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Azuma, W.A.
Kosugi, Y.
Tsuruta, K.
Lion, M.

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Time lags between crown and basal sap flows in tropical broadleaf and temperate conifer trees

W.A. Azuma[1,a], Y. Kosugi[2], K. Tsuruta[2], and Marryanna Lion[3]

[1]Graduate School of Agricultural Science, Kobe University, Hyogo, Japan; [2]Graduate School of Agriculture, Kyoto University, Kyoto, Japan; [3]Forest Research Institute Malaysia, Selangor, Malaysia

Abstract

Sap flow transportation from root to leaf in trees is explained by the cohesion of water molecules pulled up by tension due to transpiration. However, in some species, it has been observed that there can be several minutes to hours of time-lag in sap flow between the crown and the base of the stem. This time lag is assumed to be a proxy for the capacity of water storage to supply water for transpiration. To examine whole-tree water use in relation to internal stem water storage, we measured crown and basal sap flow using hand-made Granier sensors in tropical broadleaf and temperate conifer trees. Measurements on tropical broadleaf trees were conducted at the Pasoh Forest Reserve in Peninsular Malaysia with *Dipterocarpus sublamellatus* (height = 45 m, DBH = 69 cm) a dominant emergent tree species, and *Ptychopyxis caput-medusae* (height = 32 m, DBH = 38 cm), a canopy tree adjacent to *D. sublamellatus.* Measurements on temperate conifers were conducted at the Kiryu Experimental Forest in central Japan with *Chamaecyparis obtusa* (height = 20 m, DBH = 20 - 60 cm), an important plantation tree in Japan. In *D. sublamellatus*, very narrow time lags between crown and basal sap flows were observed, suggesting internal stem water storage contributed little to daytime whole-tree water use. In *P. caput-medusae* and *C. obtusa*, basal sap flow started later than crown sap flow in the morning, suggesting partial reliance on internal stem water storage for daytime whole-tree water use. Additionally, basal sap flow continued until midnight, after the crown sap flow had stopped, indicating refilling of internal stem water storage during the night.

Keywords: water relations, water storage, tall tree, rehydration, Dipterocarpaceae, Euphorbiaceae, Cupressaceae

INTORODUCTION

Sap flow transportation from root to leaf in trees is theoretically explained as water molecules linked by the cohesion of water molecules that are pulled up by tension due to transpiration (Tyree and Ewers, 1991). However, in some species, it has been observed that there can be several minutes to hours of time lag in sap flow between the crown and the base of the stem. This time lag is assumed to be a proxy for the capacity of water storage to supply water for transpiration (Meinzer et al., 2004; Phillips et al., 2003). Internal water storage in trees may have an important role in the water economy within trees as an intermediate source of water for foliar transpiration (Meinzer et al. 2001, Scholz et al. 2008). Understanding how various tree species and various forest types use internal water storage can help predict how forest water cycling responds to possible changes in land use and climate.

Here, we measured the crown and basal sap flow using hand-made Granier sensors in tropical broadleaf and temperate conifer tall trees. The time lags between the crown and basal sap flow were estimated using a cross-correlation analysis. This was a pilot study to examine whole-tree water use in relation to internal stem water storage.

MATERIALS AND METHODS

The study was conducted at two sites described below. First, a study with tropical

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[a] E-mail: wakana@port.kobe-u.ac.jp

