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Growth of regenerated tree seedlings associated with micro-climatic change in a mature larch plantation after harvesting

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Abstract

In order to further develop methods of sustainable forest management, we evaluated the effects of logging practices during the winter on micro-climatic factors and growth of four seral deciduous broad-leaved tree seedlings regenerated in a larch plantation in northern Japan. We found that winter logging practices drastically changed micro-climatic factors, especially in terms of light intensity and the vertical distribution pattern of CO₂ concentration. Harvesting overstory larch trees increased photosynthetic photon flux (PPF), which may enhance the photosynthesis of understory plants. We examined the undergrowth for tree seedlings of the following species: two late successional species, *Prunus ssiori* and *Carpinus cordata*; one gap phase species, *Magnolia hyporeuca*; and one mid-late successional species, *Quercus mongolica* var. *crispula*. All of the four studied tree species responded well to the practices of winter logging after the second year of harvesting overstoried larch trees. The current shoot diameter and current shoot length increased significantly. Therefore, we conclude that winter logging practices should improve shoot growth of deciduous broad-leaved tree seedlings regenerated in a larch plantation through the change in environmental factors that accompanies larch harvest.

Key words: winter logging, vertical profile of CO₂ concentration, current-year shoot length, deciduous broad-leaved tree species

1. Introduction

In northern Japan, vast areas of deciduous broad-leaved tree forests were converted to Japanese larch (*Larix kaempferi* Carr.) plantations in order to provide timber because Japanese larch has a relatively high growth rate (Koike et al. 2000; Ryu et al. 2009). However, there are many unmanaged larch plantations due to several weaknesses exhibited by the Japanese larch, such as reduced tolerance of biological stresses, grazing by the red-back vole, shoot blight disease, and stem and root rot (Koike et al. 2000). Recently, the commercial value of larch wood has increased rapidly due to improvements in wood-drying technology. With this increased commercial value, larch wood logging has intensified. Therefore, methods for sustainable forest management after the harvest of larch trees must be established.

In larch forests, especially those on unmanaged plantations, there are many naturally regenerated tree seedlings. Invading deciduous tree species include *Magnolia hyporeuca* Siebold et Zucc., *Magnolia praecoccisima* Koidz. var. *borealis* (Sargent) Koidz, *Quercus mongolica* Fischer ex Ledeb. var. *crispula* (Blume) Ohashi, *Prunus ssiori* F. Schmidt, *Acer mono*, *Acer amoenum* var. *matsumurae*, *Kalopanax septemlobus* (Thunb.) Koidz, *Ulmus davidiana* var. *japonica*, *Morus australis* Poir. and *Carpinus cordata* Blume (Hanada et al. 2006; Kitaoka 2004). Some of these are expected to be important sources of high-value timber.

In central Europe, deciduous broad-leaved tree seedlings that have invaded hedgerows play important roles in maintaining biodiversity and human life (Schulze and Gerstberger 1993), as well as generating wood resources (Scherer-Lorenzen et al. 2005). Therefore, evaluation of growth responses of these seedlings to larch logging would provide important information for sustainable forest management.

In northern Japan, winter logging practices are performed (Matsuda et al. 2002). Snow cover protects the forest floor and understory seedlings from disturbances associated with logging (Wolf et al. 2008). Therefore, winter logging should help protect the invading deciduous broad-leaved tree seedlings from the disturbances associated with logging. However, only limited information is available regarding environmental factors that affect the growth responses of the invading seedlings to winter logging practices (Noguchi et al. 2003).

Our previous observations indicate that specific differences in light and nitrogen affect four species of invading seral tree seedlings (Kitaoka and Koike 2004; 2005). We found that the gap phase species *M. hyporeuca* and the mid-late successional species *Q. mongolica* showed significantly higher photosynthetic rates and more efficient nitrogen use than two late successional tree species, *P. ssiori* and *C. cordata*. Therefore, we expect that growth of *M. hyporeuca* and *Q. mongolica* should be largely increased by winter logging practices, but that the late successional species *P. ssiori* and *C. cordata* would show no marked growth response

to the winter harvest.

We carried out winter logging of larch trees and investigated changes in the micro-climatic environment and growth responses of seedlings from four species that have naturally invaded larch plantations. In this study, we focused on the shoot growth of deciduous broad-leaved tree seedlings, since previous studies have suggested that shoots are highly sensitive to changes in environmental factors (Koike et al. 1997; Takenaka 1997; Ishii et al. 2003; Takahashi et al. 2006; Ishii et al. 2007). We discuss specific differences in regenerated seedlings of these deciduous broad-leaved tree species in response to environmental changes associated with the harvest.

2. Materials and methods

2.1. Site description

Our study was conducted on three unmanaged larch plantations (50 years old in 2003) on a north-facing slope in the Tomakomai Experimental Forest of Hokkaido University (TOEF), Japan (42°40'N, 141°35'E, 200-300 m a.s.l.). The stand density of larch trees was 430 individuals per ha⁻¹, and mean tree height was about 10 m. The soil type is immature volcanic ash. In the winter, snow depth reached 70 cm at the nearest weather station (Japan Meteorological Agency, URL: <http://www.data.jma.go.jp/obd/stats/data/en/smp/index.html>).

