Forest regeneration and edge effects – An ecophysiological analysis after gap-cutting

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Abstract

As continuous cover forestry is an ongoing topic in todays forest debate, questions are raised about eventual issues connected to the management. It is known that seedling performance can be poor near the edge of harvested areas, and around retained trees. This is a critical issue in transitioning toward continuous cover forestry. In the current thesis, seedling abundance and biomass was quantified as a function of the distance to overstory trees after gap-cutting. The gaps had been either planted, planted and scarified, or left as untreated controls. In each gap, sample plots (2m radius) were laid out at distances -10 m (outside the gap, under canopy), 3 m, 10 m and 20 m. Incoming radiation and soil moisture was also measured in each gap. Seedling foliar nitrogen and isotopic analyses ($^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratio) were also performed to investigate potential causes of observed patterns. Results showed a clear reduction of growth (94%) at the edge compared to the center of the gaps. Proximity to edge-trees had negative effect on both seedling density and biomass, irrespective of treatment. Nitrogen concentration and $^{15}N/^{14}N$ was lower along the gap edge, while $^{13}C/^{12}C$ showed the opposite. No signs of light and soil moisture as limiting factors for seedlings growth could be observed. The results implied that competition for nutrients, mainly N, from retained edge-trees was restraining seedlings. The results also indicated presence of a N-source accessible for center-seedlings but not edge-seedlings, which could be decomposing mycorrhizal mycelium.

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1. Introduction

The direction of today's forest management with clear-cut, scarification and planting are partly coming from decisions made long ago. When dimension-harvesting was implemented, with purpose of protecting forests, the effect was not as expected (Kardell 2004). Only larger trees were harvested to let new seedlings establish and smaller trees grow bigger before harvest. The negative effects of this practice were seen mainly in poor regeneration, where new seedlings were negatively affected by remaining trees. Due to these regeneration and growth problems, forests became sparse with trees of low quality. Later, the effect of soil treatment on regeneration was discovered and clear-cuts, mechanized soil scarification and planting became the winning forest management method for new forest stands with successful regeneration. Today, clear-cuts are a debated topic, as are alternative practices, where benefits are highlighted while the difficulties are less commonly mentioned. The problems with regeneration and seedling growth are still present and specifically important when ideas of changing forest management and reduction of harvest areas are present. This study touches the issue of seedling growth connected to retained edge-trees, in this case gap-cutting.

1.1 Alternative forest management

Decades ago, most laws concerned protection of young forests and problems with uneven logging levels (Ekelund & Hamilton 2001). Until 1993, forest politics in Sweden had its main focus on economic values, which meant that management for wood production was prioritized (Skogsstyrelsen 2021). In 1993, it was stated that forest management should include environmental goals as well as production goals. Biodiversity must be preserved and other interests such as culture and recreation must be considered when managing the forest (Swedish Forest Agency 2020). Some parts of nature conservation in forest management are particularly important. Among these are to not create large harvest sites, avoid damaging rare biotopes and to retain brush, single trees or groups of trees when harvesting. Leaving single trees, living or dead, and groups of trees at every harvest is essential today. It is not only stated in the forestry act, but also in the most common certification systems (FSC and PEFC) (Swedish Forest Agency 2022; Forest Stewardship Council n.d.; PEFC 2017).

Today, the most common management method still is rotation forestry with clearcuts and even-aged forest stands. But to ensure that goals other than production are achieved, it is necessary to reevaluate this conventional management system (Kuuluvainen et al. 2012). Continuous cover forestry (CCF) includes management methods that are not as conventional. CCF often results in less drastic changes of the environment and a common reason for avoiding clearcuts is to reduce the environmental impact and risk to biodiversity (Bengtsson & Rosell 2010). Reindeer husbandry can also motivate more gentle management methods in an area.

CCF is generally a diffuse concept and different definitions are being used depending on context. The definition of continuous cover forestry used by the Swedish Forest Agency states that a tree cover without any larger bare areas should be present at the site at all times. (Swedish Forest Agency 2021). In general, CCF includes the silvicultural systems that avoid clearcuts and has uninterrupted maintenance of forests (Pommerening & Murphy 2004). Selection systems, harvesting corridors, single tree harvesting and shelterwood are some examples of continuous cover forestry methods (Bengtsson & Rosell 2010).

Gap-cutting is another form of continuous cover forestry. This means that smaller openings are made at intervals throughout a site, rather than much larger harvest areas created in clearcut forestry (Swedish Forest Agency 2022). The gaps can have different sizes and shapes. According to the Swedish Forest Agency, the upper size-limit of a gap is 0.25 hectares, and harvested areas exceeding this are considered clearcuts (Swedish Forest Agency 2021). New seedlings establish in the gap, and as these seedlings get bigger, the gaps fill in to create an uneven stand structure in both size and age. Cutting such gaps is said to have benefits, especially for regeneration since it gives pioneer tree species a chance to establish, compared to multi-layered forests, since these trees need much light. It is also said to be a method that is easy to plan and perform compared to other management methods, since it is made like a regular clear-cut with reduced size (Hannerz et al. 2017).

