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1 **Title:** Effects of surface and light conditions of fallen logs on the emergence and
2 survival of coniferous seedlings and saplings

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Abstract

1
2 We surveyed the germination number (N_{cs}) of 2 year and a one-year-survival of
3 *Abies sachalinensis* and *Picea jezoensis* seedlings and saplings on 29 fallen logs
4 from 2004 – 2005 in a natural coniferous forest in Hokkaido, northern Japan, in
5 relation to the surface and light conditions of fallen logs. Moss height (H_{moss}), log
6 hardness (Hardness), and the area of fallen log (Area) were measured as the surface
7 conditions by each 1 m (block) from bottom to top of all fallen logs. The relative
8 photosynthetic photon flux density (rPPFD) 10 cm above the tallest seedling in each
9 block were measured as the light condition. In addition, the height of the tallest
10 seedling or sapling in each block (H_{max}), the difference between a height of each
11 seedling and sapling and the H_{max} (Shading), and a height of seedlings and saplings
12 in 2004 (H_{ini}) were considered. N_{cs} of *A. sachalinensis* was affected by Hardness
13 and Area, whereas N_{cs} of *P. jezoensis* was affected by H_{moss} , Hardness, Area, H_{max} ,
14 and rPPFD. The survival of seedlings (height < 5 cm) and saplings ($5 \leq$ height
15 < 50 cm) were affected by H_{ini} , rPPFD, and Shading for both species. However,
16 the survival of *P. jezoensis* saplings was more sensitive to decrease in rPPFD and
17 increase of Shading than that of *A. sachalinensis*. Therefore, seedling emergence was
18 influenced by surface conditions, whereas survival was affected by light conditions.
19 Furthermore, *P. jezoensis* emergence and survival were more sensitive to surface
20 and light conditions than that of *A. sachalinensis*.

1 **Keywords:** *Abies sachalinensis*, Environmental conditions, *Picea jezoensis*, Regen-
2 eration on fallen logs, Seedling dynamics.

1 Introduction

2 In boreal forests, many coniferous tree species regenerate on fallen logs (Harvey et
3 al. 1987; Suzuki et al. 1987; Taylor 1990; Szewczyk and Szwagrzyk 1996; Nakagawa
4 et al. 2001; Sugita and Tani 2001; Mori et al. 2004; Sugita and Nagaike 2005). In
5 Hokkaido, northern Japan, two dominant evergreen conifers, *Abies sachalinensis*
6 and *Picea jezoensis*, emerge and grow on both fallen logs and the forest floor, and
7 exclusively on fallen logs, respectively (Natsume 1985; Kubota et al. 1994; Takahashi
8 1994). The mortality rate of trees during early developmental stage is particularly
9 higher than that at any other developmental stage (Hett 1971; Hett and Loucks
10 1976; De Steven 1994), and the success of seedling emergence and survival strongly
11 affects the resulting number of mature trees (Pinero et al. 1984). Consequently,
12 regeneration success on fallen logs influences the population dynamics of these tree
13 species, especially *P. jezoensis* in natural forests in Hokkaido.

14 However, not all fallen logs are available for *A. sachalinensis* and *P. jezoensis*
15 recruitment. The surface conditions of fallen logs change throughout the decay
16 process (Graham and Cromack 1982), and differences in the surface conditions of
17 fallen logs cause variation in seedling and sapling density (McCullough 1948; Simard
18 et al. 1998; Takahashi et al. 2000; Narukawa et al. 2003). The surface conditions
19 on fallen logs are composed of several factors that affect *A. sachalinensis* and *P.*
20 *jezoensis* seedling and sapling density; however, which of and how these factors affect

1 seedling and sapling density has not yet been determined. Thus, the relationship
2 between these factors and the emergence and survival of these tree species on fallen
3 logs should be examined to understand their population dynamics in natural forests
4 in Hokkaido.

5 For seedlings to emerge on fallen logs, seeds need to be trapped on the logs
6 (Takahashi 1994), and sufficient water supply is necessary for germination (Taka-
7 hashi et al. 2000; Iijima et al. 2004). Takahashi (1994) reported that the number
8 of *A. sachalinensis*, *P. jezoensis*, and *Picea glehnii* seedlings and saplings on fallen
9 logs in a natural forest in Hokkaido was low on narrow logs. Iijima et al. (2004)
10 scattered *P. jezoensis* seeds on fallen logs in a natural coniferous forest in Hokkaido
11 and showed that the germination rate was significantly smaller on fallen logs with
12 a cover of thick moss (moss height > 20 mm). Although the presence of moss on
13 fallen logs improves the water status of the logs and seedlings (Iijima et al. 2006),
14 thick moss can both prevent seeds from landing on and radicles from extending into
15 the humid humus-layer beneath the moss (Harmon and Franklin 1989; Nakamura
16 1992).

17 For seedlings and saplings to survive on fallen logs, environmental conditions
18 suitable for assimilation (Harmon 1987) and root growth (Iijima et al. 2004) are
19 necessary. Iijima et al. (2004) showed that the growth of current-year seedlings of
20 *P. jezoensis* was significantly lower on fallen logs with thick moss cover than on
21 fallen logs with thin or no moss in a natural coniferous forest in Hokkaido. They

1 suggested that lower seedling growth rates resulted from shading by the tall moss.
2 Furthermore, Iijima et al. (2004) showed that 1-year-old seedlings of *P. jezoensis* on
3 hard fallen logs had lower biomass growth and higher top/root (T/R) ratios than
4 seedlings on soft fallen logs.

