*Original Paper*

# Canopy tree characteristics and the seedling-sapling occurrence of *Betula ermanii* and *B. corylifolia* in a subalpine forest, central Japan

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Canopy tree characteristics and the seedling-sapling occurrence of *Betula ermanii* and *B. corylifolia* on different microsites were investigated to clarify the probable mechanism for the coexistence of these congeneric pioneer tree species, in an old-growth stand and an adjacent heavily disturbed area, in a subalpine evergreen coniferous forest of central Japan. In the old-growth stand, both species occurred as minor members of the canopy layer. Canopy trees of *B. ermanii* were larger in size (diameter at breast height and crown area) and more common than those of *B. corylifolia*, indicating that *B. ermanii* is a typical canopy tree species. Seedlings (0.05 m≤height<1.3 m) of both species occurred on every substrate (ground, fallen logs, root mounds and rotten stumps) under canopy gaps, though they did not occur on some types of substrates (ground and rotten stumps) under a closed canopy. No *Betula* saplings (1.3 m≤height<canopy) occurred under the closed canopy, but *B. ermanii* saplings occurred on ground and rotten stumps and *B. corylifolia* saplings occurred on ground, root mounds and rotten stumps under canopy gaps. Thus, both *Betula* species seem to have similar substrate requirements under both a closed canopy and canopy gaps for their establishment. However, along a gap-size gradient, *B. ermanii* clearly requires larger gaps than *B. corylifolia* for establishment. In the area disturbed heavily by a past typhoon, very abundant large *B. ermanii* saplings appeared on every substrate, though few small *B. corylifolia* saplings appeared on some types of substrate. These results suggest that *B. ermanii* and *B. corylifolia* coexist by partitioning gap (opening) size in relation to disturbance and that small scale disturbance such as formation of small gaps promotes *B. corylifolia* and large scale disturbance promotes *B. ermanii* recruitment.

**Keywords**: canopy gaps, coexistence, disturbance, fallen logs, microsite

## Introduction

Recent studies on forest dynamics or tree regeneration have emphasized the role of natural disturbance in maintaining tree species diversity in forests because disturbances create spatio-temporal heterogeneity in the physical environment, which promotes species coexistence by partitioning the heterogeneity (*e.g.* Grubb 1977; Denslow 1980; Orians 1982; Brokaw 1985; Duncan 1993). In forests, disturbances make small openings such as canopy gaps (Whitmore 1978; Runkle 1981; Lertzman and Krebs 1991) or large openings (Oliver 1981; Lorimer 1989). Different microsites within these openings can supply favorable microenvironments for different species to establish and grow (Yamamoto 1988), determining which species can coexist in the openings.

In the subalpine coniferous forests of the central Japan, two *Betula* species, *B. ermanii* (Cham.) and *B. corylifolia* (Regel et Maxim.) co-occur as minor members in old-growth (unlogged and dominated by trees > 200 yr old) stands (Franklin *et al.* 1979). These forests are usually dominated by evergreen conifers such as *Abies* (*A. mariesii* and *A. veitchii*), *Picea* (*P. jezoensis* var.

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*hondoensis*) and *Tsuga* (*T. diversifolia*), but these deciduous broad-leaved *Betula* species, though low in importance, always occur throughout the stands (Kimura 1963; Franklin *et al.* 1979; Kohyama 1984). Investigations on the life history and regeneration characteristics of *B. ermanii* have revealed that this species is shade intolerant and requires large canopy opening or gaps on sites with exposed mineral soil (Kohyama 1984; Kimura 1991; Yamamoto 1993, 1995). On heavily disturbed area formed by large-scale disturbance, *B. ermanii* colonizes the site and builds pure stands in the pioneer stage (Kimura 1991). Also, *B. ermanii* maintains a mature stable stand at the forest limit on high mountains of central Japan (Okitsu and Satomi 1989; Okitsu 1992). On the other hand, few details are known for the life history and regeneration characteristics of *B. corylifolia*. *B. corylifolia* seems to be shade-intolerant like other *Betula* species (Osumi and Sakurai 1997), though its response to gaps and site requirements as well as the life history of the species are not known.

