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ORIGINAL ARTICLE

Effects of surface and light conditions of fallen logs on the emergence and survival of coniferous seedlings and saplings

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

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Introduction

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

However, not all fallen logs are available for *A. sachalinensis* and *P. jezoensis* recruitment. The surface conditions of fallen logs change throughout the decay process (Graham and Cromack 1982), and differences in the surface conditions of fallen logs cause variation in seedling and sapling density (McCullough 1948; Simard et al.1998; Takahashi et al. 2000; Narukawa et al. 2003). The surface conditions of fallen logs are composed of several factors that affect *A. sachalinensis* and *P. jezoensis* seedling and sapling density. However, which of and how these factors affect seedling and sapling density has not yet been determined. Thus, the relationship between these factors and the emergence and survival of these tree species on fallen logs should be examined to understand their population dynamics in natural forests in Hokkaido.

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

For seedlings and saplings to survive on fallen logs, environmental conditions suitable for assimilation (Harmon 1987) and root growth (Iijima et al. 2004) are necessary. Iijima et al. (2004) showed that the growth of current-year seedlings of *P. jezoensis* was significantly lower on fallen logs with thick moss cover than on fallen logs with thin or no moss in a natural coniferous forest in Hokkaido. They suggested that lower seedling growth rates resulted from shading by the tall moss. Furthermore, Iijima et al. (2004) showed that 1-year-old seedlings of *P. jezoensis* on hard fallen logs had lower biomass growth and higher top/root ratios than seedlings on soft fallen logs.

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

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

Materials and methods

Study site

The study was conducted in the Hidaka region in Hokkaido, northern Japan. A permanent plot (100 × 100 m) was established in a coniferous forest in the region (42°55′N, 142°45′E; 1,038 m a.s.l.) by the Northern Hidaka District Forest Office of the Japanese National Forestry Agency in 1973. No forestry operations have been conducted in the plot since its establishment. We established a 50 × 50 m subplot within the permanent plot in 2004. The density of trees > 5 cm in diameter at breast height in the subplot was highest for *Abies sachalinensis*, but the total basal area in the subplot was largest for *Picea jezoensis* (Table 1). The canopy height of the stand was 25–30 m. The undergrowth vegetation was dominated by dwarf bamboo (*Sasa senanensis* Rehd.) and a sedge (*Carex sachalinensis* Fr. Schm. var. *sachalinensis*). Mean annual precipitation recorded at the nearest meteorological station in Hidaka (42°53′N, 142°27′E; 280 m a.s.l.) was 1,374 mm from 2001 to 2004 (http://www.data.kishou.go.jp/etrn/). The mean annual temperature of the study site was estimated from as 1.2°C based on data from the meteorological station using a lapse rate of –0.6°C per 100 m.

Measurements

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

Table 1 Species composition and basal area (*BA*) in the investigated subplots

	Density (trees ha^{-1})	BA (m^2 ha^{-1})
Total	468	45.9
Abies sachalinensis	244	13.6
Picea jezoensis	144	24.9
Broad-leaf[a]	80	7.5

[a] *Betula ermanii* and *Sorbus commixta*

In 2004, we measured moss height (H_{moss}), log hardness (Hardness), and log area (Area) for each block. We measured the photosynthetic photon flux density (PPFD) as an indicator of light availability for each block under an overcast sky from late July to early October 2005 using a pair of quantum sensors (LI250; LI-COR, Lincoln, Neb., USA). The PPFD was measured five times in an open site and at 10 cm above the highest seedling in a block simultaneously, and the mean ratio was calculated (relative PPFD: rPPFD). Hardness of each block was measured three times using a Yamanaka-type soil penetrometer (LS321; IMAI, Tokyo, Japan). Area was calculated as projected area using the top and bottom diameter of each block.

Data analysis

Fallen logs found within 10 m of trees that had died within the last 5 years were excluded from analyses regarding the effect of light conditions on N_{cs} and survival. Thus, we analyzed 29 (329 blocks, 103.7 m^2) of a total of 56 fallen logs.

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

The effects of surface (H_{moss}, Hardness, and Area) and light conditions on N_{cs} were evaluated using generalized linear models (GLM; Crawley 2002), with a negative binomial error structure and a log link function. The dependent variable was N_{cs}; rPPFD, H_{moss}, Hardness, Area, height of the tallest seedling or sapling on each block (H_{max}), and the interaction between rPPFD and H_{max}, were the independent variables. We included H_{max} because the light conditions for the emergence of current-year seedlings were expected to be affected by taller seedlings and saplings in the block. GLMs were calibrated separately for each species to allow for comparisons. Model selection was performed using the Akaike information criterion (AIC) in a backward elimination procedure.

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

Results

Height distributions of seedlings and saplings on fallen logs

The numbers of current-year and other seedlings and saplings of *A. sachalinensis* on the 29 fallen logs were 157/103.7 m^2 and 477/103.7 m^2, and those of *P. jezoensis* were 899/103.7 m^2 and 1,034/103.7 m^2, respectively. The numbers of current-year and other seedlings and saplings of *P. jezoensis* were 5.7 and 2.2 times greater than those of *A. sachalinensis*. The height distribution of each species showed a typical *L*-shaped distribution (Fig. 1). However, the number of *P. jezoensis* seedlings and saplings decreased more sharply with increases in height than the number of *A. sachalinensis* seedlings and saplings.