1.2 The effect of retained trees on seedlings

Gap-size is an important factor for successful reforestation. It determines the extent of interaction with overstory trees, which influence regeneration by providing seedfall and frost protection, but also by shading, intercepting precipitation, and belowground competition for water and nutrients (mainly nitrogen) (Örlander & Karlsson 2000; Elfving & Jakobsson 2006; Erefur *et al.* 2011; Tishler *et al.* 2020). These effects are strongest around the periphery of a gap, and this area is termed the edge zone. The reported width of the edge zone varies, but generally it is between 5-10 meters. Seedling growth is lower in the edge zone than farther away from overstory trees. Reduction of both production (biomass increment) and height growth due to competition in new Scots pine stands have been seen (Erefur *et al.* 2011, Elfving & Jakobsson 2011). Stem number per hectare seems to be less affected (Elfving & Jakobsson 2007). It is likely that retained trees other than at the edge also affect seedlings.

Shelterwood is not very common in pine regeneration, and it is shown that the most successful shelterwood methods are the ones with few trees left (Tishler *et al.* 2020). Conversely, shelterwood can have positive effects on spruce regeneration, which has mainly been attributed to frost protection, increased shelterwood density promotes emergence of new Norway spruce seedlings (Nilsson *et al*. 2002). Increased seed germination of spruce seedlings is a positive effect of shelterwood compared to clearcut (Nilsson *et al*. 2006). However, growth of the seedlings decreases with increasing shelterwood density and mortality is high when removing the shelterwood (Nilsson *et al*. 2002).

There are hypotheses about retained trees predicting the opposite outcome, where trees are seen mainly as beneficial to seedlings. These thoughts are based on the concept of nutrient transport through common mycorrhizal networks between trees (Simard *et al*. 1997). Proponents of this theory argue that the large trees play a substantial role in facilitating regeneration. Trees linked in a mycorrhizal network may work as a carbon (C) supply, while young trees gain access to nutrients when linked to the network. A study made by Simard *et al*. (1997) implies C transfer between plants in the field, and similar experiments have also been performed in laboratory settings (Finlay & Read 1986), although not all have found evidence of such C transfer between plants (Wu *et al*. 2001). Simard *et al*. (1997) mention that it is necessary to consider mutualism between plants and their mycorrhizal fungi, as well as microbially mediated resource sharing.

More research is needed to understand how and when retained trees affect seedlings and establishment of a new stand. Specifically, successful forest regeneration in gaps requires a physiological understanding of the factors limiting or determining seedling establishment. The current thesis work will investigate the influence of edge trees on the regeneration of pine seedlings after gap-cutting. Seedling abundance and performance will be linked to isotopic measurements of water use efficiency and nitrogen status.

1.3 Isotopes and photosynthesis

Elements occur in several isotopes, which are atoms that differ in the number of neutrons occurring in the nucleus. Neutrons have mass but no charge, so isotopes of the same element take part in all the same reactions, but heavier isotopes will react more slowly (Fry 2006). Isotopes can be stable or unstable, where stable isotopes are non-radioactive forms of atoms and can be used in a variety of applications (International Atomic Energy Agency 2016).

When there is an isotopic difference in reaction speed, that reaction is said to cause an isotopic fractionation, or discrimination (Fry 2006). When a fractionation reaction consumes a substrate, the isotopic composition of the substrate becomes gradually heavier, whereas the isotopic composition of the product is lighter - unless the substrate is being depleted, in which case the product becomes heavier. There are many such fractionation processes in biological systems, and isotope distributions can be used to infer much about the conditions under which the process occurred or about the type of substrate used.
One such process is photosynthesis, where the enzyme RuBisCo fixes atmospheric CO_2, into carbohydrates (Farquhar et al. 1989). Atmospheric CO_2 contains both stable C isotopes, ^{12}C and ^{13}C (about 1.1 % of all C on Earth is ^{13}C, the rest is ^{12}C). In photosynthesis, atmospheric CO_2 diffuses across stomata and into leaf air spaces, and to the chloroplasts where it can be fixed.

By looking at isotopes in seedlings needles, it is possible to analyze seedling physiology and draw conclusions about their growth conditions. The influx and outflux of CO_2 are regulated by leaf stomata (Fry 2006). The enzyme RuBisCo has a slight preference for $^{12}CO_2$, so that the sugars produced have a lower $^{13}C/^{12}C$ ratio than the atmosphere (O’Leary 1988). This happens because the substrate (atmospheric CO_2) is constantly replenished via diffusion through the stomata. However, open stomata also lead to water loss from the leaf. Larger or more open stomata openings allow more CO_2 inside the leaf for enzymes to assimilate, but it also means more water will be lost to the atmosphere. When plants are exposed to water stress they close their stomata, meaning that most CO^2 will be fixed by enzymes, trapping it inside the leaf. As photosynthetic assimilation proceeds, a greater fraction of the $^{13}CO_2$ will be fixed. The ratio of water lost per assimilated C is referred to as the plant’s water use efficiency (WUE). Therefore, water-stressed plants will have increased observed ^{13}C value, which also index high WUE (Fry 2006).

1.4 Aim

This study is an ecophysiological investigation of pine seedlings growing in harvested forest gaps. The aim is to 1) quantify the edge effect on gap regeneration, and 2) to link this effect with physiological processes, based on isotopic and elemental analysis of seedlings sampled at various locations from the gap center to its edge, and under the intact canopy.
I pose the following questions:

1. How is pine regeneration affected by distance to the gap edge, regarding availability of water and nitrogen?
2. What influence does soil preparation and regeneration method have on this?