In order to infer the possible mechanism for the coexistence of these *Betula* species in subalpine forests of central Japan, the purpose of this study was to 1) compare characteristics (number and size) of canopy trees of *B. ermanii* and *B. corylifolia*, to clarify the status of both species in the canopy layer of the old-growth stand, and 2) examine the response of their seedlings and saplings a) to the substrate heterogeneity under a closed canopy and canopy gaps in the old-growth stand and in a large opening in heavily disturbed area and, b) to gap size variation.

## Study Area

The study site is on the northern Yatsugatake (36° 00' N, 138° 23' E) mountains in central Japan. The northern Yatsugatake mountains (the highest peak is 2,645 m a.s.l.) are dead volcanoes, and andesitic lava that originated in the Pleistocene or the Holocene characterize most of the surface in this area (Tsuchida 1991). The whole of this area usually has a gentle topography. The climate and vegetation have been described by Oshima *et al.* (1958), Kimura (1963), and Franklin *et al.* (1979). Annual mean temperature is about 0°C, and annual precipitation is 150–200 cm. The subalpine forests occur from 1,800 m to 2,500 m in altitude. The forests dominated by both *Abies mariesii* Masters and *A. veitchii* Lindley develop over a wide range of soil conditions and those dominated by *Tsuga diversifolia* (Maxim.) Masters on very stony soils. Mosses or herbs usually cover the floors of the *Abies* forests, but Sasa (dwarf bamboo) sometimes occurs on the floors of the *Abies* stands on deep, fine-textured volcanic-ash soils. The floors of the *Tsuga* forests are usually covered by mosses.

A typical unlogged old-growth stand (about 2,200 m a.s.l.) was sampled in a subalpine evergreen coniferous forest near the Shirakomaike pond in the northern Yatsugatake mountains. The general height of the forest canopy is 25–30 m. I also sampled a young regenerating stand (area ≥ 1.0 ha) which had been heavily disturbed by the past severe typhoon (heavily disturbed site) and was neighbouring the old-growth stand.

## Methods

The following four replacement (regeneration) categories were defined and used in this study: (i) 'canopy trees' were defined as trees reaching the canopy layer, which were usually more than 20 cm diameter at breast height (DBH); (ii) 'gapmakers' were defined as trees of more than 20 cm DBH creating a gap; (iii) 'suppressed sapling' and (iv) 'gap successor' were defined as the tallest sapling (more than 1.3 m height, including non-canopy tree species) among saplings beneath the crown of each 'canopy tree' and in each gap, respectively. Thus, only one sapling per 'canopy tree' was recorded as a 'suppressed sapling' and only one sapling per gap as a 'gap successor'. 'Gap successors' are the most probable next occupant of the canopy or the sub-canopy layer of the gaps, and include both advance regeneration and new individuals (Bormann and Likens 1979).

In the old-growth stand, species name and DBH of 'canopy trees' were recorded along a transect line using the point-centered quarter method (Cottam and Curtis 1956), which has been considered to be the most efficient one among the available distance methods (Mueller-Dombois and Ellenberg 1974). Forty-four points were selected 20–60 m apart from the former point along the transect line following constant elevational contours. Species name, number, DBH and height of *Betula* saplings ($1.3\ m \leq height < canopy$) were recorded in a $5 \times 5\ m^2$ quadrat located on the ground surface at each point. The direction of the transect line was kept constant with a compass. It was altered to the opposite direction and the transect was continued 20 m apart from the line, when the top of the line met any microtopographic changes (*e.g.* gully, small cliff). Beneath the crown of each 'canopy tree' sampled, the species name and DBH of the tallest sapling (*i.e.* suppressed sapling) were recorded and the species name and number of *Betula* seedlings ($0.05\ m \leq height < 1.3\ m$) in a $1 \times 1\ m^2$ quadrat located on the ground surface were also recorded. Relative densities of 'canopy trees' and 'suppressed saplings' in the stand were calculated from the point-centered quarter-data. I sampled canopy trees of *Betula* randomly from *Betula* canopy trees recorded by the point-centered quarter method and measured the largest distance between crown edges (length) and the largest distance perpendicular to length (width), and the crown area was calculated by the formula for a circle using the mean value of the length and the width.

