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Author(s)	Yano, Keisuke; Shibuya, Masato
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Title: Site preference and occurrence patterns of *Picea jezoensis* and *Abies sachalinensis* on decayed logs in natural coniferous forests in Hokkaido, northern Japan

Authors: Keisuke Yano[1,2] · Masato Shibuya[1]

Address: [1]Gradeate School of Agriculture, Hokkaido University, Sapporo, Hokkaido 060-8589, Japan

[2] Present address: Forestry and forest products research institute, Forest tree breeding center, Ishi 3809-1, Juo town, Hitachi, Ibaraki 319-1301, Japan

Corresponding author: K. Yano

Tel: +81-294-39-7048, Fax: +81-294-39-7352,

E-mail: yanokei@affrc.go.jp, Postal address: Forestry and forest products research institute, Forest tree breeding center, Ishi 3809-1, Juo town, Hitachi, Ibaraki, 319-1301, Japan

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Abstract

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

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

Keywords *Abies sachalinensis* ·decayed logs ·disturbance ·natural regeneration ·*Picea jezoensis*

Introduction

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

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

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

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

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

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

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

Materials and Methods

Study sites

Two study plots (P1: 43°39' N, 143°6' E; P2: 43°6' N, 143°9' E) were set up in the eastern part of Daisetsuzan National Park in Hokkaido.

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

P2 was set up in June 2000 in flat terrain at an altitude of about 700 m a.s.l. in a natural forest, and was 30 m × 30 m in area. The mean annual temperature is 4 °C, and August (mean 18 °C) and January (mean –11 °C) are the warmest and coldest months, respectively, according to the records at the nearest meteorological station in Nukabira (20 km from P2, 540 m a.s.l.). The annual precipitation is 1298 mm in Nukabira. P2 was dominated by *A. sachalinensis*. The DBH distribution was unimodal, with a peak at 30–40 cm (Fig. 1). P2 had been severely damaged by a typhoon in 1954 (Tamate et al. 1977), and 27%–87% of the trees in and around this stand were damaged by the typhoon (Takebe 2003).

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

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

Occurrence patterns of seedlings and saplings on decayed logs

The occurrence patterns of the seedlings and saplings of *P. jezoensis* and *A. sachalinensis* on decayed logs were examined at P1 and P2. In this part of the research, we defined seedlings as less than 30 cm in height, and saplings as 30–200 cm in height. We set up 178 quadrats on 22 decayed logs at P1, and 256 quadrats on 30 decayed logs at P2. We included 34 quadrats on four decayed logs adjacent to P1 to provide enough samples. To calculate the area of each quadrat, we assumed the quadrat to be trapezoidal. The length of each quadrat along the log stem was fixed at 1 m, and the stem diameters at both ends were assumed to be the top and bottom lines of a trapezoid. Quadrat areas ranged from 0.112 to 0.815 m^2. The total areas of the quadrats were 89.2 and 86.4 m^2 at P1 and P2, respectively. We measured the heights of all the seedlings and saplings in the quadrats.

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

We further examined the influence of differences in the habitats of the seedlings and the effect of competitive exclusion on the occurrence patterns of seedlings and saplings. If the competitive exclusion between the two species exerts a strong effect on their cohort dynamincs, it is expected that the occurrence patterns of the two species would shift until they grew into a pure cohort dominated by either *P. jezoensis* or *A. sachalinensis*. All the quadrats were classified into one of three growth stages based on the height of the tallest individual occurring in each quadrat: S1 (the tallest < 10 cm), S2 (10 cm ≤ the tallest < 30 cm), and S3 (30 cm ≤ the tallest < 200 cm). At P1, 88, 38, and 86 quadrats were classified into S1, S2, and S3, respectively, and at P2, 52, 84, and 120 quadrats were classified into S1, S2, and S3, respectively. We measured the individual densities for *P. jezoensis* and *A. sachalinensis* in each quadrat.

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

$$C_\delta = 2\sum_{i=1}^{q} n_{xi} n_{yi} \Big/ (\delta_x + \delta_y) N_x N_y .$$

We calculated δ_x and δ_y with the following equations:

$$\delta_x = \sum_{i=1}^{q} n_{xi}(n_{xi} - 1) \Big/ N_x(N_x - 1), \quad \delta_y = \sum_{i=1}^{q} n_{yi}(n_{yi} - 1) \Big/ N_y(N_y - 1).$$

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

Results

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

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

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

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

In the S1 growth stage at P1, the interspecific overlap index (C_δ) was 0.750, and the seedlings of *P. jezoensis* and *A. sachalinensis* co-occurred (Table 2, Fig. 3). The trends observed for S1 were also observed for S2. In contrast, *A. sachalinensis* dominated in S1 and S2 at P2 (Fig. 3). In S3, C_δ was 0.560 for P1 (Table 2), and the saplings of both species were present in many quadrats (Fig. 3). In the S3 at P2, C_δ was 0.199, and either of the species dominated in most quadrats (Table 2, Fig.3). The occurrence patterns of the saplings tended toward exclusive. The sapling density of *A. sachalinensis* was low in the quadrats dominated by *P. jezoensis*, and vice versa (Fig. 3).

Discussion

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

Seedlings of both species in the S1 growth stage co-occurred at P1 (Table 2, Fig. 3), although we observed that the habitats of the seedlings were different between the two species (Fig. 2). This may have resulted from the heterogeneous thicknesses of the moss mats and litter layers on the logs, caused by factors such as bark crevices. The thicknesses may have been heterogeneous at a scale sufficiently small for the co-occurrence of the seedlings. Takahashi et al. (2000) suggested that the surface conditions on decayed logs are heterogeneous even when the logs are in the same decay class. Considerable spatial heterogeneity in the thicknesses of moss mats and litter layers may occur generally, even in a small area in a natural forest in Hokkaido. Therefore, differences in the habitats of the seedlings of the two species do not seem to have caused any spatial segregation just after their establishment on the decayed logs.

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

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

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

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

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

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

The occurrence patterns of saplings on logs were different between P1 and P2 (Fig. 3). There was a catastrophic disturbance at P2 in 1954 but not at P1 (Tamate et al. 1977; Takebe 2003), as indicated by DBH distributions. Kubota (1995) suggested that the frequency and magnitude of the disturbances influence the regeneration of the understorey trees through the stand structure. Disturbances change forest stand structures and the environment such as the frequency of fallen logs in each decay class, the abundance of seed trees, and the canopy gap area, that influence tree regeneration (Greene et al. 1999; Takahashi et al. 2000). After the catastrophic disturbance at P2 in 1954, the species composition of the seed trees probably changed and *A. sachalinensis* gradually became dominant (Figs 1 and 3). At P1, which has not been affected by any severe disturbance in the last 45 years, there are many seed trees of both *P. jezoensis* and *A. sachalinensis* (Fig. 1). Consequently, it seems that seed dispersal and the abundance of available decayed logs, which were responsible for the differences in the occurrence of *P. jezoensis* and *A. sachalinensis* between P1 and P2, are significant factors in the natural regeneration of conifers in Hokkaido.

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

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Figure Legends

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

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

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

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 clssified into S1, S2, and S3 depending on the height of the tallest individual in the quadrat. See in the text for detail.

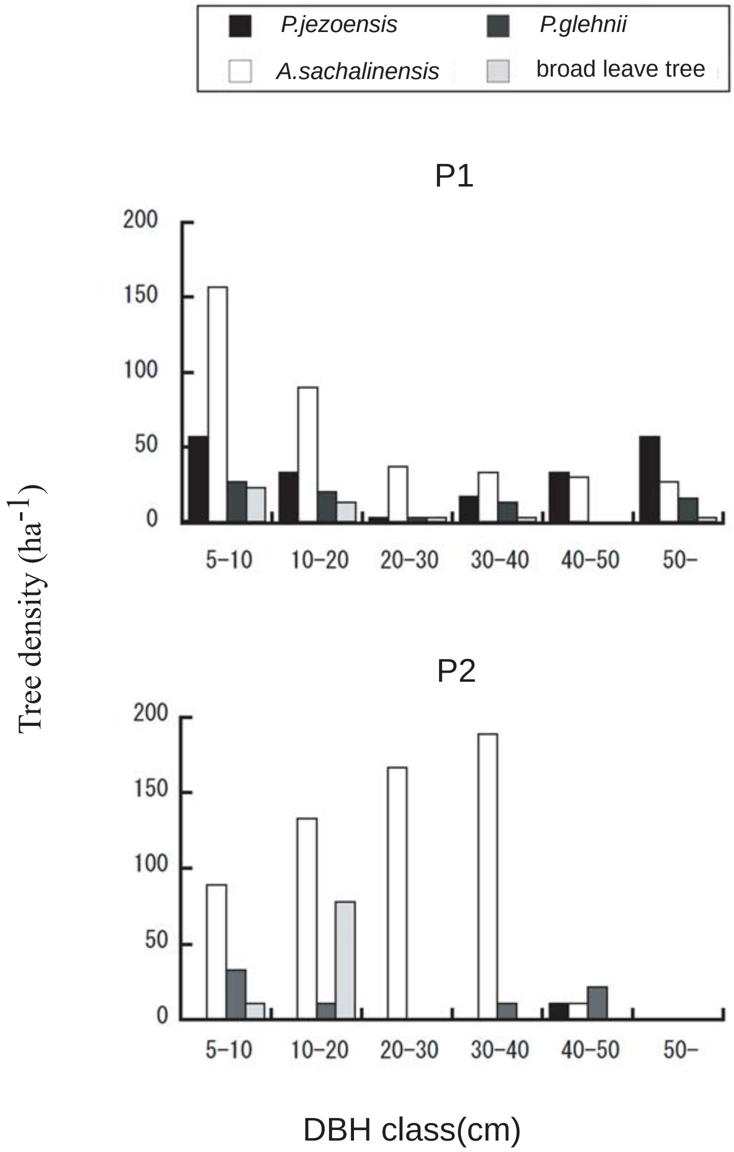

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Fig. 1.

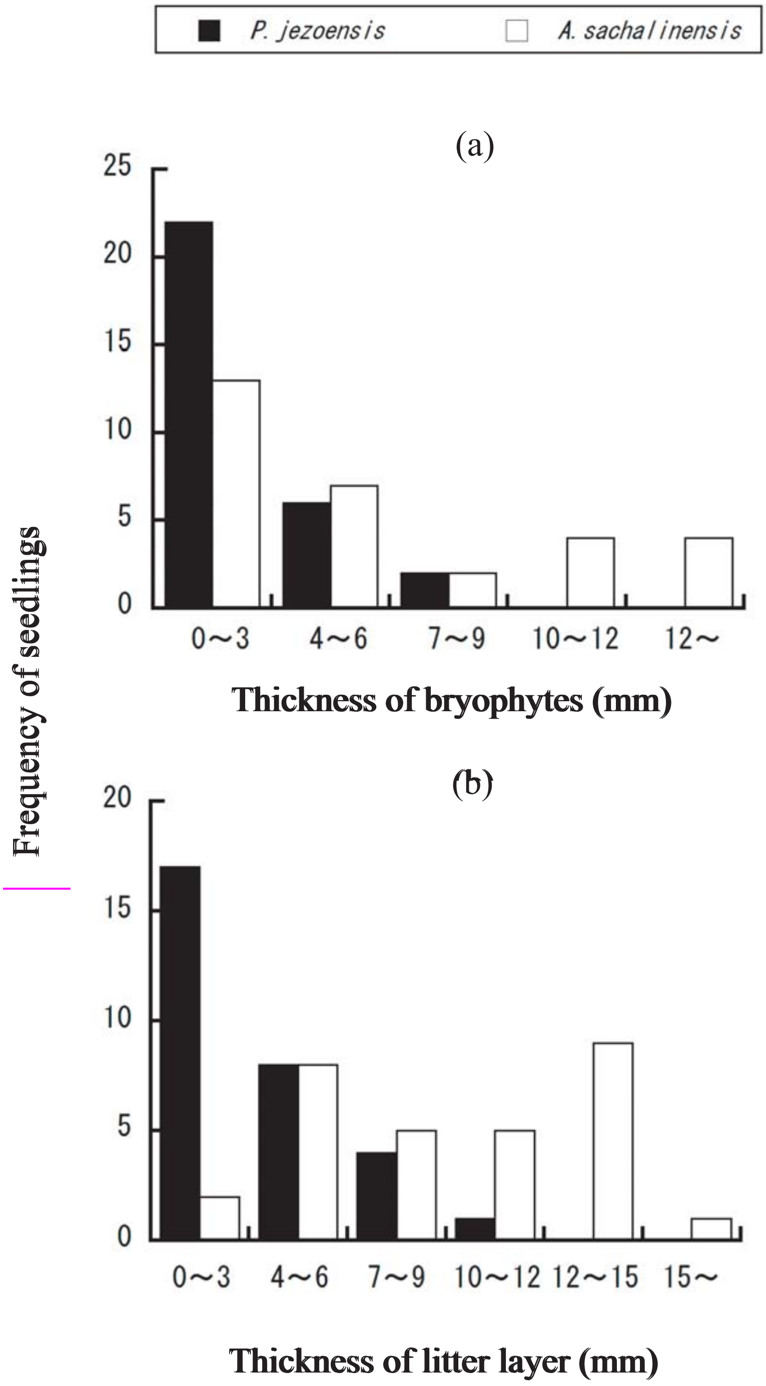

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Fig. 2.

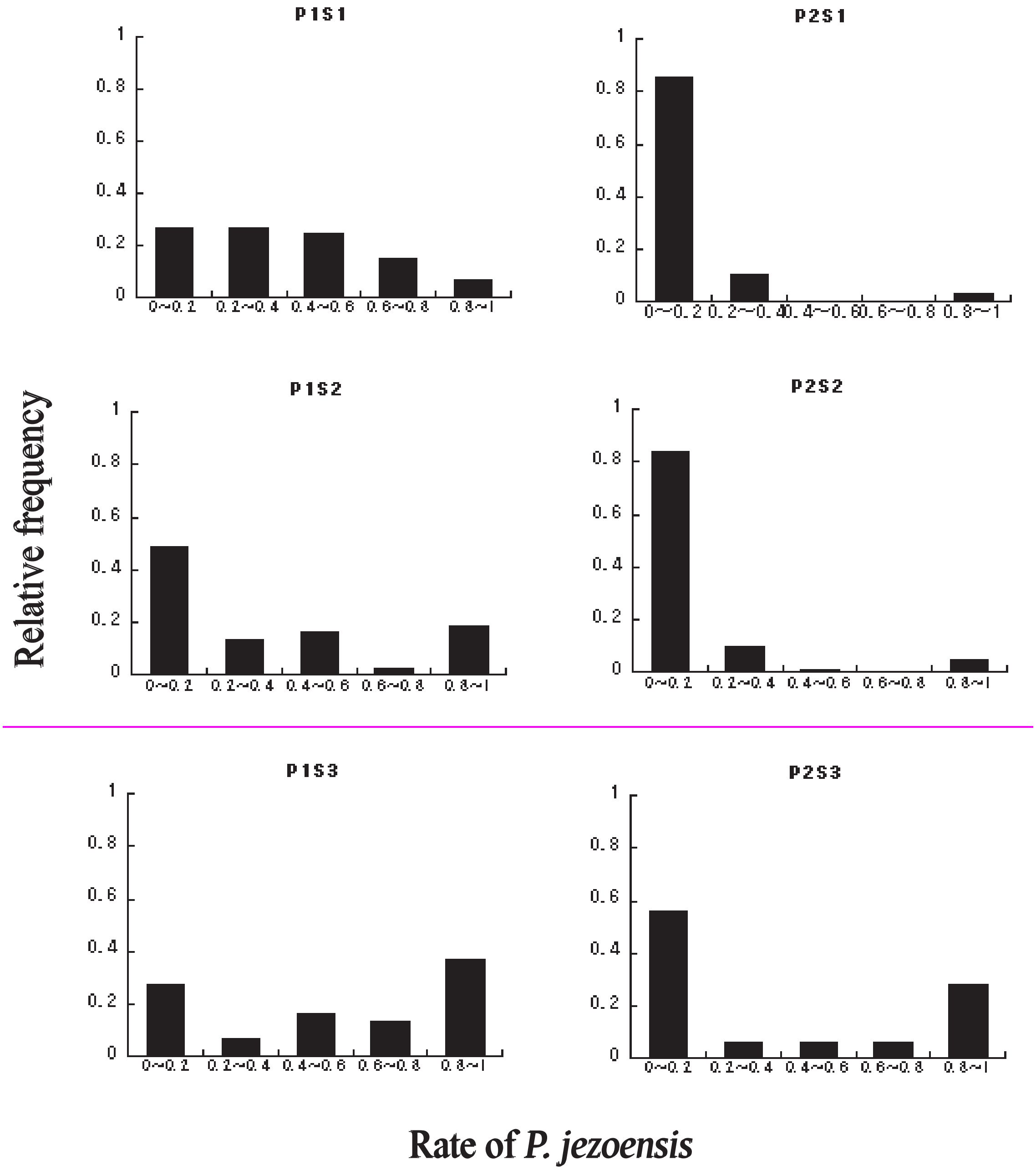

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Fig. 3.