Hypotheses:

1. Total production (g dry weight/ha) is lower near the gap edge. This leads to loss of potential productive area.

2. Seedlings near edge-trees have a higher $^{13}C/^{12}C$ ratio and lower foliar nitrogen concentration. Hypothetically this is because edge-trees compete with plants for water and nitrogen, leading to lower total seedling production near the edge.

3. Seedlings far from retained trees have higher $^{15}N/^{14}N$ ratio. After harvest, big parts of the mycorrhizal network in the ground die and nitrogen is released. The fungi have a higher ^{15}N signature because of the isotopic fractionation that occurs when they export N to their host trees. Thus, uptake of decomposing ectomycorrhizal mycelium would lead to higher ^{15}N signature in the seedlings. Also, ^{15}N is higher in plants after soil scarification, due to disturbance in the soil.

2. Material and method

2.1 Site description

The study site is located close to Sveg in Härjedalen, Jämtland county (62.1955201 13.8323131). It is a demonstration area called “Rånddalen” and a part of the project “Alternative management methods in Rånddalen”. The area is important to Mittådalens sami village as winter grazing area, making it suitable for gentle forest management. The area consists of moraine with some podsolation Scots pine (*Pinus sylvestris*) forest of 135 years. The soil is moraine with some podsolation and a thin humus layer covered with mosses, lichens and *Ericacea* species. Stem number per hectare is 420-460, site index is T16 (Edlund 2017). The forest is uneven in terms of diameter, height and stem density. The area was fertilized in 1998 and then left until February 2016.

The area of 30 ha was divided into three parts with different sized gaps (35, 50 and 70 m diameter). For this study, the gaps with 50m diameter were chosen. A total of 12 gaps were harvested in 2016. After harvest, three of these were left untouched, five were scarified and four both scarified and re-planted. Gentle soil scarification was done in spring 2017 using a metal ball behind a tractor (see appendix). Autumn 2017, *P. sylvestris* was planted in three gaps and *P. contorta* in one gap.

2.2 Experimental design

Nine gaps with a diameter of 50 m were chosen for the current study. In three of the gaps, soil scarification and planting (*P. sylvestris*) were performed; three were scarified but not planted (natural regeneration); and the final three were left untouched as control gaps (Fig. 1). In each gap, two transects were laid out in directions north and south respectively to get data in both light angles. Four circular sample plots with radius 2 m were laid out in each transect with following distances from the edge: 20m, 10m, 3m and –10m (Fig. 2). The fourth plot (-10m) was laid out 10m from the edge into the surrounding forest, representing a pre-treatment control.

In some gaps, adjustments had to be made to this design. If the fourth plot (-10 m) ended up within 10 meters of the adjacent gap, the transect was relocated a few meters to the east or west. Two of the gaps had a tree retained from harvest, if a sample plot was laid out close to the tree, it was moved 10m from the stem of the retained tree.