5 The differences in the conditions available for emergence and survival of seedlings
6 on fallen logs should be examined between *A. sachalinensis* and *P. jezoensis*. Current-
7 year *A. sachalinensis* seedlings are larger than current-year *P. jezoensis* seedlings
8 (*A. sachalinensis*, 3.6 ± 0.5 cm; *P. jezoensis*, 2.1 ± 0.5 cm; Kitabatake 2001). *A.*
9 *sachalinensis* saplings are more shade-tolerant than *P. jezoensis* (Kubota et al.
10 1994; Kubota and Hara 1996, but opposite result was obtained in Hiura et al.
11 1996). Current-year seedling size may affect the competition with moss on fallen
12 logs, whereas shade tolerance may affect their survival in low light. In this study,
13 shade-tolerance was defined the ability to survive under low light condition (Kobe
14 et al. 1995). These species-specific traits may result in differences in the conditions
15 available for seedling emergence and survival between these species.

16 Therefore, our objectives of this study were (1) to determine factors affecting the
17 emergence and survival of *A. sachalinensis* and *P. jezoensis* seedlings and saplings
18 on fallen logs and (2) examine how these factors result in differential emergence and
19 survival of these species on fallen logs, in order to clarify the effect of the surface
20 and light conditions of fallen logs on their population dynamics in natural coniferous
21 forest in Hokkaido.

1 Methods

2 Study site

3 The study was conducted in the Hidaka region in Hokkaido, northern Japan. A
4 permanent plot (100 × 100 m) was established in a coniferous forest in the region
5 (42° 55' N, 142° 45' E; 1038 m a.s.l.) by the Northern Hidaka District Forest Office
6 of the Japanese National Forestry Agency in 1973. No forestry operations have been
7 conducted in the plot since its establishment. We established a 50 × 50 m subplot
8 within the permanent plot in 2004. The density of trees > 5 cm in diameter at breast
9 height (DBH) in the subplot was highest for *Abies sachalinensis*, but the total basal
10 area (BA) in the subplot was largest for *Picea jezoensis* (Table 1). The canopy height
11 of the stand was 25 – 30 m. The undergrowth vegetation was dominated by dwarf
12 bamboo (*Sasa senanensis* Rehd.) and a sedge (*Carex sachalinensis* Fr. Schm. var.
13 *sachalinensis*). Mean annual precipitation recorded at the nearest meteorological
14 station in Hidaka (42° 53' N, 142° 27' E; 280 m a.s.l.) was 1374 mm from 2001
15 to 2004 (<http://www.data.kishou.go.jp/etrn/>). The mean annual temperature of
16 the study site was estimated from as 1.2 °C based on data from the meteorological
17 station using a lapse rate of – 0.6 °C per 100 m.

1 Measurements

2 We examined each of the 56 fallen logs within the subplot. Their total projected
3 area was 190 m², comprising 7.9 % of the subplot area. This value was similar to
4 that determined in previous studies (6.0 – 11.0 %, Graham and Cromack 1982; 6.0
5 %, Christy and Mack 1984; 9.9 %, Harmon 1989; 2.6 – 6.0 %, Takahashi 1994; but
6 13.2 – 15.5 %, Narukawa and Yamamoto 2002). We divided the fallen logs into 1-
7 m-long sections, hereafter “blocks.” Seedlings and saplings were defined as < 5 cm
8 in height and 5 cm ≤ height < 50 cm, respectively; they accounted for 96 % of all
9 *A. sachalinensis* and *P. jezoensis* individuals on the fallen logs investigated. From
10 August to October 2004, we measured the height and diameter at root collar (DRC)
11 of all seedlings and saplings on each fallen log, except current-year seedlings, and
12 counted the number of current-year seedlings (N_{cs}) on each block. Both current-
13 year and older seedlings and saplings were identified by color tags. We checked the
14 survival of all seedlings and saplings and surveyed N_{cs} of newly emerged on each
15 block in September and October 2005.

16 In 2004, we measured moss height (H_{moss}), log hardness (Hardness), and log area
17 (Area) for each block. We measured the photosynthetic photon flux density (PPFD)
18 as an indicator of light availability for each block under an overcast sky from late
19 July to early October 2005 using a pair of quantum sensors (LI250; LI-COR, Lincoln,
20 NE, USA). The PPFD was measured five times in an open site and at 10 cm above

1 the highest seedling in a block simultaneously, and the mean ratio was calculated
2 (relative PPFd: rPPFD). Hardness of each block was measured three times using
3 a Yamanaka-type soil penetrometer (LS321; IMAI Corp., Tokyo, Japan). Area was
4 calculated as projected area using the top and bottom diameter of each block.

5 Data analysis

6 Fallen logs found within 10 m of trees that had died within the last 5 years were
7 excluded from analyses regarding the effect of light conditions on N_{cs} and survival.
8 Thus, we analyzed 29 (329 blocks, 103.7 m²) of a total of 56 fallen logs.

9 The relationships between H_{moss} and Hardness, and between the DRC of the
10 thickest seedling in each block and Hardness were analyzed using Spearman's rank
11 correlation coefficient to determine changes in the surface conditions of fallen logs
12 with decay. We used Hardness as an index of time lapsed after the occurrence of a
13 fallen log, because Hardness is assumed to decrease gradually with decay.

