

Understory removal increases carbon gain and transpiration in the overstory of birch (*Betula ermanii*) stands in northern Hokkaido, Japan: trends in leaf, shoot and canopy

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Key words: canopy, dwarf bamboo, leaf dynamics, photosynthesis, shoot

Causes and consequences of understory development

In boreal, sub-boreal and cool-temperate forests, deciduous (summer-green) trees often dominate, but their densities are not very high. The leafing period of these trees is relatively short. Therefore, the overstory is not completely closed in such forests, making space available for understory plants on the forest floor. The understory is often densely and almost purely dominated by evergreen plants, e.g., *Sasa* spp. in eastern Asia and *Vaccinium* spp. in Siberia, that have shade tolerance/avoidance ability and rapid/continuous clonal growth characteristics. Having leaves in winter enhances their functions (e.g. gas exchange activity) before and after the overstory leafing period. These traits are often detectable in satellite images/aerial photographs and flux measurements. Thus, the roles of understory plants in forest ecosystems have become increasingly relevant to the processes of CO₂ and H₂O exchange/flux/cycle.

In the distinctly two layered cool-temperate deciduous forests in Japan, the understory accounts for a large fraction of the biomass and photosynthetic production of the forests (Nishimura et al. 2004, Ito et al. 2005). The peaks of carbon gain in the understory occur in early spring and late autumn when the understory is not severely shaded by the overstory (Lei & Koike 1998, Nishimura et al. 2004, Sakai & Akiyama 2005). In other periods, overstory shading limits light availability in the understory while understory shading limits light availability for the tree seedlings at the bottom of the understory. Therefore, a dense understory (heavy shade) prevents the seedlings of canopy trees from becoming established, which, in turn, prevents regeneration of the forest (Kobayashi et al. 2004).

The overstory and understory vegetation also limit each other by competing for water and nutrients in the soil. Such limitation of resources would induce changes in photosynthetic productivity and water use of plants not only at the leaf level but also at the shoot (twig) and canopy levels. However, little is known about the physiological effects of understory vegetation on the overstory trees. Although a few studies (e.g., Price et al. 1986, Kume et al. 2003) examined the effects of the understory on the overstory gas exchange characteristics at the leaf level, they did not examine the effects at the shoot or canopy levels.

In the present study, we conducted an understory removal experiment in secondary forests of Japanese mountain birch (*Betula ermanii*, a deciduous broad-leaf tree) in a sub-boreal area, northern Japan (Uryu Experimental Forest of Hokkaido University). We surveyed leaf demography, gas exchange and shoot/canopy structure in the overstory in areas with and without an understory in order to estimate shoot and forest canopy (overstory) carbon gain and transpiration.

Understory removal experiment

On Mt. Jinja in Moshiri, Uryu Experimental Forest of Hokkaido University, secondary birch forests were established after removal of above-ground vegetation and the rototilling of soil and roots near the ground surface, a traditional method of 'scarification' for artificial forest regeneration in this area (Umeki 2003). After the scarification, many tiny seeds of birch are dispersed on the surface of the bare ground, and the birch seedlings emerge simultaneously and grow rapidly. Subsequently, the forest, which is almost purely dominated by

even-aged birch trees, develops. In the processes of this forest development, dwarf bamboo (*Sasa kurilensis*, an evergreen clonal plant; ca. 2.0-2.5 m height) often invades the understory by vegetative reproduction. This species of dwarf bamboo is a typical dominant in the relatively less shady cool-temperate and sub-boreal forests in the snowy region of eastern Eurasia.

In two birch stands ('OLD', ca. 30-yr-old and 'YOUNG', ca. 20-yr-old), an understory dwarf-bamboo removal treatment was conducted in 1998. All dwarf-bamboo shoots in the dwarf-bamboo removal plot were cut by hand at the stem base (ground surface) and were removed from the plot. Thereafter, some new shoots of dwarf bamboo were also removed. A dwarf-bamboo intact plot (control) was also set up in each stand. Plot sizes were 20m × 20m in the OLD stand and 15m × 15m in the YOUNG stand. The removal plot and the control plot were separated by buffer zones that were 30 m wide in the OLD stand and 60 m wide in the YOUNG stand. Canopy access towers adjacent to the plots were established both in the OLD stand (ca. 12m height) and the YOUNG stand (ca. 9m height).

