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Tree Regeneration in Artificial Canopy Gaps Established for Restoring Natural Structural Variability in a Scots Pine Stand

Seppo Rouvinen and Jari Kouki

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In Finland and elsewhere in Europe, many protected forest areas include also stands that were previously managed and that lack several naturally occurring stand characteristics. In these areas, ecosystem restoration can be used to facilitate and accelerate the formation of structural and habitat features resembling those of natural forests. For example, by creating small gaps it could be possible to diversify forest structure and tree species composition and to produce dead wood while still maintaining mostly continous canopy coverage. We examined experimentally the effects of artificial gap formation on post-disturbance tree regeneration in the gaps in a young protected, but formerly commercially managed pine (*Pinus sylvestris* L.) dominated forest. In the experimental sites, gap size and the portion of girdled trees out of all treated trees (girdled and felled trees combined) in the gaps varied. Natural and artificial (direct seeding of silver birch *Betula pendula* Roth) tree regeneration and development was monitored both on disturbed (scarified soil patches) and undisturbed forest floor during three growing seasons. Results show that gaps can be valuable in diversifying stand structure but to be successful and rapid, tree regeneration needs disturbed forest floor. Pine regenerated numerously, but birch had clearly lower regeneration, especially on small-sized gaps. In conclusion, increasing tree diversity in young pine-dominated forests seems to be difficult when only small artificial gaps are used. But even small gaps can be used to create and maintain diverse cohort structure of the dominant species and thus they can contribute to restoration goals.

Keywords ecosystems, diversity, restoration
Addresses University of Eastern Finland, School of Forest Sciences, Joensuu, Finland
E-mail jari.kouki@uef.fi, seppo.rouvinen@uef.fi
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1 Introduction

The human influence on forests varies considerably in different part of boreal vegetation zone. Natural or semi-natural forests still prevail over large regions in northern Canada and Russia, but in more populated regions, such as in Fennoscandia, forest ecosystems have been fundamentally altered by past human utilization. This applies not only to managed forests, but also many protected, currently unmanaged areas have a long history of utilization before they were established as reserves (Metsähallitus… 2000, Working group… 2000, Josefsson et al. 2009). This causes a challenge for forest conservation, since the conservation value of these forests is also reduced because of the habitat degradation. Degraded forests will eventually return to more natural habitats but ecosystem restoration can be used to accelerate the formation of structural and habitat features resembling those of natural forests (Kuuluvainen et al. 2002). Restoration of natural ecological characteristics in young, managed stands is particularly challenging, because there are typically no large quantities of living or dead wood available and because the deciduous phase has often been removed from the early succession of managed forests. The restoration of natural young stands are very rarely studied and – especially in Fennoscandia – they remain as a major challenge when developing restoration guidelines (Kouki et al. 2001, 2011).

Ecosystem restoration often aims at initiating long-term natural developmental processes, such as tree successions and dead tree formation, or paludification (Tukia 2000, Working group… 2003). In Finland, most of the restoration studies have focused on drained peatlands, while restoration of forests on mineral soils has received much less attention (Kuuluvainen et al. 2002, Komonen and Kouki 2008, Kouki et al. 2011). Lack of dead wood in the forests is obvious in Fennoscandia (Siitonen 2001). Consequently, many current restoration methods aim at increasing the amount and diversity of dead wood, so that habitat requirements of threatened forest biota can be met (Tikkanen et al. 2006, Kouki et al. 2011). Current methods of restoration on mineral soils include prescribed burning of stands, which increases the amount of dead wood and initiates a natural succession, forming dead wood artificially by girdling or felling, and imitating gap dynamics by creating small openings (gaps) in even-aged stands (Tukia 2000, Tukia et al. 2001, Kouki et al. 2001). During the period 2003–2009, over 15 000 ha (2140 ha/year) of forest land in protected areas was restored in Finland, mainly using gap felling and related procedures. For the period 2010–2016, additional 13 000 ha (1850 ha/year) is planned to be restored. There is urgent need to understand what are the ecological consequences of these recent and widely applied activities.