In this study, the ground area directly under a canopy opening ($5\ m^2 \leq area < 0.1\ ha$) was defined as a 'gap'; equivalent to canopy gaps defined by Runkle (1981); areas with canopies < 10 m high are defined as gaps. All gaps whose visual center was within 10 m on either side of the transect line were recorded. For each gap, the largest distance between gap edges (length) and the largest distance perpendicular to length (width) were recorded and the gap area was calculated by the formula for a circle using the mean value of the length and the width. Species name, DBH and the state (live or dead) of 'gapmakers' were recorded and also the mode of death or injury (*i.e.* standing dead, trunk-broken, uprooted or branch-broken) were recorded. In each gap, the followings were recorded: 1) the species name and DBH of the 'gap successor', 2) species name and number of *Betula* saplings in a $5 \times 5\ m^2$ quadrat and those of *Betula* seedlings in five $1 \times 1\ m^2$ quadrats randomly located on the surface ground within the gap. Densities of gaps and 'gapmakers' were calculated in the total surveyed area. Cases where there were no 'suppressed saplings' beneath the crown of a recorded 'canopy tree' or no 'gap successor' in a gap, were recorded as 'not existing'.

*Betula* regeneration on logs, mounds, and stumps were measured separately from regeneration on the ground surface. All visible fallen logs, root mounds, and rotten stumps within 10 m either side of the transect line were recorded. For fallen logs, their species name (if identified) was recorded, and the length and the diameter at mid-length were measured. The surface area of the fallen logs was calculated using the formula for half of the surface area of the side of a cylinder. When established seedlings or saplings of *Betula* were found on the fallen logs, their species name, number, DBH (only for saplings) and height were recorded. For root mounds, potential area which can be established by seedlings and saplings was calculated by the formula of the ellipse using the mound thickness and the mound width (Peterson *et al*. 1990). When established seedlings or saplings of *Betula* were found on the root mounds, their species name, number, DBH (only for saplings) and height were recorded. For rotten stumps, the diameter at a mid-height between the top and the base of the stump was measured and the potential area which can be established by seedlings and saplings was calculated by the formula of the circle using this value. When established seedlings or saplings of *Betula* were found on the rotten stumps, their species name, number, DBH (only for saplings) and height were recorded. The area investigated was 461.0 $m^2$ for fallen logs, 44.9 $m^2$ for root mounds, and 55.4 $m^2$ for rotten stumps.

Total surveyed area was calculated by multiplying the width of belt transects (*i.e.* 20 m) by the total length of the transect lines and was 1.78 ha. Based on the total number of 'gapmakers' and 'gap successors' in the total area surveyed in the old-growth stand, relative densities of 'gapmakers' or 'gap successors' in each tree species were calculated. Relative frequency was calculated as the percentage of the occurrence of a species at a sampling point to total sampling points. In the old-growth stand, twenty-seven gaps (the range of gap size was 14.1–350.5 $m^2$) were sampled by the point-centered quarter method and additional eight gaps (area ranging 46.4–878.3 $m^2$) were sampled independent of the investigation using the point-centered quarter method for detecting the response of both *Betula* species to the gap size variation.

Three 5×5 $m^2$ quadrats randomly located at representative on the heavily disturbed site, and species name, number, DBH and height of *Betula* saplings were recorded with descriptions of their rooting substrate. All field studies were conducted from August to October, 1995. Nomenclature follows Ohwi (1972)