Deciduous broad-leaved tree seedlings invaded the understory of the larch plantation (Kitaoka and Koike 2004; 2005). In December 2001, the winter logging sites and control sites were set up following a Latin square design. At the winter logging sites, we harvested all of the overstory larch trees; the minimum diameter of the larches was 10 cm at breast height, with a total of 80 individuals. Each study site was 25 m $\times$ 25 m with three site replicates.

2.2. Monitoring of environmental factors

Seasonal changes in relative light intensity at the forest floor were monitored in 2002. We followed the method of Kitaoka and Koike (2004; 2005) and this determined the relative photosynthetic photon flux (rPPF) by the percentages of the PPF at seedling tops as compared to PPF in an open space. PPF was measured with two LI-190 sensors (Li-Cor, Lincoln, NE, USA). One sensor was used to monitor PPF at the center of each plot at seedling top height. The other sensor was set on the top of a 12 m canopy access tower to monitor PPF in open space. All of the measurements were carried out between 11 am and 1 pm on cloudy days.

Vertical distributions of CO₂ concentration ([CO₂]) were monitored by a six-channel [CO₂] monitoring system (Dalton, Sapporo, Japan; see Koike et al. 2001) with a single-beam infrared gas analyzer (IRGA) (ZFP5, Fuji Electric Systems, Tokyo, Japan). Gas samplers were set at six different heights (0.2, 2, 4, 6, 8 and 12 m) from the forest floor with use of a canopy access

tower. The sampling interval at each height was one hour. The monitoring was conducted for 10 consecutive days in each month and at 20-day intervals from mid-April to mid-November in 2001 and 2002, from before to after the winter harvest of larches.

Soil respiration rates were also monitored by a six-channel soil-respiration monitoring system (Hokkaido Dalton, Sapporo, Japan; see Kitaoka et al. 2002) with IRGA (GMM222, Vaisara, Finland). In 2002, three soil respiration chambers were put at the center of the control sites, and three other chambers were put at the center of canopy opening sites for a total of six chambers. For calibration of both vertical [CO₂] and soil respiration monitoring systems, three known standard gases (pure N₂, 342 ppm CO₂, 880 ppm CO₂) were used.

We collected core soil samples for determination of soil pH and nitrogen content in August 2002 and 2003. Each soil core volume was 100 ml, and four soil cores were collected at each site, with three site replicates in both control and winter logging treatment; in total, 24 soil cores were used for determination of soil pH. Soil samples (10 g) were used for soil pH measurements. Soil pH measurements were performed according to the protocol proposed by Kayama et al. (2002). The rest of the fresh soil samples were air dried and used for analysis of nitrogen content. Soil nitrogen content was determined with an NC analyzer (NC-900, Shimadzu, Kyoto, Japan). The nitrogen content was calibrated and checked against a known standard (acetanilide, N = 10.36%, C = 71.09%; Wako Chemical Co. Ltd., Osaka, Japan). Soil water content at a

depth of 10-20 cm was monitored by soil moisture sensors at one-hour intervals (EC-20, Decagon, Washington, USA) at three sites for both winter logging and control treatments.

2.3. Plant materials, measurements of shoot growth and leaf mass per area, and statistical analysis

For this study, we selected four seral tree species that had invaded a larch plantation. *Magnolia hyporeuca* Siebold et Zucc. and *Quercus mongolica* Fischer ex Ledeb. var. *crispula* (Blume) Ohashi grew near gaps, while *Carpinus cordata* Blum and *Prunus ssiori* F. Schmidt naturally regenerated on the forest floor of three replicate larch plantation sites (Kitaoka and Koike 2004; 2005). In 1999, the mean age and height of the seedlings were 3-4 years and approximately 95 cm, respectively. Shoot growth was measured in late October of 2001, 2002, 2003 and 2008. We investigated the growth of four shoot replicates at each plot and three plot replicates. In total, 24 shoots were measured per species.

We measured the length and diameter of current-year main shoots with a metal scale and digital calipers, respectively. Current-year shoot volume (CSV) was estimated according to the cone volume formula:

$$CSV = \frac{1}{3} \times l \times \left(\frac{d}{2}\right)^2 \times \pi \quad (1),$$

where l is shoot length, d is shoot diameter, and π is approximated as 3.14.

After measuring shoot length and diameter, we obtained two leaf disks (2 cm² in total) from the sampled shoot. The leaf disks were dried at 60°C for 48 h and weighed for the determination of leaf mass per area (LMA).

Statistical analyses were carried out using R ver. 2.70 (R Development Core Team 2007, URL: <http://www.R-project.org>).

