



Title	Site preference and occurrence patterns of <i>Picea jezoensis</i> and <i>Abies sachalinensis</i> on decayed logs in natural coniferous forests in Hokkaido, northern Japan
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Citation	Journal of Forest Research, 15(2), 108-114 https://doi.org/10.1007/s10310-009-0162-4
Issue Date	2010-04
Doc URL	http://hdl.handle.net/2115/42947
Rights	The original publication is available at www.springerlink.com
Type	article (author version)
File Information	JFR15-2_108-114.pdf



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1 **Title:** Site preference and occurrence patterns of *Picea jezoensis* and
2 *Abies sachalinensis* on decayed logs in natural coniferous forests in
3 Hokkaido, northern Japan

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20 **Article type:** original articles

21 **Subject area and field:** biology and ecology

22 **Pages:** 21 pages including title page

23 **Tables and Figures:** 2 tables and 3 figures

1 **Abstract**

2

3 The objectives of this study were to investigate differences in the
4 site preferences of seedlings of *Picea jezoensis* and *Abies sachalinensis*
5 on decayed logs, and to examine the occurrence patterns of seedlings and
6 saplings of the two species and whether they occur together or separately
7 on logs. We characterized the habitats of 1–2-year-old seedlings of the
8 two species on logs and examined the relationship of the two species on
9 logs by growth stages in two plots. One plot had been disturbed about 50
10 years ago, whereas another had not for a long time.

11 Although the thickness of moss and litter layer in the habitats of
12 1–2-year-old seedlings were significantly different between the two
13 species, the two species could occur together. In one study plot,
14 seedlings and saplings of the two species occurred together. The initial
15 occurrence pattern of the seedlings influenced the occurrence patterns of
16 the saplings on logs. The occurrence patterns of the seedlings and
17 saplings of the two species on logs seemed to be affected by the
18 abundance of seed trees. In another study plot, the saplings of the two
19 species occurred separately, but one species was not always
20 competitively superior to the other species. Disturbance history
21 influenced the occurrence patterns of the saplings of the two species on
22 decayed logs at the two study plots. Consequently, it is concluded that
23 seed dispersal and the abundance of available logs, which are usually
24 influenced by disturbance, are significant factors in the natural
25 regeneration of conifers in Hokkaido.

1

2 **Keywords** *Abies sachalinensis* ·decayed logs ·disturbance ·natural

3 regeneration ·*Picea jezoensis*

1 **Introduction**

2

3 In boreal forests, many conifers regenerate on decayed logs
4 (Harmon and Franklin 1989; Szewczyk and Szwagrzyk 1996;
5 Marie-Josee et al. 1998; Mori et al. 2004). In Hokkaido, northern Japan,
6 *Picea jezoensis* and *Abies sachalinensis*, both dominant evergreen
7 coniferous trees, regenerate mainly on decayed logs, because fungi
8 attack their seeds and the intensive suppression of their seedlings by
9 dwarf bamboos prevents their natural regeneration on the ground
10 (Natsume 1985; Cheng 1989; Takahashi 1991; Hiura et al. 1996;
11 Narukawa et al. 2003). Consequently, the investigation of their
12 regeneration on decayed logs is important to understand the regeneration
13 processes of these two coniferous species, especially *P. jezoensis*
14 (Natsume 1985; Kubota and Hara 1996b), in natural forests in Hokkaido.

15 Many studies have examined the differences in the ecological traits
16 of tree species influencing the natural regeneration in the natural forests
17 of Hokkaido. For example, Kubota and Hara (1995) showed that there
18 was little or symmetrical interspecific competition between adult trees
19 taller than 2 m among four canopy tree species, *P. jezoensis*, *A.*
20 *sachalinensis*, *Betula ermanii*, and *Picea glehnii*, in a natural forest.
21 They concluded that the population dynamics of the saplings (less than 2
22 m in height) govern the coexistence of the canopy trees (Kubota and
23 Hara 1995; Kubota and Hara 1996b). Therefore, it is important to
24 investigate the regeneration patterns of the two major species, *P.*
25 *jezoensis* and *A. sachalinensis*, on decayed logs when we examine the

1 stand dynamics in the natural coniferous and conifer-broadleaved forests
2 of Hokkaido.

3 Kubota and Hara (1996a) indicated habitat segregation between the
4 saplings of *P. jezoensis* and *A. sachalinensis* on decayed logs. They
5 suggested that there is asymmetric competition between the two species
6 on decayed logs, and that the saplings of *P. jezoensis* are competitively
7 excluded during sapling growth. However, *Picea*-dominated sites on
8 decayed logs are frequently observed in the natural forests of Hokkaido
9 (Natsume 1985; Takahashi et al. 2000), and the cause of their dominance
10 at these sites has not yet been examined.

11 Site preference in seedling establishment can influence the spatial
12 distribution of tree species (Niiyama 1990; Lusk 1995; Jakobsson and
13 Eriksson 2002). In general, the thicknesses of the moss mats and the
14 litter layers on decayed logs influence the seedling establishment of
15 coniferous tree species (Harmon and Franklin 1989; Nakamura 1992).
16 Logs with moss mats and litter layers of moderate thickness are suitable
17 to the establishment of conifers (Harmon 1987; Nakamura 1992;
18 Narukawa et al. 2003; Iijima et al. 2004). On the other hand, excessively
19 thick moss mats and litter layers prevent the establishment and growth of
20 the seedlings (Cross 1981; Harmon and Franklin 1989; Hörnberg et al.
21 1997; Iijima et al. 2004). This negative effect depends on the size of the
22 current-year seedlings; larger current-year seedlings are better than
23 smaller ones at becoming established on sites with thick moss mats and
24 litter layers (Knapp and Smith 1982; Nakamura 1992). Because
25 current-year seedlings of *P. jezoensis* are generally smaller than those of

1 *A. sachalinensis* (Kitabatake 2001), the seedlings of *P. jezoensis* are
2 expected to favor sites with thin moss mats and litter layers during their
3 natural regeneration on decayed logs, although the seedlings of *A.*
4 *sachalinensis* can establish at sites with thick moss mats and litter layers
5 on decayed logs.

6 In this study, we examined two questions regarding the regeneration
7 traits of *P. jezoensis* and *A. sachalinensis* growing on decayed logs in
8 natural forests of Hokkaido. First, does the thickness of the moss mats
9 and litter layers differ between the two species at the sites of seedling
10 establishment (hereafter, we refer to these as ‘habitats’)? Second, do the
11 seedlings and saplings of the two species occur together or separately on
12 decayed logs, and are there any dynamic changes in the occurrence
13 patterns of saplings on logs with growth?

14 To examine these questions, we analyzed the differences in the
15 habitats of seedlings of the two coniferous species and the occurrence
16 patterns of the seedlings and saplings of the two species on decayed logs
17 in two natural forests of Hokkaido. We also discussed the factors
18 influencing the occurrence patterns of seedlings and saplings of the two
19 species on decayed logs.

20

21 **Materials and Methods**

22

23 Study sites

24

25 Two study plots (P1: 43°39' N, 143°6' E; P2: 43°6' N, 143°9' E)

1 were set up in the eastern part of Daisetsuzan National Park in Hokkaido.

2 P1 was set up in September 2001 on a southeast slope with a
3 gradient of 15° at an altitude of about 950 m above sea level (a.s.l.) in a
4 natural forest, and was 60 m × 70 m in area. The mean annual
5 temperature is 5 °C, and August (mean 19 °C) and January (mean -9 °C)
6 are the warmest and coldest months, respectively, according to the
7 records at the nearest meteorological station in the town of Kamikawa
8 (30 km from P1, 350 m a.s.l.). The annual precipitation is 1314 mm at
9 Kamikawa. *Picea jezoensis* and *A. sachalinensis* were the dominant
10 species at P1. The distribution of tree diameters at breast height (DBHs)
11 was reverse J-shaped (Fig. 1). P1 had not suffered from a catastrophic
12 disturbance for a long time, and had been only slightly affected by a
13 typhoon in 1954 (Tamate et al. 1977). Some researches (Takahashi et al.
14 2000; Narukawa et al. 2003; Narukawa and Yamamoto 2003; Iijima et al
15 2004) has been conducted near P1, because this area is a typical
16 old-growth coniferous forest in Hokkaido.

17 P2 was set up in June 2000 in flat terrain at an altitude of about 700
18 m a.s.l. in a natural forest, and was 30 m × 30 m in area. The mean
19 annual temperature is 4 °C, and August (mean 18 °C) and January (mean
20 -11 °C) are the warmest and coldest months, respectively, according to
21 the records at the nearest meteorological station in Nukabira (20 km
22 from P2, 540 m a.s.l.). The annual precipitation is 1298 mm in Nukabira.
23 P2 was dominated by *A. sachalinensis*. The DBH distribution was
24 unimodal, with a peak at 30–40 cm (Fig. 1). P2 had been severely
25 damaged by a typhoon in 1954 (Tamate et al. 1977), and 27%–87% of the

1 trees in and around this stand were damaged by the typhoon (Takebe
2 2003).

3

4 Site preference for seedling establishment of *P. jezoensis* and *A.*
5 *sachalinensis*

6

7 We examined the site preferences for seedling establishment of *P.*
8 *jezoensis* and *A. sachalinensis* at P1. We selected 12 logs in or near P1,
9 on which seedlings of the two species frequently occurred and on which
10 the tallest seedlings were less than 10 cm, because we wanted to examine
11 the habitat characteristics just after seedling establishment. We selected
12 30 seedlings of each species that were one or two years old. We
13 measured the thicknesses of the moss mat (green part of the moss) and
14 litter layer (L layer) at the positions of the seedlings as characteristics of
15 the seedling habitats. The difference in the mean moss mat and litter
16 layer thicknesses between the two species was tested by a *U* test,
17 assuming that the thicknesses of the moss mats and litter layers would
18 not differ significantly between the two species if the favorable habitat
19 of the seedlings do not differ from one another.

20

21 Occurrence patterns of seedlings and saplings on decayed logs

22

23 The occurrence patterns of the seedlings and saplings of *P. jezoensis*
24 and *A. sachalinensis* on decayed logs were examined at P1 and P2. In
25 this part of the research, we defined seedlings as less than 30 cm in

1 height, and saplings as 30–200 cm in height. We set up 178 quadrats on
2 22 decayed logs at P1, and 256 quadrats on 30 decayed logs at P2. We
3 included 34 quadrats on four decayed logs adjacent to P1 to provide
4 enough samples. To calculate the area of each quadrat, we assumed the
5 quadrat to be trapezoidal. The length of each quadrat along the log stem
6 was fixed at 1 m, and the stem diameters at both ends were assumed to be
7 the top and bottom lines of a trapezoid. Quadrat areas ranged from 0.112
8 to 0.815 m². The total areas of the quadrats were 89.2 and 86.4 m² at P1
9 and P2, respectively. We measured the heights of all the seedlings and
10 saplings in the quadrats.

11 We classified the degree of decay of the logs, because it influences
12 the natural regeneration of tree species (Takahashi et al. 2000). Graham
13 and Cromack (1982) classified the decay classes of fallen logs into five
14 categories (decay classes I–V). We classified all the decayed logs at P1
15 and P2, including the supplementary four logs near P1, according to
16 Graham and Cromack (1982). We examined relationships between
17 disturbance history of stands investigated and the decay class
18 distribution of fallen logs.

19 We further examined the influence of differences in the habitats of
20 the seedlings and the effect of competitive exclusion on the occurrence
21 patterns of seedlings and saplings. If the competitive exclusion between
22 the two species exerts a strong effect on their cohort dynamics, it is
23 expected that the occurrence patterns of the two species would shift until
24 they grew into a pure cohort dominated by either *P. jezoensis* or *A.*
25 *sachalinensis*. All the quadrats were classified into one of three growth

1 stages based on the height of the tallest individual occurring in each
 2 quadrat: S1 (the tallest < 10 cm), S2 (10 cm ≤ the tallest < 30 cm), and
 3 S3 (30 cm ≤ the tallest < 200 cm). At P1, 88, 38, and 86 quadrats were
 4 classified into S1, S2, and S3, respectively, and at P2, 52, 84, and 120
 5 quadrats were classified into S1, S2, and S3, respectively. We measured
 6 the individual densities for *P. jezoensis* and *A. sachalinensis* in each
 7 quadrat.

8 To examine whether the two species co-occur or occur separately,
 9 we calculated the interspecific overlap index (C_δ ; Morisita 1959) for
 10 each growth stage at each study plot. We defined n_{x_i} and n_{y_i} as the
 11 densities of *P. jezoensis* and *A. sachalinensis*, respectively, in the
 12 quadrat i ($i = 1, 2, \dots, q$), and N_x and N_y as the sums of n_{x_i} and n_{y_i} . We
 13 calculated C_δ with the following equation:

$$14 \quad C_\delta = 2 \sum_{i=1}^q n_{x_i} n_{y_i} / (\delta_x + \delta_y) N_x N_y.$$

15 We calculated δ_x and δ_y with the following equations:

$$16 \quad \delta_x = \sum_{i=1}^q n_{x_i}(n_{x_i} - 1) / N_x(N_x - 1), \quad \delta_y = \sum_{i=1}^q n_{y_i}(n_{y_i} - 1) / N_y(N_y - 1).$$

17 If the ratio of the density of *P. jezoensis* to that of *A. sachalinensis*
 18 is stable in every quadrat, C_δ will be 1. If the two species never occur in
 19 the same quadrat, C_δ will be 0.

20

21 **Results**

22

1 Differences in the habitats of *P. jezoensis* and *A. sachalinensis* seedlings

2

3 The thicknesses of the moss mats and litter layers in the habitats of
4 1–2-year-old seedlings of *P. jezoensis* and *A. sachalinensis* are shown in
5 Fig. 2. The mean thickness of the moss mats in the habitats of *P.*
6 *jezoensis* was 2.3 ± 2.1 mm (mean \pm SD), whereas that of *A.*
7 *sachalinensis* was 5.6 ± 5.0 mm. The mean thickness of the litter layers
8 in the habitats of *P. jezoensis* was 3.6 ± 2.5 mm, whereas that of *A.*
9 *sachalinensis* was 9.4 ± 4.2 mm. The thickness of both the moss mats and
10 litter layers in the seedling habitats of *A. sachalinensis* were
11 significantly greater than those of *P. jezoensis* (*U* test, $P < 0.05$ for moss
12 mat thickness; $P < 0.01$ for litter layer thickness).

13

14 Distribution of log decay class and occurrence patterns of seedlings and
15 saplings of the two species on logs

16

17 At P1, we observed logs of decay classes II–V. Logs of decay
18 classes II and V were relatively abundant (Table 1). At P2, we found no
19 logs of decay class I or II, whereas many logs were considerably decayed
20 and 80% of the logs were in decay classes IV and V (Table 1).

21 In the S1 growth stage at P1, the interspecific overlap index (C_δ)
22 was 0.750, and the seedlings of *P. jezoensis* and *A. sachalinensis*
23 co-occurred (Table 2, Fig. 3). The trends observed for S1 were also
24 observed for S2. In contrast, *A. sachalinensis* dominated in S1 and S2 at
25 P2 (Fig. 3). In S3, C_δ was 0.560 for P1 (Table 2), and the saplings of

1 both species were present in many quadrats (Fig. 3). In the S3 at P2, C_s
2 was 0.199, and either of the species dominated in most quadrats (Table 2,
3 Fig.3). The occurrence patterns of the saplings tended toward exclusive.
4 The sapling density of *A. sachalinensis* was low in the quadrats
5 dominated by *P. jezoensis*, and vice versa (Fig. 3).

6

7 **Discussion**

8

9 The thicknesses of the moss mats and litter layers in habitats of
10 1–2-year-old seedlings of *A. sachalinensis* were significantly greater
11 than those of *P. jezoensis* (Fig. 2). Although, seedlings of *A. sachalinensis*
12 established at sites with thick moss mats and litter layers on decayed
13 logs, we did not find the seedlings of the *P. jezoensis* at such a sites.
14 Iijima et al. (2004) indicated that thick moss mats prevented the
15 germination of the *P. jezoensis* on decayed logs. And Kitabatake (2001)
16 showed that *A. sachalinensis* was greater at the establishment of the sites
17 with thick litter layer than *P. jezoensis* because current-year seedlings of
18 *A. sachalinensis* are larger than those of *P. jezoensis*. Therefore, it is
19 assumed that seedlings of *A. sachalinensis* tend to occur at sites with
20 thicker moss mats and litter layers than do those of *P. jezoensis*.

21 Seedlings of both species in the S1 growth stage co-occurred at P1
22 (Table 2, Fig. 3), although we observed that the habitats of the seedlings
23 were different between the two species (Fig. 2). This may have resulted
24 from the heterogeneous thicknesses of the moss mats and litter layers on
25 the logs, caused by factors such as bark crevices. The thicknesses may

1 have been heterogeneous at a scale sufficiently small for the
2 co-occurrence of the seedlings. Takahashi et al. (2000) suggested that
3 the surface conditions on decayed logs are heterogeneous even when the
4 logs are in the same decay class. Considerable spatial heterogeneity in
5 the thicknesses of moss mats and litter layers may occur generally, even
6 in a small area in a natural forest in Hokkaido. Therefore, differences in
7 the habitats of the seedlings of the two species do not seem to have
8 caused any spatial segregation just after their establishment on the
9 decayed logs.

10 At P2, on the other hand, seedlings of *A. sachalinensis* apparently
11 dominated on the decayed logs (Fig. 3). At P2, most of the canopy trees
12 with DBHs larger than 30 cm, which could be seed trees (Matsuura 1980),
13 were *A. sachalinensis* (Fig. 1), so that the dispersed seeds of *A.*
14 *sachalinensis* could have been much more abundant than those of *P.*
15 *jezoensis* over the past several years. Furthermore, we noticed that logs
16 of decay classes IV and V accounted for 80% of all the logs investigated
17 at P2 (Table 1). In a natural forest in central Hokkaido, seedlings of *P.*
18 *jezoensis* smaller than 10 cm were more abundant on logs of decay class
19 III than on logs of decay classes IV and V. However, seedlings of *A.*
20 *sachalinensis* smaller than 10 cm were abundant on logs of decay classes
21 III–V (Takahashi et al. 2000). Consequently, seedlings of *A.*
22 *sachalinensis* dominated the S1 and S2 growth stages at P2 because the
23 seed source of that species was larger and the logs were more decayed.

24 At P1, the seedlings and saplings of *P. jezoensis* and *A.*
25 *sachalinensis* occurred together in all the growth stages (S1, S2, and S3;

1 Fig. 3), although Kubota and Hara (1996a) suggested that the two
2 species were spatially separated in the sapling stage in a natural forest in
3 Hokkaido. Our results, shown in Fig. 3, suggest that there is no
4 competitive exclusion between *P. jezoensis* and *A. sachalinensis* at P1,
5 because P1 has not been intensively disturbed in several decades and
6 S1–S3 are assumed to form a chronosequence under stable stand
7 conditions

8 At P2, the saplings of *P. jezoensis* and *A. sachalinensis* tended to
9 occur exclusively on decayed logs in the S3 growth stage (Table 2), but
10 one species was not always superior to the other species. If one-way
11 competitive exclusion strongly influenced the growth and survival of the
12 seedlings on decayed logs, one species would be dominant on many logs
13 as the seedlings grew. Although Kubota and Hara (1996a) reported that *A.*
14 *sachalinensis* was competitively superior to *P. jezoensis* on decayed logs,
15 our study showed that *P. jezoensis* was also dominant in many quadrats
16 in the S3 growth stage at P2. From these results, which show the
17 co-occurrence of the two species during the S1–S3 growth stages in P1,
18 we conclude that one-way competitive exclusion between *P. jezoensis*
19 and *A. sachalinensis* did not strongly affect the occurrence patterns of
20 the seedlings and saplings on the decayed logs in the stands investigated.
21 Kubota and Hara (1996a) concluded that the difference in crown shape
22 between the species affected their growth dynamics and the competition
23 between them. However, Narukawa and Yamamoto (2003) suggested that
24 competition among the roots on the surfaces of decayed logs was greater
25 than any competition among the shoots of the saplings on those logs.

1 Other factors, such as the allocational acclimation of the seedlings to
2 environmental conditions (Iijima et al. 2004), might have influenced the
3 occurrence patterns of the saplings of the two species on the logs. It is
4 necessary to take factors other than the competition between the
5 aboveground parts of the seedlings and saplings into account when
6 examining the growth and competition dynamics of *P. jezoensis* and *A.*
7 *sachalinensis* on decayed logs.

8 At P2, the relationships of density between *P. jezoensis* and *A.*
9 *sachalinensis* in the S1 and S2 growth stages were different from that in
10 the S3 growth stage. At P2, at present, the seedlings of *P. jezoensis* are
11 hardly regenerating because most of the fallen logs are very decayed
12 (Takahashi et al. 2000). Considering the disturbance history, the current
13 DBH distribution (Fig. 1), and the species composition in the S1–S3
14 growth stages in P2, we infer that many *P. jezoensis* were established on
15 fallen logs after the catastrophic disturbance caused by the typhoon in
16 1954, and that the regeneration of *A. sachalinensis* gradually increased
17 on decayed logs thereafter. Therefore, it seems that the occurrence
18 patterns of the seedlings and saplings at P2 have been influenced by the
19 disturbance history of the stand and the temporal dynamics of the
20 distribution of the log decay class.

21 The occurrence patterns of saplings on logs were different between
22 P1 and P2 (Fig. 3). There was a catastrophic disturbance at P2 in 1954
23 but not at P1 (Tamate et al. 1977; Takebe 2003), as indicated by DBH
24 distributions. Kubota (1995) suggested that the frequency and magnitude
25 of the disturbances influence the regeneration of the understorey trees

1 through the stand structure. Disturbances change forest stand structures
2 and the environment such as the frequency of fallen logs in each decay
3 class, the abundance of seed trees, and the canopy gap area, that
4 influence tree regeneration (Greene et al. 1999; Takahashi et al. 2000).
5 After the catastrophic disturbance at P2 in 1954, the species composition
6 of the seed trees probably changed and *A. sachalinensis* gradually
7 became dominant (Figs 1 and 3). At P1, which has not been affected by
8 any severe disturbance in the last 45 years, there are many seed trees of
9 both *P. jezoensis* and *A. sachalinensis* (Fig. 1). Consequently, it seems
10 that seed dispersal and the abundance of available decayed logs, which
11 were responsible for the differences in the occurrence of *P. jezoensis* and
12 *A. sachalinensis* between P1 and P2, are significant factors in the natural
13 regeneration of conifers in Hokkaido.

14 In conclusion, the habitats of the seedlings on decayed logs were
15 fundamentally different for *P. jezoensis* and *A. sachalinensis*, but the two
16 species could co-occur on decayed logs in the natural forests of
17 Hokkaido. The occurrence patterns of the seedlings and saplings of the
18 two conifer species were different, depending on the stands. However,
19 the occurrence patterns did not result from one-way competitive
20 exclusion between the species, but were instead affected by the
21 disturbance histories of the stands. Seed dispersal and seedbed
22 availability affected the spatial distribution of the saplings of the two
23 species on decayed logs.

24

25 **Acknowledgments**

1 We are grateful to Drs. H. Tanouchi, S. Abe, and Mr. H. Utsugi, of the
2 Forestry and Forest Product Research Institute and Dr. K. Takahashi,
3 Emeritus Professor of Hokkaido University, for their assistance and
4 variable comments. We also thank the many members of the Research
5 Group of Forest Resource Science, Hokkaido University, for their
6 assistance in the field survey. We also acknowledge two anonymous
7 reviewers for helpful comments for improving the manuscript.

8

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1 **Figure Legends**

2

3 **Fig. 1** DBH (diameter at breast height) distributions in investigated
4 stands.

5

6 **Fig. 2** Frequencies of 1- and 2-year-old seedlings of *Picea jezoensis* and
7 *Abies sachalinensis* by the thicknesses of moss mat (a) and litter layer
8 (b) at P1.

9

10 **Fig. 3** Relative frequency distributions of the rate of seedlings and
11 saplings of *P. jezoensis* in each quadrat by growth stage. The growth
12 stages of the quadrats are divided by the tallest individuals in the
13 quadrat, as follows: S1, tallest individuals < 10 cm; S2, 10 cm \leq tallest
14 | individuals < 30 cm; and S3, 30 cm \leq tallest individuals < 200 cm.

Table 1 Decay class distribution at each plot

Decay class*	P1 (%)	P2 (%)
I	0	0
II	33	0
III	10	20
IV	14	49
V	43	31

* According to Graham and Cromack (1982).

1

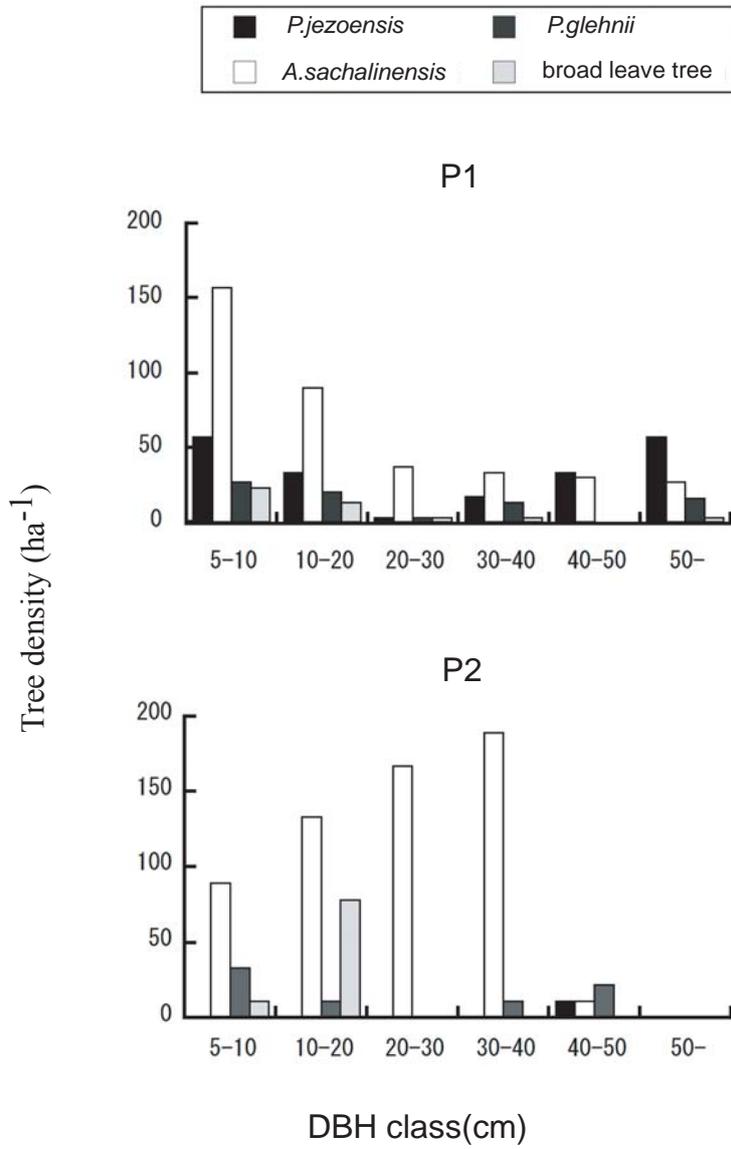
Table 2 Interspecific overlap index (C_{δ}) by growth stages at plots P1 and P2

Growth stage*	P1	P2
S1	0.750	0.252
S2	0.531	0.432
S3	0.560	0.199

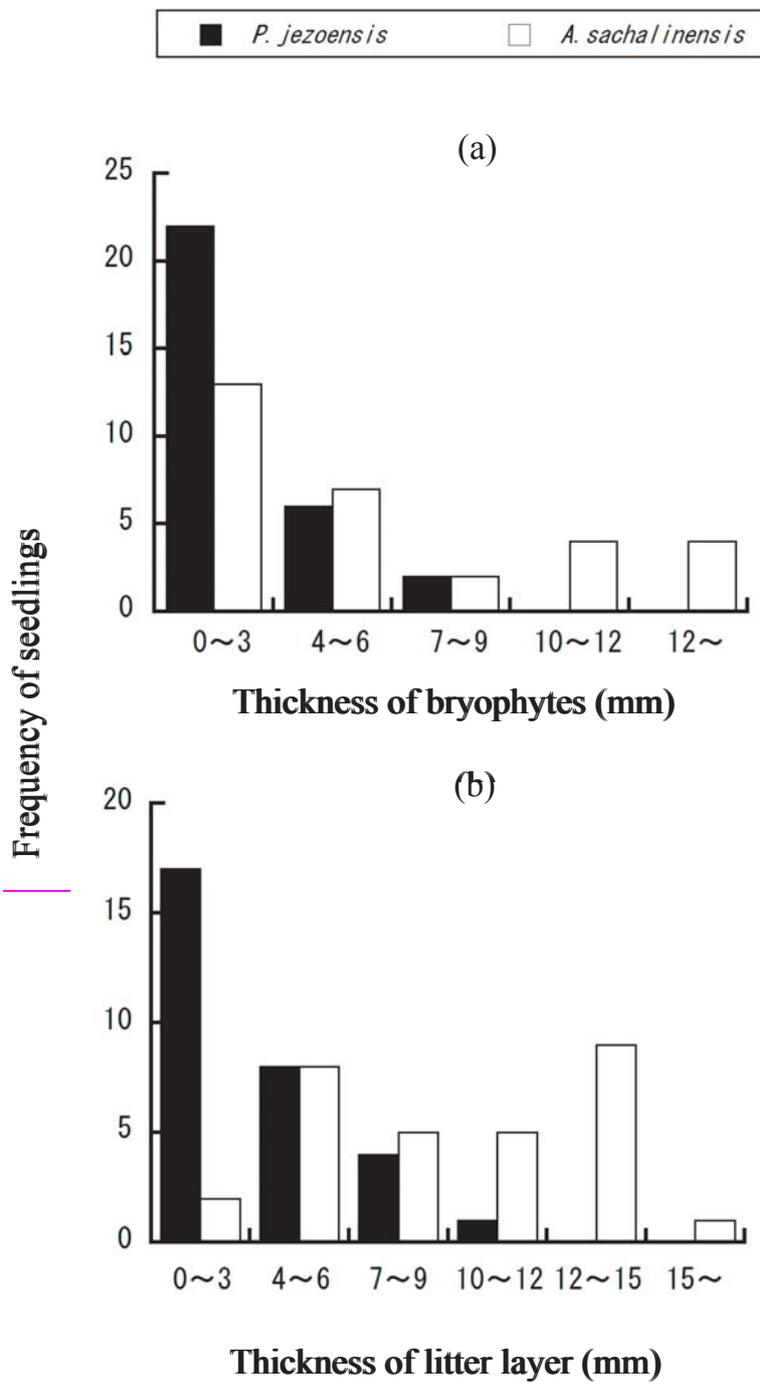
Values in the table are the C_{δ} -index.

* One-meter quadrats for seedling and sapling census are classified into S1, S2, and S3 depending on the height of the tallest individual in the quadrat. See in the text for detail.

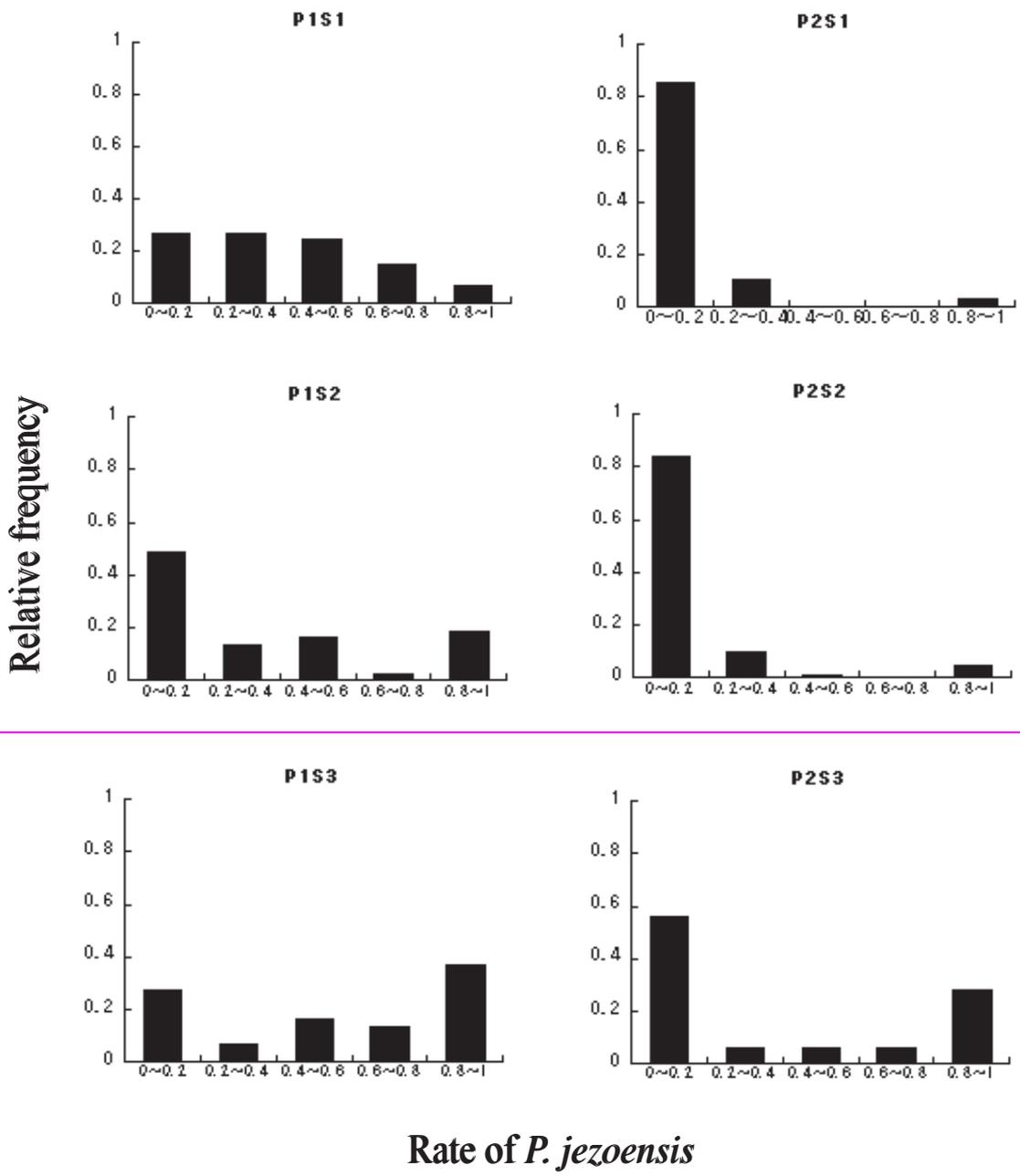
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Fig. 1.



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Fig. 2.



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Fig. 3.