Insignificant effects of culm age on transpiration in a managed Moso bamboo forest, Kyoto, Japan

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Abstract:

The expansion of Moso bamboo forests in Japan might change transpiration and therefore reduce the availability of water resources. Moso bamboo stands are often composed of culms with various ages and older culms may have lower sap flux density (F_d), which may in turn affect individual culm transpiration (Q_t), probably because vascular bundles do not regenerate after sprouting. Information related to the differences of F_d and Q_t between younger and older culms would be important for (i) understanding the effects of culm age structure changes on stand-scale transpiration (E_c), and (ii) developing sampling strategies for E_c estimates in Moso bamboo forests. We conducted sap flux measurements for 15 individuals from four culm age classes in a managed Moso bamboo forest in Kameoka, Kyoto, Japan. Differences in F_d were not significant among the four culm age classes with almost the same stem diameter at breast height (DBH). Q_t was related to DBH across four age classes, indicating that culm age had no apparent effect on Q_t in the forest. Our results suggest the effects of culm age structure changes on E_c are small, and contribute to development of sampling strategy without considering culm age structure for E_c estimates at this site.

KEYWORDS age structure; Moso bamboo; sap flux; water use

INTRODUCTION

More than 70 genera of Bamboo occur naturally in tropical, subtropical and temperate regions around the world, from sea level to 4000 m a.s.l. although they are naturally absent in Europe (e.g., Gratani *et al.*, 2008). Moso bamboo (*Phyllostachys pubescens*) is a useful plant in terms of providing food and materials for humans, and is often planted and cultivated. However, a decline of the bamboo industry has caused many Moso bamboo plantations to be abandoned. Left unmanaged, the fast-growing Moso bamboo forests have been expanding and are replacing surrounding vegetation such as coniferous plantation forests and natural broad-leaved forests in eastern Asia, such as in Japan (e.g., Shinohara *et al.*, 2014), Taiwan (e.g., Chiou *et al.*, 2009) and

mainland China (Song *et al.*, 2011).

Transpiration is one of the major components of the forest water cycle, and therefore affects water yield (e.g., Oishi *et al.*, 2010). Characterizing transpiration of bamboo species is necessary to allow an assessment of the potential effects of the expansion of bamboo species on local water cycles. The sap flux measurement technique is a useful method for investigating stand-scale transpiration especially in mountainous areas with a mosaic of vegetation coverage, because this technique is not limited by complex terrain and spatial heterogeneity (e.g., Wilson *et al.*, 2001). Several studies have examined transpiration in bamboo forests based on sap flux measurements (Dierick *et al.*, 2010; Kume *et al.*, 2010b; Komatsu *et al.*, 2010). Previous studies quantified stand-scale transpiration in Moso bamboo forests in Fukuoka, Japan, indicating greater stand-scale transpiration occurs in Moso bamboo forests when compared with surrounding coniferous forests (Komatsu *et al.*, 2010; Ichihashi *et al.*, 2015). The larger amounts of transpiration observed in the Moso bamboo forests (~100–300 mm yr⁻¹ larger when compared with surrounding forests) may be attributable to larger canopy conductance in Moso bamboo forest compared to other forest types (Komatsu *et al.*, 2012), the strong ability of this species to transport water from the roots to the leaves (Imaji *et al.*, 2013) and the ability of the species to generate high root pressure (Wang *et al.*, 2011; Cao *et al.*, 2012).

Although previous studies have characterized stand-scale transpiration for Moso bamboo, currently no studies have considered the potential effects of culm age structure of a stand (relative composition of older and younger culms) on stand-scale transpiration in Moso bamboo forests.

Firstly, Moso bamboo tends to show a 2-year cycle of new shoot production; a year with new shoots is described as an on-year and a following off-year production cycle (Li *et al.*, 1998). The newly emerged shoots reach the canopy (typically >10 m) within 1 or 2 months (Isagi *et al.*, 1997). In a bamboo stand in China, about one-third of the bamboo culms in a stand were replaced by new culms every 2 years (Li *et al.*, 1998). Thus, inter-annual variations in age structure are significant in bamboo stands. Unlike tree species, established bamboo culms do not show stem diameter growth and renewal of xylem vessels or tracheids after their initial establishment. The aging of a culm without the renewal of vascular bundles might be associated with

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decreasing functionality of the hydraulic transport system caused by cavitation. This could lead to a decrease in leaf stomatal conductance and/or leaf area (e.g., Sperry, 1993; Meinzer *et al.*, 1995; Dierick *et al.*, 2010) and, hence, result in a decrease in the individual culm transpiration rate in older culms. Thus, to understand the potential effects of culm age structure changes on stand-scale transpiration, we need to clarify sap flux and individual culm transpiration in response to the aging of culms.

