



Title	Removal of understory dwarf bamboo ( <i>Sasa kurilensis</i> ) induces changes in water-relations characteristics of overstory <i>Betula ermanii</i> trees
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1 Removal of understory dwarf bamboo (*Sasa kurilensis*) induces changes in  
2 water-relations characteristics of overstory *Betula ermanii* trees

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1 Removal of understory dwarf bamboo (*Sasa kurilensis*) induces changes in  
2 water-relations characteristics of overstory *Betula ermanii* trees

3  
4 **ABSTRACT**

5 We investigated how removal of understory dwarf bamboo (*Sasa kurilensis* Makino et  
6 Shibata) affected growth and water-use of young *Betula ermanii* Cham. trees in a  
7 secondary forest in northern Japan. We compared current-year shoot morphology, leaf  
8 water-relations characteristics and whole-tree water use of *B. ermanii* trees growing with  
9 dwarf bamboo in the understory (intact plot) to those of trees growing where dwarf  
10 bamboo was experimentally removed (removal plot). Current-year shoot length and  
11 internode frequency increased, while internode length and individual leaf area decreased in  
12 response to dwarf bamboo removal. Carbon isotope composition ( $\delta^{13}\text{C}$ ) of leaves did not  
13 change indicating that leaf water-use efficiency was unaffected by the presence/absence of  
14 dwarf bamboo. Pressure-volume analysis indicated that leaves in the removal plot had  
15 lower water uptake ability. During mid-summer, trees in the removal plot sustained high  
16 sap flow velocity after peaking at midday, while that of trees in the intact plot declined. In  
17 addition, whole-tree sap flux and soil-to-leaf hydraulic conductance were both higher for  
18 trees in the removal plot. We inferred that the observed changes reflect hydraulic  
19 homeostasis of *B. ermanii* trees to maintain constant water-use efficiency in response to  
20 belowground competition with dwarf bamboo. Removal of dwarf bamboo is, therefore, an  
21 effective silvicultural prescription to enhance growth of overstory trees by relieving  
22 belowground competition for soil water.

23  
24 **Key Words:** hydraulic homeostasis, sap flow, shoot morphology, understory management,  
25 water relations

## 1 **Introduction**

2 Dwarf bamboos (genus *Sasa*; clonal evergreen plants) are prominent understory  
3 species of many temperate forests in East Asia, including Japan (Oshima 1961; Franklin et  
4 al. 1979). Dwarf bamboo cover is especially thick in areas of heavy snowfall, where culms  
5 reach over 2 m in height. In such areas, leaf area index (LAI: total leaf area per unit ground  
6 area) of dwarf bamboo may be as high as 4 to 6 and relative light intensity on the forest  
7 floor is less than 5% (Oshima 1962; Konno 2001; Kobayashi et al. 2004). Thick dwarf  
8 bamboo cover inhibits tree regeneration by preventing seedling establishment and  
9 suppressing sapling growth (Oshima 1962; Taylor and Qin 1988; Kobayashi et al. 2004).  
10 As a result, stands with thick dwarf bamboo cover completely lack sub-canopy trees and  
11 only consist of two layers of vegetation: overstory trees and understory dwarf bamboo  
12 (Franklin et al. 1979).

13 In contrast to the many studies conducted on the negative effects of dwarf bamboo  
14 on tree regeneration (e.g., Nakashizuka 1988; Hiura et al. 1996; Takahashi 1997), its effect  
15 on the growth of overstory trees has received less attention. Dense understory vegetation  
16 competes with overstory trees for nutrients and water (Sands and Nambiar 1984; Oren et al.  
17 1987; Riegel et al. 1992; Miller et al. 1998). For example, in secondary *Pinus densiflora*  
18 Sieb et Zucc. stands in south-central Japan, maximum net photosynthetic rate and stomatal  
19 conductance of needles increased (Kume et al. 2003) and diameter growth increased  
20 (Sakamoto et al. 2004) in response to removal of understory vegetation. This suggests that  
21 stand productivity could be considerably increased through adequate control of understory  
22 vegetation.

23 In northern Japan, dwarf bamboo is the dominant understory species in many  
24 secondary forests and plantations (Noguchi and Yoshida 2005). It is likely that overstory  
25 trees and dwarf bamboo compete for belowground resources such as water and nutrients.

1 Takahashi et al. (2003) found that diameter-growth rate of young *Betula ermanii* Cham. in  
2 Hokkaido, northern Japan, increased in the two years following experimental removal of  
3 dwarf bamboo. This and subsequent studies in the same stand indicated that soil water and  
4 N availability both increased after dwarf bamboo removal (Takahashi et al. 2003; Tripathi  
5 et al. 2006). A separate study showed that photosynthetic rate of *B. ermanii* leaves  
6 decreased as soil water potential decreased during the growing season in the stand with  
7 understory dwarf bamboo (Takahashi et al. 2004). The fine and coarse roots of both dwarf  
8 bamboo and *B. ermanii* are concentrated in the top 20 cm of the soil (Tripathi et al. 2005).  
9 Therefore, removal of dwarf bamboo is expected to increase the growth of overstory *B.*  
10 *ermanii* trees by relieving belowground competition for water and nutrients.

