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Effects of Snow Avalanche Disturbance on Regeneration of Subalpine *Abies mariesii* Forest, Northern Japan

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Abstract

We examined the effects of snow avalanche on stand structure and the subsequent regeneration of subalpine *Abies mariesii* Mast forest in northern Japan, and discussed whether gap formation after avalanche disturbance leads to immediate seedling establishment or not. Tree size and age, tree-ring chronology, and seedling density were compared between, on, and around a relatively large avalanche path, which was created in the mid-1980s within Hachimantai National Park. On the avalanche path, only smaller and younger trees (height <5 m, 50–100 yr old) escaped the mechanical damage of avalanche by leaning into the remaining snowpack, and old canopy trees were mostly killed by stem breakage. Tree size structure of the avalanche path, including both living and dead individuals, was relatively similar to that of nearby undisturbed forest, indicating that a mature stand (>ca. 200 yr old) had been previously developed on the avalanche slope without large-scale disturbances in the past. Most of the surviving, younger trees showed abrupt growth release during the few years (1987–1989) after the avalanche event. However, densities of both post-avalanche (<15 yr old) and pre-avalanche (≥15 yr old) seedlings were much lower on the avalanche path than in the nearby forest, especially at microsites covered with dense dwarf bamboo (*Sasa kurilensis*) shrub. The pre-avalanche seedlings on the avalanche path sharply increased annual height growth rates after the mid-1980s avalanche, but such positive growth response did not continue longer than 6 to 7 yr. These findings suggested that gap formation following the infrequent, large-scale avalanche disturbance did not necessarily lead to immediate seedling recruitment and/or further growth release of pre-avalanche seedlings. The constraint of seedling establishment was primarily explained by the lack of potential seed supply, and shading effect of the dwarf bamboo bush. Consequently, post-avalanche regeneration of the subalpine fir forest was likely to depend on the smaller individuals (2–5 m in height) that were able to avoid both the mechanical damage of avalanche and mortality from shading by the dwarf bamboo.

Introduction

Snow avalanche is one of major disturbance agents affecting landscape, vegetation patterns, and forest development in subalpine areas worldwide, especially near upper treelines (Potter, 1969; Akifyeva et al., 1978; Erschbamer, 1989; Smith et al., 1994; Veblen et al., 1994; Walsh et al., 1994). Mature forests rarely develop due to repetitive mechanical damage on the steep slopes where avalanche occurs frequently. On such avalanche-prone sites, meadows, broad-leaved shrubs, and younger conifer stands are generally established, although dominant vegetation types vary locally depending on impact and frequency of avalanches (e.g., Butler, 1979; Johnson et al., 1985; Johnson, 1987; Pattern and Knight, 1994).

In Japan, many disastrous snow avalanches occur every winter, especially in Hokkaido Island and northern parts of Honshu Island (Nakamura et al., 1995). Avalanche events in these snowy regions have been well studied from various viewpoints, such as avalanche-prone terrain (Takahashi and Ueda, 1937; Wakabayashi, 1966), forest protection and silviculture treatment (Takahashi et al., 1968), and mechanical damage upon trees (Onodera and Wakabayashi, 1969, 1970). Some researchers have also tried to reconstruct impact and frequency of past avalanche events on forest structure using tree-ring patterns and snow damage scars (Wakabayashi et al., 1970;

Wakabayashi, 1971; Shimokawa, 1983). These earlier studies, however, mostly dealt with avalanche events at lower elevations, and comparable field studies on subalpine forests are still considerably limited (e.g., Nashimoto and Ishii, 1999).

Subalpine conifer forests in the northern parts of Honshu Island are generally dominated by *Abies mariesii* Mast, which are distributed above 1000 to 1100 m in elevation along the main mountain range, the Ohu mountains. However, the fir forests are sparse or excluded in some extremely snowy mountains (Shidei, 1952; Yamanaka et al., 1973; Sugita, 1992). Besides, the upper forest-limit often occurs at lower elevations, especially on east-facing leeward slopes with heavy snow accumulation (Shidei, 1956). On such snowy sites, individual trees suffer from snow-loading damage (Yoshii, 1949; Ishizuka, 1981). For example, Kajimoto et al. (2002) showed that intensive snow-loading damage occurred repetitively after snowy winters, and largely controlled both individual growth and stand development of *A. mariesii* near the upper forest-limits. Recently, Daimaru et al. (2000) reported that snow avalanches occurred infrequently, but caused large-scale destruction in the upper or higher *A. mariesii* forests in this region, indicating that avalanche is another important agent of snow-related disturbances.

Following these infrequent avalanche events (>several decades), relatively large openings or gaps (e.g., 1–3 ha in area) are created near the upper forest limit (Daimaru et al., 2000). Such gap

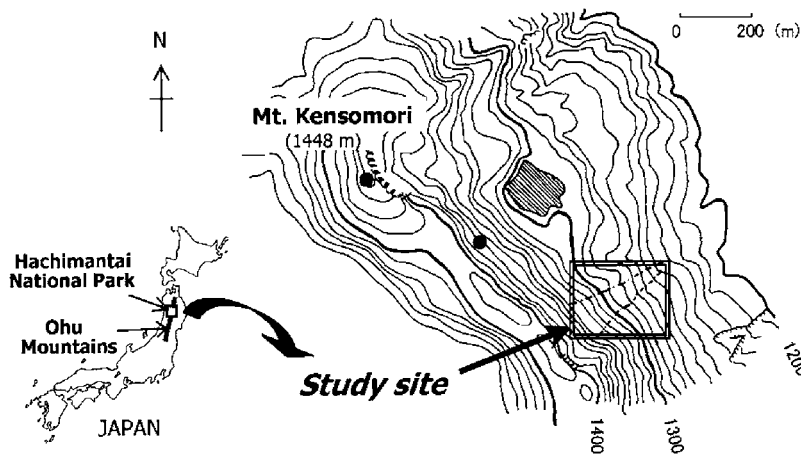


FIGURE 1. Location map of the study site near Mt. Kensomori within Hachimantai National Park. A dashed line indicates the boundary between the mid-1980s avalanche path and surrounding undisturbed forest.

