established culms in a $G. apus$ clump, daily sap flux of freshly sprouted leafless culms was estimated to be 79% lower than the corresponding values of a $G. apus$ clump where established culms had not been removed (Figure 5); the latter was assessed indirectly by applying the ratio of 0.63 between $J_s$ of $G. apus$ and $B. vulgaris$ (Appendix Figure S5). Taking into account uncertainties in the ratio (range: 0.55 to 0.84), the corresponding relative difference of $J_s$ between cutting and control clump is between 76 and 84%.
DISCUSSION

It is generally accepted that micrometeorological factors such as solar radiation and vapor pressure deficit are the main drivers of day-to-day fluctuations in tree water use and that limited soil water availability can constrain tree water use (O’brien et al., 2004; Kume et al., 2007). However, water use patterns may vary under special circumstances, e.g., in freshly sprouted leafless bamboo culms. In our study, we found that diurnal \( J_s \) patterns in freshly sprouted bamboo culms changed from the leafless to the well-leaved period (Figures 2, 3). During the leafless period, diurnal \( J_s \) patterns in freshly sprouted bamboo culms typically differed from patterns in neighboring established culms, i.e., freshly sprouted culms had high sap flux during the night and low sap flux during the daytime. The nighttime maxima imply that the \( J_s \) pattern of freshly sprouted bamboo culms are not always controlled by the classic micrometeorological drivers, particularly during the early growing stages when culms are still without leaves and branches. The neighboring established culms most likely play an important supportive role for the freshly sprouted culms (Fraser et al., 2006; Liese and Köhl, 2015). As such, when all the established culms in a \( G. \) apus clump in our study were cut, \( J_s \) in neighboring, newly sprouted culms was reduced by 79% (Figure 5).

Tentatively applying the available adjusted \( J_s \) formula as specified for established bamboo culms (Mei et al., 2016) to the rhizomes and freshly sprouted culms in our study suggests that during the first 4 months after emerging, 48% of the daily sap flow of freshly sprouted culms was provided by established culms via the rhizomes (Appendix Figure S6). It may well be that freshly sprouted culms not only receive water from the nearest directly connected established culm, but from several sources interconnected via the underground rhizome network. Generally, the dependency of freshly sprouted culms on established culms may vary with their distances to established culms; as such, a previous study on water transfer between poplar ramets found that ramets benefited more from proximal root connection than from distal ones (Adonsou et al., 2016). The current elongation stage of a given newly sprouted culm may further impact its dependency on established culms.

![Graph showing daily contribution (%) of nighttime to whole-day sap flow in freshly sprouted culms, established culms and the connecting rhizomes of three culm pairs of \( B. \) vulgaris in the first months after sprouting. The gray area indicates the leafing period of freshly sprouted culms, i.e., the transition phase from a leafless to a well-leaved state.](image-url)
neighbors and thus the patterns and amounts of water it receives from donor culms.

Despite some previous indications of water transfer via rhizomes in bamboos (Dierick et al., 2010; Zhao et al., 2016), the mechanisms remain unclear. As such, the possible trade-offs between daytime sap flow of established culms and nighttime sap flow of freshly sprouted culms as well as the driving forces leading to the water transfer from the established donor culms to meet the water demand of the dependent freshly sprouted culms yet remain to be studied. Our results indicate that water supply from established donor culms to leafless freshly sprouted culms was reduced during the daytime, when the transpiration demand of established culms was high (more than 90% of whole-day transpiration; Figures 2, 3). In contrast, water transfer to leafless freshly sprouted culms was high during the nighttime, when transpiration of established culms is marginal. Such sap flow patterns indicate competition for water within bamboo clumps, particularly during the phenological period of bamboo sprouting.

