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Stand structure and growth patterns of understorey trees in a coniferous forest, Taisetsuzan National Park, northern Japan

YASUHIRO KUBOTA,[1]* YASUO KONNO[1] AND TSUTOM HIURA[2]

[1]*Laboratory of Environmental Botany, Faculty of Agriculture, Obihiro University of Agriculture and Veterinary Medicine, Nishi 2-11, Inada-cho, Obihiro, Hokkaido 080 and* [2]*Nakagawa Experiment Forest, Hokkaido University of Agriculture, Otoineppu 098-25, Hokkaido, 080 Japan*

Stand structure was studied with special reference to growth and mortality patterns of sapling and understorey trees in a coniferous *Picea jezoensis* and *Abies sachalinensis* forest in Taisetsuzan National Park, Hokkaido, northern Japan. *Picea jezoensis* was dominant in the basal area, while *A. sachalinensis* was abundant in large numbers in the canopy. Estimated mortalities increased significantly with diameter at breast height (DBH) for both *P. jezoensis* and *A. sachalinensis* in the canopy, but the tendency was different between the two species. *Picea jezoensis* had a lower mortality rate than *A. sachalinensis*, especially at small DBH classes. The spatial distribution of understorey individuals of *A. sachalinensis* did not show any significant correlation with the spatial distribution of canopy gaps, but that of *P. jezoensis* showed a significant correlation. *Abies sachalinensis* can grow higher than *P. jezoensis* under suppressed conditions; while *P. jezoensis* requires canopy gaps for steady height growth. This growth pattern leads to a different waiting height in the understorey (≥ 2 m in height and 10 cm in diameter at breast height). *Abies sachalinensis* waited for an improvement in light conditions at higher strata (max. 7 m), while *P. jezoensis* waited at lower strata (max. 3 m). The estimated mortality of understorey *A. sachalinensis* increased with size, while that of understorey *P. jezoensis* decreased. Therefore, *P. jezoensis* gives priority to survival while *A. sachalinensis* gives priority to understorey growth. The difference in the 'waiting pattern' between the two species in the understorey was considered a significant feature for the canopy recruitment process of *P. jezoensis* and *A. sachalinensis*.

Key words: *Abies sachalinensis; Picea jezoensis;* understorey tree; waiting pattern.

INTRODUCTION

Picea jezoensis Carr. and *Abies sachalinensis* Masters are co-occurring species in sub-boreal forests, in Hokkaido, northern Japan. The structure and dynamics of *P. jezoensis* and *A. sachalinensis* forests have not been completely investigated. Several hypotheses on the co-existence mechanisms for *Picea* and *Abies* in northern coniferous forests have been proposed with respect to life-history traits of the two species. Oosting and Reed (1952) and Veblen (1986) suggested that the two species co-exist by having different life-history characteristics: *P. engelmanii* Parry has a lower recruitment rate and greater longevity in the canopy layer, while *A. lasiocarpa* Hook has a higher recruitment rate and higher mortality of canopy trees. However, these life-history traits, especially canopy recruitment rate, are affected by environmental factors such as natural disturbance. Regeneration sites formed by gap disturbance show various characteristics that have a wide range in size, and heterogeneous light environments in each formation pattern (Nakashizuka 1985; Canham 1988b; Poulson & Platt 1989; Lieberman *et al.* 1989). The difference in the growth pattern brings about different responses against various gap disturbance regimes (Hartshorn 1978; Denslow 1980; Canham 1988a). Therefore,

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*Present address: Department of Biology, Faculty of Science, Tokyo Metropolitan University, Tokyo, 192-03 Japan.

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it is important to understand the growth pattern more clearly, and to investigate the species-specific performance of component species with respect to the disturbance regime.

In this paper, the differences in the growth pattern of understorey trees of *P. jezoensis* and *A. sachalinensis* are studied. The 'waiting pattern' of understorey trees is shown to be a significant characteristic related to the recruitment into the canopy. Finally, the difference in the 'waiting pattern' is discussed between *P. jezoensis* and *A. sachalinensis.*

STUDY SITE

This study was carried out in a *Picea–Abies* forest (1000 m a.s.l.) on the ESE slope of Mt Onsen, Taisetsuzan National Park, Hokkaido, northern Japan. Precipitation is approximately 1500 mm per year. Mean daily temperatures during the warmest month (August) and the coldest month (January) are 17.7°C and − 10.7°C, respectively. The warmth index (Kira 1977) is 44.1, indicating that the region is located between the cool-temperate and sub-boreal zones. Snow cover on the forest floor is usually from November until the following May. The soil is predominantly brown forest soil, with local distribution of block streams by periglacial formation.