14 The effects of surface (H_{moss} , Hardness, and Area) and light conditions on N_{cs}
15 were evaluated using generalized linear models (GLM; Crawley 2002), with a neg-
16 ative binomial error structure and a log link function. The dependent variable was
17 N_{cs} ; rPPFD, H_{moss} , Hardness, Area, height of the tallest seedling or sapling on
18 each block (H_{max}), and the interaction between rPPFD and H_{max} were the indepen-
19 dent variables. We included H_{max} because the light conditions for the emergence of
20 current-year seedlings were expected to be affected by taller seedlings and saplings

1 in the block. GLMs were calibrated separately for each species to allow for compar-
2 isons. Model selection was performed using the Akaike Information Criterion (AIC)
3 in a backward elimination procedure.

4 The effects of surface (H_{moss} and Hardness) and light conditions on survival were
5 evaluated using GLMs with a binomial error structure and a logit link function. The
6 dependent variable was survival; rPPFD, H_{moss} , Hardness, initial height of each
7 seedling and sapling (H_{ini}), the differences between the height of each seedling and
8 sapling and H_{max} in each block (Shading), and the interaction of rPPFD and Shading
9 were the independent variables. Shading indicated the shading of a subject seedling
10 and sapling by taller seedlings and saplings. GLMs were calibrated separately for
11 each species to allow for comparisons. Model selection was performed using the AIC
12 in a backward elimination procedure. Furthermore, we calculated Akaike weight
13 (w) and the relative importance of variable (Burnham and Anderson 2002; Johnson
14 and Omland 2004) for comparing the importance of each variable. Akaike weight
15 is defined as $w_i = \frac{\exp(-\Delta_i/2)}{\sum_{r=1}^R \exp(-\Delta_r/2)}$, where $\Delta_i = AIC_i - AIC_{min}$ is the difference
16 between an AIC of each model and the minimum AIC among all candidate models
17 (including null model and full model). This value, referred to as the Akaike weight,
18 provides a relative weight of evidence for each model. The relative importance of
19 predictor variable can be calculated as the sum of the Akaike weights over all of
20 the models in which the parameter of interest appears. All statistical analyses were
21 performed using R (R Development Core Team 2005).

1 Results

2 Height distributions of seedlings and saplings on fallen logs

3 The numbers of current-year and other seedlings and saplings of *A. sachalinensis*
4 on the 29 fallen logs were 157/103.7 m² and 477/103.7 m², and those of *P. jezoensis*
5 were 899/103.7 m² and 1034/103.7 m², respectively. The numbers of current-year
6 and other seedlings and saplings of *P. jezoensis* were 5.7 and 2.2 times greater than
7 those of *A. sachalinensis*. The height distribution of each species showed a typical
8 L-shaped distribution (Fig. 1). However, the number of *P. jezoensis* seedlings and
9 saplings decreased more sharply with increases in height than the number of *A.*
10 *sachalinensis* seedlings and saplings.

11 The relationship between the surface conditions of fallen logs and seedling 12 and sapling size

13 H_{moss} was negatively related to Hardness (Fig. 2). Tall moss was found only on soft
14 fallen logs. The DRC of the thickest seedling or sapling was also negatively related
15 to Hardness (Fig. 3). Saplings were only found on soft fallen logs, and seedlings
16 were observed on both soft and hard fallen logs.

17 Effects of surface and light conditions on seedling emergence

18 Only Hardness and Area significantly affected the N_{cs} of *A. sachalinensis* in both
19 2004 and 2005 (Table 2). The N_{cs} of *A. sachalinensis* was low on hard and narrow

1 fallen logs.

2 Conversely, all surface conditions, except the interaction between rPPFD and
3 H_{max} , significantly affected the N_{cs} of *P. jezoensis* in both 2004 and 2005 (Table 2).
4 The N_{cs} of *P. jezoensis* was low on shaded, hard, and narrow fallen logs, and on
5 fallen logs with tall moss and tall seedling or sapling.

6 Effects of surface and light conditions on seedling and sapling survival

7 The mortality rates of *A. sachalinensis* and *P. jezoensis* seedlings were 23.6 and
8 26.8 %/year, respectively, which appeared to be higher than the mortality rates
9 of saplings (between 5 and 50 cm in height) of both species (5.4 and 3.5 %/year,
10 respectively). We therefore analyzed the effect of surface and light conditions on
11 the survival of seedlings and saplings, separately.

12 The survival of *A. sachalinensis* seedlings was significantly affected by H_{ini} ,
13 rPPFD, Shading, and the interaction between rPPFD and Shading (Table 3). The
14 effects of factors other than the interaction were positive. H_{ini} and Shading were
15 relatively important variables (Table 4). The survival of *A. sachalinensis* saplings
16 was significantly affected by H_{ini} , rPPFD, and Shading; all effects were positive (Ta-
17 ble 3). H_{ini} and rPPFD had large effect on the survival of *A. sachalinensis* saplings
18 (Table 4).

19 In *P. jezoensis*, H_{ini} , Moss, rPPFD, and Shading significantly affected the sur-
20 vival of seedlings (Table 3). Among them, H_{ini} and rPPFD substantially affected the

1 survival of *P. jezoensis* seedlings (Table 4). Only the effect of Shading was negative.
2 H_{ini} , rPPFD, and Shading greatly affected the survival of saplings, and the effects of
3 H_{ini} and rPPFD were positive. H_{ini} , rPPFD, Shading, and the interaction of rPPFD
4 and Shading had large effect on the survival of *P. jezoensis* saplings although the
5 interaction of rPPFD and Shading was not selected in the best model (Table 4).