Secondly, stand transpiration estimates based on sap flux normally use a limited number of samples in a stand. For single species plantations, samples are generally selected based on tree size (i.e., Diameter at Breast Height; DBH), because DBH is a major determinant of the transpiration of trees, and biased sampling with regard to tree sizes could cause a significant error in estimating stand-scale transpiration (Čermák *et al.*, 1995; Kume *et al.*, 2010a). In the case of bamboo, if aging results in decreased individual culm transpiration caused by a dysfunction of the hydraulic system, samples should be selected with consideration of culm age structure as well as culm size distribution in the stand for precise stand transpiration estimates. Thus, clarifying the effects of culm age on the individual culm transpiration rate is necessary for robust transpiration estimates based on sap flux for bamboo stands where culm age structures vary inter-annually.

The objective of this study is 1) to examine the potential effects of age structure changes on interannual variations in stand-scale transpiration, and 2) to examine whether or not samples should be selected with the consideration of culm age structure for stand-scale transpiration estimates, as the first step in obtaining robust transpiration estimates of bamboo stands. We conducted sap flux measurements for a total of 15 individuals that were classified into four age classes in a managed Moso bamboo forest in Kyoto, Japan. Then, we compared the sap flux density and individual culm transpiration among the four age classes.

METHODS

Site characterization

Sap flux measurements were conducted in a Moso bamboo (*P. pubescens*) forest at Kameoka City, Kyoto Prefecture, Japan (34.99°N, 135.61°E, 150 m a.s.l.) from August 29 to October 31, 2014. Annual mean air temperature of 14.6°C and annual mean precipitation of 1452 mm were recorded between 2003 and 2012 at the nearest meteorological observatory in Kameoka, 5 km from the study site. The 1.0 ha bamboo forest of the study site has been producing shoots for over five decades. This forest has clay soil and has been managed as follows: rapeseed meal fertilization (18.0 ton ha⁻¹ yr⁻¹), thinning of older culms (older culms develop a yellow color and have fewer leaves), removal of bamboo shoot heads before some bamboo shoots have completely sprouted to keep the vegetation height low, and covering soil surface with a soil dressing annually to efficiently locate new early stage bamboo shoots (Ueda, 1963).

Air temperature, relative humidity (RSW-20S, ESPEC MIC Corp., Aichi, Japan) and rainfall (K5606QG, Yokogawa Denshikiki Co., Ltd., Tokyo, Japan) measurements were conducted at an open area in the study site every 10 minutes.

Mean volumetric soil water content at the depth of 0–30 cm was measured at the study plot at 30 minute intervals using a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA) with three 30-cm long time domain reflectometers (CS650, Campbell Scientific Inc.). Solar radiation (CMP11, Kipp & Zonen, Delft, The Netherlands) was recorded on average every 30 min on the flat roof of a building at Kyoto University, 25 km from the study site.

Stand structure measurements

The 100 m² (10 × 10 m) plot was established in a flat area of the study site. The mean bamboo height, mean culm DBH and the bamboo density of the plot were approximately 7.1 m, 7.5 cm and 6800 culms ha⁻¹, respectively. Mean leaf area index of 3.7 m² m⁻² was measured using a plant canopy analyzer (LAI-2000, Li-Cor Inc., Lincoln, NE, USA) at the plot on December 9, 2014. To identify culm age, bamboo shoots grown in 2014 (1 yr) and 2013 (2 yr) were marked with paint on the culm surfaces. Excluding the bamboo culms that appeared in 2013 and 2014, the age of bamboo culms appearing before 2012 were separated into younger (> 3 yr_y) or older (> 3 yr_o) classes based on the white wax line at the bamboo nodes. In this study, bamboo culms with and without white wax lines on the node were categorized as belonging to the younger and older age classes, respectively, because the white wax line disappears based on culm age (Shinohara *et al.*, 2013).