According to the source-sink theory, resource translocation among connected herbaceous plants depends on resource availability; the resource is transferred from resource-abundant regions (source) to resource-scarce regions (sink; Marshall, 1996). The theory could explain the opposite water use patterns observed for freshly sprouted and established bamboo culms in our study. The established bamboo culms transpired a lot of water during the daytime, probably also retrieving water stored in the culms (Yang et al., 2015; Mei et al., 2016). During the nighttime, along with the largely reduced transpiration and the refilling of the culm water storage via root pressure mechanisms (Cao et al., 2012; Yang et al., 2015), water demand in established culms is largely reduced, while demand for water in freshly sprouted culms become relatively higher than in the established culms. Such resource allocation relies largely on resource availability of the donor individuals, which can be simulated with models (Caraco and Kelly, 1991) and which has previously been observed for several tree species (Fraser et al., 2006; Baret and DesRochers, 2011; Adonsou et al., 2016) and herbaceous species (Alpert and Mooney, 1986; Lau and Young, 1988; Chapman et al., 1992; Kroon et al., 1996; Stueffer et al., 1996; Wang Z. et al., 2011; Zhang et al., 2012). The dependency of freshly sprouted culms on established culms was largely relieved after they had fully developed leaves (Figures 2B,C). However, some water transfer among the young culms and the interconnected established culms continued for several weeks after leaf flushing. Substantial resource translocation could potentially be reactivated at a later time, e.g., in case of resource stress of individual culms (Marshall, 1996). For example, differences in soil water availability, which have been reported even for small patches, could be balanced via interconnected rhizome networks (Hutchings and Wijesinghe, 1997; Wang Y. et al., 2011; Zhang et al., 2012).

Another finding is that for the first 4 months after emergence, freshly sprouted culms kept active nighttime sap flow regardless of whether they were with or without leaves, contributing 69, 52, and 35% of total daily sap flow over the leafless, leafing and well-leaved periods, respectively (Figure 4). Reduced competitive water uptake from rhizomes by the established culms during the night could be a potential reason, while another could include carbohydrate translocation from the established culms to freshly sprouted culms during the night. It has been observed that non-structural carbohydrates in established culms were largely reduced during the period of sprouting of neighboring shoots, and it was assumed that they had been transferred into the freshly sprouted culms (Song et al., 2016). Carbohydrate transport from the source (usually the leaves) to the sink (e.g., rhizome or freshly sprouted culm) is believed to be driven by hydrostatic pressure gradients in the phloem (Münch, 1930). In the carbohydrate transport process, the phloem has to withdraw water from the surrounding tissues (usually the xylem), which usually equilibrates the water potential between the phloem and the surrounding tissues (Thompson and Holbrook, 2003; Hölttä et al., 2006). However, drawing water from the xylem is more difficult when the water potential in the xylem is more negative; carbohydrate transport in the phloem thus likely occurs during the nighttime, when xylem water potential is less negative (Hölttä et al., 2009; Savage et al., 2015). Without substantial transpiration demand and with the water storage refilling via

![Figure 5](Slide05.png)

**Figure 5** | Normalized sap flux densities \( J_s \) in freshly sprouted culms of *G. apus* in cutting (dashed lines) and control clumps (solid line). In the cutting experiment clump, all established culms were removed, leaving only freshly sprouted culms. Due to missing measured data, we estimated \( J_s \) of freshly sprouted *G. apus* culms in the control clump by multiplying \( J_s \) of freshly sprouted *B. vulgaris* culms in a nearby clump by a ratio of 0.63 (see section “Materials and Methods” and Appendix Figure S5). Averaged data from 3 and 5 culms for the control and cutting clump, respectively, normalized by setting the hourly maximum and minimum of both datasets to one and zero. Lines represent means and error corridors around the lines indicate standard deviations.
root pressure mechanisms, the less negative water potential in established culms during the night further promotes the phloem to draw water and transport carbohydrates to freshly sprouted culms. However, the underlying mechanisms for water movement from established culms to freshly sprouted culms as well as its relationship with carbohydrate translocation remain unclear and will need to be addressed in future studies.

CONCLUSION

In the period of sprouting, young bamboo culms receive water resources from neighboring established culms via the underground rhizome network. The freshly sprouted culms show a high share of nighttime water fluxes. This resource support may facilitate the very fast growth of the bamboo shoots, and enable the colonizing of new places.

DATA AVAILABILITY

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

DF contributed to the experimental design, field installations, data analysis, and wrote and revised the manuscript. Particularly, DF conducted all the data analysis and figure-making, and wrote the preliminary draft of the manuscript. TM contributed to the experimental design, field installations, and revision for the manuscript. AR contributed to the field installations and revision for the manuscript. DH contributed to the experimental design and revision for the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpls.2019.00786/full#supplementary-material
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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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