Stand development and regeneration during a 33-year period in a seral *Picea glehnii* forest, northern Japan

Koichi Takahashi[1*], Masaru Yogo[2†] and Satoshi Ishibashi[3]

[1] *Department of Biology, Faculty of Science, Shinshu University, Matsumoto 390-8621, Japan,* [2] *Department of Forest Science, Faculty of Agriculture, Hokkaido University, Sapporo 060-0809, Japan, and* [3] *Hokkaido Research Station, Forestry and Forest Products Research Institute, Sapporo 062-8516, Japan.*

---

* Author to whom correspondence should be addressed. Present address. Department of Biology, McGill University, 1205 Docteur Penfield, Montreal, Quebec H3A 1B1, Canada. Email: koichit@gipac.shinshu-u.ac.jp.

† Present address: Tomoku Co. Ltd., Marunouchi-Mitui Bilding, Marunouchi, Tokyo 100-0005, Japan.

This manuscript consists of the text of 22-typed pages, 3 tables and 6 figures.

Abstract Stand development and regeneration were studied during a 33-year period (1965 to 1998) in a 1-ha plot in a seral *Picea glehnii* forest in northern Japan. *P. glehnii* was mono-dominant in the upper canopy layer, but its understory trees were rarely found in 1965. Other species were scarcely observed in 1965. Many saplings of *Abies sachalinensis* recruited over 5 cm DBH by 1998 had come to be dominant in the understory layer. Mortality of *P. glehnii* canopy trees was low. Therefore, the stand basal area increased during the census period due to the growth of surviving canopy trees. Stand development brought about intense competition among trees by increasing local crowding for each tree, and promoted dominance of larger trees and suppression of smaller trees. Although growth rates of understory trees of the two conifers decreased with the increase of local crowding, the growth rate of *A. sachalinensis* was consistently higher than that of *P. glehnii* at all extents of local crowding. The recruitment rate (growing to ≥ 5 cm DBH) of the two conifers was less affected by local crowding. However, the number of recruits of *P. glehnii* was only about a quarter of that of *A. sachalinensis* during the census period because the regeneration of *P. glehnii* was largely restricted to fallen logs and trunk vicinity. Therefore, our long-term study suggests that *A. sachalinensis* will dominate over *P. glehnii* in the seral forest because of higher recruitment and growth rates of *A. sachalinensis* in the understory than those of *P. glehnii*.

Keywords *Abies sachalinensis*, Coniferous forest, Forest succession, Long-term study, *Picea glehnii*

Introduction

Picea glehnii Mast. and *Abies sachalinensis* Fr. (Schm.) Mast. are dominant conifers in subalpine forests of Hokkaido in northern Japan (Tatewaki 1958). *P. glehnii* often dominates after large-scale disturbances such as volcanic eruption, forest fire and landslide, while *A. sachalinensis* invades in later stages of succession (Tatewaki and Yamanaka 1940; Tatewaki 1958; Osawa 1992). Therefore, it is considered that *P. glehnii* is replaced by *A. sachalinensis* late in the rotation. However, there are few reports that how actually monitored forest succession of seral *P. glehnii* forests.

Regeneration of each species is determined by demographic rates such as mortality, growth and recruitment. These three demographic rates are often density dependent, i.e., higher growth and recruitment rates and lower mortality in less crowded conditions, and *vice versa* in more crowded conditions (Weiner 1984; Welden et al. 1991; Takahashi 1996a; Umeki and Kikuzawa 1999; He and Duncan 2000). Therefore, tree competition (caused by local crowding) largely influences tree regeneration. Forest floors are heterogeneous with fallen logs, root-mounds, pits and understory vegetation cover. Use of microhabitats for seedling establishment is different among species, and therefore, is another important aspect of the recruitment process (Duncan 1991). For example, seedlings of conifers often occur on fallen logs and the importance of logs as sites of regeneration is widely recognized both in North America (Christy and Mack 1984; Harmon and Franklin 1989; Taylor 1990) and in Japan (Nakamura and Obata 1985; Suzuki and Tsukahara 1987; Suzuki et al. 1987; Sugita and Tani 2001). Fungal attack reduces seed germination and seedling growth, therefore, seedlings are then confined to elevated woody substrates such as fallen logs and stumps (Veblen et al. 1977; Franklin et al. 1979; Taylor and Qin 1988), where fungal attacks are less frequent. In order to understand the forest succession of seral *P. glehnii* forests, we need to know how local crowding affects the demographic rates of *P. glehnii* and *A. sachalinensis*, and how the use of microhabitats affects their recruitment rates.

Long-term observation is of great importance for understanding forest dynamics because forest size structure and species composition are not stable in time and space. Long-term measurements of mortality, growth and recruitment rates provide useful information to analyze factors affecting population dynamics and species coexistence (Nakashizuka 1991a). Recently, many long-term studies in various types of forest ecosystems have been published (Manokaran and Kochummen 1987; Nakashizuka 1991b; Namikawa 1996; Tsuyuzaki and Haruki 1996; Bunyavejchewin 1999; Umeki and Kikuzawa 1999; Woods 2000a, b; Takahashi et al. 2003a). However, there have been few long-term studies that investigated regeneration, including the effect of tree competition (caused by local crowding) on the demographic rates, of seral *P. glehnii* forests.

Our long-term study examined the stand development and regeneration in a seral *P. glehnii* forest in Hokkaido, northern Japan, using 33-year data (1965 to 1998) of trees ≥ 5 cm in diameter at breast height (DBH) in a 1-ha plot. Firstly, we describe stand development during the 33-year period. Secondly, we compare the use of microhabitats for seedling establishment and demographic rates (mortality, growth and recruitment) between *P. glehnii* and *A. sachalinensis*, in relation to tree competition.

Methods

Study site

Field research was conducted in a seral *P. glehnii* forest on the slope of Mt. Meakan (43° 23'N, 143° 90'E, about 720 m above sea level) in Hokkaido, northern Japan. The forest around this region was partly denuded by a volcanic eruption of Mt. Meakan ca. 240 years ago (Yamada 1958), after which *P. glehnii* colonized the site. Some of the first generation of *P. glehnii* fell down, and then *A. sachalinensis* invaded. Subordinate trees were all deciduous hardwoods: *Betula ermanii* Cham., *Sorbus commixta* Hedl., *Acer ukurunduense* Trantv. et Mey, *Tilia japonica* (Miq.) Simonk. and *Kalopanax pictus* (Thunb.) Nakai. The forest floor was partly covered with dwarf bamboo *Sasa nipponica* Makino, but its abundance was almost negligible (Takahashi 1997).