formation may lead to regeneration success through seedling recruitment and/or growth release of pre-avalanche seedlings in response to improvement of light environment. This scenario of post-disturbance regeneration process, so called gap dynamics, has been well demonstrated for old subalpine conifer forests located in central parts of Honshu Island (e.g., Kohyama, 1982, 1983, 1984; Kanzaki, 1984; Kimura et al., 1986; Yamamoto, 1993, 1995). On these subalpine forests, however, gaps are mainly created by wind-related disturbances, such as stem breakage, treefall, and uprooting of canopy trees due to wind storms (i.e., typhoon) (Komiya et al., 1981; Kanzaki and Yoda, 1986; Yamamoto, 1992). Disturbance regimes differ in frequency, average gap size, and subsequently environmental changes among the major types of disturbance agents, such as fire, wind storms and insect outbreaks (Oliver et al., 1985; Veblen, 1989; Turner et al., 1997). As for snow avalanches, Johnson (1987) reported that re-establishment of dominant tree species differed largely even within a given avalanche slope due to difference in average event frequency. Thus, post-avalanche regeneration of *A. mariesii* forest on openings is not likely to occur as in the same scenario of wind-induced gap dynamics.

Undergrowth of dwarf bamboos often interferes with seedling recruitment in some forest types worldwide (e.g., Veblen et al., 1977; Taylor and Zisheng, 1988). Likewise, dwarf bamboo (*Sasa* spp.) shrubs are distributed widely in the snowy regions of northern Japan, which affects seedling establishment in the mountain beech (*Fagus crenata* Blume) forest (Nakashizuka, 1987; 1988) and subalpine mixed conifer forest (Takahashi, 1994, 1997; Hiura, et al., 1996). Particularly, *Sasa kurilensis* (Rupr.) Makino et Shibata densely covers the ground of subalpine *A. mariesii* forests, so that seedling recruitment may be restricted even in the gaps (Makita, 1997). Thus, to understand postavalanche regeneration of the fir forest, we need to evaluate the disturbance regime endemic to avalanche, but also effects of the undergrowth on seedling establishment following the disturbance.

To examine these two processes, we made field observations and sampled on a relatively large avalanche path created within Hachimantai National Park. Tree size and age structure, individual growth response, and seedling recruitment were compared between the two sites, inside the avalanche path and in the nearby undisturbed forest. Based on these results, we discussed roles of the avalanche disturbance in development of the subalpine *A. mariesii* forest, focusing on the question whether relatively large gap formation following the avalanche leads to immediately seedling establishment or not.

Materials and Methods

STUDY SITE

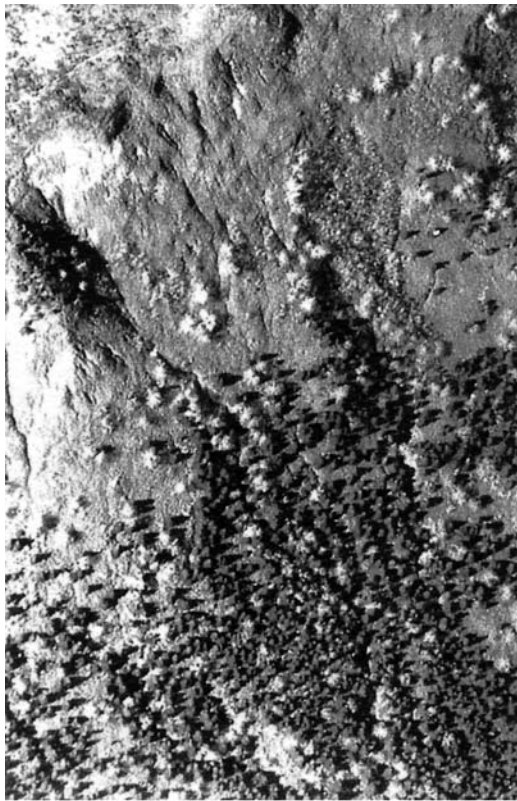
The study site is located near Mt. Kensomori (1448 m a.s.l.) in the Ohu mountain range, within Hachimantai National Park, northern Honshu Island (39°45'N, 140°45'E) (Fig. 1). In the study area, major peaks are extinct volcanoes, and bedrocks consist of andesite and volcanic sediments (e.g., welded tuff). Monthly mean air-temperatures are about 16°C in August and -11°C in January near the summit of Mt. Kensomori; estimated by applying a lapse rate (-0.6°C/100 m) to the data at meteorological station (Daimaru et al. 2002). Snowfall generally begins in late October and lasts until early May. Snow accumulation differs locally due to effects of topography and predominant northwest wind (Daimaru et al., 2002). For example, maximum snow depth is less than 1 m on the windward ridges, but exceeds 3 m in the *A. mariesii* forest on the eastern, leeward slope around Mt. Yumori (1472 m a.s.l., about 15 km south to this study site) (Kajimoto et al., 1998; 2002).

Subalpine forests in the study area are dominated by *Abies mariesii* at higher elevation (1000–1500 m), and are mixed with *Tsuga diversifolia* (Maxim.) Masters, *Pinus parviflora* Sieb. et Zucc., and *Betula ermanii* Cham at lower elevation (<1300 m). Around Mt. Kensomori, the fir forest expands up to the summit on the western slope, while its upper forest-limit declines about 100 m below the main ridge on the eastern slope. Dwarf bamboo (*Sasa kurilensis*) (1–2 m in height) occurs throughout the area, and densely covers the ground surface inside *A. mariesii* forests, except for some microsites, such as just below the crowns of larger canopy trees.

