ORIGINAL ARTICLE

Regeneration of forest floor-grown seedlings of Sakhalin fir can be promoted through shading by shelter trees

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ABSTRACT

Natural regeneration of forest-floor seedlings of Sakhalin fir (*Abies sachalinensis*) is expected to contribute to low-cost afforestation. However, removal of canopy trees often causes photoinhibitory damage in forest-floor seedlings of Sakhalin fir as a typical shade-tolerant species. In the present study, we investigated factors related to solar radiation influencing survival rate and growth of Sakhalin fir seedlings after a canopy tree cutting in 62-year-old forest plantations. Survival rates, derived from aerial photographs taken by an unmanned aerial vehicle, could be predicted by the maximum consecutive direct solar radiation and shade period calculated from the sun track simulated by hemispheric photographs. Needle shedding rate of old shoots, which were developed under shade, increased with increasing daily integrated direct solar radiation in the first summer after the winter cutting of canopy trees. Conversely, growth rates of current-year-old shoots in the second summer after the winter cutting of canopy trees decreased with increasing daily integrated direct solar radiation. Needle shedding might suppress the growth rate of current-year-old shoots in the second summer, possibly due to the decreased nitrogen supply from the old needles. Thus, shading achieved by topography (e.g. north-faced slope) and retained shelter trees would be of relevance for the natural regeneration of forest-floor seedlings of Sakhalin fir, a typical shade-tolerant species.

Introduction

Sakhalin fir (*Abies sachalinensis*) is known as a typical shade-tolerant conifer species, commonly distributed in Hokkaido, northern Japan, as well as few nearby places, i.e. southern Kuril islands and Sakhalin island (Kubota et al. 1994; Matsuda et al. 2002). Seedlings of Sakhalin fir can survive under deep shade for a long time as Sakhalin fir is a climax species in the course of forest succession (Kikuzawa 1983; Koike 1988). Especially in the eastern part of Hokkaido, forest floor-grown seedlings of Sakhalin fir were commonly observed since less amount of snowfall in the eastern part prevents infection by *Racodium* snow blight (*Racodium therryanum* Thuem) (Nakagawa et al. 2001; Sakamoto and Miyamaoto 2005). As a trial of low-cost afforestation, regeneration of forest floor-grown seedlings of Sakhalin fir is expected after the removal of canopy trees for saving the planting cost of seedlings. However, damage in forest floor-grown seedlings of Sakhalin fir, e.g. brownish discoloration in shoots as a typical symptom, is often observed in springtime after a winter cutting of canopy trees in Hokkaido (Nakagawa et al. 2017), where canopy tree harvesting is usually conducted in winter to prevent soil compaction and disturbance of forest floor under snow cover (Hashimoto et al. 2018). Fully shade-acclimated seedlings of Sakhalin fir often suffer severe photooxidative damage by strong irradiance when canopy trees are removed (Kitao et al. 2000, 2018, 2019, 2022).

The development of new shoots in evergreen coniferous trees is afforded by photosynthetic carbon gain in pre-existing old shoots in early spring, which has been well demonstrated by feeding labelled CO_2 ($^{14}CO_2$) (Hansen and Beck 1994) and detailed analyses of various carbohydrates in old shoots around budbreak (Egger et al. 1996). Thus, springtime photoinhibition in the forest floor-grown seedlings of Sakhalin fir after the winter cutting of canopy trees caused a reduction in current shoot growth due to photosynthetic decline and defoliation of 1-year-old needles in the first year (Kitao et al. 2018). Furthermore, in the second year after the cutting, even though the newly developed needles under full sunlight acclimated to high light condition, reductions in the current shoot growth sustained due to the defoliation of old needles in the first year, probably because of the limitation of N re-allocation (Wyka et al. 2016; Kitao et al. 2019). Thus, growth suppression related to photoinhibitory damage might be sustained in the succeeding years, which may retard the regeneration of Sakhalin fir seedlings. These findings can explain that several years are needed for the recovery from growth suppression in Sakhalin fir seedlings after a clear-cutting (Noguchi and Yoshida 2007; Yoshida and Noguchi 2010; Nakagawa et al. 2017).

Regarding sustainable forest management with natural regeneration, ecosystem-based silvicultural systems, such as shelterwood and seed-tree harvesting, have been developed; the former improves light conditions for sapling growth and recruitment, and the latter, which is a variant of clear-cutting with a small number of retained canopy trees, provides seed sources for seedling establishment (de Freitas and Pinard 2008; Klopcic and Boncina 2012; Kern et al. 2017; Montoro Girona et al. 2018). Conversely, retaining some canopy trees as shelter trees would also aid in preventing photoinhibition

by alleviating abrupt increases in irradiance (Ball 1994; Man and Lieffers 1999). As the degree of photoinhibition is proportional to the integrated amount of irradiance (Werner et al. 2001), and the recovery of photoinhibition is expected under shade (Verhoeven et al. 1999; Miyata et al. 2014; Kromdijk et al. 2016; Kaiser et al. 2018), interruption of sun track by the remaining canopy trees would improve the survival rate and growth of forest floor-grown seedlings. Based on the field observation, we observed a considerable variation in growth and survival of Sakhalin fir seedlings even in the clear-cutting sites (Kitao et al. 2019), probably because of heterogenous light conditions.

Here, we hypothesized that heterogeneous light conditions due to the topography, including standing adjacent to the clear-cutting sites and remaining broadleaf trees in the clear-cutting sites, might influence the survival rate and growth of forest floor-grown seedlings by modifying photoinhibitory damage, where strong solar irradiance might adversely affect the survival rate and growth. To test this hypothesis, we investigated the relationship between light environments, derived from hemispheric photographs, and survival rate and growth in forest-floor seedlings of Sakhalin fir after clear-cutting. Based on the relationship, we discuss the role of shelter trees for natural regeneration of Sakhalin fir, regarding circumvention of photoinhibitory damage.

Materials and methods

Study site

A study site was established in 62-year-old forest plantations of Sakhalin fir, managed by the Konsen Seibu regional forest office of the Forestry Agency, Japan, located at Shibecha, Hokkaido, Japan (43.25°N, 144.59°E, 90 m a.s.l.). Details of the study site are described in Kitao et al. (2018, 2019). In the present study, we focused on the two clear-cutting plots (100% cutting) in the study site. The area was ≈1.3 ha for both clear-cutting plots, with approximately 60% of forest floor covered mostly by seedlings of Sakhalin fir before cutting. The forest-floor seedlings were approximately 20 years old and 60 cm tall. Based on field observations, spring budbreak of the seedlings occurred at the end of May in the study site. The density of canopy trees was ≈700 trees ha^{-1}, with an approximately 0.3 m of breast height diameter and about 20 m height on average. In the two clear-cutting plots, canopy tree cuttings were conducted at the end of October 2015 and at the end of January 2016, respectively. In total, 12 sub-plots were set within the plots, where 3–5 neighboring seedlings were randomly selected as representatives for each sub-plot to investigate the growth and needle shedding responses. There was no difference observed in photoinhibition between the plots as a function of light dose (Kitao et al. 2018, 2019).

Parameters related to solar track

Light environment for each sub-plot was evaluated using hemispheric photographs, which were taken by a digital camera (Coolpix 900, Nikon, Tokyo, Japan) combined with a fisheye lens (Fisheye Lens, FC-E8, Nikon) above the seedlings. Hemispheric photographs were taken at 18 sub-plots in total as we also chose 6 sub-plots additional to those described above, where seedlings were severely damaged. Based on the photographs, direct solar radiation not intercepted by the remaining trees was estimated using a canopy analysis software (HemiView 2.1 SR5, Delta-T Devices, Cambridge, UK). In the present study, as we assumed that light environment during the recovery from winter dormancy in spring might be relevant for photoinhibitory damage (Kitao et al. 2018, 2019), a diurnal change in the solar radiation was estimated at each sub-plot on 15 April. Based on the diurnal change, we derived the total duration of shaded period (<50 W m^{-2}) during daytime (S$_{time}$), the maximum amount of consecutive solar radiation (R$_{cons}$) (>300 W m^{-2}) not interfered by the remaining trees or adjacent stands, and the daily integrated direct solar radiation (R$_{int}$). We set the threshold values described above based on the preliminary analyses with highest values of r^2 between survival rate and S$_{time}$ and R$_{cons}$ using different values: 50, 100, 200, 300 and 400 W m^{-2} for R$_{cons}$ and 5, 10, 25, 50, 100 and 200 W m^{-2} for S$_{time}$.

Survival rate

Aerial photographs were taken by a 4K resolution digital camera (FC300X, DJI, Shenzen, China) equipped on an unmanned aerial vehicle (UAV) (Phantom 3 professional, DJI) in July 2016. The spatial resolution of aerial photograph, taken from the mean flying altitude of 26.7 m above the ground, was 1.1 cm at the ground. Stereoscopic measurement was conducted with Stereo Viewer Pro (Photec, Sapporo, Japan) to carefully identify alive and dead seedlings using the stereo-paired original aerial photographs. Distribution of alive and dead seedlings is shown in Figure 1. Survival rates were determined by [alive seedlings/total seedlings] within a 3-m radius of the sub-plot, at the center of which hemispheric photographs were taken.

Initial impact of solar radiation on old pre-existing shoots after the removal of canopy trees

We evaluated the initial damage on the old shoots, developed under shade in the forest floor, by means of the rate of shed needles to total needles in the first summer (July in 2016) after the winter cutting of canopy trees. In this analysis, we used the data of 1-year-old shoots sampled in July 2016, which corresponded to 2-year-old shoots in 2017. We estimated the total dry mass of needles based on the shoot length [needle dry mass (g) = 0.0416 × shoot length (cm) − 0.0328 (r^2 = 0.65)] (Kitao et al. 2018). The rate of shed needles was calculated as follows: shed needle rate = [(total needle dry mass) − (attached needle dry mass)]/(total needle dry mass) × 100%.

Growth of current-year shoots in the second summer after the removal of canopy trees

We investigated the effects of solar radiation on the growth of Sakhalin fir seedlings in the second summer in 2017. Growth rate of current-year shoot was evaluated by the ratio of dry weight of current-year shoots to the weight of 1-year-old needles (Kitao et al. 2018, 2019). The data of dry weight represent the shoots of Sakhalin fir seedlings sampled in July 2017, in the second summer after the removal of canopy trees.

Figure 1. Aerial photograph of the clear-cutting site taken by a UAV. White points indicate alive seedlings, whereas black points indicate dead seedlings.
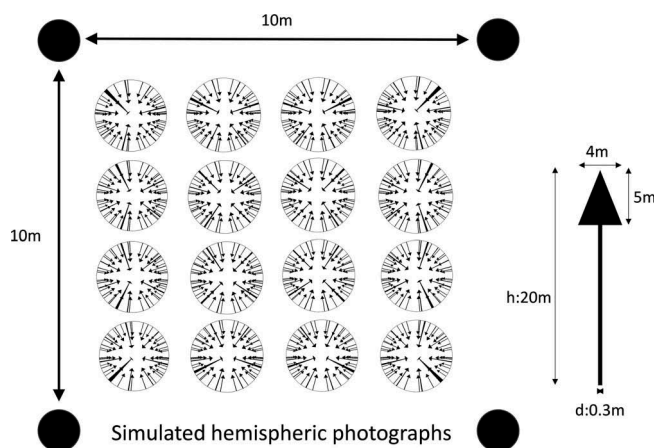

Figure 2. An example of simulated hemispheric photographs with a 10 × 10 m layout of shelter trees in both south–north and east–west directions. The average size of shelter tree was assumed to be 20 m in height, 5 m in canopy depth, 4 m in canopy width, and 0.3 m in stem diameter.

Estimation of survival rate with various layouts of reserved canopy trees

Based on the predicting model of survival rate from direct solar radiation, described below in statistical analyses, we mapped the survival rate with various layouts of reserved canopy trees: (1) 10 m (north–south) × 10 m (east–west direction), (2) 10 m (north–south) × 40 m (east–west direction), (3) 20 m (north–south) × 20 m (east–west), and (4) 40 m (north–south) × 40 m (east–west direction). A reserved canopy tree was assumed to have a tree height of 20 m, a stem diameter of 30 cm, a canopy width of 4, and a canopy depth of 5 m, which was the typical size of canopy trees grown at the experimental site. We arranged totally 54 shelter trees, and then produced hemispheric photographs at several points inside a simulating area of 40 m × 40 m (Figure 2). Then, we estimated the time-course of direct solar radiation by using a canopy analysis software (HemiView 2.1 SR5, Delta-T Devices).

Statistical analysis

The effects of light environments on the survival rate were analyzed by a multiple logistic regression analysis using the glm function of R (R Core Team and R Development Core Team 2020), where initial explanatory factors were (1) the total duration of shaded period during the daytime (S_{time}), (2) the maximum amount of consecutive solar radiation (R_{cons}), and (3) the daily integrated direct solar radiation (R_{int}). A stepwise method for variable selection of multiple logistic regression analysis was used for quantitative evaluation of the influence of the explanatory factors. Stepwise regressions were used to define the subset of effects that would altogether provide the smallest corrected Akaike information criterion (AIC) in subsequent modeling. Regarding needle shed rate in 2016 and growth rate of current-year shoot in 2017, a linear mixed model was applied to analyze the effects of solar radiation. In this model, S_{time}, R_{cons}, and R_{int} were set as initial fixed effects, and individuals in sub-plots as a random factor to account for variance due to differences among individual plants within a sub-plot. We used the lmer function of the R package lmerTest for the model fitting (Kuznetsova et al. 2017). Step-down model-building approach was used to simplify the fixed effects structure. The level of significance was $\alpha = 0.05$.

Results

Survival rate predicted by direct solar radiation

Diurnal changes in direct solar radiation, not including diffusive indirect solar radiation, were estimated from hemispheric photographs taken at 18 sub-plots across two clear-cutting sites. Higher survival rates appear to be observed in sub-plots where the sun track was intercepted by stands adjacent to the clear-cutting sites, or remaining broadleaf trees (Figure 3). It should be noted that while survived seedlings did not die, they suffered considerable photoinhibitory damage in their needles in the first year after the canopy tree removal (cf. Kitao et al. 2018).

a   Survival rate = 0.92   c   Survival rate = 0.18
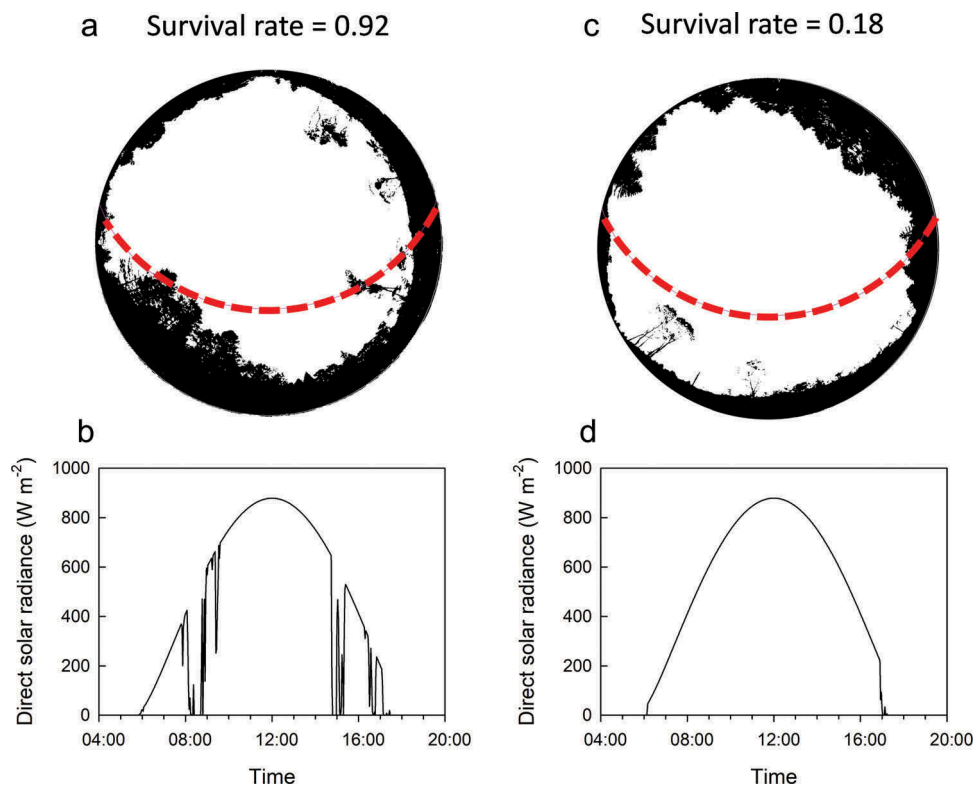
Figure 3. Hemispheric photographs (a, c) and diurnal direct solar radiation (b, d) in sub-plots with highest (a, b) and lowest (c, d) survival rates. Dashed curve lines in the hemispheric photographs indicate sun tracks on 15 April.

Table 1. Summary of multiple logistic regression of survival rate in seedlings of Sakhalin fir after the removal of canopy trees.

Analysis	Intercept	Regression coefficients				
		Variable	Coefficients	t-value	P	VIF
Full model	−7.75	S_{time} (min)	0.0171	3.50	<.001	2.03
(= Best model)		R_{cons} (MJ m^{-2})	−0.223	−6.01	<.001	2.15
AIC = 130		R_{int} (MJ m^{-2})	0.445	0.25	.077	3.55
Predictive model	2.09	S_{time} (min)	0.0113	3.10	<.01	1.06
AIC = 131		R_{cons} (MJ m^{-2})	−0.177	−6.88	<.001	1.06

Initial explanatory variables affecting survival rate: total shaded period < 50 W m^{-2} (S_{time}), maximum consecutive direct solar radiation > 300 W m^{-2} (R_{cons}), and daily integrated direct solar radiation (R_{int}). Stepwise regressions were undertaken to define the subset of effects that would altogether provide the smallest corrected Akaike information criterion (AIC) in subsequent modeling. As a measure of multi-collinearity, variance inflation factor (VIF) is demonstrated.

A multiple logistic regression analysis was conducted for the survival rate of Sakhalin fir seedlings, setting S_{time}, R_{cons}, and R_{int} as initial explanatory factors. We used a threshold of light intensity for S_{time} at ≤50 W m^{-2}, and that of R_{cons} at >300 W m^{-2}, based on preliminary analyses regarding the relationship between survival rate and those factors. After a stepwise method for variable selection, survival rate could be predicted by S_{time}, R_{cons}, and R_{int} with lowest AIC (Table 1). We eliminated R_{int} from the explanatory factors to avoid multi-collinearity as it had relatively high value of variance inflation factor (VIF, 3.55), and the exclusion of R_{int} practically did not affect AIC (130 vs 131). Using S_{time} and R_{cons} as explanatory factors, survival rate = 1/(1 + EXP (−2.09 + 0.177 R_{cons} − 0.0113 S_{time})), we can predict survival rate of seedlings of Sakhalin fir (Figure 4).

Initial impact of canopy tree cutting on leaf shedding

As a result of the step-down model-building approach, a simplified model predicting the ratio of shed needles uses R_{int} as an explanatory variable (Table 2). Higher shedding rate was observed with increasing amount of R_{int} (Figure 5).

Growth of current-year shoots in the second summer after the removal of canopy trees

A simplified model predicting the growth rate of current-year shoot also uses R_{int} as an explanatory variable (Table 3). Lower growth rate was observed in the second summer in 2017 with increasing amount of R_{int} (Figure 6).

Simulation of survival rate by the predicting model with shade period and the maximum consecutive solar radiation

We simulated survival rate of Sakhalin fir seedlings in a 40 × 40 m area with various shelter tree layouts based on the predicting model as described in Table 1. Most of the seedlings would survive with a 10 × 10 m layout of shelter trees (Figure 7a), whereas only one-third of seedlings would survive with a 40 × 40 m layout (Figure 7d). It should be noted that even if the number of shelter trees per ha was the same (25 trees/ha), average survival rate was higher in 10 m (south–north) × 40 m (east–west), which was ≈63% (Figure 7c) and higher than in the 20 × 20 m layout of shelter trees (55%) (Figure 7b). Except
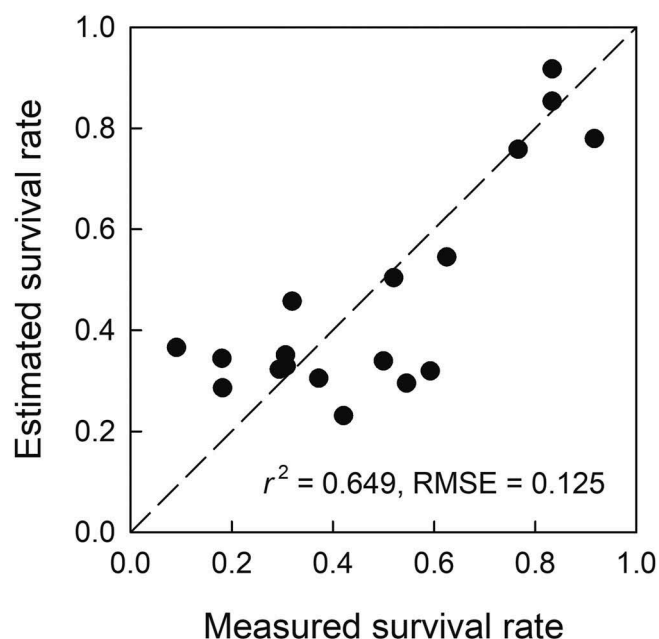
Figure 4. Relationship between measured and estimated survival rate of Sakhalin fir seedlings grown in clear-cutting plots. Dashed line indicates 1:1 relationship.

$r^2 = 0.649$, RMSE = 0.125
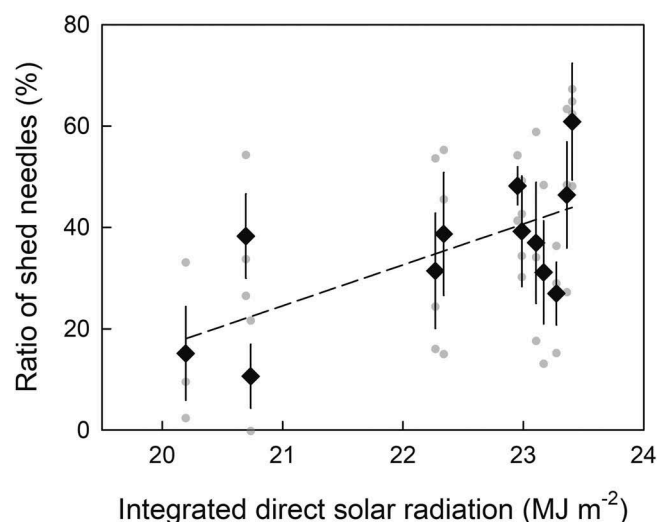
Figure 5. Relationship between the ratio of shed needles in the old shoots developed at the forest understory, and integrated direct solar radiation in the seedlings of Sakhalin fir in the first summer after winter cutting of canopy trees. Grey circles indicate individual seedlings. Closed diamonds and error bars indicate mean ± SE ($n = 3$–5) for each sub-plot, where a hemispheric photograph was taken. Data of 1-year-old shoots sampled in July 2016 were used. Linear regression analysis was conducted for the pooled data across the sub-plots (dashed line).

Table 2. Summary of multiple regression of the ratio of shed needles in seedlings of Sakhalin fir in the first summer after removal of canopy trees.

Analysis	Intercept	Variable	Coefficients	t-value	P	VIF
			Regression coefficients			
Full model	−149	S_{time} (min)	0.0356	0.177	.868	6.26
		R_{cons} (MJ m^{-2})	0.538	0.329	.750	3.64
		R_{int} (MJ m^{-2})	7.66	0.712	.495	11.39
Simplified model	−145	R_{int} (MJ m^{-2})	8.06	2.87	<0.05	−

Initial explanatory variables affecting the ratio of shed needles were set as: total shaded period < 50 W m^{-2} (S_{time}), maximum consecutive direct solar radiation > 300 W m^{-2} (R_{cons}), and daily integrated direct solar radiation (R_{int}). Step-down model-building approach was used to simplify the fixed effects structure.

Table 3. Summary of multiple regression of the growth rate of current-year shoot in the seedlings of Sakhalin fir in the second summer after the removal of canopy trees.

Analysis	Intercept	Variable	Coefficients	t-value	P	VIF
			Regression coefficients			
Full model	38.0	S_{time} (min)	−0.0182	−1.05	.321	6.29
		R_{cons} (MJ m^{-2})	−0.0204	0.151	.884	3.44
		R_{int} (MJ m^{-2})	−1.42	−1.60	.147	11.06
Simplified model	20.9	R_{int} (MJ m^{-2})	−0.721	−2.82	<0.05	−

Initial explanatory variables affecting the ratio of shed needles were set as: total shaded period < 50 W m^{-2} (S_{time}), maximum consecutive direct solar radiation > 300 W m^{-2} (R_{cons}), and daily integrated direct solar radiation (R_{int}). Step-down model-building approach was used to simplify the fixed effects structure.

for the 10 × 10 m layout, survival rate appeared substantially heterogenous within the 40 × 40 m area.

Discussion

Survival and mortality of regenerating trees define the regeneration of forests and are major drivers of the dynamics of forest formation, development, and establishment of natural forests (Kubota et al. 1994; Messier et al. 1999; Matsuda et al. 2002). Increasing the survival of regenerating seedlings of target trees in artificial forests is critical in the forestry practice too, including enhancing the regeneration of forest floor-grown seedlings of Sakhalin fir (Nakagawa et al. 2001; Kern et al. 2017; Montoro Girona et al. 2018). Regarding

ecosystem-based silvicultural systems, such as shelterwood and seed-tree harvesting, we further showed that an interruption of direct solar radiation might improve the survival and growth of forest floor-grown Sakhalin fir seedlings after the clear-cutting of canopy trees. As the degree of photoinhibition might be proportional to the amount of intercepted light (Werner et al. 2001; Nishiyama et al. 2011; Pospíšil 2016), and might recover under low light (Verhoeven et al. 1999; Miyata et al. 2014; Kromdijk et al. 2016; Kaiser et al. 2018), it seems reasonable that survival rate of Sakhalin fir seedlings was affected by the maximum consecutive direct solar radiation and total shade period.

In a previous study, we showed that the amount of remained intact needles of 2-year-old shoots of Sakhalin fir
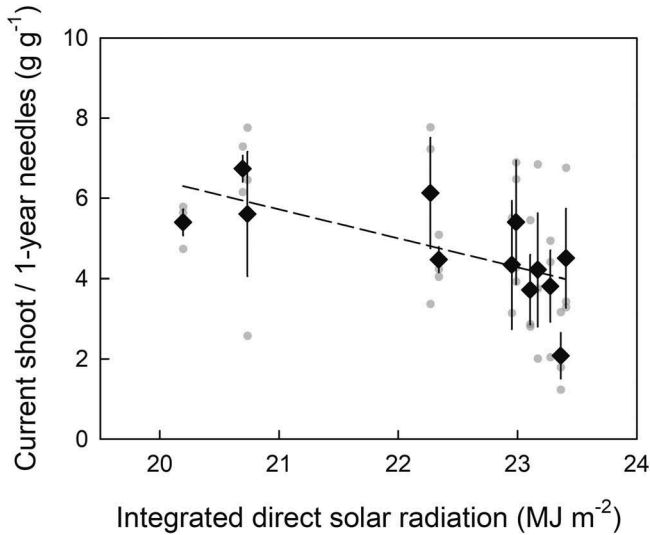
Figure 6. Relationship between the growth rate of current shoot in the seedlings of Sakhalin fir in the second summer after the removal of canopy trees and integrated direct solar radiation. Grey circles indicate individual seedlings. Closed diamonds and error bars indicate mean ± SE ($n = 3$–5) for each sub-plot, where a hemisphere photograph was taken. Linear regression analysis was conducted for the pooled data across the sub-plots (dashed line).

seedlings in the clear-cutting sites might be a constraint of newly developed current-year-old shoots (Kitao et al. 2019). Regarding development of new shoots in evergreen trees, carbohydrates might be provided as photosynthate from young shoots (1-year-old shoots), while nitrogen might be transferred from older shoots (2-year-old or older shoots in Sakhalin fir seedlings) (Miyazawa et al. 2004; Millard and Grelet 2010; Wyka et al. 2016; Kitao et al. 2019). In this context, needle shedding exacerbated by the greater integrated solar radiation, probably due to photoinhibitory damage, would be a main factor decreasing the growth of current-year-shoot in the next summer. Conversely, limited solar radiation under shade also restricted shoot growth of

Sakhalin fir seedlings, as the growth rate of current-year shoot increased from 3 (forest floor) to 6 g g^{-1} (66% and 100% canopy tree cutting), and then declined with further increase in solar radiation within the clear (100%) cutting sites (Figure 6, cf. Kitao et al. 2019). Thus, the growth rate of ≈6 g g^{-1} observed at R_{int} from 20 to 21 MJ m^{-2} (Figure 6) was considered to be the maximum value in the seedlings of Sakhalin fir across variable light conditions. As the range of R_{int} was not so wide in the clear-cutting sites (≈20.0 to 23.5 MJ m^{-2}) (cf. Figures 5 and 6), a relatively short period of light shielding (10% or so of reduction in integrated solar radiation) would be enough to protect Sakhalin fir seedlings from needle shedding due to photoinhibitory damage (cf. Figures 3 and 5).

A suppression of growth in forest-floor seedlings of Sakhalin fir was often observed after a canopy tree removal, and several years were needed for recovery (Noguchi and Yoshida 2007; Yoshida and Noguchi 2010; Nakagawa et al. 2017). Such a sustained suppression in growth might be attributed to the photoinhibition and needle shedding after a canopy tree removal in the pre-existing shoots developed under shade (Kitao et al. 2018, 2019). From the viewpoint of forestry, suppression in shoot growth lasting several years would be a major disadvantage in competing against herbaceous species including the sasa bamboo, which imposes a serious limitation on the initial afforestation and regeneration by a thick coverage (Harayama et al. 2022; Kitao et al. 2022). An appropriate arrangement of shelter trees, preventing sustained growth suppression, would be of relevance for the success of regeneration of forest-floor seedlings of Sakhalin fir.

Shelter trees for the survival of seedlings have been proposed as a strategy to circumvent photoinhibition, especially in cold regions since photoinhibitory stress is exacerbated under low temperature (Ball 1994; Man and Lieffers 1999; Egerton et al. 2000), as is the case in northern Japan, Hokkaido (Sugai et al. 2023). To illustrate the effects of shelter trees, a simulation was conducted to create a map of survival
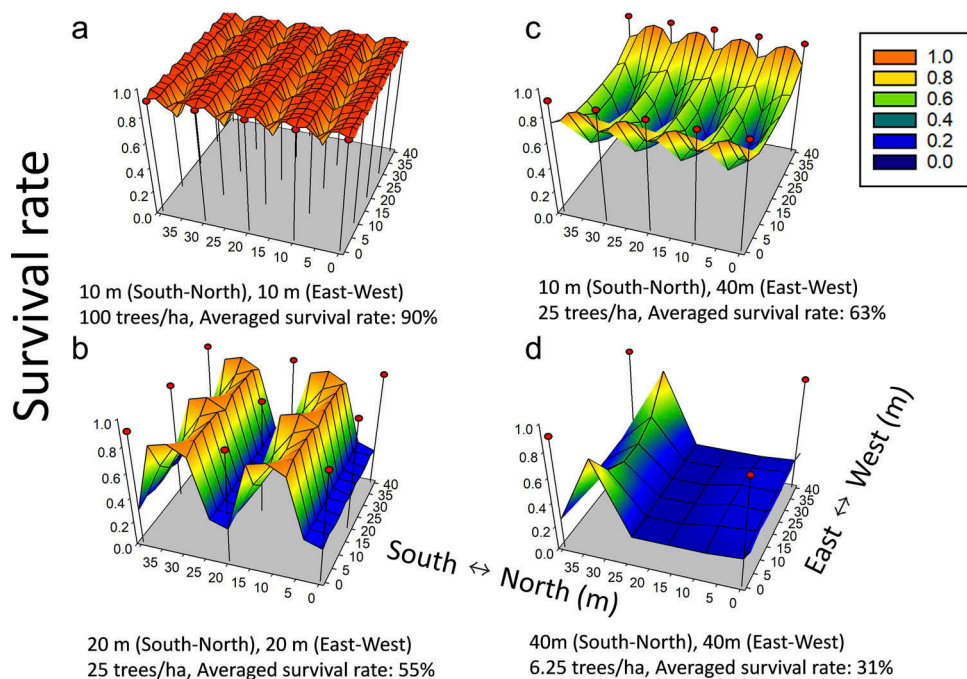
Figure 7. Survival rate estimated from the predicting model with various shelter tree layouts: 10 m (north–south) × 10 m (east–west direction) (a), 10 m (north–south) × 40 m (east–west direction) (b), 20 m (north–south) × 20 m (east–west) (c), and 40 m (north–south) × 40 m (east–west direction) (d). Vertical bars with red bulbs indicate shelter tree positions.

rate with various layouts of shelter trees using the predictive model described above. As a result of simulation, a greater number of remaining shelter trees generally resulted in higher survival rate, whereas survival rate was heterogenous with fewer shelter trees, depending on the arrangement of shelter trees. This suggests a possibility to control survival rate in expected areas in a clear-cutting site by an appropriate arrangement of a limited number of shelter trees.

Natural regeneration of forest-floor seedlings might be hindered by forestry operation using heavy machines during harvesting, where compaction of soils and mechanical damage of seedlings might have adverse effects (Cambi et al. 2017; Hashimoto et al. 2018; Mariotti et al. 2020; Picchio et al. 2020). Planning of skid roads and winching corridors to minimize mechanical damage of seedlings would be a possible approach to promote natural regeneration of forest-floor seedlings. In addition to such an approach, shading by shelter trees on intact areas would improve survival rate and growth of forest-floor seedlings of Sakhalin fir, a typical shade-tolerant species, leading to successful natural regeneration. Advantage of shading for the regeneration of shade-tolerant (sun-intolerant) tree species, as shown in the present study, would provide an additional supportive insight into the ecosystem-based silviculture systems, such as shelterwood and seed-tree harvesting, which aims to maintain habitat diversity as well as forest productivity (Raymond et al. 2009; Kern et al. 2017; Montoro Girona et al. 2018; Yamaura et al. 2018, 2022).

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Disclosure statement

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