3. Results

3.1. Environmental factors

Seasonal change in the rPPF at the winter logging sites was different as compared with that at the control sites (Figure 1). Clear seasonal changes in rPPF were observed at the control sites. The rPPF gradually decreased from May to July, remained constant until mid-October, and then increased toward November. In contrast, at the winter logging sites, the rPPF ranged from 50 to 60% and showed no marked changes throughout the growing season. Both before and after winter logging, [CO₂] gradually decreased from early morning to afternoon and increased from evening to night (Figure 2). Winter logging practice caused the change in the vertical distribution of [CO₂] in spring. In contrast, little change in the vertical distribution of [CO₂] was

observed in summer and autumn. Soil respiration rates at the winter logging sites significantly increased in July, whereas there was no significant difference observed in May or October (Figure 3). Soil pH was significantly reduced by winter logging (Table 1), whereas winter logging did not affect soil nitrogen content. Soil water content showed different responses to treatment throughout the season; soil water content was significantly higher at the winter logging sites than at the control sites from April to mid-June and from late September to the beginning of October (Figure 4). However, the opposite trend was observed from mid-June to July.

3.2. Shoot growth characteristics in response to winter logging

Winter logging significantly increased the LMA of all four tree species (Table 2). There was a significant interaction between winter logging and yearly variation for the LMA of *C. cordata*. Other three species didn't show the interaction between winter logging practice and yearly variation (Table 2).

Shoot diameter and current-year shoot length of all four tree species were significantly increased by winter logging (Table 2). Significant interactions between winter logging and yearly variation in shoot diameter and current-year shoot length were also observed in the four tree species. There was no reaction in the first year after logging, but all trees increased shoot

growth in the following years. In the second year after winter harvesting, however, the shoot diameter and current-year shoot length of *M. hyporeuca*, *Q. mongolica* and *P. ssiori* were significantly increased by the treatment. Furthermore, winter logging significantly increased the shoot diameter and current-year shoot length of all tree species in the sixth year after treatment (except for the shoot diameter of *P. ssiori*).

In all of the investigated years after logging, shoot volume was significantly increased by the winter harvest (Figure 5). There were significant interactions between harvesting and yearly variation in the current-year shoot volume of the four species. In the first year after the winter harvest, a significant increase in the current-year shoot volume was only observed in *P. ssiori*, but all species demonstrated a significant increase in the current-year shoot volume in the second and sixth years after treatment.

4. Discussion

4.1. Environmental factors

The rPPF and other environmental factors were greatly affected by winter logging (Figures 1 to 4, Table 1). Previous reports suggest that soil water content is increased by the harvest of canopy-composing trees, due to reduced transpiration among the trees making up the canopy (Ishizuka et al. 2002). However, in this study, soil water content was lower at the harvest sites

than at the control sites from the beginning of June through July (Figure 4). Because our study sites were an unmanaged larch plantation, it is possible that the transpiration of canopy-composing larch was relatively low and, as a result, that the soil in the control plot retained moisture. Moreover, the soil at the study sites mainly contained pumice and volcanic ash, which stopped water uptake through the capillary tube and may have suppressed extra evaporation from the soil surface. In addition, there is a possibility that snow depth affected the differences in soil water content in the spring; generally, snow depth under the canopy is less than that without the canopy.

On the other hand, winter harvesting increased the degree of vegetation cover, including several herbaceous plant species (Kitaoka 2004). Furthermore, the light intensity at the forest floor was higher at the winter logging sites than at the control sites (Figure 1). In general, leaf transpiration increases with increasing light intensity and temperature. No marked difference was found in air temperature between the control and winter logging sites (Qu et al. 2004). Therefore, an increase in the light intensity-induced stimulation of transpiration of herbaceous plant species may explain the decrease in soil water content at the winter logging sites. The increased degree of cover observed for several herbaceous plant species following winter logging may partly explain the decrease in $[\text{CO}_2]$ near the forest floor during the day in the spring, and of course wind would significantly affect the vertical profile of $[\text{CO}_2]$ (Bazzaz and

Williams 1991). Generally, under the calm wind conditions in closed forests, $[\text{CO}_2]$ at the forest floor have the highest values (Bazzaz and Williams 1991).

Before canopy opening, the distribution pattern of $[\text{CO}_2]$ during summer, especially at night, was lower than during spring and autumn. This would be partly attributed to the cold summer and relatively high humidity of the air (Japan Meteorological Agency, <http://www.data.jma.go.jp/obd/stats/data/en/smp/index.html>). Cold and cloudy weather might affect respiration from plants, and high humidity might affect CO_2 flux from the soil.

The increased light intensity at the forest floor of winter logging sites leads to increased soil temperature (Bazzaz 1996; Qu et al. 2004). In the present study, the soil respiration rates, which is highly dependent on soil temperature, was increased at the winter logging sites (Figure 3). Because the activity of nitrifying bacteria greatly depends on soil temperature, there is a possibility that the nitrification rate at the winter harvesting sites was higher than that at the control sites. It is well known that protons are released during the nitrification process (Shibata 2004). Therefore, the reduction in the soil pH is mainly attributed to increased nitrification due to increased soil temperature.