The study site is dominated by *Picea jezoensis* Carr., *Abies sachalinensis* Masters, *Betula ermanii* Cham. and *Picea glehnii* Masters; *Acer ukruenduense* Trautv. et Mey. and *Sorbus commixta* Hedl. are also found but only locally. The vertical stand structure is multi-layered, where canopy trees of *P. jezoensis, B. ermanii* and *P. glehnii* overtop the canopy formed by *A. sachalinensis.* Two types of forest floor vegetation are recognized; *Sasa* and *Carex* on the brown soil and *Vaccinium, Rhododendron* and *Menziesia* on the block stream.

METHODS

A study plot of 1.8 ha (100 m × 180 m) was established in 1989. The whole area was covered with a 10 × 10 m grid system for field survey. Three life phases were defined for trees: (i) sapling (30 cm $\leqslant$height $<$ 200 cm); (ii) understorey tree (height $\geqslant$ 200 cm and diameter at breast height $<$ 10 cm); and (iii) canopy tree (diameter at breast height $\geqslant$ 10 cm).

The diameter at breast height (DBH) at 1.3 m was measured for all living and dead trees $\geqslant$ 2 m in height. Height growth rate and release height (defined as the height where the average stem growth of the initial 5 years was at least twice the average for the following 5 years) of understorey trees was determined by detecting scars of branch whorls that formed annually on the trunk. For this purpose, the authors climbed up to the tree crowns using a ladder.

Dead trees $\geqslant$ 10 cm in DBH were identified to species level by examining samples of tissues sectioned under a microscope (*Picea jezoensis* and *Picea glehnii* were dealt with as the genus *Picea*) and were classified into four types according to the estimated causes of death; bole snapping, base snapping, uprooting and standing dead. Treefall direction was also measured. The damage ratio of trees at each DBH class for each species was defined $M_i = D_i/(L_i + D_i)$, where L_i and D_i were the numbers of living and dead trees, respectively, at DBH class i. The decay class of fallen logs was classified into six categories according to structural integrity and vegetation coverage on the logs (Graham & Cromack 1982; Arthur & Fahey 1989). Class 1 boles were essentially undecayed with most or all of the bark and branches intact. At the other extreme, class 6 boles were decayed nearly perfectly and detectable only by their outline on the forest floor. Class 2, 3, 4 and 5 fitted into a continuum between these two extremes.

Subplots 2 m × 2 m in area were regularly settled on the ground at each grid cell intersection in the plot (180 subplots in total). Furthermore, 81 subplots of various sizes were set up on elevated surfaces such as fallen logs, mounds and stumps formed by gap disturbances. The number of saplings in each subplot was recorded, and the crown depth (a), crown width (1) and stem growth in the past 5 years were measured for each sapling. The relative height growth rate (RHGR = $[\log H_{1989} - \log H_{1984}]/5$; H_{1989} and H_{1984} were the tree heights in 1989 and in 1984, respectively of saplings investigated. Furthermore, crown shape index (CSI = $\log [a/1]$; *sensu* Nakamura & Obata 1982) for saplings was compared between *P. jezoensis* and *A. sachalinensis.* Sapling density at each site was estimated as sapling number per subplot area.

Gaps were defined by the vertical projection area where no stems reached 10 m in height or 10 cm in DBH. The size of gaps was calculated as an ellipse by measuring the long and short axes (Runkle 1982). Understorey trees beneath each gap, designated gap successors, were recorded (133 trees in total). Gap ages were determined from the release dates based on the increment of annual rings in cores obtained from the two to four tallest stems in each gap. Illuminance at 0, 0.5, 1.0 and 2.0 m above ground was measured regularly at the centers of 90 grid cells in summer. All the measurements were carried out under overcast cloudy conditions using photoelectric illuminometers (Toshiba SPI-5, Tokyo). These illuminance values were divided by the illuminance in the open site to obtain relative illuminance.