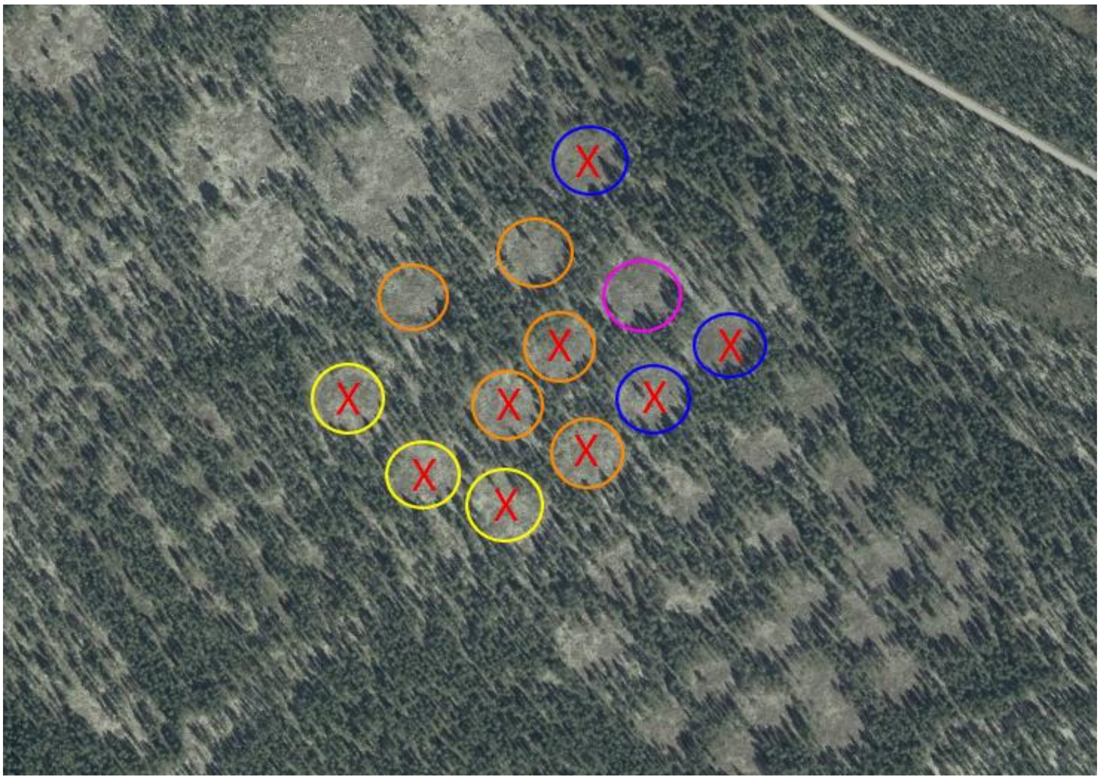

Figure 1. Demonstration area "Rånddalen", where gap-cutting was performed with different treatments. Each gap has a diameter of 50m. Gaps left untouched after harvest in yellow, scarified with natural regeneration in orange and scarified and re-planted in blue (pine) and pink (lodgepole pine). Nine gaps were chosen for the current study (marked with red X).

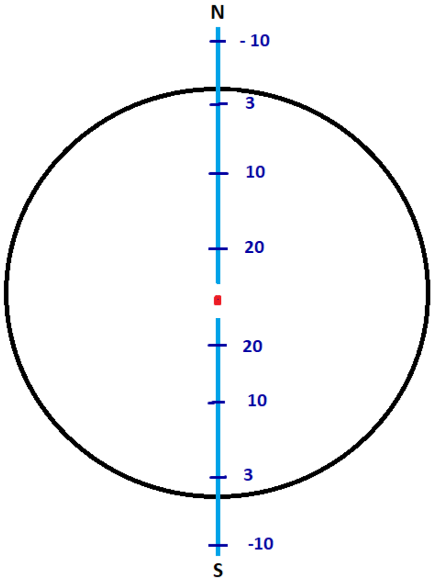

Figure 2. Overview of experimental design in each 50m gap. Transects in directions north and south. Sample plots with radius 2m lied out at different distances (in metres) from the edge of the gap. -10m works as control in surrounding standing forest. Other distances were chosen to show eventual differences at different distances from edge. In total, 9 gaps were studied. With 8 sample plots in each gap, a total of 72 sample plots were inventoried.

2.3 Field measurements and sample preparation

Field measurements were made in September. Soil moisture and light conditions were measured with Hydrosense II (Campbell Scientific, Logan, U.T., USA) and LAI-2200 (Li-Cor Biosciences, Lincoln, N.E., USA) in all 72 sample plots. In each sample plot, all pine seedlings were counted. Seedlings are here defined as all living Scots pine seedlings up to 5 years, both planted and naturally regenerated. Since the seedling size varied a lot, they were divided into three size classes: 1-14cm (S), 15-31cm (M) and above 31cm (L). At each plot, three seedlings were excavated including root system (coarse roots). If at least one seedling of every size class was present in the plot, one of each size was excavated. If not, two of the most common size class and one of the less common was chosen. The three sample seedlings were subjectively chosen as average representatives of each size class in the plot. Height above ground, shoot weight and root weight was measured and noted for the sample seedlings. Samples of current year foliage was collected from the leading shoot of all sample seedlings for further analysis. For seedlings with little number of needles, defining the annual shoot was difficult and the whole green part was saved. At one of the gaps (scarification and planting), whole seedlings were taken as samples with root and shoot separated to be used for further calculations.

In the laboratory, all samples were put in an oven, at 65°C, until completely dry. Dry weight was measured for the samples with both root and shoot, then dry weight ratio was calculated and used to get dry weight for remaining samples. A small number of needles were taken from each sample and was milled to powder using Retsch MM 400 (Retsch GmbH, Haan, Germany). The milled samples were dried in preparation further analysis. When completely dry, the powder was weighed and prepared for isotope analysis in small tin capsules.

2.4 Isotopic analysis

Samples were analyzed using Elemental Analyzer-Isotope Ratio Mass Spectrometer (carried out at SLU Stable Isotopes Laboratory, SSIL). Through combustion, the samples emerge as gas (CO_2 and N_2) which is analyzed in the isotope ratio mass spectrometer. The resulting values from the analysis denote a difference relative to standards and have the notation δ.

The samples were analyzed for:

1. Mass fraction of C and N (g C or N per g dry mass)
2. Isotopic ratio. $\Delta^{13}C = {}^{13}C/{}^{12}C$ and $\delta^{15}N = {}^{15}N/{}^{14}N$.
3. Fractional abundance. Isotopic amount $F = {}^{13}C/({}^{12}C+{}^{13}C)$ or ${}^{15}N/({}^{14}N+{}^{15}N)$. Often denoted as atom percent, where atom% = F*100.

2.5 Calculations and data analysis

The data from field measurements and sample analysis were analysed in JMP Pro 16. Tests for data were made as regression analyses at plot and gap level to explore correlation patterns between data variables. To see if there were any statistically significant differences in plant characteristics within the different treatments and distances from edge, analysis test of variance (ANOVA), Tukey-Kramer HSD and t-tests were done. The interaction between direction and distance to parameters like edge trees to incoming radiation and soil moisture, was tested by fitting a multiple linear regression model.

For areal calculations of production and needle biomass, gaps were divided in three parts (fig. 3). The edge zone (nr 1 in Fig. 3) of the division was based on a subjective estimation of the distance from edge trees to established regeneration (see appendix). The intermediate zone (nr 2) and center zone (nr 3) part was based on the distance for sample plots, where the middle of plot 10m and 20m, at 15m, was used in calculations. The proportion of needles in the saved seedlings was calculated to 0.66 for small seedlings and 0.57 for both medium and large. Since no large seedlings were saved for weighing, the value for large is copied from weighed medium sized seedlings.

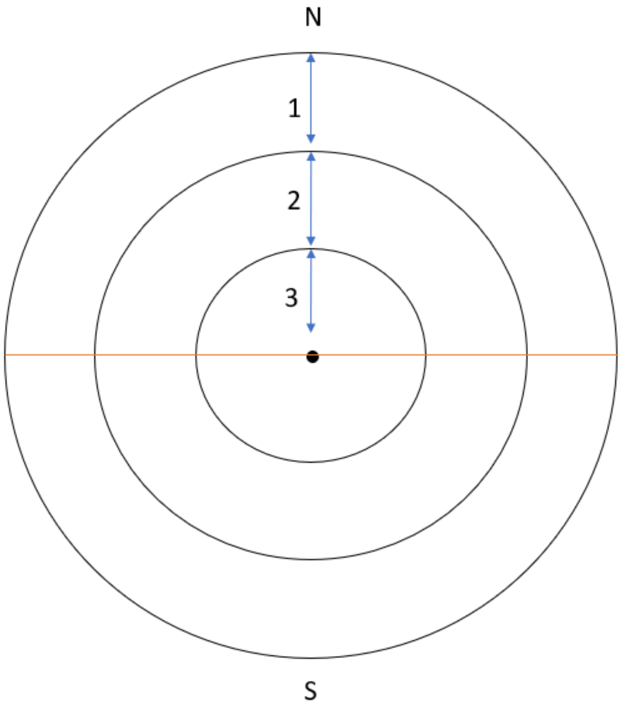

Figure 3. Design of gap division for areal calculations. Distance 1 based on subjective estimation of meters from edge trees to established regeneration, which is different for each gap. Distance 2 placed in the middle of sample plot 10m and 20m (2=15m-distance 1). Distance 3 based on gap center and middle of plot 10m and 20m (3=25m-15m).

3. Results

3.1 Environmental factors

Incoming radiation was significantly lower under the forest canopy (-10 m, Fig. 4a), than in the gaps ($p < 0.001$), but did not differ between north and south-facing transects ($p = 0.33$). It was 58 ± 7 % darker under forest canopy compared to the center of the gap (20 m).

Similarly, soil moisture was affected by distance ($p = 0.04$), but without significant differences between the north and south sides of the gaps ($p = 0.33$). Distances 10 m and -10 m were significantly different from each other (21.6 ± 1.3 % and 16.7 ± 1.3 % soil moisture, respectively) but neither was significantly different from 3 m or 20 m. The soil was driest at -10 m, increasing at 3 m (20.3 ± 1,3 %) with a peak at 10 m to then decrease slightly again at 20 m (20.2 ± 1,3 %) (Fig. 4b). Soil scarification and regeneration method did not have any significant effect on soil moisture or incoming radiation ($p = 0.33$ and $p = 0.14$, respectively).

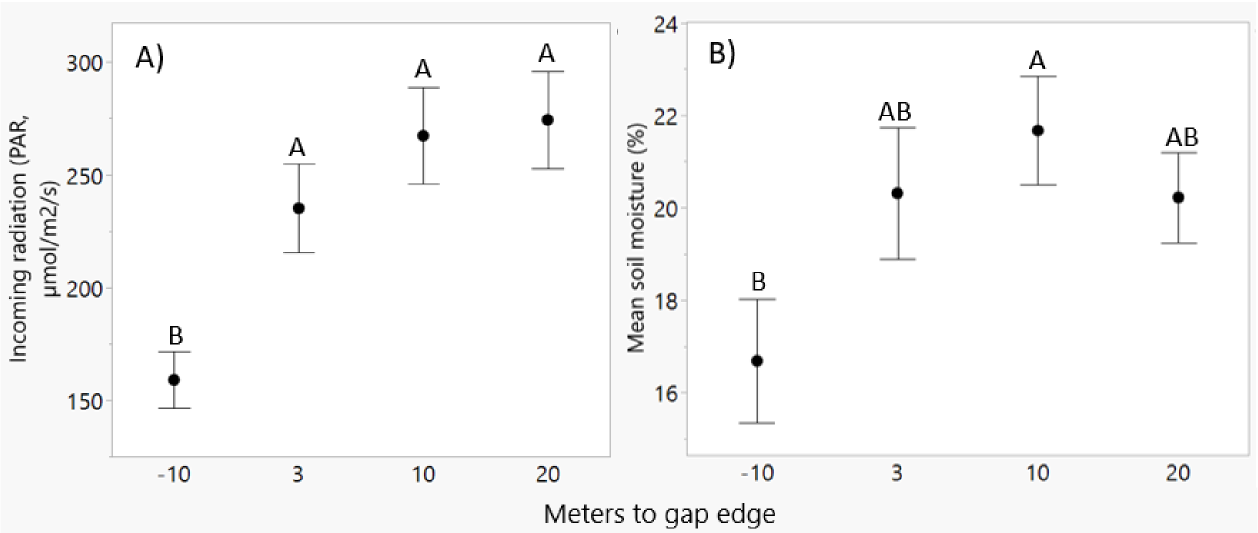

Figure 4. A) Mean incoming radiation (Photosynthetically active radiation, µmol m^{-2} s^{-1}) by meters to gap edge. Radiation increased towards the centre of the gaps. The increase was highest from standing forest (-10 m) to the first sample plot close to the edge (3 m). The other distances had more similar radiation values. B) Mean soil moisture (%) by meters to gap edge. Soil moisture increased towards the centre, but highest soil moisture was found at 10 m from edge.

