# Effects of understory dwarf bamboo on soil water and growth of overstory trees in a dense secondary *Betula ermanii* forest, northern Japan

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This manuscript consists of 16-typed pages including figure legends, 2 tables and 3 figures.

Effects of understory dwarf bamboo (*Sasa kurilensis*) on soil water and the growth of overstory trees were studied in a dense secondary forest of *Betula ermanii* in northern Japan. Four plots were established in a dense *Betula ermanii* forest with *Sasa kurilensis* in the understory, and *Sasa* was removed in two plots of the four. Annual increment of trunk diameter of each tree was measured in the first two years from the beginning of the experiment. Soil water potential was similar between the plots with and without *Sasa* just after significant rainfall, but was less negative between rainfall events in the plot without *Sasa* than in the plot with *Sasa*. This suggests that the *Sasa* removal slows the reduction of soil water after rainfall events. The relative growth rate of trunk diameter of *Betula ermanii* increased with tree size in all plots because taller trees strongly suppressed smaller ones in this dense forest. The growth rates of *Betula ermanii* were higher in the plots without *Sasa* than in the plots with *Sasa*. However, the difference in growth rates between the plots with and without *Sasa* tended to be smaller at smaller size classes, probably because smaller trees were strongly suppressed by larger ones, irrespective of the presence/absence of *Sasa*. Therefore, the *Sasa* removal increases soil water and growth of larger *Betula ermanii* in this dense forest during the first two years after the *Sasa* removal. This study suggests that *Sasa* reduces the growth of larger *Betula ermanii* in this dense stand, at least partially, by decreasing available soil water to these trees.

**Key words:** *Betula ermanii*; Competition; Dwarf bamboo; Growth; *Sasa kurilensis*; Soil water availability

## INTRODUCTION

Forest understory vegetation is often dominated by herbaceous species in temperate and boreal forests (Roberts *et al*. 1980; Nakashizuka & Numata 1982; Taylor & Qin 1988; Kojima 1994; Gratzer *et al*. 1999; Takahashi *et al*. 1999). Dwarf bamboos, the genus *Sasa*, form dense undergrowth in Japanese forests (Suzuki 1961, 1962). Leaf area index (total leaf area per unit ground area, LAI) of dwarf bamboo sometimes exceeds 5.0 in open habitats (Oshima 1962; Kitamura *et al*. 1996). When dwarf bamboo is abundant, soil surface is heavily shaded. Konno (2001) reported that the relative light intensity under the dense foliage of *Sasa tsuboiana* Makino was only ca. 1%. Many researchers have reported that tree species hardly regenerate in forests with bamboo cover, and therefore, many attempts have been made to reveal the effects of dwarf bamboo on tree seedling establishment (Nakashizuka & Numata 1982; Nakashizuka 1988; Takahashi 1997; Kudoh *et al*. 1999). However, there have been few studies on the effects of dwarf bamboo on the growth of overstory trees.

Plants compete for resources such as light, soil water and nutrients. In terms of competition for light in dense stands, taller plants suppress the growth of smaller ones due to light interception (i.e., asymmetric competition). Although understory *Sasa* cannot shade overstory trees, it is likely to affect growth of overstory trees through belowground competition for soil resources (water and/or nutrients) because belowground competition is supposed to be symmetric (cf. Weiner 1990). Therefore, resources in the soil are competed between overstory and understory plants. However, little empirical evidence is available to show if understory *Sasa* affects the growth of overstory trees through belowground competition for resources in the soil. Examining this prediction is essential for understanding forest dynamics, especially in Japan, where

*Sasa* abundance is high.

The present study attempts to reveal whether or not the presence of understory dwarf bamboo (*Sasa kurilensis* Makino et Shibata) reduces soil water and the growth of overstory trees in a dense secondary *Betula ermanii* Cham. forest in northern Japan. We established two experimental plots with *Sasa* understory and two others without *Sasa* understory, then compared soil water potential and the growth rates of *Betula ermanii* between the plots with and without *Sasa* understory.