## Results

### 1. Number and size of canopy trees

About 20% of the total number of canopy trees was *Betula* species (Table 1). The density of *B. corylifolia* was about half of that of *B. ermanii* and the basal area of *B. corylifolia* was one-sixth of that of *B. ermanii*. The relative frequency of *B. ermanii* was higher than that of *B. corylifolia*. The mean DBH of *B. ermanii* was significantly larger than that of *B. corylifolia* (Mann-Whitney $U$-test, $p<0.001$). The DBH range of *B. ermanii* (20–70 cm) was wider than that of *B. corylifolia* (20–40 cm) for both canopy trees and gapmakers (Fig. 1). The mean crown area of *B. ermanii* was 125.1±60.5 $m^2$ (maximum=283.2 $m^2$) and that of *B. corylifolia* was 57.9±21.8 $m^2$ (maximum=105.4 $m^2$), and the former was significantly larger than the latter (Mann-Whitney $U$-test, $p<0.01$). Crown area increases linearly with DBH for both species (Fig. 2). The coefficient of the simple regression line for *B. ermanii* ($Y=2.667X$, $R^2=0.913$) was larger than that for *B. corylifolia* ($Y=2.116X$, $R^2=0.936$).

### 2. Occurrence of seedlings and saplings

Both *Betula* species had gapmakers with the

Table 1. Density ($ha^{-1}$), relative density (%), relative frequency (%), mean DBH±S.D. (cm), and basal area ($m^2$ $ha^{-1}$) for canopy trees in the old-growth stand. Maximum DBH was given in parentheses.

| | Density | Relative density | Relative frequency | DBH | Basal area |
|---|---|---|---|---|---|
| Evergreen conifers | | | | | |
| *Abies veitchii* | 75.9 | 15.3 | 56.8 | 37.1±7.7 (54.0) | 8.54 |
| *Abies mariesii* | 110.1 | 22.2 | 43.2 | 35.1±8.2 (52.6) | 11.25 |
| *Picea jezoensis* var. *hondoensis* | 70.4 | 14.2 | 63.6 | 49.9±11.7(75.3) | 14.52 |
| *Tsuga diversifolia* | 140.9 | 28.4 | 43.2 | 42.5±10.7(76.5) | 21.27 |
| Deciduous broad-leaved trees[1] | | | | | |
| *Betula ermanii* | 62.0 | 12.5 | 43.2 | 48.4±11.7(69.8) | 12.06 |
| *Betula corylifolia* | 33.7 | 6.8 | 25.0 | 27.9±4.8 (37.6) | 2.12 |

[1]A canopy tree of *Sorbus commixta* occurred (DBH=38.6 cm)

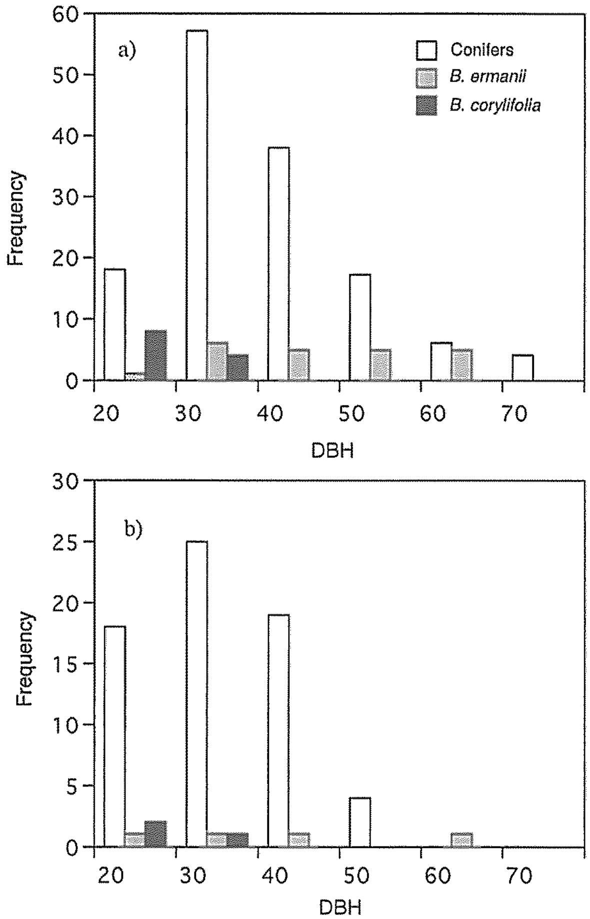


Fig. 1. DBH (cm) class frequency (no. /total area surveyed) distribution of canopy trees (a) and gapmakers (b) of conifers, *Betula ermanii* and *B. corylifolia* in the old-growth stand.