6 Discussion

7 Effects of surface and light conditions on seedling emergence

8 Based on the height distributions (Fig. 1), the recruitment of both *A. sachalinensis*
9 and *P. jezoensis* seemed to occur continuously on the fallen logs in the investigated
10 plot. However, the sharp decrease in *P. jezoensis* seedlings and saplings may indicate
11 a lower survival rate than for *A. sachalinensis* seedlings and saplings, although the
12 observed 1-year survival rates for these species did not differ greatly.

13 H_{moss} and the DRC of the thickest seedling or sapling in each block tended to
14 increase as fallen logs became softer and older (Figs. 2, 3), indicating that the
15 surface conditions of a fallen log changes over time; *i.e.*, the logs decay.

16 The N_{cs} of both species was low on narrow and hard fallen logs (Table 2). Con-
17 cerning with the effect of a diameter of fallen log, Takahashi (1994) also recognized
18 that the number of coniferous seedlings and saplings was low on narrow fallen logs <
19 20 cm in diameter. While, with regard to the effect of Hardness of fallen logs, Iijima

1 et al. (2004) reported that the germination rate of *P. jezoensis* seeds scattered on
2 fallen logs was not affected by Hardness. Then, the small numbers of current-year
3 seedlings on hard fallen logs may have resulted from the difficulty in trapping seeds
4 on the hard log surface.

5 The N_{cs} was smaller for *P. jezoensis* on fallen logs with a thick than with a thin
6 covering of moss (Table 2), although not for *A. sachalinensis*. This species-specific
7 response to H_{moss} was assumed to have resulted from the difference in seed size be-
8 tween *A. sachalinensis* and *P. jezoensis* (mean seed mass: *A. sachalinensis*, 9.8 mg;
9 *P. jezoensis*, 2.4 mg; Asakawa 1981). Several studies have found close relationships
10 between seed size and the recruitment sites of tree species. For example, small-
11 seeded species tend to regenerate on mounded sites where the litter layer is thinner
12 than on the flat forest floor (Lusk and Kelly 2003). Furthermore, Kitabatake (2001)
13 showed that the germination rate of *P. jezoensis* is more sensitive to the thickness
14 of the litter layer than that of *A. sachalinensis*. Therefore, the emergence of *P.*
15 *jezoensis* is probably more sensitive to H_{moss} than that of *A. sachalinensis*.

16 The N_{cs} of *P. jezoensis* (but not *A. sachalinensis*) was lower on shaded fallen logs
17 and logs with tall seedlings and saplings than on logs that received a high amount
18 of light. In laboratory tests, light conditions do not affect the germination rate
19 of *P. jezoensis* (Inokuma and Asakawa 1961; Yagi et al. 1971). Furthermore, the
20 germination rate of *P. jezoensis* was independent of light conditions in a previous
21 field study (Iijima et al. 2004). One of the causes of this discrepancy between

1 our results and those of the aforementioned studies is probably the timing of the
2 investigation. We examined the N_{cs} in September, although the germination of *P.*
3 *jezoensis* began in early July (Iijima, personal observation). It is possible that some
4 of the current-year seedlings that emerged on shaded fallen logs had already died
5 by the time of the investigation in September.

6 The N_{cs} of both species increased with decreases in Hardness (Table 2), *i.e.*, with
7 the decay of fallen logs. However, H_{moss} also increased with decreases in Hardness
8 (Fig. 2), which causes unfavorable conditions for the emergence of seedlings of *P.*
9 *jezoensis* (Table 2). Therefore, suitable fallen logs for seedling emergence are more
10 severely limited for *P. jezoensis* than for *A. sachalinensis* in this natural forest.

11 **Effects of surface and light conditions on seedling and sapling survival**

12 An increase in rPPFD positively affected the survival of both species seedlings and
13 saplings (Table 3). However, the effect of rPPFD on the survival of *P. jezoensis*
14 seedlings was higher than that of *A. sachalinensis* seedlings although there was not
15 so much difference of relative importance of rPPFD in saplings (Table 4). Fur-
16 thermore, the survival of *P. jezoensis* saplings decreased with increased Shading,
17 whereas that of *A. sachalinensis* increased. Relative importance of Shading had
18 strong effect on the survival of *P. jezoensis* saplings, but not on the survival of *A.*
19 *sachalinensis* saplings (Table 4). Although the reason for the increase in survival of
20 *A. sachalinensis* with increases in Shading is unknown, these results indicate that

1 the shade tolerance of *A. sachalinensis* was higher than that of *P. jezoensis*. Some
2 previous studies in Hokkaido support this inference (Kubota et al. 1994; Kubota
3 and Hara 1996; cf., Hiura et al. 1996). Kubota and Hara (1996) suggested that
4 the shade tolerance of *P. jezoensis* was lower than that of *A. sachalinensis* because
5 the mortality rates of *P. jezoensis* (30-200 cm in height) was higher than that of
6 *A. sachalinensis* in natural coniferous forest in Hokkaido. Our results (Table 3)
7 are more reliable than those of the aforementioned studies because we measured
8 the light conditions of each block and considered the ontogeny of the seedlings or
9 saplings (Sack and Grubb 2001; Lusk 2004; Kneeshaw et al. 2006; Niinemets 2006).

10 With the exception of *P. jezoensis* seedlings, the survival of both species was
11 not affected by Hardness or H_{moss} , which were assumed to influence seedling root
12 extension. Surface conditions of fallen logs, such as Hardness and H_{moss} , had little
13 effect on the survival of the two conifers.

