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Author(s)	Iijima, Hayato; Shibuya, Masato
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Title: Evaluation of suitable conditions for natural regeneration of *Picea jezoensis* on fallen logs

Authors: Hayato Iijima[1), *] and Masato Shibuya[2)]
Address: 1) Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan

Corresponding author
Name: Hayato Iijima
Address: Graduate School of Agriculture, Hokkaido University, Sapporo 060-8589, Japan
TEL: +81-11-706-4180
FAX: +81-11-706-3346
E-mail: hayato.iijima@gmail.com
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*Present address: Yamanashi Forest Research Institute, 2290-1, Saishoji, Masuho, Yamanashi 400-0502, Japan.
TEL: +81-556-22-8001
FAX: +81-556-22-8002

Abstract

The abundance of *Picea jezoensis*, a major conifer tree species in Hokkaido, northern Japan, is currently decreasing due to the lack of suitable conditions for recruitment and intensive harvests. To contribute to the development of sustainable forest management in Hokkaido, suitable substrates for natural regeneration of *P. jezoensis* were evaluated during a 4-year experimental study using seed additions in a natural coniferous forest. The environmental conditions (moss height, log hardness, extent of the humus layer, and light conditions) of fallen logs were measured. Moss height was categorized into three groups: 0 mm, Bark; 0 – 20 mm, Mthin; and ≥ 20 mm, Mthick. The germination rates of *P. jezoensis* were highest on Mthin, intermediate on Bark, and lowest on Mthick. Survival rates were low on Mthick, did not differ between Bark and Mthin, and increased with enhanced light. Growth increased with light, but the root allocation of seedlings was not affected by any environmental conditions. From these results, we determined that fallen logs with no or thin moss cover under bright conditions were most suitable for *P. jezoensis* regeneration. We discussed the generality of our results in relation to a co-occurring tree species in Hokkaido and the results of other regions.

Keywords: Fallen logs; Light conditions; Log hardness; Moss height; *Picea jezoensis*

Introduction

In boreal forests, fallen logs are recognized as favorable substrates for tree regeneration, as the seedlings of many tree species establish on these microenvironments (Harvey 1987; Taylor 1990; Sugita and Nagaike 2005). However, because several studies have reported large variations in seedling densities on fallen logs, not all fallen logs provide safe regeneration sites (McCullough 1948; Simard et al. 1998; Narukawa et al. 2003). For tree regeneration, the limitations in establishment (substrate) conditions are equally or sometimes even more important than the limitations in seed sources (dispersion of adults, adult fecundity, or dispersal distances of seeds; Clark et al. 1998; LePage et al. 2000; Astrup et al. 2008). Therefore, clarification of suitable establishment conditions of fallen logs is crucial for promoting natural regeneration in boreal forests.

There are two problems to clarify suitable establishment condition of fallen logs for trees species. One problem is the adoption of "decay rate" as the indices of environmental conditions. Previous studies have used decay rates to evaluate the effect of environmental conditions of fallen logs on tree regeneration (McCullough 1948; Graham and Cromack 1982; Christy and Mack 1984; Simard et al. 1998; Narukawa et al. 2003) with the exceptions of Harmon (1989) and Harmon and Franklin (1989). However, the decay rates were determined qualitatively using shape and other non-quantitative factors. The environmental conditions of fallen logs should instead be assessed using a quantitative and biologically more meaningful index. The other one is the shortage of seed additional study. Seed scatter, which can exclude the effects of the competition with larger saplings and the limitation of seed supply, are necessary to precisely determine the suitable conditions of fallen logs for seedling dynamics.

Specific environmental conditions were suggested to affect the establishment of tree species on fallen logs. Furthermore, the suitable conditions differed even among germination, survival and growth of seedlings (Schupp 1995; Makana and Thomas 2004; Mori et al. 2004; Caspersen and Saprunoff 2005; Bellingham and Richardson 2006). For successful germination, seeds must extend their roots into Humus-layer on fallen logs, which consists from inner bark and decomposed moss and logs (Nakamura 1992), and suck up water. However, fallen logs are harder substrate than soil, and vertical root extension of seedlings is inhibited on logs (Narukawa and Yamamoto 2003; Doi et al. 2008). It was suggested that the radicle extension of germinated seeds was difficult on recently fallen (*i.e.* hard) logs (Narukawa et al. 2003). Fallen logs with moss harbor more moisture than those without moss (Takahashi et al. 2000; Iijima et al. 2006), but a thick covering of moss can prevent root extension into the humus layer (Nakamura 1992). Such masking effect of moss or litter on water source is usually strong for small-seeded species (Lusk and Kelly 2003). Consequently, the condition that is easy for seeds to extend their radicles is favourable for successful germination. However, the effects of each environmental condition were not evaluated at the same time in previous studies because of the usage of decay rate or the measurement of one of the environmental conditions.

Especially, the amount of Humus was rarely determined in previous studies.