## METHODS

### Study site

This study was carried out at the Uryu Experimental Forest of Hokkaido University in northern Japan (44˚ 20' N, 142˚ 15' E). Mean annual temperature was 3.0˚C, and the mean temperatures of July and January were 17.9˚C and –12.1˚C, respectively, during 1961–1980. Annual precipitation was 1572 mm. The vegetation of the Uryu Experimental Forest consists of coniferous species such as *Abies sachalinensis* Mast. and *Picea glehnii* Mast. and deciduous broad-leaved species such as *Quercus crispula* Blume, *Acer mono* Maxim., *Acer palmatum* subsp. *matsumurae* Koidz., *Betula ermanii, Magnolia obovata* Thunberg and *Tilia japonica* Shimonkai (Takahashi *et al*. 2003). Nomenclature follows Ohwi (1975), Satake *et al*. (1993) and Ohashi (2001). Leaf emergence of deciduous broad-leaved tree species begins in late May or early June, and leaves completely fall by mid- or late October.

The study site was located at a flat ridge on Mt. Jinja (580 m above sea level) in the Uryu Experimental Forest. This area was a secondary forest of *Betula ermanii*. The forest floor was covered with dwarf bamboo (*Sasa kurilensis*). The height of *Sasa kurilensis* was up to ca. 2.5 m. LAI of the understory *Sasa* layer was 0.9, and LAI of the overstory tree layer was 4 (our unpublished data).

### Plot survey

In 1998, two 15-m × 15-m plots (Plot-1a and Plot-1b) were established in a dense secondary *Betula ermanii* stand with 6-m trunk height. The other pair of 20-m × 30-m plots (Plot-2a and Plot-2b) was established in another dense stand with 9-m trunk height (1 km away from the first pair of the plots). There were no canopy gaps in the four plots. The distance between Plot-1a and Plot-1b was 60 m, and that between Plot-2a and Plot-2b were 30 m.

All trees within the four plots were tagged at breast height in late September (the very end of the growing season) in 1998. The trunk height and the trunk circumference 5-cm below the number label of each tree were measured. After the measurement of the trunk height and trunk circumference, all *Sasa* within Plot-1b, Plot-2b and a 5-m buffer were cut with trimmers and sickles, and then were transformed to the outside of the plots. The trunk circumference was re-measured carefully at the exact location in late September in 1999 and 2000, and the dead trees during 1998–2000 were also recorded.

### Soil water potential

Soil water potential at a depth of 25 cm was manually monitored in the four plots with tensiometers from July to October at about 10-day intervals in 1998 (before *Sasa* removal) and 1999 (after *Sasa* removal). Air pressure inside the tensiometers was measured with a handy manometer (PG-100, Copal Electronics Corp., Tokyo). Replicates of the tensiometers were ca. 10–20 in each plot in each year (1998 or 1999).

The tensiometers were randomly placed within each plot. The measurements were conducted around noon. Daily rainfall was measured at the station of the experimental forest (5 km away from the study area).

### Data analyses

The effect of *Sasa* removal on seasonal changes in soil water potential was analyzed using a repeated measures ANOVA with one between-subject factor (*Sasa* treatment) and one within-subject factor (day). The analysis was conducted for each of the two growing seasons, 1998 (before *Sasa* removal) and 1999 (after *Sasa* removal). Although we measured soil water potential in all the plots in both the years (1998 and 1999), most of the tensiometers installed in Plot-1a could not be measured at each measurement time in 1999 because the height of water inside the tensiometers were too low to measure. Therefore, we could not compare soil water potential between Plot-1a and Plot-1b. The low height of water inside the tensiometers in Plot-1a with *Sasa* indicates drier conditions in the soil in this plot than in Plot-1b without *Sasa*. In addition, some tensiometers could not be measured also in the other plots because of the reduced water inside the tensiometers. These tensiometers were excluded from the analysis.

The relative growth rate of trunk diameter at breast height (DBH) was calculated for each tree for each of the two growing periods (from 1998 to 1999, and from 1999 to 2000) as ($\ln D_1 - \ln D_0$), where $D_0$ and $D_1$ are DBHs at the beginning and the end of the measurement period, respectively. Trees in Plot-1a and Plot-1b were divided into six size classes at 1-cm intervals between 1.0 and 7.0 cm in DBH, and trees in Plot-2a and Plot-2b were divided into five classes at 2-cm intervals between 2.0 and 12.0 cm in DBH. The relative growth rates of DBH were compared between the plots with and without *Sasa*, by using a repeated measures ANOVA with two between-subject factors (*Sasa* treatment, DBH class) and one within-subject factor (year). The analysis was performed for each pair of the plots.