broadleaf trees was conducted at the Pasoh Forest Reserve (PFR) of the Forest Research Institute Malaysia in Peninsular Malaysia (2°58'N, 102°18'E, 75–150 m a.s.l.) where the annual mean air temperature and precipitation measured from 2003 to 2017 were 25.5 °C and 1872 mm year^{-1}, respectively. The site was covered with a primary lowland mixed dipterocarp forest (tropical evergreen broad-leaved forest), which consisted of various species of *Shorea* and *Dipterocarpus*. We selected two study trees accessible from a 30-m-high triangular canopy walkway; *Dipterocarpus sublamellatus* (height = 45 m, DBH = 69 cm) known as a dominant emergent tree species, and an individual of *Ptychopyxis caput-medusae* (height = 32 m, DBH = 38 cm) that was adjacent to the *D. sublamellatus* tree. Secondly, a study with a temperate conifer was conducted at the Kiryu Experimental Forest (KEW) in central Japan (34°58′N, 136°00′ E, 200–250 m a.s.l.) where the annual mean air temperature and precipitation measured from 2008 to 2017 were 13.5 °C and 1784 mm year^{-1}, respectively. The site was covered with mostly 55-year-old *Chamaecyparis obtusa* (Japanese cypress), with some 100-year-old *C. obtusa* remaining. We selected one 55-year-old *C. obtusa* accessible from a 30-m-high canopy tower (height = 20 m, DBH = 20 cm) and two 100-year-old *C. obtusa* accessible by single rope climbing technique (height = 22 m, DBH = 55 cm) for use in our study.

Sap flux density was measured by the thermal dissipation method with Granier-type sensors (Granier 1987). The sensor consisted of a pair of 20-mm-long and 2 mm in diameter probes. Each probes were inserted into the sapwood approximately 15 cm apart, vertically. The upper probe included a heater which was supplied with a constant 0.2 W of power. The temperature difference between the upper and lower probes was recorded as an average every 10 min and converted to sap flux density (cm^{3} m^{-2} s^{-1}) according to Granier (1987). At the PFR site, the sap flow sensors were inserted at a height of 32 m in a branch and at 1.3 m in the stem of *D. sublamellatus*, and at 30 m in a branch and 1.3 m in the stem of *P. caput-medusae*. We measured the sap flow in September 2016, September 2017, July 2018, December 2018, and July 2019. At the KEW site, the sap flow sensors were installed at a height of 18 m and 1.3 m in the stem of the 55-year-old *C. obtusa*, and at 20 m and 1.3 m in the stem of the 100-year-old *C. obtusa* trees. At the KEW site we measured the sap flow from August 2016 to December 2016 and from August 2018 to July 2019.

To estimate the time lags between the sap flow at the base of the stem and in the canopy branches, we used a cross-correlation analysis (Phillips et al. 1999) with R ver. 3.6.1 (R Development Core Team 2019), which is useful for determining the time delay between two signals. The maximum correlation coefficient indicates the point in time at which the two data sets are best aligned. For cross-correlation analysis, we used a sap flow data set from 2 days to 1 week which was measured on clear days.

As meteorological data at each site, we measured solar radiation (W m^{-2}; MR22, Eko Instruments, Tokyo, Japan at PFR, CMP-6, Kipp & Zonen, Delft, the Netherlands at KEW), temperature (℃; HMP45A, Vaisala, Helsinki, Finland), and vapor pressure deficit (kPa) at 29 m in height from the canopy towers at each site. We also measured rainfall (mm; 34-T, Ota Keiki Seisakusho, Tokyo, Japan) and volumetric soil water content (m^{3} m^{-3}; CS615 or CS616, Campbell Scientific, Logan, UT, USA). All meteorological variables were recorded every 30 min.

RESULTS AND DISCUSSION

Figure 1 shows the meteorological characteristics of the PFR site during our measurements. As the PFR site is located at a lowland tropical forest, temperature was constant and solar radiation had two small peaks each year. A typical monsoonal rainfall can be seen with two major peaks between April and May and between October and December forming a bimodal pattern at this site (Lion et al. 2017). In 2017, rain fall was a little higher than the preceding or following years. Soil volumetric water content corresponded with rain fall.

Figure 2 shows the meteorological characteristics of the KEW site during our measurements. The KEW site is located at a temperate forest, with a clear seasonal change in temperature, solar radiation, and vapor deficit. Rain fall was high in June, July, and September. Soil volumetric water content corresponded with rainfall and vapor deficit, and clearly decreased in mid-late August.