In the birch forests after the understory dwarf bamboo removal, the following characteristics were found in the removal plots in comparison with the intact plots. 1) Soil temperature at 5cm depth was 3-4°C greater right after the snow melt season (mid-May) due to the incidence of much sunlight on the forest floor (Takahashi et al. 2002). 2) Soil nitrogen availability was greater because decomposition of the remaining detritus from the understory (dead dwarf-bamboo roots) increased and the nutrient uptake by the understory decreased (Tripathi et al. 2005, 2006). 3) Soil water availability was greater because the water use by the understory decreased (Takahashi et al. 2003). 4) Growth rates of birch trees forming the overstory was greater due to the release from resources competition with understory (Takahashi et al. 2003). This raises the question of whether the photosynthetic productivity and water consumption of birch trees was also altered by the dwarf bamboo removal.

Leaf gas exchange capacity in relation to leaf demography and shoot structure

Leaf-level net CO₂ assimilation rate and transpiration rate were measured near saturating irradiance (more than 1000 μmolCO₂ m⁻² s⁻¹) at 25°C leaf temperature, 50-60% relative air humidity and 360 μmol mol⁻¹ air CO₂ concentration using a LI-6400 Portable Gas Exchange Measurement System (Li-Cor) for several well-developed

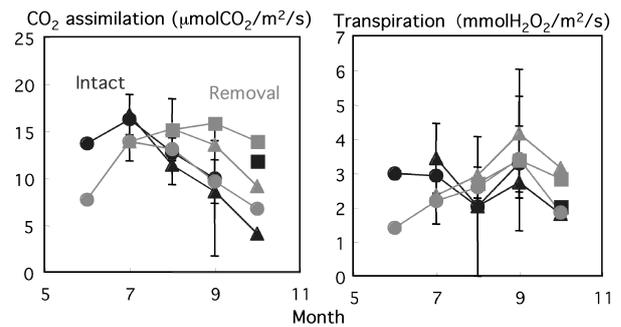


Fig. 1 Seasonal changes in gas exchange rates near saturating irradiance of canopy leaves of birch forest with (intact) and without (removal) dwarf-bamboo understory (11-12m height) (OLD, 2003). ●, 1st leaf from the shoot base (spring leaf); ▲, 4th leaf (early summer leaf); ■, 7th leaf (late summer leaf).

leaves collected from the birch canopy. In the latter part of the growing season, both rates tended to be greater in the leaves from the upper canopy (11m-12m height in the OLD stand) of the removal plot than in those of the intact plot (Fig. 1). From the middle to lower canopy (7m-11m), leaf gas exchange capacity was not clearly affected by dwarf-bamboo removal. The dwarf bamboo removal did not seem to have a strong effect on leaf-level gas exchange capacity in the birch trees.

In forests where evergreen coniferous trees form the canopy, needle-level photosynthetic rates and stomatal conductance were clearly higher in areas where the understory had been removed than in areas where it had not been removed (Price et al. 1986; Kume et al. 2003). In Douglas fir (*Pseudotsuga menziesii*) and Japanese red pine (*Pinus densiflora*), whose needles usually flush during a short period in the growing season, understory removal had positive effects on needle photosynthetic rates and stomatal conductance throughout the needles' relatively long life-span (several years). On the other hand, the leaves of deciduous birch trees emerge successively during the growing season and their life-span is relatively short (several weeks)(Koike 1995). Plants with a successive leaf-emergence strategy show a high leaf turnover rate with rapid leaf development and senescence but keep a constant photosynthetic productivity at the shoot level during the growing season (Kikuzawa 2003). If the resources availability increased,

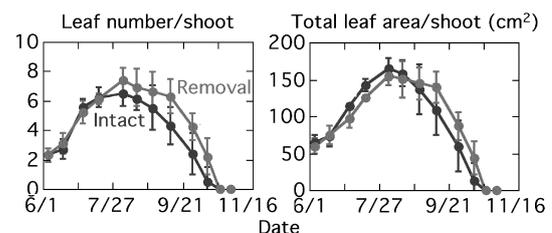


Fig. 2 Seasonal changes in leaf number and total leaf area per shoot of birch trees at 11-12m height in the forests of understory dwarf-bamboo intact and removed (OLD, 2003).

such plants would increase the number of leaves per shoot to increase shoot productivity. In support of this assumption, understory removal was found to increase leaf number and total leaf area per current-year shoot (long shoot) in the canopy of birch trees and to delay the time of peak of these values in the growing season (Fig. 2). These trends were also found in the YOUNG stand.