11 In this study, we investigated how removal of dwarf bamboo influenced the water-  
12 relations characteristics of overstory *B. ermanii* trees in a young secondary forest in  
13 northern Japan. We compared current-year shoot morphology, leaf water-relations  
14 characteristics and whole-tree water use of *B. ermanii* trees growing with dwarf bamboo in  
15 the understory to those of trees growing where dwarf bamboo was experimentally  
16 removed. From these results, we inferred the ecophysiological mechanisms that lead to  
17 increased growth rate of *B. ermanii* trees in response to dwarf bamboo removal and  
18 evaluated the effectiveness of this silvicultural prescription for enhancing the growth of  
19 stands with dense understory dwarf bamboo cover.

20

## 21 **Materials and Methods**

### 22 *Study site and sample trees*

23 The study was conducted in an even-aged, pure stand of *B. ermanii* (ca. 25-year-  
24 old) located atop the flat ridge of Mt. Jinja (580 m above sea level), Moshiri Village, in the  
25 Uryu Experimental Forest of Hokkaido University in Hokkaido Prefecture, northern Japan

1 (44° 20' N, 142° 15' E). The total stand area is ca. 5 ha. Mean annual temperature in the  
2 region is 3.0°C ranging from -12.1°C mean monthly temperature in January to 18.1°C in  
3 August. Annual mean precipitation is ca. 1500 mm. Snow depth during the winter months  
4 (December–March) reaches more than 2 m.

5 The *B. ermanii* stand initiated after dwarf bamboo (*Sasa kurilensis* Makino et  
6 Shibata) was removed in 1973 using a bulldozer to enhance tree regeneration; (scarification  
7 cf., Umeki 2003; Yoshida et al. 2005). Following dwarf-bamboo removal, *B. ermanii*  
8 regenerated naturally from seed. In the following years, dwarf bamboo recovered from  
9 clonal growth of surviving rhizomes in the soil and formed a dense understory. According  
10 to measurements made by Takahashi et al. (2003) in 1998 (the year of experimental  
11 removal of dwarf bamboo, see below), the average height of the dwarf bamboo was 2.5 m  
12 with an LAI of 0.9. The LAI of the overstory trees was 4. Stand density and basal area of  
13 overstory trees in 1998 were: 5165 trees ha<sup>-1</sup> and 18.2 m<sup>2</sup> ha<sup>-1</sup> (Takahashi et al. 2002).

14 At the beginning of the growing season in 1998, all above-ground parts of dwarf  
15 bamboo were pruned in a 20 x 30 m rectangular area of the stand (here after: removal plot)  
16 and along a 5-m buffer zone on all sides to study the effects of dwarf bamboo removal on  
17 the growth and physiology of overstory *B. ermanii*. Pruning of dwarf bamboo was  
18 conducted every year for the following three years until no new shoots emerged from  
19 surviving rhizomes. Some herbaceous plants established after dwarf bamboo removal but  
20 their cover and height were small. As a control, a 20 x 30 m plot was created ca 50 m from  
21 the removal plot in the area of the stand where dwarf bamboo was left intact (hereafter:  
22 intact plot). Both plots were within the same continuous stand of *B. ermanii* with a canopy  
23 height of ca. 11 m. Because the stand is located at the top of a flat ridge, stand conditions  
24 are homogeneous and the canopies of both plots are fully exposed in all directions. There  
25 was no difference in tree size between the two plots in 1998 before removal of dwarf

1 bamboo (Takahashi et al. 2002).

2

### 3 *Shoot morphology*

4           In 2001, one scaffolding tower (13 m tall) was erected in each of the plots to study  
 5 the canopy of *B. ermanii* trees. Five dominant trees near each tower were chosen as sample  
 6 trees (Table 1). These trees composed the upper canopy of the stand and the crown surface  
 7 of each tree was well exposed to direct sunlight. Toward the end of the growing season  
 8 (September 7, 2001), we selected six current-year shoots from the crown surface of each  
 9 sample tree for measurement of shoot morphology. For each current-year shoot, we  
 10 measured shoot length ( $L_s$ ) and number of internodes ( $N_i$ ). We measured the area of each  
 11 leaf ( $A_L$ ) using a leaf area meter (LI-3100-C, LiCor Inc., Lincoln, NE). The leaves were  
 12 then oven-dried to constant weight at 80°C to determine leaf dry mass. This was used to  
 13 calculate leaf mass per area (LMA). *Betula ermanii* exhibits successive leaf emergence  
 14 (Kikuzawa 1982) and early leaves had already fallen at the time of measurement.  
 15 Therefore, morphological data could only be measured on late leaves.

16

### 17 *Leaf water relations*

18           To compare water-use efficiency of leaves, the dried leaf samples were ground to  
 19 a fine powder. We analyzed carbon isotope composition of leaves using a system  
 20 consisting of an elemental analyzer (EA1108, Carlo-Erba, Milan, Italy) for combustion, an  
 21 interface (Finnigan MAT Confro, Bremen, Germany) and a stable isotope ratio mass  
 22 spectrometer (Finnigan MAT 252). Two duplicate samples (0.1–0.2 mg) were measured  
 23 for each leaf and  $\delta^{13}\text{C}$  (‰) values were calculated as:

$$24 \quad \delta^{13}\text{C} = \{(R_{\text{sample}}/R_{\text{standard}}) - 1\} \times 1000, \quad (3)$$

25 where  $R$  is the  $^{13}\text{C}/^{12}\text{C}$  ratio. Relative error between duplicates from the same leaf were less

1 than 1.0%. Measurements from the duplicates were averaged to obtain mean  $\delta^{13}\text{C}$  values  
2 for each leaf. Less negative values of  $\delta^{13}\text{C}$  reflect greater integrated water-use efficiency  
3 (carbon gain per water transpired) of leaves under field conditions (Farquhar et al. 1989).

4 We compared leaf water relations characteristics using the pressure-volume  
5 technique (Tyree and Hammel 1972). One current-year shoot was sampled from the crown  
6 surface of each sample tree toward the end of the growing season when leaf emergence and  
7 shoot elongation had ceased (September 5, 2001). Immediately after cutting, the branches  
8 were recut under water, sealed in plastic bags with moist paper, transported to the  
9 laboratory and kept under darkness overnight. Leaf water potential measurements were  
10 made on one fully expanded, mature leaf from each current-year shoot using a Scholander-  
11 type pressure chamber (Model 600, PMS Instruments Co., Corvallis, OR). Measurements  
12 were repeated with natural dehydration in the laboratory until well after turgor loss (five to  
13 six additional data points). The leaves were then oven-dried to constant weight for  
14 measurement of dry mass.

15 Leaf osmotic potential at saturation ( $\Psi_{\pi, \text{sat}}$ ), leaf water potential at turgor loss ( $\Psi_{l, \text{tlp}}$ )  
16 and relative water content at turgor loss ( $\text{RWC}_{\text{tlp}}$ ) were obtained from the pressure-  
17 volume curve for each leaf. Bulk modulus of elasticity of leaf tissue ( $\epsilon$ ) was determined for  
18 each leaf from the slope of the linear relationship between leaf water potential ( $\Psi_{\pi, \text{sat}}$  to  $\Psi_{l, \text{tlp}}$ )  
19 and free water content (Maruyama and Morikawa 1983).

#### 20 21 *Field observations of whole-tree water use*

22 We measured whole-tree sapflow velocity in four of the five sample trees from  
23 July to September of 2001 (Table 1). Thermal Dissipation Probes (TDP-30, Dynamax Inc.,  
24 Houston, TX) were inserted in opposite sides of the trunk of each tree at 1.3 m above  
25 ground level and insulated with styrofoam and reflective lining to measure sapflow velocity

1 by the heat dissipation technique (Granier 1987; Clearwater et al. 1999). The TDP-30  
 2 consisted of two probes, 1.2 mm in diameter and 30 mm in length. The two probes were  
 3 inserted into the main stem of the tree at 40 mm vertical spacing. The upper probe received  
 4 0.2 W of current which was dissipated as heat into the sapwood. Temperature difference  
 5 between the upper and lower probes ( $\Delta T$ , °C) was measured every 10 seconds by a  
 6 thermocouple and 30-minute averages were recorded on a data logger (CR10, Cambell  
 7 Scientific, Logan, UT). We calculated sapflow velocity ( $U$ , mm s<sup>-1</sup>) using the following  
 8 equation proposed by Granier (1987).

$$9 \quad U = 0.0119 k^{1.231} \quad (1)$$

$$10 \quad k = (\Delta T_M - \Delta T) / \Delta T \quad (2)$$

11 where,  $\Delta T_M$  is the temperature difference between the upper and lower probes during the  
 12 stable period at night when there is no sap flow. Equations (1) and (2) have been applied to  
 13 a wide variety of species and sites (Wullschlegel et al. 1998). However, because sapflow  
 14 velocity varies with depth from the cambium, accurate estimation of sapflow requires an  
 15 understanding of the radial profile of sap flux density along the length of the probe along  
 16 with measurements of sapwood area to develop species-specific empirical equations (Zang  
 17 et al. 1996; Wullschelger and King 2000; Nadezhina et al. 2002; Kubota et al. 2005). We  
 18 failed to obtain these data and our estimates of sapflow velocity may, therefore, be  
 19 inaccurate. However, assuming that the radial profile of sapflux does not change, our  
 20 estimates would still be valid for comparing sap flow velocity of total sapwood area  
 21 between the two stands relative to each other.

22 The calculated values of sapflow velocity were converted to m hr<sup>-1</sup> to facilitate  
 23 comparison with daily values for whole-tree sap flux. We calculated whole-tree sap flux  
 24 (m<sup>3</sup> m<sup>-2</sup> day<sup>-1</sup>) for clear days during the growing season by integrating the 30-min averages  
 25 of sapflow velocity of each tree over a 24-hour period centered around 12:00.

1           We measured diurnal changes in leaf water potential at the crown surface of the  
2 sample trees in the field using the pressure chamber. Measurements were taken on five  
3 fully expanded, mature leaves on two of the five sample trees in each plot (tree numbers: 1,  
4 3, 739, 765), six times during a 24-hour period on clear days (August 20, 30 and September  
5 5, 2001) at predawn, morning, noon, afternoon, late afternoon and predawn of the  
6 following day. We estimated soil-to-leaf hydraulic conductance from the relationship  
7 between diurnal measurements of leaf water potential and the corresponding measurement  
8 of sapflow velocity. Assuming a steady-state water flow within the soil-plant-air  
9 continuum, we estimated soil-to-leaf hydraulic conductance (unscaled) from the slope of  
10 the relationship between leaf water potential and sapflow velocity using data from all  
11 measurements of leaf water potential in the field.

12           We obtained meteorological data on daily solar radiation and precipitation from  
13 the weather station at the Moshiri Field Station of Hokkaido University about 5 km from  
14 the study site as a reference for weather conditions during measurement. Takagi et al.  
15 (2001) give a detailed description of the meteorological measurement system.

16

### 17 *Statistical analyses*

18           For logistic reasons, the experimental unit in this study, the stand, could not be  
19 replicated. However, given homogeneous stand conditions and proximity of the two plots,  
20 we assumed that the experimental design was sufficient to infer that any observed  
21 differences between plots in tree-level characteristics would be due to the effect of dwarf  
22 bamboo removal.

23           For leaf water relations and shoot morphology, mean values were compared  
24 between the intact and removal plots using the two-sample *t*-test by pooling data from all  
25 sampled leaves in each plot upon finding no significant difference between sample trees.

1 For sapflow velocity and whole-tree sap flux, we considered measurements made on the  
 2 four sample trees in each plot as replicates and compared plots using two-way ANOVA  
 3 with plot and sampling time as the two main effects. We compared the slope of the  
 4 relationship between leaf water potential and sapflow velocity between the plots using  
 5 regression analysis.

6

## 7 **Results**

### 8 *Shoot morphology*

9 Shoot length ( $L_s$ ) was longer in the removal plot than in the intact plot (Table 2,  $t$   
 10 = 2.19,  $P = 0.03$ ). This was because shoots in the removal plot had more internodes ( $t =$   
 11 5.59,  $P < 0.01$ ), although internode lengths ( $L_i$ ) were shorter than in the intact plot ( $t =$   
 12 7.95,  $P < 0.001$ ). Both leaf area ( $A_L$ ) and leaf mass per area (LMA) were smaller in the  
 13 removal plot than in the intact plot ( $t = 8.36$ ,  $P < 0.01$  and  $t = 2.77$ ,  $P < 0.01$ , respectively).

14

### 15 *Leaf water relations*

16 Carbon isotope composition ( $\delta^{13}C$ ) of leaves was similar for the two plots ( $t =$   
 17 0.482,  $P = 0.642$ ) indicating that integrated leaf water-use efficiency was not affected by  
 18 presence/absence of dwarf bamboo. Pressure-volume measurements indicated that leaves  
 19 in the removal plot lost turgor at higher leaf water potentials than leaves in the intact plot  
 20 (Table 3). Both leaf water potential ( $\Psi_{l, \text{tlp}}$ ) and relative water content at turgor loss point  
 21 ( $RWC_{\text{tlp}}$ ) were higher for leaves in the removal plot than for those in the intact plot ( $t =$   
 22 2.20,  $P = 0.03$  and  $t = 2.50$ ,  $P = 0.02$ , respectively). Although not statistically significant,  
 23 osmotic potential at saturation ( $\Psi_{\pi, \text{sat}}$ ) tended to be higher for leaves in the removal plot ( $t$   
 24 = 1.19,  $P = 0.29$ ). Bulk modulus of elasticity ( $\varepsilon$ ) was lower for leaves in the removal plot  
 25 than for leaves in the intact plot ( $t = 2.71$ ,  $P = 0.02$ ).

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*Field observations of whole-tree water use*

Maximum sapflow velocity was similar between the two plots ranging from 0.118 – 0.261 m h<sup>-1</sup> in the removal plot and 0.167 – 0.247 m h<sup>-1</sup> in the intact plot during July – September ( $F = 0.019$ ,  $P = 0.089$ ). However, comparison of diurnal patterns of sapflow velocity indicated that, on clear days, sapflow velocity of trees in the removal plot began to increase earlier in the day and maximum sapflow velocity was sustained until later in the day than trees in the intact plot (Figure 1). For example, on a typical clear day during the early growing season (July 27), sap flow velocity began to increase in tree 739 in the removal plot at 7:00 indicating that transpiration had begun. In contrast, sapflow velocity did not start until 8:00 for tree 4 in the intact plot. On this day, sapflow velocity reached peak values (0.227–0.263 m hr<sup>-1</sup>) at 12:30 in both plots. Subsequently, sapflow velocity of trees in the intact plot decreased more rapidly than that of trees in the removal plot. At 17:00, sapflow velocity of tree 4 of the intact plot had decreased to 0.265 (0.061 m hr<sup>-1</sup>) of the daily maximum, whereas that of tree 739 in the removal plot had only decreased to 0.575 (0.151 m hr<sup>-1</sup>). On a typical clear day during the mid-growing season (August 13), there was a one-hour difference between tree 739 and tree 4 in the time of initiation of sapflow. Sapflow velocity increased rapidly in the morning and reached peak values (0.227–0.266 m hr<sup>-1</sup>) around 10:30–11:30 in both plots. Subsequently, sapflow velocity of trees in the intact plot decreased rapidly, whereas trees in the removal plot sustained relatively high sapflow velocity until about 17:00. The difference between the plots in the diurnal pattern of sapflow velocity was more marked than during the early growing season. On a typical clear day during the late growing season (September 6), the diurnal patterns of sapflow velocity was similar for trees in both plots.

On clear days during the growing season, whole-tree sap flux was higher for trees

1 in the removal plot than for trees in the intact plot (Figure 2,  $F = 14.50$ ,  $P < 0.01$ ). Average  
2 daily sap flux on clear days (the mean of all observations shown in Figure 3) was  $1.37 \text{ m}^3$   
3  $\text{m}^{-2} \text{ day}^{-1}$  for the removal plot and  $1.17 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$  for the intact plot. The largest  
4 differences between the two plots were observed on August 21 after a prolonged dry period  
5 and during September 2-3. On these dates, sap flux in the removal plot was  $0.544\text{--}0.614$   
6  $\text{m}^3 \text{ m}^{-2} \text{ day}^{-1}$  greater than in the intact plot.

7         The relationship between sapflow velocity and leaf water potential indicated that  
8 soil-to-leaf hydraulic conductance was higher for trees in the removal plot than for those in  
9 the intact plot (Figure 3,  $F = 6.57$ ,  $P = 0.01$ ). Although sapflow velocity was similar  
10 between the plots at higher leaf water potentials, at leaf water potentials lower than  $-1.0$ ,  
11 sapflow velocity was higher for trees in the removal plot than for trees in the intact plot.  
12 Linear regression estimates of the slope of the relationship were  $-4.42$  and  $-5.83$  for trees  
13 739 and 765 in the removal plot and  $-6.31$  and  $-7.10$  for trees 1 and 3 in the intact plot.

14

## 15 **Discussion**

16         Our results showed that removal of understory dwarf bamboo caused plastic  
17 responses in the water use of *B. ermanii* trees through changes in morphological and water-  
18 relations characteristics at the leaf, shoot and whole-tree levels. Despite similar upper-  
19 canopy light conditions, we observed differences in shoot and leaf morphology between the  
20 intact and removal plots. Removal of dwarf bamboo increased both shoot length and  
21 internode frequency of current-year shoots, suggesting that shoot elongation and leaf  
22 production decreased in the intact plot due to belowground competition with dwarf  
23 bamboo. Dwarf bamboo removal also decreased LMA. Under water-stressed conditions,  
24 both shoot elongation and leaf expansion are suppressed, resulting in shorter internodes,  
25 smaller leaf area and greater LMA (Hsiao 1973; Morgan 1984). In our study, however,

1 shoot length was shorter, but internode length was longer and both leaf area and LMA were  
2 greater in the intact plot. Because the study site receives moderate summer precipitation  
3 and below ground water from snow melt, the decrease in soil water availability in the intact  
4 plot may not have been so great as to cause water stress. Therefore, we inferred that the  
5 observed changes are the result of homeostatic responses to maintain constant leaf water-  
6 use efficiency under variable water availability (hydraulic homeostasis *sensu* Meinzer et al.  
7 2004; Buckley and Roberts 2005).

8         Similar values of  $\delta^{13}\text{C}$  in both the plots indicated that water-use efficiency of  
9 leaves during the growing season was not affected by the presence/absence of dwarf  
10 bamboo. This contradicts results obtained for *Pinus densiflora* where understory vegetation  
11 restricted water uptake by leaves and leaf water-use efficiency (inferred from  $\delta^{13}\text{C}$  values)  
12 was higher than in the managed stand where understory vegetation was removed (Kume et  
13 al. 2003). The apparent homeostasis in leaf water-use efficiency of the *B. ermanii* trees in  
14 this study seems to have been realized through complementary changes in water-relations  
15 characteristics at the leaf and whole-tree levels.

16         In the intact plot, greater individual leaf area would increase leaf-level  
17 transpiration, while greater LMA would increase transpiration rate per leaf area. Pressure-  
18 volume measurements indicated that leaves of trees in the intact plot have greater water  
19 uptake ability than leaves in the removal plot. These changes would compensate for the  
20 reduction in leaf number (fewer internodes) to maintain constant water-use efficiency at the  
21 shoot level for trees in the intact plot. The increased water uptake ability of individual  
22 leaves in the intact plot would not be effective if leaf longevity was reduced. In general,  
23 leaf longevity is positively correlated with LMA (Kudo 1996; Wright et al. 2005). We  
24 observed that leaf longevity was not noticeably reduced in the intact plot (T. Kobayashi,  
25 unpublished data). Therefore, we inferred that increased water uptake ability of leaves in

1 the intact plot reflect hydraulic homeostasis to maintain constant leaf-level water-use  
2 efficiency in response to belowground competition with dwarf bamboo.

3         Although removal of dwarf bamboo increased the growth rate of overstory *B.*  
4 *ermanii*, stand-level LAI did not increase (A. Sumida, unpublished data), suggesting that  
5 tree-level leaf area might also be maintained. At the whole-tree level, trees in the removal  
6 plot maintained higher sapflow velocity than trees in the intact plot during the afternoon in  
7 early- to mid-summer when evapotranspirational demand was high. In addition, whole-tree  
8 sap flux and soil-to-leaf hydraulic conductance increased in response to dwarf bamboo  
9 removal. These results suggested that water use of trees in the intact plot was negatively  
10 affected by the presence of dwarf bamboo. Photosynthetic capacity of *B. ermanii* decreases  
11 with decreasing soil water availability due to decreasing leaf stomatal conductance (Kitao  
12 et al. 2003; Takahashi et al. 2004). Because the growing season in northern Japan is  
13 relatively short, maintaining transpiration and photosynthetic production on clear days  
14 during the early- to mid-summer may be an important factor controlling the annual growth  
15 rate of trees. Therefore, the restrictions on whole-tree water use during this period may be a  
16 determining factor for the lower growth rate of *B. ermanii* in the intact plot compared with  
17 the removal plot (Takahashi et al. 2003).

18         Both stomatal regulation of leaf water potential and whole-tree hydraulic  
19 conductance are important for maintaining stomatal conductance and hence photosynthetic  
20 capacity (Sperry et al. 2002; Tyree 2003). Under field conditions, stomatal conductance  
21 may be maintained by either 1) increasing the water uptake capacity of leaves by lowering  
22 the leaf water potential; or 2) increasing the water absorption capacity of the whole tree by  
23 increasing the soil-to-leaf hydraulic conductance (Ishida et al. 1992; Nardini et al. 1999).  
24 For trees in the intact plot, the greater water uptake ability of leaves may compensate for  
25 the lower soil-to-leaf hydraulic conductance and maintain leaf gas exchange capacity under

1 conditions of belowground competition with dwarf bamboo. Cienciala et al. (1994) found  
2 that irrigation increased basal area increment, but water-use efficiency (dry matter  
3 production per unit water transpired) was similar among irrigated, control and drought-  
4 treated stands of 24-year-old *Picea abies* L. Karst. in Sweden.

5 We should also note that hydraulic sufficiency can also be maintained by  
6 modifying the relationship between conducting area and leaf area (Sobrado 2003).  
7 Although we did not measure sapwood area and tree-level leaf area in this study, it can be  
8 conceived that trees in the intact plot had more conducting area relative to leaf area and  
9 thus maintained similar water-use efficiency as trees in the removal plot. Tripathi et al.  
10 (2005) found that fine-root proportion of *B. ermanii* in the soil increased in response to  
11 dwarf bamboo removal, whereas fine-root biomass was not affected. This suggested that  
12 relative biomass allocation to belowground was greater in the intact plot, which could have  
13 also contributed to maintaining hydraulic sufficiency.

14 The allocation of water between overstory trees and understory vegetation is  
15 critical to tree productivity in managed stands (Sands and Nambiar 1984; Oren et al. 1987;  
16 Miller et al. 1998). Minimizing understory evapotranspiration is especially important  
17 during early stages of stand growth when the potential growth rate of overstory trees is  
18 high, but more open canopy conditions promote development of thick understory  
19 vegetation. In addition to inhibiting regeneration and growth of overstory trees, dwarf  
20 bamboo contributes a large fraction of the transpiring leaf area, biomass and photosynthetic  
21 production in many Japanese forests (Sakai and Akiyama 2005). Removal of dwarf  
22 bamboo in relatively young stands may greatly enhance productivity of overstory trees in  
23 the long-term. The most recent study in this stand showed that removal of understory dwarf  
24 bamboo increased net carbon gain and transpiration rates of overstory *B. ermanii* trees  
25 (Kobayashi et al. 2006) indicating that dwarf bamboo removal is an effective silvicultural

1 prescription not only to improve the understory light environment for enhancing tree  
2 seedling establishment, but also to enhance growth of overstory trees by relieving  
3 belowground competition.

4

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16 *globulus* with position in sapwood and use of a correction coefficient. *Tree Physiol*  
17 16:697-703
- 18
- 19

- 1 Table 1. Structural properties of the sample trees of *Betula ermanii* growing with and  
 2 without understory dwarf bamboo (*Sasa kurilensis*) in northern Japan (intact plot and  
 3 removal plot, respectively).

Tree	Height (m)	DBH (cm)
Intact plot		
1*	11.5	11.0
2*	10.7	10.1
3*	11.7	9.6
4*	10.9	10.1
5	11.4	8.6
Removal plot		
739*	11.2	8.6
738*	12.2	10.9
737*	12.7	12.5
765*	12.3	11.3
811	11.6	8.0

- 4 \* trees used for sapflow measurement.

1 Table 2. Comparison of shoot and leaf morphology of *Betula ermanii* trees growing with  
 2 and without understory dwarf bamboo (*Sasa kurilensis*) in northern Japan (intact plot and  
 3 removal plot, respectively). Mean values  $\pm$  one standard deviation are shown for 30 current-  
 4 year shoots sampled from six trees in each plot.

Treatment	$L_s$ (mm)	$N_i$	$L_i$ (mm)	$A_L$ (cm <sup>2</sup> )	LMA (g m <sup>-2</sup> )
Intact plot	229.8 $\pm$ 94.1	7.1 $\pm$ 2.2	45.6 $\pm$ 10.7	42.8 $\pm$ 9.8	85.5 $\pm$ 10.5
Removal plot	275.2 $\pm$ 66.9*	9.7 $\pm$ 1.4*	36.3 $\pm$ 9.2*	34.9 $\pm$ 7.6*	80.5 $\pm$ 12.7*

6  $L_s$ : length of current-year shoot

7  $N_i$ : number of internodes per current-year shoot

8  $L_i$ : internode length

9  $A_L$ : leaf area

10 LMA: leaf mass per area

11 \*: Significantly different from intact plot (Two-sample *t*-test,  $P < 0.05$ ).

1 Table 3. Carbon isotope composition and leaf water-relations characteristics of *Betula*  
 2 *ermanii* trees growing with and without understory dwarf bamboo (*Sasa kurilensis*) in  
 3 northern Japan (intact plot and removal plot, respectively). Mean values  $\pm$  one standard  
 4 deviation are shown for each plot.