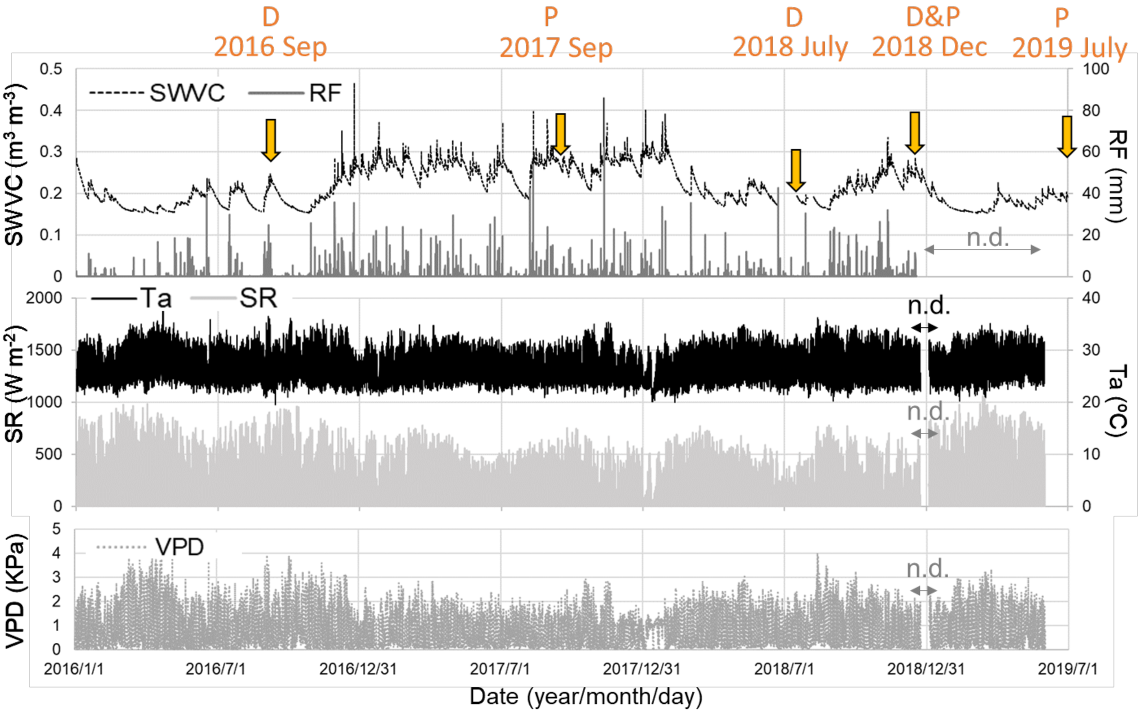


Figure 1. The meteorological characteristics of the PFR site during our measurement. SWVC: soil water volumetric content (m^3 m^{-3}), RF: rain fall (mm), Ta: temperature (℃), SR: solar radiation (W m^{-2}), VPD: vapor pressure deficit (kPa), n.d.: no data