RESULTS

Stand structure and gap formation pattern

The basal area and density of canopy trees of the main canopy species (*P. jezoensis, P. glehnii, A. sachalinensis* and *B. ermanii*) were 27.1 m^2 and 355 per hectare, respectively. The density of understorey trees of canopy species was 247 per hectare. The basal area of *Picea* spp. exceeded that of *A. sachalinensis*, but *A. sachalinensis* occurred in greater number. The DBH frequency distributions of canopy trees were inversely J-shaped. *A. sachalinensis* showed a peak in stem number at 10 cm DBH class and declined sharply in larger size classes, while *Picea* spp. and *B. ermanii* showed a gradual decrease in stem number (Table 1).

Table 2. The cause of death for *Picea spp., A. sachalinensis* and *B. ermanii.*

Cause of death	*Picea* spp.	*A. sachalinensis*	*B. ermanii*
Base snapping	50	65	4
Bole snapping	11	36	5
Standing dead	8	38	6
Uprooting	31	87	11

Forty-five per cent of fallen stems fell from east to south, which was the aspect of the slope. The bole snapping, base snapping and uprooting were the majority (85%) of the causes of death. The causes of death were not significantly different among species (Table 2, χ^2 test, $P > 0.1$). The DBH frequency distribution of bole snapping stems of *Picea* spp. differed significantly from that of *A. sachalinensis* (Mann-Whitney *U*-test, $P < 0.01$).

The damage ratio increased with DBH class for *Picea* spp. and *A. sachalinensis* (Kendall rank correlation test, $P < 0.05$), but *B. ermanii* did not show any significant correlations between mortality and size. The increasing tendencies of damage ratio differed between *Picea* spp. and *A. sachalinensis* (Table 3). Therefore, the estimated mortality of *Picea* spp. was lower, especially in small DBH classes, than that of *A. sachalinensis.*

The size of gaps ranged from 5 to 1245 m^2. The total gap area was 3467 m^2, or 19.3% of the whole study plot, showing a lognormal frequency distribution (Fig. 1). This agreed with the results reported by Foster and Reiners (1986), White *et al.* (1985) and Taylor (1990). Relative illuminance increased with height and showed an inverse J-shaped fre-

Table 1. DBH class distribution of living and dead stems.

DBH class (cm)	Number of stems (per 1.8 ha) *P. jezoensis*	*P. glehnii*	*A. sachalinensis*	*B. ermanii*
0–10	47 (6)	50	275 (47)	72 (-)
10–20	28 (13)	36	136 (56)	36 (1)
20–30	25 (13)	25	84 (58)	27 (3)
30–40	22 (19)	16	58 (45)	25 (9)
40–50	23 (25)	15	14 (48)	18 (9)
50–60	9 (18)	6	2 (16)	15 (2)
60–70	7 (10)	0	0 (0)	5 (0)
80–90	2 (2)	0	1 (2)	2 (1)
80–90	1 (2)	0	0 (1)	1 (2)

Dead stems are shown in parentheses.

Table 3. Changes in a damage ratio with DBH class.

DBH class (cm)	Damage ratio (%) *Picea* spp.	*A. sachalinensis*	*B. ermanii*
0–10	14.6	11.3	—
10–20	16.9	29.2	2.7
20–30	20.6	40.8	10.0
30–40	33.3	43.7	26.5
40–50	39.7	77.9	33.3
50–60	54.5	88.9	11.8
60–70	58.8	—	0.0
70–80	50.0	66.7	33.3
80–90	66.7	100.0	66.6

quency distribution at each height (Fig. 2). The lower relative illuminance at 0–0.5 m height may be ascribed to the foliage layer of *Sasa kuriensis*.

Establishment site of seedlings and saplings

The density of saplings on different forest floor substrata is shown in Table 4. Saplings of *A. sachalinensis* were most abundant, which was twice the density of *P. jezoensis*. Occurrences of *P. jezoensis, A. sachalinensis* and *B. ermanii* were mainly restricted to fallen logs. As was reported by Christy and Mack (1984) and Stewart (1989), establishment occurred primarily on fallen logs and mounds. Establishment sites were mostly restricted to fallen logs, especially for *P. jezoensis*. Most fallen logs were in decay class 2 and decay class 3. The highest sapling density for all the species was found in decay class 2 (Table 5).