With respect to survival and growth of seedlings, light condition is the important factor. Bright condition will enhance the survival and growth of seedlings on fallen logs (Iijima et al. 2007). A thick covering of moss can shade small seedlings, which causes the mortality of seedlings on fallen logs (Harmon and Franklin 1989; Iijima et al. 2004). Harmon and Franklin (1989) proposed 5 cm of moss as the crucial height for the survival of *Picea sitchensis* and *Tsuga heterophylla*. However, too bright condition inhibits the survival of seedlings on fallen logs (Harmon 1987) and the crucial height of moss in relation to the shade of seedlings differs depending on the initial size of species (Nakamura 1992). Therefore, suitable condition for survival and growth of seedlings on fallen logs should be examined in the targeting species.

In Hokkaido, northern Japan, conifer tree species often regenerate on fallen logs (Kubota et al. 1994). The conifer *Picea jezoensis* Carr cannot regenerate on the forest floor and regenerates exclusively on fallen logs (Takahashi 1994; Narukawa et al. 2003); thus, substrate limitation is the primary limiting factor in the natural regeneration of *P. jezoensis* (Kubota and Hara 1996b). Recruitment limitation, intensive harvesting, and difficulty of plantation have led to sharp decreases in the populations of *P. jezoensis* (Koshika 1995; Koshika and Seino 1996). Furthermore, *P. jezoensis* compete with *Abies sachalinensis*, which also regenerates on fallen logs in Hokkaido (Kubota et al. 1994; Takahashi 1994; Narukawa et al. 2003; Iijima et al. 2007). Therefore, suitable environmental conditions for *P. jezoensis* on fallen logs must be examined in relation to *A. sachalinensis* for the conservation and promotion of the natural regeneration of this species.

Consequently, the objective of this study was to determine suitable conditions for the establishment of *P. jezoensis* on fallen logs. We measured the quantitative environmental conditions of fallen logs, germination rates, survival rates, growth, and root allocation of seedlings on fallen logs for 4 years after experimental seed addition; this approach make it possible to evaluate the effects of each environmental condition on the establishment of seedlings on fallen logs quantitatively which was impossible in previous studies. Our results will contribute to promote natural tree regeneration and develop sustainable forest management systems in Hokkaido.

Materials and Methods

Study site

The study was conducted in a coniferous forest of the Taisetsuzan National Park in central Hokkaido, northern Japan (43º 39' N, 143º 06' E, 950m a.s.l.). A permanent plot (100 × 200 m) was established by the Hokkaido Research Center of the Forestry and Forest Products Research Institute (FFPRI), Hitsujigaoka, Sapporo, Japan. The tree density and total basal area (BA) of trees greater than 5 cm in diameter at breast height (DBH) in the plot were 642 trees ha^{-1} and 53.8 m^{2} ha^{-1}, respectively. *Picea glehnii*

Masters, *P. jezoensis*, *Abies sachalinensis* Masters and broadleaved trees accounted for 43, 29, 28, and 0.1 % of the BA, respectively. The canopy height of the stand was 25-30 m, and ground vegetation was dominated by dwarf bamboo (*Sasa senanensis* Rehd). Because no forestry operations have occurred in the plot since a strong typhoon in September 1954, many fallen logs are scattered throughout the plot. The mean annual precipitation at the nearest meteorological station in Sou-unkyo (43º54'N, 142º55'E; 540 m a.s.l.) during the research period (2003 – 2006) was 1,423 mm (Japan Meteorological Agency; http://www.data.jma.go.jp/obd/stats/etrn/index.php). The mean air temperature recorded at the study site by a thermo-humidity sensor (RS-10, Espec Mic. Co., Aichi, Japan) during July and October of the research period (2003 – 2006) was 11.9 ºC

Log selection

In May 2003, we selected 26 fallen logs for seed additions and measurements of environmental conditions. In this site, the surface area of fallen logs occupied only 4.4 % of the forest floor (Narukawa et al. 2003), which is relatively small value in boreal forests (6.0–11.0 %, Graham and Cromack 1982; 6.0 %, Christy and Mack 1984; 6.5-9.8 %, Spies et al. 1988; 9.9 %, Harmon 1989; 2.6-6.0 %, Takahashi 1994). To include a variety of environmental factors in the study, we selected seven logs with no moss (Bark), ten with thin (< 20 mm; Mthin) moss cover, and nine with thick (≥ 20 mm; Mthick) moss cover. Log species of Mthin and Mthick could not be identified, however, those of Bark were limited to *P. glehnii* or *P. jezoensis* with bark because the bark of these species had many cracks that prevented our scattered seeds from falling off before germination. Moss cover was used as the basis for the selection of fallen logs because the environmental conditions of these substrates vary with the extent of moss cover (Iijima et al. 2007). Furthermore, Iijima et al. (2004) reported sharp decreases in the germination of *P. jezoensis* on fallen logs with moss cover thicker than 20 mm. The dominated moss species in Mthin and Mthick were *Campylium squarrosulum* (Broth & Card.) Kanda and *Hylocomium splendens* (Hedw.) Schimp. or *Pleurozium schreberi* (Brid.) Mitt., respectively. A 15 × 15-cm quadrat was established on each fallen log by tagging pink tapes on the surface of the log at the same time of the selection of fallen logs.