Based on the results obtained from the measurement of environmental factors, we conclude that the micro-climatic changes due to winter logging were greatly affected by the activity of herbaceous plant species and/or soil microbial populations at the forest floor.

4.2. Shoot growth in response to winter logging

We predicted that winter harvesting would not promote shoot growth in the two late successional tree species, *P. ssiori* and *C. cordata*. However, by six years after the winter logging treatment, all four of the tree species studied had well-developed current-year shoots (Table 2 and Figure 5). Hence, winter logging is effective for accelerating the growth of deciduous broad-leaved tree seedlings that have invaded larch plantations.

Improved shoot growth among the four tree species in the winter logging sites may be due in part to changes in LMA. Increased LMA is one of the most important responses of leaves during acclimation to strong light intensity, serving to speed up the rate of photosynthesis (Björkman 1981; Koike 1986; Koike 1988). *P. ssiori* and *C. cordata* grown in the winter logging sites exhibited increased LMA, as did *M. hyporeuca* and *Q. mongolica*. However, the degree of increase was lower in the late successional tree species than in the other tree species; the three year average increment rates of LMA values at winter logging treatment sites were 55% in *M. hyporeuca* and 56% in *Q. mongolica*, while the increment rates were 30% in *P. ssiori* and 26% in *C. cordata*. This phenomenon reflects the differences in successional traits among the tree species.

Observed yearly variations in the d , l and current-year shoot volume (CSV) indicate the time lag of shoot growth stimulation in response to winter logging. Hashimoto and Aoki (1996) reported that *Quercus serrata* Murray grown under shady conditions in northern Japan had a higher shoot-root ratio; hence, lower water uptake occurred due to insufficient root growth. The time lag of shoot growth stimulation is related to water uptake and was greater in *C. cordata* than in the other three tree species (Table 2). This trend was also observed with regard to LMA (Table 2). *C. cordata* exhibits variable LMA in humid conditions and is relatively sensitive to drought (Masaki et al. 1992; Park and Morikawa 2002; Kitaoka 2004). Therefore, *C. cordata* may need a longer time to achieve increased water uptake capacity (i.e., root growth) in response to a rapid increase in the water requirement due to high light intensity and drought, both of which are induced by winter logging.

5. Conclusion

In the present study, we carried out a winter harvest of larch trees and investigated the resulting changes in the micro-climatic environment and shoot growth responses of *M. hyporeuca*, *Q. mongolica*, *P. ssiori* and *C. cordata* that had invaded larch plantations. Winter logging greatly affected the micro-climatic environment. Seedlings of *M. hyporeuca*, *Q. mongolica*, *P. ssiori* and *C. cordata* showed robust acclimation to the micro-climatic changes, as well as enhanced shoot growth. Therefore, we conclude that winter logging is effective for

acceleration of the growth of deciduous broad-leaved tree seedlings that have invaded a larch plantation, through logging-related changes in environmental factors, including light conditions, CO₂ concentration and soil nutrients.

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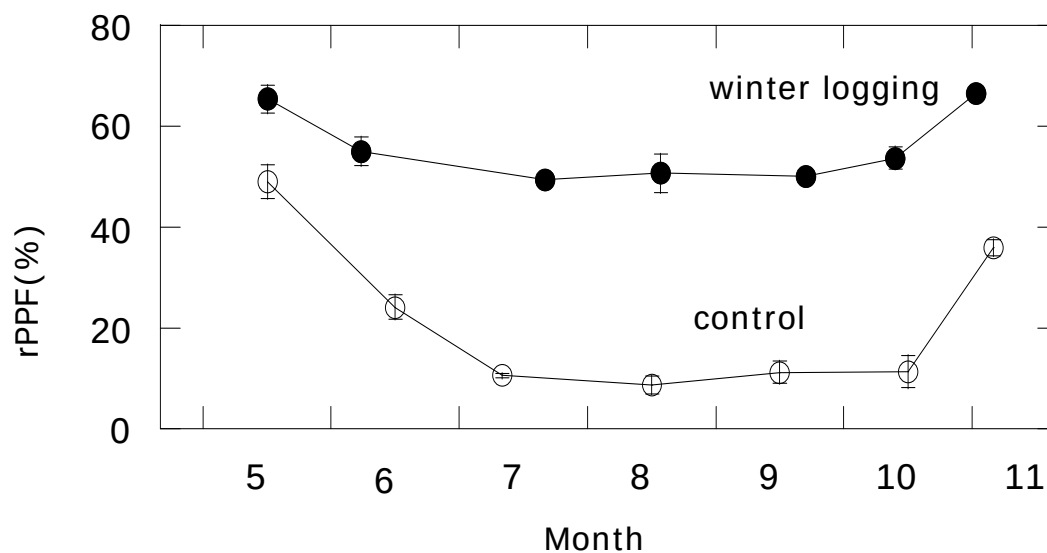
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Figure 1 Seasonal changes in relative photosynthetic photon flux (rPPF). Open symbols indicate the control sites, and closed symbols indicate the winter logging practice sites (mean values of 3 site replicates). The error bars indicate standard error.