Field measurements

Three 100 m × 100 m permanent plots were established in the seral *P. glehnii* forest in 1965 by the Obihiro Regional Forestry Office, to examine volume recovery after selective logging (Ishibashi et al. 1996). Two of the three plots were subject to selective logging, while the other one plot was intact. This study analyzed the data from the intact plot.

The plot was sub-divided into 100 quadrats of 10 m × 10 m in 1998. All trees ≥ 5 cm DBH were tagged, and their DBH was measured in 1965, 1970, 1975, 1980, 1990 and 1998. Dead trees and newly recruited trees, growing to ≥ 5 cm DBH, during successive censuses were also recorded. To examine use of microhabitats for seedling establishment of *P. glehnii* and *A. sachalinensis*, saplings (0.5–2.0 m tall) were assigned to four types of microhabitats (ground, root-mounds, fallen logs and trunk vicinity), according to Takahashi (1994, 1997). Trunk vicinity was defined as the area within 1 m of the trunk base of any living tree ≥ 20 cm DBH. This survey was conducted in ten quadrats of 10 m × 10 m (0.1 ha in total) within the 1-ha plot in 1998.

Data analysis

We analyzed the effects of tree competition on DBH growth rates of target trees, applying the following equation (cf., Kohyama 1992, 1993; Hara et al. 1995; Nakashizuka and Kohyama 1995; Takahashi and Kohyama 1999; Takahashi et al. 2003a),

$$G(t, x) = a_0 + a_1 x + a_2 B(t, x),$$

where $G(t, x)$ is the absolute growth rate in DBH (mm/year) of size x at time t, and $B(t, x)$ is the local crowding expressed as the cumulative basal area (cm^2/m^2) of neighboring trees ≥ size x at time t. Coefficient a_0, a_1 and a_2 are constants. Target individual trees were divided into five arbitrary DBH classes chosen to arrange similar vertical strata

(5.0–9.9, 10.0–19.9, 20.0–39.9, ≥ 40.0 cm DBH). We defined the neighboring trees if they satisfied the following two conditions: trees belonging to the same or larger size class of the target individual tree because the primary interest of this analysis was to express competition for light; trees in the same 10 m × 10 m quadrat in which the target tree was located. Local crowding (i.e., $B(t, x)$) was calculated for each target tree. Multiple linear regression analysis was conducted for the $G(t, x)$ equation.

In order to examine whether competition intensity changed with time due to the stand development during the 33-year period, the competition analysis was performed separately for each of the two periods (1965 to 1980, and 1980 to 1998). The competition analysis was not performed for *A. sachalinensis* because its frequency was low (only three trees in 1965) and because the variation in DBH was small (only understory trees throughout the examined period). Alternatively, the growth rates of understory trees (5–15 cm DBH) were compared between *P. glehnii* and *A. sachalinensis* for the period 1980 to 1998 because many *A. sachalinensis* invaded by 1980. The growth rates of the two conifers were compared by the analysis of covariance (ANCOVA). Local crowding was set as the covariate.

Recruitments and mortality of the two conifers were also analyzed for each of the two periods (1965 to 1980, 1980 to 1998). Recruitment rate per 10 m × 10 m quadrat during each period was analyzed for each species by the Pearson correlation test, in order to examine whether the recruitment rates of the two conifers were reduced by the local crowding of trees ≥ 5 cm DBH within the quadrat.

Mortality of each species is expected to be a function of local crowding. However, the number of dead trees during the 33-year period was not enough to analyze mortality in relation to local crowding. Therefore, mortality was analyzed, irrespective of local crowding. We calculated annual mortality at 10 cm DBH intervals from 5 to 65 cm, according to Sheil et al. (1995).

Results

Stand development

The DBH frequency distribution of *P. glehnii* in 1965 showed a bell-shaped pattern with a median of 32.6 cm (Fig. 1). *A. sachalinensis* and the other broad-leaved tree species were only 3 and 9 trees/ha, respectively, in 1965 (Table 1). *P. glehnii* occupied 97.8% of the total density and 99% of the total basal area in 1965 (Table 1). Both total density and basal area increased from 1965 to 1998 (Table 1). The total number of *P. glehnii* slightly decreased from 523 to 490 trees/ha, due to the death of understory trees and small number of new recruits during the 33-year period (Table 1, Figs. 2a, 2d). The mean DBH of *P. glehnii* slightly increased during the census period, while skewness of the size structure unchanged (Fig. 2b, 2c). These showed that the size structure of *P. glehnii* moved toward a larger size without frequent recruitment. On the contrary, the number of *A. sachalinensis* at the smallest size class increased from 3 to 157 trees/ha during the 33-year period, and that of the other broad-leaved tree species also increased from 9 to

126 trees/ha (Table 1, Fig. 1). The number of *A. sachalinensis* recruits tended to increase with time (Fig. 2d). The increase of skewness for the size structure of *A. sachalinensis* corresponded to their high recruitment (Figs. 2c, 2d). Thus, *A. sachalinensis* had come to be dominant in the understory layer with the progress of stand development in this seral *P. glehnii* forest.

Mortality, growth and recruitment during the 33-year period

Mortality of *P. glehnii* was analyzed separately for early and later half of the examined periods (1965 to 1980, and 1980 to 1998). Smaller *P. glehnii* showed greater mortality in the early half period (Fig. 3). It was expected that the death at the smallest size class (5–15 cm in DBH) was due to local crowding. However, there was no statistical difference between dead and surviving trees in terms of the extent of local crowding (51.1 ± 27.2 cm^2/m^2 for dead trees versus 48.5 ± 24.6 cm^2/m^2 for surviving trees, Kolmogorov-Smirnov two sample test, $P > 0.05$). Mortality of *P. glehnii* at the smallest size class decreased in the later half period, and was similar to that of *A. sachalinensis* in the same period (Fig. 3).