14 There were differences in the effects of surface and light conditions depending
15 on the seedling and sapling developmental stages (Tables 2, 3). The emergence
16 of seedlings was influenced mainly by the surface conditions of fallen logs, such as
17 Area, Hardness, and H_{moss} . However, the survival of seedlings and saplings were
18 fundamentally affected by light conditions and the size of the seedlings and saplings.
19 The discrepancy in the conditions favorable for the emergence and survival of tree
20 seedlings and saplings has been reported in previous studies (Schupp 1995; Coates
21 2002; Mori et al. 2004). Surface conditions such as Hardness and H_{moss} probably

1 only significantly affect the early developmental stage of seedlings (Bellingham and
2 Richardson 2006).

3 Consequently, we showed (1) the Area, Hardness, H_{moss} , and rPPFD influenced
4 N_{cs} , and rPPFD affected the survival of *A. sachalinensis* and *P. jezoensis*; and
5 (2) the effects of these factors were species-specific. In particular, the conditions
6 available for the emergence and survival of *P. jezoensis* were more limited than
7 those for *A. sachalinensis*. In this forest, *P. jezoensis* may mitigate its limited site
8 availability and low survival rate by having a large N_{cs} (in Results) and rapid growth
9 rate (Kubota and Hara 1996). Furthermore, if *P. jezoensis* once reach canopy layer,
10 *P. jezoensis* can stay in a stand for a longer time than *A. sachalinensis* because
11 mean life time of *P. jezoensis* is much longer than that of *A. sachalinensis* (200
12 – 400 years in *P. jezoensis* and 100 – 250 years in *A. sachalinensis*; Honda 1926;
13 Nakamura 1929). A large N_{cs} , rapid growth rate, and a long life span may make it
14 possible for *P. jezoensis* to maintain their population in natural coniferous forest.
15 A survey of seedling emergence and growth rates on fallen logs and the changing
16 rates of the surface conditions of fallen logs would allow a more precise evaluation
17 of the effects of surface and light conditions on the dynamics *A. sachalinensis* and
18 *P. jezoensis* seedlings and saplings on fallen logs in relation to the stand dynamics
19 in natural forests in Hokkaido.

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1 References

- 2 Asakawa S (1981) The seeds of Japanese trees –Conifer trees– [In Japanese]. Japan
3 Forest Tree Breeding Association, Tokyo, Japan
- 4 Bellingham PJ, Richardson SJ (2006) Tree seedling growth and survival over 6 years
5 across different microsites in a temperate rain forest. *Can J For Res* 36:910-918
- 6 Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A
7 Practical Information-Theoretic Approach. Springer USA
- 8 Christy EJ, Mack RN (1984) Variation in demography of juvenile *Tsuga heterophylla*
9 across the substratum mosaic. *J Ecol* 72:75-91
- 10 Coates KD (2002) Tree recruitment in gaps of various size, clearcuts and undisturbed
11 mixed forest of interior British Columbia, Canada. *For Ecol Manag* 155:387-398
- 12 Crawley MJ (2002) Statistical computing: An introduction to data analysis using
13 S-plus. John Wiley England
- 14 De Steven D (1994) Tropical tree seedling dynamics: recruitment patterns and their
15 population consequences for three canopy species in Panama. *J Trop Ecol* 10:369-
16 383
- 17 Graham RL, Cromack K Jr (1982) Mass, nutrient content and decay rate of dead
18 boles in rain forest canopy gaps. *Ecology* 78:2458-2473
- 19 Harmon ME (1987) The influence of litter and humus accumulations and canopy
20 openness on *Picea sitchensis* (Bong.) and *Tsuga heterophylla* (Raf.) Sarg. seedlings
21 growing on logs. *Can J For Res* 17:1475-1479
- 22 Harmon ME (1989) Retention of needles and seeds on logs in *Picea sitchensis* –
23 *Tsuga heterophylla* forests of coastal Oregon and Washington. *Can J Bot* 67:1833-
24 1837
- 25 Harmon ME, Franklin JF (1989) Tree seedlings on logs in *Picea-Tsuga* forests of
26 Oregon and Washington. *Ecology* 70:48-59
- 27 Harvey AE, Jurgensen MF, Larsen MJ, Graham RT (1987) Relationship among soil
28 microsite, ectomycorrhizae, and natural conifer regeneration of old-growth forests
29 in western Montana. *Can J For Res* 17:58-62
- 30 Hett JM (1971) A dynamic analysis of age in sugar maple seedlings. *Ecology* 52:1071-
31 1074
- 32 Hett JM, Loucks OL (1976) Age structure models of balsam fir and eastern hemlock.
33 *J Ecol* 64:1029-1044