Sap flux measurements

Sap flux density per unit cross sectional area of culm (F_d ; cm³ m⁻² s⁻¹) was measured using the thermal dissipation method with Granier-type sensors (Granier, 1987). The pair of probes was inserted into the stem, about 15 cm apart, in a vertical direction. Constant heat was supplied to the upper probe, while the lower probe recorded the stem temperature. The heat was dissipated into the xylem, and gave an estimate of the vertical sap flux surrounding the probes. For bamboo, we used 10-mm long and 2-mm diameter probes with a 0.15 W constant power supply to the upper probes based on Kume *et al.* (2010a) and Ichihashi *et al.* (2015). A sensor was inserted into each culm at breast height (approximately 1.3 m). All sensors were installed facing north on the culms and were fully insulated to avoid solar radiation and penetration by rain water. The temperature differences were scanned every 30 s and recorded on average every 30 min using a data logger (CR1000) with a peripheral multiplexer (AM16/32, Campbell Scientific Inc.). The temperature difference was converted to F_d as described by Granier (1987) with a modified empirical constant proposed by Onozawa *et al.* (2009) and Kume *et al.* (2010a). Mean air temperature, vapor pressure deficit (VPD), and volumetric soil water content during the study period were 17.4°C, 0.51 kPa and 0.27 m³ m⁻³, respectively.

Individual culm transpiration (Q_c ; cm³ s⁻¹) was calculated from multiplying the F_d by the cross sectional area of culm (A_{s_b} ; cm²). For A_{s_b} estimates, the culm thickness was measured for all sample bamboo by drilling a 2.5 mm diameter hole at breast height prior to the sap flow measurements, and the measurements were taken as the mean of two orthogonal measurements. A_{s_b} was calculated from the DBH and the culm thickness. We assumed that the culm cross-sections were circular.

Table I. Data summary of samples used for sap flux measurement

Culm age class	Mean DBH* (cm)	Mean tree height (m)	Mean culm sectional area (cm ²)
1 yr (<i>n</i> = 4)**	8.7 (1.1)***	7.1 (1.9)	23.2 (4.7)
2 yr (<i>n</i> = 4)	8.2 (1.4)	7.5 (1.6)	20.3 (4.9)
>3 yr_y (<i>n</i> = 4)	8.9 (1.8)	8.3 (1.0)	24.0 (6.9)
>3 yr_o (<i>n</i> = 3)	8.4 (1.4)	7.4 (2.1)	22.0 (5.1)

* Diameter at breast height; ** Number of bamboo for sap flux measurement; *** A numeral in the parenthesis indicates the standard deviation.

To characterize the response of daily mean F_d to daily mean VPD , the exponential saturation was used (e.g., Ewers *et al.*, 2008):

$$F_d = a(1 - e^{-bVPD}) \quad (1)$$

where a is the saturation parameter and b is the curvature (response) parameter. Nonlinear fits were performed using the Levenberg-Marquardt method (Fujita *et al.*, 1994) in KaleidaGraph (version 4.1.1, Synergy Software, Reading, PA, USA). The differences in the curvature parameter b among four age classes were tested with one-way analysis of variances.

The period mean daily F_d and Q_t were obtained by the following procedures. 30-min data of F_d and Q_t were first averaged and summed during 24 hours, respectively. The daily data was then averaged over the study period.

We selected three to four bamboos from each culm age class for sap flux measurement. Four samples of bamboos were selected from each culm age class of 1 yr, 2 yr, and >3 yr_y, and three samples of bamboos were selected from culm age class of >3 yr_o (Table I). Samples of bamboos were evenly selected across various DBH ranges in each age class.

RESULTS

Stand structure

DBH ranged from 5.1 cm to 11.3 cm (mean 7.5 cm; mode 8.6 cm; Figure 1a). Numbers of culms for 2 yr (*n* = 25) were largest in the four age classes, and were comparable with those for >3 yr_y (*n* = 20) and >3 yr_o (*n* = 17). Numbers of culms for 1 yr (*n* = 6) were the smallest in the four age classes (Figure 1a).

Mean DBH was not significantly different among four age classes (Figure 1b; $p = 0.26$). Culm thickness ranged from 0.8 to 1.1 cm (mean 0.9 cm), which was moderately related to DBH ($R = 0.68$, $p < 0.001$). Basal area and total cross-sectional area of culm walls were 31.1 and 12.6 m² ha⁻¹, respectively.

Diurnal and day-to-day variations in sap flux

Figure 2 shows the diurnal courses of mean F_d for three or four individuals for each of four age classes, R_s , and VPD on given days without rain. The peaks of the diurnal patterns of F_d occurred at noon, and the peaks of the F_d have considerable variations within and among age classes. In the cross-correlation analysis, the diurnal variations in mean F_d for each age class showed maximum correlation with VPD

Figure 1. (a) Frequency distributions of stem diameter at breast height (DBH) with respect to each culm age class; 1 year old (1 yr), 2 years old (2 yr), more than 3 years with relatively younger (>3 yr_y), and older (>3 yr_o) culms, (b) Mean DBH and standard deviation among the four culm age classes analyzed here

after a time lag of 1.0 h ($R = 0.84$ – 0.85) and with R_s after a time lag of 0.5–1.0 h ($R = 0.83$ – 0.85). No clear differences in the time lag among four age classes were observed.

Figure 3 shows the relationship between daily mean VPD and daily mean F_d of each individual for the four age classes. The F_d was correlated to VPD for all individuals ($R = 0.60$ – 0.84). The differences in the responses of F_d to VPD among the four age classes were not significant (Supplement Table SII; $p = 0.53$). An apparent decline of F_d at the higher range of VPD for older age classes was not observed.

Effects of culm age on relationship between DBH and individual culm transpiration

Period mean daily F_d measured at each individual ranged from 4.5 to 25.1 cm³ m⁻² s⁻¹ (Figure 4). F_d was weakly and

Figure 2. Diurnal variations in (a) vapor pressure deficit (VPD ; thick line), solar radiation (R_s ; thin line) and sap flux density (F_d) of four different age classes; (b) 1 year old (1 yr), (c) 2 years old (2 yr), (d) more than 3 years with relatively younger age (> 3 yr_y), and (e) more than 3 years with relatively older age (> 3 yr_o). The number of culms for sap flux measurements was also shown in (b)–(e). Vertical bars represent standard error

insignificantly related to DBH (Figure 4b; $R = 0.44$, $p < 0.1$). No significant difference of F_d among four age classes was observed ($p = 0.66$).

Period mean daily Q_t measured at each individual ranged from 0.74 to 5.5 $kg d^{-1}$. Q_t was correlated to DBH across four age class (Figure 4c; $R = 0.74$, $p < 0.001$) because of a strong positive correlation between DBH and A_{s_b} (Figure 4a; $A_{s_b} = 3.7503DBH - 9.6601$, $R = 0.98$). The difference in period mean daily Q_t among four age classes was also not significant ($p = 0.85$).

DISCUSSION AND CONCLUSIONS

The lack of a renewal of vascular bundles may cause older culms to have a lower F_d because of the decline in hydraulic conductance of the soil–leaf pathway. Normally, the highest rates of water transport are mostly found in the youngest and

Figure 3. Relationship between daily mean vapor pressure deficit (VPD) and daily mean sap flux density (F_d) for four different aged culm classes; (a) 1 year old (1 yr), (b) 2 years old (2 yr), (c) more than 3 years with relatively younger (> 3 yr_y), and (d) older (> 3 yr_o) culms. Numeral of each legend indicates diameter at breast height. Parameters of the curve fits are listed in Supplement Table SI

outermost vessels in tree species (e.g., Tateishi *et al.*, 2008; Tsuruta *et al.*, 2010; Umebayashi *et al.*, 2010; Kume *et al.*, 2012). On the other hand, in this study, F_d and its response to VPD did not show apparent differences among culm age classes (Figure 3 and 4b). Also, time lags between VPD , R_s , and F_d among the culm age classes did not show clear differences, and were comparable with a previous study (Kume *et al.*, 2010a). Variations in Q_t were almost explained by variations in DBH (Figure 4c). These results suggest that culm age may not affect F_d and Q_t in the Moso bamboo forest.

Figure 4. Relationship between diameter at breast height (DBH) and (a) cross sectional area of a culm ($A_{s,b}$), (b) sap flux density (F_d), and (c) whole-bamboo transpiration (Q_t) for four different aged culm classes; 1 year old (1 yr), 2 years old (2 yr), more than 3 years with relatively younger (>3 yr_y), and older (>3 yr_o) ages. Black lines in (a) and (c) represent regression equations derived across the four aged culm classes ($A_{s,b} = 3.7503\text{DBH} - 9.6601$; $R = 0.98$, $Q_t = 993.0\text{DBH} - 5431.4$; $R = 0.74$, respectively)

Forest management practices at the study site may have an influence on our results. The study site is managed using local management practices (Ueda, 1963) including near-annual thinning of relatively old bamboo culms that turned yellow and had lost many leaves. It is still possible that much older bamboos than were analyzed in the present study may show a decline in F_d when compared with younger culms. Indeed, Moso bamboo culms sometimes live longer than 10 years (Isagi *et al.*, 1997). Root pressure could be another possible reason for insignificant effects of culm age. Cao *et al.* (2012) reported high levels of root pressure in giant bamboo species, suggesting that hydraulic dysfunction in Moso bamboo might be moderated through the creation of root pressure caused by the refilling of cavitated conduits with a positive root pressure induced by sap.

Several studies have reported that Q_t was correlated with DBH for many tree species (e.g., Čermák *et al.*, 2004; Tsuruta *et al.*, 2008; Takagi, 2013) as found in this research (Figure 4). The daily amount of Q_t in a 90-year-old Japanese cypress forest ranged from approximately 7.0 to 13.0 kg d⁻¹ with DBH ranging from 25.0 to 35.0 cm (Takagi, 2013). Tsuruta *et al.* (2008) also reported the daily amount of Q_t in a 23-year-old Japanese cypress forest, showing that Q_t ranged from 4.1 to 9.0 kg d⁻¹ with DBH ranging from 8.4 to 12.6 cm. The daily amount of Q_t of bamboos for this study with DBH ranging from 7.0 to 11.3 cm (Figure 3c; 0.74–5.5 kg d⁻¹) was comparable with that of the 23-year-old Japanese cypress forest.

Previous studies reporting larger stand-scale transpiration in Moso bamboo forests than that of the surrounding coniferous forests (Komatsu *et al.*, 2010; Ichihashi *et al.*, 2015) have not considered the effects of culm age on transpiration. This could lead to the following two problems. 1) Uncertainty of stand-scale transpiration estimates of Moso bamboo forests caused by a failure to consider variabilities in stand-scale transpiration; this variation is probably caused by significant interannual variations of age structure in Moso bamboo forests (Li *et al.*, 1998), and 2) inaccurate sap flux-based stand-scale transpiration estimates based on sampling without consideration of culm age structure (i.e., biased sampling). Our results suggest that interannual variations in stand-scale transpiration caused by culm age structure changes are small, in addition, samples can be selected without consideration of culm age structure for sap flux measurements at this site.

Ichihashi *et al.* (2015) reported that the mean stand F_d averaged over all sample culms in a dense unmanaged Moso bamboo forest was smaller than that of a recently thinned Moso bamboo forest in Fukuoka, Japan (Supplement Table SII). Canopy stand transpiration as the multiple of mean stand F_d and stand sapwood area was similar between the unmanaged and thinned Moso bamboo forests despite a much higher culm density in the unmanaged bamboo forest. The unmanaged bamboo forest probably has a higher proportion of older culms because no thinning had been conducted when compared with a managed bamboo forest. Therefore, it is still possible that old culms might have a low F_d in the unmanaged bamboo forest.

In addition, increased Q_t in the managed (thinned) bamboo forest compared with that of the unmanaged (un-thinned) forest at a given DBH might be another reason for the comparable stand-scale transpiration between the unmanaged and managed Moso bamboo forests. Previous studies in tree species reported increases of F_d after thinning that were probably caused by high sunlight exposure of individual crowns in a thinned forest (Morikawa *et al.*, 1986; Sun *et al.*, 2014).

We found almost the same F_d among the four age classes at the given DBH in the managed Moso Bamboo forest in Kyoto in the present study. This result contributes to robustness of random sampling for long-term sap flux-based stand-scale transpiration estimates. However, future studies will still need additional sap flux measurements on older culms in unmanaged bamboo forests with variations in culm density to accurately characterize stand-scale transpiration in Moso bamboo forests.

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SUPPLEMENTS

Table SI. Parameters for the relationship between daily mean sap flux density (F_d) and daily mean vapor pressure deficit (VPD) for each bamboo (Equation (1); Figure 3)

Table SII. Comparison of sap flux measurements in Moso bamboo stands

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