The effect of tree competition on the DBH growth rate of *P. glehnii* was examined for the two periods (1965 to 1980, and 1980 to 1998), in order to investigate how competitive interaction changed during the 33-year period. Multiple regression analysis revealed that larger trees grew faster and that growth rate was reduced by competition with neighboring trees in both periods (Table 2). However, the partial regression coefficient for competition (a_2) in the later half period (1980 to 1998) was about two times greater than that in the early half period (1965 to 1980). Furthermore, the partial regression coefficient for size (a_1) in the later half period was about four times greater than that in the early half period. The competition term was excluded from the G (t, x) equation to compare the size dependency of growth rates of *P. glehnii* between the two periods, and a simple linear regression including only DBH as the independent variable was used. The slope of the simple linear regression was significantly greater in the later half period than in the early half period ($F_{1,943} = 45.9$, $P < 0.001$, Fig. 4). Therefore, the growth rates of smaller *P. glehnii* reduced and those of larger *P. glehnii* increased with stand development (Fig. 4).

The growth rates of understory trees (5–15 cm DBH) during 1980 to 1998, in response to local crowding, were compared between *P. glehnii* and *A. sachalinensis*. Although the growth rates of understory trees of the two conifers decreased with the increase of local crowding, the growth rate of *A. sachalinensis* was greater than that of *P. glehnii* at any extent of local crowding (ANCOVA, $F_{1,75} = 15.1$, $P < 0.001$, Fig. 5).

Recruitment rates, growing over 5 cm DBH, of the two conifers were less affected by local crowding (Fig. 6). A significant negative correlation was detected only in the recruitment of *A. sachalinensis* during 1965 to 1980 (Pearson correlation coefficient $R = -0.21$, $P < 0.05$). The total number of recruits of *P. glehnii* was only about a quarter of that of *A. sachalinensis* during the census period (45 versus 159 recruits ha^{-1} 33 years^{-1}, Table 1). Saplings (0.5–2.0 m tall) of *P. glehnii* were largely restricted to fallen logs and trunk vicinity (Table 3). On the contrary, most of *A.*

sachalinensis saplings regenerated on soil (Table 3). Furthermore, the sapling densities of *A. sachalinensis* were greater than those of *P. glehnii* in all microhabitats (Table 3). Thus, *A. sachalinensis* had more vigorous regeneration capacities than *P. glehnii*.

Discussion

The size structure of *P. glehnii* was a bell-shaped pattern in 1965, suggesting that *P. glehnii* invaded during a short period after the eruption of Mt. Meakan. In addition, the size-dependent growth rate was more evident in the later half of the examined period (1980 to 1998) than in the early half of the examined period (1965 to 1980), i.e., the growth rate of smaller trees reduced while that of larger trees increased. Generally, competition for light is intense as self-thinning occurs in even aged populations, and growth rates are clearly size-dependent because larger trees strongly suppress the growth of smaller ones (i.e., one-sided competition) (e.g., Kikuzawa 1988; Hara et al. 1991; Takahashi et al. 2003b). The total stand basal area increased from 48.5 m^2/ha to 61.3 m^2/ha during the 33-year period. The total basal area of 61.3 m^2/ha is quite high compared with other mature coniferous and deciduous broad-leaved forests in Japan (e.g., Nakashizuka et al. 1992; Yamamoto et al. 1995; Takahashi 1997; Umeki and Kikuzawa 1999; Takahashi et al. 2003a). In forests with stand basal area less than in our study site, tree competition is either not recognized, or weak (e.g., Hara et al. 1995; Hiura and Fujiwara 1999; Takahashi et al. 2003a). Ishibashi et al. (1996) compared the growth rates of *P. glehnii* between the plots with and without selective logging in this seral *P. glehnii* forest, and reported that the growth rate of *P. glehnii* was greater in the plot with selective logging than in the plot without selective logging. The result of Ishibashi et al. (1996) is the experimental evidence that the seral *P. glehnii* forest was so developed that tree growth was reduced by competition. Therefore, it is considered that stand development brought about the strong one-sided competition during the 33-year in this stand.

The number of recruits, growing over 5 cm DBH, of *A. sachalinensis* largely increased with the stand development, although the competition was increased due to the stand development for the growth of trees ≥ 5 cm DBH. The increase in *A. sachalinensis* recruits was probably due to the increase of seed supply from the surrounding forest. On the contrary, the recruitment of *P. glehnii* was infrequent throughout the 33-year period. This was largely due to the fact that regeneration of *P. glehnii* was restricted to fallen logs and trunk vicinity. *P. glehnii* cannot establish on ground unless mineral soil is exposed (Ishizuka 1961; Matsuda et al. 1978). The difficulty of seedling establishment on ground for *P. glehnii* is probably due to its small seed size compared with *A. sachalinensis* (0.3 g per 100 seeds for *P. glehnii* versus 1.0 g for *A. sachalinensis*, after Yatoh 1977). Accumulation of litter often reduces seedling establishment especially for species with small seeds, and therefore, the regeneration of these species is restricted to soil-disturbed sites and elevated woody substrates (Taylor and Qin 1988; Nakashizuka 1989; Lusk 1995). In addition, seeds of *P. glehnii* are susceptible to soil pathogens (Cheng and Igarashi 1988), which in turn reduces seed germination and seedling establishment of *P. glehnii*. In contrast, small seeds of *P.*

glehnii are amenable to wide dispersal, and therefore, *P. glehnii* can colonize after large-scale soil disturbances such as landslide and volcanic eruption (Tatewaki 1958). Newly deposited volcanic ash contains few pathogens, and *P. glehnii* regenerates well on the ground. Thus, *P. glehnii* can be regarded to posses a ruderal characteristic (*sensu* Grime 1977).