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

H_{moss} was negatively related to Hardness (Fig. 2). Tall moss was found only on soft fallen logs. The DRC of the thickest seedling or sapling was also negatively related to Hardness (Fig. 3). Saplings were only found on soft fallen

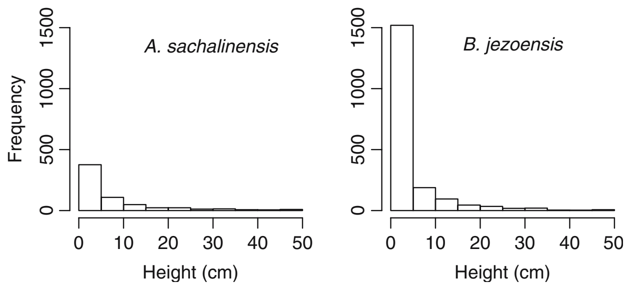

Fig. 1 Height distributions of seedlings and saplings of *Abies sachalinensis* and *Picea jezoensis* on fallen logs

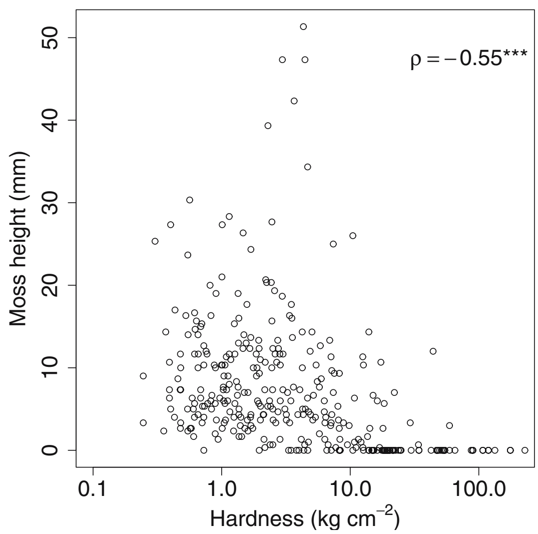

Fig. 2 The relationship between Hardness and H_{moss}. ρ Spearman rank correlation coefficient, *** $P < 0.001$

logs, and seedlings were observed on both soft and hard fallen logs.

Effects of surface and light conditions on seedling emergence

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

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

Effects of surface and light conditions on seedling and sapling survival

The mortality rates of *A. sachalinensis* and *P. jezoensis* seedlings were 23.6 and 26.8%/year, respectively, which

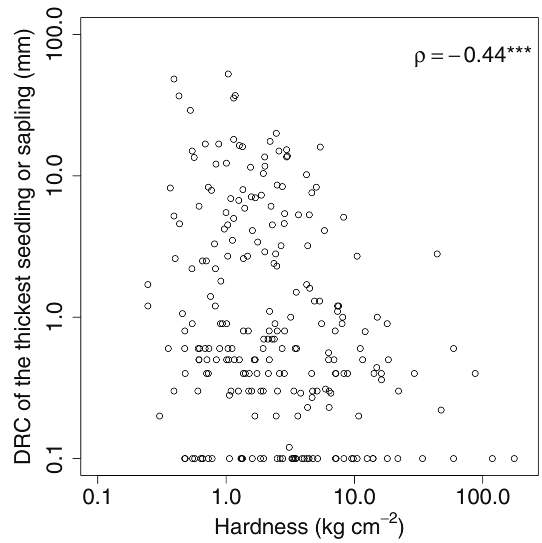

Fig. 3 The relationship between Hardness and DRC of the thickest seedling or sapling in each block. ρ Spearman rank correlation coefficient, *** $P < 0.001$

appeared to be higher than the mortality rates of saplings (between 5 and 50 cm in height) of both species (5.4 and 3.5%/year, respectively). We therefore analyzed the effect of surface and light conditions on the survival of seedlings and saplings separately.

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

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

Discussion

Effects of surface and light conditions on seedling emergence

Based on the height distributions (Fig. 1), the recruitment of both *A. sachalinensis* and *P. jezoensis* seemed to occur

Table 2 GLM results on the effects of surface and light conditions on the N_{cs} of *Abies sachalinensis* and *Picea jezoensis*

Dependent variable	*Abies sachalinensis*		*Picea jezoensis*	
	2004	2005	2004	2005
Regression coefficient				
rPPFD	NS	NS	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	NS	–0.032	–0.027
H_{max}	NS	NS	–0.012	–0.010
rPPFD × H_{max}	NS	NS	NS	NS
Error distribution (Negative binomial)				
Null deviance (*df*)	270.2 (328)	332.3 (328)	428.3 (328)	383 (328)
Residual deviance (*df*)	214.2 (325)	247.2 (326)	317 (323)	284.1 (323)

NS Non-significant variable

Table 3 GLM results on the effects of surface and light conditions on survival of *Abies sachalinensis* and *Picea jezoensis*