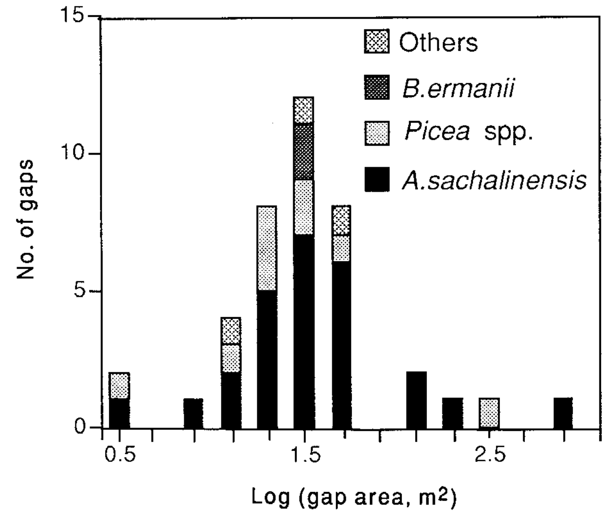

Fig. 1. Size distribution of gaps in the plot.

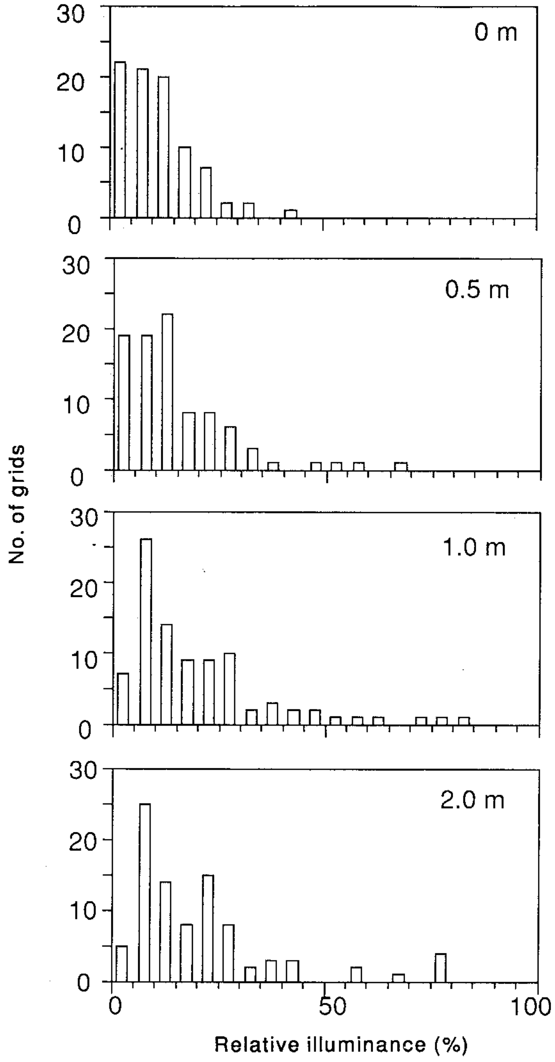

Fig. 2. Frequency distributions of relative illuminance at different heights of 0, 0.5, 1.0 and 2.0 m.

Table 4. Occurrences of saplings in forest floor substrata.

	Sapling density (per m^2) *P. jezoensis*	*A. sachalinensis*	*B. ermanii*
Fallen log	4.7	8.8	1.8
Mound	0.3	0.8	0.5
Ground	0.0	0.2	0.1

Table 5. The frequency of fallen logs and density (per m^2) of established saplings for all the species on each decay class.

Decay class	1	2	3	4	5	6
Frequency	35	82	25	25	34	74
Sapling density	0.0	16.7	9.8	6.3	7.9	5.6

Growth pattern and crown shape of saplings

The relative height growth rate (RHGR) of saplings showed no significant difference between *P. jezoensis* and *A. sachalinensis*, except saplings at 100–200 cm (*t*-test, $P > 0.05$; Fig. 3). The RHGR of saplings in gaps was significantly higher than that beneath canopies ($P < 0.001$). Most saplings of *B. ermanii* were distributed beneath gaps, and RHGR was higher than that of the other species (*t*-test, $P < 0.01$). This would indicate that *B. ermanii* depends on gaps as a regeneration site at an earlier life stage than conifers. The relationship between RHGR and the crown shape index (CSI) for saplings was analyzed (Fig. 4). If a tree has a slender crown shape, CSI > 0. If the crown is an umbrella-shape, which is the most effective shape for matter production under shaded conditions (Horn 1971; Kohyama 1980; Küppers 1989), CSI < 0. The CSI decreased more rapidly for *P. jezoensis* with decreasing RHGR than *A. sachalinensis* (analysis of covariance, $P < 0.001$), indicating that *P. jezoensis* tended to have an umbrella-shape crown under poor conditions for growth.

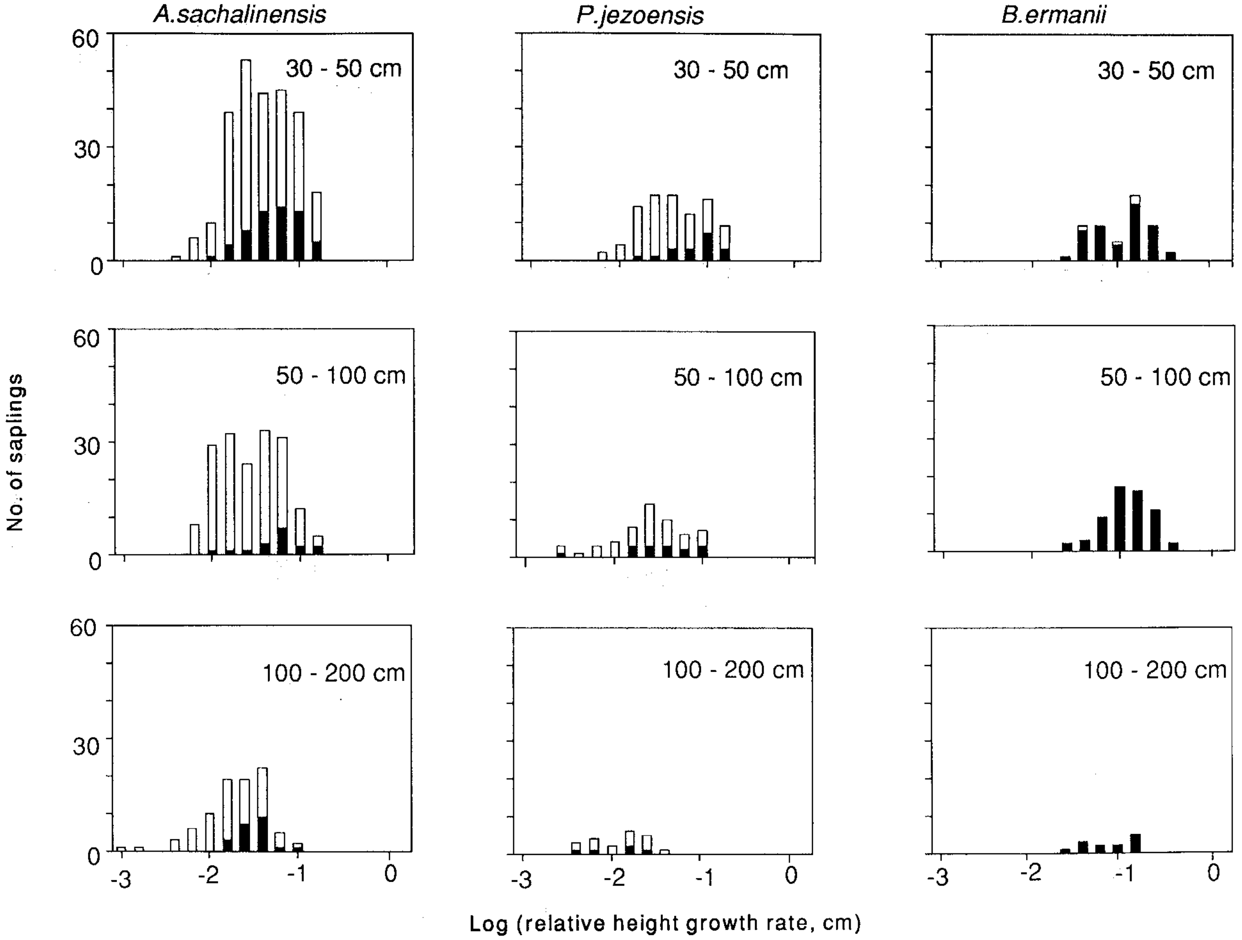

Fig. 3. Frequency distributions of relative height growth rate (RHGR) of saplings during the last 5 years. Upper, middle and lower rows show RHGR for saplings of 30–50, 50–100 and 100–200 cm in height, respectively. Solid parts indicate saplings beneath canopy gaps and open parts show those under the closed canopy.

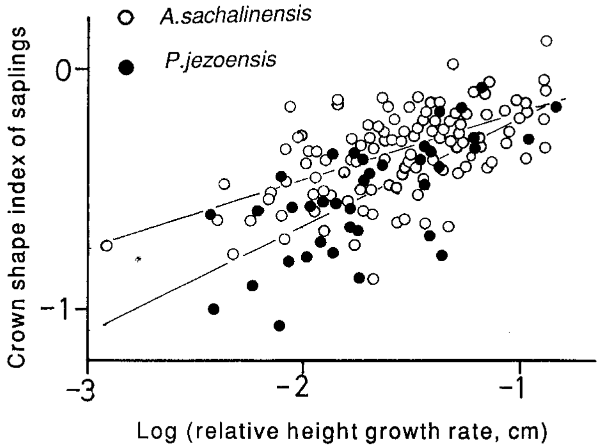

Fig. 4. Relationship between relative height growth rate (RHGR) and crown shape index (CSI) for saplings.

Waiting pattern of understorey trees

Individuals of *A. sachalinensis* were released at a significantly higher layer (max. 7 m) than those of *P. jezoensis* (max. 3 m; Mann-Whitney *U*-test, $P < 0.001$; Fig. 5). This suggests that understorey trees of *A. sachalinensis* wait for gap formation at higher layers, while those of *P. jezoensis* wait at lower layers. Percentages of gap successors (GSER after Leemans [1991]) for each DBH class were examined, and an association with gaps was tested by the χ^2 test of goodness of fit (the null hypothesis is that the ratio of the gap successors to waiting trees under the closed canopy is 19.3 : 80.7, according to the

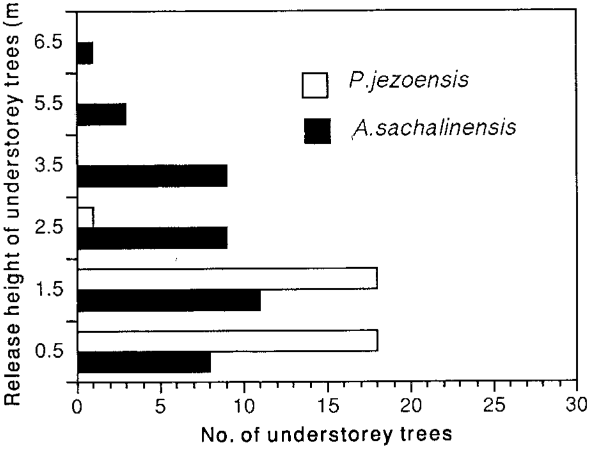

Fig. 5. Frequency distribution of release heights for understorey trees. Abbreviations as for those in Fig. 4.