## RESULTS

### Plot description

*Betula ermanii* occupied 96% of the total density in both Plot-1a and Plot-1b, and 72% in both Plot-2a and Plot-2b (Fig. 1). Subordinate trees were all deciduous broad-leaved species: *Phellodendron amurense* Rupr., *Sorbus commixta* Hedland, *Salix caprea* L. and *Aralia elata* Seem.

Although the size structure was not largely different between the paired plots in each stand, total densities were lower in Plot-1a and Plot-2b than in Plot-1b and Plot-2a, respectively (Fig. 1). On the contrary, mean DBHs were larger in Plot-1a and Pot-2b than in Plot-1b and Plot-2a, respectively. Thus, Plot-1a and Plot-2b developed slightly more than Plot-1b and Plot-2a, respectively, because there were many smaller trees in Plot-1b and Plot-2a. As for the four plots established in this study, the slope of the regression was –1.51 when log-transformed mean volume of individual trees within a plot was plotted against log-transformed tree density of the plot (data not shown). This indicates that these stands were over-crowded and self-thinning occurred, because the slope of the regressions is expected to be –1.5 for stands under self-thinning process (cf. Yoda *et al*. 1963; Kikuzawa 1988).

### Soil water potential

In 1998 (before *Sasa* removal), seasonal trends in soil water potential at a depth of 25 cm were similar between Plot-2a and Plot-2b (Fig. 2, Table 1, $p = 0.989$ for treatment).

Although soil water potential in each plot changed in response to rainfall (Fig. 2, Table 1, ANOVA, $p < 0.001$ for day), there were no consistent differences in soil water potential between the two plots before *Sasa* removal (e.g., soil water potential was more negative in Plot-2a than in Plot-2b on day 207, but was less negative on days 217 and 230). In 1999 (after *Sasa* removal in Plot-2b), soil water potential was more negative in Plot-2a with *Sasa* than in Plot-2b without *Sasa* throughout the growing season (Fig. 2, Table 1, ANOVA, $p < 0.001$ for treatment). The absolute difference in soil water potential between the two plots was larger between significant rainfall events than just after significant rainfall (Table 1, ANOVA, $p < 0.001$ for day × treatment interaction).

### Growth of *Betula ermanii*

For each pair of the plots, the relative growth rates of DBH of *Betula ermanii* were different between the two growing seasons (Fig. 3, Table 2, $p < 0.05$ for year). Especially in Plot-1a and Plot-1b, the relative growth rate decreased at all size classes in 2000. The relative growth rates were different among size classes in each stand, i.e., the relative growth rates were lower at smaller size classes for each pair of the plots (Fig. 3, Table 2, $p < 0.001$ for size). As for the effect of understory *Sasa* on the growth of overstory *Betula ermanii*, the relative growth rates were lower in the plot with *Sasa* than those in the plot without *Sasa* for each pair of the plots (Fig. 3, Table 2, at least $p < 0.005$ for treatment). This tendency was more conspicuous at larger size classes in the comparison between Plot-1a and Plot-1b (Fig. 3, Table 2, $p < 0.001$ for treatment × size interaction). Although the relative growth rates at larger size classes also seemed to be lower in Plot-2a with *Sasa* than those in Plot-2b without *Sasa*, statistical significance was not detected (Fig. 3, Table 2, NS for treatment × size interaction).

## DISCUSSION

Soil water potential was more negative in Plot-2a with *Sasa* than in Plot-2b without *Sasa* in 1999, although soil water potential was similar between the two plots in 1998 (before *Sasa* removal). This suggests that *Sasa* removal increased soil water. Several researchers also reported that removal of understory vegetation increased soil water (Lambert *et al*. 1971; Kelliher & Black 1986; Oren *et al*. 1987), apparently as a result of decreased transpiring leaf area. Roberts *et al*. (1980) and Kelliher & Black (1986) reported that transpiration of understory plants was ca. 20–30% of total forest transpiration. Probably, the water uptake by *Sasa* transpiration cannot be ignored also in our study site. In addition, *Sasa* may reduce soil water not only by their transpiration but also by their rain interception. However, the difference in soil water potential between the plots with and without *Sasa* was larger between the significant rainfall events compared with just after the rainfall events. This suggests *Sasa* reduces soil water mainly by their transpiration rather than by their rain interception.

The relative growth rate of DBH of *Betula ermanii* increased with tree size in all the plots, which suggests intense asymmetric competition for light in this dense stand, i.e., taller trees suppressed smaller ones but hardly *vice versa* (cf. Cannell *et al*. 1984; Schmitt *et al*. 1987; Weiner 1990). As for the effect of understory *Sasa* on the growth of overstory *Betula ermanii*, the growth rates of *Betula ermanii* tended to be lower in the plots with *Sasa* than in the plots without *Sasa*. Our previous study revealed that the maximum photosynthetic rate of *Betula ermanii* decreases as soil water potential gets more negative (Takahashi *et al*., unpublished data). This is probably due to stomatal closure in response to the limitation of soil water availability (Babalola *et al*. 1968; Bréda *et al*. 1995; Granier & Bréda 1996; Kallarackal & Somen 1997; Cienciala *et al*.

1998; Miller *et al*. 1998; Oren *et al*. 1998). Therefore, it seems that lower growth rates of *Betula ermanii* in the plots with *Sasa* than in the plots without *Sasa* are partly due to lower photosynthetic production in response to the limitation of soil water availability due to competition for water with *Sasa*. On the other hand, the difference in the growth rates between the plots with and without *Sasa* tended to be smaller at smaller size classes, especially in the pair of Plot-1a and Plot-1b. The small differences are probably because smaller trees were strongly suppressed by larger ones, irrespective of the presence/absence of *Sasa*. Therefore, it is likely that *Sasa* reduces the growth of larger *Betula ermanii* trees by reducing available soil water to these trees in this dense forest. However, this scenario must be treated with caution because we could not eliminate other possible factors affecting the growth of *Betula ermanii*. In particular, competition for nutrients is probably important, i.e., *Betula ermanii* might grow more in the plots without *Sasa* than in the plots with *Sasa* as a result of increased access to soil nutrients rather than soil water. Recently, Kume *et al*. (2003) showed that the presence of understory vegetation decreases both water and nutrient supplies for overstory pine trees (*Pinus densiflora* Sieb. et Zucc.). Thus, competition for nutrients is probably another important factor affecting the growth of *Betula ermanii*. In addition, Takahashi *et al*. (2002) showed that the daily maximum soil-temperature at a depth of 5 cm was slightly higher (1 ~ 2˚C) during summer in the plots without *Sasa* than in the plots with *Sasa* because much solar radiation penetrates to the soil surface if *Sasa* is absent. High soil temperature possibly enhances microbial activity in the soil, which increases the decomposition rate of organic matter in the soil (Van Cleve *et al*. 1983), which in turn supplies more nutrients for overstory trees. Unfortunately, we do not have enough information to evaluate the relative importance of soil nutrients on the growth of *Betula ermanii* compared with soil water.

We concluded that the *Sasa* removal increases soil water and the growth of larger *Betula ermanii* in the first two years after the *Sasa* removal. Therefore, this study suggests that understory *Sasa* possibly reduces the growth of larger *Betula ermanii*, at least partially, through competition for water. However, further studies are necessary to evaluate the relative importance of competition for nutrients between understory *Sasa* and overstory *Betula ermanii*.

## ACKNOWLEDGEMENTS

We thank D. Mitsuishi and the staff of Uryu Experimental Forest of Hokkaido University for their support in the field. Our thanks are also due to T. Kobayashi for fruitful comments on the earlier version of this manuscript. Financial support was partly provided by the Ministry of Education, Science, Sports and Culture of Japan (No. 13460060) and by the Joint Research Program of the Institute of Low Temperature Science, Hokkaido University.

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## FIGURE LEGENDS

**Fig. 1** Frequency distributions of trunk diameter at breast height (DBH) in the four plots in a dense secondary *Betula ermanii* forest in 1998 (before *Sasa* removal in Plot-1b and Plot-2b). Shaded and open bars indicate *Betula ermanii* and other species, respectively. Mean DBH (± SD, cm), total density (trees/ha) and total basal area (BA, $m^2$/ha) of each plot are presented in the figures.

**Fig. 2** Daily rainfall (mm) and soil water potential (MPa) at a depth of 25 cm in Plot-2a (solid circle) and Plot-2b (open circle) in a dense secondary *Betula ermanii* forest in 1998 (before *Sasa* removal, left figure) and 1999 (after *Sasa* removal, right figure). Summary of ANOVA with repeated measures for soil water potential is shown in Table 1.

**Fig. 3** Relative growth rate (with positive standard deviation) of trunk diameter at breast height (DBH) of *Betula ermanii* in the four plots during the two growing seasons (1999–2000). DBH is depicted in 1-cm classes beginning at 1-cm DBH in the upper figure, and in 2-cm classes beginning at 2-cm DBH in the lower figure. Summary of ANOVA with repeated measures for relative growth rate in DBH is shown in Table 2.

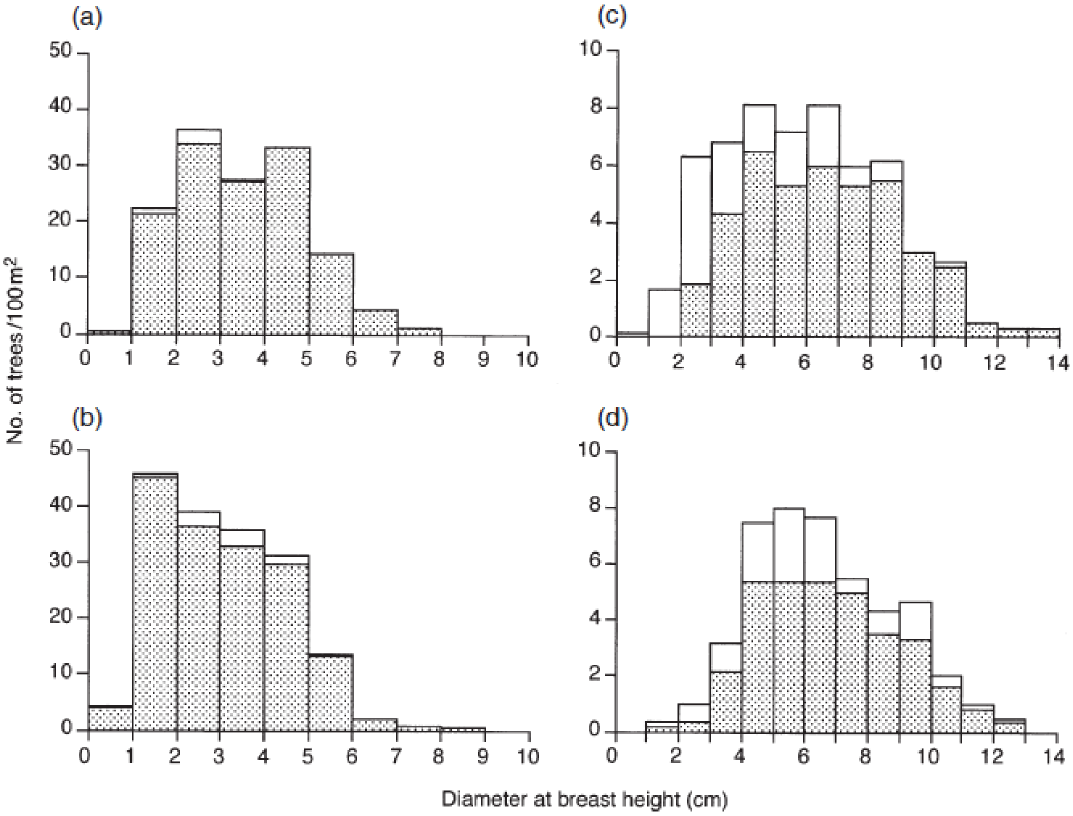
(a)
(b)
(c)
(d)
No. of trees /100m²
Diameter at breast height (cm)
0
10
20
30
40
50
0
2
4
6
8
10
0
1
2
3
4
5
6
7
8
9
10
0
2
4
6
8
10
12
14