Values not connected by the same letter are significantly different. Error bars show standard error.

3.2 Seedlings and production

Total number of seedlings increased four-fold from below the forest canopy to the center of the gaps (from 5216 ± 636 to 20779 ± 636 seedlings ha^{-1}, $p < 0.001$, Table 1). There was no difference in seedling density between the north and south transects ($p = 0.63$). The increase was highest from -10 m to 10 m, while the difference closer to the center (10 and 20 m) was small (Table. 1). Total seedling biomass (dry weight, kg ha^{-1}) increased as distance to edge increased. Number of seedlings was almost the same at 10 and 20 meters, while weight was higher at 20m indicating bigger plants in the middle. Soil scarification did not affect total number of seedlings or biomass at different distance from edge ($p \geq 0.13$ for all distances). Scarification and planting did not affect the total number of seedlings or total seedling biomass per area ($p \geq 0.38$ for all distances), but it significantly improved the proportion of large seedlings at 20m ($p = 0.04$), but not closer to the edge.

Table 1. Values from sample plots at -10m, 3m, 10m and 20m from gap edge. Values are shown as means from all 9 gaps. Total number of seedlings per ha, total seedling weight and proportion of each size is showed for all distances, including p-values. All values are significantly connected to distance, except for proportion of medium sized seedlings. Direction did not significantly affect the values, thus the data is not separated for north and south. Values not connected by the same letter (A, B, C) are significantly different.

Meters to edge	**-10**	**3**	**10**	**20**	**p-value**
Tot. nr of seedlings (nr/ha)	5216^{A} ± 636	9903^{A} ± 636	20955^{B} ± 636	20779^{B} ± 636	$p < 0.001$
Tot. Seedling weight (kg/ha)	$4,3^{C}$ ± 49.9	27^{BC} ± 49.9	186^{B} ± 47.1	370^{A} ± 47.1	$p < 0.001$
Proportion L of total (%)	1^{B} ± 0.04	5^{B} ± 0.04	28^{A} ± 0.04	33^{A} ± 0.04	$p < 0.001$
Proportion M of total (%)	41^{A} ± 0.05	30^{A} ± 0.05	30^{A} ± 0.05	34^{A} ± 0.05	$p = 0.39$
Proportion S of total (%)	58^{A} ± 0.06	65^{A} ± 0.06	42^{BC} ± 0.06	33^{C} ± 0.06	$p < 0.001$

Seedling size distribution varied with the distance from the gap edge (Table 1). Proportion of large plants of total number of plants is significant to both distance (Table 1) and direction (p = 0.047). Proportion of large plants at 10 and 20m is not significantly different from each other, but from -10 m and 3 m (Table 1). In south, the mean proportion of large plants is 8 ± 3.7 % lower compared to the north transect. Medium-sized plants cannot be explained by either distance or direction, while small plants are affected by distance to edge (Table 1).