Measurements

Environmental conditions of fallen logs

The moss height (Hmoss), log hardness (Hardness), amount of humus layer (Humus), and photosynthetic photon flux density (PPFD) were measured on sampled quadrats. Hmoss was categorized into three groups as stated above (0 mm, Bark; 0-20 mm, Mthin; and ≥ 20 mm, Mthick). Hardness was measured three times using a Yamanaka-type soil penetrometer (LS321; Imai, Tokyo, Japan). Humus was measured as the dry mass of the humus layer per unit area. The humus layer just beside the quadrat on each fallen log was dug out after the removal of bark and moss. The harvested humus layers were dried at

105 ºC for 72 h and weighed. The PPFD was measured under an overcast sky in early September 2006 using a pair of quantum sensors (LI250; LI-COR, Lincoln, NE, USA). The PPFD was measured five times, each time simultaneously in an open site and at 10 cm above the surface of each fallen log. The mean ratio of relative PPFD: rPPFD was calculated.

Seedling dynamics

One hundred seeds of *P. jezoensis* were sown within the 15 × 15-cm quadrat of each fallen log in May 2003. Germinated seedlings were tagged once per week until October 2003. Therefore, tagged seedlings were the same age and they were emerged during growing season of 2003. The survival of the tagged seedlings was surveyed weekly from May to October 2003 and monthly from May 2004 to October 2006. The observation interval for current-year (*i.e.*, 2003) seedlings was short because the monitoring of germination (during the growing season of 2003) was conducted once per week.

Ten surviving seedlings on each fallen log were harvested very carefully, including the roots, in October 2006. If there was any loss of roots in the harvested seedling, the seedling was not included in the analysis. All seedlings were harvested from fallen logs for which the number of surviving seedlings was less than 10. The harvested seedlings were separated into needles, branches, and roots. These organs were dried at 70 ºC for 48 h and weighed.

Statistical analysis

The effects of environmental conditions on the germination rate, survival rate, seedling growth (seedling mass), and root allocation were analyzed using a hierarchical Bayes model. In all analyses, Hmoss, Hardness, and rPPFD were included as fixed effects. Humus was excluded from the analyses because this variable was strongly correlated to Hardness (see Fig. 1). The model structures of all analyses were as follows:

Germination rate ~ Binomial(p), $p = 1/\{1 + \exp[-(\beta_1 * \text{Hmoss} + \beta_2 * \text{Hardness} + \beta_3 * \text{rPPFD})]\}$

We assumed that the germination rate followed a binomial distribution of probability p. βs are coefficients of fixed effects. β_1 was divided into β_{11} and β_{12}, which correspond to coefficients of Mthin and Mthick because the coefficient of Hmoss was calculated as a relative value when the coefficient of Bark was set to 0.

Survival rate ~ Binomial(p), $p = 1/\{1 + \exp[-(\beta_1 * \text{Hmoss} + \beta_2 * \text{Hardness} + \beta_3 * \text{rPPFD})]\}$

We assumed that the survival rate followed a binomial distribution of probability p. βs are the same as above.

Seedling growth ~ Normal(μ, $1/\tau$), $\log(\mu) = \beta_1 * \text{Hmoss} + \beta_2 * \text{Hardness} + \beta_3 * \text{rPPFD} + r$

We assumed that the seedling mass followed a Gaussian (normal) distribution of mean μ and variance $1/\tau$. We used a log-link function to estimate the mean parameter μ, because the seedling mass was log-normally distributed. βs are as above, and r is a random effect of fallen logs. Because the mean parameter μ of seedling growth was expected to be affected by random effects derived from each fallen log, the random effect parameter of each fallen log is incorporated into the statistical model of seedling growth.

Root mass ~ Normal(μ, $1/\tau$), $\log(\mu) = \alpha$ * Seedling mass, $\alpha = 1/\{1 + \exp[-(\beta_1$ * Hmoss + β_2 * Hardness + β_3 * rPPFD + d * Seedling mass + $r)]\}$

We assumed that the root mass of a seedling followed a Gaussian distribution of mean μ and variance $1/\tau$. We used a log-link function for the estimation of the mean parameter μ, because root mass was log normally distributed. βs and r are the same as in the models of germination rate and seedling growth, respectively. α is the allocation ratio of root mass to whole seedling mass. To set the range of α between 0 and 1, we used a logit-link function to estimate the allocation ratio parameter α; $\alpha = 1$ indicates that a seedling fully allocates its resources to its root. d is the ontogenetic effect on root allocation (*i.e.*, α) and was incorporated into the model because ontogenetic changes of allocation to roots have been observed in many previous studies (*e.g.*, Walters and Reich 1999).

The priors for fixed effect parameters are non-informative Gaussian distributions, and those of random-effect parameters are Gaussian distributions of mean 0 and variance

$1/\tau$. The variance parameter τ is referred to as a hyperparameter of which the prior distributions are non-informative Gamma distributions, because the inverse-Gamma distribution is the conjugate prior for the variance (Dietze et al. 2008). Prior and hyperprior distributions of all of these parameters are listed in Table 1.

Bayesian inference with Markov Chain Monte Carlo (MCMC) simulations (McCarthy 2007) was used to estimate parameters and test for significance. The posterior samples were obtained using three independent MCMC samplings, in each of which 900 values were sampled with a 10-step interval after 1000 burn-in MCMC steps. For calculations, we used WinBUGS ver. 1.4 (Spiegelhalter et al. 2003) through R2WinBUGS (Sturtz et al. 2005) in R (R Development Core Team 2008). The mean value of posterior samples was adopted as an estimated parameter. An estimated coefficient was considered significant if 95 % of the credible interval of the coefficient did not overlap 0.

Results

The relationships among the environmental conditions are presented in Fig. 1. Hardness decreased with Hmoss, whereas Humus increased with Hmoss. Therefore, there was negative relationship between Hardness and Humus. rPPFD decreased slightly with Hmoss.

Germination and survival dynamics were shown for each moss category (Fig. 2).

Germination began in early July 2003 and was nearly complete in October 2003. Seedling mortality was intense during the first two years of the study (2003 and 2004). Sharp decreases in the survival of 1-year-old (2004) seedlings were only observed on Mthick.

Germination was significantly affected by all environmental conditions (Table 2). Germination rates varied with Hmoss (Mthin > Bark > Mthick), increased with Hardness, and decreased with rPPFD (Fig. 3). However, the effects of Hardness and rPPFD on germination were not as strong as those of Hmoss (Fig. 3). The survival rate of seedlings over the 4-year study was significantly affected by Hmoss and rPPFD (Table 2). The survival rates increased with rPPFD and were low on Mthick (Fig. 4). The seedling mass increased with rPPFD (Table 3; Fig. 5). The root allocation of the seedlings was not affected by any of the environmental factors (Table 3).

Discussion

Suitable conditions of fallen logs for regeneration

The suitable conditions for the regeneration of *P. jezoensis* evaluated using decay rates have differed across studies (Haruki 1982; Takahashi et al. 2000; Narukawa et al. 2003). For example, Haruki (1982) showed the seedling density of *P. jezoensis* was highest on decay rate I; however, Takahashi et al. (2000) claimed that the seedling density of *P. jezoensis* was highest on decay rate III. Furthermore, because the definition of the decay rate is qualitative and differs among studies (Graham and Cromack 1982; Taylor 1990;

Simard et al. 1998; Lee and Sturgess 2001), its value for a particular fallen log is researcher-dependent and therefore unreliable.

The germination rate of *P. jezoensis* was low on Mthick (Fig. 3). Iijima et al. (2007) reported that low germination rates in Mthick were likely caused by the interference of thick moss with the radicle extension of germinated seeds attempting to reach the humus layer for access available water. In contrast, seeds were able to germinate on Bark and germination rates were higher on Bark than on Mthick (Fig. 3). This result counters the conclusions of previous studies that germination on fresh, hard logs with no moss is difficult: in the studies of Takahashi et al. (2000) and Narukawa et al. (2003), few current-year seedlings were found on such substrates. One possibility of the difference between our result and previous studies is the experimental design. We added a certain number of seeds on each fallen log. However, previous studies targeted naturally regenerated seedlings. It was difficult to distinguish the effects of environmental conditions of fallen logs and the limitation of seed supply on the number of germinated seeds in such situation. The other possibility is the presence and type of bark of fallen logs (Harmon 1989; Narukawa et al. 2003). Seed entrapment was affected by the surface morphology of substrate (Chambers 1991). In this study, we used fallen logs with bark of *Picea* species as Bark and never used fallen logs with no bark or bark of other species like *Abies sachalinensis* or *Betula ermanii*. The bark of *Picea* species had many cracks and prevented our scattered seeds from falling off before germination. In contrast, fallen logs with no bark or the bark of *A. sachalinensis* or *B. ermanii* are flat and difficult to trap seeds. In natural forests, there are fallen logs with no bark which might be occurred standing dead of the trees or bark sliding off after they were fallen on soil and fallen logs with bark of *A. sachalinensis* or *B. ermanii*. Although no information about the presence and type of bark was available in Takahashi et al. (2000) and Narukawa et al. (2003), the presence and type of bark can affect the results of them. Therefore, our approach evaluated the substrate conditions more reliably than previous studies (Takahashi et al. 2000; Narukawa et al. 2003). Furthermore, even though fallen logs with no moss (Bark in this study) were hard, they harboured similar (small) amounts of humus as logs with Mthin (Fig. 1), indicating that a water source was available to germinated seeds even on recently fallen logs. However, fallen logs with no moss lost water more readily than those with moss cover (Iijima et al. 2006). Because water conditions strongly affect seed germination (Facelli and Chesson 2008; Daws et al. in press), differences in the germination rates on Bark and Mthin may have been caused by differences in moisture.

Hardness positively affected the germination rate (Table 2). However, it is difficult to consider the positive effect of Hardness on germination rate biologically and visually (Fig. 3). One of the causes of this phenomenon might be too strong effect of moss category. Germination rate was especially low on Mthick (Figure 3) and Hardness of Mthick was also lowest among fallen logs of moss category. The low germination rate at low value of Hardness might cause the detection of positive effect of Hardness on germination rate. It seems more appropriate to interpret that the result indicates that Hardness is not important factor for germination on fallen logs with bark.

The survival rates did not differ between fallen logs with Bark and Mthin, but were extremely low on Mthick (Fig. 4). Seedlings on fallen logs with thick moss cover can be shaded by the moss (Harmon and Franklin 1989). In a subalpine natural coniferous forest in central Japan, Nakamura (1992) attributed the lower survival rates of *Tsuga diversifolia* seedlings (compared to those of *Abies veitchii*) to its lower mean height relative to that of the moss on fallen logs (the mean height of *A. veitchii* was similar to that of the moss). The mean height of current-year seedlings of *P. jezoensis* in a natural coniferous forest in Hokkaido was 2.0 cm, suggesting that *P. jezoensis* seedlings experience difficulty surviving on fallen logs with thick moss cover over 20 mm (Iijima et al. 2004). The observation that strong mortality of 1-year-old (*i.e.* 2004) seedlings only occurred on Mthick (Fig. 2) further supports the hypothesis that small seedlings are shaded by a thick moss cover.

At this study site, the seedling survival rates increased with the rPPFD in the range from 5 to 26 % (Fig. 4). Increases in light availability are typically important for the survival of seedlings in temperate or subalpine forests (Makana and Thomas 2004; Bellingham and Richardson 2006). However, brighter conditions may also inhibit the survival of seedlings on fallen logs. Harmon (1987) demonstrated that the survival of *Picea sitchensis* on fallen logs in Oregon increased with the canopy opening up to 33 %

of open sky but decreased with canopy openings above the level, perhaps due to desiccation in high-light conditions. Accordingly, assessments of suitable light conditions for seedling survival on fallen logs should consider both the climate of the region (Heinemann and Kitzberger 2006) and species-specific traits, such as light demands and water-use properties (Battaglia et al. 2000; Gómez-Aparicio et al. 2008).

The growth of *P. jezoensis* seedlings increased with rPPFD but was not affected by the other environmental conditions of the fallen logs on which they grew (Table 3; Fig. 5). Furthermore, the root allocation of the seedlings was also unaffected by the all measured environmental factors (Table 3) and the seedling survival was not affected by Hardness (Table 2). Therefore, the growth of seedlings on fallen logs was primarily affected by light conditions even on recently fallen, fresh, and hard logs.

The most suitable conditions for *P. jezoensis* seedlings differed for their germination, survival, growth, and root allocation. The most critical factor for seedlings might shift from water uptake via sufficient root extension to light interception via bright conditions or release from moss shading. Consequently, fallen logs with no or thin moss cover under high-light conditions were most suitable for the recruitment of *P. jezoensis* although fallen logs with no moss is available only when there is the bark of *Picea* species.

Implications for promoting natural regeneration

In natural forests, various species compete with each other for similar environmental conditions. Thus, the suitable environmental conditions described above may not necessarily lead to substantial natural regeneration of *P. jezoensis*.

On fallen logs with thin moss cover, *P. jezoensis* is likely to intensively compete with *Abies sachalinensis*, which is co-occurring tree species with *P. jezoensis* in natural coniferous forests of Hokkaido, because *A. sachalinensis* regenerate on fallen logs (Kubota et al. 1994; Takahashi 1994; Narukawa et al. 2003; Iijima et al. 2007). Furthermore, the germination of *A. sachalinensis* was less affected by thick moss or litter cover than that of *P. jezoensis* (Kitabatake 2001; Iijima et al. 2007) and the shade tolerance of *A. sachalinensis* is higher than that of *P. jezoensis* (Kubota et al. 1994; Kubota and Hara 1996a; Iijima et al. 2007). However, recently fallen logs with little to no moss cover harbor many germinated seedlings of *P. jezoensis* but not of *A. sachalinensis* (Iijima et al. 2007). It takes several years to emerge moss on fallen logs after the occurrence of fallen logs (Hövemeyer and Schauermann 2003). Unlike *Picea* species, *Abies* species tend to have difficulty establishing on less vegetated substrates, such as fallen logs with no moss (Knapp and Smith 1982; LePage et al. 2000; Astrup et al. 2008). Because *P. jezoensis* exhibits intermediate germination rates (Fig. 3), high survival rates (Fig. 4), and minimal competition with *A. sachalinensis* on recently fallen logs with no moss, recently fallen logs with no moss potentially provide the most suitable substrates for *P. jezoensis*. Accordingly, *P. jezoensis* can occupy its suitable but limited condition by establishment on fallen logs located under bright condition soon after the emergence of them; while *A. sachalinensis* is suggested to be able to maintain its populations by the adaptation to broader environmental conditions including fallen logs with thick moss cover and shaded conditions even if *P. jezoensis* already establishes on the recruitment site.

In conclusion, recently fallen logs with no moss or thin moss cover (under 20 mm in height) and sited in bright conditions appear to be the most suitable substrates for the regeneration of *P. jezoensis*. The suitable conditions we showed indicate that naturally fallen or artificially cut logs are available to *P. jezoensis* soon after the emergence of fallen logs. In future studies, modelling of temporal change of environmental conditions of fallen logs should be conducted. The modelling will contribute to precise prediction of natural regeneration of *P. jezoensis* make planned forest management of forests in Hokkaido.

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Tables

Table 1 Definitions of prior distribution of parameters. The ‘distribution’ column shows the name of the probability distribution used as the prior distribution for each parameter. The ‘mean’ and ‘variance’ columns show the mean and variances of the posterior distribution, respectively.

Parameters		Distribution	Mean	Variance
β_{11}	Mthin (fixed effect)	Gaussian	0	10^3
β_{12}	Mthick (fixed effect)	Gaussian	0	10^3
β_2	Hardness (fixed effect)	Gaussian	0	10^3
β_3	rPPFD (fixed effect)	Gaussian	0	10^3
r	Fallen logs (random effect)	Gaussian	0	$1/\tau_r$
α	Allocation ratio of root	Gaussian	0	10^3
d	Ontogenetic effect (fixed effect)	Gaussian	0	10^3
τ_r	Variance parameter of r	Gamma	1	10^3

Table 2 Summary of posterior samples of environmental conditions for the analyses of germination and survival of *P. jezoensis* evaluated by hierarchical Bayes model.

Parameters	Germination			Survival		
	Mean	2.5 %*	97.5 %**	Mean	2.5 %	97.5 %
β_{11} Mthin (fixed effect)***	1.23	0.80	1.75	n.s.		
β_{12} Mthick (fixed effect)	-0.67	-1.24	-0.10	-2.06	-3.43	-0.76
β_2 Hardness (fixed effect)	0.03	0.01	0.04	n.s.		
β_3 rPPFD (fixed effect)	-0.04	-0.06	-0.02	0.13	0.09	0.18

n.s. indicates 95 % of credible interval of a parameter overlapped 0. *, **; 2.5 % and 97.5 % points of credible intervals of posterior samples. ***; coefficients of Hmoss were calculated as relative values when the coefficient of Bark was set to 0.

Table 3 Summary of posterior samples of environmental conditions for the analyses of growth and root allocation of *P. jezoensis* evaluated by hierarchical Bayes model.

Parameters		Growth			Root allocation		
		Mean	2.5 %*	97.5 %**	Mean	2.5 %	97.5 %
β_{11}	Mthin (fixed effect)***	n.s.			n.s.		
β_{12}	Mthick (fixed effect)	n.s.			n.s.		
β_2	Hardness (fixed effect)	n.s.			n.s.		
β_3	rPPFD (fixed effect)	0.08	0.02	0.15	n.s.		
d	Ontogenetic effect (fixed effect)	—			n.s.		

n.s. indicates 95 % of credible interval of a parameter overlapped 0. *, **; 2.5 % and 97.5 % points of credible intervals of posterior samples. ***; coefficients of Hmoss were calculated as relative values when the coefficient of Bark was set to 0.

Figure captions

Figure 1: Boxplots of environmental conditions of fallen logs.
(a), The relationship between moss category and Hardness; (b), moss category and Humus; (c), moss category and rPPFD.

Figure 2: Germination and survival dynamics of seedlings.
(a), Bark; (b), Mthin; (c), Mthick; Empty circle indicates the total number of germinated seeds at each point from the start of germination in each moss category (Bark, Mthin, and Mthick) and filled circle indicates the total number of seedlings in each moss category. Then, the difference in open and filled circles indicates the mortality number of seedlings. The dynamics during current-year (left side of each figure) was expanded.

Figure 3: Effects of environmental conditions on germination rate on fallen logs.
(a), The effect of moss category; (b), The effect of Hardness; (c), The effect of rPPFD on germination rate; □, Bark; ○, Mthin; △, Mthick

Figure 4: Effects of moss height and light condition on survival of seedlings on fallen logs.
Legends of figure are the same as Figure 3. Solid, dashed, and doted lines indicate predicted regression line of Bark, Mthin, and Mthick for survival rate, respectively. The regression parameters of this figure were shown at Table 2.

