


RESEARCH ARTICLE

Differences in seasonality and temperature dependency of stand transpiration and canopy conductance between Japanese cypress (Hinoki) and Japanese cedar (Sugi) in a plantation

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Abstract

In this paper, we present an investigation of interspecies differences in transpiration of the 2 most common plantation forest tree species in Japan, both in the family Cupressaceae with different northern limits of native distribution, Japanese cypress (Hinoki; *Chamaecyparis obtusa* Sieb. et Zucc.) and Japanese cedar (Sugi; *Cryptomeria japonica* D. Don). The stem sap flow rate was measured in 2 nearby stands of similar leaf area index in a 42-year-old plantation. Single-tree and stand-scale transpiration rates (E_{tre} and E_{sta} , respectively) were observed during an ideal autumn environment. At the stand scale, mean sap flux density of Hinoki was greater than that of Sugi, whereas total sapwood area per ground area was smaller in Hinoki than Sugi. Because the 2 variables had counterbalancing effects on transpiration, E_{sta} of Hinoki was similar to (94% of) that of Sugi. This offset was also found between the mean E_{tre} of the 2 species. E_{sta} was similar between the stands from May to October, whereas E_{sta} of Sugi was notably greater than that of Hinoki from February to April. During these 3 months, the difference in cumulative E_{sta} was 21.7 mm, which accounted for 79% of the difference in annual E_{sta} between Hinoki and Sugi (192 and 219 mm/year, respectively). We found that canopy conductance (G_c) and its sensitivity to the mean vapour pressure deficit during daylight hours in Sugi were particularly high in early spring, whereas those in Hinoki shifted gradually throughout the growing season. This difference was related to the optimal temperature of G_c in Sugi, which was approximately 10 °C lower than that in Hinoki. Our results suggest that plantations of water-conserving species such as Hinoki produce timber slowly but yield water resources generously. Moreover, for plantations of trees sensitive to high temperature, such as Sugi, managers should be concerned about possible future decline caused by anticipated global warming.

KEYWORDS

Chamaecyparis obtusa, *Cryptomeria japonica*, Cupressaceae, global warming, heat dissipation method, interspecies difference, sap flux density, sapwood area

1 | INTRODUCTION

The rate of temperature change predicted in this century is likely to be unprecedented for trees (Saxe, Cannell, Johnsen, Ryan, & Vourlitis, 2001). Because of elevated temperatures and, in some areas, accompanying drought, amplified tree die-off is already occurring in some locations (Allen et al., 2010; Anderegg, Kane, & Anderegg, 2013). In the Japanese archipelago, plantations of two conifer species occupy approximately 19% of the total land area (Japan Forestry Agency,

2013): Japanese cedar, *Cryptomeria japonica* D. Don (Sugi) and Japanese cypress, *Chamaecyparis obtusa* Sieb. et Zucc. (Hinoki). Many plantations cover the slopes of montane regions that form the headwaters of rivers. Sound management of these plantations is thus important for conservations of land and water resources in Japan. A decline of Sugi trees has been observed over the past two decades in low-lying plains of some regions in Japan probably because of temperature increase and drought (Matsumoto, Shigenaga, Miura, Nagakura, & Taoda, 2006; Shigenaga, Matsumoto,

Taoda, & Takahashi, 2005; Ueda, Amano, Waguchi, Yoneda, & Shibata, 2006). Previous studies using leaf gas-exchange measurements suggested that Sugi is susceptible to water stress (Matsumoto, Maruyama, & Morikawa, 1992). But the ecophysiological trait in the leaves does not necessarily explain the long-term behaviour of the species at the individual or stand scale. Moreover, the attribute of a species can be characterized by understanding the differences from other species. Thus, it is essential to observe the long-term transpiration at the stand scale and to discover the difference between the two species.

To better understand the water use traits of the two species, the dominant component of the variation at the stand-scale, the transpiration rate (E_{sta} ; mm/day), is the central issue. E_{sta} can be derived from the mean sap flow rate and total stand sapwood area as (e.g., Oren, Phillips, Katul, Ewers, & Pataki, 1998)

$$E_{sta} = J_s \times \frac{A_{ssta}}{A_g}, \quad (1)$$

where J_s is the mean sap flux density of measured trees ($\text{m}^3 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), A_{ssta} is the total sapwood area for all trees in the plot (m^2), and A_g is the horizontal plot area (m^2). Intraspecies variation in E_{sta} has been clarified for each of the study species in prior studies. For Sugi, Kumagai, Tateishi, Shimizu, and Otsuki (2008) found that J_s was similar between lower and upper slope positions irrespective of the differences in tree size and soil conditions, indicating that A_{ssta} is a strong determinant of the spatial variation of E_{sta} along a slope. For Hinoki, a similar approach was used to show that differences of E_{sta} are caused by differences in both J_s and A_{ssta} (Kume et al., 2015).

To understand the interspecies differences in transpiration, the components of E_{sta} must be observed in the two species under similar conditions. Comparing the results from different sites or published results of separate studies is useful only when interspecies differences are large, because such differences reflect not only interspecies differences in physiological activity or stand architecture but also factors such as measurement methods, tree age, soil and atmospheric conditions, season, and year (see Saito, Tanaka, Tanabe, Matsumoto, & Morikawa, 2003). However, the long-term differences in transpiration rates between Hinoki and Sugi stands have still not been clarified at either the single-tree or the stand scale. In particular, the annual cycle and environmental response of E_{sta} in Hinoki is not sufficiently characterized. Also, the physiological causes of the observed Sugi decline are not fully understood. Moreover, the annual cycle in E_{sta} reflects both the direct effects of variations in environmental conditions and physiological changes that produce season-to-season differences in transpiration response to environmental variables. Thus, comparing environmental responses of E_{sta} across the range of seasonally varying conditions is essential to clarify the interspecies differences in E_{sta} over the long term.

The aim of this study is to elucidate the physical and physiological processes that contribute to interspecies difference in transpiration at the stand scale. In particular, we focus on determining E_{sta} of Hinoki and Sugi on monthly and annual timescales. Also, this comparison will shed light on the physiological mechanism of the observed Sugi decline in Japan. Measurements for each species were conducted using the

same method and over the same time period. The nearby stands of the two species were similar in maturity and had similarly adequate soil moisture. The results will identify differences in the mechanisms of E_{sta} variation in monospecific communities of these two Cupressaceae family conifer species.

2 | MATERIALS AND METHODS

2.1 | Study site

Observations were conducted in the Yayama experimental catchment (YEC; 2.98 ha, 33°31'N, 130°39'E, 304–406 m a.s.l.) in Fukuoka Prefecture, western Japan. Saito et al. (2015) described the topography and stand structure of the YEC. Observations for E_{sta} commenced in December 2010, and data from January 1 to December 31, 2011 (12 months) were analysed. The two study plots were located at midslope positions, both inclined at approximately 20° (Table 1). The 15 × 15 m Hinoki plot stood on a northwest-facing slope. The 15 × 16 m Sugi plot, located ~65 m away, was on a northeast-facing slope. The Hinoki trees were shorter and had a smaller diameter at breast height (DBH) than did the Sugi trees, but tree density was greater in the Hinoki stand than in the Sugi stand. The stand density management diagram (Ando, 1968) estimates of stem volumes of the Hinoki and Sugi stands were 427 and 613 m^3/ha , respectively. These correspond to 0.88 and 0.87 of the yield index, indicating similar levels of maturity. Chiwa et al. (2015) reported that stream water in the basin contained high NO_3^- concentrations and that the site experienced a high bulk atmospheric N deposition rate, suggesting N saturation in the YEC.

2.2 | Meteorology and soil water conditions

Saito et al. (2013) described protocols for observing meteorological variables at a weather station and measuring the leaf area index of the area including the sap flow plots. Those variables were precipitation (P_r , mm), solar radiation (R_s , W/m^2), air temperature (T_{air} , °C), relative humidity (RH, %), and wind speed (m/s^1). Missing T_{air} data from August 21 to October 3 and relative humidity from October 6 to November 2 were filled using data from the Iizuka Observatory (Japan Meteorological Agency; 15 km NNE of the study site; 37 m a.s.l.) after calibration.

Soil water was monitored at the three points randomly scattered across each plot. At each point, two types of sensors were installed at 10, 30, and 50 cm from the ground surface in the soil profile. Volumetric water content (θ ; m^3/m^3) was monitored with dielectric sensors (EC-5, Decagon Devices, Pullman, WA, USA). At each time interval, the weighted mean of θ in 0–60 cm depth (θ_{0-60}) was obtained by $\theta_{0-60} = (\theta_{10} \times 20 + \theta_{30} \times 20 + \theta_{50} \times 20)/60$, where, θ_{10} , θ_{30} , and θ_{50} were the mean of the three measurements of θ at each depth. Soil matric potential (Ψ ; kPa) was monitored by tensiometers (DIK-3023, Daiki Rika Kogyo, Tokyo, Japan). The continuous data of Ψ at 30 cm (Ψ_{30}) at one of the three points were used. Data were recorded every hour.