Increasing evidence points to the importance of small-scale disturbances in different types of boreal forest ecosystems (Steijlen and Zackrisson 1986, Leemans 1991, Kuuluvainen 1994, Kuuluvainen et al. 1998, Rouvinen 2002, Kneeshaw and Bergeron 1998, Lewis and Lindgren 2000). Although the significance of small-scale disturbances has been recognized for decades in Fennoscandia (e.g. Sernander 1936, Sirén 1955), it has received relatively little attention in comparison to large-scale disturbances such as fires (e.g. Zackrisson 1977, Wallenius 2011). Small-scale disturbances are, however, important since they create structural heterogeneity on multiple scales, from the pit-and-mound microtopography formed by uprooted trees to the deaths of small understorey trees, canopy trees or groups of trees. All these contribute to local tree regeneration and succession (Kuuluvainen 1994, Kuuluvainen and Juntunen 1998, Ulanova 2000). In addition, if the fallen trees are left in the gaps, creation of small openings rapidly accelerates the formation of forest structures, such as dead wood (coarse woody debris, CWD).

Forests with a wide range of gap sizes can be expected to offer good possibilities for the regeneration of trees. Microhabitats vary among gaps, within gaps, at the gap / closed canopy interface (gap edge) and within the forest stand matrix (Coates and Burton 1997). In reality, the observed patterns of tree recruitment are the result of a broad suite of factors. In addition to gap characteristics, annual variation in seed production, seed dispersal opportunities (abundance, location and arrangement of parent trees), type and distribution of seedbeds and their favorability, microclimate, potential for vegetative reproduction and the abundance of seed and seedling predators affect regeneration (Grubb 1977, Greene et al. 1999, Wagner and Lundqvist 2005). All these factors can cause major spatial and temporal variation in seedling recruitment, making it difficult to show the effects of that gap characteristics cause. Obviously, rigorous and controlled field experiments can be valuable in separating the significance of gap characteristics on tree recruitment.

The most important gap characteristics seem to be related to light. Light availability can vary sharply inside gaps and, thus, within-gap variation is considered to be critically important to the growth of individual tree seedlings (Wayne and Bazzaz 1993, Sipe and Bazzaz 1995). Light available at ground level throughout forest stands are directly related to gap size, shape, canopy height orientation and latitude (Canham et al. 1990). Although light availability is clearly important, many studies have shown that also other factors play important role in regeneration success (e.g. Kuuluvainen 1994, Gray and Spies 1997, Kuuluvainen and Juntunen 1998, Wright et al. 1998, Kobayashi and Kamitani 2000) and the actual effects of light still require further exploration.

More refined studies on how canopy gaps influence tree regeneration hold the most promise for better predicting tree regeneration and successional dynamics following restoration activities in boreal forests. In this study, we focused on effects of small, artificial gaps as a restoration method in a young Scots pine (*Pinus sylvestris* L.) dominated forest on mineral soil. By creating small gaps, it may be possible to diversify forest structure and tree species composition and to produce more dead wood while still maintaining continous forest cover and typical microclimate. The aims of this study were to examine the effects of artificial gap formation and forest floor disturbance on regeneration of pine and broadleaf species and their development over three growing seasons. The effects of gap characteristics (gap size and canopy openness), within-gap variation and within-gap microhabitat variability (disturbed vs. undisturbed forest floor) were experimentally manipulated and examined in field settings.

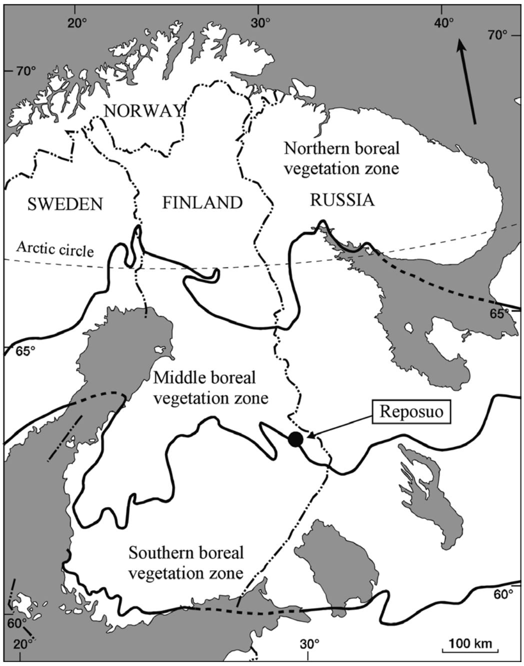

Fig. 1. Geographical location of the Reposuo study area.

2 Material and Methods

2.1 Study Area

The study area was located in Reposuo (63°20’N, 30°14’E) in North Karelia, eastern Finland, in the transition zone between the southern and middle boreal vegetation zones (*sensu* Ahti et al. 1968) (Fig. 1). The area is state-owned (administrated by Metsähallitus), protected and included in the Natura 2000 conservation network of the European Union. The area is located at approximately 125 m a.s.l. The mean temperature of the coldest month (February) was –9.8°C and of the warmest month (July) +17.5°C during the period 2000–2010 (data from nearby Mekrijärvi Research Station). The annual precipitation is 601 mm, half of which falls as snow (Drebs et al. 2002). The growing season is approximately 150 days (from early May to early October) and the effective temperature sum is 1050 degree days (threshold value of +5°C for the daily mean temperature) (Alalammi 1988). A permanent snow cover is normally present from the middle of November to early May (Solantie et al. 1996).

The study area was located on a dryish *Vaccinium* type forest (rather poor fertility, class VT according to *V. vitis-idaea*, based on the Finnish site type classification, Cajander 1926). The dominant tree layer was composed of 30–35 years old Scots pines. There were also scattered individuals of birch (*Betula pendula* Roth and *B. pubescens* Ehrh.), aspen (*Populus tremula* L.), willow (*Salix caprea* L.), rowan (*Sorbus aucuparia* L.) and spruce (*Picea abies* (L.) Karst.), but they did not occur in the dominant canopy layer. The understorey vegetation consisted mainly of dwarf shrubs (*Vaccinium vitis-idaea*, *V. myrtillus*, *Calluna vulgaris*), mosses (*Pleurozium schreberi*, *Hylocomium splendens*, *Dicranum* spp.) and lichens (*Cladina* spp.).

The dominant height of trees was 7 m, the basal area was 12 m^2 ha^{-1} (of which pine composed 99.2%) and the volume of the growing stock was 55 m^3 ha^{-1}. The forest was regenerated by artificial sowing after clear cutting in the late 1960s. Thinning was carried out 15 years after seeding, but other silvicultural treatments, like second thinning and fertilisation, were not applied.

2.2 Study Design and Field Measurements

The study was conducted on an area of 22 ha. Within the area, circular artificial canopy gaps with random locations were established, with a minimum distance between gaps of 30 m. Gap diameter was scaled to the dominant height (h_{dom}) of the adjacent forest (h_{dom} ranged from 6 to 10 m within the study area): the gap diameter to tree height ratios for the four gap sizes were 0.5, 1.0, 1.5 and 2.0 (thus, absolute gap diameter variation was 3–20 m). All trees within gaps were either felled or girdled, but their proportions varied. The proportion of felled trees was 0, 25, 50, 75 or 100%, which was denoted as “canopy openness”. Each gap size / canopy openness combination was replicated three times, and thus the total number of gaps was 60 (4 gap size classes x 5 canopy openness classes x 3 replicates = 60 treatments, i.e. gaps). Gaps were created in April 2003 by chainsaw felling or girdling (bark removal, one vertical band of about 40 cm that completely encircled the tree) all pines over 1.3 m tall within the gap perimeter. All felled trees were left on the area. Standing dead trees present before gap creation were not felled, and fallen dead trees were disturbed as little as possible.

In late May 2003, tree regeneration study was initiated. In the two small-sized gaps (classes 0.5 and 1.0), four 40 x 60 cm seeding plots were established. The litter and humus layer was removed on two of the plots: one plot was left unseeded (referred as ‘disturbed’), the other was seeded with 60 seeds of silver birch (*B. pendula* Roth) on two rows of 30 seeds (‘disturbed and seeded’), and the humus layers were put upside down as mounds beside the plots. On the remaining two plots, humus layer was not disturbed: one was left unseeded (‘undisturbed’), the other was seeded by 60 seeds of birch (‘seeded’). These four plots were established around the central pole of the gap with 1.0 m distance, the first north-east, the second south-east, the third south-west and the fourth north-west of the central pole, and the treatments were randomly assigned on the plots. In the two large-sized gaps (classes 1.5 and 2.0), 12 seeding plots were established on three west-east lines with 1.5 m plot distance along the line and the treatments were randomly assigned on the plots. To study regeneration on different parts of the gap, three transects were established: 1) on the center, 2) on the southern half and 3) on the northern half of the gap. The distance of the southern and northern lines from the gap edge were standardized to be 1.5 m. All the plots were established on a level ground without rocks, stumps or other similar structures. The sites were rather homogeneous and suitable level ground was readily available everywhere. In total, each larger gap included 12 experimental plots. Seeds used were of local origin and their source was unambiguously identified (EY/FIN/M29-93-0004). According to the standard germination test (International Seed… 1985), the viability (21-day test) of seed was 64%. In the artifical seeding trials we used only silver birch (*B. pendula*) seedlings but not pines for two reasons: 1) we wanted to study if birch can establish into gaps but the natural seeding was probably very low because of the shortage of birches in the study sites, and 2) adult pines were so common and seed source therefore secured.

Tree regeneration was measured at the end of the first (2003), second (2004) and third (2005) growing season. The number of living seedlings of each tree species was counted and the germination year was recorded. Seedling height was measured at the end of the third growing season (2005). Since small birch seedling are hard to identify to species level and since there is a possibility that also naturally originated *B. pubescens* seedlings are included in the data, we use the term *Betula* spp. when presenting results.

2.3 Statistical Analyses

Depending on the normality of the variable distributions and homogeneity of the variances, the parametric analysis of variance (ANOVA) or non-parametric Kruskal-Wallis test was used to analyse the differences in the number of seedlings and seedling size among the gap sizes, canopy openings and in the larger gaps also among gap positions. If a significant difference ($p < 0.05$) in dependent variable was observed, pairwise comparisons were applied, using Tukey test (when ANOVA was used) or with the comparable non-parametric method introduced by Zar (1974: 156) (when Kruskal-Wallis was used). Mann-Whitney test was used to analyse the effect of artificial seeding on birch regeneration on disturbed forest floor. The analyses were performed only on data measured in year 2005.

3 Results

3.1 Seedling Establisment

No birch seedlings were found on the undisturbed plots in years 2003 and 2004, but in 2005 there was one pine seedling on those plots. As the number of seedlings was insignificant on the undisturbed plots, those plots were excluded from the rest of the analyses.

On the disturbed plots there were a total of 82, 1264 and 869 living seedlings present in year 2003, 2004 and 2005, respectively (Table 1). In each year, most of the seedlings were pines and although birch was also found, the number of birch seedlings was low. There were more birch seedlings in the plots disturbed and seeded compared to plots disturbed only. Scattered aspens and rowans, as well as one willow, were of root sucker origin.

Table 1. Total number of seedlings found on the disturbed ground plots in September 2003, 2004 and 2005 by the year of establishment and tree species. The values are represented as pooled data and birch (*Betula pendula* and *B. pubescens*) also by treatment classes in parentheses ('disturbed' + 'disturbed + seeded').

Year of measurement Species	Year of germination 2003	 2004	 2005
2003			
Pinus sylvestris	68		
Betula spp.	10 (0+10)		
Populus tremula	4		
2004			
Pinus sylvestris	43	1114	
Betula spp.	5 (0+5)	94 (17+77)	
Populus tremula	2	5	
Sorbus aucuparia	–	1	
2005			
Pinus sylvestris	31	613	135
Betula spp.	4 (0+4)	47 (8+39)	21 (8+13)
Populus tremula	2	5	9
Sorbus aucuparia	–	1	–
Salix spp.	–	–	1

Seedlings found in year 2005 were predominantly established in the previous year, although many seedlings established in year 2004 had died in 2005 (Table 1). Only 55% of pines and 50% of birches established in year 2004 were found in the following year. The same decreasing pattern with time was also detected in pines and birches established in year 2003, but as time went on mortality rate of seedlings decreased. The number of established pines and birches in year 2004 was high compared to years 2003 and 2005.

3.2 Tree Regeneration on Disturbed Forest Floor and Gap Characteristics

No birches were found in the smallest gaps (gap size 0.5) (Fig. 2). The intermediate sized gaps (gap sizes 1.0 and 1.5) had some birch seedlings and the amount of birch seedlings (per study plot) was highest in the large sized gaps (gap size 2.0). The number of birch seedlings was higher on the disturbed and seeded plots compared to plots disturbed only in each gap size, but the differences due to seeding were not statistically significant. Pooled birch data (seedlings on the disturbed and disturbed and seeded plots combined together) differed significantly between gap sizes, and the pairwise post-hoc tests showed that the difference was statistically significant only between gap sizes 0.5 and 2.

Pine from natural seeding regenerated significantly better compared to birch. The highest mean for the gapwise numbers of pine seedlings was obtained for the smallest gaps (gap size 0.5), but the difference between gap sizes was not statistically significant.

No birches were found in the gaps in which all of the trees were girdled (canopy opening = 0), and usually the highest number of birches (per study plot) was found in the gaps that had mixture of girdled and felled trees (Fig. 3). The mixture of girdled and felled trees also seemed to favour establishment of pines. However, the differences were not statistically significant.

On an average, there were more birch seedlings in the center and southern part of the larger sized gaps (Fig. 4), especially in gaps of diameter 2.0, where the difference among gap locations was statistically significant so that center and northern part differed each other. Pine regenerated abundantly in all the gap locations.

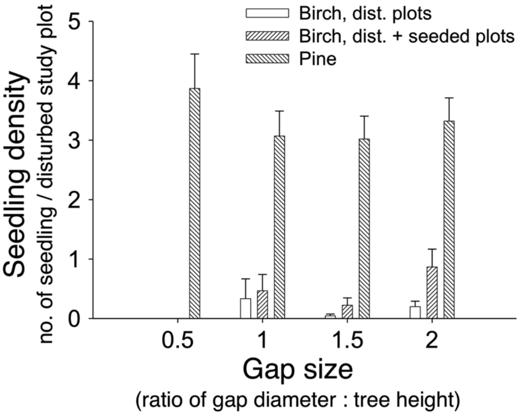

Fig. 2. Mean density of birch (*Betula pendula* and *B. pubescens*) and Scots pine (*Pinus sylvetsris*) seedlings in year 2005 by gap size on disturbed ground plots. Pine is represented as pooled data (seedlings on the disturbed and disturbed and birch seeded plots combined together) and birch by treatments: “Birch, dist. plots” = birch found on the disturbed plots, “Birch, dist. + seeded” = birch found on the disturbed and birch seeded plots. Error bars represent one standard error of the mean.

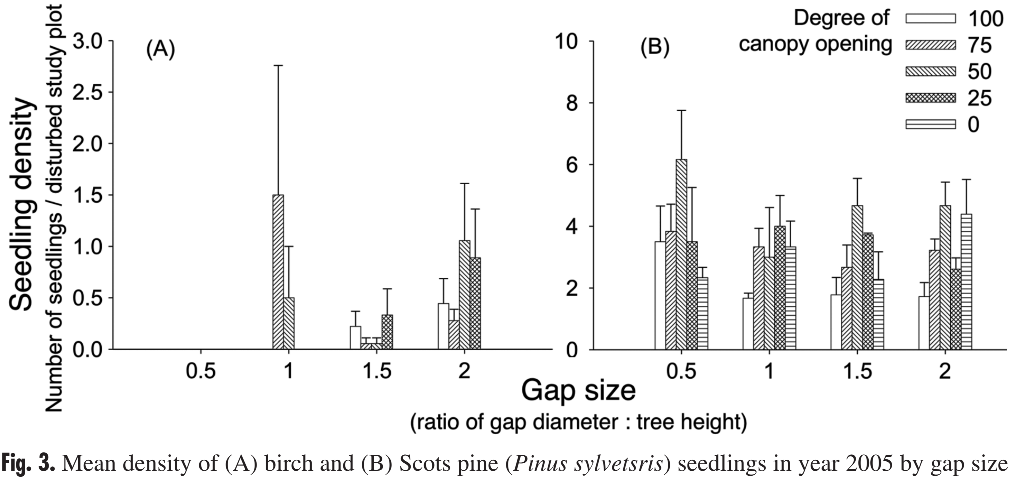

Fig. 3. Mean density of (A) birch and (B) Scots pine (*Pinus sylvetsris*) seedlings in year 2005 by gap size and canopy opening on disturbed ground plots. Error bars show one standard error of the mean.

Table 2. Mean seedling height, cm (± standard deviation) of Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula* and *B. pubescens*) in year 2005 by germination year and gap size. Number of seedlings is presented in parentheses. For larger gaps (gap sizes 1.5 and 2.0), data are pooled for all gap locations.

Species & germination year	Gap size			
	0.5	1.0	1.5	2.0
P. sylvestris, 2003	4.67 ± 2.08 (3)	6.20 ± 2.59 (5)	4.18 ± 0.98 (11)	5.33 ± 1.83 (12)
P. sylvestris, 2004	2.81 ± 0.67 (97)	3.00 ± 0.86 (74)	2.81 ± 0.70 (215)	2.93 ± 1.00 (227)
P. sylvestris, 2005	2.06 ± 0.25 (16)	1.54 ± 0.52 (13)	2.11 ± 0.43 (46)	2.03 ± 0.37 (60)
Betula spp., 2003	–	–	2.50 ± 0.71 (2)	20.00 ± 9.90 (2)
Betula spp., 2004	–	2.75 ± 1.28 (8)	1.80 ± 0.84 (5)	3.94 ± 2.27 (34)
Betula spp., 2005	–	1.25 ± 0.50 (4)	1.0 ± 0.00 (5)	1.25 ± 0.45 (12

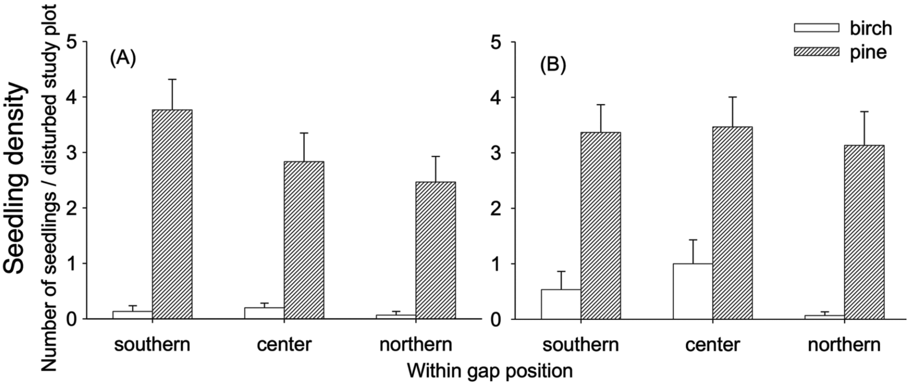

Fig. 4. Mean density of birch (*Betula pendula* and *B. pubescens*) and Scots pine (*Pinus sylvetsris*) seedlings in year 2005 by within gap position on disturbed ground plots of (A) gap size 1.5 and (B) gap size 2.0. Error bars show one standard error of the mean.

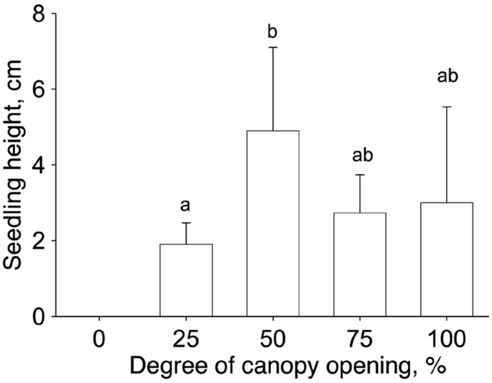

Fig. 5. Mean height of two years old birch (*Betula pendula* and *B. pubescens*) seedlings by canopy opening. Error bars show standard deviations. The different letters indicate significant difference at the $p < 0.05$ level between the canopy openness classes (Tukey test).

3.3 Seedling Size and Gap Characteristics

Size of pine and birch seedlings that germinated in year 2003 varied greatly within the gap size classes (Table 2), but the difference between classes was not statistically significant. Average size of younger seedlings, those germinated in 2004 or 2005, varied slightly between gap sizes but the difference was not statistically significant.

Pine height by germination years did not differ between the canopy openness classes. Birch seedlings germinated in 2004 were taller in the gaps that had both girdled and felled trees (Fig. 5), but those germinated in 2005 did not differ in height. Oldest birches were found only in the gaps that had all treated trees as felled ones (canopy opening = 100%).

Table 3. Mean seedling height, cm (± standard deviation) of Scots pine (*Pinus sylvestris*) and birch (*Betula pendula* and *B. pubescens*) in year 2005 by germination year and within gap position on the large sized gaps (gap size 1.5 and 2.0). Number of seedlings is presented in parentheses. The various letters indicate significant difference at the $p < 0.05$ level between the within gap position classes.

Species & germination year	Within gap position southern	 center	 northern
P. sylvestris, 2003	4.75 ± 1.71 (4)	5.40 ± 1.78 (10)	4.11 ± 1.05 (9)
P. sylvestris, 2004	2.85 ± 0.99 (172)^{b}	3.11 ± 0.86 (131) ^{a}	2.68 ± 0.64 (139) ^{b}
P. sylvestris, 2005	2.00 ± 0.33 (38)	2.10 ± 0.37 (48)	2.00 ± 0.55 (20)
Betula spp., 2003	–	14.00 ± 12.53 (3)	3.00 ± 0.00 (1)
Betula spp., 2004	2.70 ± 2.36 (10) ^{ab}	4.27 ± 2.11 (26) ^{a}	1.67 ± 0.58 (3) ^{b}
Betula spp., 2005	1.0 ± 0.00 (10) ^{b}	1.43 ± 0.53 (7) ^{a}	–

Pines germinated in 2003 and 2005 did not show within-gap variation in height, but those germinated in 2004 did (Table 3). Height of birch seedlings germinated in 2004 and 2005 also differed within gap position.

4 Discussion

Three growing seasons after logging, tree seedling recruitment was insignificant on plots that situated on undisturbed forest floor. Depending on tree species, recruitment on disturbed forest floor was abundant (pine) or scanty (birch and other deciduous trees). The observed pattern is not surprising: the favorability of microsites with exposed mineral soil for pine and birch regeneration has been recognized for decades (e.g. Aaltonen 1919, Lehto 1956, Yli-Vakkuri 1961a, b, Hagner 1965, Kuuluvainen and Juntunen 1998). As noted by the previous authors, the presence of undisturbed layer has several effects on germination: it has poor water holding capacity and different thermal properties than mineral soil, and it may present a barrier to root penetration of germinants to underlying soil. The presence of ground and floor layer vegetation may impose competitive effects on tree seedlings (Nilsson and Wardle 2005).

In our study sites, pine regenerated more vigorously than birch on the disturbed plots, although it was not artificially seeded. There can be several reasons for that. Firstly, birch is shade-intolerant tree species while pine is more shade tolerant (Nikolov and Helmisaari 1992). Thus, low light level on a gap can prohibit regeneration and development of birch more than that of pine. Lack of birch regeneration in low light level can be seen as an absence of birch seedlings on small sized and shady (=low level of canopy opening) gaps. Secondly, our study site was dryish and quite infertile. Although birch is rather drought- and nutrient-stress-tolerant, it requires higher soil moisture and more nutritious soil compared to Scots pine (Nikolov and Helmisaari 1992). Thirdly, nearly all of the few pre-logging birches (*Betula* spp.) that we found were young and small-sized, certainly not able to form seed crops. Dominant pines were 30–35 years old and capable to produce seeds (Nikolov and Helmisaari 1992). Consequently, natural birch seeding was not able to compensate possible failures in artificial, direct birch seeding. In addition, seed crops of birch were poor in our study area in studied years (Finnish Forest… 2006), as evidenced by lack of birch in unseeded disturbed study plots. Pine regeneration, instead, did not suffer from the lack of seeds as seed crops of pine were abundant, especially in year 2004 (Finnish Forest… 2006). These tree- and stand-level factors are likely to explain the failure of birch regeneration and the success of pine regeneration in our study sites.

Many of the new seedlings died during the first winter and next summer. The loss continued during the following winter and summer, but after that the mortality rate of seedling cohorts decreased. This is in agreement with regeneration studies done in Finland (Yli-Vakkuri 1961a, b), Sweden (Steijlen et al. 1995, Beland et al. 2000), Canada (Wright et al. 1998) and Alaska (Zasada et al. 1992). During the first winter, small seedlings are most vulnerable to factors like frost heaving and freezing, and microsite flooding and drought probably cause mortality during the second growing season.

Regeneration of a disturbed site often occurs over a period of several years rather than all at once (Zasada et al. 1992). The establishment of new, natural regeneration in any given year depends on the coincident occurrence of abundant viable seeds, seedbed conducive to germination of a given species, and favorable microenvironment for germination and establishment. Each year, these factors differ, and regeneration of a given species consequently fluctuates. In our study, most seedlings found in 2005 were established in 2004. There are probably several reasons for that. Firstly, there was a better seed crop of especially pine in year 2004 compared to years 2003 and 2005 (Finnish Forest… 2006). Secondly, as seeding plots were prepared in late May 2003, some of the pine seed rain of 2003 may have landed before plots were done since the seed rain typically begins earlier in spring (Heikinheimo 1932, 1937, Hannerz et al. 2002). Thirdly, during the latter years, re-vegetation already partly covered the disturbed plots and in the gaps with girdled trees also fallen bark was accumulating on the ground (personal observation). The decreasing trend with time in tree seedling establishment on prepared soil surface has been detected in several studies (e.g. Beland et al. 2000, Karlsson and Örlander 2000) but it is also clear that our study period is still rather short and that trends we observed may be transient.

Birch, one of the least shade-tolerant species in these forests (Nikolov and Helmisaari 1992) had greatest densities in large-sized gaps and was totally missing in the smallest-sized gaps. Recruitment of pine was completely unaffected by gap sizes, canopy openness classes and within-gap variability, demonstrating a wider amplitude in micro-habitat for pine regeneration. Scattered aspen, rowan and willow regeneration was of root sucker origin, and hence initial distribution of these species is more strongly tied to parent tree location and soil surface disturbance than to other gap characteristics. It is notable, however, that the gaps in our study were rather small (up to 20 m at most). Such gap sizes are typically used in restoration activites in Fennoscandia but whether larger gaps could provide advantages remains to be studied.

Interception of radiation and precipitation by tree crowns may reduce seed germination and seedling growth (Kuuluvainen et al. 1993), but several studies have indicated that in dry pine forests, seedling growth and survival is more affected by below-ground competitive interactions than by competition for light (Aaltonen 1919, Kalela 1942, Kuuluvainen and Juntunen 1998). Also the current results emphasize the importance of forest floor disturbance in seedling germination, growth and survival of pine.

Number of pine seedlings tended to be highest when a gap included both girdled and felled trees on site. Thus, the mixture of tree-level restoration treatments improves regeneration, possibly by moderating microclimate or providing spatial heterogeneity. Previous studies indicate that shade from logs may facilitate seedling establishment in gaps by providing moist or cool microsites (Aaltonen 1919, Gray and Spies 1997). Studies in clearcuts have found that shade of coarse woody debris and stumps enhances seedling survival, often more effectively than shade from live vegetation (Gray and Spies 1997 and references therein). Our study indicates that partial shade of standing dead trees may be important for successful regeneration. Birch germination, however, did not show any clear relationship to canopy opening, except that there were no birch seedlings on the gaps where all the treated trees were girdled. However, the results on birch germination variation within gap position demonstrate that overstory and understory shaded microsites can also favour birch establishment. Several studies have indicated that germination and early survival rates may be lowest in the exposed north end of gaps due to drought stress and high surface temperatures caused by direct solar radiation (e.g. Gray and Spies 1996, Coates 2002).

Mean seedling height did not differ among the gap sizes and the detailed analyses showed differences between canopy openness classes only for birches germinated in 2004. Seedling height within the large-sized gaps, however, differed: mean height of seedlings was greatest in the center of gaps. Similar results of height separation have been reported for many tree species (Aaltonen 1919, Gray and Spies 1996, Coates 2000, Page and Cameron 2006) but our study period is still too short to draw more general or final conclusions on seedling heights.

In conclusion, increasing diversity of trees in young pine-dominated forests seems to be difficult when small artificial gaps are used. However, even small gaps can be effective in creating size and age variation of the dominant species and, thus, to increase structural heterogeneity. Our results also suggest that availability of suitable substrates is the primary factor limiting seedling recruitment following gap logging. It is thus possible that some site preparation may be necessary to achieve the goals of restoration but such preparations should closely mimic naturally occurring disturbances if implemented in conservation areas. The differences on seedling number and height between gap size, canopy openness class and gap position were usually small, especially in pine. However, it must be kept in mind that our study was done on a homogeneous site that does not represent all the circumstances found in comparable pine forests in Finland. Furthermore, longer-term recruitment studies are needed to verify the regeneration patterns in the gaps. For example, it is not clear if the favorable locations for emergence and early establishment of germinants are also favorable for growth and survival of established seedlings (Schupp 1995). Several studies from temperate forests have indicated that this is not necessarily so (e.g. Wright et al. 1998, Coates 2002, Page and Cameron 2006). Obviously, there must be a better understanding of the role of microhabitats in regeneration dynamics and maintenance of tree species mixtures and different cohorts of each tree species when silvicultural and ecological restoration systems emulating natural structural and compositional features for pine forests are developed.

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