Figure 5: Effect of light condition on growth of seedlings on fallen logs.
Legends of figure are the same as Figure 3. Solid line denotes predicted regression line for growth of seedlings. The regression parameters of this figure were shown at Table 3.

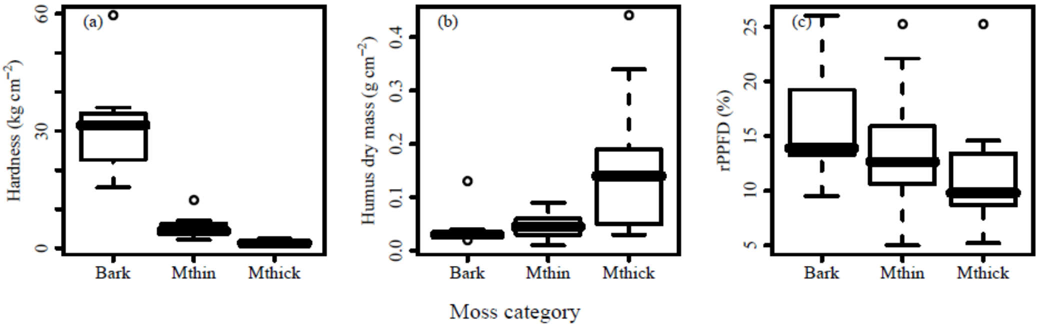
(a)
Hardness (kg cm^{-2})
0
30
60
Bark
Mthin
Mthick
(b)
Humus dry mass (g cm^{-2})
0.0
0.1
0.2
0.3
0.4
Bark
Mthin
Mthick
(c)
rPPFD (%)
5
10
15
20
25
Bark
Mthin
Mthick
Moss category

Figure 1

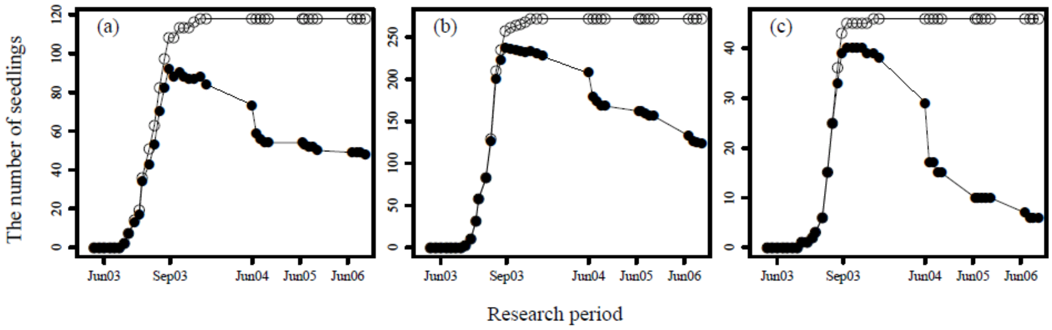
(a)
(b)
(c)
The number of seedlings
Research period
0
20
40
60
80
100
120
0
50
100
150
200
250
0
10
20
30
40
Jun03
Sep03
Jun04
Jun05
Jun06

Figure 2

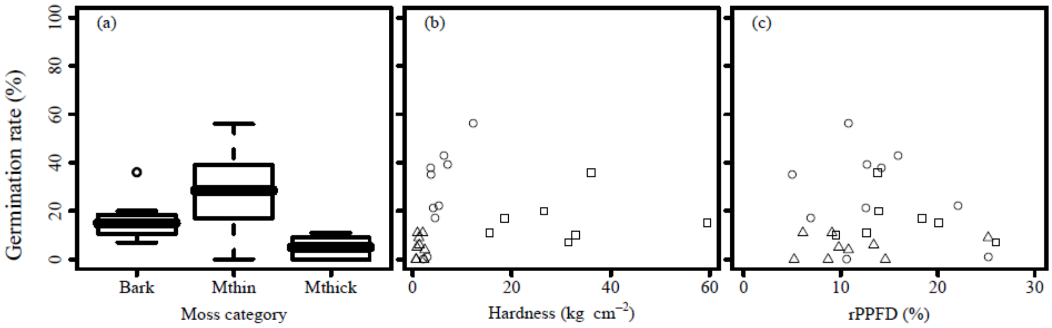
(a)
(b)
(c)
Germination rate (%)
0
20
40
60
80
100
Bark
Mthin
Mthick
Moss category
0
20
40
60
Hardness (kg cm^{-2})
0
10
20
30
rPPFD (%)