TABLE 1 Stand characteristics of the Hinoki and Sugi plot in the Yayama experimental catchment

Species		<i>Chamaecyparis obtusa</i> (Hinoki)	<i>Cryptomeria japonica</i> (Sugi)
Age	(yr)	42	42
Plot horizontal area	(m ²)	197.0	212.9
Number of trees		33	27
Number of measuring trees ^a		16 (3 or 7)	9 (3)
Tree density	(trees/ha)	1,675	1,268
Mean height	(m)	16.0	20.2
Mean DBH	(cm)	19.9	25.7
Range of DBH	(cm)	14.3–23.3	18.6–38.1
Basal area	(m ² /ha)	52.5	68.3
Sapwood area	(m ² /ha)	14.9	25.3
LAI (direct)	(m ² /m ²)	3.7	2.8
LAI (optical)	(m ² /m ²)	3.8 ± 0.1	3.5 ± 0.1
Canopy openness	(%)	2.2 ± 0.3	3.0 ± 0.2

Note. Number with ± operator indicates mean ± standard deviation. Leaf area index (LAI; direct) and LAI (optical) was obtained by tree harvesting and LAI-2000, respectively. DBH = diameter at breast height.

^aThe numbers are from the intensive period from September to December 2011, and the numbers in parentheses are from the reference period.

2.3 | Sap flow measurements

A heat dissipation sensor (Granier, 1987) was installed in the sapwood of each sample tree stem at approximately 1.6 m above the ground. Each sensor consisted of a pair of 20-mm-long probes with a vertical separation of ~15 cm. The upper probe was heated with constant electric power of 0.2 W. The temperature difference between the two probes was scanned every 30 s, and the mean value was recorded every 10 or 30 min by a data logger (CR1000, Campbell Scientific Inc., Logan, UT, USA) via a multiplexer (AM16/32, Campbell Scientific Inc.). All sensors were installed in the north sides of tree stems to avoid direct sunlight (Kumagai et al., 2005). The area of the trunk around the sensors was covered by a rectangular aluminium dish (16 cm × 25 cm), the edges of which were sealed to the bark except for the lower side. In Hinoki, the sensors were installed only in the first depth (0–20 mm). In Sugi, the sensors were installed in the first (0–20 mm) or first and second depth (0–20 and 20–40 mm) according to the tree sapwood depth (SWD). The average SWD for sample trees was 17.2 ± 2.7 mm and 29.6 ± 8.0 mm in Hinoki and Sugi, respectively.

Sap flux density (F_d ; m/s) was estimated based on the empirical equation of Granier (1987) as $F_d = 1.19 \{(\Delta T_{\max} - \Delta T)/\Delta T\}^{1.23} \times 10^{-4}$, where ΔT is the temperature difference between the two probes and ΔT_{\max} is the daily maximum ΔT observed in each daily cycle (from 0500 to 0500 the next day). If part of the probe was out of contact with sapwood, ΔT was replaced by the calibrated temperature

difference (ΔT_{sw}), using an equation as: $\Delta T_{sw} = (\Delta T - b\Delta T_{\max}) / a$, where a was the fraction of the probe in contact with sapwood and $b = 1 - a$ (Clearwater, Meinzer, Andrade, Goldstein, & Holbrook, 1999).

2.4 | Estimates of tree and stand transpiration rates

Saito et al. (2015) described the estimation of sapwood area in a stem cross-sectional area (A_{stre} ; m²). In Hinoki, the daily transpiration rate for each tree (E_{tre} ; kg/day) was calculated as $E_{tre} = F_d \times A_{stre}$. The daily integral F_d (m/d; from 0500 to 0500 the next day) was used for this calculation. In six Sugi trees, the same calculation was performed for E_{tre} for each tree equipped with a sensor in the first depth. For the other three Sugi trees with sensors in the first and second depths, E_{tre} was estimated as $E_{tre} = E_{20} + E_{res}$ where E_{20} is daily mass of sap flow (kg/day) in the first depth ($E_{20} = F_{d20} \times A_{s20}$), and E_{res} is that in the residual SWD ($E_{res} = F_{dres} \times A_{sres}$). F_{d20} and F_{dres} are the daily integral F_d (m/d) at 0–20 mm and residual SWD, respectively. The ratio of F_{dres} to F_{d20} was 0.59, 0.25, and 0.56, respectively, in the three sample trees.

The average E_{tre} of all F_d sample trees was obtained for the entire study period as $E_{tre} = \Sigma E_{tre,i} / n$, where $\Sigma E_{tre,i}$ is the sum of E_{tre} in all sample trees and n was the number of sample trees (i.e., 16 and nine, in Hinoki and Sugi, respectively). The study period was separated into “a reference period” and “an intensive period” as described below. During the reference period using a limited sample size, $\Sigma E_{tre,i}$ was estimated

TABLE 2 Parameters for equations fitted to the relationships of J_s or E_{sta} against D_{day}

Equation	Parameter	<i>Chamaecyparis obtusa</i> (Hinoki)	<i>Cryptomeria japonica</i> (Sugi)
$J_s = a \times (1 - \exp(D_{day} \times b)) + c$	a	2.62	0.98
	b	-0.57	-1.30
	c	-0.18	-0.14
$E_{sta} = g \times (1 - \exp(D_{day} \times h)) + i$	g	3.90	2.47
	h	-0.57	-1.30
	i	-0.28	-0.34

with the sum of E_{tre} of the reference trees by linear equations. These equations were constructed during the intensive period. In Hinoki, the equation for sums of E_{tre} in three reference trees (E_{tre3}) was $\Sigma E_{tre,i} = 11.7 E_{tre3} - 4.9$ ($R^2 = 0.96$). The equation for seven reference trees (E_{tre7}) was $\Sigma E_{tre,i} = 4.8 E_{tre7} - 3.7$ ($R^2 = 0.99$). In Sugi, the equation for three reference trees was $\Sigma E_{tre,i} = 3.6 E_{tre3} - 7.4$ ($R^2 = 0.97$).

The mean stand sap flux density (J_s ; $m^3 \cdot m^{-2} \cdot day^{-1}$) was estimated for each sample plot using Equation 2:

$$J_s = \frac{\Sigma E_{tre,i}}{\Sigma A_{stre,i}} \quad (2)$$

where $\Sigma A_{stre,i}$ is the sum of A_{stre} for all F_d sample trees.

2.5 | Periods for intensive and reference measurement

Monitoring E_{sta} by the Granier method requires a large, stable electric power supply, which is normally not available in plantations in montane regions (see Zimmermann et al., 2000). However, long-term monitoring was achieved in this study by supplying sufficient power during parts of the observation period and extrapolating the results to the other period.

The continuous observations from January 1 to December 31, 2011 consisted of two periods: (a) “the reference period” from January 1 to September 16 in Hinoki or to September 14 in Sugi. Those

reference periods were followed by (b) “the intensive periods” ending December 31 for both species. In Hinoki, the reference measurement was carried out on three trees before August 3, then, on seven trees until September 16. In Sugi, the reference measurement was conducted using three trees until September 14. During the intensive period, 16 Hinoki and nine Sugi trees were measured. Those trees included the trees used in the reference period.

2.6 | Effective days for analysis and gap filling

The effective days for analysis were 177 days in Hinoki (48%) and 171 days in Sugi (47%) during the year 2011 observation period (365 days). Data were not used for days with minimum $T_{air} < 0^\circ C$ (from January 1 to February 6), or any day with $P_r > 2$ mm/d and for one subsequent day. Besides these days, data were excluded for any other days influenced by large P_r amounts (≥ 45 mm/day), an abrupt increase of ΔT at night, and malfunctions in the data logger.

After gap filling, the continuous daily data were used in the calculation of monthly and annual values of E_{sta} and J_s . The missing data of daily J_s were filled using estimates derived from an equation as $J_s = a \times (1 - \exp(D_{day} \times b)) + c$, where D_{day} (kPa) is the mean vapour pressure deficit during daylight hours (0600–1800), and a , b , and c are the constants shown in Table 2. This equation was also used for filling the gaps in daily E_{sta} .