Treatment	$\delta^{13}\text{C}$ (‰)	$\text{RWC}_{\text{tlp}}$	$\Psi_{\text{l, tlp}}$ (MPa)	$\Psi_{\pi, \text{sat}}$ (MPa)	$\varepsilon$ (MPa)
Intact plot	$-28.50 \pm 0.68$	$0.83 \pm 0.013$	$-2.17 \pm 0.09$	$-1.25 \pm 0.13$	$14.73 \pm 1.36$
Removal plot	$-28.25 \pm 0.71$	$0.85 \pm 0.011^*$	$-2.02 \pm 0.10^*$	$-1.16 \pm 0.08$	$11.33 \pm 2.11^*$

6  $\delta^{13}\text{C}$ :  $[(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$ , where  $R$  is the  $^{13}\text{C}/^{12}\text{C}$  ratio.

7  $\text{RWC}_{\text{tlp}}$ : relative water content at turgor loss point,

8  $\Psi_{\text{l, tlp}}$ : leaf water potential at turgor loss point,

9  $\Psi_{\pi, \text{sat}}$ : osmotic potential at saturation

10  $\varepsilon$ : bulk modulus of elasticity

11 \*: Significantly different from intact plot (Two-sample  $t$ -test,  $P < 0.05$ ).

## 1 **Figure captions**

2

3 Figure 1. Diurnal patterns of relative sapflow velocity (sapflow velocity relative to the  
4 daily maximum value for each tree) of *Betula ermanii* trees growing with and without  
5 understory dwarf bamboo (*Sasa kurilensis*) in northern Japan (intact plot and removal plot,  
6 respectively). Typical diurnal patterns on clear days in July, August and September are  
7 shown for two of the four sample trees in each plot: intact plot (trees 2 and 4, thick lines)  
8 and removal plot (trees 739 and 765, thin lines). Diurnal changes in temperature (thin line)  
9 and solar radiation (thick line) are shown above.

10

11 Figure 2. Whole-tree sap flux ( $\text{m}^3 \text{m}^{-2} \text{d}^{-1}$ ) of *Betula ermanii* trees growing with and  
12 without understory dwarf bamboo (*Sasa kurilensis*) in northern Japan (intact plot and  
13 removal plot, respectively). Daily sap flux on clear days during the growing season were  
14 calculated for each plot (intact plot: filled symbols, removal plot: open symbols) based on  
15 measurements of total daily sapflow for the four sample trees in each plot. Error bars  
16 indicate one standard deviation. Measurements for the intact plot in early July were lost  
17 due to mechanical failure. Bars show daily precipitation measured at the weather station  
18 near the study site.

19

20 Figure 3. Relationship between sapflow velocity and leaf water potential of *Betula ermanii*  
21 trees growing with and without understory dwarf bamboo (*Sasa kurilensis*) in northern  
22 Japan (intact plot and removal plot, respectively). Common symbols indicate  
23 measurements from the same tree: intact plot (filled symbols and thick lines), removal plot  
24 (open symbols and thin lines)