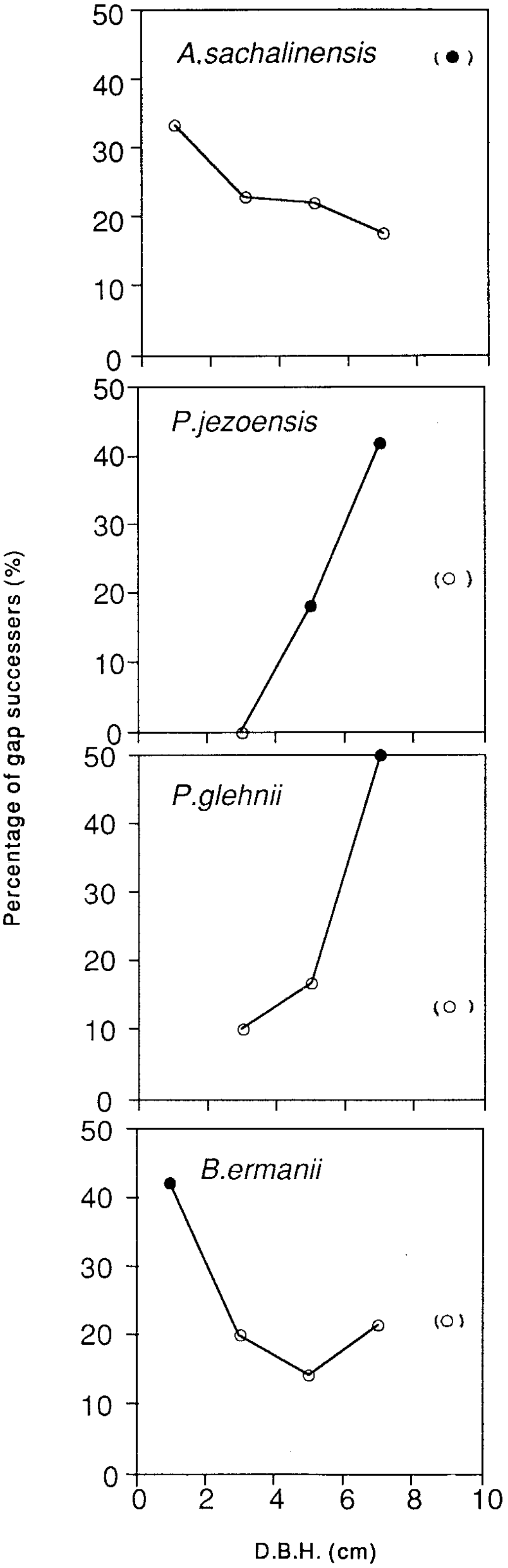

Fig. 6. Changes in the ratio of understorey individuals occurring in canopy gaps to that of total understorey individuals with DBH class. Solid symbols show significant occurrence ($P < 0.05$) in the canopy gaps. The data points in parentheses are omitted because of uncertainty of appearance in canopy gaps or beneath the closed canopy.

actual canopy gap ratio; Fig. 6). The density of understorey trees of *P. jezoensis* and *A. sachalinensis* was 26 and 153 per hectare, respectively. Understorey trees of *A. sachalinensis* demonstrated no significant association with gaps, even in large size classes (DBH = 8 cm), while *P. jezoensis* showed a significant gap association ($P < 0.05$) with increasing DBH class.

Understorey trees of *P. jezoensis* showed greater height growth with increasing DBH class, while *A. sachalinensis* had no such tendencies (Fig. 7a). The coefficients of variation (CV) of height growth rate of *A. sachalinensis* increased with DBH class, but the CV of *P. jezoensis*, which was smaller than that of *A. sachalinensis*, had no relation to DBH class (Fig. 7b). Skewness of height growth rate of *A. sachalinensis* showed constantly negative values in all DBH classes (Fig. 7c). However, that of *P. jezoensis* changed from positive to negative at 2–6 cm DBH, which was the size significantly associated with gaps (Fig. 6). The dead stem ratio of *A. sachalinensis*, which can be regarded as estimated mortality, increased in 2–6 cm DBH classes, then declined. However, that of *P. jezoensis* decreased constantly with DBH class (Fig. 7d).

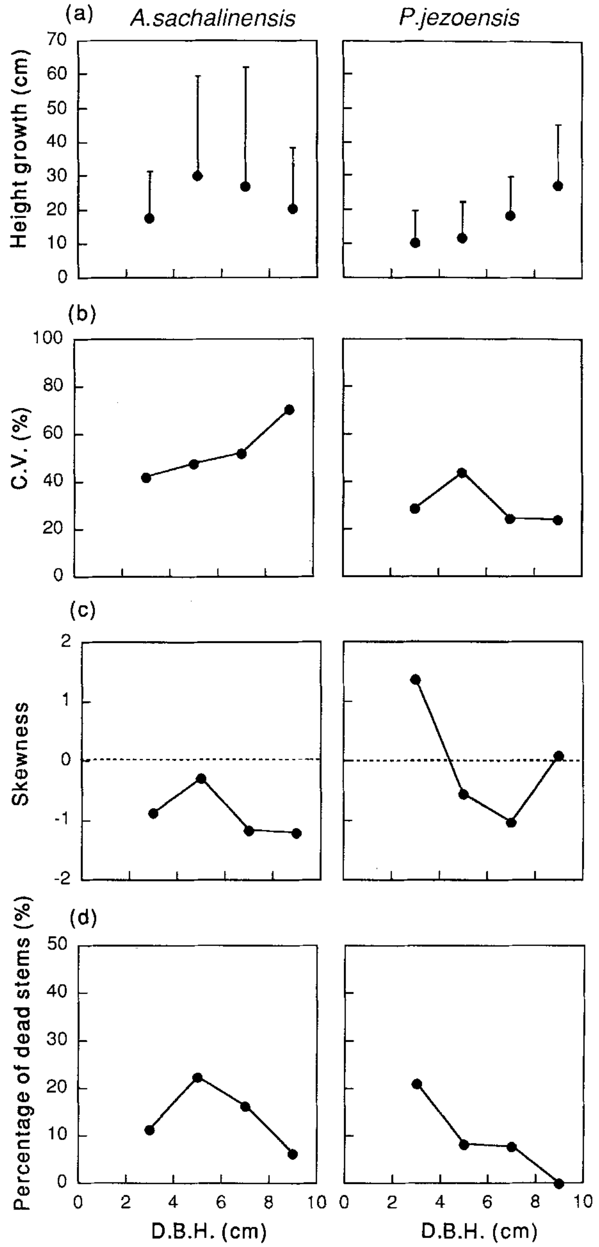

Fig. 7. (a) Relationships beteen DBH class and height growth in a 2 year period for understorey trees. Symbols show means + s.d. (with bar) of height growth. (b) The relationships between DBH class and coefficient of variance of the distribution of height growth rate in each DBH class for understorey trees. (c) The relationships between DBH class and skewness of the distribution of height growth rate in each DBH class for understorey trees. (d) Changes in dead stem ratio of understorey trees with DBH class. The dead stem ratio was calculated by dividing the number of dead stems by the sum of living and dead stems.

DISCUSSION

Veblen (1986) explained the coexistence mechanism of *Picea engelmanii* and *Abies lasiocarpa* based on percentage frequencies of fallen trees and occupants of treefall sites, which represent mortality and recruitment rate, respectively. The present results were similar: the damage ratio of canopy trees of *A. sachalinensis* exceeded that of *P. jezoensis*, and *A. sachalinensis* occurred in a greater number of understoreys. However, the abundance of understorey trees prior to gap creation does not necessarily lead to a high probability of filling canopy gaps (Lertzman 1992). To accept the canopy recruitment rate as a parameter for coexistence is essential in elucidating the growth and mortality patterns of understorey trees. These patterns of understorey trees indicate that *A. sachalinensis* can grow into higher layers even under suppressed conditions while *P. jezoensis* requires canopy gaps for height growth (Figs 5–7a). These different patterns between *P. jezoensis* and *A. sachalinensis* understorey may be regarded as the two extremes of life-history traits against shade (Canham 1989). *Picea jezoensis* has shade tolerance and individuals can persist in the understorey, but appreciable net growth occurs only after formation of gaps, while *A. sachalinensis* can grow slowly and consistently even beneath a closed canopy (Canham 1988c). Light conditions for understorey trees are variable corresponding to the vertical distribution of light. In the canopy layer, light intensity decreases exponentially from the top to the lowest branches with increasing cumulative foliage mass (Monsi & Saeki 1953). However, Horn (1971) and Kikuzawa *et al.* (1988) report that the light conditions in the understorey are poorest beneath the umbra due to the lowest branches of canopy trees, then become better away from the canopy layer. This implies that understorey trees of *P. jezoensis* suffer less from suppression by canopy trees than *A. sachalinensis* and had a lower mortality because of waiting at a lower layer. However those of *A. sachalinensis* suffer higher mortality because of shading by lower branches of canopy trees (Fig. 7d). *Picea jezoensis* gives priority to surviving and *A. sachalinensis* to growing in the understorey.

Picea jezonensis and *A. sachalinensis* exhibit different life-history traits. *Picea jezoensis* has a greater life span (> 300 years) and begins to produce cones at larger sizes (DBH > 40 cm), and *A. sachalinensis* has a short life span (< 100–200 years) and begins to produce cones at smaller sizes (DBH > 20 cm; Hiura *et al.* 1992; Kubota unpubl. data). Considering the growth and mortality patterns of understorey trees and the life-history traits of both of these species, it is assumed that lower mortality of *P. jezoensis* in the understorey may compensate for its smaller number of understorey trees, and the consistent growth of *A. sachalinensis* in the understorey enables more individuals to enter the canopy layer and earlier onset of reproduction, compensating for its shorter life span. Therefore, the 'waiting pattern' of understorey trees suggests an important feature in the life-history pattern of *P. jezoensis* and *A. sachalinensis*.

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