Dependent variable	*Abies sachalinensis*		*Picea jezoensis*	
	Small[a]	Large[b]	Small[a]	Large[b]
Regression coefficient				
H_{ini}	0.206	0.079	0.212	0.088
Hardness	NS	NS	NS	NS
H_{moss}	NS	NS	0.015	NS
rPPFD	0.061	0.169	0.075	0.183
Shading	0.023	0.019	–0.006	–0.034
rPPFD × Shading	–0.001	NS	NS	NS
Error structure (Binomial)				
Null deviance (*df*)	403.1 (368)	108.8 (257)	1,755 (1,508)	129.7 (423)
Residual deviance (*df*)	392.9 (364)	93.81 (254)	1,710 (1,504)	114.2 (420)

NS Non-significant variable

[a] Seedling, $H_{ini} < 5$ cm

[b] Sapling, 5 cm $\leq H_{ini} < 50$ cm

Table 4 Relative importance of variables in GLM of seedlings and saplings survival of *A. sachalinensis* and *P. jezoensis*

	Abies sachalinensis		*Picea jezoensis*	
	Seedling[a]	Sapling[b]	Seedling[a]	Sapling[b]
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 × Shading	0.41	0.50	0.35	0.59

[a] Seedling $H_{ini} < 5$ cm

[b] Sapling 5 cm $\leq H_{ini} < 50$ cm

continuously on the fallen logs in the investigated plot. However, the sharp decrease in *P. jezoensis* seedlings and saplings may indicate a lower survival rate than for *A. sachalinensis* seedlings and saplings, although the observed 1-year survival rates for these species did not differ greatly.

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

The N_{cs} of both species was low on narrow and hard fallen logs (Table 2). Concerning the effect of the diameter of a fallen log, Takahashi (1994) also recognized that the number of coniferous seedlings and saplings was low on narrow fallen logs < 20 cm in diameter. While with regard to the effect of Hardness of fallen logs, Iijima et al. (2004) reported that the germination rate of *P. jezoensis* seeds scattered on fallen logs was not affected by Hardness. The small numbers of current-year seedlings on hard fallen logs may have resulted from the difficulty in trapping seeds on the hard log surface.

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

The N_{cs} of *P. jezoensis* (but not *A. sachalinensis*) was lower on shaded fallen logs and logs with tall seedlings and saplings than on logs that received a high amount of light. In laboratory tests, light conditions do not affect the germination rate of *P. jezoensis* (Inokuma and Asakawa 1961; Yagi et al. 1971). Furthermore, the germination rate of *P. jezoensis* was independent of light conditions in a previous field study (Iijima et al. 2004). One of the causes of this discrepancy between our results and those of the aforementioned studies is probably the timing of the investigation. We examined the N_{cs} in September, although the germination of *P. jezoensis* began in early July (Iijima, personal observation). It is possible that some of the current-year seedlings that emerged on shaded fallen logs had already died by the time of the investigation in September.

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

Effects of surface and light conditions on seedling and sapling survival

An increase in rPPFD positively affected the survival of both species seedlings and saplings (Table 3). However, the effect of rPPFD on the survival of *P. jezoensis* seedlings was higher than that of *A. sachalinensis* seedlings although there was not so much difference in relative importance of rPPFD in saplings (Table 4). Furthermore, the survival of *P. jezoensis* saplings decreased with increased Shading, whereas that of *A. sachalinensis* increased. Relative importance of Shading had a strong effect on the survival of *P. jezoensis* saplings, but not on the survival of *A. sachalinensis* saplings (Table 4). Although the reason for the increase in survival of *A. sachalinensis* with increases in Shading is unknown, these results indicate that the shade tolerance of *A. sachalinensis* was higher than that of *P. jezoensis*. Some previous studies in Hokkaido support this inference (Kubota et al. 1994; Kubota and Hara 1996; cf., Hiura et al. 1996). Kubota and Hara (1996) suggested that the shade tolerance of *P. jezoensis* was lower than that of *A. sachalinensis* because the mortality rates of *P. jezoensis* (30–200 cm in height) was higher than that of *A. sachalinensis* in natural coniferous forest in Hokkaido. Our results (Table 3) are more reliable than those of the aforementioned studies because we measured the light conditions of each block and considered the ontogeny of the seedlings or saplings (Sack and Grubb 2001; Lusk 2004; Kneeshaw et al. 2006; Niinemets 2006).

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

There were differences in the effects of surface and light conditions depending on the seedling and sapling developmental stages (Tables 2, 3). The emergence of seedlings was influenced mainly by the surface conditions of fallen logs, such as Area, Hardness, and H_{moss}. However, the survival of seedlings and saplings were fundamentally affected by light conditions and the size of the seedlings and saplings. The discrepancy in the conditions favorable for the emergence and survival of tree seedlings and saplings has been reported in previous studies (Schupp 1995; Coates 2002; Mori et al. 2004). Surface conditions such as Hardness and H_{moss} probably only significantly affect the early developmental stage of seedlings (Bellingham and Richardson 2006).

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

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