- 1 Hiura T, Sano J, Konno Y (1996) Age structure and response to fine-scale distur-
2 bances of *Abies sachalinensis*, *Picea jezoensis*, *Picea glehnii*, and *Betula ermanii*
3 growing under the influence of a dwarf bamboo understory in northern Japan.
4 *Can J For Res* 26:289-297
- 5 Honda S (1926) Recruitment state of natural coniferous forest in Hokkaido [In
6 Japanese]. *J Jpn For Soc* 33:12-31
- 7 Iijima H, Shibuya M, Saito H, Takahashi K (2004) The effect of moss height on
8 survival and growth of *Picea jezoensis* seedlings on fallen logs [In Japanese with
9 English summary]. *J Jpn For Soc* 86:358-364
- 10 Iijima H, Shibuya M, Saito H, Takahashi K (2006) The water relations of *Picea*
11 *jezoensis* seedlings on fallen logs. *Can J For Res* 36:664-670
- 12 Inokuma T, Aasakawa S (1961) Germination behavior of *Picea jezoensis* and *Picea*
13 *glehnii* seeds [In Japanese with English summary]. *J Jpn For Soc* 43:166-168
- 14 Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends*
15 *Ecol Evol* 19:101-108
- 16 Kitabatake T (2001) The effect of the depth of litter layer and the size of seedlings on
17 the emergence and survival of seedlings [In Japanese]. *J Jpn For Environ* 43:23-26
- 18 Kneeshaw DD, Kobe RK, Coates KD, Messier C (2006) Sapling size influences shade
19 tolerance ranking among southern boreal tree species. *J Ecol* 94:471-480
- 20 Kobe RK, Pacala SW, Silander Jr JA (1995) Juvenile tree survivorship as component
21 of shade tolerance. *Ecol Appl* 5:517-532
- 22 Kubota Y, Hara T (1996) Allometry and competition between saplings of *Picea je-*
23 *zoensis* and *Abies sachalinensis* in a sub-boreal coniferous forest, northern Japan.
24 *Ann Bot* 77:529-537
- 25 Kubota Y, Konno Y, Hiura T (1994) Stand structure and growth patterns of un-
26 derstorey trees in a coniferous forest, Taisetsuzan National Park, northern Japan.
27 *Ecol Res* 9:333-341
- 28 Lusk CH (2004) Leaf area and growth of juvenile temperature evergreens in low
29 light: species of contrasting shade tolerance change rank during ontogeny. *Funct*
30 *Ecol* 18:820-828
- 31 Lusk CH, Kelly CK (2003) Interspecific variation in seed size and safe sites in a
32 temperate rain forest. *New Phytol* 158:535-541
- 33 McCullough HA (1948) Plant succession on fallen logs in a virgin spruce-fir forest.
34 *Ecology* 29:508-513

- 1 Mori A, Mizumachi E, Osono T, Doi Y (2004) Substrate-associated seedling recruit-
2 ment and establishment of major conifer species in an old-growth subalpine forest
3 in central Japan. *For Ecol Manag* 196:287-297
- 4 Nakagawa M, Kurahashi A, Kaji M, Hogetsu T (2001) The effects of selection cutting
5 on regeneration of *Picea jezoensis* and *Abies sachalinensis* in the sub-boreal forests
6 of Hokkaido, northern Japan. *For Ecol Manag* 146:15-23
- 7 Nakamura K (1929) Natural *Picea jezoensis* and *Abies sachalinensis* forest in
8 Sakhalin experimental forest [In Japanese]. *J Jpn For Soc* 11:187-194
- 9 Nakamura T (1992) Effect of bryophytes on survival of conifer seedlings in subalpine
10 forests of central Japan. *Ecol Res* 7:155-162
- 11 Narukawa Y, Yamamoto S (2002) Effects of dwarf bamboo (*Sasa* sp.) and forest
12 floor microsites on conifer seedling recruitment in a subalpine forest, Japan. *For*
13 *Ecol Manag* 163:61-70
- 14 Narukawa Y, Iida S, Tanouchi H, Abe S, Yamamoto S (2003) State of fallen logs and
15 the occurrence of conifer seedlings and saplings in boreal and subalpine old-growth
16 forests in Japan. *Ecol Res* 18:267-277
- 17 Natsume S (1985) Studies on the habitat conditions and early growth in the natural
18 regeneration of *Picea jezoensis* Carr. [In Japanese with English summary]. *Res*
19 *Bull Coll Exp For Fac Agric Hokkaido Univ* 42:47-107
- 20 Niinemets Ü (2006) The controversy over traits conferring shade-tolerance in trees:
21 ontogenetic changes revisited. *J Ecol* 94:464-470
- 22 Pinero D, Martinez-Ramos M, Sarukhan J (1984) A population model of *Astro-*
23 *caryum mexicanum* and a sensitivity analysis of its finite rate of increase. *J Ecol*
24 72:977-991
- 25 R Development Core Team (2005) R: A language and environment for statistical
26 computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-
27 900051-07-0 URL <http://www.R-project.org>.
- 28 Sack L, Grubb PJ (2001) Why do species of woody seedlings change rank in relative
29 growth rate between low and high irradiance? *Funct Ecol* 15:145-154
- 30 Schupp EW (1995) Seed-seedling conflicts, habitat choice, and patterns of plant
31 recruitment. *Am J Bot* 82:399-409
- 32 Simard MJ, Bergeron Y, Sirois L (1998) Conifer seedling recruitment in a south-
33 eastern Canadian boreal forest: the importance of substrate. *J Veg Sci* 9:575-582
- 34 Suzuki E, Ota K, Igarashi T, Fujiwara K (1987) Regeneration process of coniferous
35 forests in northern Hokkaido I. *Abies sachalinensis* forest and *Picea glehnii* forest.
36 *Ecol Res* 2:61-75

- 1 Sugita H, Tani M (2001) Differences in microhabitat-related regeneration patterns
2 between two subalpine conifers, *Tsuga diversifolia* and *Abies mariesii* on Mount
3 Hayachine, northern Honshu, Japan. *Ecol Res* 16:423-433
- 4 Sugita H, Nagaike T (2005) Microsites for seedling establishment of subalpine
5 conifers in a forest with moss-type undergrowth on Mt. Fuji, central Honshu,
6 Japan. *Ecol Res* 20:678-685
- 7 Szewczyk J, Szwagrzyk J (1996) Tree regeneration of rotten wood and on soil in
8 old-growth stand. *Vegetatio* 122:37-46
- 9 Takahashi K (1994) Effect of size structure, forest floor type and disturbance regime
10 on tree species composition in a coniferous forest in Japan. *J Ecol* 82:769-773
- 11 Takahashi M, Sakai Y, Ootomo R, Shinozaki M (2000) Establishment of tree
12 seedlings and water-soluble nutrients in coarse woody debris in an old-growth
13 *Picea-Abies* forest in Hokkaido, northern Japan. *Can J For Res* 30:1148-1155
- 14 Taylor AH (1990) Disturbance and persistence of sitka spruce (*Picea sitchensis*
15 (Bong) Carr.) in coastal forests of the pacific northwest, North America. *J Bio-*
16 *geogr* 17:47-58
- 17 Yagi K, Hatano K, Watanabe A (1971) Germination behavior of *Picea jezoen-*
18 *sis* seeds, with special reference to natural regeneration of the spruce stand [In
19 Japanese]. *J Jpn For Soc* 53:19-21