Fig. 1

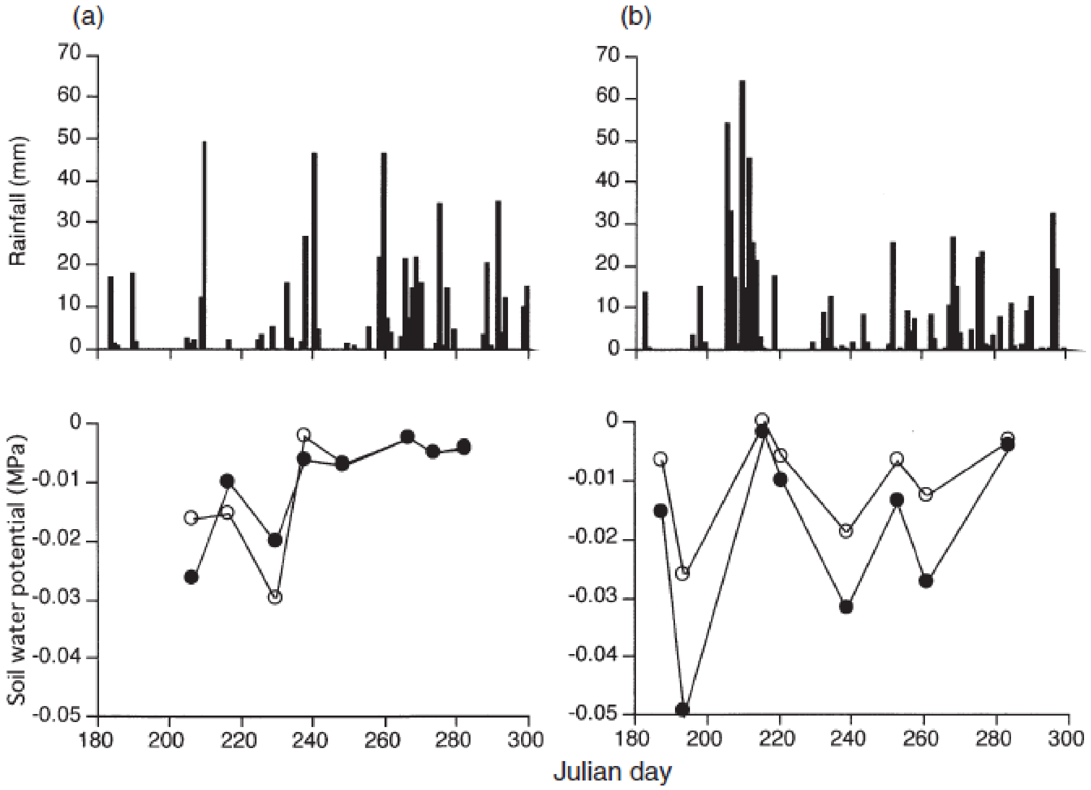
(a)
(b)
Rainfall (mm)
0
10
20
30
40
50
60
70
Soil water potential (MPa)
0
-0.01
-0.02
-0.03
-0.04
-0.05
180
200
220
240
260
280
300
Julian day

Fig. 2

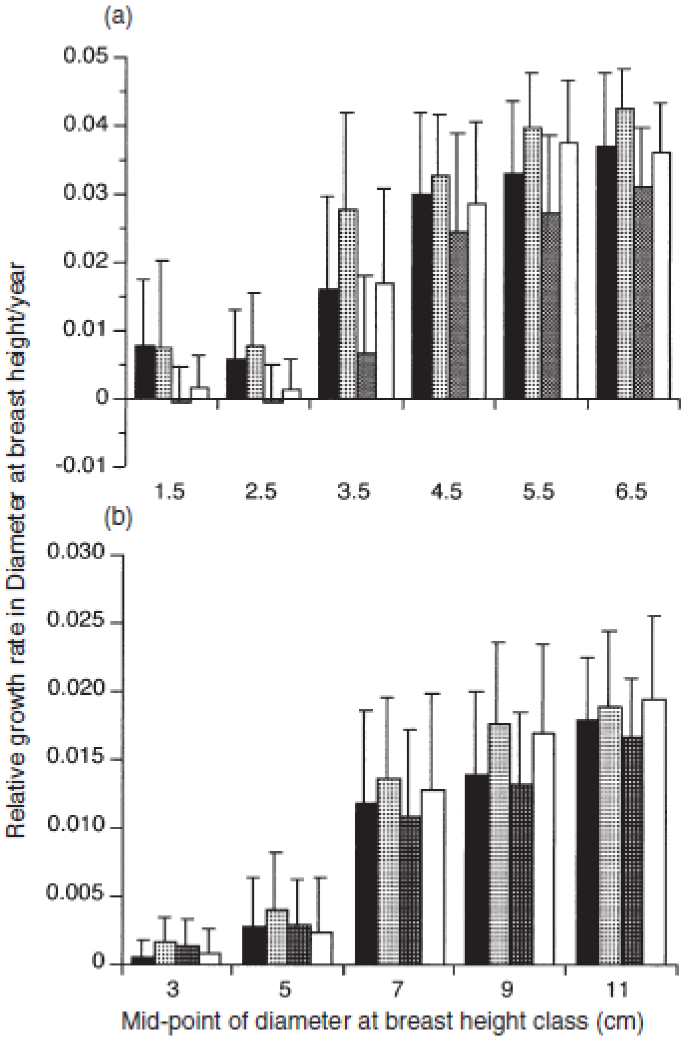
(a)
0.05
0.04
0.03
0.02
0.01
0
-0.01
1.5
2.5
3.5
4.5
5.5
6.5
(b)
0.030
0.025
0.020
0.015
0.010
0.005
0
3
5
7
9
11
Relative growth rate in Diameter at breast height/year
Mid-point of diameter at breast height class (cm)