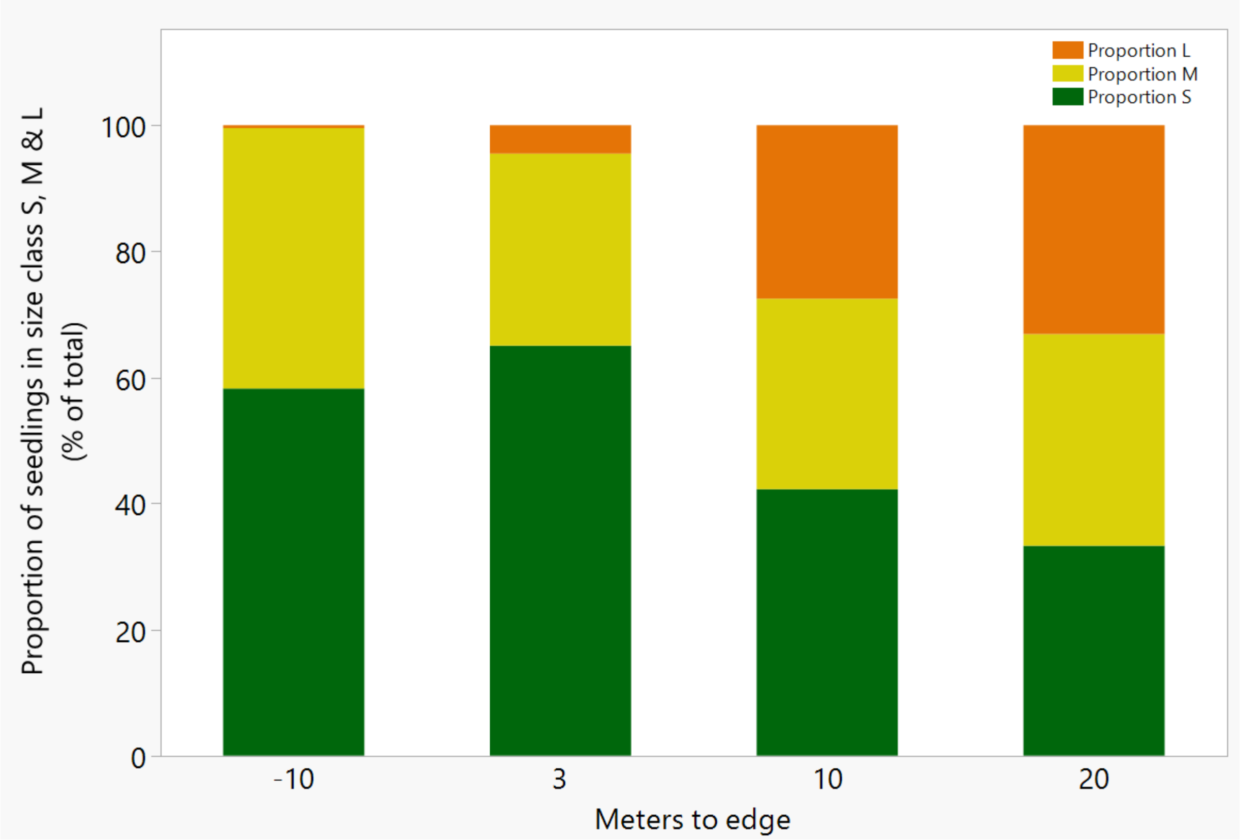

Figure 4. Proportion of seedlings in size class large (orange), medium (yellow) and small (green) at distances -10 m, 3 m, 10 m and 20 m from gap edge. The graph is showing mean values for every distance, with data from north and south transects combined. Large plants are more common closer to the center, while medium and small sized plants have a higher proportion close to edges and under the forest canopy (-10 m).

Total seedling production per unit area was estimated by dividing all gaps in three concentric circular areas, as described in the methods section, and using the values from sample plots 3 m, 10 m and 20 m. The edge zone, closest to the gap edge, was calculated (as a mean of all 9 gaps) to 1074 m^2. Intermediate zone was calculated to 574 m^2 and center zone (in the gap center) to 314 m^2. The estimated biomass production per area was thus 21,1 kg/ha (edge zone). 210,1 kg/ha (intermediate zone). 370,1 kg/ ha (center zone). Seedling production was thus

94% lower in the edge zone than in the intermediate zone, and 89 % lower than in intermediate zone. A steady increase of seedling biomass was seen from the gap edge to the center (Fig. 5). When treatments were analysed separately (Fig. 6), no significant effect of regeneration method ($p > 0.43$ for all zones) or soil scarification ($p > 0.20$ for all zones) was found.

The estimated needle N content had a steady increase from the edge zone to the center zone. Calculated N content (Table 2) was 0.13 ± 0.37 kg/ha closest to the edge (edge zone), then 1.32 ± 0.37 kg/ha (intermediate zone) and 2.42 ± 0.37 kg/ha in the center (center zone) (Table 2).

Table 2. Values for area, biomass (kg dry weight per hectare) and nitrogen amount (kg N per hectare) is shown for the three parts of the gap. Area 1 is adjacent to the gap edge, area 2 is in the middle and area three is the center part of the gap. Values not connected by the same letter are significantly different.

Part of gap	**Edge zone**	**Intermediate zone**	**Center zone**	**p-value**
Area (m^2)	1074	574	314	
Biomass (kgDW/ha)	21.1^{A} ± 56	210.1^{AB} ± 56	370.1^{B} ± 56	$p < 0.01$
Nitrogen (kgN/ha)	0.13^{A} ± 0.37	1.32^{AB} ± 0.37	2.42^{B} ± 0.37	$p < 0.01$

Mean distance for the edge effect is 8.2 ± 0.6 m, thus 55 ± 1.8 % of the total gap area is affected by the edge trees. There is no significant difference between the north and south transect ($p = 0.3$). The average distance for edge effect was higher in scarified gaps compared to non-scarified; 9.3 ± 0.6 m and 7.8 ± 0.4 m respectively. Despite this, the difference is not significant ($p = 0.08$). With regeneration method, the distance in planted gaps is 7 ± 0.4 m compared to 8.9 ± 0.3 m in the naturally regenerated gaps. This difference is significant ($p = 0.01$).