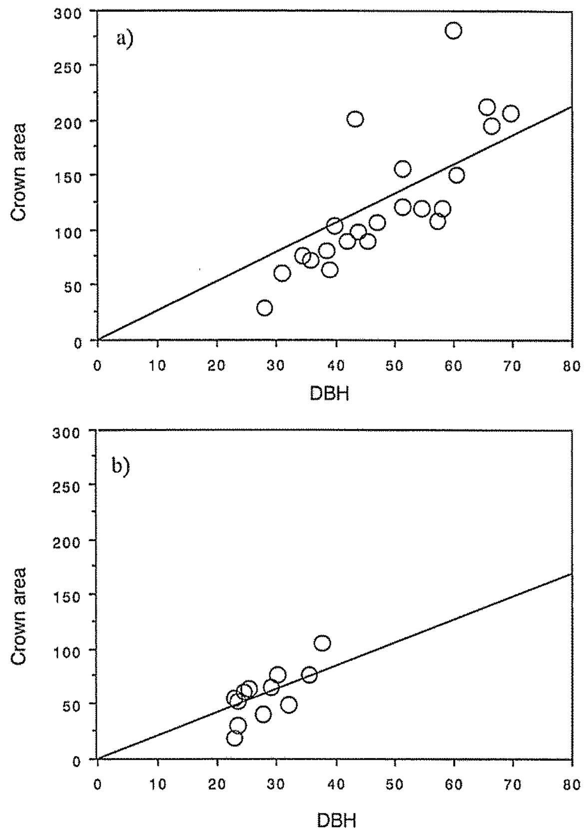


Fig. 2. Relationship between DBH (cm) and crown area ($m^2$) of *Betula ermanii* (a) and *B. corylifolia* (b).

Table 2. Relative density (R.D., %), mean DBH±S.D. (cm) and basal area (B.A., $m^2ha^{-1}$) of gapmakers, suppressed saplings and gap successors for *Betula ermanii* and *B. corylifolia*. Maximum DBH is given in parentheses.

| | Gapmakers[1)] | | | Suppressed saplings | | | Gap successors | | |
|---|---|---|---|---|---|---|---|---|---|
| | R.D. | DBH | B.A. | R.D. | DBH | B.A. | R.D. | DBH | B.A. |
| *B. ermanii* | 3.7 | 40.8±15.4 (65.2) | 0.596 | — | — | — | 5.9 | 5.3±3.0 (8.3) | 0.014 |
| *B. corylifolia* | 3.7 | 24.3±8.0 (37.0) | 0.205 | 0.6 | 11.4[2)] (11.4) | 0.010 | 1.2 | 0.8[2)] (0.8) | 0.000 |

[1)]Total number of gapmakers was 108 trees.
[2)]Only one suppressed sapling or gap successor occurred.

same relative density (Table 2). Only *B. corylifolia* occurred, though very low in relative density, as suppressed saplings, while both species occurred as gap successors; the relative density of gap successors for *B. corylifolia* was lower than that for *B. ermanii*.

Seedlings of both species occurred on every substrate under canopy gaps, though they did not occur on ground and rotten stump and moreover *B. corylifolia* did not occur on the root mound under a closed canopy (Table 3). Under a closed canopy, many *B. corylifolia* seedlings occurred on fallen logs and many *B. ermanii* seedlings occurred on root mounds. Under gaps, seedling density was lower on ground than on other substrates, while seedling height was higher on ground than on other substrates, for both species. Although these differences of substrate requirement were present for both species, differences between species were not so apparent.