MID-1980s AVALANCHE PATH

For our field study, a relatively large avalanche path (a wedge-like opening, Fig. 1) was selected from some avalanche slopes found at east-facing slopes of Mt. Kensomori (Daimaru et al., 2000). Slope angle was >25 to 30° on the upper parts (>1300 m a.s.l.), and was gradually reduced to 15 to 20° at the lower end of slope.

Preliminary examination of the aerial photographs, which were taken at 5-yr intervals since 1965 (Fig. 2), indicated that the avalanche path was created in mid-1980s (between 1984 and 1988). According to other evidence, such as avalanche scars retained on the stems of some broadleaved trees (*Betula ermanii*), a full-depth avalanche likely occurred in the early spring of 1986 (Daimaru et al., 2000). Snow crack formation may have triggered the avalanche at the uppermost part of the slope (1350–1380 m a.s.l., about 150 m in width). Around this starting zone, where the ground surface had been previously covered with dwarf bamboo bush, many bare ground patches appeared after the



A



B

FIGURE 2. Aerial photographs of the study slope taken (A) before (on 15 October 1983) and (B) after (on 23 September 1988) the disturbance of mid-1980s avalanche (photos No. 83-35 C6A-3, 88-33, C6-24; Japan Forestry Agency). On the photo in 1988 (B), much bare ground appeared at the starting zone (seen as white patches occurring in bow-shape at upper slope), indicating that ground surface erosion together with rhizomes of dwarf bamboo (*Sasa*) occurred due to the full-depth avalanche. At the lower end of slope, woody debris consisting of many broken stems was also recognized.

avalanche (see white patches in 1988 photograph; Fig. 2B), indicating that ground surface erosion was caused including rhizomes of *Sasa* shrubs. Runout length of the avalanche was estimated to be about 300 m, and woody debris of many broken stems was found at the lower end of slope (Fig. 2B).

TREE SURVEY

Tree census was conducted on the avalanche path and surrounding undisturbed forest. The boundary of these two sites was determined by comparing the two aerial photographs taken before and after the mid-1980s avalanche (Fig. 2). On the avalanche path (about 1.7 ha in area), spatial positions of all living trees of *A. mariesii* (height > 1.3 m) were mapped, and their stem diameters at heights of 1.3 m (DBH) and 30 cm (D_{30}), and tree heights (H) were measured. For *B. ermanii*, only larger individuals (H > 1.3 m, but DBH < 20 cm) were measured for spatial positions and DBH. Dead trees were classified into three types; standing dead trees without any signs of mechanical damage, stem-broken trees (i.e., broken snags), and uprooted trees. For the stem-broken trees, their diameters (both DBH and D_{30} , or only D_{30}) and breakage heights were recorded. The tree census of the undisturbed forest was made within the area restricted to 20–30 m outside the boundary (about 2 ha in total area).

TREE-RING ANALYSIS

Tree age and ring-width patterns were examined for all living *A. mariesii* trees ($n = 34$) on the avalanche path by sampling stem cores at

30 to 50 cm in height, except for some larger trees (at 80–120 cm in height). We removed only one or two cores from each tree, since destructive sampling was restricted within the National Park. On the undisturbed forest, stem cores were sampled from some larger canopy trees (DBH > 30 cm, $n = 26$) located on the northern half of the tree census area. For each core sample, the number of annual rings was counted, and annual ring-widths were measured using a microscope (0.01 mm in accuracy). Cross-dating was made visually using pointer-years, such as narrow rings or abrupt growth release (Fritts, 1976; Schweingruber, 1996).

Ring-width patterns were analyzed by separating the study slope into upper and lower parts for both the avalanche path and undisturbed forest (a boundary is defined in Fig. 3). For this analysis, relatively old trees (>90 yr old) without any signs of physiological deterioration (e.g., tip dieback) were selected among the core-sampled trees of the avalanche path ($n = 9$ from upper slope, and $n = 8$ from lower slope). Individual ring-width index curve was approximated by fitting either simple linear or inverse-exponential regression according to the standard method (e.g., Fritts, 1976), and then average ring-width index curve (since 1940) was calculated for each slope. In the same manner, individual and average ring-width index curves (since 1900) were determined for some older (>170 yr old), healthy individuals selected from the core-sampled trees on the undisturbed forest ($n = 8$ for upper slope, and $n = 11$ for lower slope). In the analysis of tree-ring chronology, we focused on abrupt changes of ring-width pattern to detect tree growth response to the mid-1980s avalanche and/or other past disturbance events. Other statistical methods were not applied to reconstruction of disturbance events in details, such as the event-

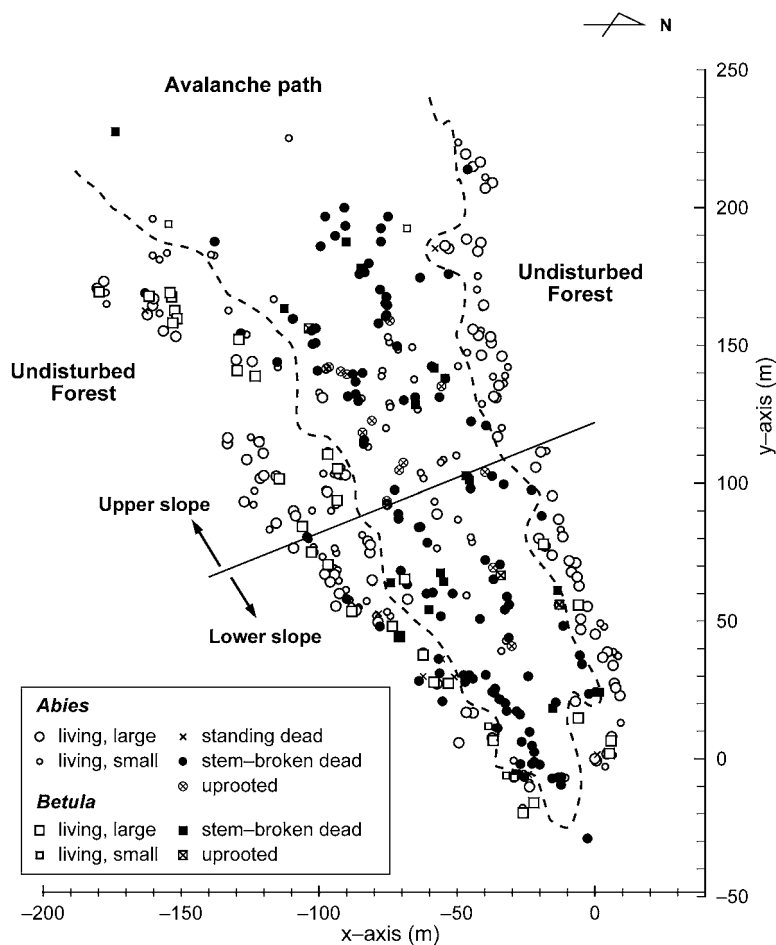


FIGURE 3. Spatial location map of *A. mariesii* and *B. ermanii* trees in the study site. Two different size symbols indicate larger (DBH > 30 cm) and smaller (≤ 30 cm) living trees of each species; *B. ermanii* trees smaller than 20 cm were excluded. Each tree position is plotted on the two dimensional plane: x- and y-axes indicate north-south and east-west directions, respectively. A dotted curve shows the boundary between the avalanche path and surrounding undisturbed forest, and a straight line across the avalanche path (about 80–100 m on y-axis) indicates the boundary between the upper and lower slope parts.

response index using the beginning years of compression wood formation (Carrara, 1979; Shroder, 1980; Butler and Malanson, 1985; Rayback, 1998), since the our samples (i.e., one or two cores per tree) were too small to apply such index with a relatively high cut-off value. Besides, we confirmed that wide compression wood rings were recognized in some core samples, but were mostly formed in early growth stage of each tree (<5 cm in stem diameter at each core sampling height); the patterns of simultaneously abrupt growth release detected in our analysis were free of such compression wood rings.

SEEDLING SURVEY

The density of living *A. mariesii* seedlings ($H < 130$ cm) was examined using square quadrats (each 2×2 m² in area). On the avalanche path, 14 quadrats (i.e., seven pairs) were established on two different microsites: around stem-broken dead trees of *A. mariesii* (designated as site AC; $n = 7$) and inside *Sasa* shrubs (AS; $n = 7$) (2–3 m away from each AC). These quadrats were located along down the middle of the avalanche slope (>20 m inside the boundary). On the undisturbed forest, 20 census quadrats (ten pairs) were established on two corresponding microsites: below crowns of living *A. mariesii* trees (FC; $n = 10$) and in nearby *Sasa* shrubs (FS; $n = 10$) along the northern boundary. We selected the larger individuals for the two microsites (AC, FC). The mean values were 35 cm (D_{30}) and 1.8 m (stem breakage height) for the stem-broken dead trees of AC, and 47 cm (DBH) and 14.1 m (H) for the living trees of FC, respectively. As for each *Sasa* shrub site (AS, FS), undergrowth conditions appeared relatively similar in terms of culm density and height (1–1.5 m), although these parameters were not compared statistically.

The age of *A. mariesii* seedlings was determined by counting the numbers of interbranch nodes along the stem. This nondestructive method was applicable for younger seedlings (<30 yr) (Kajimoto et al., 2002), but it often underestimated ages for older seedlings because of their portions of underground stems (e.g., Tanaka, 1986). Thus, the age of older seedlings was determined destructively by counting the numbers of annual rings above the root collar. Comparisons of seedling density among the four microsites were made by Steel-Dwass multiple comparison test, by separating the seedlings into two age-groups, pre-avalanche (>15 yr old at the sampling year 2000) and postavalanche seedlings (≤ 15 yr old): they were defined as the individuals that germinated before and after the mid-1980s avalanche, respectively. To examine height growth response to the avalanche disturbance, annual stem elongation rates in the last 25 yr (1975–2000) were measured for some medium-size, pre-avalanche seedlings ($H = 20$ –40 cm, >26 yr old) selected from each of the four microsites ($n = 12$), except for AS ($n = 5$; all target size samples).

Results

TREE SIZE AND AGE STRUCTURE

We observed 166 *A. mariesii* and 22 *B. ermanii* trees inside the avalanche path, including living and dead trees (Fig. 3). For both species, larger trees ($D_{30} > 20$ cm) were mostly killed by either stem breakage or uprooting (Fig. 4A). The proportion of stem-broken trees (0.83) was much higher than that of the uprooted trees (0.17) for each species. On the undisturbed forest, the proportions of stem-broken and standing dead trees of *A. mariesii* were almost the same (0.58 vs. 0.42), and there were no uprooted trees (Fig. 4B). Overall, for both living and

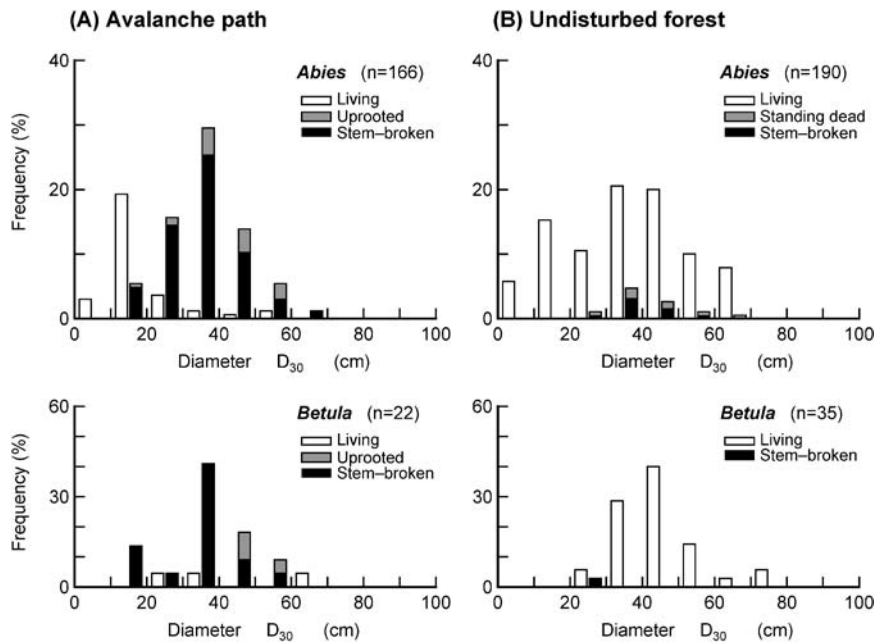


FIGURE 4. Relative frequency distribution of stem diameters at 30 cm height (D_{30}) for living and dead trees of *A. mariesii* and *B. ermanii* in the (A) avalanche path and (B) nearby undisturbed forest.

dead *A. mariesii* trees, peaks of D_{30} -frequency diagrams appeared in the same class (30–40 cm) in both the avalanche path and undisturbed forest, although the size distribution differed statistically between the two sites ($P < 0.01$, Kolmogorv-Smirnov goodness of fit test).

The counts of annual rings of living *A. mariesii* trees on the avalanche path mostly ranged from 50 to 150 yr (Fig. 5). Only three large individuals ($D_{30} > 30$ cm) exceeded 180 yr; one was stem-broken (3 m in height), and the others were healthy ($H = 9$ and 16 m), but retained typical avalanche scars on their stems on the upslope side (3–5 m in height). On the undisturbed forest, the numbers of annual rings of the canopy trees ranged from 140 to 270 yr.

SPATIAL PATTERN OF DAMAGED TREES

On the avalanche path, living *A. mariesii* trees were mainly distributed within the mid-central of the study slope (about 70–150 m on the y-axis in Fig. 3), as well as uprooted dead trees. Stem-broken dead trees were observed throughout the slope, with breakage heights ranging from 0.2 to 6 m. Breakage heights were related to spatial

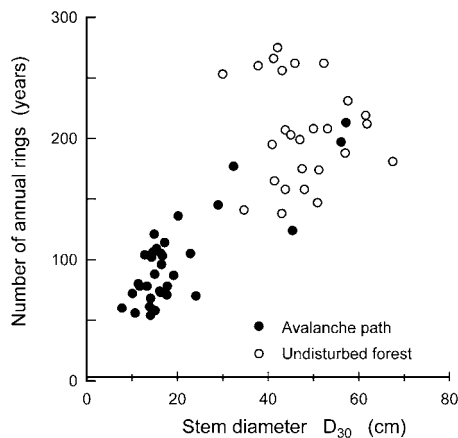


FIGURE 5. Relationships between stem diameters at 30 cm height (D_{30}) and ages for the *A. mariesii* trees in the avalanche path ($n = 34$) and undisturbed forest ($n = 26$). The numbers of annual rings were determined at aboveground heights of 30 to 50 cm, but at 80 to 120 cm for larger trees.

location, since breakage occurred less than 2 m in aboveground height for the most of individuals located on the upper half of avalanche slope ($>$ about 80–100 m on the y-axis) (Fig. 6A). Around the boundary of the upper and lower slopes, where the maximum heights of stem breakage differed drastically, the slope angle sharply increased ($> 30^\circ$), and then decreased (Daimaru et al., 2000). In contrast, heights of all living *A. mariesii* trees on the upper slope were lower than 5 m, and only a few taller trees ($H > 8$ m) existed on the lower part of avalanche slope (Fig. 6B).

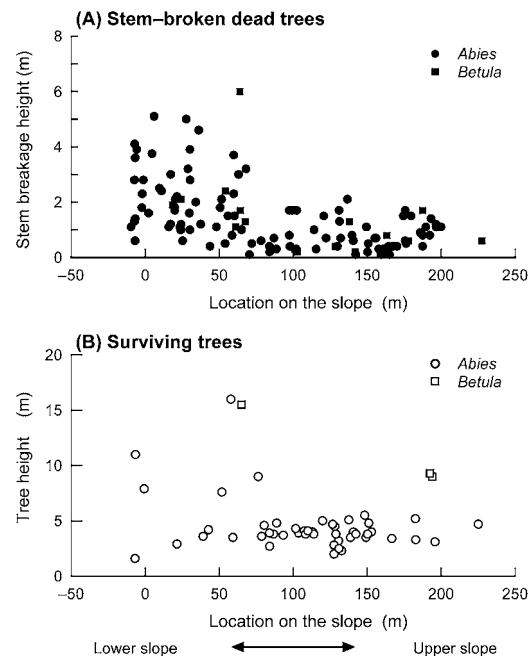


FIGURE 6. Relationships between tree position and (A) stem breakage height of dead trees, and (B) height of living trees in the avalanche path. Each tree position is expressed as a horizontal distance along the y-axis (see Fig. 3) with east-west (or upper-lower) direction in the study slope.

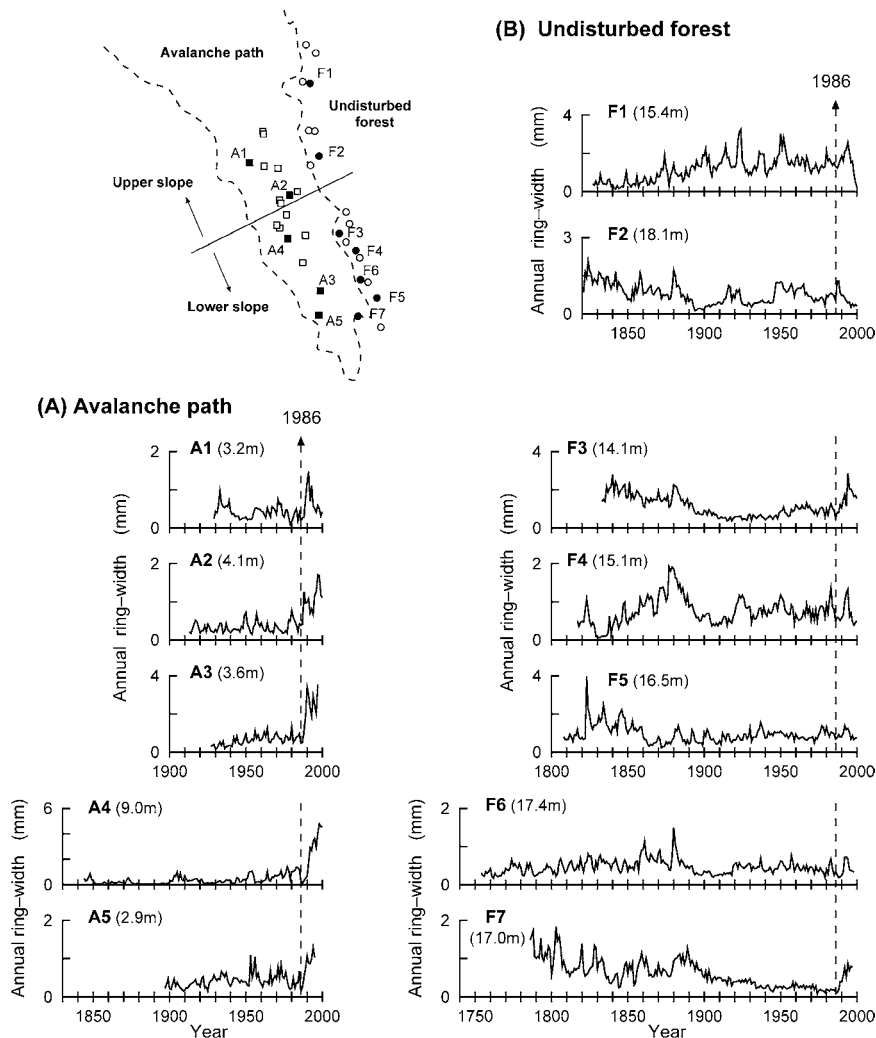


FIGURE 7. Examples of individual ring-width patterns of *A. mariesii* trees sampled from the (A) avalanche path (A1–A5) and (B) undisturbed forest (F1–F7). A small map shows locations of the sample trees used for calculation of average ring-width index curves for four different slope parts: upper and lower slopes of the avalanche path and undisturbed forest. Tree height is shown in parenthesis of each diagram of tree-ring chronology.

TREE-RING-WIDTH PATTERNS

Living *A. mariesii* trees on the avalanche path increased diameter growth rates sharply after the mid-1980s avalanche. About 62% of the core-sampled trees ($n = 21$) showed a pattern of abrupt growth release during the consecutive three years (1987–1989) (e.g., tree No. A1–A5) (Fig. 7A). Similarly, positive growth response was also observed for old canopy trees sampled from the edge of undisturbed forest (F1–F7), although the extent of such growth release pattern differed among the individuals (Fig. 7B). Before the mid-1980s avalanche, some canopy trees on the upper (F1, F2) and lower slope (F4) experienced abrupt growth release patterns several times during the last 80 yr (e.g., in early 1910s and late 1940s), while the other sample trees showed relatively constant tree-ring patterns.

Average ring-width index curves were significantly correlated between the sample trees of upper and lower slopes on the avalanche path ($P < 0.001$, simple correlation coefficient $r = 0.68$) (Fig. 8A). For both upper and lower slopes, values of ring-width index increased two times or more just after the mid-1980s avalanche. Average ring-width index curves of old canopy trees taken from the undisturbed forest were also correlated between the upper and lower slopes ($P < 0.001$, $r = 0.91$) (Fig. 8B). However, the abrupt growth release just after the mid-1980s avalanche was more conspicuous for the canopy trees located on the lower slope than those on the upper slope, as indicated in some individual tree-ring patterns (Fig. 7B). During the last 80 yr, abrupt growth release

common to the samples of both slope areas was remarkable only in late 1940s (Fig. 8B).

SEEDLING RECRUITMENT AND GROWTH RESPONSE

The density of post-avalanche seedlings in the undisturbed forest was significantly higher on FC microsites (below crowns) (2.1 m^{-2}) than on FS microsites (inside *Sasa* shrubs) (0.4 m^{-2}) ($P < 0.05$, Steel-Dwass comparison test) (Table 1). On the avalanche path, the densities of the post-avalanche seedlings (0.0 m^{-2}) did not differ between the two corresponding microsites, AC (around stem-broken dead trees) and AS (inside *Sasa* shrubs) ($P > 0.05$), and were as low as that of FS. The densities of pre-avalanche seedlings in these three microsites (FS, AC, and AS) were also much lower ($< 1.3 \text{ m}^{-2}$) than that of FC (5.0 m^{-2}) ($P < 0.05$). For the pre-avalanche seedlings on the avalanche path, however, the density was slightly higher on AC (1.3 m^{-2}) than on AS (0.3 m^{-2}) ($P < 0.05$). Total seedling density was the highest on FC (7.1 m^{-2}), which was about 5 to 20 times those of the other microsites (Table 1).

Stem elongation rates of the advance seedlings on the undisturbed forest varied within a relatively small range ($0.5\text{--}1.0 \text{ cm yr}^{-1}$) during the recent 25 yr (Fig. 9B); annual fluctuation did not differ between the two microsites (FC and FS) ($P < 0.05$, $r = 0.47$). For the pre-avalanche seedlings on the two microsites (AC and AS) of the avalanche path, annual fluctuations of stem growth rates were also correlated ($P <$

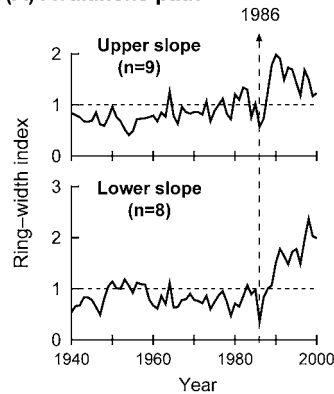
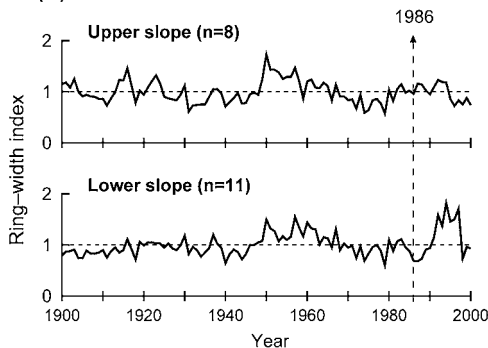
(A) Avalanche path**(B) Undisturbed forest**

FIGURE 8. Average ring-width index curves of *A. mariesii* samples determined for upper and lower slope parts of the (A) avalanche path and (B) undisturbed forest. A vertical dotted line indicates the occurrence year of mid-1980s avalanche.

0.001, $r=0.78$), and abrupt growth release occurred remarkably in 1987 (i.e., a year after the mid-1980s avalanche) (Fig. 9A). However, the growth rates decreased gradually during the following 6 to 7 yr, and were reduced to a level (about 1.0 cm yr^{-1}) similar to those of the previous 10 yr (1975–1985).

Discussion

Mechanical damage from the mid-1980s avalanche primarily depended on tree size (or height). Namely, smaller trees ($D_{30} < 20$ cm, $H < 5$ m) could escape the damage on the upper slope, and larger trees were mostly killed by stem breakage (Figs. 3, 4, 6). Similarly, size-dependent avalanche damage was reported for subalpine conifer species in other geographic regions, e.g., *Pinus contorta* and *Picea engelmannii* in the Canadian Rockies (Johnson, 1987), and *P. engelmannii* and *Abies lasiocarpa* in Cascade Canyon, Grand Teton National Park (Pattern and Knight, 1994). In our study site, the avalanche damage was also associated closely with spatial position: stem breakage mostly occurred less than 2 m in aboveground height for the trees on the upper part of slope (Figs. 3, 6A). This suggests that the smaller trees were buried in the snowpack (about 2 m in depth) and survived the incident. The inferred snowpack level is, however, at least few meters lower than the maximum height of the surviving trees (about 5 m), or the threshold of tree height against the avalanche damage. This discrepancy might be explained by the fact that *A. mariesii* has a flexible trunk (or younger) growth stages, and can tolerate snow pressure by leaning considerably in the snowpack (Ishizuka, 1981). For example, in the *A. mariesii* forest on Mt. Yumori near the present study site, all smaller trees ($H < 4$ m) and 30 to 40% of medium size trees ($H = 4\text{--}6$ m) were completely buried in the snowpack (about 3 m in depth) during mid-winter (Kajimoto et al., 2002).

TABLE 1

Densities of post- and pre-avalanche seedlings of *A. mariesii* on the avalanche path and undisturbed forest. Each value shows a median and range (min.–max.) of seedling density (m^{-2}) for each microsite ($n = 7$ for AC and AS; $n = 10$ for FC and FS). Values with same small letter in each column are not significantly different ($P > 0.05$; Steel-Dwass multiple comparison test)

Site	Post-avalanche seedlings (≤ 15 yr old)	Pre-avalanche seedlings (> 15 yr old)
Avalanche path		
Around dead tree (AC)	0.0 ^a (0.0–0.3)	1.3 ^a (0.3–3.5)
Inside <i>Sasa</i> shrub (AS)	0.0 ^a (0.0–1.3)	0.3 ^b (0.0–1.0)
Non-disturbed forest		
Below crown (FC)	2.1 ^b (0.5–9.3)	5.0 ^c (1.0–20.5)
Inside <i>Sasa</i> shrub (FS)	0.4 ^a (0.0–1.0)	0.5 ^{ab} (0.0–2.3)

^a Insert explanation here.

^b Insert explanation here.

^c Insert explanation here.

Reconstructed stand structure in the avalanche path, including both living and dead trees, was relatively similar to that of nearby undisturbed forest (Fig. 4). This indicates that a mature *A. mariesii* stand (>200 yr old) had previously developed inside the avalanche slope until the mid-1980s, without any large-scale disturbances. During the last 80 yr before the mid-1980s, however, the canopy trees on the nearby forest, especially on the upper slope, showed abrupt growth release in some periods (Figs. 7B, 8B). This evidence suggests that rather small-scale disturbances, such as avalanche influencing only the upper slope, may have occurred several times, because avalanche return interval becomes shorter at upper parts than lower parts within a given slope (Potter, 1969; Butler, 1979; Johnson, 1987).

The younger, surviving *A. mariesii* trees enhanced growth rates sharply following the gap formation by the mid-1980s avalanche. On the avalanche path, however, post-avalanche seedling recruitment was

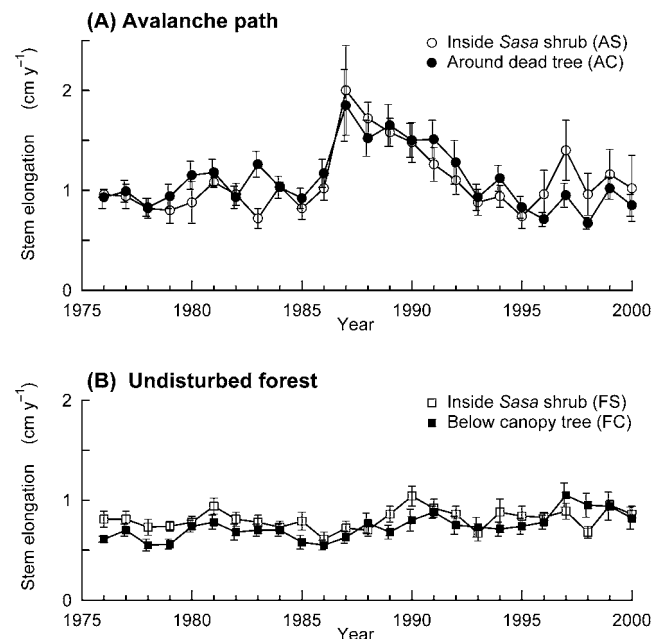


FIGURE 9. Annual stem elongation patterns of pre-avalanche seedlings (>15 yr old) of *A. mariesii* taken from the two microsities of the (A) avalanche path and (B) undisturbed forest. Each value shows mean \pm SE of the samples on each microsite ($n = 12$ in AC, FC and FS; $n = 5$ in AS).

not promoted in both below the damaged trees (AC) and inside *Sasa* shrubs (AS) (Table 1). This might be explained by the lack of seed supply due to death of cone-producing canopy trees. Since mature seeds of *A. mariesii* tend to fall below the crowns of larger trees (Hibino et al., 1981), potential wind-dispersed seed supply from the nearby undisturbed forest might be restricted, or may be reduced gradually with a distance from the edge of forest.

Seedling density, both post- and pre-avalanche seedlings, was much lower in *Sasa* shrubs on both the avalanche path and nearby forest (AS and FS) (Table 1), indicating that seedling recruitment and survivorship were considerably limited by the undergrowth. Generally, *Sasa* communities (including *S. kurilensis*) have large leaf area indices (about 5 m² m⁻²), which results in low light intensity on the ground surface (about 2–3%) (Oshima, 1961). Makita (1997) reported that mortality of newly recruited seedlings was high (67% at the end of first season) under dense coverage of *S. kurilensis* (relative light intensity was 4–5%) in the *A. mariesii* forest on Mt. Hakkoda, northern Japan. Most seedling recruitment of *A. mariesii* occurs just below the crowns of larger trees, where *Sasa* shrubs are locally sparse or absent (Hibino et al., 1981; Hamao and Osawa, 1984). Thus, the constraint of seedling establishment inside the *Sasa* shrubs in our study site might be primarily due to mortality by insufficient light.

It still remains unclear why density of the pre-avalanche seedlings around the stem-broken dead trees on the avalanche path (AC) was much lower than that of corresponding microsites (FC) on the undisturbed forest (Table 1). We expected that seedling establishment on these two microsites has occurred at a similar rate until the mid-1980s avalanche. According to our observations at 15 yr after the avalanche, most of these stem-broken dead trees (i.e., broken snags) on the avalanche path are partially covered with *Sasa* bush. Thus, mortality of the advance seedlings likely occurred to some extent even around such damaged trees from shading by the newly invaded dwarf bamboo. This possibility is supported by the fact that growth enhancement of the pre-avalanche seedlings on both microsites (AC, AS) did not continue longer than 6 to 7 yr after the mid-1980s avalanche disturbance (Fig. 9A).

Seedling recruitment of *A. mariesii* is generally confined in below the crowns of large trees, where *Sasa* grows sparsely or rare, but also occurs on some elevated microsites, such as stumps, fallen logs, and uprooted mounds (Sugita and Tani, 2001; Narukawa and Yamamoto, 2002). Among these microhabitats, we did not examine seedling establishment on fallen logs and uprooted mounds. However, in our study site, the uprooting damage was much less than stem breakage on the avalanche path (Fig. 4). Besides, fallen logs that were produced by the avalanche did not remain in situ, and were considerably transported into the lower end of slope. The avalanche disturbance may not contribute to producing such elevated microhabitats favorable for seedling recruitment.

Our field study suggested that gap formation following the infrequent, large-scale avalanche disturbance enhanced growth of the surviving, younger individuals, but did not necessarily lead to immediately seedling recruitment and/or further growth release of advance seedlings. The constraint of seedling establishment was primarily related to the avalanche-endemic disturbance regime, i.e., lack of seed supply by intensive damage upon canopy trees, and was also caused by the dense undergrowth, i.e., mortality from shading of the dwarf bamboo. Consequently, forest development after the avalanche is likely to depend on the smaller-size individuals (2–5 m in height) that were able to avoid both the mechanical damage and shading mortality. This implies that postavalanche regeneration differs from the scenario of wind-induced gap dynamics suggested for many subalpine conifer forests in central Japan: seedling establishment occur immediately from the seedling banks on gaps (Yamamoto, 1992). In the study region, however, frequency of avalanche events may be

much lower than that of wind-induced disturbances, such as windstorms (e.g., typhoons) which occur almost every summer. For example, Daimaru et al. (2000) reported another event of full-depth avalanche within Hachimantai National Park (about 5 km north to Mt. Kensomori), which happened in the spring 1999 on the east-facing slope, and destroyed the upper part of *A. mariesii* forests, as did the mid-1980s avalanche. In this study area, such destructive avalanches have not occurred at least during the last 30 to 40 yr. Thus, avalanche is an important agent causing relatively large-scale destruction intermittently on the subalpine fir forests in this region, especially at higher elevations. To generalize our findings, we need further case studies on the interactions between the avalanche disturbance, undergrowth, and seedling establishment, by paying attention to differences in disturbance scale and event return interval.

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