Fig. 3

**Table 1** Summary of ANOVA with repeated measures for soil water potential in a dense secondary *Betula ermanii* stand in 1998 (before *Sasa* removal) and 1999 (after *Sasa* removal). "Treatment" compares Plot-2a and Plot-2b. "Day" refers to the eight times when soil water potential was measured in each year.

| | 1998 | | | | 1999 | | | |
|---|---|---|---|---|---|---|---|---|
| Source | df | MS | *F* | *p* | df | MS | *F* | *p* |
| Between subjects | | | | | | | | |
| Treatment | 1 | 2.52 | < 0.001 | 0.989 | 1 | 335676.2 | 16.0 | 0.001 |
| Error | 36 | 13559.4 | | | 18 | 20947.8 | | |
| Within subject | | | | | | | | |
| Day | 7 | 286403.7 | 46.0 | < 0.001 | 7 | 302023.5 | 88.1 | < 0.001 |
| Day × Treatment | 7 | 32888.4 | 5.28 | < 0.001 | 7 | 28643.4 | 8.36 | < 0.001 |
| Error | 252 | 6226.7 | | | 126 | 3426.4 | | |

**Table 2** Summary of ANOVA with repeated measures for relative growth rate in DBH of *Betula ermanii* during the two growing seasons (1999–2000). "Treatment" compares the two plots (*Sasa* cut and not cut). "Size" compares across six and five size classes for Plot-1 and Plot-2, respectively. "Year" refers to the two times when relative growth rate of DBH was measured during the two growing seasons.

| | Plot-1 | | | | Plot-2 | | | |
|---|---|---|---|---|---|---|---|---|
| Source | df | MS | *F* | *p* | df | MS | *F* | *p* |
| Between subjects | | | | | | | | |
| Treatment | 1 | 0.004379 | 23.77 | < 0.001 | 1 | 0.000397 | 8.09 | 0.005 |
| Size | 5 | 0.030139 | 163.61 | < 0.001 | 4 | 0.007163 | 145.72 | < 0.001 |
| Treatment × Size | 5 | 0.000754 | 4.10 | 0.001 | 4 | 0.000079 | 1.63 | 0.167 |
| Error | 539 | 0.000184 | | | 406 | 0.000049 | | |
| Within subject | | | | | | | | |
| Year | 1 | 0.006897 | 150.20 | < 0.001 | 1 | 0.000041 | 5.78 | 0.017 |
| Year × Treatment | 1 | 0.000033 | 0.71 | 0.400 | 1 | 0.0000034 | 0.47 | 0.495 |
| Year × Size | 5 | 0.000237 | 5.17 | < 0.001 | 4 | 0.0000038 | 0.53 | 0.716 |
| Year × Treatment × Size | 5 | 0.000036 | 0.78 | 0.563 | 4 | 0.000015 | 2.15 | 0.074 |
| Error | 539 | 0.000046 | | | 406 | 0.0000072 | | |