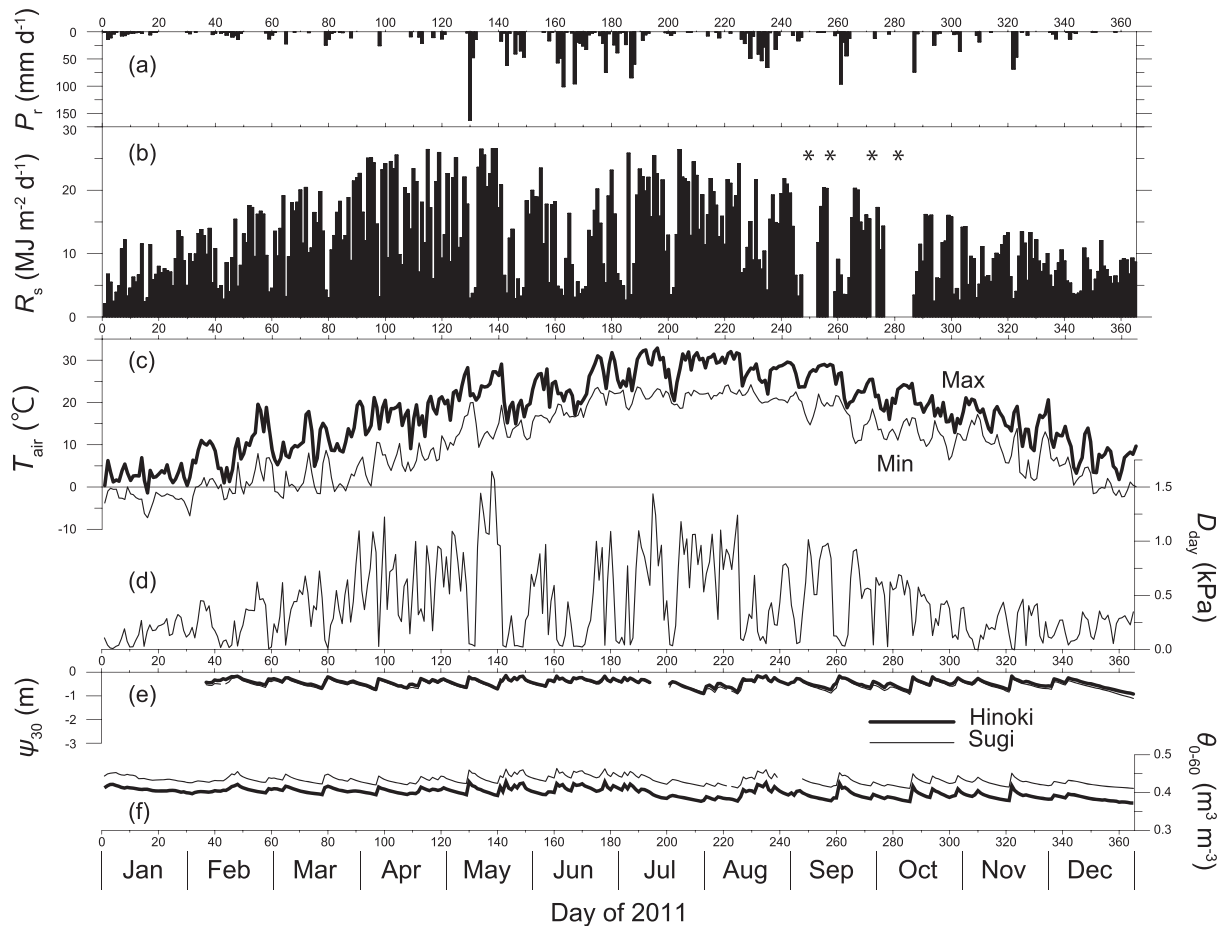


FIGURE 1 Meteorological data from 2011 at the weather station beside the study stands for (a) precipitation (P_r), (b) solar radiation (R_s), (c) daily maximum and minimum air temperature (T_{air}), and (d) vapour pressure deficit during daylight hours from 6:00–18:00 (D_{day}). Also shown are (e) soil matrix potential at 30 cm depth (ψ_{30}) and (f) soil volumetric water content in the 0–60 cm depth range (θ_{0-60}). * in R_s indicates dates of missing data

2.7 | Potential sources of error

We considered four possible sources of error in the transpiration estimates. First, the natural temperature gradient between the two probes (ΔT_{net}) was found to have only a minor effect on estimated daily F_d . ΔT_{net} was observed by the sensors installed but unheated during the reference period, and ΔT_{net} in a diurnal cycle was normally within ± 0.6 °C except on rainy days. At 0.6 °C, ΔT_{net} would account for roughly 8% of mean daily F_d . However, fluctuation in the ΔT_{net} above and below zero within a diurnal cycle naturally cancels out any deviations in its contribution to the daily cumulative values of F_d .

Second, nighttime sap flow was considered to be negligible. The nocturnal transpiration (Dawson et al., 2007) potentially causes underestimation of ΔT_{max} (Lu, Urban, & Zhao, 2004; Oishi, Oren, & Stoy, 2008). However, nighttime humidity is high in the YEC because the site is located in a montane area with a high frequency of rainfall throughout a year. The nights (0000–0600, 1800–2400) with the vapour pressure deficit < 0.1 kPa for at least 1 hour, amounted to 77% of the all nights in a year (i.e., 280/365). Therefore, we suggest that underestimation of ΔT_{max} played a minor role in the estimation of F_d .

Third, the error in estimating J_s by the azimuthal variation of F_d was minimized. The azimuthal variation in F_d is represented in the tree-to-tree variation of F_d (Kumagai et al., 2005). Sample size of this study was a statistically sufficient (i.e., 16 and nine in Hinoki and Sugi, respectively). Kume et al. (2010) reported 15 is a sufficient sample size in Hinoki with a coefficient of variation $< 12\%$. Kumagai, Aoki, Shimizu, and Otsuki (2007) reported 10 is a sufficient sample size in Sugi with a coefficient of variation $< 10\%$. In addition, previous studies have tied the variation of F_d to the variation of SWD (Tsuruta et al., 2010; Vertessy, Hatton, Reece, O'Sullivan, & Benyon, 1997). However, SWD for the four azimuthal directions did not vary significantly ($p > .05$).

Fourth, errors related to uncertainty in sapwood area were minimized in this study (Saito et al., 2015). A_{stre} and A_{ssta} were estimated based on observed SWD in the two species. Kumagai et al. (2005, 2007) used A_{stre} where depth equalled the probe length (i.e., 20 mm; Lu et al., 2004). They also treated the intermediate wood ("white band") of Sugi as a part of conducting xylem when estimating A_{stre} and A_{ssta} . However, in this study, A_{stre} and A_{ssta} did not include the area of the intermediate wood in the stem cross section. In Hinoki, the

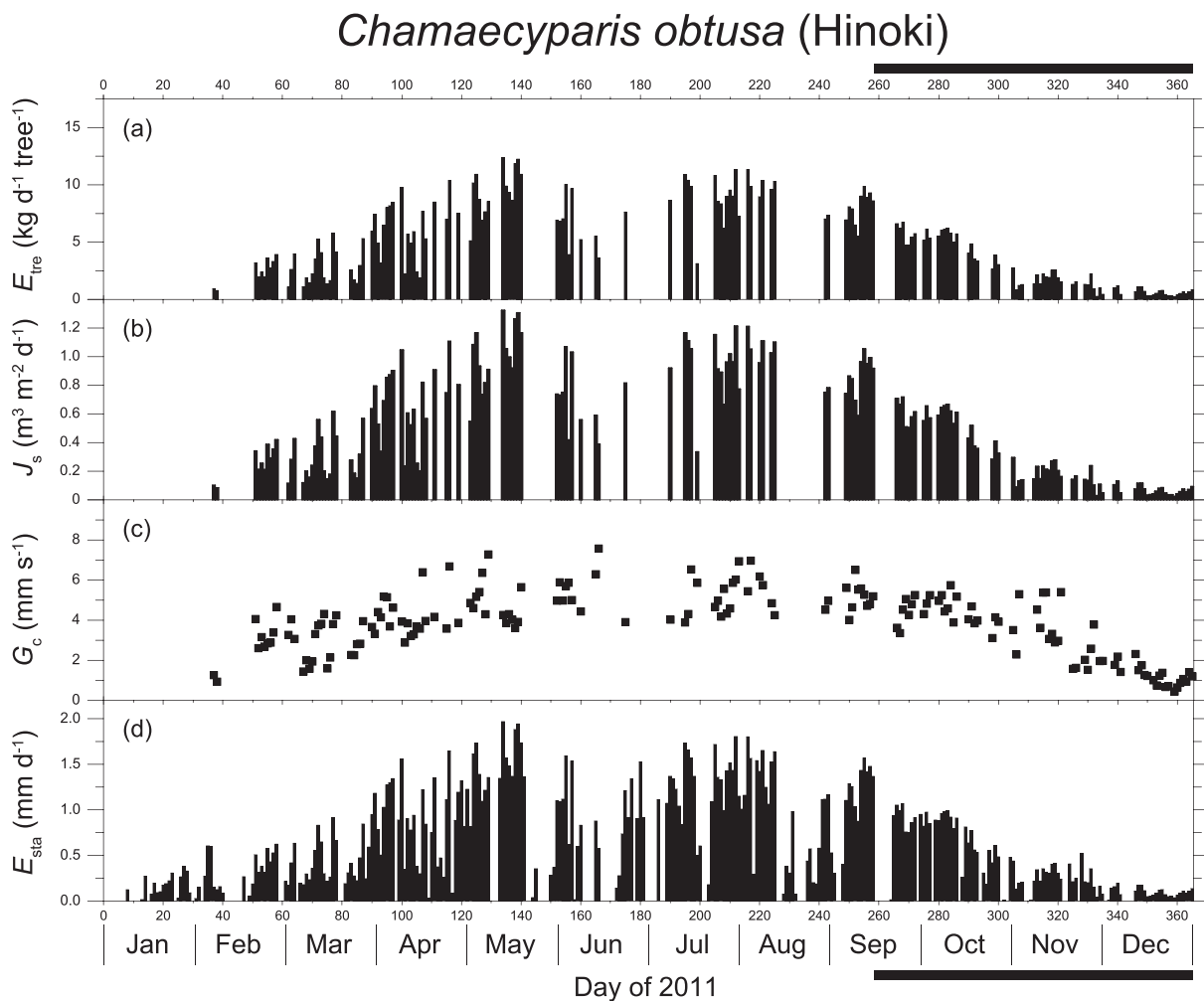


FIGURE 2 Daily sap flow properties in the Hinoki plot: (a) tree transpiration rate (E_{tre}), (b) mean stand sap flux density (J_s), (c) canopy conductance (G_c), and (d) stand transpiration rate (E_{ssta}). The number of effective observation days for analyses was 177. Missing E_{ssta} data were estimated using a regression curve of E_{ssta} versus D_{day} (Figure 5b). The black band beside the abscissa indicates the intensive measurement period ($n = 16$) beginning September 16. The period before the band was the reference measurement period ($n = 3$ or $n = 7$)

above changes resulted in changes of +12%, +27%, and +27% in E_{tre} , J_s , and E_{sta} , respectively. In Sugi, the changes resulted in changes of +8%, +15%, and -11%.