The gas exchange rate was estimated for the birch leaves essentially by the procedure of Hikosaka et al. (1999). Then, gas exchange rate per total leaf area in the current-year-old shoot was determined as the product of area-based leaf gas exchange rate and total leaf area per shoot. We found that the net CO₂ assimilation and transpiration rates of birch trees at the shoot level were greater in the removal plot than in the intact plot (Fig. 3). Especially, in the middle and lower canopy, this trend was found throughout the growing season. Thus, we suggest that birch trees respond to changes in competitive intensity and resources availability due to the dwarf bamboo removal mainly by altering leaf demography and shoot structure, and therefore by altering the gas exchange capacity at the shoot level rather than that at the single leaf level.

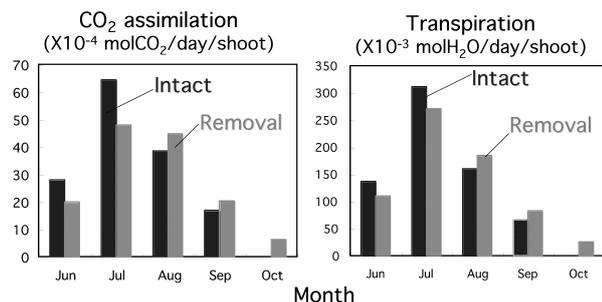


Fig. 3 Seasonal changes in gas exchange rates per shoot of birch trees at 11-12m height in the forests of understory dwarf-bamboo intact and removed (OLD, 2003).

Possible carbon gain and transpirational water loss in the overstory

We measured the plant area index and leaf density of the birch canopy, and the vertical light intensity gradient in the birch canopy in the removal and intact plots. Then, gas exchange rate per birch canopy was determined as the product of area-based leaf gas exchange rate and leaf area of canopy level. We found that the amounts of canopy-level carbon gain and transpiration in the removal plot were twice those of the control plot in July (Fig. 4).

The birch leaf density at the shoot level was greater in the removal plot than in the intact plot, but birch leaf density at the canopy level didn't show such a trend. The light intensity profile in the canopy in the

removal plot was similar to that in the intact plot. Therefore, the types of foliage and/or population structure of birch trees that would contribute to the canopy gas exchange rate appear to be different between the plots. We are now trying to 1) analyze the changes in the crown and population structures of birch trees after understory removal, 2) analyze three-dimensional foliage and light intensity distribution in the canopy, 3) estimate gas exchange rates in both the overstory and the understory, and 4) compare the values of gas exchange rate derived from traditional ecological procedures and those from flux measurements at the stand level.

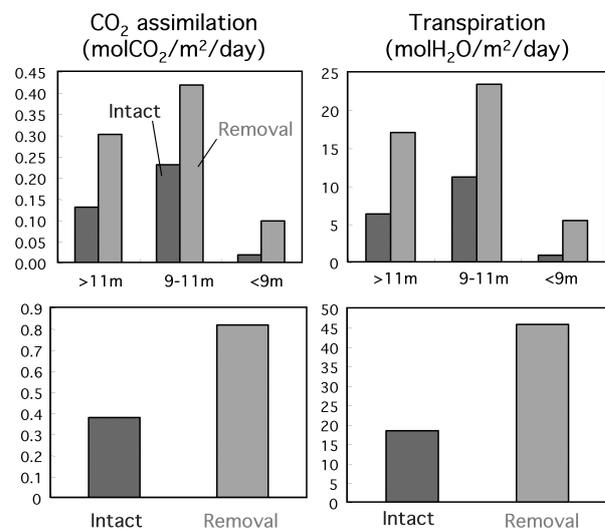


Fig. 4 Seasonal changes in canopy gas exchange rates of a birch forest with (intact) and without (removal) dwarf-bamboo undersory (OLD, July 2003). Upper, three class of canopy height; Lower, total canopy.

Acknowledgements

We thank the staff and members of the Uryu Experimental Forest and the Biosphere Dynamics Research Group of the Institute of Low Temperature Science for their support and help.

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