Table 1: Species composition and basal area (BA) in the investigated subplots. *, *Betula ermanii* and *Sorbus commixta*.

	Density (trees ha ⁻¹)	BA (m ² ha ⁻¹)
Total	468	45.9
<i>Abies sachalinensis</i>	244	13.6
<i>Picea jezoensis</i>	144	24.9
Broad-leaf*	80	7.5

Table 2: GLM results on the effects of surface and light conditions on the N_{cs} of *Abies sachalinensis* and *Picea jezoensis*. n.s., non-significant variable.

Dependent variable		<i>Abies sachalinensis</i>		<i>Picea jezoensis</i>	
		2004	2005	2004	2005
Regression coefficient	rPPFD	n.s.	n.s.	0.094	0.076
	Area	3.373	3.950	4.073	3.771
	Hardness	-0.017	-0.032	-0.019	-0.023
	H_{moss}	0.025	n.s.	-0.032	-0.027
	H_{max}	n.s.	n.s.	-0.012	-0.010
	$rPPFD \times H_{max}$	n.s.	n.s.	n.s.	n.s.
Error distribution		Negative binomial			
Null deviance (d.f.)		270.2 (328)	332.3 (328)	428.3 (328)	383 (328)
Residual deviance (d.f.)		214.2 (325)	247.2 (326)	317 (323)	284.1 (323)

Table 3: GLM results on the effects of surface and light conditions on survival of *Abies sachalinensis* and *Picea jezoensis*. n.s., non-significant variable. * Seedling, $H_{ini} < 5$ cm; ** Sapling, $5 \text{ cm} \leq H_{ini} < 50$ cm

Dependent variable	<i>Abies sachalinensis</i>		<i>Picea jezoensis</i>		
	Small*	Large**	Small*	Large**	
Regression coefficient	H_{ini}	0.206	0.079	0.212	0.088
	Hardness	n.s.	n.s.	n.s.	n.s.
	H_{moss}	n.s.	n.s.	0.015	n.s.
	rPPFD	0.061	0.169	0.075	0.183
	Shading	0.023	0.019	-0.006	-0.034
	rPPFD×Shading	-0.001	n.s.	n.s.	n.s.
Error structure	Binomial				
Null deviance (d.f.)	403.1 (368)	108.8 (257)	1755 (1508)	129.7 (423)	
Residual deviance (d.f.)	392.9 (364)	93.81 (254)	1710 (1504)	114.2 (420)	

Table 4: Relative importance of variables in GLM of seedlings and saplings survival of *A. sachalinensis* and *P. jezoensis*. * Seedling, $H_{ini} < 5$ cm; ** Sapling, $5 \text{ cm} \leq H_{ini} < 50$ cm

	<i>Abies sachalinensis</i>		<i>Picea jezoensis</i>	
	Seedling*	Sapling**	Seedling*	Sapling**
H_{ini}	0.79	0.78	0.99	0.82
Hardness	0.43	0.28	0.35	0.48
H_{moss}	0.30	0.34	0.45	0.29
rPPFD	0.40	0.68	1.00	0.66
Shading	0.59	0.42	0.41	0.93
rPPFD \times Shading	0.41	0.50	0.35	0.59

1 Captions

2 Figure 1. Height distributions of seedlings and saplings of *Abies sachalinensis* and

3 *Picea jezoensis* on fallen logs.

4 Figure 2. The relationship between Hardness and H_{moss} . ρ , Spearman rank correla-

5 tion coefficient. ***, $p < 0.001$.

6 Figure 3. The relationship between Hardness and DRC of the thickest seedling or

7 sapling in each block. ρ , Spearman rank correlation coefficient. ***, $p < 0.001$.

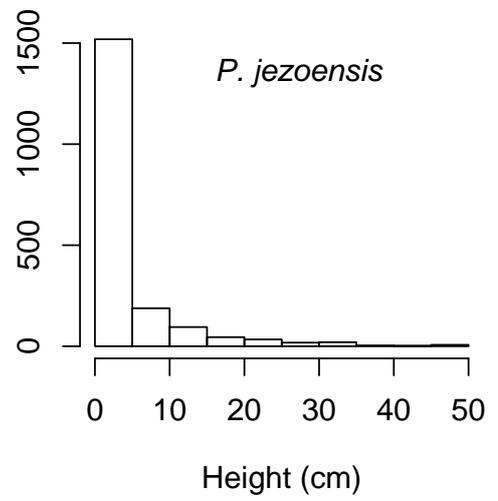
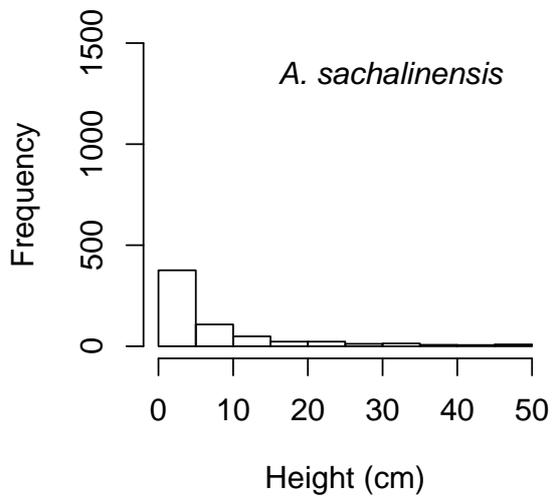