No *Betula* saplings occurred under a closed canopy. Under canopy gaps, the sapling density of both species was nearly equal, while mean DBH, height and basal area of *B. ermanii* were larger than those of *B. corylifolia* (Table 4). *B. ermanii* saplings occurred on ground and rotten stumps and *B. corylifolia* saplings occurred on ground, root mounds and rotten stumps (Table 5).

Responses of each species' seedlings and saplings to gap size variation were different (Table 6). *B. corylifolia* occurred in smaller gaps than *B. ermanii* for both seedlings and saplings.

In the heavily disturbed area, *B. ermanii* saplings were much more abundant and larger than *B. corylifolia* saplings (Table 7). The density of *B. ermanii* saplings was about elevenfold that of *B. corylifolia* saplings. On this site, *B. ermanii* saplings occurred on every substrate (Table 8); only *Betula* occurred on root mound and *B. ermanii* saplings were found with much higher relative density than *B. corylifolia* on this substrate. However, *B. corylifolia* saplings occurred only on fallen logs and root mounds with much lower relative density overall.

## Discussion

### 1. Characteristics of canopy trees

*Betula* often occurs in the canopy layer of many subalpine old-growth forests dominated by evergreen conifers, though its importance in the canopy layer is too low (Franklin *et al.* 1979;

Table 3. Mean density ($ha^{-1}$) and height (mean±S.D., cm) of *Betula ermanii* and *B. corylifolia* seedlings (0.05 ≤height<1.3 m) on different substrates (ground, fallen logs, root mound and rotten stump) under closed canopy and canopy gaps.

| | Ground[1] | | Fallen logs[2] | | Root mound[3] | | Rotten stump[4] | |
|---|---|---|---|---|---|---|---|---|
| | Closed canopy | Gap | Closed canopy | Gap | Closed canopy | Gap | Closed canopy | Gap |
| Density | | | | | | | | |
| *B. ermanii* | — | 400 | 46.8 | 727.3 | 2776.4 | 4393.6 | — | 3578.3 |
| *B. corylifolia* | — | 514.3 | 1264.2 | 2383.9 | — | 6736.9 | — | 1789.2 |
| Height | | | | | | | | |
| *B. ermanii* | — | 110.4 ±21.3 | 5.0 | 19.5 ±17.2 | 24.3 ±8.7 | 48.4 ±48.5 | — | 49.4 ±37.3 |
| *B. corylifolia* | — | 79.1 ±31.4 | 14.1 ±9.2 | 22.8 ±29.1 | — | 57.7 ±38.3 | — | 28.6 ±24.5 |

[1]Number of quadrats (1×1 $m^2$) investigated was 176 (176 $m^2$ in area) under a closed canopy and 175 quadrats (175 $m^2$ in area) under gaps.
[2]Number of fallen logs investigated were 49 (213.6 $m^2$ in area) under a closed canopy and 52 (247.4 $m^2$ in area) under gaps.
[3]Number of root mounds investigated was 7 (10.8 $m^2$ in area) under a closed canopy and 26 (34.1 $m^2$ in area) under gaps.
[4]Number of rotten stumps investigated was 11 (10.7 $m^2$ in area) under a closed canopy and 13 (44.7 $m^2$ in area) under gaps.

Table 4. Density ($ha^{-1}$), DBH (mean±S.D., cm) basal area (B.A., $m^2ha^{-1}$) and height (mean±S.D., m) of *Betula ermanii* and *B. corylifolia* saplings (height≥1.3 m) under canopy gaps. Maximum DBH and height were given in parentheses. Thirty-five 5×5 $m^2$ quadrats were investigated.

| | Density | DBH | B.A. | Height |
|---|---|---|---|---|
| *B. ermanii* | 217.1 | 3.16±2.57 (8.30) | 0.025 | 5.10±3.01 (9.45) |
| *B. corylifolia* | 228.6 | 1.37±0.72 (3.69) | 0.004 | 2.67±0.98 (6.47) |

Table 5. Mean density ($ha^{-1}$) of *Betula ermanii* and *B. corylifolia* saplings (height≥1.3 m) on different substrates (ground, fallen logs, root mound and rotten stump) under canopy gaps.

| | Ground | Fallen logs | Root mound | Rotten stump |
|---|---|---|---|---|
| *B. ermanii* | 80.0 | – | – | 137.1 |
| *B. corylifolia* | 137.1 | – | 22.9 | 68.6 |

Table 6. Density ($ha^{-1}$) of seedlings (0.05 < height < 1.3 m) and saplings (height≥1.3 m) of *Betula ermanii* and *B. corylifolia* and the frequency of gap successors (the tallest sapling in a gap) occurred in different gap size ($m^2$) classes.

| | Gap size class | | | | |
|---|---|---|---|---|---|
| | 40– | 80– | 160– | 320– | 640– |
| Density | | | | | |
| Seedlings | | | | | |
| *B. ermanii* | – | – | – | 700 | – |
| *B. corylifolia* | – | – | 2,000 | 700 | – |
| Saplings | | | | | |
| *B. ermanii* | – | – | 2,400 | 400 | 3,600 |
| *B. corylifolia* | 107 | – | 800 | 1,500 | 400 |
| Frequency of gap successors | | | | | |
| *B. ermanii* | – | – | 1 | 1 | 3 |
| *B. corylifolia* | – | 1 | – | – | – |

Table 7. Mean density ($ha^{-1}$), DBH (mean±S.D., cm) basal area (B.A., $m^2$ $ha^{-1}$) and height (mean±S.D., m) of *Betula ermanii* and *B. corylifolia* saplings (height≥1.3 m) on the heavily disturbed site. Three 5×5 $m^2$ quadrat were investigated.

| | Density | DBH | B.A. | Height |
|---|---|---|---|---|
| *B. ermanii* | 4525 | 3.68±1.35 | 9.21 | 5.78±1.52 |
| *B. corylifolia* | 400 | 1.16±0.79 | 0.12 | 1.97±0.23 |

Table 8. Relative density (%) of *Betula ermanii* and *B. corylifolia* saplings (height≥1.3 m) on different substrates (ground, fallen logs, root mound and rotten stump) in the heavily disturbed site.

| | Ground | Fallen logs | Root mound | Rotten stump |
|---|---|---|---|---|
| *B. ermanii* | 13.5 | 39.5 | 83.4 | 50.0 |
| *B. corylifolia* | – | 5.3 | 16.6 | – |
| Other tree species | 86.5 | 55.2 | 0 | 50.0 |

Kohyama 1984; Kanzaki 1984; White *et al.* 1985; Kanzaki and Yoda 1986; Taylor and Qin 1988). Similarly, in this study, two *Betula* species, *B. ermanii* and *B. corylifolia*, together composed about 20% of the total number of canopy trees. However, the status of each *Betula* species was different in canopy abundance, frequency and size. *B. ermanii* canopy trees were more abundant, more frequent and larger in size than *B. corylifolia* trees. As a seed source, abundant and frequent occurrence of seed trees leads to a higher probability of catching a favorable establishment site and larger crown size increases the potential area for seed bearing (Harper 1977). Both *Betula* have light winged seeds which can disperse long distances by wind as is usual with species in the genus *Betula* (Yanagisawa 1961; Kinnaird 1974; Osumi and Sakurai 1997). However, due to its greater abundance, frequency and size, *B. ermanii* has an advantage in colonizing or exploiting favorable sites for its establishment compared with *B. corylifolia*. This advantage might explain why very abundant *B. ermanii* seedlings or saplings appeared in the heavily disturbed area.

Difference of longevity is considered to be an important cause for tree species coexistence (Schmida and Ellner 1984; Veblen 1986). Longevity of *B. ermanii* exceeds 250 years (Watanabe 1979), but that of *B. corylifolia* is not known. It has not been reported that large differences exist between their longevities, although the size distribution of both *Betula* (Fig. 1) suggests that their longevities may be different.

## 2. Occurrence of seedlings and saplings

*Betula* is a typical shade-intolerant pioneer genus and can not survive and grow under forest shade (Koïke and Sakagami 1985; Koike 1987, 1995; Wayne and Bazzaz 1993). In this study, only one suppressed sapling of *B. corylifolia* and no saplings of *B. ermanii* could be found under a closed canopy in the old-growth stand. Since seedlings of both species occurred on fallen logs or root mound under a closed canopy, their seedlings can survive on elevated surfaces such as these substrates. Exposed mineral soil such as soil on root mounds has been considered to be a favorable establishment site for many *Betula* species (Kimura 1991; Yamamoto 1993, 1995; Osumi and Sakurai 1997). Under canopy gaps, seedlings of both species occurred on every substrate including the ground surface, implying that formation of canopy gaps makes every substrate favorable establishment sites for the establishment of both *Betula* species. However, any substrate under canopy gaps is not always favorable for growth and survival of *Betula* saplings, because saplings occurred only on some types of substrate. Although I found slight differences in substrate requirements for each *Betula* species, considering these results altogether and totally, the substrate requirement for establishment may not be substantially different for the two *Betula* species in the old-growth stand.

Both *Betula* species strongly required canopy gaps for their establishment. However, along a gap size gradient, both seedlings and saplings of *B. corylifolia* occurred in smaller gap sizes compared with those of *B. ermanii*. This result and the fact that one suppressed sapling of *B. corylifolia* occurred under a closed canopy suggest that *B. corylifolia* is more shade-tolerant than *B. ermanii*.

In the heavily disturbed area, very abundant large *B. ermanii* saplings appeared on every substrate. On this site, *B. ermanii* may be able to establish and grow irrespective of substrate difference. On the other hand, few small *B. corylifolia* saplings appeared on some types of substrate. These results clearly imply that the colonizing or establishment abilities of *B. ermanii* are much stronger than those of *B. corylifolia* in heavily disturbed areas.

In conclusion, these *Betula* species may coexist by partitioning gap (opening) size along gap size gradient (Denslow 1980) in relation to natural disturbance and not by differentiation for substrate requirement. Small-scale disturbance promotes *B. corylifolia* and large-scale disturbance promotes *B. ermanii* for the recruitment.

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## 中部日本亜高山帯林におけるダケカンバとウラジロカンバの林冠木特性と稚幼樹の出現

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同属近縁の先駆樹種であるダケカンバとウラジロカンバの共存メカニズムを明らかにする目的で，両樹種の林冠木特性と異なるマイクロサイト上での稚幼樹の出現を，中部日本亜高山帯常緑針葉樹林の老齢林分と隣接する台風による大規模撹乱地で調査した。両樹種とも老齢林分の林冠層の非優占樹種であった。ダケカンバの林冠木がウラジロカンバの林冠木よりも，胸高直径や樹冠面積が大きく，より普遍的に出現したことは，ダケカンバが顕著な林冠樹種であることを示している。両樹種の稚樹（0.05 m≦高さ<1.3 m）は，林冠ギャップ下ではすべての基質上（地表面，倒木，根返りマウンド，腐朽株）で出現したが，閉鎖林冠下では地表面と腐朽株上で出現しなかった。両樹種の幼樹（1.3 m≦高さ<林冠層）は閉鎖林冠下では出現しなかったが，林冠ギャップ下ではダケカンバは地表面と腐朽株上で，ウラジロカンバはさらに根返りマウンド上でも出現した。したがって，両樹種は閉鎖林冠下でも林冠ギャップ下でも，その定着に適した基質は類似しているようである。しかしながら，ダケカンバはウラジロカンバよりも定着に対してより大きなギャップを必要とする。台風による大規模撹乱地では，あらゆる基質上で多数の大サイズのダケカンバの幼樹が出現したが，ウラジロカンバの幼樹はいくつかのタイプの基質上でわずかしか出現しなかった。これらの結果は，ダケカンバとウラジロカンバは撹乱と関係してギャップサイズを分割することによって共存しており，小ギャップ形成のような小規模撹乱はウラジロカンバの定着を，大規模撹乱はダケカンバの定着を促進することを示唆している。

キーワード：ギャップ，共存，自然撹乱，先駆樹種，マイクロサイト