2.8 | Canopy conductance

Daily mean canopy conductance (G_c : mm/s) was calculated using the following equation (e.g., Alsheimer, Köstner, Falge, & Tenhunen, 1998):

$$G_c = \frac{E_{sta}}{D_{day}} \cdot \frac{R \cdot (T_{day} + 273.15)}{M_w} \times \frac{10^3}{43200}, \quad (3)$$

where R is a gas constant ($8.314 \text{ J} \cdot \text{K}^{-1} \cdot \text{mol}^{-1}$) and M_w is molar mass of water (18.015 g/mol). E_{sta} (mm/d) is the daily integral stand transpiration, but G_c was obtained as the average value for daylight hours divided by $60 \times 60 \times 12$. T_{day} ($^{\circ}\text{C}$) is the mean air temperature during daylight hours (0600–1800), which were the same periods of D_{day} (kPa). A factor of 10^3 is needed for unit conversion from m/day to mm/day. Applying Equation 3 stands on two assumptions. First, the canopy is well coupled with the atmosphere. The mean value of the

coupling coefficient (Ω) was as small as 0.22 in the stands of both species. Canopies of conifer plantations have large roughness values; thus, the boundary-layer resistance is approximately 0 (Kumagai et al., 2008). Second, E_{sta} estimated from F_d at breast height equals the true transpiration rate in the canopy. The diurnal changes of stored water in the stem have a negligible influence because of daily aggregated datasets.

2.9 | Data statistics

In the D_{day} - G_c diagrams, the upper envelope of the scattered points was used for analysis, because these points represent the response of G_c to D_{day} when other environmental variables are at their optimum levels. Boundary line analysis was conducted using select points along the upper envelope, as follows (e.g., Schäfer, Oren, & Tenhunen, 2000). (a) Select G_c data for periods with $R_s > 8.64 \text{ MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ($=200 \text{ W/m}$ averaged for 12 hours in a day). (b) Classify the selected G_c data into D_{day} intervals of 0.2 kPa, starting from $D_{day} = 0.4 \text{ kPa}$. Note that the range of the interval (i.e., 0.2 kPa) was expanded up to 0.4 kPa, when the number of G_c values was less than 4. (c) Obtain the mean and standard deviation (σ) of G_c in each interval. (d) Remove outliers ($p < .05$;

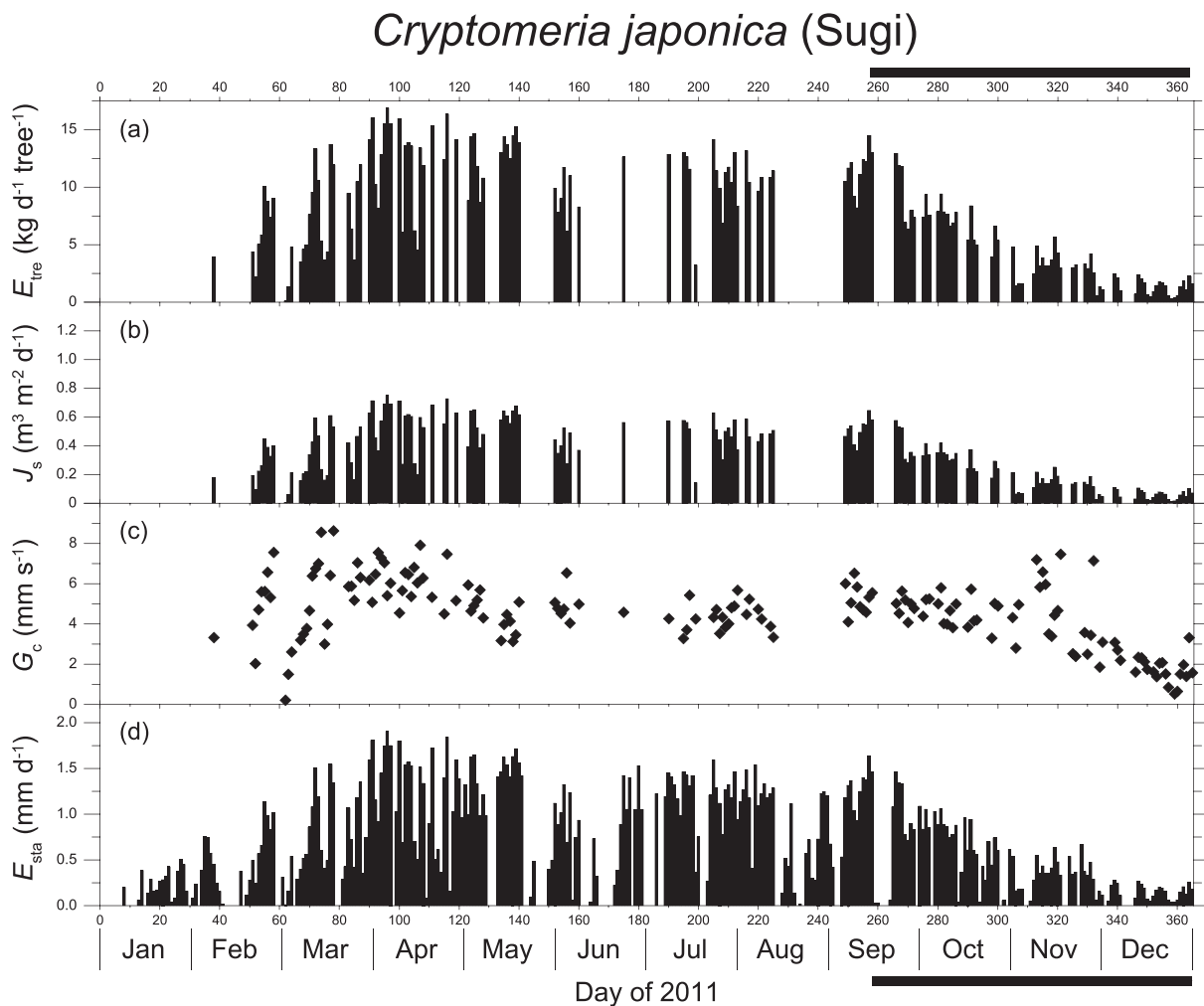


FIGURE 3 Daily sap flow properties in the Sugi plot: (a) tree transpiration rate (E_{tre}), (b) mean stand sap flux density (J_s), (c) canopy conductance (G_c), and (d) stand transpiration rate (E_{sta}). The number of effective observation day for analyses was 171. Missing E_{sta} data were estimated using a regression curve of E_{sta} versus D_{day} (Figure 5b). The black band under the abscissa indicates the intensive measurement period ($n = 9$) beginning September 14. The period before the band was the reference measurement period ($n = 3$)

Dixon's test for $n \leq 25$ and Grubbs' test for $n > 25$; Sokal & Rohlf, 1995). (e) Find the data $> \text{mean} + 1\sigma$ in the interval with $n \geq 4$ G_c data. (f) Use least squares regression to select values of G_{cref} and m in the following equation (e.g., Oren et al., 1999):

$$G_c = G_{\text{cref}} - m \ln D_{\text{day}}, \quad (4)$$

The slope (m ; $=dG_c/d(\ln D_{\text{day}})$) and intercept (G_{cref} : the reference value of G_c at $D_{\text{day}} = 1$ kPa of the regression lines) were used to evaluate the response of G_c to variations in D_{day} .

3 | RESULTS

3.1 | Meteorology and soil water conditions

Annual P_r was 2,469 mm with a pronounced rainy season during June and July (Figure 1a). Snowfall occurred frequently from January to early February. R_s peaked at approximately 26 MJ m^2/day in April and May (Figure 1b). After the rainy season, R_s peaked again at that level in July and August. The highest and lowest T_{air} were 32.9 °C in August and -7.3°C in January, respectively (Figure 1c). D_{day} exceeded 1.0 kPa on sunny days from April to September (Figure 1d). The high values and narrow range of ψ_{30} and θ_{0-60} indicated soil moisture conditions were relatively moist in both stands (Figure 1e,f). ψ_{30} never fell below -1.11 m and θ_{0-60} remained in the range from 0.37 to 0.46 m^3/m^3 in the two stands.

3.2 | Seasonal trends of tree and stand transpiration rate

E_{tre} in Hinoki increased gradually from February to April, peaking in mid-May (12.4 $\text{kg}\cdot\text{day}^{-1}\cdot\text{tree}^{-1}$; Figure 2a), then decreased gradually from September to December. The same pattern was observed for J_s and E_{sta} (Figure 2b and 2d), which peaked at 1.3 $\text{m}^3\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ and 2.0 mm/day in May, respectively. G_c plateaued at 6–8 mm/s from May to October (Figure 2c).

In Sugi (Figure 3a), a clear peak was found in E_{tre} from March to April (16.9 $\text{kg}\cdot\text{day}^{-1}\cdot\text{tree}^{-1}$) and a relatively stable plateau was seen from July to September (~13 $\text{kg}\cdot\text{day}^{-1}\cdot\text{tree}^{-1}$). The same pattern was observed in J_s and E_{sta} (Figure 3b and 3d), which peaked at 0.8 $\text{m}^3\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ and 1.9 mm/day in early April, respectively. Two peaks appeared in G_c (Figure 3c), a first clear peak (8.6 mm/s) in March, and the second moderate peak (7.5 mm/s) in November. Those peak values were rather higher than the peak value (~6 $\text{mm}\cdot\text{s}^{-1}\cdot\text{tree}^{-1}$) observed at that time in the Kahoku experimental watershed (KHEW; Kumagai et al., 2008).