Fig. 1:

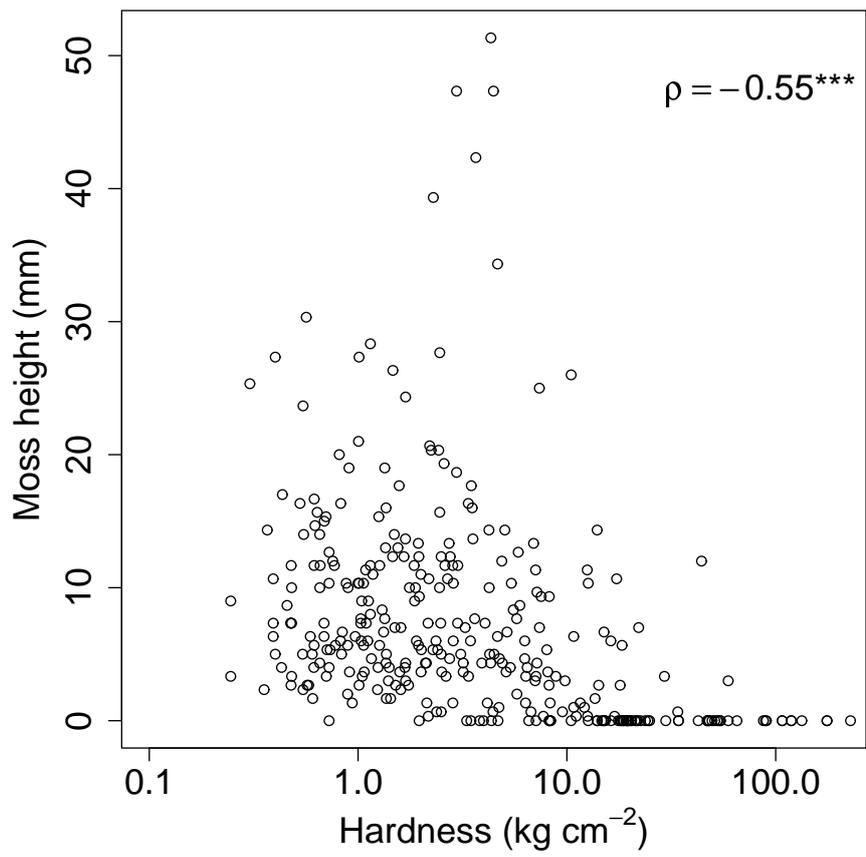


Fig. 2:

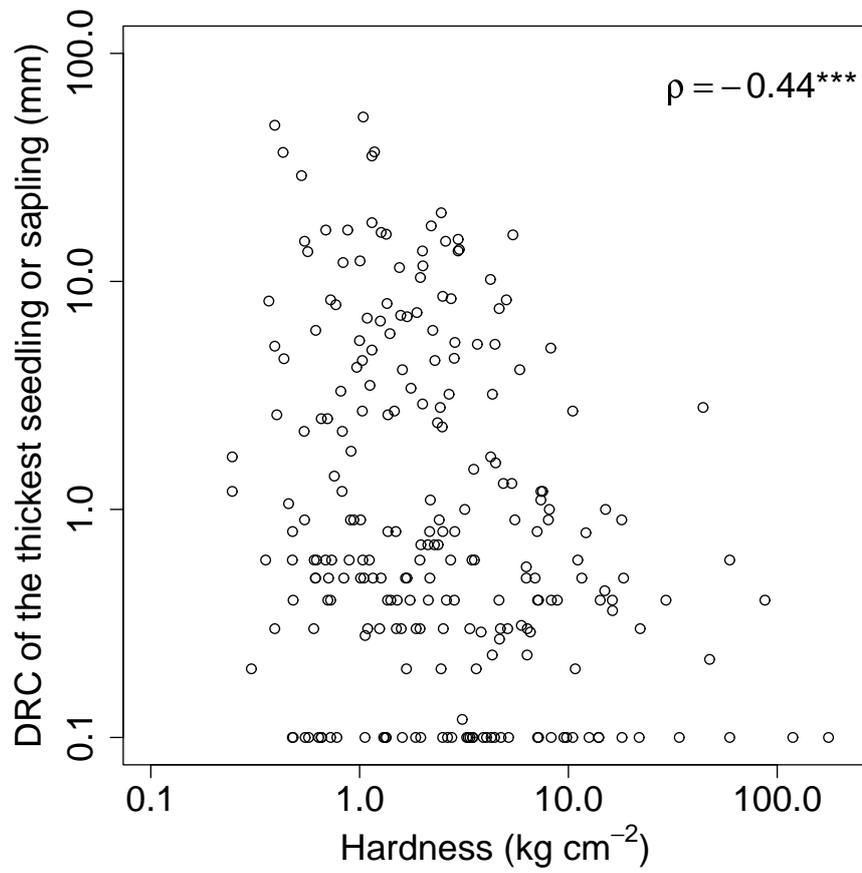


Fig. 3: