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Early response of *Pinus sylvestris* and *Picea abies* seedlings to an experimental canopy gap in a boreal spruce forest

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Abstract

We studied the early response of size and morphology of *Pinus sylvestris* (Scots pine) and *Picea abies* (Norway spruce) seedlings to an experimental canopy gap and the consequent distribution of photosynthetically active radiation (PAR) in a boreal Norway spruce forest. Because of the asymmetric distribution of radiation in the gap and its surroundings, which was due to solar geometry at high latitudes, the highest amount of radiation was received several metres north of the gap centre. As a result, seedlings growing under the canopy at the northern edge of the gap received amounts of radiation similar to those received by seedlings growing in the southern part of the gap. Seedling size (aboveground dry biomass, height, and projected leaf area) of both species increased with increasing radiation, but shade-intolerant *P. sylvestris* responded more strongly than shade-tolerant *P. abies*. *P. sylvestris* seedlings reached their maximum aboveground dry biomass in the northwestern part and *P. abies* seedlings in the northern half of the gap. As height difference between species was small, the greater aboveground dry biomass of *P. sylvestris* seedlings was explained by its larger projected leaf area compared to *P. abies*. In addition, *P. sylvestris* responded to radiation with a more flexible morphology than *P. abies*, allowing *P. sylvestris* to increase its needle length with increasing radiation. Longer needles contributed to increased aboveground dry biomass, projected leaf area, and specific leaf area$_p$. Consequently, with increasing radiation, *P. sylvestris* seedlings allocated proportionally more aboveground dry biomass to assimilating parts versus structural parts compared to *P. abies*. This allowed *P. sylvestris* to capture more light and compete better for resources than *P. abies* in gap and gap-edge environments.

Keywords: Morphology; Norway spruce; Radiation; Scots pine; Spatial pattern

1. Introduction

Small-scale gap disturbance and regeneration are an integral part of the dynamics of boreal forests (Bergeron et al., 1999; Engelmark and Hytteborn, 1999). In naturally dynamic boreal forests of Fennoscandia, catastrophic events, such as stand-replacing fires or severe storms, are relatively infrequent, and small gaps are commonly created by minor perturbations, e.g. surface fire, strong winds, pathogens, or heavy snow loads (Sernander, 1936; Liu and Hytteborn, 1991; Kuuluvainen, 1994, 2002; Zackrisson et al., 1995; Kuuluvainen et al., 1998).

Gap environments are heterogeneous with fine-scale environmental variation in regeneration microhabitats (Kuuluvainen and Juntunen, 1998) superimposed by

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large-scale within-gap gradients in competitive interference for light, water, and nutrients by the dominant trees surrounding a gap (Aaltonen, 1919; Goldberg, 1990; Kuuluvainen et al., 1993; Palik et al., 1997). Surrounding trees also have a strong effect on the environmental conditions and processes in the gap area, especially in the vicinity of gap edges (Chen et al., 1993, 1995; Matlack, 1993; Cadenasso et al., 1997; Matlack and Litvaitis, 1999). These effects modify the distribution of resources along the gap-edge zone, which can lead to gap partitioning.

Although conifer seedling establishment has been studied for several decades (Yli-Vakkuri, 1961), the early development of size and morphology of conifer seedlings under natural conditions has only recently been addressed (Zobel and Antos, 1991; Klinka et al., 1992; Wang et al., 1994; Chen et al., 1996; Gray and Spies, 1996; Chen, 1997; Chen and Klinka, 1998; Mailly and Kimmins, 1997; Kneeshaw et al., 1998). This topic is important because seedling growth patterns and morphological characteristics play an important role in determining succession dynamics after a disturbance, giving rise to variation in competitive ability for establishment, and promoting increased growth (Goulet and Bellefleur, 1986; Zobel and Antos, 1991; Tremmel and Bazzaz, 1995). Even small differences in morphology and growth may be ecologically important for survival (Walters and Reich, 1996), especially on sites where competition from ground vegetation is strong (Nilsson et al., 1996; Örlander et al., 1996; Jäderlund et al., 1997).

A better understanding of tree regeneration in relation to gap-edge effects is important since forest management methods using natural disturbances as a template are being developed (Attiwill, 1994; Angelstam, 1996, 1998; Bergeron and Harvey, 1997; Bergeron et al., 1999; Franklin et al., 2002; Harvey et al., 2002; Kuuluvainen, 2002). These silvicultural methods often include the use of small and/or irregularly shaped clearcuts that are broken with islands of retention trees (Coates and Burton, 1997). However, the promoted use of small-scale silvicultural methods means that more regeneration area is in a gap-edge environment (Matlack and Litvaitis, 1999). Accordingly, a better understanding of tree regeneration ecology in gap-edge environments is needed to understand natural forest dynamics (Steijlen and Zackrisson, 1986; Leemans, 1991; Kuuluvainen, 1994; Angelstam, 1996; Kuuluvainen and Juntunen, 1998) and to develop improved natural regeneration and direct seeding methods for forest management. In direct seeding, the timing of germination can be affected by seed pre-treatment. As such, moist chilling relieves dormancy of collected boreal tree seeds and widens the environmental range for germination (Gosling and Peace, 1990; Leinonen and Rita, 1995; Leinonen, 1997).

In this study, we examined the early development of seedlings of shade-intolerant *Pinus sylvestris* L. (Scots pine) and shade-tolerant *Picea abies* (L.) Karst. (Norway spruce) in relation to an experimental canopy gap in a boreal Norway spruce forest on a mesic *Myrtillus* site type (MT). We made a spatially explicit description of the radiation environment and of the size and morphological development of the seedlings. We asked the following specific questions: (1) What is the early response of size and morphology of *P. sylvestris* and *P. abies* seedlings to the canopy gap? (2) How does moist chilling of seeds affect the development of above-ground size and morphology of *P. sylvestris* and *P. abies* seedlings?

2. Methods

2.1. Study site

The experimental work was set in an even-aged 80-year-old coniferous stand (2 ha) located 6.5 km from the Hyytiälä Forestry Field Station of the University of Helsinki, Finland (61°48′N; 24°20′E; 140 m in altitude). The dominant species in the stand is *P. abies*, which accounts for 94.4% of the stems, while *P. sylvestris* and *Betula pendula* Roth. (silver birch) represent 2.9 and 2.7% of the stems, respectively. In order to create a gap-edge zone, trees were removed in winter 1995 from a circular gap about 50 m in diameter (2200 m^2) in the centre of the stand. Before cutting, the growing stock density was 462 stems ha^{-1}, volume 256 $m^3\ ha^{-1}$, and the average height 20.2 m. The stand is located on a glacial delta formation of fine sand (particle size 0.2–0.02 mm) and the soil type is podzolic. The annual mean temperature on the site is +2.9 °C, January being the coldest month (mean −8.9 °C) and July the warmest (mean +15.3 °C); the annual precipitation averages 709 mm (Finnish

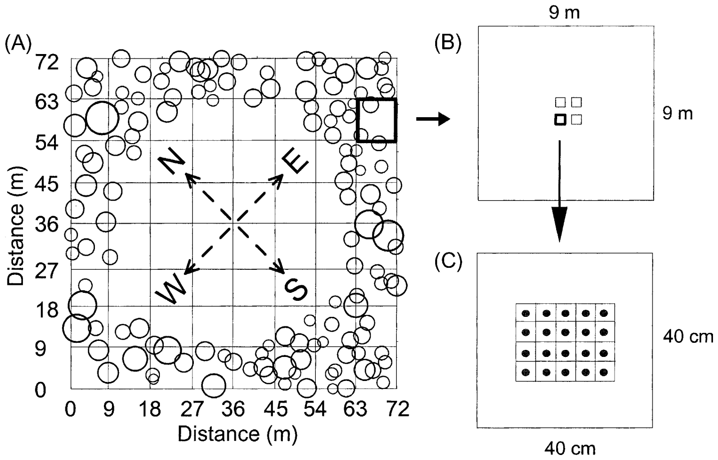

Fig. 1. Overview of the study area divided into 64 blocks (A); diagrammatic representations of the subdivision of a block into four plots of 40 cm × 40 cm (B); and a plot into a 22 cm × 18 cm sowing area with 20 sowing spaces (C). Circles in (A) represent the location of trees over the study site and are drawn proportionally to stem diameter.

Meteorological Institute, 1991). According to the Finnish classification of forest types (Cajander, 1925), the site is a *Myrtillus* site type. The understorey vegetation consisted of mosses during growing season 1995, and light *Deschampsia* spp. and *Calamagrostis* spp. growth during growing season 1996.

2.2. Experimental design

In order to get a radiation gradient from the centre of the gap to all directions, an experimental area of 72 m × 72 m was placed over the gap and its edges, and divided into 64 blocks of equal size (9 m × 9 m), in an 8 × 8 grid pattern (Fig. 1A). In each block, four plots of 40 cm × 40 cm in area, and a few centimetres deep into the humus, were scalped to the mineral soil (Fig. 1B). Scalping to the mineral soil was done in order to provide better conditions for seed germination and seedling survival (Yli-Vakkuri, 1961; Kuuluvainen, 1994; Carlton and Bazzaz, 1998). In the centre of each of these 256 plots, a sowing area of 22 cm × 18 cm was marked and subdivided into 20 sowing spaces of equal size, in a 5 × 4 grid pattern (Fig. 1C). Each sowing space received one seed. The study material consists of a direct seeding experiment which took place on 6 June 1995. A 2 × 2 factorial design (species × moist chilling) was used, allocated randomly between plots in each block, each patch containing 20 seeds of the same species and treatment.

In natural conditions, seeds of *P. sylvestris* and *P. abies* usually overwinter in cones and disperse on snow or cold moist soil in the spring (Heikinheimo, 1937). In order to reproduce the natural conditions occurring in boreal forests, moist chilling was used on collected seeds. Moist chilling was induced by storing *P. sylvestris* and *P. abies* seeds (from the same seed source as unchilled seeds) at 3 ± 1 °C on moist filter paper under cool white light (16 h photoperiod; 25–30 μmol m^{-2} s^{-1}) during 4 weeks. The 16 h photoperiod was used in order to mimic natural light conditions in the field during spring.

2.3. Seedling measurements

Total needle dry biomass, stem dry biomass, projected leaf area, mean needle length, and height were measured on a sample of seedlings in order to evaluate aboveground seedling size and morphology. Every 10th surviving *P. sylvestris* and *P. abies* seedling was sampled in October 1996. Since only living seedlings were considered for the sampling, each patch provided 2, 1, or even 0 seedlings, for a total of 77 and 74 *P. sylvestris* seedlings, and 42 and 58 *P. abies* seedlings from unchilled and moist-chilled seeds, respectively. Seedlings were cut at the root collar and stored at 0 ± 1 °C in individually identified plastic bags until measured. Sampled seedlings were dried for 24 h at 65 °C and cooled to room temperature in a desiccator before being weighed for total needle and stem dry biomass (±0.0001 g). For each seedling, projected leaf area and mean needle length were measured using a scanned image of all needles (including cotyledon needles), which was then interpreted by WinNeedle (1995) software. Height of all surviving seedlings, whether sampled or not, was measured from the root collar to the tip of the terminal bud (±1 mm).

In addition to the dimensional variables measured directly on seedlings, some indices expressing seedling morphology were calculated. In order to determine whether *P. sylvestris* and *P. abies* allocate resources differently between photosynthesising and structural parts along the gap-edge zone, the distribution of dry biomass between needle and stem was calculated. Specific leaf area$_p$ (projected leaf area/total needle dry biomass) is an indirect evaluation of relative growth rate (Reich et al., 1998; Wright and Westoby, 2001), and was measured to determine differences in growth strategies between species. Aboveground seedling morphology shows how seedlings compete for space and light, and is evaluated on the basis of height/stem dry biomass and mean needle length.

2.4. Radiation modelling

Among the environmental variables affecting seedling development, the amount of solar radiation reaching seedlings is directly dependent on the presence of gaps in the canopy, and therefore on management practices. Radiation penetrating through canopy gaps influences other variables, such as soil and air temperature, soil water and nutrient availability. For this reason, radiation was chosen to characterise the gap-edge zone. Because empirical measurements of radiation over the growing season in numerous locations (256) would have been very tedious, we adopted a modelling approach to describe the radiation regime. For this task, radiation values at each seedling location were predicted by a radiative transfer model specially calibrated and evaluated for the study stand. A complete description of the model theory and application to the specific study area is reported in Cescatti (1997a,b).

The hourly amount of radiation reaching each sowing patch was estimated using a 3-D transfer model which takes into account the geometry and architecture of the canopy, length of light beam penetrating through the crown, leaf area density along beam paths and extinction coefficient (Cescatti, 1997a). The 3-D geometrical description of the canopy required the measurement of the crown heights (at top, at base and at greatest width), length of crown radii in four orthogonal directions and crown shape coefficient for each tree in a 2-ha area (890 trees) overlaying the experimental site. The coordinates of all trees and sowing plots were recorded using a tachymetre (Rouvinen and Kuuluvainen, 1997). Leaf area of single trees in the canopy was calculated according to species-specific biometric models between leaf area and stem diameter (Marklund, 1988). Since there was no defoliation problem in the stand, the vertical distribution of leaf area density within crowns was assumed to be uniform (Cescatti, 1997b). Considering that light coming from the lower zenithal angles is negligible because of shading effects from trees surrounding the gap (Cescatti, 1997b), the understorey vegetation and soil preparation do not affect the radiation regime of seedlings in the mineral plots, and their effects were not included in the radiation model.

Incoming radiation (averaged 5-min interval), measured at the Hyytiälä Forestry Field Station, was used as input for the radiative transfer model. Partitioning between direct and diffuse radiation was done according to Weiss and Norman (1985). The predicted hourly radiative fluxes were integrated from May to the end of September to compute the total amount of photosynthetically active radiation (PAR, 400–700 nm, MJ m^{-2}) received at each microsite since seed sowing. To determine the amount of PAR received by 2-year-old seedlings, the amounts of PAR received during the two summers (May–September) were summed.

To validate the model predictions, a Plant Canopy Analyser (PCA) was used to measure diffuse radiation in overcast conditions 2 m above ground at 200 points evenly spaced over the gap and its edges. The 2 m measuring height was selected in order to avoid interference (shading) from the operator on the measurements. Diffuse light conditions were preferred in order to avoid the high temporal variability in direct radiation that would have increased uncertainty in the measurements. However, the radiative transfer model used for the simulation is able to take into consideration the distribution of the direct radiation and can generate the radiative field at every specific height in the canopy space (Cescatti, 1997a,b). Using this specific feature of the model, the light simulation used in the analysis of the microclimate was obtained for the ground level where seedlings were growing and took into consideration the availability of direct and diffuse radiation measured at a nearby meteorological station. The canopy gap fraction was estimated as the ratio of the simultaneous PCA reading in the stand over the PCA reading of a sensor installed in a clearing next to the experimental forest. When compared with observed values, the model predicted most of the spatial variability of diffuse fluxes ($R^2 = 0.97$) (Cescatti, 1997b).

2.5. Statistical analysis

2.5.1. Analysis of variance

The effects of block, species, and moist chilling on seedling size (aboveground dry biomass, projected leaf area, height) and morphology (specific leaf area$_\mathrm{p}$, needle/stem dry biomass ratio, height/stem dry biomass ratio, and needle length) were tested using analysis of variance. The following model was used:

$$Y_{ijkl} = \mu + \sigma_i + \alpha_j + \beta_k + \alpha\beta_{jk} + \sigma\alpha_{ij} + \varepsilon_{ijkl} \qquad (1)$$

where Y is the seedling size or morphology variable, μ the mean; σ_i the block effect, α_j the species effect, β_k the moist chilling effect, $\alpha\beta_{jk}$ the interaction between species and moist chilling, $\sigma\alpha_{ij}$ the interaction between block and species, and ε_{ijkl} is the error. In cases when there were two seedlings per plot, the average was used in the analysis. Block represents spatial location and includes the variation in radiation, soil properties, water availability, competition, and other variables along the gap-edge zone. The model parameters were estimated and tested using the GLM procedure of SAS (SAS Institute Inc., 1989).

Among the response variables, projected leaf area, aboveground dry biomass, height/stem dry biomass, and needle length were log-transformed (base-e log) for the ANOVA, as the variances were positively correlated with the means (Zar, 1999, p. 275). Residuals were plotted to verify the normality of variable distributions.

2.5.2. Partial Mantel test

The amount of radiation seedlings received was autocorrelated to their location along the gap-understorey gradient, which produced autocorrelation of the seedling variables data. As the observations were not independent, standard linear models could not be used. Instead, partial Mantel statistics were used to remove the effect of spatial autocorrelation. Since the Mantel test is based on similarity or distance matrices (Mantel, 1967), the partial Mantel statistic measures how well the variation in one matrix corresponds to the variation in a second matrix, while controlling for the effect of variation in a third one (Legendre and Fortin, 1989; Legendre and Legendre, 1998). In this case, we measured how well the variation in seedling size or morphology corresponds to the variation in radiation, while controlling for the effect of spatial location along the gap-edge zone. The effect of radiation on seedling size and morphology was analysed separately for each species and moist chilling treatment.

2.5.3. Spatial description

The arrangement of the experiment in a regular grid over the study area (Fig. 1) facilitated the description of the spatial distribution of seedling and environmental variables. For this purpose, experimental data were spatially interpolated using geostatistical techniques, i.e. semivariance analysis and Kriging interpolation (Cressie, 1989). First, experimental semivariograms were computed for seedling variables and radiation (Cressie, 1993). Then the exponential model was fitted to the experimental semivariograms. The fit of the models was relatively good ($r^2 = 0.76$–0.95, mean $= 0.90$). Finally, maps of the spatial distribution of variables were drawn based on values obtained using Kriging interpolation (Rossi et al., 1992; Cressie, 1993, pp. 105–209). Seedlings from both moist chilling treatments were combined to draw the maps of variables, since moist chilling was not a significant factor.

3. Results

3.1. Distribution of radiation in the study area

Fig. 2 shows the spatial distribution of the total amount of PAR received in the experimental area during the summers of 1995 and 1996 (May–September), when the experiment was running. The highest amount of PAR was received several metres north of the gap centre. From this maximum, radiation

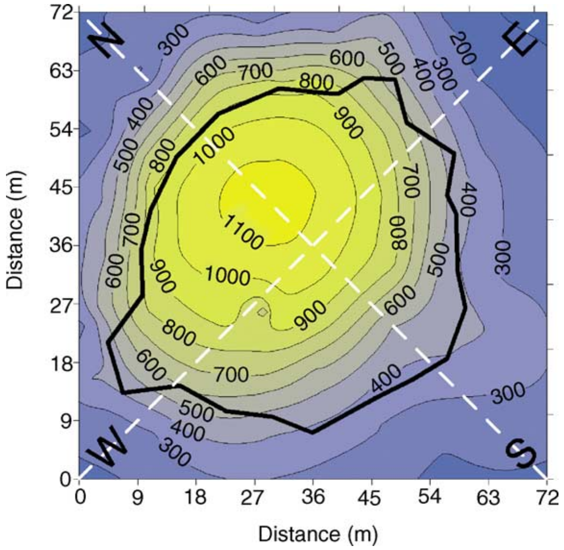

Fig. 2. Isopleths of cumulative photosynthetically active radiation (PAR, MJ m^{-2}) received since seed sowing by 2-year-old seedlings during the two growing seasons. The gap area is delimited by a thick black line, and the orientation is indicated by broken white lines.

decreased gradually towards gap edges and the decrease was slightly steeper towards the northern than the southern edge. The radiation sum over the two growing seasons varied from 100 MJ m^{-2} under the forest canopy to a maximum of 1100 MJ m^{-2} in the northern part of the gap (Fig. 2).

Because of the asymmetric distribution of radiation in the gap and its surroundings, which is due to solar geometry at high latitudes, seedlings growing under the canopy at the northern edge of the gap received amounts of radiation that were similar to those received by seedlings growing in the southern part of the gap (Fig. 2). In the gap, seedlings received 20–62% of the radiation received over the same period of time in an open area (1824 MJ m^{-2}) near the experimental site. Under the canopy, the proportion of radiation received compared to that in an open area ranged from as high as 50% at the northern edge of the gap to as low as 4% further into the forest.

3.2. *Response of seedling size to canopy gap*

3.2.1. *Aboveground dry biomass*

After two growing seasons, for a given amount of radiation received, *P. sylvestris* had attained a significantly larger aboveground dry biomass than *P. abies*

Table 1
ANOVA results for the effect of block (spatial location), species, and moist chilling on the size and morphology of 2-year-old *P. sylvestris* and *P. abies* seedlings

	d.f.	MS	*F*	*P*
Aboveground dry biomass ($R^2 = 0.841$)				
σ_i	61	1.677	4.28	<0.001
α_j	1	21.437	54.65	<0.001
β_k	1	1.117	2.85	0.096
$\alpha\beta_{jk}$	1	0.160	0.41	0.525
$\sigma\alpha_{ij}$	50	0.491	1.25	0.185
ε_{ijkl}	77	0.392		
Total	191			
Height ($R^2 = 0.734$)				
σ_i	61	392.53	2.16	<0.001
α_j	1	1095.40	6.03	0.016
β_k	1	57.30	0.32	0.576
$\alpha\beta_{jk}$	1	245.50	1.35	0.249
$\sigma\alpha_{ij}$	50	241.42	1.33	0.130
ε_{ijkl}	77	181.75		
Total	191			
Projected leaf area ($R^2 = 0.837$)				
σ_i	61	1.578	4.07	<0.001
α_j	1	23.726	61.12	<0.001
β_k	1	0.546	1.41	0.239
$\alpha\beta_{jk}$	1	0.120	0.31	0.580
$\sigma\alpha_{ij}$	50	0.467	1.20	0.229
ε_{ijkl}	77	0.388		
Total	191			
Specific leaf area$_p$ ($R^2 = 0.754$)				
σ_i	61	2.74E+6	2.61	<0.001
α_j	1	0.12E+6	0.12	0.735
β_k	1	7.44E+6	7.09	0.010
$\alpha\beta_{jk}$	1	3.02E+6	2.87	0.094
$\sigma\alpha_{ij}$	50	1.31E+6	1.24	0.193
ε_{ijkl}	77	1.05E+6		
Total	191			
Needle/stem dry biomass ($R^2 = 0.753$)				
σ_i	61	1.044	1.82	0.007
α_j	1	9.301	16.18	<0.001
β_k	1	0.018	0.03	0.861
$\alpha\beta_{jk}$	1	0.826	1.44	0.234
$\sigma\alpha_{ij}$	50	1.005	1.75	0.014
ε_{ijkl}	77	0.575		
Total	191			
Height/stem dry biomass ($R^2 = 0.850$)				
σ_i	61	0.489	4.14	<0.001
α_j	1	9.156	77.61	<0.001
β_k	1	0.549	4.65	0.034
$\alpha\beta_{jk}$	1	0.132	1.12	0.293
$\sigma\alpha_{ij}$	50	0.180	1.52	0.048

Table 1 (*Continued*)

	d.f.	MS	*F*	*P*
ε_{ijkl}	77	0.118		
Total	191			
Mean needle length ($R^2 = 0.936$)				
σ_i	61	0.187	3.58	<0.001
α_j	1	31.958	611.79	<0.001
β_k	1	0.170	3.25	0.076
$\alpha\beta_{jk}$	1	0.011	0.22	0.640
$\sigma\alpha_{ij}$	50	0.132	2.53	<0.001
ε_{ijkl}	77	0.052		
Total	191			

The model used for ANOVA: $Y_{ijkl} = \mu + \sigma_i + \alpha_j + \beta_k + \alpha\beta_{jk} + \sigma\alpha_{ij} + \varepsilon_{ijkl}$. Y, seedling size or morphology variable; μ, mean; σ_i, block effect; α_j, species effect; β_k, moist-chilling effect; $\alpha\beta_{jk}$, interaction between species and moist chilling; $\sigma\alpha_{ij}$, interaction between block and species; ε_{ijkl}, error.

(Table 1, Fig. 3A). For both species, the effect of the gap on aboveground dry seedling biomass was also revealed in ANOVA by the significant effect of spatial location (block) in the experimental area (Table 1, Fig. 4A and B). When averaged over the whole experimental area, the mean aboveground dry biomass was 0.16 g for *P. sylvestris* and 0.06 g for *P. abies* (Fig. 3A).

The partial Mantel correlation between radiation and seedling aboveground dry biomass was significant for both *P. sylvestris* and *P. abies* (Table 2), indicating that aboveground dry biomass increased with increasing radiation (Fig. 3A). *P. sylvestris* responded more strongly to radiation than *P. abies* (Table 2, Fig. 4A and B). The correlation can be observed by comparing the maps displaying the spatial distributions of radiation and aboveground dry biomass over the experimental area (Figs. 2, 4A and B). The spatial distributions of radiation and aboveground dry biomass were asymmetrical with the gap limits, such that

Table 2

Partial Mantel statistics and probabilities between seedling variables (Y) and radiation (R), removing the effect of spatial location (L), for 2-year-old seedlings from each species and moist chilling treatment

	P. sylvestris		*P. abies*	
	r (YR.L)	*P*	*r (YR.L)*	*P*
Aboveground dry biomass				
Moist-chilled	0.472	0.001	0.180	0.006
Unchilled	0.340	0.001	0.339	0.001
Projected leaf area				
Moist-chilled	0.473	0.001	0.185	0.006
Unchilled	0.425	0.001	0.276	0.001
Height				
Moist-chilled	0.286	0.001	0.116	0.023
Unchilled	0.195	0.001	0.196	0.003
Specific leaf area$_p$				
Moist-chilled	0.286	0.001	0.005	0.397
Unchilled	0.259	0.001	0.162	0.012
Needle/stem dry biomass				
Moist-chilled	0.457	0.001	0.004	0.402
Unchilled	0.353	0.001	−0.054	0.149
Height/stem dry biomass				
Moist-chilled	0.319	0.001	0.169	0.004
Unchilled	0.312	0.001	0.420	0.001
Mean needle length				
Moist-chilled	0.484	0.001	−0.050	0.167
Unchilled	0.417	0.001	0.026	0.288

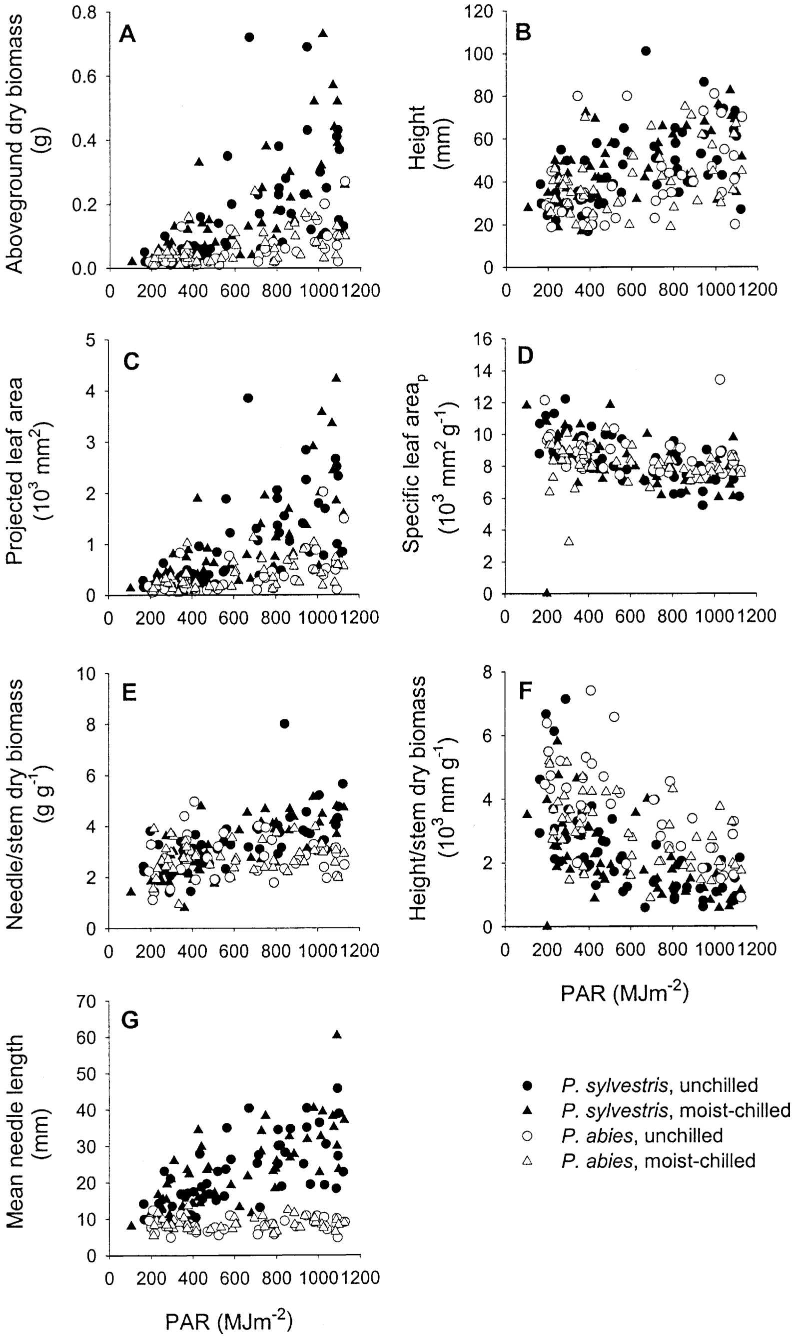

Fig. 3. Scatter plots of the distribution of seedling variables in relation to PAR for 2-year-old *P. sylvestris* and *P. abies* seedlings from moist-chilled and unchilled seeds: aboveground dry biomass (A); height (B); projected leaf area (C); specific leaf area$_p$ (D); needle/stem dry biomass (E); height/stem dry biomass (F); and mean needle length (G).

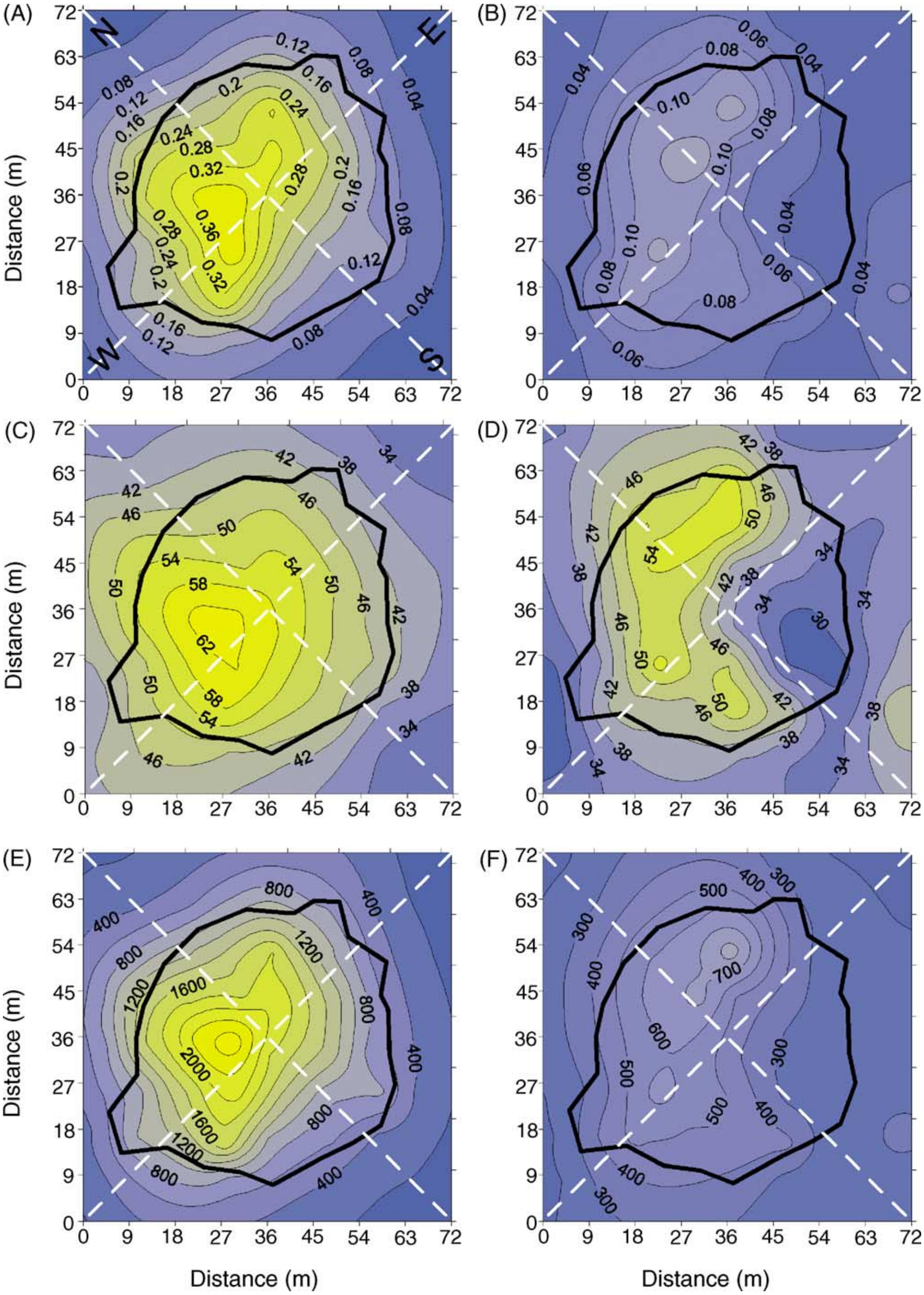

Fig. 4. Isopleths of aboveground dry biomass of *P. sylvestris* (A) and *P. abies* (B); height of *P. sylvestris* (C) and *P. abies* (D); and projected leaf area of *P. sylvestris* (E) and *P. abies* (F) 2-year-old seedlings growing along a gap-edge zone. Seedlings from moist-chilled and unchilled seeds were combined since moist chilling did not affect size significantly. The gap area is delimited by a thick black line, and the orientation is indicated by broken white lines.

maximum values were reached in the northern part of the gap. However, the location of maximum aboveground dry biomass of *P. sylvestris* and *P. abies* did not coincide with the location of maximum radiation.

P. sylvestris reached their maximum aboveground dry biomass several metres northwest of the gap centre, southwest of the radiation maximum (Fig. 4A). From this peak value (0.36 g), the aboveground dry biomass of *P. sylvestris* decreased gradually towards the gap edges and into the forest, down to 0.04 g (Fig. 4A). As a result of the asymmetric response of seedling biomass to the gap, the aboveground dry biomass of *P. sylvestris* seedlings growing in the southern part of the gap was similar to that of seedlings growing under the canopy at the northern edge of the gap (Fig. 4A).

The maximum aboveground dry biomass of *P. abies* seedlings was also attained in the northern part of the gap (Fig. 4B). However, the response of *P. abies* to the gap and increased radiation was not as strong as that of *P. sylvestris*. This was shown by the range of aboveground dry biomass attained by *P. abies* (0.04–0.12 g, Fig. 4B), which was narrower than for *P. sylvestris*. The area of maximum aboveground dry biomass attained by *P. abies* was diffuse and spread over the location of highest radiation (Figs. 2 and 4B). The isopleths of aboveground dry biomass of *P. abies* were more asymmetrical in relation to the gap limits than those of *P. sylvestris* (Fig. 4A and B). In the southeastern part of the gap, *P. abies* seedlings showed no response to the gap and increased radiation, aboveground dry biomass being as low as for seedlings growing under the canopy (Fig. 4B).

3.2.2. Height

For a given amount of radiation received, *P. sylvestris* seedlings were significantly taller than *P. abies* (Table 1), though the height difference was small. The average height after two growing seasons was 47 mm for *P. sylvestris* and 40 mm for *P. abies* (Fig. 3B). Both species showed a significant response to the gap (Table 1), such that seedling height increased with increasing radiation (Table 2). However, the response of *P. sylvestris* to radiation was slightly stronger than that of *P. abies* (Table 2, Fig. 4C and D). The spatial distribution of *P. sylvestris* and *P. abies* seedling height in relation to the gap was similar to the distribution of aboveground dry biomass (Fig. 4A–D). *P. sylvestris* were tallest in the northwestern part of the gap, several metres from the gap centre (Fig. 4C). Because of the asymmetric response of *P. sylvestris* seedlings to the gap, seedlings growing in the southern part of the gap attained heights similar to that of seedlings growing under the canopy at the northern edge of the gap (Fig. 4C). The tallest *P. abies* seedlings were found in the northern and southwestern parts of the gap (Fig. 4D). Similarly as for the spatial pattern of aboveground dry biomass, *P. abies* seedling height was shortest in the southeastern part of the gap, where seedlings were even shorter than under the canopy (Fig. 4D).

3.2.3. Projected leaf area

For both species, projected leaf area increased with increasing radiation (Table 2), i.e. projected leaf area was larger in the gap than under the canopy (Table 1, Fig. 3C). The response of *P. sylvestris* to radiation was much stronger than that of *P. abies* (Table 2, Fig. 3E and F). Accordingly, projected leaf area was larger for *P. sylvestris* ($938\ \mathrm{mm}^2\ \mathrm{g}^{-1}$) than for *P. abies* ($383\ \mathrm{mm}^2\ \mathrm{g}^{-1}$) seedlings (Fig. 3C, Table 1). For both species, the spatial distribution of projected leaf area was similar to that of seedling height (Fig. 4).

3.3. Response of seedling morphology to canopy gap

3.3.1. Specific leaf area$_p$

Specific leaf area$_p$ varied with spatial location, being lower in the gap than under the canopy for both species (Fig. 3D), as indicated by the significant effect of block (Table 1). Specific leaf area$_p$ decreased with increasing radiation (Fig. 3D), though the effect of radiation was significant for *P. sylvestris* only (Table 2). Specific leaf area$_p$ did not differ significantly between species (Table 1, Fig. 3D).

3.3.2. Needle/stem dry biomass

P. sylvestris and *P. abies* responded differently to the gap, as indicated by the significant effects of block and block × species interaction (Table 1). Needle/stem dry biomass ratio, which reflects the allocation of aboveground dry biomass to assimilating versus structural parts, increased with increasing radiation for *P. sylvestris* seedlings (Fig. 3E, Table 2). In other words, *P. sylvestris* seedlings allocated proportionally more biomass to needles than to the stem with increasing radiation (Fig. 3E). In contrast, *P. abies* did not show a significant response to radiation (Fig. 3E, Table 2). The average needle/stem dry biomass ratio was larger for *P. sylvestris* (3.20 g g^{-1}) than for *P. abies* (2.78 g g^{-1}) (Fig. 3E, Table 1).

3.3.3. Height/stem dry biomass

For both species, height/stem dry biomass ratio was higher under the canopy than in the gap (Fig. 3F, Table 1), indicating that stems were proportionally taller and thinner with decreasing radiation (Table 2). The height/stem dry biomass ratio of *P. sylvestris* was smaller than that of *P. abies* (Fig. 3F, Table 1), indicating that *P. sylvestris* had proportionally shorter and thicker stems than *P. abies*. The significant interaction between species and spatial location (block effect) shows that species responded differently to the gap (Table 1), such that the ratio decreased more sharply between the understorey and the gap centre for *P. abies* than for *P. sylvestris* (Fig. 3F).

3.3.4. Needle length

P. sylvestris and *P. abies* responded differently to the gap: mean needle length of *P. sylvestris* increased with increasing radiation, while needle length of *P. abies* did not show a significant response to radiation (Fig. 3G, Table 2). This was also shown in ANOVA, with a significant interaction between spatial location (block) and species (Table 1). *P. sylvestris* had longer needles than *P. abies* (Table 1), the average length being ca. 23 mm for *P. sylvestris* and ca. 9 mm for *P. abies* (Fig. 3G).

3.4. Response of seedling size and morphology to moist chilling

Our results showed that after two growing seasons, the moist chilling treatment did not have a significant effect on variables describing *P. sylvestris* and *P. abies* seedling size, i.e. aboveground dry biomass, height and projected leaf area (Table 1). However, some of the morphological characteristics did show a response to moist chilling.

Specific leaf area$_p$ was significantly higher for seedlings from unchilled than from moist-chilled seeds (Table 1). For *P. sylvestris*, mean specific leaf area$_p$ was 8447 and 8534 mm^2 g^{-1} and for *P. abies*, 8079 and 8812 mm^2 g^{-1} for moist-chilled and unchilled seeds, respectively (Fig. 3D, Table 1). However, *P. sylvestris* and *P. abies* did not respond differently to moist chilling, as indicated by the non-significant interaction between species and moist chilling (Table 1).

In addition, seedlings from unchilled seeds had a higher height/stem dry biomass ratio than seedlings from moist-chilled seeds (Table 1). When averaged over the whole experimental area, the mean height/stem dry biomass ratio was 2110 and 2270 mm g^{-1} for *P. sylvestris*, and 2960 and 3650 mm g^{-1} for *P. abies* from moist-chilled and unchilled seeds, respectively (Fig. 3F).

On the other hand, the moist chilling treatment did not have a significant effect on needle/stem dry biomass ratio and on mean needle length in either of the species (Table 1).

4. Discussion

After two growing seasons, *P. sylvestris* attained larger sizes, i.e. aboveground dry biomass, height, and projected leaf area, than *P. abies* across the gap-edge zone (Figs. 3 and 4). Though the size of both species increased with increasing radiation, the response was stronger for *P. sylvestris* than for *P. abies* (Table 2). As the difference in seedling height between species was small, the larger aboveground dry biomass of *P. sylvestris* seedlings is explained by its greater projected leaf area compared to *P. abies* (Fig. 3A–C). Also, shade-intolerant *P. sylvestris* responded to increasing radiation with a more variable morphology than did shade-tolerant *P. abies* (Table 2). *P. sylvestris* had longer needles than *P. abies*, and mean needle length of *P. sylvestris* increased sharply with increasing radiation, while that of *P. abies* did not vary significantly with radiation (Table 2, Fig. 3G). Accordingly, *P. sylvestris* has evolved a mechanism that allows it to increase its needle length with increasing radiation, contrary to *P. abies*, which lacks this property. As a consequence, mean needle length contributed to the greater aboveground dry biomass and projected leaf area of *P. sylvestris* seedlings compared to those of *P. abies* (Fig. 3A and C). And accordingly, *P. sylvestris* allocated proportionally more dry biomass to needles than to the stem, i.e. to assimilating parts rather than to structural parts, with increasing radiation compared to *P. abies* seedlings (Fig. 3E). A high biomass distribution to leaves means an increased potential for photosynthesis. The longer needles of *P. sylvestris* also contributed to larger specific leaf area$_p$ compared to *P. abies* (Fig. 3D). A high specific leaf area provides more leaf surface to capture light while investing less in leaf biomass, thus enhancing relative growth rate (Reich et al., 1998; Wright and Westoby, 2001). Therefore, shade-intolerant *P. sylvestris* underwent changes that allowed it to capture more light than *P. abies*, both in the gap and under the canopy. As shade-intolerant *P. sylvestris* has a higher photosynthetic capacity than shade-tolerant *P. abies* (Ceulemans and Saugier, 1991), *P. sylvestris* can compete for resources better than *P. abies*, and grow larger. However, high growth rates under the canopy have been shown to decrease seedling survival in the long run (Kobe et al., 1995).

The maps of spatial distribution show that there were differences in symmetry between the isopleths of seedling size variables and radiation (Figs. 2 and 4). The spatial pattern of radiation was relatively symmetrical in all directions, whereas the spatial pattern of seedling size varied more in shape. In addition, radiation and seedling variables converged to different locations: the location of the highest radiation was several metres north of the gap centre, with the largest *P. sylvestris* seedlings several metres west of it, and the largest *P. abies* several metres east. If seedling size were affected solely by radiation, the spatial pattern of size variables would be equal along a same radiation level, whether located in the gap or under the canopy. However, with equal radiation, *P. sylvestris* seedling size varied more under the canopy at the northern edge of the gap than in the southern part of the gap (Fig. 4). For *P. abies*, the opposite was true (Fig. 4). This suggests that gap-edge zone characteristics other than radiation also influence seedling size.

Apart from radiation, the development of seedlings is also affected by other factors along the gap-edge zone, such as root competition for water and nutrients by ground vegetation and mature trees (Caldwell et al., 1995; Nilsson et al., 1996; Örlander et al., 1996; Jäderlund et al., 1997), and herbivory (Hulme, 1996; Nystrand and Granstrom, 2000). These effects, as well as early seedling growth, are likely to depend on within-gap position, since the competition of large trees retards the growth of ground vegetation at gap edges (Kuuluvainen et al., 1993). It is possible that these contrasting factors affecting seedling growth lead to some type of gap partitioning between species, as observed in previously published results (Wayne and Bazzaz, 1993a,b; Bazzaz and Wayne, 1994; Sipe and Bazzaz, 1995; Gray and Spies, 1996).

One should keep in mind that gap partitioning originates from different seedling survival rates in different parts of the gap, due to varying environmental conditions (radiation, water, nutrients, competition from grasses, etc.). However, once seedlings are established, their growth is related to these same environmental conditions, such that *P. sylvestris* and *P. abies* may become dominant in different parts of the gap. Evidence of this was observed already after two growing seasons, with the largest *P. sylvestris* and *P. abies* seedlings found on opposite sides (east and west) of the location of highest radiation. In addition, being located in the southeastern part of the gap was detrimental to size growth of *P. abies* seedlings, such that *P. sylvestris* also dominated that area. Since *P. sylvestris* did not show reduced sizes in the southeastern part of the gap, strong competition by roots for nutrients and water is not a likely explanation for the small size of *P. abies*. However, *P. abies* emergence was slightly delayed in that area (unpublished data), which could account for the small seedling sizes. The fact that seedlings grew better in some parts of the gap than others may also be due to interactions between the mineral seedbed and microclimate. For example, the western part receives most radiation in the morning when environmental conditions are most favourable for photosynthesis, i.e. when temperatures are low and relative humidity is high (Wayne and Bazzaz, 1993a). Gap partitioning may become clearer after a longer regeneration period.

Both light quantity and quality affect seedling morphology, and as such, the phenomenon of etiolation confounds the effect of radiation on seedling morphology. *P. sylvestris* has been shown to be taller and have higher height/stem dry biomass at low red:-far-red levels, i.e. in shade (de la Rosa et al., 1998). The fact that seedlings had a high height/stem dry biomass ratio at low radiation levels, especially at <600 MJ m^{-2}, shows that seedlings were etiolated under the canopy. Decreasing stem diameters have been reported with decreasing radiation (Wang et al., 1994; Chen, 1997; Chen and Klinka, 1998; Küßner et al., 2000). A smaller diameter infers a lower stem dry biomass, and thus for a given height, a proportionally greater height/stem dry biomass. However, since red:far-red levels were not measured in this study, it is impossible to know whether the high height/stem dry biomass ratios were due to low radiation, to reduced red:far-red, or both. In this study, *P. abies* had a higher height/stem dry biomass ratio than *P. sylvestris* at all radiation levels, which means that seedlings had proportionally taller and thinner stems. This morphological characteristic infers reduced mechanical strength (Ganade and Westoby, 1999). Therefore, *P. sylvestris* had higher resistance to mechanical damage, which improved its competitive ability for establishment over *P. abies*.

In forest regeneration by direct seeding, seed moist chilling is used to widen the environmental range for germination by relieving seed dormancy (Gosling and Peace, 1990; Leinonen and Rita, 1995; Leinonen, 1997). As such, moist-chilled seeds can germinate earlier than unchilled seeds, and seedlings can benefit from a longer growing season. Nonetheless, our results show that moist chilling had a negligible effect on seedling size after two growing seasons. However, some seedling morphological variables were affected by moist chilling. Seedlings from moist-chilled seeds had lower specific leaf area$_p$ than seedlings from unchilled seeds (Table 1, Fig. 3D). Since seedlings from moist-chilled seeds germinated earlier than seedlings from unchilled seeds (unpublished results), this result is in accord with Sellin and Fenner (2001), who reported that specific leaf area$_p$ decreases with foliage age. Also, seedlings from unchilled seeds had higher height/stem dry biomass than seedlings from moist-chilled seeds (Table 1, Fig. 3F). Having germinated earlier (unpublished results), seedlings from moist-chilled seeds may have begun diameter growth at the time of measurement, contrary to seedlings from unchilled seeds. Stem diameter growth implies increased stem dry biomass for a lower height/stem dry biomass ratio.

Differences in aboveground seedling size and morphology affect the abilities of each species for competition and establishment (Goulet and Bellefleur, 1986; Zobel and Antos, 1991; Tremmel and Bazzaz, 1995). However, the overall competitive ability of a species is given by the combination of morphological strategy and physiological features. Although early development is important for establishment success, the physiological capacity (photosynthesis and respiration) of seedlings was not measured in this study. Consequently, our results cannot predict with certainty that *P. sylvestris* will outcompete *P. abies* in similar gap environments. Shade-intolerant *P. sylvestris* is more sensitive to shade and, therefore, may be less competitive than shade-tolerant *P. abies* at gap edges or in a shelterwood silvicultural system. In addition, *P. abies* is able to survive better than *P. sylvestris* when growing in the presence of competing vegetation (Jonsson, 1999).

One limitation of this study is the lack of replication in several gap-edge zones. As such, the results show only one possible outcome of seedling establishment in a gap-edge environment. Also, the fact that our seedbed was mineral soil limits the application of these results to regeneration from seeding, either artificial or natural, in combination with soil preparation to expose the mineral soil.

5. Conclusions and practical implications

Because of the asymmetric distribution of PAR in the gap and its surroundings, which was due to solar geometry at high latitudes, the highest amount of radiation was received several metres north of the gap centre. As a result, seedlings growing under the canopy at the northern edge of the gap received amounts of radiation that were similar to those received by seedlings growing in the southern part of the gap.

During the early development of seedlings, shade-intolerant *P. sylvestris* underwent size and morphological modifications that allowed it to capture more light and compete better for resources than shade-tolerant *P. abies* in gap and gap-edge environments. Size of both species increased with increasing radiation, but *P. sylvestris* responded more strongly than *P. abies*. As height difference between species was small, the greater aboveground dry biomass of *P. sylvestris* seedlings was explained by its larger projected leaf area compared to *P. abies*.

In addition, *P. sylvestris* responded to radiation with a more flexible morphology than *P. abies*, allowing *P. sylvestris* to increase its needle length with increasing radiation. Longer needles contributed to increased aboveground dry biomass, projected leaf area, and specific leaf area$_p$. Consequently, with increasing radiation *P. sylvestris* seedlings allocated proportionally more aboveground dry biomass to assimilating parts versus structural parts compared to *P. abies*. However, the lack of convergence between the spatial distributions of seedling size variables and radiation indicates that seedlings were also affected by environmental factors other than radiation.

It can be judged from the asymmetric distributions of radiation and seedling size responses in relation to the circular gap (see Figs. 2 and 4) that in order for seedlings to benefit optimally from radiation, gaps should have an elongated shape and they should have a north–south orientation. This shape and orientation of gaps would maximise the area receiving the most radiation in the central part of the gap, while simultaneously minimising the area receiving the least radiation at the southern edge of the gap.

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