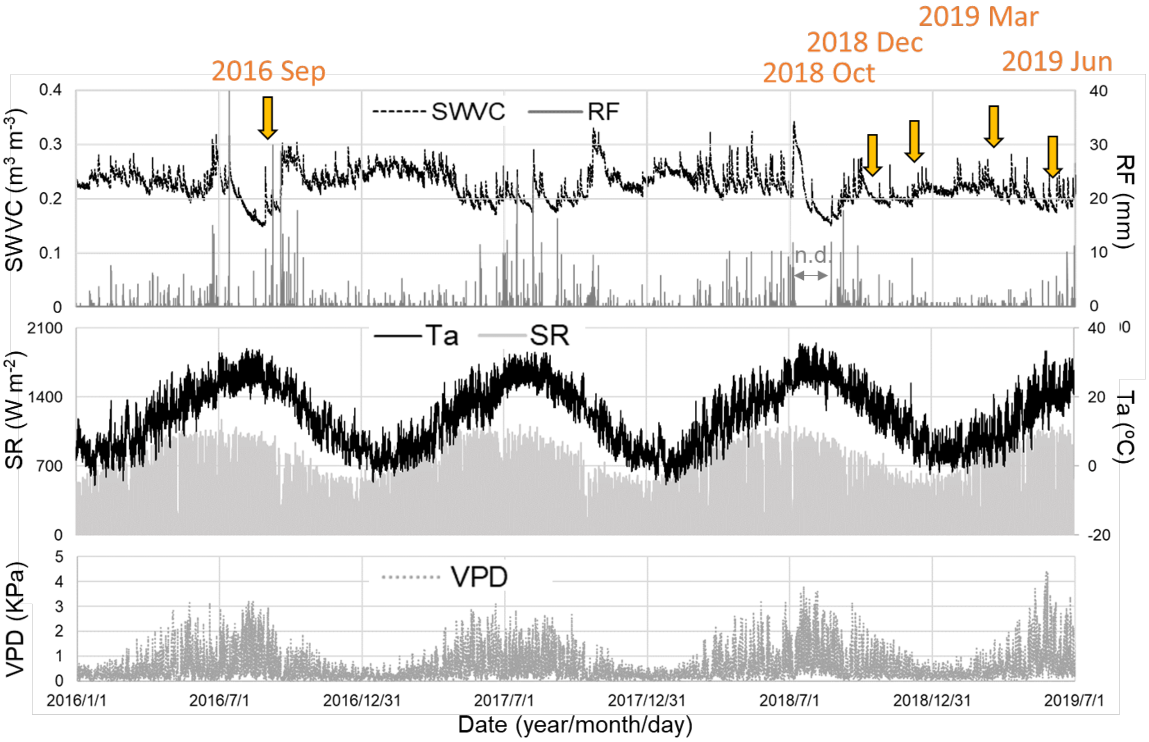


Figure 2. The meteorological characteristics of the KEW site during our measurement. Abbreviation as for Figure 1.

The daily course of sap flux density in *D. sublamellatus* and *P. caput-medusae* at the PFR site is shown in Figure 3, and that of *C. obtusa* at the KEW site is shown in Figure 4. During the course of the day a typical pattern of sap flow was observed, with an increase in the early morning and a decrease in the afternoon.

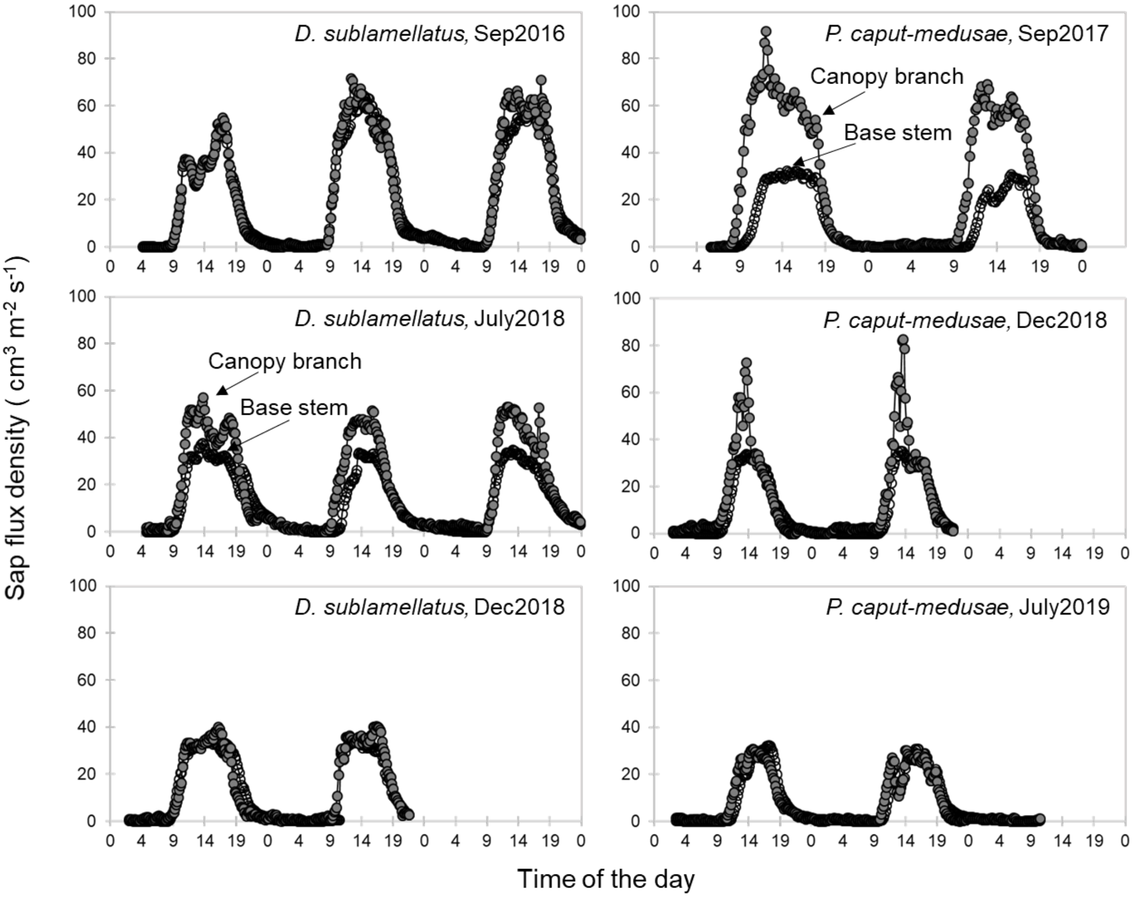


Figure 3. The daily course of crown and basal sap flux density in *D. sublamellatus* and *P. caput-medusae* at the PFR site.

Cross-correlation analysis between the crown and basal sap flux density of *D. sublamellatus* and *P. caput-medusae* at the PFR site showed maximum correlation at a time lag of 0 - 10 min and 20- 50 min, respectively. This means that in *D. sublamellatus*, the sap flow at the crown and stem base are relatively synchronous within the daily time course, while in *P. caput-medusae*, the basal sap flow started later than crown sap flow in the morning when transpiration increased. In both species, basal sap flow continued until midnight after the crown sap flow had stopped. Differences in the time course of basal sap flow and crown sap flow could be explained as a period of discharge and recharge of water from internal stem water storage. Also, a higher hydraulic resistance could cause larger time lags because hydraulic resistance decreases water uptake at a given water potential difference between soil and leaves (Kumagai, 2001). In *D. sublamellatus*, our results suggested that hydraulic resistance along the conductive pathway did not limit water transport and the internal water storage capacity was small. Narrow time lags between canopy transpiration and basal sap flow were also reported in emergent trees in a tropical rainforest in Borneo, Malaysia (Kume et al. 2008). In *P. caput-medusae*, the time lag was a little larger than in *D. sublamellatus*, suggesting partial reliance on internal stem water storage for daytime whole-tree water use. Previous studies conducted in a neo-tropical forest ecosystem reported significant time lags of 40–120 min between transpiration and basal stem sap flow in emergent trees (Goldstein et al., 1998; Phillips et al., 1999). Our results indicate that the daily pattern of internal water use differs among tall tree species, even if they are growing in the same stand.

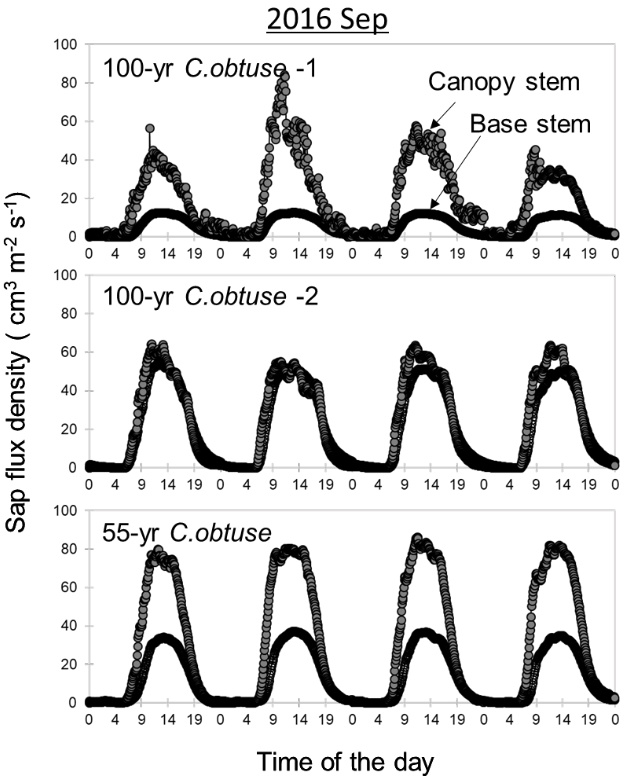
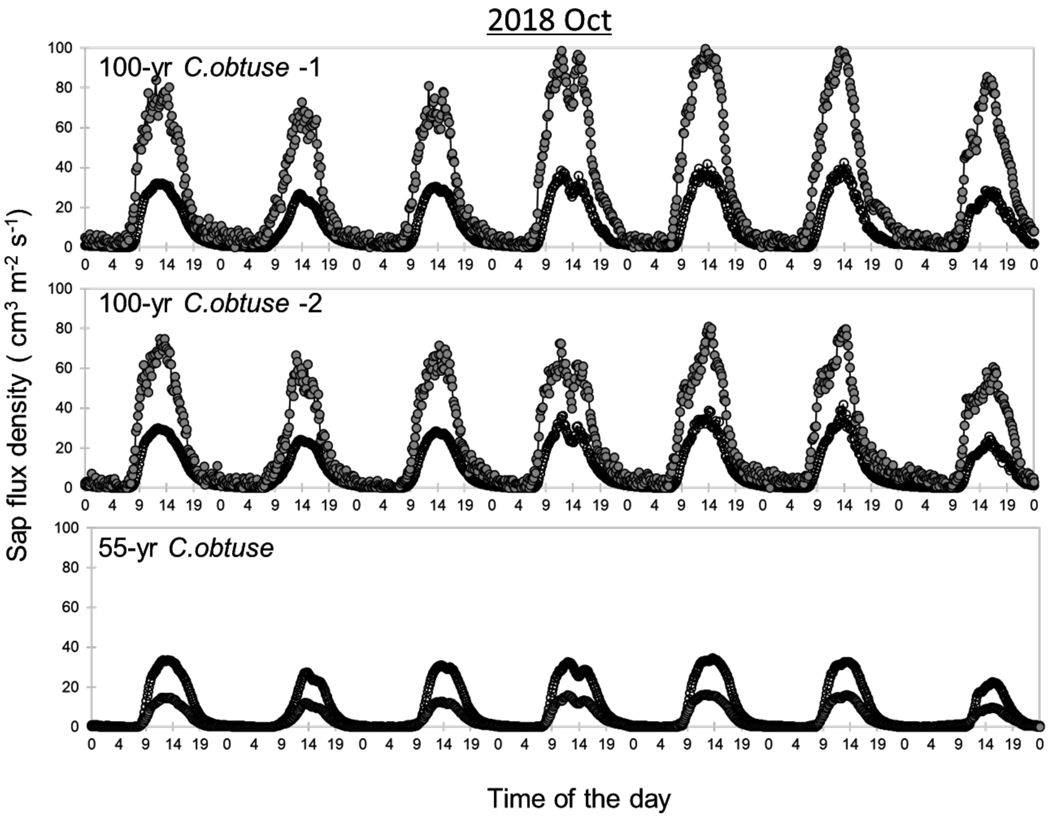
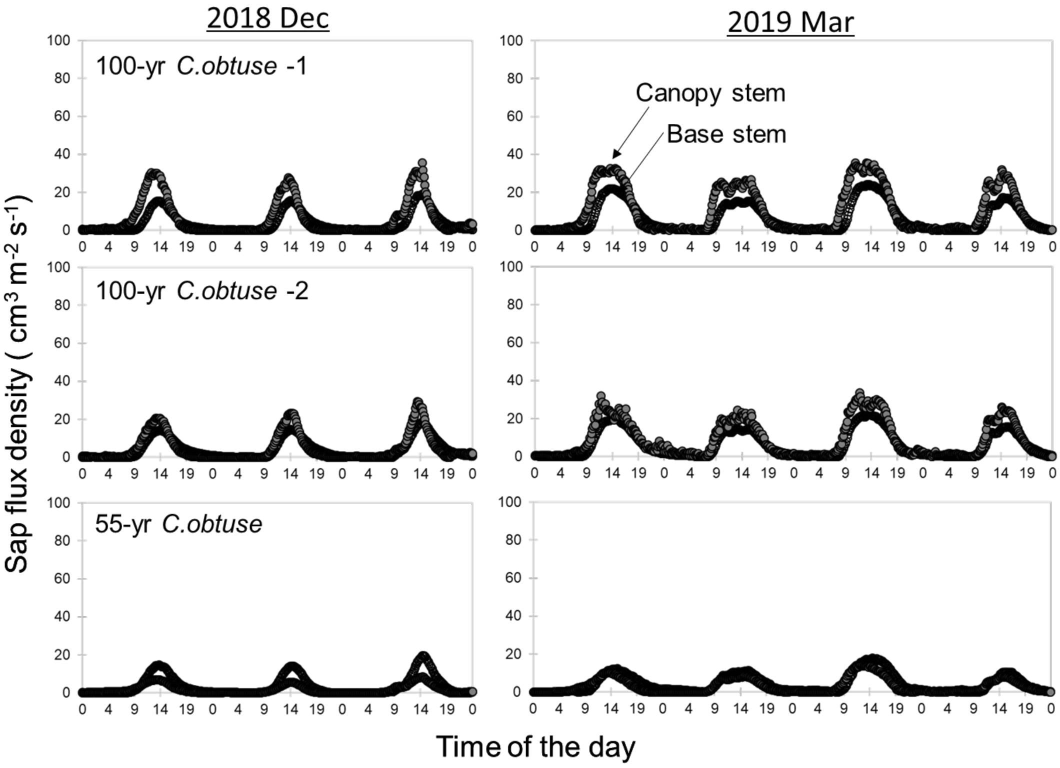


Figure 4a. The daily course of crown and basal sap flux density in 55-yr and 100- yr old of *C. obutusa* at the KEW site.





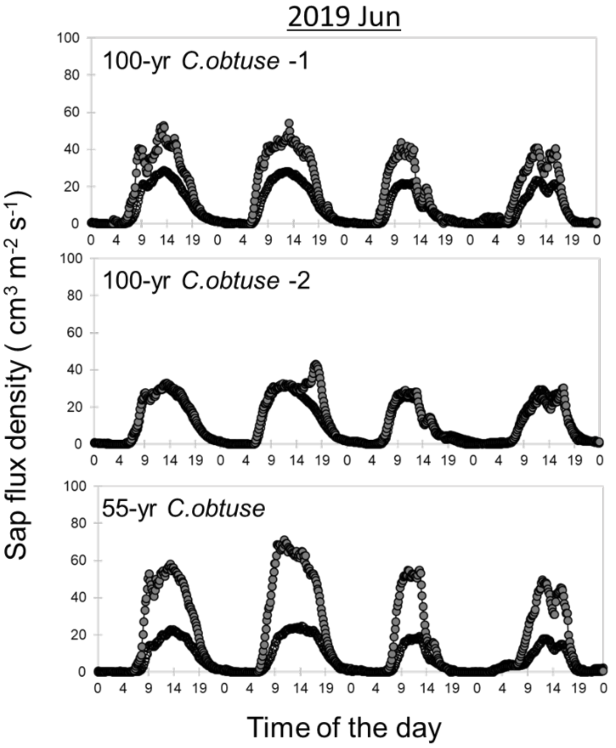


Figure 4b. The daily course of crown and basal sap flux density in 55-yr and 100- yr old of *C. obutusa* at the KEW site.

Cross-correlation analysis for the crown and basal stem sap flux density in the 55-year-old and 100-year-old of *C. obtusa* at the KEW site showed maximum correlation at a time lag of 0 - 60 min and 0- 70 min, respectively. In coniferous forest stands, internal water storage depended on the amount of sapwood and is associated with tree size (Phillips et al., 2003). On the other hand, our results indicated that the time lag was not always dependent on tree size in temperate conifer trees. The results of this study also indicated that hydraulic resistance along the conductive pathway and reliance on internal water storage change seasonally, as show in the time course of these changes among the three study trees (Fig. 5). Some previous studies showed soil water decline could cause larger time lags due to increasing hydraulic resistance (Kumagai, 2001; Sperry and Pockman, 1993). In *C. obtusa*, it was reported that soil drought caused a decline in diurnal and seasonal variations in sap flux density (Tsuruta et al., 2018). In this study, our data set was too small to analyze the relationship between the time lag and meteorological factors. Further continuous measurements would reveal how internal water storage use relates to meteorological conditions.

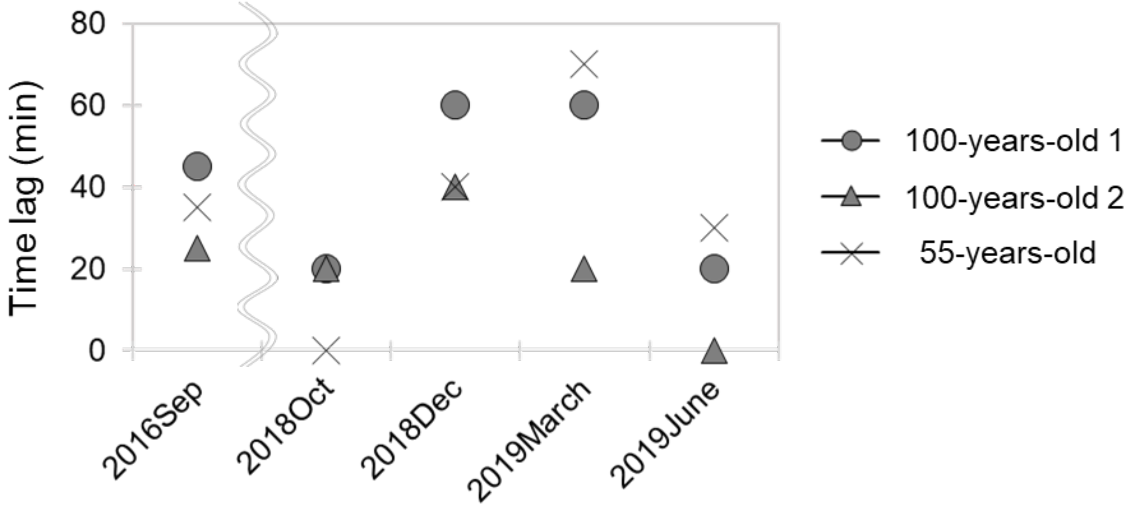


Figure 5. Seasonal variation of time lags (the maximum correlation coefficient) between crown and basal sap flux density in 55-yr and 100- yr old of *C. obutusa* at the KEW site.

CONCLUSIONS

In this study, a very narrow time lags between crown and basal sap flow was observed in *D. sublamellatus*, suggesting internal stem water storage contributed little to daytime whole-tree water use. In *P. caput-medusae* and *C. obtusa*, basal sap flow started later than crown sap flow in the morning, suggesting partial reliance on internal stem water storage for daytime whole-tree water use. Additionally, basal sap flow continued until midnight after the crown sap flow had stopped, indicating refilling of internal stem water storage during the night. However, the use of internal water storage differs seasonally and among species growing in the same stand.

Further long-term monitoring will need to investigate the relationship between use of internal water storage and meteorological factors. From the examination of the time lag pattern in this study, we would like to extend it to quantify the contribution of internal water storage in the daily water balance of trees.

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