Figure 1

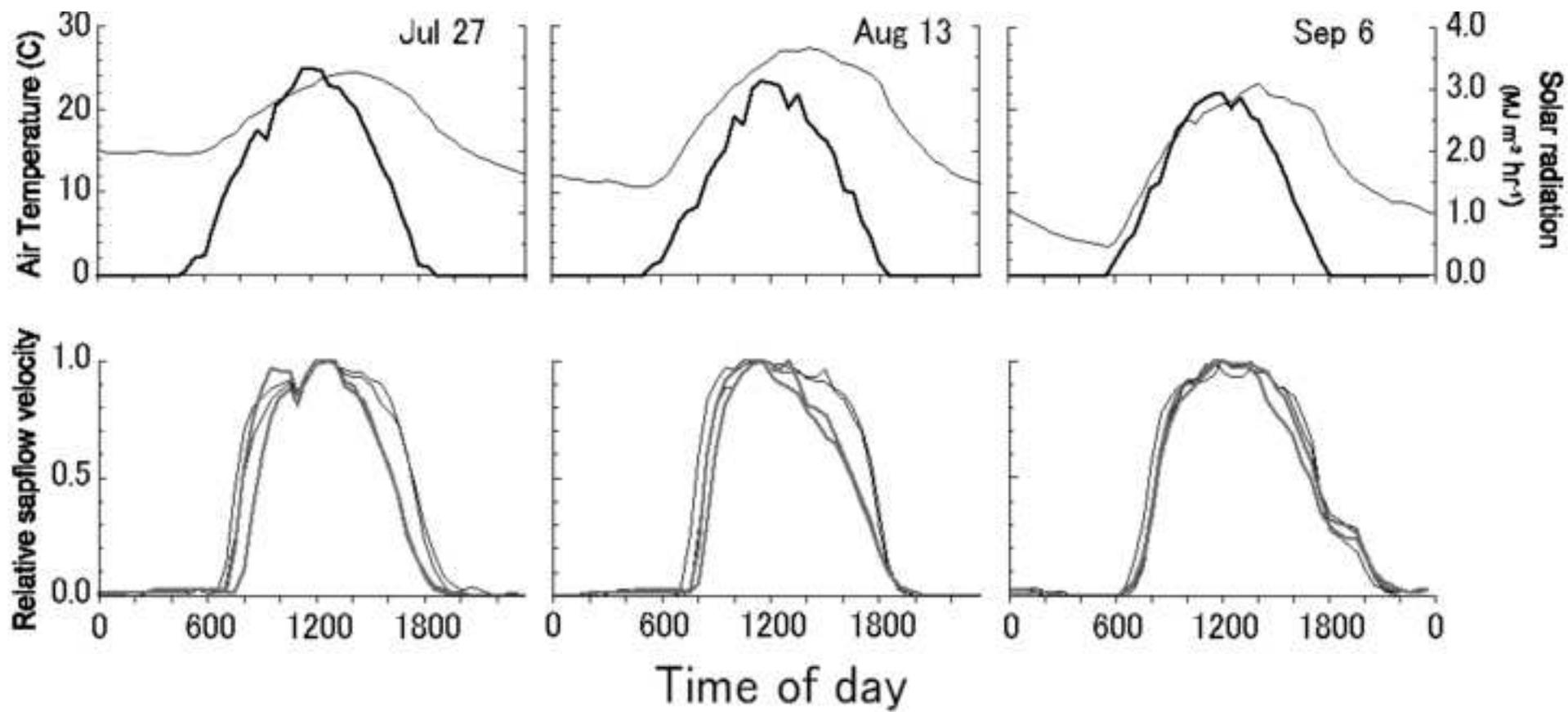


Figure2

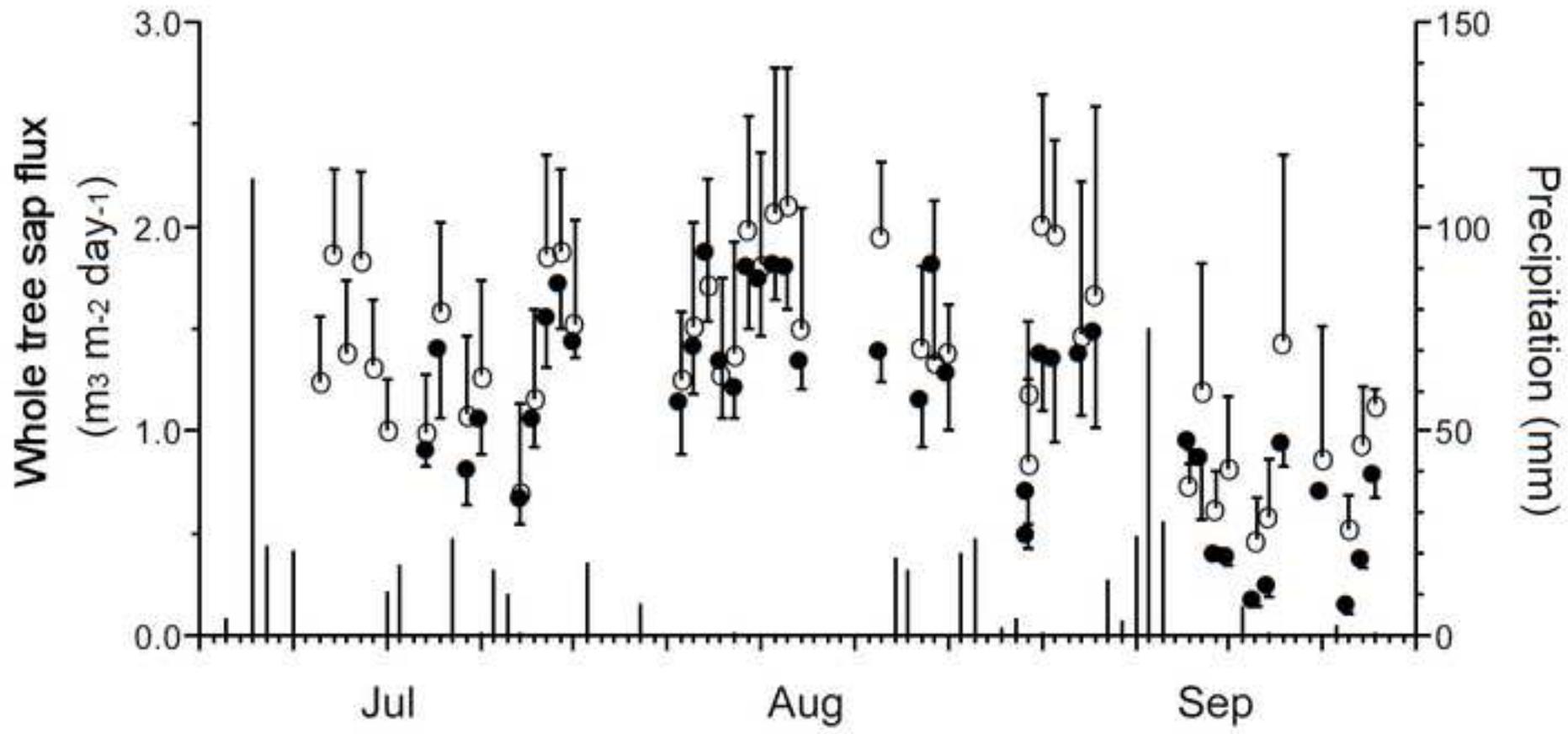


Figure3