3.3 | Short-term species differences in tree and stand transpiration rates

The first step in our analysis was to examine the intra and interspecies differences in E_{tre} . For each sample tree, E_{tre} ($\text{kg}\cdot\text{d}^{-1}\cdot\text{tree}^{-1}$) averaged for 24 days with available estimates during the period September 16 to October 31 was calculated. During the period, most days were sunny ($R_s > 8.64$ $\text{MJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) with moderate atmospheric humidity

($0.5 < D_{\text{day}} < 1.0$; Figure 1b and 1d). Daily F_d across A_{stre} for each tree (F_{dtre} ; $\text{m}^3\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) was calculated as $F_{\text{dtre}} = E_{\text{tre}}/A_{\text{stre}}$.

Tree size might be expected to explain the observed intraspecies variations of F_{dtre} , A_{stre} , and E_{tre} . However, F_{dtre} had no significant relationship with DBH in Hinoki ($R^2 = 0.10$, $p = .24$) or in Sugi ($R^2 = 0.14$,

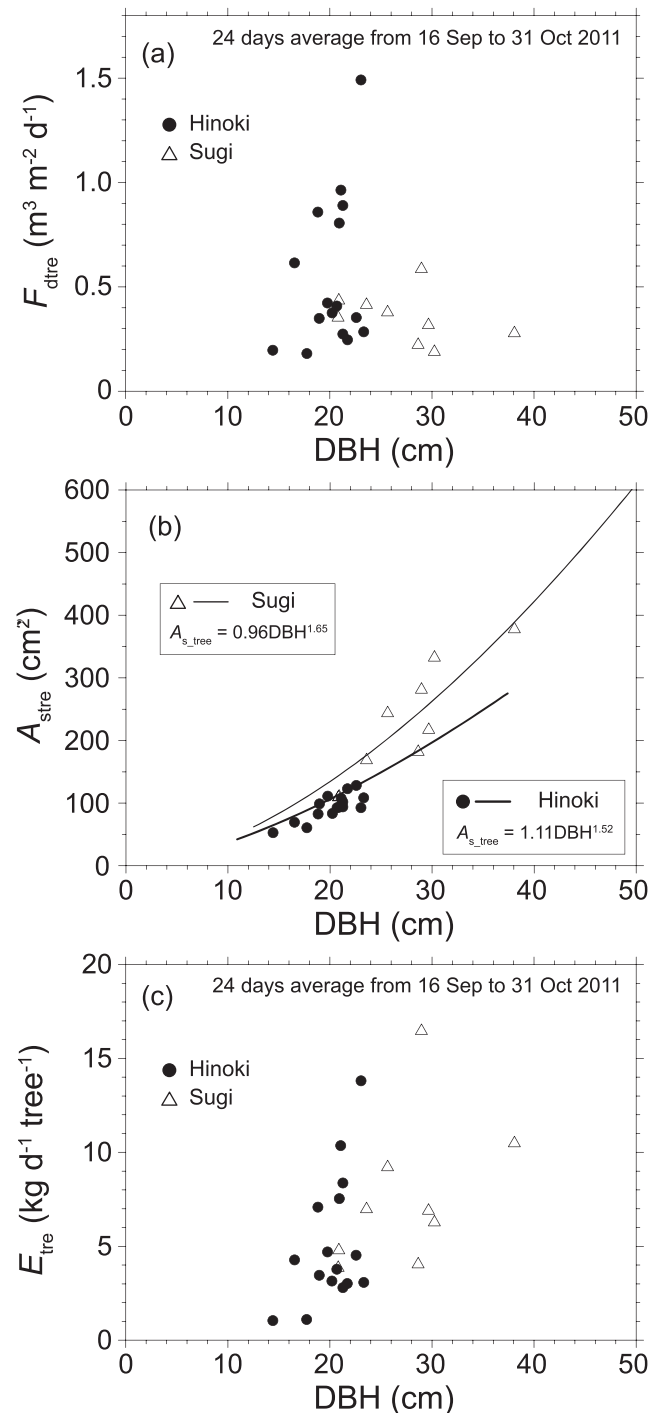


FIGURE 4 (a) Daily sap flux density across sapwood area (F_{dtre}) for each tree averaged from September 16 to October 31 (24 days) in relation to tree diameter at breast height (DBH). The number of trees was 16 and nine in Hinoki and Sugi, respectively. (b) Sapwood area for each tree (A_{stre}) is presented in relation to DBH. The values of the sample trees (symbols) are presented with the regression curves obtained across the catchment (Saito et al., 2015). (c) Daily transpiration rate for each tree averaged during the 24 days (E_{tre}) is shown in relation to DBH

$p = .32$). $F_{d\text{tre}}$ in Hinoki varied more widely than that in Sugi (Figure 4a). The independence of $F_{d\text{tre}}$ from tree size parameters was also suggested by Kumagai et al. (2005) in Sugi and by Kume et al. (2010) in Hinoki. A_{stre} versus DBH in the study plots were almost on the exponential curve obtained across the YEC area (Saito et al., 2015). The variation of A_{stre} with DBH in Hinoki was smaller than that in Sugi because of the smaller size (Figure 4b). E_{tre} was not significantly related to DBH in either Hinoki ($R^2 = 0.21$, $p = .08$) or Sugi ($R^2 = 0.20$, $p = .22$). The range of individual variation in E_{tre} in Hinoki was roughly similar to that of Sugi across a similar tree size range (i.e., DBH, 20–30 cm; Figure 4c).

Among the variables tested, E_{tre} of Hinoki had a close relationship with $F_{d\text{tre}}$ ($R^2 = 0.95$, $p < .01$) but not with A_{stre} ($R^2 = 0.05$, $p = .41$). However, in Sugi, E_{tre} had a weak, nonsignificant relationship with $F_{d\text{tre}}$ ($R^2 = 0.37$, $p = .08$) and A_{stre} ($R^2 = 0.36$, $p = .09$). Therefore, the variation of E_{tre} in Hinoki was caused by the variation of $F_{d\text{tre}}$, and that in Sugi was caused by variations in both $F_{d\text{tre}}$ and A_{stre} .

Concerning interspecies differences, mean $F_{d\text{tre}}$ of 16 Hinoki trees ($0.54 \pm 0.36 \text{ m}^3 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) was larger by a factor of 1.55 than the mean of nine Sugi trees ($0.35 \pm 0.12 \text{ m}^3 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), but the difference was not significant ($p = .14$). However, the mean A_{stre} in Hinoki ($93.7 \pm 20.7 \text{ cm}^2$) was significantly smaller (42%; $p < .01$) than that of Sugi ($224.6 \pm 93.5 \text{ m}^2$). Consequently, the mean E_{tre} of Hinoki ($5.13 \pm 3.46 \text{ kg/day}$) was 33% smaller than that of Sugi ($7.66 \pm 3.98 \text{ kg/day}$), though the difference was not significant ($p = .11$).

At the stand scale, J_s of Hinoki ($0.55 \text{ m}^{-3} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) was 160% that of Sugi ($0.34 \text{ m}^{-3} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) during the 24 days, and A_{ssta}/A_g of Hinoki was 59% that of Sugi (Table 1). Therefore, mean E_{sta} of the 24 days in Hinoki (0.81 mm/day) was similar to (94% of) that in Sugi (0.86 mm/day).

3.4 | Species difference in responses to environmental variables

The second step of the analysis was the examination of interspecies differences in environmental responses of J_s and E_{sta} . In the plot of J_s against D_{day} , J_s of Hinoki was greater than that of Sugi at a given value of D_{day} (Figure 5a). At $D_{\text{day}} = 1.0 \text{ kPa}$, J_s of Hinoki ($0.95 \text{ m}^3 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$) was 165% that of Sugi ($0.58 \text{ m}^3 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), based on the regression curves. However, in the plot of E_{sta} against D_{day} , the greater J_s in Hinoki was counterbalanced by the smaller A_{ssta}/A_g (Figure 5b). Thus, E_{sta} of Hinoki (1.42 mm/day) was 97% that of Sugi (1.46 mm/day) on the regression curves at $D_{\text{day}} = 1.0 \text{ kPa}$. Table 2 summarizes parameters of the regression curves. The regression curve of Sugi was more convex than that of Hinoki, but the difference was very slight at the annual time scale.

The data of E_{sta} in 2011 were classified into four seasons: January–February and December (DJF; winter), March–May (MAM; spring), June–August (JJA; summer), and September–November

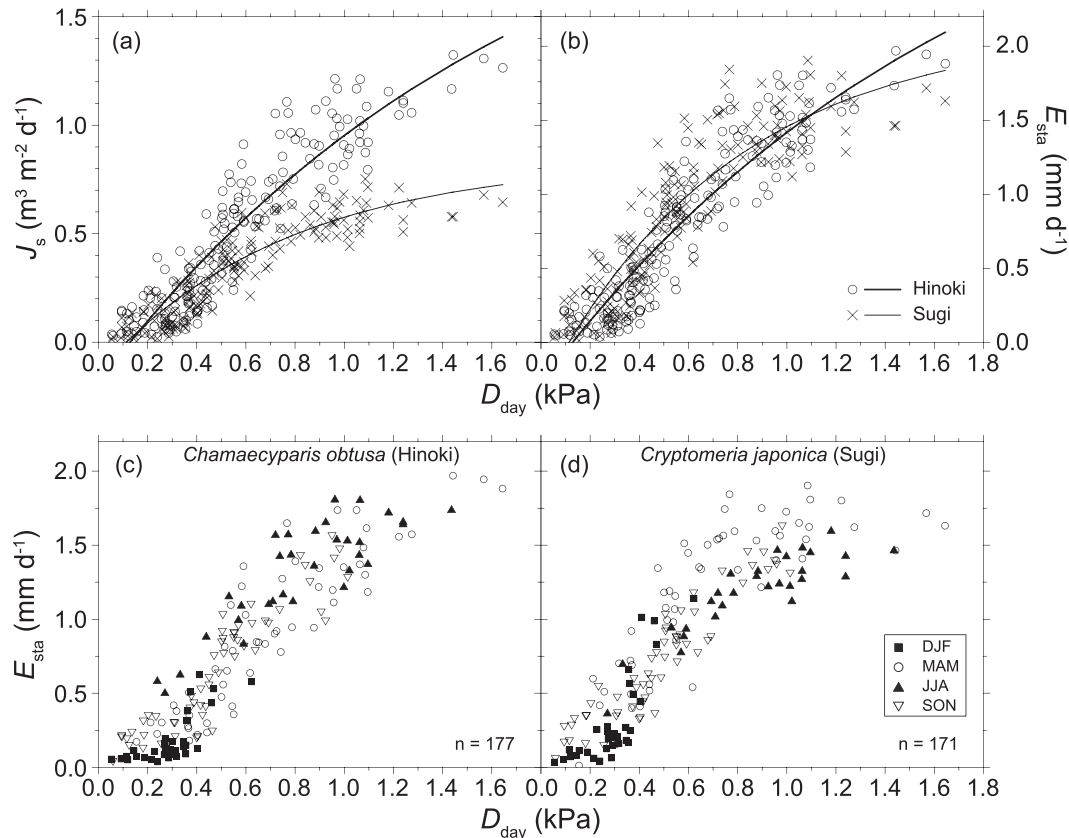


FIGURE 5 (a) Daily mean stand sap flux density (J_s) in relation to mean vapour pressure deficit during daylight hours from 0600 to 1800 (D_{day}). (b) Daily stand transpiration rate (E_{sta}) is shown in relation to D_{day} throughout the measurement period. Table 2 shows the parameters of the regression curves. The same data set of $E_{\text{sta}}-D_{\text{day}}$ relationship was shown (c) for Hinoki and (d) for Sugi, separately. The data of E_{sta} were divided into four seasons: January, February, and December (DJF); March–May (MAM); June–August (JJA); and September–November (SON) in 2011

(SON; autumn). At a given D_{day} , the E_{sta} values for Hinoki were distributed similarly across the growing season (i.e., MAM, JJA, and SON; Figure 5c). However, in Sugi, the points in MAM were higher than those in the other seasons (Figure 5d). In addition, the plots of E_{sta} against R_s also exhibited a positive relationship (data not shown), although the relationship did not show clear species differences.

3.5 | Stand transpiration rate in monthly and annual scales

The third step of the analysis was examination of interspecies differences in seasonality of J_s and E_{sta} . The seasonal pattern of J_s in Hinoki showed a moderate plateau from April to October (Figure 6a). The

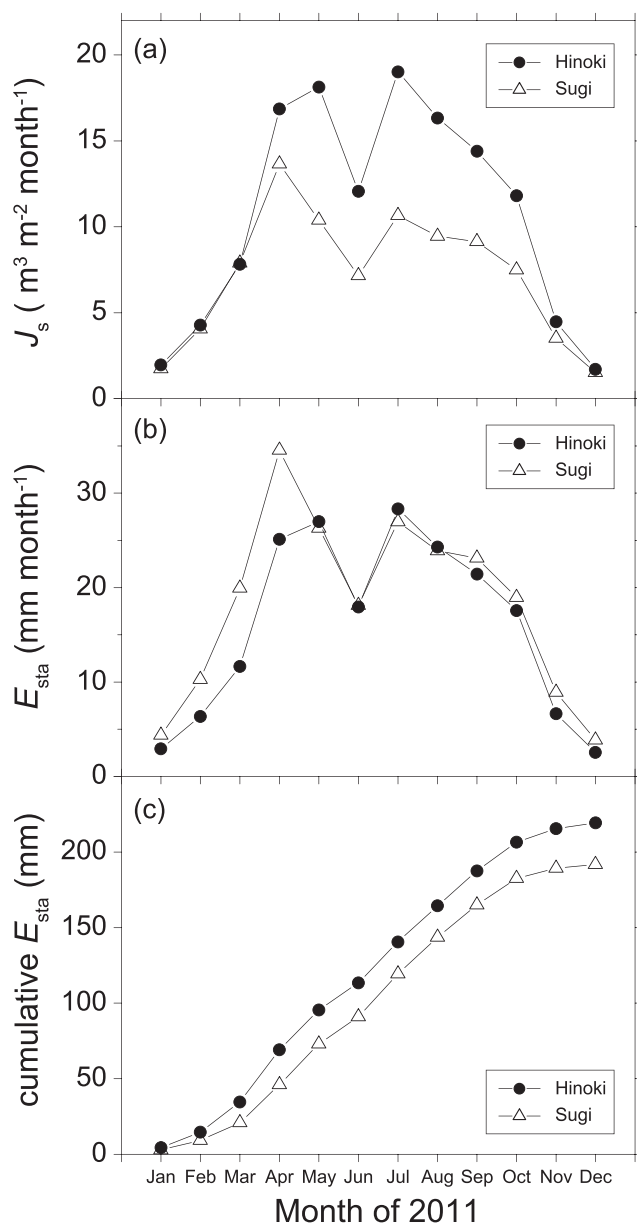


FIGURE 6 (a) Monthly mean stand sap flux density (J_s). (b) Monthly stand transpiration rate (E_{sta}). (c) Cumulative E_{sta} , which is calculated by monthly E_{sta} cumulated from January to December. The continuous daily data after gap filling were used for calculating the monthly J_s , monthly E_{sta} , and cumulative E_{sta}

temporal decline in June was caused by the high frequency of rainfall and small D_{day} (Figure 1a and 1d). In contrast, the pattern in Sugi peaked sharply in April. The J_s of Hinoki from May to October was >1.5 times higher than that in Sugi but that in the other seasons was 1.0–1.3 times that in Sugi.

From May to October, E_{sta} was similar for the two species, but E_{sta} of Sugi was clearly greater than that of Hinoki from February to April (Figure 6b). During this period, the difference of cumulative E_{sta} between Hinoki and Sugi was 21.7 mm, which accounted for 79% of the annual difference (27.5 mm; Figure 6c). That is, the sharp peak in E_{sta} of Sugi in early spring induced a greater annual cumulative E_{sta} of Sugi than that of Hinoki.

The goal of our analysis was comparison of annual E_{sta} between the two species. The annual E_{sta} in Hinoki (192 mm/year) was 87% that of Sugi (219 mm/year). Yearly, J_s in Hinoki was 149% that in Sugi, but A_{sssta}/A_g in the Hinoki stand was only 59% that of Sugi. Thus, the annual transpiration from the Hinoki stand depends more on the sap flow rate, but that from Sugi stand depends more on sapwood area. Our values are low, when compared with a similar Hinoki stand in central Japan (441.0 mm/year, Sun et al., 2014), because of the relatively high number of rainy days in the YEC.

3.6 | Response of canopy conductance to environmental variables

Before the analyses, we expected that D_{day} and T_{day} were the factors responsible for controlling G_c , using Jarvis type multiplicative functions (Jarvis, 1976; Kobayashi et al., 2014). Indeed, the temporal variation of soil moisture (i.e., Ψ_{30} and θ) did not play a role in the variation of G_c (data not shown). Although the dependency of G_c on R_s was not clear, the data obtained in very low R_s ($<8.64 \text{ MJ}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) was removed in further analyses of G_c versus humidity or temperature.

Species differences were found in the upper envelope of the plot of G_c against D_{day} on an annual basis (Figure 7a,b). The data of G_c in 2011 were classified into the four seasons. In Hinoki, the seasonal shifts in the response of G_c to D_{day} were moderate year round except for during DJF. However, in Sugi, G_c in MAM was higher and more sensitive to D_{day} when compared with G_c in other seasons. The select points in Hinoki were from MAM (7/19; indicating seven MAM points out of the 19 selected points), JJA (11/19), and SON (1/19), whereas the select points in Sugi were from DJF (1/15) and MAM (14/15). In addition, G_c near $D_{\text{day}} = 1 \text{ kPa}$ was consistently observed throughout March to November in both species. This contradicts the possibility of experimental artefacts (e.g., sensor degradation) in extrapolating the sum of E_{tre} in the intensive period to that in the reference period.

The interspecies difference observed in the seasonal shift of the $D_{\text{day}}-G_c$ relationship can be understood by the interspecies difference in temperature dependency of G_c . The data of G_c were distributed in a convex pattern over the range of T_{day} in both species (Figure 7c,d). The select points in the $D_{\text{day}}-G_c$ relationships (Figure 7a,b) were superimposed on Figure 7c and 7d. The select points for Hinoki were distributed in the range of T_{day} from 12.3 to 28.1 °C, and the points for Sugi were distributed from 6.1 to 22.2 °C. The mean value of Sugi (13.7 ± 3.9 in mean \pm SD) was significantly lower than that of Hinoki (23.2 ± 4.3 ; $p < .01$).

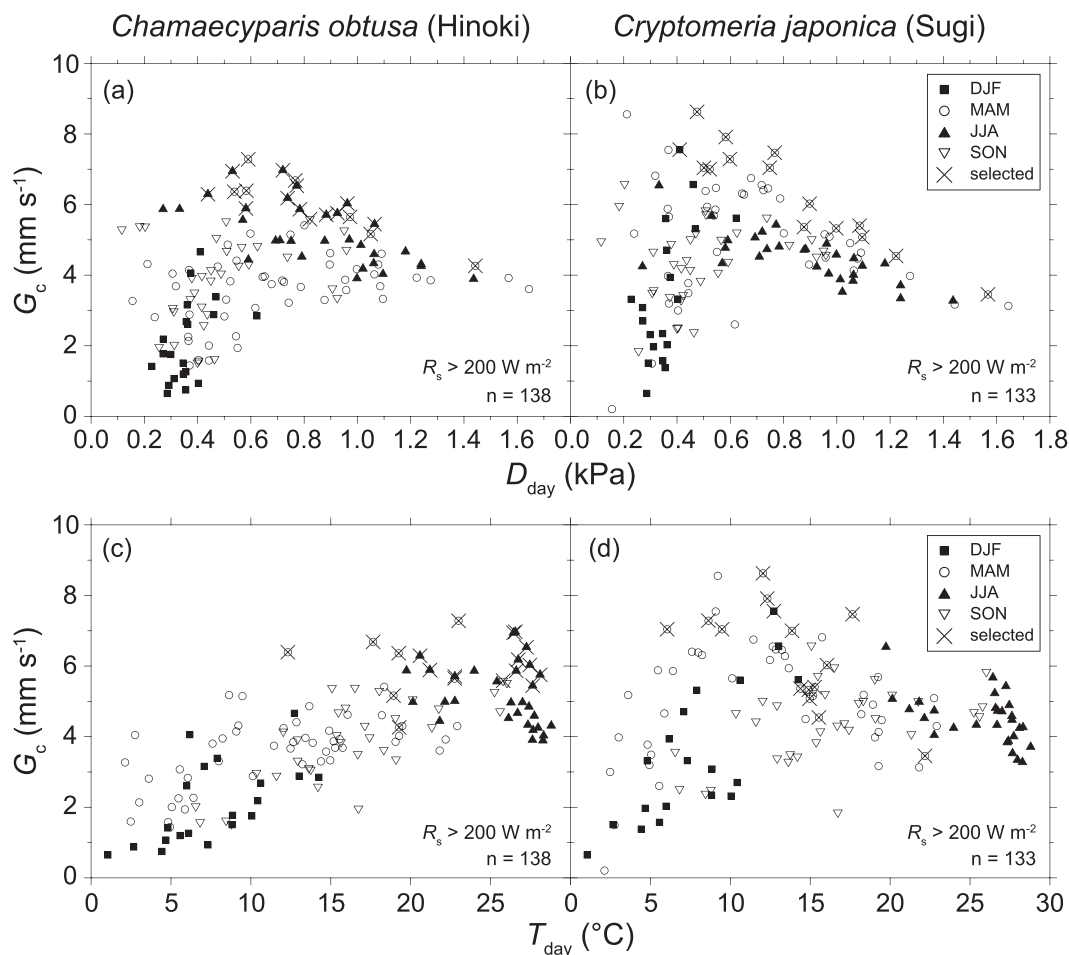


FIGURE 7 Canopy conductance (G_c) is presented in relation to (a, b) to mean vapour pressure deficit during daylight hours (0600–1800; D_{day}), and (c, d) mean air temperature during the daylight hours (T_{day}). The data of G_c above threshold value of R_s ($8.64 \text{ MJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1} = 200 \text{ W/m}^2$ averaged for 12 hours in a day) were used for the analyses. The points in upper envelopes in G_c versus D_{day} across 2011 are indicated by crosses (x). The data of G_c were separated by four seasons as January, February, and December (DJF); March–May (MAM); June–August (JJA); and September–November (SON) in 2011

3.7 | Stomatal sensitivity to atmospheric humidity

Values of G_c in Figure 7a and 7b are plotted against $\ln D_{day}$ (Figure 8a, b). The regression lines fitted to the select points exhibited significant interspecies differences in their slopes ($p = .013$, analysis of covariance; Figure 9a). The annual proportionality of m/G_{cref} was 0.33 in Hinoki and 0.61 in Sugi (Table 3). Thus, G_c of Hinoki is less sensitive to D_{day} when compared with that of Sugi on an annual basis. The seasonal shift of the lines was not significant in Hinoki ($p > .07$; Figure 8c) but was significant in the slope in Sugi ($p < .01$; Figure 8d). Also, the decrease in m/G_{cref} from MAM to JJA was larger in Sugi than in Hinoki (Table 3). Thus, the sensitivity of G_c to humidity is relatively stable in Hinoki but declines during the growing season in Sugi.

Comparing the species in MAM, the slope (m) was significantly smaller for Hinoki than Sugi ($p = .05$; Figure 9a), indicating low sensitivity in Hinoki. In JJA, m of Hinoki was not different from Sugi ($p = .95$), but G_{cref} was significantly higher ($p < .001$; Figure 9b) than that of Sugi. This indicates that G_c of Hinoki in JJA is relatively high, irrespective of the similarity to Sugi in D_{day} sensitivity. In addition, the m and m/G_{cref} of Sugi were generally higher than those in KHEW (Table 3), thus, the stomatal sensitivity of Sugi in YEC is generally greater than that in KHEW.

4 | DISCUSSION

4.1 | A process of interspecies difference in stand transpiration rate

Typically, a Hinoki tree grows more slowly and is, therefore, smaller than a Sugi tree of the same age. However, the smaller A_{stre} of Hinoki is cancelled out by its larger F_{dtre} , resulting in similar E_{tre} by Sugi (Figure 4c). Also, between the two stands with similar maturity, the smaller A_{ssta}/A_g of Hinoki was counterbalanced by a larger mean sap flux density; therefore, E_{sta} was similar in both stands. These results were derived during ideal autumn conditions, but a similar situation existed from May to October (Figure 6b).

At an annual time scale, the environmental response of E_{sta} must be considered. In the distribution of E_{sta} against D_{day} across a year, the difference between these two species was not clear (Figure 5b). However within the year, a seasonal shift of the relationship was prominent in a curve of Sugi (Figure 5d). Because interspecies difference in E_{sta} at a given D_{day} depended on the season, the seasonal course of E_{sta} showed different patterns between the two species

(Figure 6b). The difference was prominent, especially in early spring, which was responsible to the greater annual E_{sta} of Sugi than that of Hinoki (Figure 6c). Thus, our results suggest that the Hinoki stand uses less water than the Sugi stand on annual base, because E_{sta} of Sugi notably increases in early spring.

Many previous studies have demonstrated that the variation of E_{sta} among stands was explained by differences in total sapwood area (Alsheimer et al., 1998; Roberts, Vertessy, & Grayson, 2001). Indeed, the annual E_{sta} of Hinoki was smaller than that of Sugi, and A_{ssta}/A_g of Hinoki was smaller than that of Sugi. Also, Tateishi, Xiang, Saito, Otsuki, and Kasahara (2015) observed a decrease in June to October E_{sta} after thinning 50% of the stems at our site. However, we found that the interspecies difference of annual E_{sta} was produced by the pronounced J_s of Sugi during early spring (Figure 6a). This indicates that high-physiological activity in this season induced the greater annual E_{sta} of Sugi.

4.2 | Seasonal change in canopy conductance

The seasonal shift in the response of E_{sta} to D_{day} resulted from the shift in stomatal regulation of transpiration at the stand scale. We found that the response of G_c to D_{day} shifted differently between the two species. The G_c at a given D_{day} and the sensitivity to D_{day} in the Hinoki stand stayed at similar levels from MAM through JJA (Figures 7a and 8c). In the Sugi stand, however, a larger G_c and greater sensitivity to D_{day} occurred in MAM but not later in the growing

season (Figures 7b and 8d). Those interspecies differences in seasonality were related to the difference in the optimum temperature for G_c , which was 9.4 °C higher in Hinoki than in Sugi (Figure 7c,d). This difference seems consistent with the difference in the northern limits of their natural distributions. The limit of Hinoki is on Mt. Akaidake (37°10'N) and that of Sugi is 400 km farther north on Mt. Yagurayama (40°68'N; Hayashi, 1951). The annual mean temperature is about 2 °C higher for the northern limit for Hinoki than that for Sugi.

The G_c in Sugi increases particularly in early spring and then decreases and stabilizes (Figure 3c), whereas that in Hinoki remains stable from spring to autumn (Figure 2c). Those shifts seem to correspond with the respective seasonal courses of stem growth of Sugi and Hinoki reported in western (Yamashita, Kasuya, Nishimura, & Takeda, 2004) and eastern (Yamashita, Okada, & Kamo, 2006) Japan. In those two studies, stem growth of the two species increased rapidly from the beginning of April. At the end of June, about 90% of the annual growth was complete in Sugi. However, the growth still was about 60% complete at the end of June in Hinoki and only reached 90% in September. Yamashita et al. (2006) pointed out that, in Sugi, late wood formation started after June. In contrast, in Hinoki, early wood and late wood formed one after another from July; then late wood formed from September onward. Therefore, the robust water use in Sugi in early spring suggests that it is related to rapid growth during early wood formation. In contrast, stable water use in Hinoki throughout the growing season appears to be related to the moderate growth of this species.

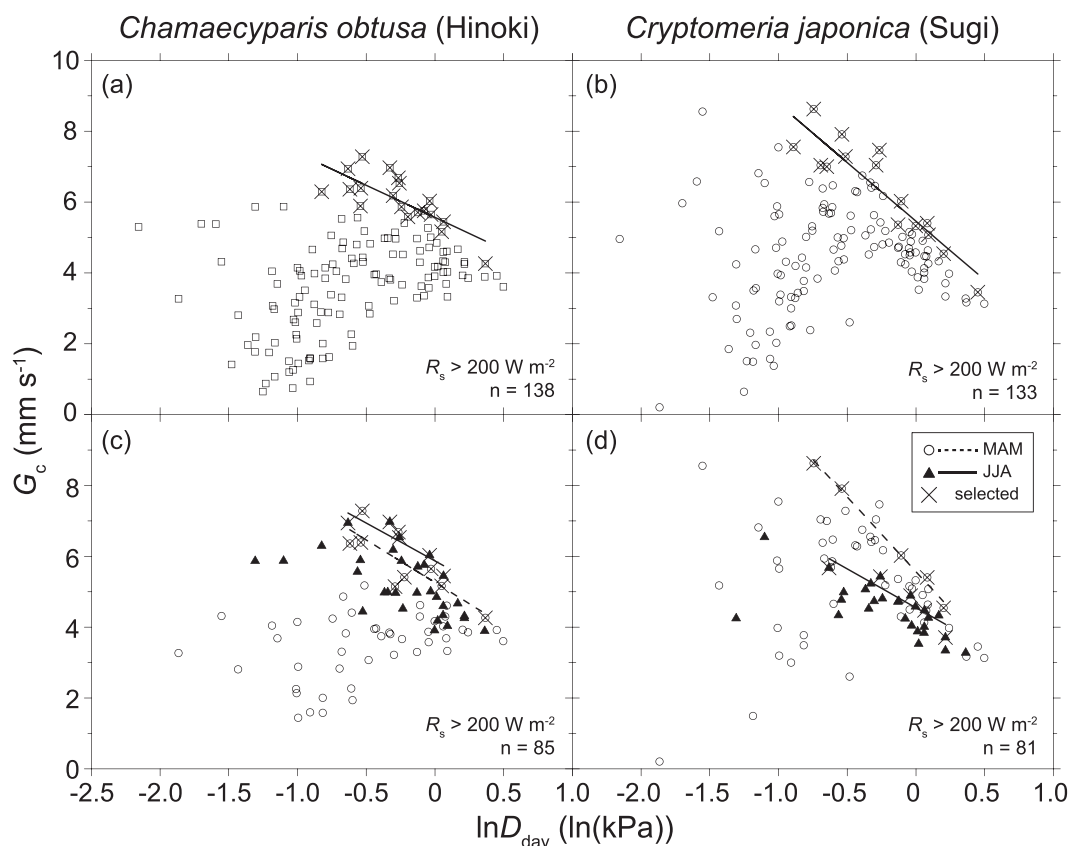


FIGURE 8 (a, b) Canopy conductance (G_c) in relation to natural logarithm of mean vapour pressure deficit during daylight hours (0600–1800; $\ln D_{day}$) throughout a year. The dataset for each species corresponds with that in Figure 7a, and 7b, where the data in upper envelopes are indicated by crosses (x). (c, d) The data of G_c during March–May (MAM) or June–August (JJA) are presented separately. The data in upper envelopes for each season are indicated by crosses (x). Lines and dotted lines indicate the regression lines on the selected data, whose parameters are shown in Figure 9 and Table 3

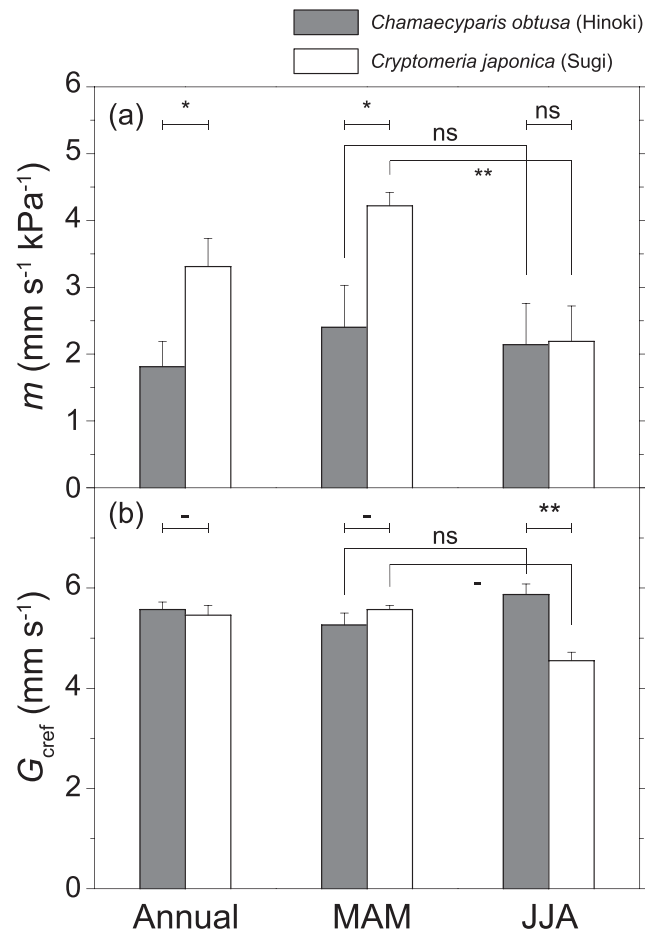


FIGURE 9 The parameters of regression lines on the plots of canopy conductance (G_c) versus natural logarithm of mean vapour pressure deficit during daylight hours (0600–1800; $\ln D_{\text{day}}$). m ($=dG_c/d(\ln D_{\text{day}})$) and G_{cref} indicates the slope and intercept of the regression line, respectively. The leading bars indicate the results on an annual basis (annual; Figure 8a, b). The following bars indicate the results during March–May (MAM; Figure 8c,d) and those during June–August (JJA), separately. Symbols indicate the statistical significances indicated by analysis of covariance for * ($p < .05$), ** ($p < .01$), ns (not significant), and - (comparison not possible)

TABLE 3 Parameters of the linear regression for the plots of G_c against $\ln D_{\text{day}}$

Site	Species	Period	G_{cref} (mm/s)	m (mm·s ⁻¹ ·kPa ⁻¹)	m/G_{cref} (kPa ⁻¹)	R^2
YEC (this study)						
	Hinoki	Annual	5.57 ± 0.15	1.81 ± 0.38	0.33	0.57**
		MAM	5.26 ± 0.24	2.40 ± 0.63	0.46	0.67**
		JJA	5.87 ± 0.21	2.14 ± 0.62	0.36	0.80*
	Sugi	Annual	5.46 ± 0.19	3.31 ± 0.42	0.61	0.83**
		MAM	5.57 ± 0.08	4.22 ± 0.20	0.76	0.99**
		JJA	4.55 ± 0.17	2.19 ± 0.53	0.48	0.85*
KHEW (Kumagai et al., 2008)						
	Sugi_UP	2005	3.67 ± 0.28	0.93 ± 0.26	0.25	
		2006	3.92 ± 0.37	1.68 ± 0.32	0.43	
	Sugi_LP	2005	5.02 ± 0.33	2.06 ± 0.36	0.41	
		2006	5.39 ± 0.29	2.63 ± 0.29	0.49	

Note. Data were obtained in the Yayama experimental catchment (YEC) and the Kahoku experimental watershed (KHEW). G_{cref} (reference G_c) indicates G_c at $D_{\text{day}} = 1$ kPa. Number with \pm operator indicates mean \pm standard error.

*Statistical significance of regression coefficient at $p < .05$ level.

**Statistical significance of regression coefficient at $p < .01$ level.

4.3 | Application to plantation management

Nagakura, Shigenaga, Akama, and Takahashi (2004) showed that Hinoki displayed more water-conserving characteristics than Sugi in potted seedlings based on a soil drought experiment. Our results show that annual transpiration of Hinoki was 87% that of Sugi in mesic soil conditions at the stand scale. Based on these results for seedlings and our results for adult trees, Hinoki can be characterized as exhibiting conservative water use traits at the single-tree and stand scales when compared with Sugi. This water-conserving trait of Hinoki will contribute to its ability to grow in drought-prone parts of a slope or to survive for a longer period when soil drought occurs in comparison with Sugi. Moreover, G_c of Hinoki was optimal when $T_{\text{day}} > 16$ °C, so this species will potentially provide ecosystem services more effectively than Sugi in warm sites.

In contrast, the faster growth rate of Sugi provides the benefit of producing greater timber volume. G_c of Sugi was optimal when $T_{\text{day}} < 17$ °C so that a Sugi plantation will be expected to produce over longer growing seasons than Hinoki, especially in colder locations. Unusual meteorological events in early spring, such as high temperature or severe drought perhaps caused by anticipated global warming may inhibit the growth of Sugi.

The variation in water use between the stands of the two species potentially affects the water yield from the catchment. In follow-on work, E_{sta} and the other evaporation components, such as canopy interception loss (Saito et al., 2013), will be summed to get evapotranspiration (ET) for each stand. This evaluation will be validated by the ET obtained with the soil water budget (e.g., Daly & Porporato, 2006). Moreover, the ET of each stand can be scaled up to the catchment scale using stand structural parameters across the catchment. Saito et al. (2015) has established a less labour-intensive method for evaluating A_{ssta}/A_g for each species in the catchment using airborne LiDAR technology. Those future studies will lead us to more complete understanding of the hydrologic cycle of these plantations.

5 | CONCLUSIONS

Our results show that the interspecies difference in annual E_{sta} was mainly produced by the difference in E_{sta} during a few months in early spring. During most of the growing season, E_{sta} of the Hinoki stand was similar to that of the Sugi stand. This is because the smaller total sapwood area per ground area of Hinoki was counterbalanced by the greater sap flux density. We found that the canopy conductance of Sugi is particularly high and sensitive in early spring. Our results suggest that a Sugi plantation in future will be expected to produce over a shorter growing seasons than present because of the effects of higher temperatures due to global warming.

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