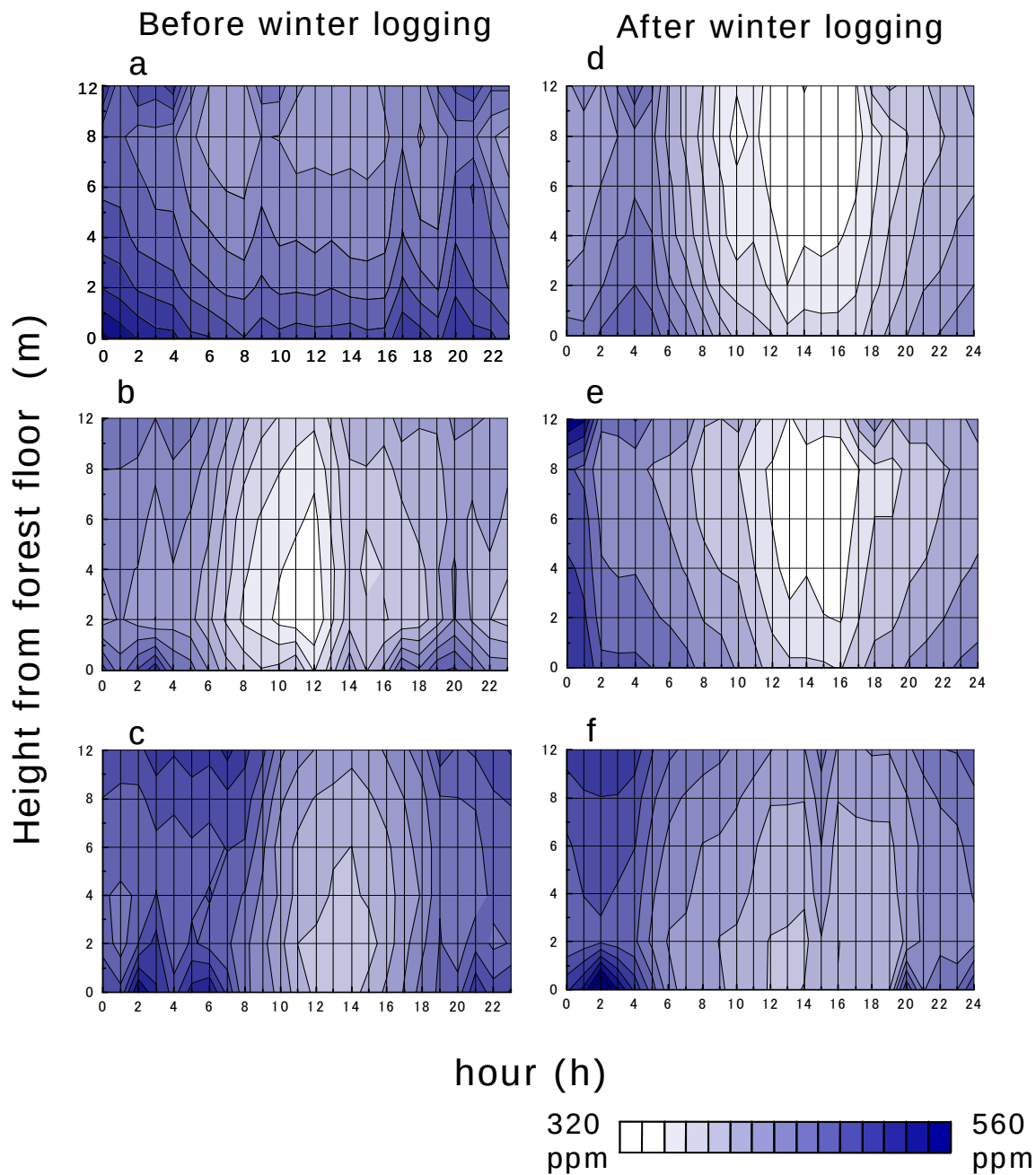


Figure 2 Diurnal course of the vertical distribution of CO₂ concentration at the larch plantation. Left (a, b and c): before winter logging practice; right (d, e and f): after winter logging practice; upper (a and d): spring (April-May); middle (b and e): summer (June-August) and lower (c and f): autumn (September-November). The monitoring was conducted for 10 continuous days in each month at 20-day intervals, from mid-April to mid-November. Values are mean values during the above measurement period in each season.