Figure 3

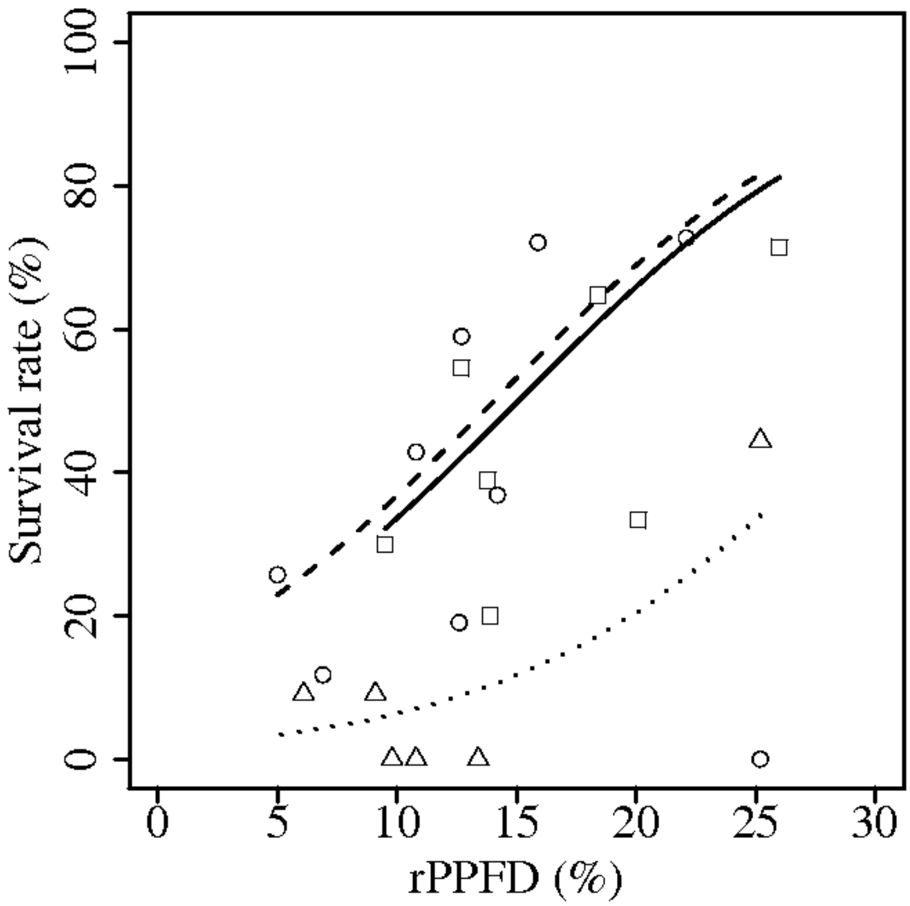

Figure 4

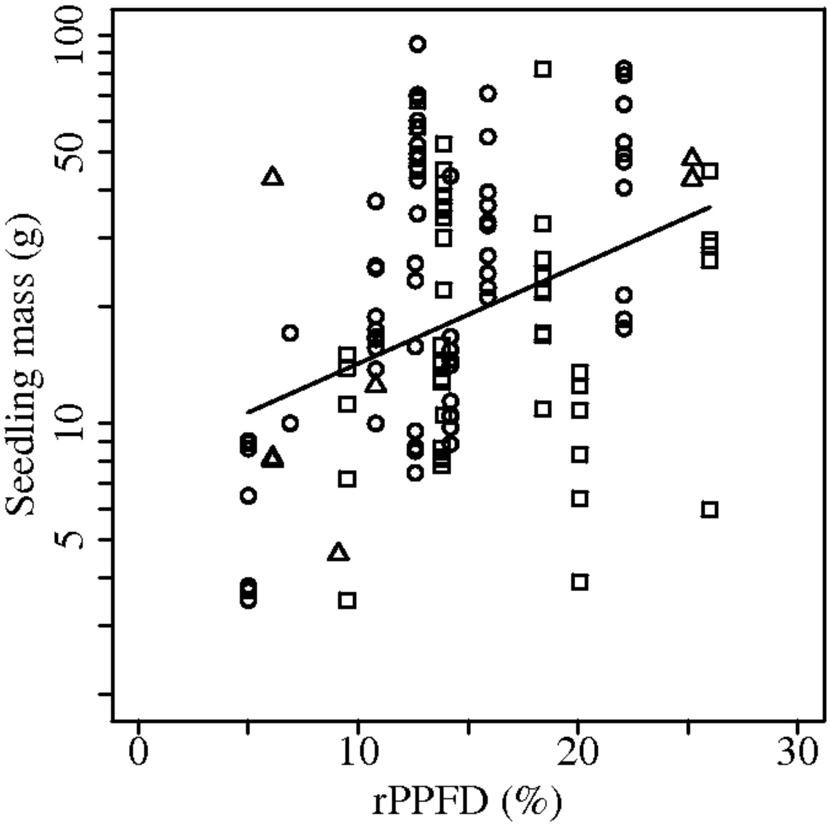

Figure 5