The growth rate of *A. sachalinensis* understory trees was greater than that of *P. glehnii* at any extent of local crowding. Higher growth rate, coupled with the frequent recruitment, of *A. sachalinensis* enables it to regenerate well in seral *P. glehnii* forests. Takahashi and Kohyama (1999) predicted the abundance of the two conifers (*P. glehnii* and *A. sachalinensis*) in relation to the undergrowth dwarf bamboo *Sasa*, using a simulation model incorporating the observed density-dependencies of the demographic rates. They showed that abundance of the two conifers was largely determined by the recruitment, i.e., *P. glehnii* and *A. sachalinensis* dominate in forests with and without *Sasa*, respectively, because *Sasa* reduces seedling establishment mainly on the ground and less frequently on fallen logs and trunk vicinity (Takahashi 1997). There was no *Sasa* cover in the seral *P. glehnii* forest examined in this study. Therefore, *A. sachalinensis* will dominate over *P. glehnii* later in this forest succession. In addition, natural disturbances caused by typhoons or strong winds do not provide much chance of regeneration for *P. glehnii*. Hasegawa and Tsujii (1989) examined the recovery process of a seral *P. glehnii* forest without *Sasa* after wind disturbances. They concluded that *A. sachalinensis* would dominate in future because sapling density of *P. glehnii* did not increase after the wind disturbances. Therefore, *P. glehnii* needs a large-scale soil disturbance to re-dominate in this region without *Sasa* (Takahashi 1996b).

Our long-term study concluded that (1) stand development during the 33-year period brought about intense one-sided competition by increasing local crowding for each tree, i.e., the size hierarchy (dominance and suppression) was developed with time, and that (2) forest succession was promoted by vigorous regeneration of *A. sachalinensis* largely due to its higher growth and recruitment rates compared with *P. glehnii*, irrespective of the extent of local crowding. Therefore, our long-term monitoring suggests that *A. sachalinensis* will dominate over *P. glehnii* in this seral forest.

Acknowledgements We wish to thank Obihiro Regional Forestry Office for providing the long-term data. Our thanks are also due to the members of Laboratory of Forest Management, Faculty of Agriculture, Hokkaido University, for field assistance in 1998.

References

Bunyavejchewin S (1999) Structure and dynamics in seasonal dry evergreen forest in northeastern Thailand. J Veg Sci 10:787–792.

Cheng D, Igarashi T (1988) Histopathology of Yezo spruce and Glehn's spruce seeds infected by the dard snow-blight causal fungus *Racodium therryanum*. J Jpn For Soc 70:344–351.

Christy EJ, Mack RN (1984) Variation in demography of juvenile *Tsuga heterophylla* across the substratum mosaic. J Ecol 72:75–91.

Duncan RP (1991) Competition and the coexistence of species in a mixed podocarp stand. J Ecol 79:1073–1084.

Franklin JF, Maeda T, Ohsumi Y, Matsui M, Yagi H, Hawk GM (1979) Subalpine coniferous forests of central Honshu, Japan. Ecol Monogr 49:311–334.

Grime PJ (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194.

Hara T, Kimura M, Kikuzawa K (1991) Growth patterns of tree height and stem diameter in populations of *Abies veitchii*, *A. mariesii* and *Betula ermanii*. J Ecol 79:1085–1098.

Hara T, Nishimura N, Yamamoto S (1995) Tree competition and species coexistence in a cool-temperate old-growth forest in southwestern Japan. J Veg Sci 6:565–574.

Harmon ME, Franklin JF (1989) Tree seedlings on logs in Picea-Tsuga forests of Oregon and Washington. Ecology 70:48–59.

Hasegawa S, Tsujii T (1989) Dynamics of coniferous forests in Mt. Oakan. In: Report of basic studies on natural environments near Akan Lake, The Maeda Ippo Foundation, Akan, pp. 6–37 (in Japanese).

He F, Duncan RP (2000) Density-dependent effects on tree survival in an old-growth Douglas-fir forest. J Ecol 88:676–688.

Hiura T, Fujiwara K (1999) Density-dependence and co-existence of conifer and broad-leaved trees in a Japanese northern mixed forest. J Veg Sci 10:843–850.

Ishibashi S, Shiraishi N, Sano M, Ono Y (1996) Studies on a selective cutting system of natural forests (4) Growth analysis of Akaezomatsu (*Picea glehnii* Masters) natural forest at the foot of Mt. Meakan. Trans Ann Meet, Hokkaido br Jpn For Soc 44:146–148 (in Japanese).

Ishizuka K (1961) A relict stand of *Picea glehnii* Masters on Mt. Hayachine, Iwate Prefecture. Ecol Rev 15:155–162.

Kikuzawa K (1988) Intraspecific competition in a natural stand of *Betula ermanii*. Ann Bot 61:727–734.

Kohyama T (1992) Size-structured multi-species model of rain forest trees. Func Ecol 6:206–212.

Kohyama T (1993) Size-structured tree poplations in gap-dynamic forest: the forest architecture hypothesis for the stable coexistence of species. J Ecol 81:131–143.

Lusk CH (1995) Seed size, establishment sites and species coexistence in a Chilean rain forest. J Veg Sci 6:249–256.

Manokaran N, Kochummen KM (1987) Recruitment, growth and mortality of tree species in a lowland dipterocarp forest in Peninsular Malaysia. J Trop Ecol 3:315–330.

Matsuda K, Haruki M, Hasegawa S, Yajima T, Sekine M, Mayama R (1978) Studies on the *Picea glehnii* forest. (V) Species composition and regeneration of the southernmost natural community of the *Picea glehnii* on Mt. Hayachine. Jpn J Ecol 28:347–356 (in Japanese).

Nakamura T, Obata K (1985) Differences in ecological character between *Abies veitchii* and *Tsuga diversifolia*. II: Distribution of seedlings on the moss-covered floor of

Tsuga forests on Mt. Fuji. Bull Tokyo Univ For 74:67–79 (in japanese).

Nakashizuka T (1989) Role of uprooting in composition and dynamics of an old-growth forest in Japan. Ecology 70:1273–1278.

Nakashizuka T (1991a) The importance of long-term studies of forest dynamics in large plots. Jpn J Ecol 41:45–53 (in Japanese).

Nakashizuka T (1991b) Population dynamics of coniferous and broad-leaved trees in a Japanese temperate mixed forest. J Veg Sci 2:413–418.

Nakashizuka T, Iida S, Tanaka H, Shibata M, Abe S, Masaki T, Niiyama K (1992) Community dynamics of Ogawa Forest Reserve, a species rich deciduous forest, central Japan. Vegetatio 103:105–112.

Nakashizuka T, Kohyama T (1995) The significance of the asymmetric effect of crowding for coexistence in a mixed temperate forest. J Veg Sci 6:509–516.

Namikawa K (1996) Stand dynamics during a 12 year period in an old-growth, cool temperate forest in northern Japan. Ecol Res 11:23–33.

Osawa A (1992) Development of a mixed-conifer forest in Hokkaido, northern Japan, following a catastrophic windstorm: A "parallel" model of plant succession. In: Kelty MJ, Larson BC, Oliver CD (eds) The ecology and silviculture of mixed-species forests. Kluwer Academic Publishers, Dordrechtpp, pp. 29–52.

Peet RK (1981) Forest vegetation of the Colorado front range. Vegetatio 45:3–75.

Sheil D, Burslem DFRP, Alder D (1995) The interpretation and misinterpretation of mortality rate measures. J Ecol 83:331–333.

Sugita H, Tani M (2001) Difference in microhabitat-related regeneration patterns between two subalpine conifers, *Tsuga diversifolia* and *Abies mariesii*, on Mount Hayachine, northern Honshu, Japan. Ecol Res 16:424–433.

Suzuki E, Tsukahara J (1987) Age structure and regeneration of old growth *Cryptomeria japonica* forests on Yakushima Island. Bot Mag Tokyo 100:223–241.

Suzuki E, Ota K, Igarashi T, Fujiwara K (1987) Regeneration process of coniferous forests in northern Hokkaido I. *Abies sachalinensis* forest and *Picea glehnii* forest. Ecol Res 2:61–75.

Takahashi K (1994) Effect of size structure, forest floor type and disturbance regime on tree species composition in a coniferous forest in Japan. J Ecol 82:769–773.

Takahashi K (1996a) Plastic response to crown architecture to crowding in understorey trees of two co-dominating confers. Ann Bot 77:159–164.

Takahashi K (1996b) Mechanisms determining coexistence and exclusion between two co-dominating species in subalpine forests. Ph.D. Dissertation, Hokkaido University, Sapporo.

Takahashi K (1997) Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understorey. J Veg Sci 8:529–536.

Takahashi K, Kohyama T (1999) Size-structure dynamics of two conifers in relation to understorey dwarf bamboo: a simulation study. J Veg Sci 10:833–842.

Takahashi K, Mitsuishi D, Uemura S, Suzuki J, Hara T (2003a) Stand structure and dynamics during a 16-year period in a sub-boreal conifer-hardwood mixed forest, northern Japan. For Ecol Manage 174:39–50.

Takahashi K, Uemura S, Suzuki J, Hara T (2003b) Effects of understory dwarf bamboo on soil water and growth of overstory trees in a dense secondary *Betula ermanii* forest, northern Japan. Ecol Res 18:767–774.

Tatewaki M (1958) Forest ecology of the islands of the North Pacific Ocean. J Fac Agr, Hokkaido Univ 50:371–486.

Tatewaki M, Yamanaka T (1940) Phytosociological study on *Picea glehnii* forests at Mt. Kikin in Kitami. Trans Sapporo Nat Hist Soc 157:1–54 (in Japanese).

Taylor AH (1990) Disturbance and persistence of sitka spruce (*Picea sitchensis* (Bong) Carr.) in coastal forests of the Pacific Northwest, North America. J Biogeogr 17:47–58.

Taylor AH, Qin Z (1988) Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong Natural Reserve, Sichuan, China. J Ecol 76:1204–1218.

Tsuyuzaki S, Haruki M (1996) Tree regeneration patterns on Mount Usu, northern Japan, since the 1977–1978 eruptions. Vegetatio 126:191–198.

Umeki K, Kikuzawa K (1999) Long-term growth dynamics of natural forests in Hokkaido, northern Japan. J Veg Sci 10:815–824.

Veblen TT, Ashtom DH, Schlegel FM, Veblen AT (1977) Distribution and dominance of species in the understory of a mixed evergreen-deciduous *Nothofagus* forest in south-central Chile. J Ecol 65:815–830.

Weiner J (1984) Neighbourhood interference amongst *Pinus rigida* individuals. J Ecol 72:183–195.

Welden CW, Hewett SW, Hubbell SP, Foster RB (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. Ecology

72:35–50.

Woods KD (2000a) Dynamics in late-successional hemlock-hardwood forests over three decades. Ecology 81:110–126.

Woods KD (2000b) Long-term change and spatial pattern in a late-successional hemlock-northern hardwood forest. J Ecol 88:267–282.

Yamada S (1958) Studies on the history of volcanic eruptions of alluvium epoch in Hokkaido on the basis of depositional features of the pyroclastics. Chidankensenpo 8:1–40 (in Japanese).

Yamamoto S, Nishimura N, Matsui K (1995) Natural disturbance and tree species coexistence in an old-growth beech-dwarf bamboo forest, southwestern Japan. J Veg Sci 6:875–886.

Yatoh K (1977) Trees of Japan. Asakura Shoten, Tokyo (in Japanese).

Figure legends

Fig. 1 Frequency distribution of trunk diameter at breast height (DBH) of *Picea glehnii* (shaded bar) and *Abies sachalinensis* (open bar), larger than 5 cm DBH, in 1965 (a), 1980 (b) and 1998 (c).

Fig. 2 Tree density (a), mean DBH (b) and skewness of DBH frequency distribution (c) and the number of recruits (d) of *Picea glehnii* (solid circle) and *Abies sachalinensis* (open circle).

Fig. 3 Mortality of *Picea glehnii* during 1965 to 1980 (solid circle) and during 1980 to 1998 (open circle), and *Abies sachalinensis* during 1980 to 1998 (solid triangle). Mortality of *Picea glehnii* was calculated at 10 cm DBH intervals, and that of *Abies sachalinensis* was calculated only at the smallest size class (5–10 cm in DBH).

Fig. 4 Relationship between DBH and the growth rate in DBH for *Picea glehnii* during 1965 to 1980 (a) and during 1980 to 1998 (b). Regression equations are (a) $Y = 1.033 + 0.016X$ ($r = 0.199$, $F_{1,473} = 19.5$, $n = 475$, $P < 0.001$) and (b) $Y = -0.127 + 0.050X$ ($r = 0.541$, $F_{1,470} = 194.3$, $n = 472$, $P < 0.001$).

Fig. 5 Relationship between local crowding and the growth rate in DBH during 1980 to 1998 for understory trees (5–15 cm in DBH) of *Picea glehnii* (solid circle) and for *Abies* *sachalinensis* (open circle). Regression equations are $Y = 1.151 – 0.0077\ X$ ($r = –0.357$, $F_{1,35} = 5.11$, $n = 37$, $P = 0.030$) for *Picea glehnii* (solid line) and $Y = 1.942 – 0.0098\ X$ ($r = –0.28$, $F_{1,39} = 3.33$, $n = 472$, $P = 0.076$) for *Abies sachalinensis* (broken line).

Fig. 6 Relationship between local crowding and the number of recruits per 10 m × 10 m quadrat during 1965 to 1980 and during 1980 to 1998 for *Abies sachalinensis* (a, c) and *Picea glehnii* (b, d). A Pearson correlation coefficient (R) with its significance level was shown in each figure ($n = 100$).

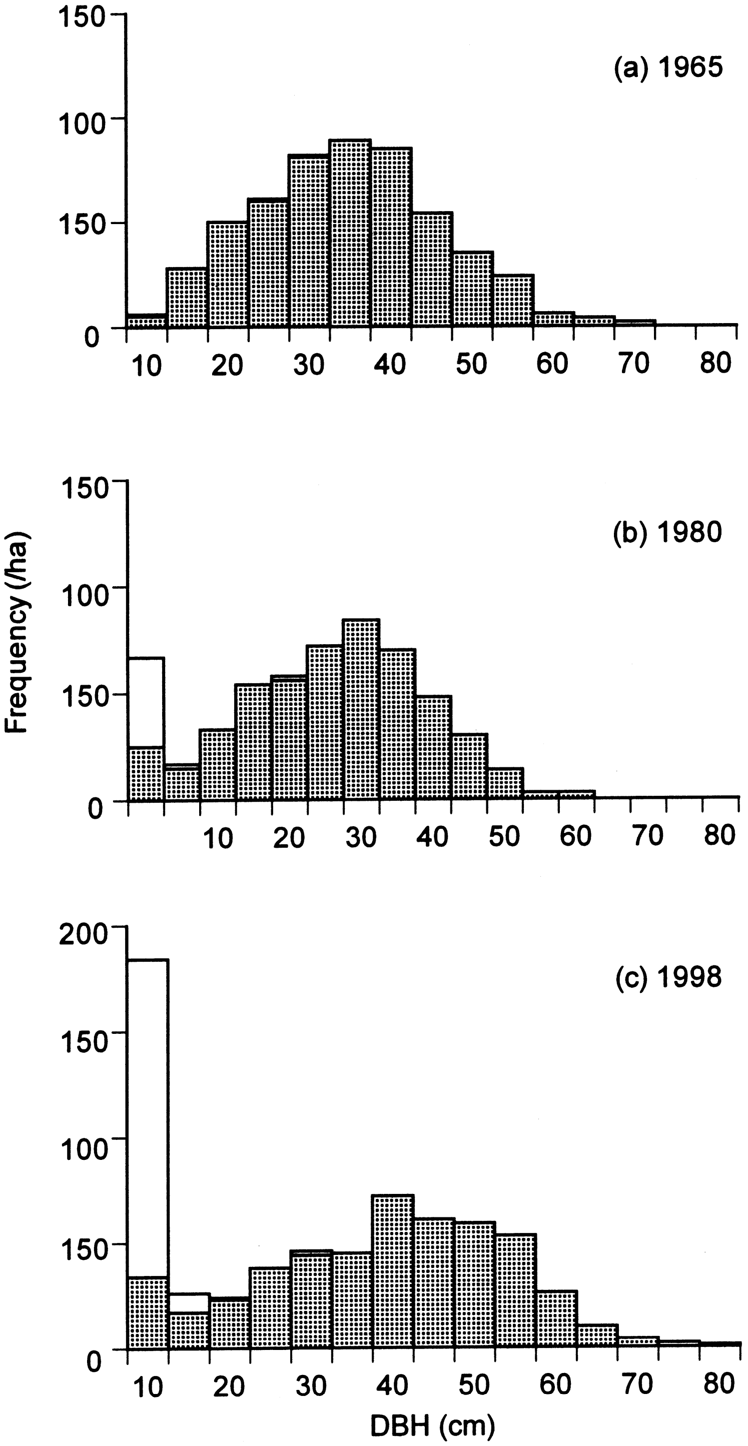
(a) 1965
150
100
150
0
10
20
30
40
50
60
70
80
(b) 1980
150
100
150
0
10
20
30
40
50
60
70
80
(c) 1998
200
150
100
150
0
10
20
30
40
50
60
70
80
Frequency (/ha)
DBH (cm)

Fig. 1

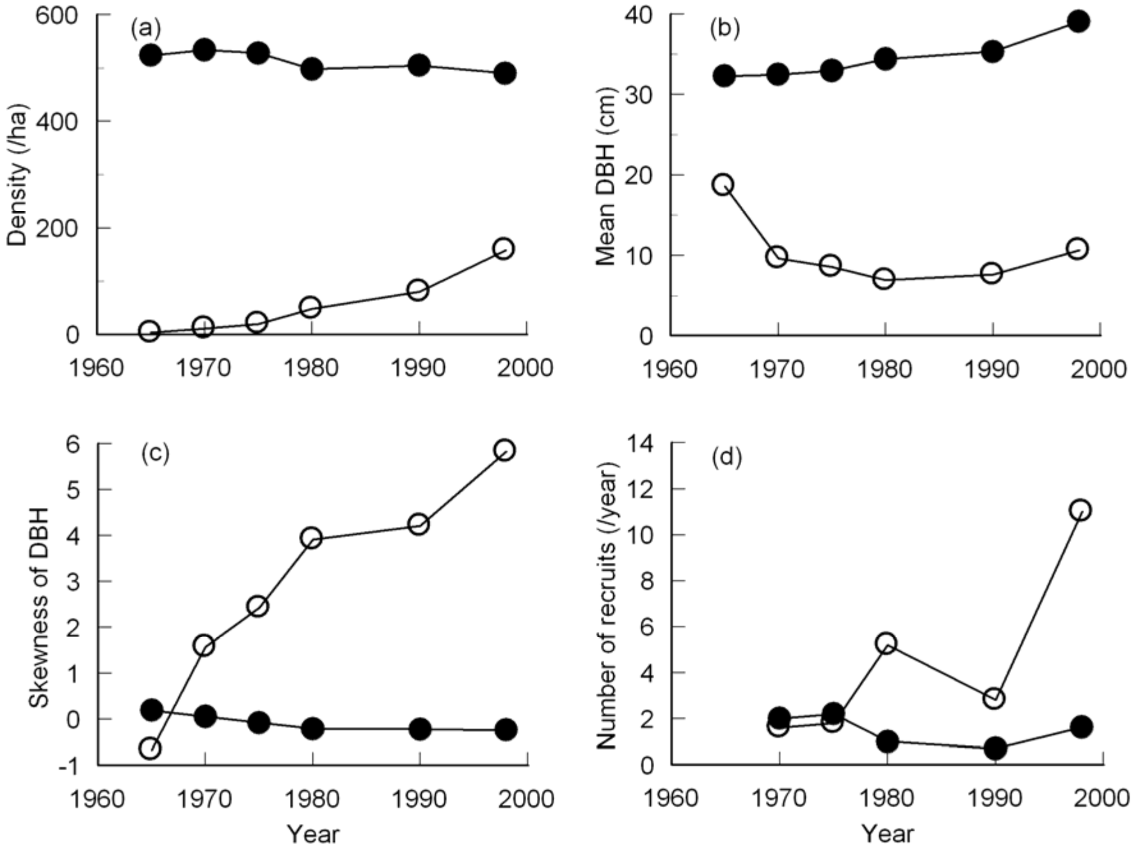
(a)
Density (/ha)
600
400
200
0
1960
1970
1980
1990
2000
(b)
Mean DBH (cm)
40
30
20
10
0
(c)
Skewness of DBH
6
5
4
3
2
1
0
-1
Year
(d)
Number of recruits (/year)
14
12
10
8
6
4
2
0
Year

Fig. 2

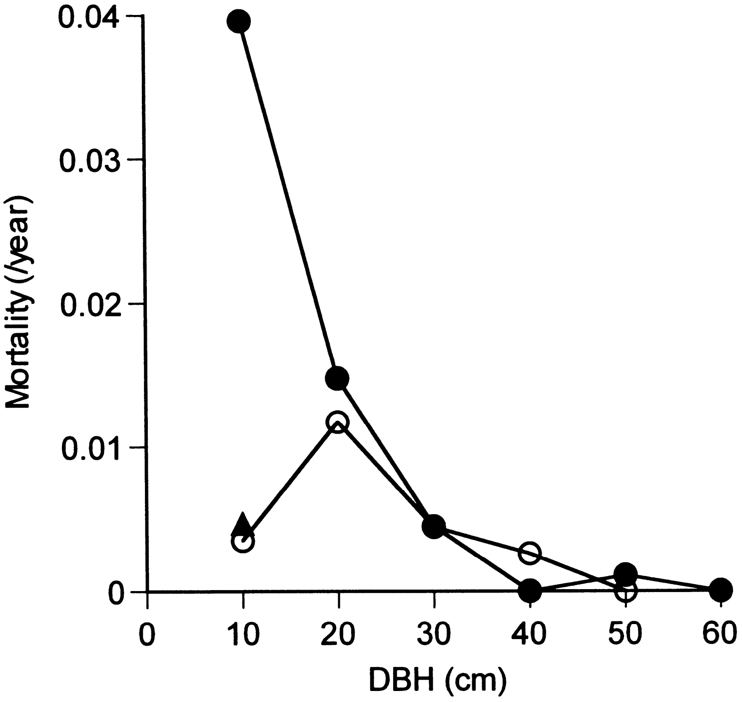

Fig. 3

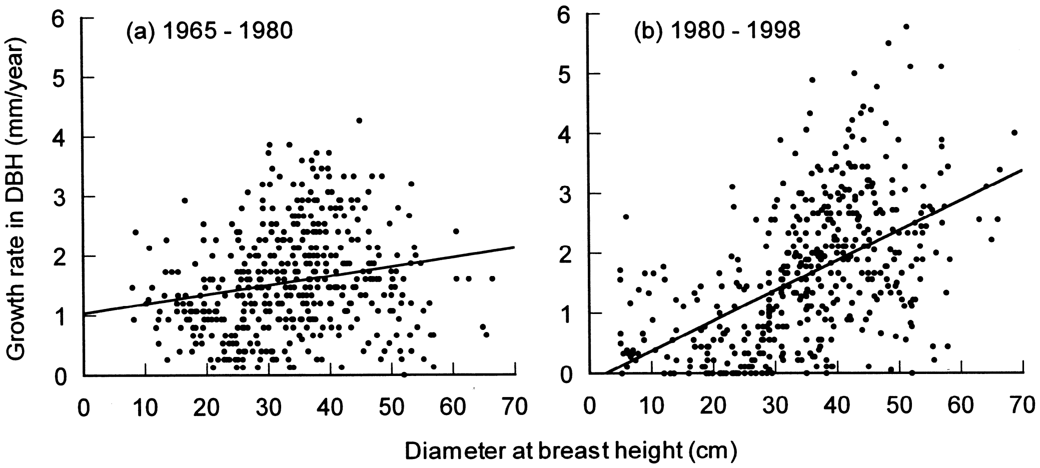
(a) 1965 - 1980
(b) 1980 - 1998
Growth rate in DBH (mm/year)
0
1
2
3
4
5
6
0
10
20
30
40
50
60
70
Diameter at breast height (cm)

Fig. 4

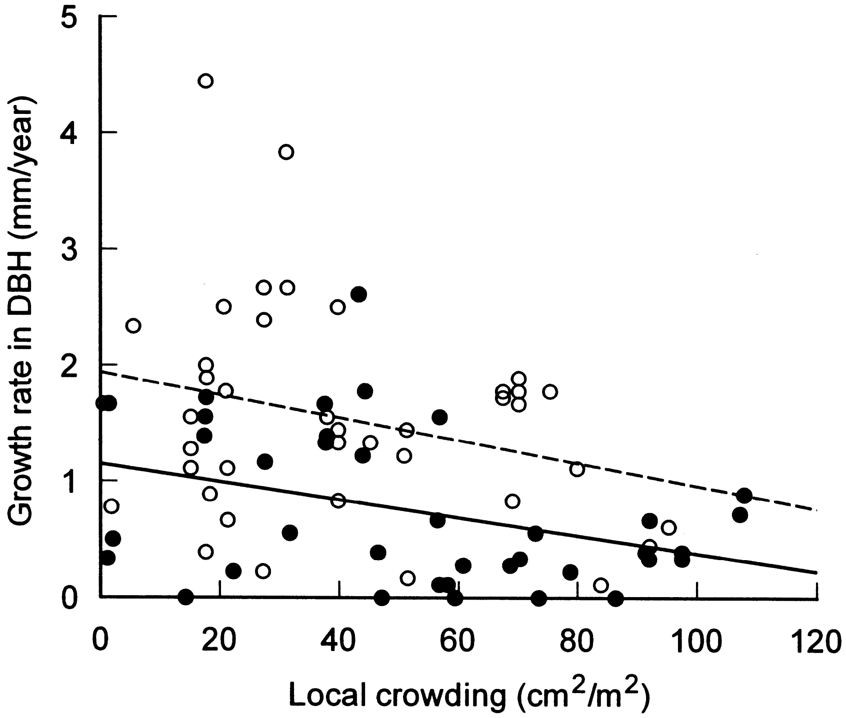
5
4
3
2
1
0
Growth rate in DBH (mm/year)
0
20
40
60
80
100
120
Local crowding (cm²/m²)

Fig. 5

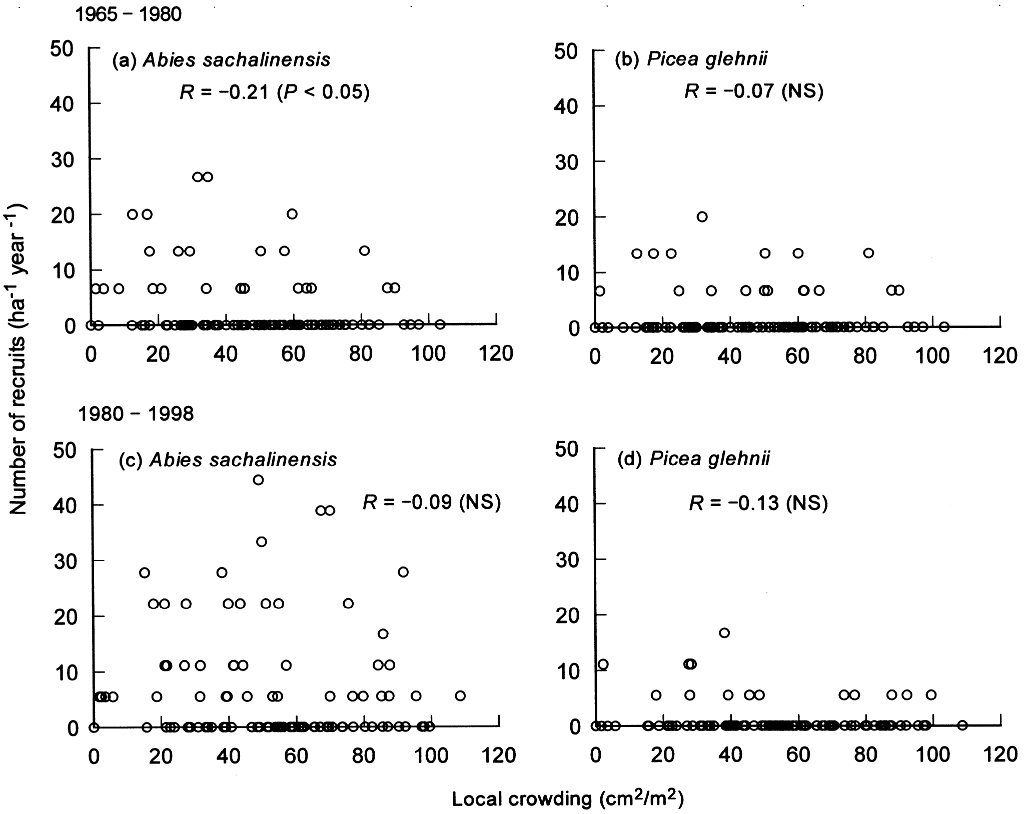
1965 - 1980
(a) *Abies sachalinensis*
$R = -0.21$ ($P < 0.05$)
(b) *Picea glehnii*
$R = -0.07$ (NS)
1980 - 1998
(c) *Abies sachalinensis*
$R = -0.09$ (NS)
(d) *Picea glehnii*
$R = -0.13$ (NS)
Number of recruits (ha^{-1} $year^{-1}$)
Local crowding (cm^2/m^2)
0
10
20
30
40
50
0
20
40
60
80
100
120

Fig. 6

Table 1 Changes in basal area and density of trees larger than 5 cm DBH between 1965 and 1998 for each species within a 1-ha plot in a seral *Picea glehnii* forest, northern Japan.

	Basal area (cm^2/m^2)		Density (/ha)			
	1965	1998	1965	1998	Dead	Recruit
Abies sachalinensis	0.1	0.7	3	157	5	159
Picea glehnii	48.1	60.1	523	490	78	45
Other species	0.3	0.5	9	126	26	143
Total	48.5	61.3	535	773	109	347

Table 2 Results of multiple linear regression analysis for the G (t, x) equation of *Picea glehnii*. Degrees of freedom for the whole-model F-values are $F_{2,\, n\text{-}3}$.

Period	a_0	a_1	a_2	n	R	F-value
1965 to 1980	1.49^{***}	0.0098^{*}	-0.0063^{**}	475	0.247	15.4^{***}
1980 to 1998	0.70^{***}	0.041^{***}	-0.011^{***}	471	0.587	122.8^{***}

*; $P < 0.05$, **; $P < 0.01$, ***; $P < 0.001$.

Table 3 Density (/0.1 ha) and relative frequency (%) in parentheses of saplings (0.5–2.0 m tall) on the four microhabitats (ground, fallen logs, root-mounds and trunk vicinity) in a seral *Picea glehnii* forest, northern Japan.

	Microhabitat				
Species	Ground	Fallen logs	Root-mounds	Trunk vicinity	*n*
Abies sachalinensis	181 (69.9)	38 (14.7)	0 (0)	40 (15.4)	259
Picea glehnii	5 (13.2)	13 (34.2)	0 (0)	20 (52.6)	38

n, number of observations (/0.1 ha).