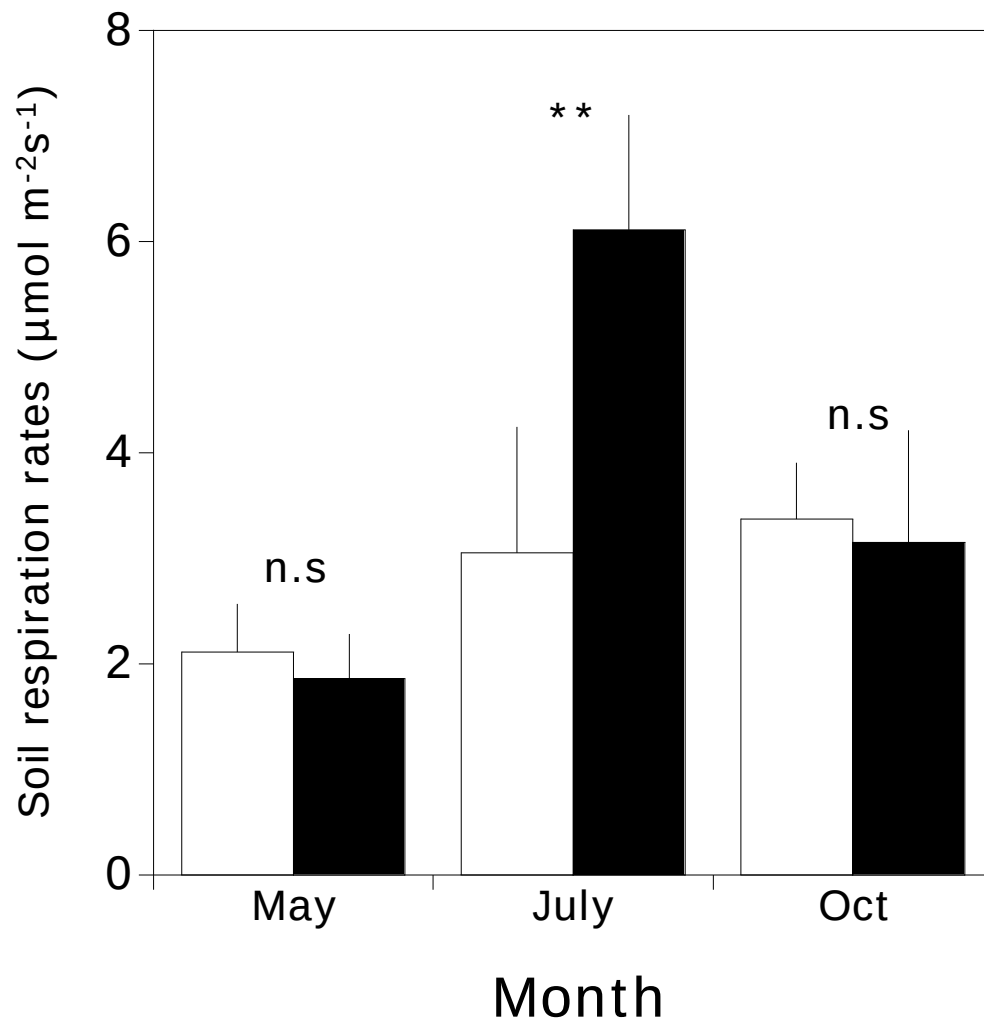


Figure 3 Seasonal changes in the soil respiration rates at the control sites (white) and winter logging practice sites (black). Vertical lines on the bars indicate standard error (n=3). Statistical differences were analyzed by t-test. ** indicates significant differences between control and winter logging ($p < 0.01$), and n.s. indicates non-significant differences between winter logging and control.

Table 1 Soil pH and nitrogen content in both winter logging and control sites in the first and second years after winter logging. Data are presented as mean (SE). Each mean and SE value represents are three site replications. The significance of the main effects of winter logging (wl) and yearly variation (yr) and the significance of the interaction between winter logging and yearly variation (wl $\times$ yr) are shown as symbols (*: $p < 0.05$, **: $p < 0.01$) or as non-significant (n.s.).

parameters	year	control	winter logging	ANOVA
soil pH	1 yr	5.09 (0.03)	4.66 (0.18)	wl: *
	2 yr	4.92 (0.32)	4.80 (0.10)	yr: n.s.
				wl $\times$ yr: n.s.
soil nitrogen content	1 yr	7.16 (1.36)	8.46 (0.36)	wl: n.s.
	2 yr	8.30 (1.81)	6.31 (1.03)	yr: n.s.
				wl $\times$ yr: n.s.

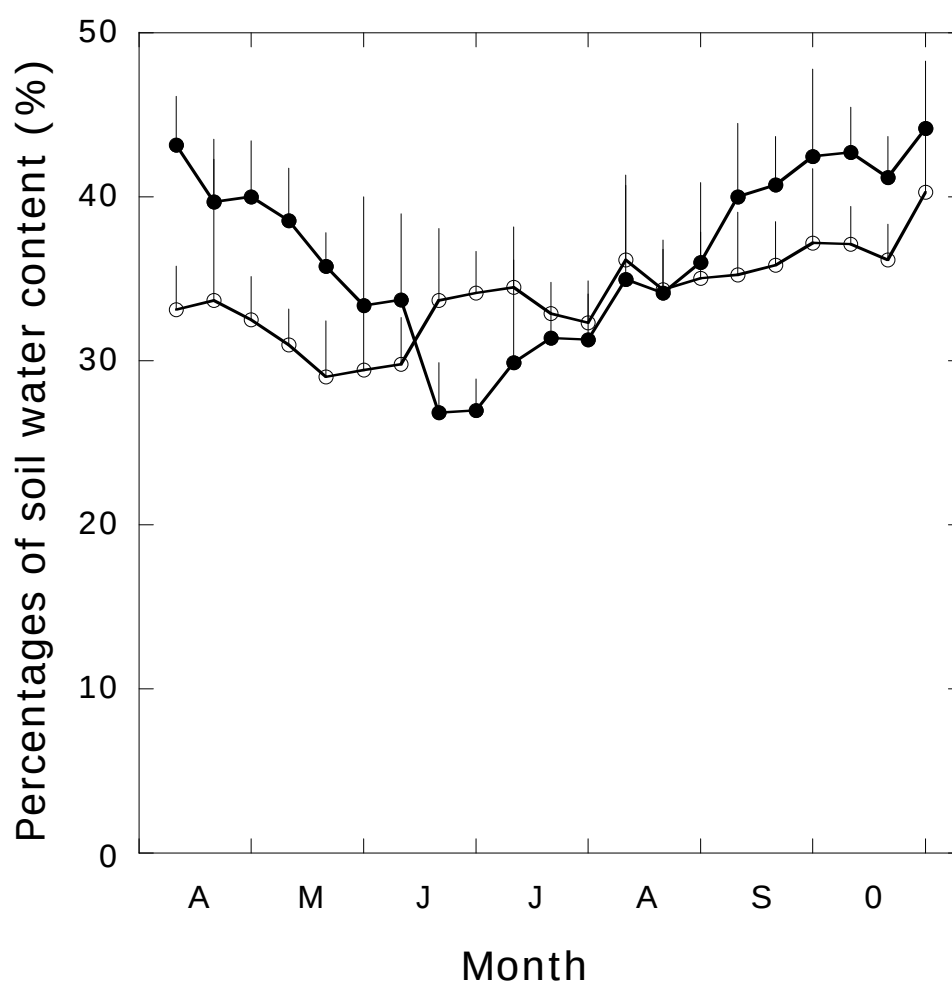


Figure 4 Seasonal changes of soil water content at the study sites. The data are the mean values of three site replicates; open symbols indicate the control, and closed symbols indicate winter logging. Error bars indicate standard error (n=3).

Table 2 Current-year shoot diameter (d), shoot length (l) and leaf mass per area (LMA). Values are presented as mean (SE), calculated from three site replicates. The significance of main effects of winter logging (wl) and yearly variation (yr) and the significance of the interaction between winter logging and yearly variation (wl $\times$ yr) are shown as symbols (*: $p < 0.05$, **: $p < 0.01$) or as non-significant (n.s.). When a significant interaction between winter logging and yearly variation was detected, the Holm post-hoc test was performed to identify significant differences among the 6 values (2 treatments $\times$ 3 years). Values with different letters indicate significant differences at $p < 0.05$ in each species.

species	year	parameters								
		d (mm)			l (mm)			LMA (g m ⁻²)		
		control	winter	ANOVA	control	winter logging	ANOVA	control	winter	ANOVA
<i>M. hyporeuca</i>	1yr	2.98 (1.99)bc	2.78 (0.71)c	wl: **	45.91 (30.78)c	86.75 (22.17)c	wl: **	36.97 (2.64)	52.23 (13.0)	wl: **
	2yr	3.57 (0.86)bc	7.52 (2.51)a	yr: **	68.00 (18.23)c	188.00 (20.18)b	yr: **	36.99 (7.24)	55.19 (8.16)	yr: n.s.
	6yr	4.55 (1.99)b	8.64 (1.87)a	wl $\times$ yr: **	60.00 (40.46)c	341.57 (80.10)a	wl $\times$ yr: **	34.50 (6.37)	59.84 (8.7)	wl $\times$ yr: n.s.
<i>Q. mongolica</i>	1yr	2.78 (1.54)b	3.31 (0.92)ab	wl: **	23.84 (6.83)d	47.06 (20.80)cd	wl: **	32.40 (4.67)	44.00 (6.19)	wl: **
	2yr	2.57 (0.30)b	4.74 (2.04)a	yr: *	38.83 (15.19)cd	109.66 (25.51)b	yr: **	32.00 (6.85)	57.03 (19.30)	yr: *
	6yr	2.09 (0.58)b	3.68 (1.11)a	wl $\times$ yr: *	82.16 (41.79)bc	206.16 (54.31)a	wl $\times$ yr: **	41.00 (3.30)	62.48 (7.51)	wl $\times$ yr: n.s.
<i>P. ssiori</i>	1yr	1.98 (0.35)c	3.18 (2.01)bc	wl: **	26.33 (2.73)c	36.48 (6.78)c	wl: **	37.23 (4.22)	47.61 (5.49)	wl: **
	2yr	2.46 (1.79)c	5.91 (1.14)a	yr: **	29.50 (6.15)c	69.85 (11.20)b	yr: **	32.80 (6.14)	45.66 (4.63)	yr: **
	6yr	1.98 (0.65)bc	4.03 (1.80)b	wl $\times$ yr: **	54.50 (13.17)bc	209.33 (62.16)a	wl $\times$ yr: **	48.55 (7.20)	59.77 (1.67)	wl $\times$ yr: n.s.
<i>C. cordata</i>	1yr	1.64 (0.32)c	1.25 (0.24)d	wl: **	31.40 (14.74)cd	16.60 (4.21)d	wl: **	31.61 (3.54)b	40.24 (3.45)at	wl: **
	2yr	2.05 (0.44)bc	3.90 (2.53)ab	yr: **	28.76 (6.61)c	38.10 (7.83)c	yr: **	30.69 (2.75)b	36.53 (2.46)b	yr: **
	6yr	2.87 (1.27)b	4.13 (0.96)a	wl $\times$ yr: **	199.16 (87.38)b	328.60 (24.99)a	wl $\times$ yr: **	37.97 (4.73)b	50.91 (9.39)a	wl $\times$ yr: **

mean ($\pm$ se), wl: winter logging, yr: year, *: $p < 0.05$, **: $p < 0.01$

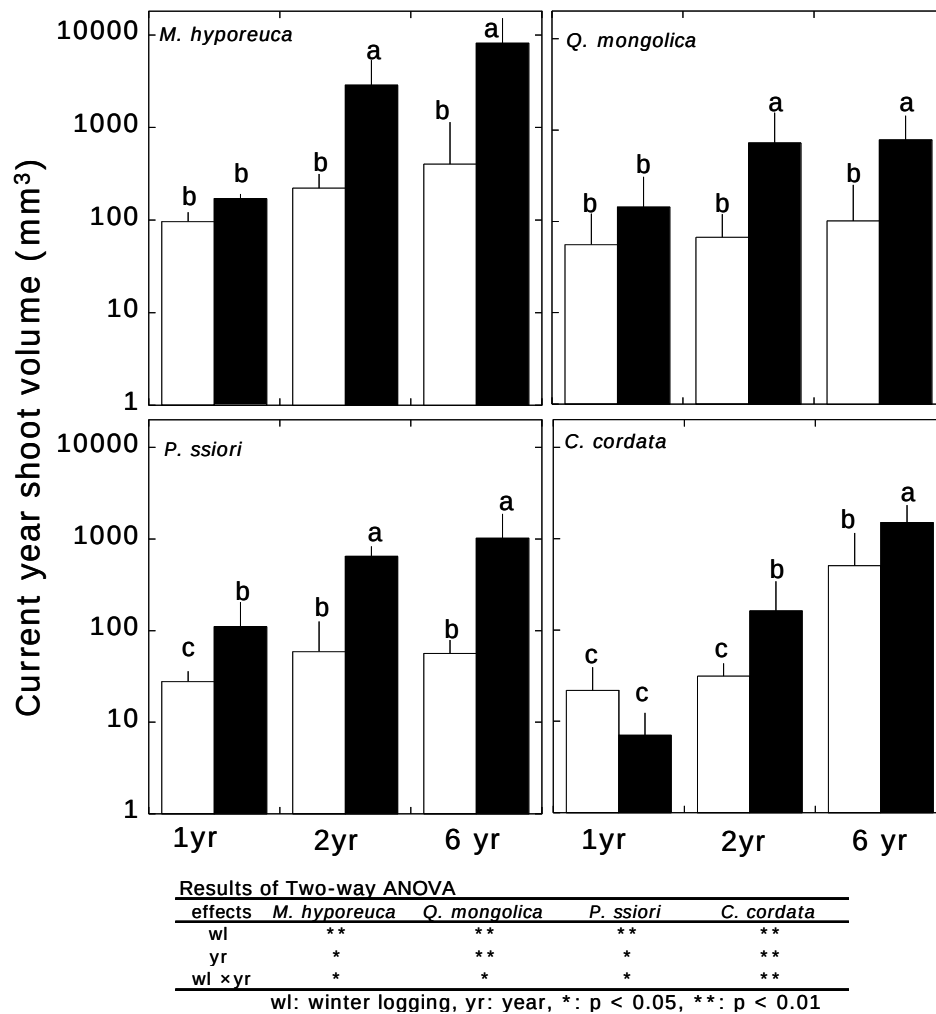


Figure 5 Current-year shoot volume of four deciduous tree species at the control sites (white) and winter logging practice sites (black). Columns and error bars denote means $\pm$ SE. Each value represents three site replicates. The significance of the main effects of winter logging (wl) and yearly variation (yr) and the significance of the interaction between winter logging and yearly variation (wl $\times$ yr) are shown as symbols (*: $p < 0.05$, **: $p < 0.01$) or as non-significant (n.s.). When a significant interaction between winter logging and yearly variation was detected, the Holm post-hoc test was performed to identify significant differences among the 6 values (2 treatments $\times$ 3 years). Values with different letters indicate significant differences at $p < 0.05$ in each species.