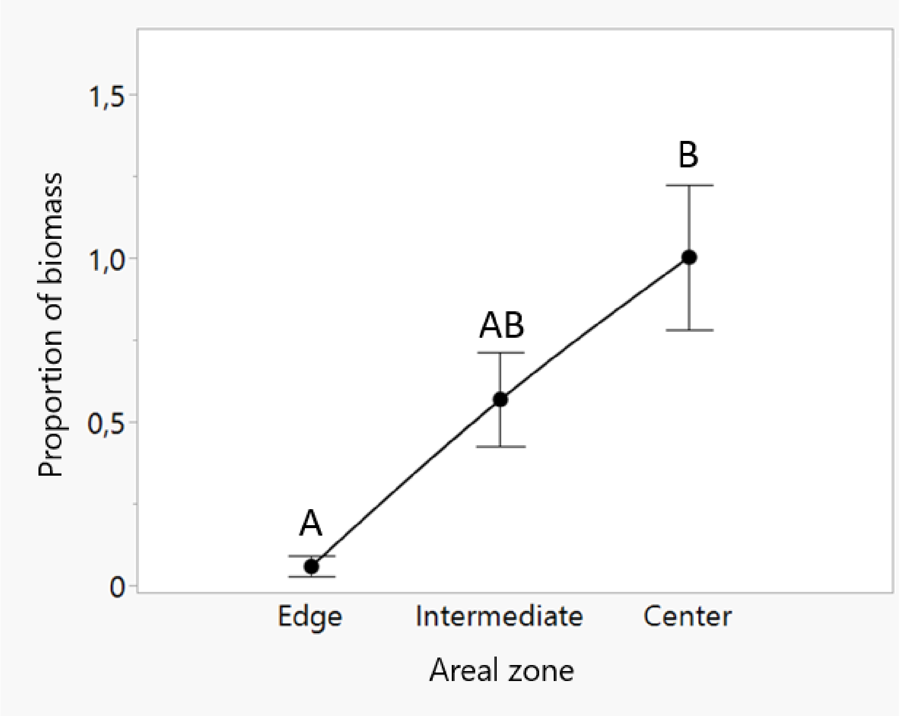

Figure 5. Proportion of total biomass in three gap zones, with data from treatments and directions combined. Nearly all the seedling biomass in the gaps was produced in the intermediate and center zones. The production in the edge zone represented less than 10% of the total. Values not connected by the same letter (A, B) are significantly different. Error bars show standard error.

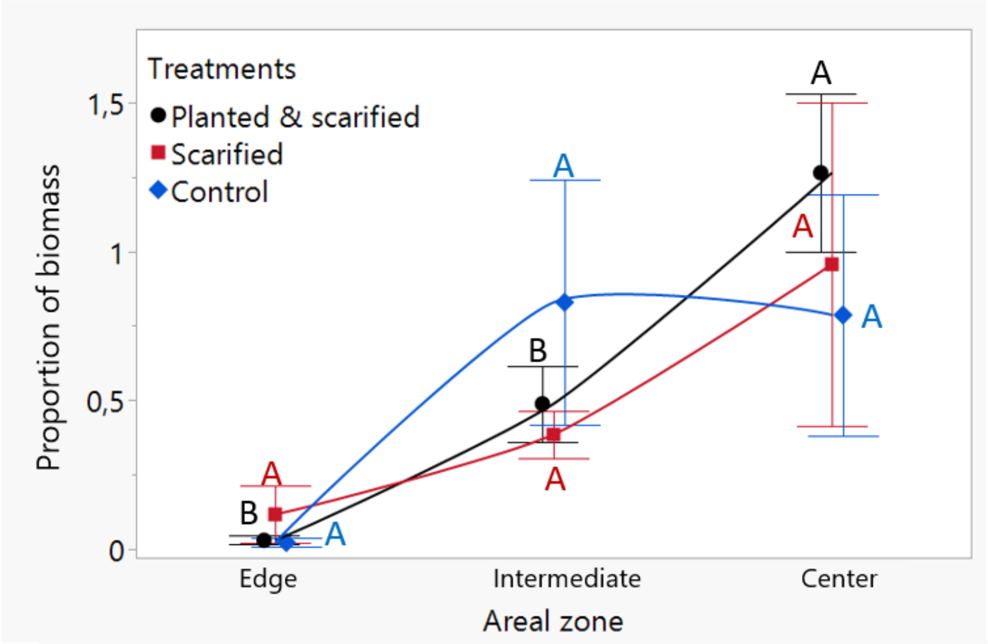

Figure 6. Proportion of total biomass in three zones in a gap. Data from both north and south transects are used. The three treatments (planted & scarified, scarified and untouched control) are showed separetely. Gaps with planting and scarification or only scarification had higher biomass compared to closer to the edge. The untouched control plots had highest biomass at 10m, to decrease slightly towards 20m. Values at distances internal for treatments that are not connected by the same letter are significantly different. Error bars show standard error.

3.3 Physiological characteristics

3.3.1 Seedling foliar nitrogen

Needle N concentration (% of dry weight) was found to increase towards the center of the gaps (Fig. 9a) ($p < 0.001$), without effect of direction ($p = 0.42$). Scarification had no significant effect on foliar N concentration at the time of sampling ($p = 0.56$), but there was a significant effect of regeneration method at -10 m and 3 m with data from both transects combined ($p = 0.05$ and $p = 0.03$, respectively). Nitrogen concentration was 0.13 ± 0.06 % (-10 m) and 0.13 ± 0.05 % (3 m) higher when planted, compared to naturally regenerated. Analyses comparing isotopic data from each sample plot at -10m was done to see eventual differences due to the gap's location, but no correlation of data values and gap's location was seen.

The isotopic $^{15}N/^{14}N$ ratio (Fig. 9b) of seedling foliage increased by 4.9 ± 0.7 ‰, from the sampling location beneath the forest canopy (-10 m) to the center of the gaps ($p < 0.001$), and there was no difference between the north and south transects. Overall, $\delta^{15}N$ was 2 ± 0.7 ‰ higher in scarified gaps, than in non-scarified controls ($p = 0.003$). Separate analysis at each distance from the gap edge revealed that this scarification effect was only significant at the 10 m sampling location. The effect of regeneration was not significant ($p = 0.06$).

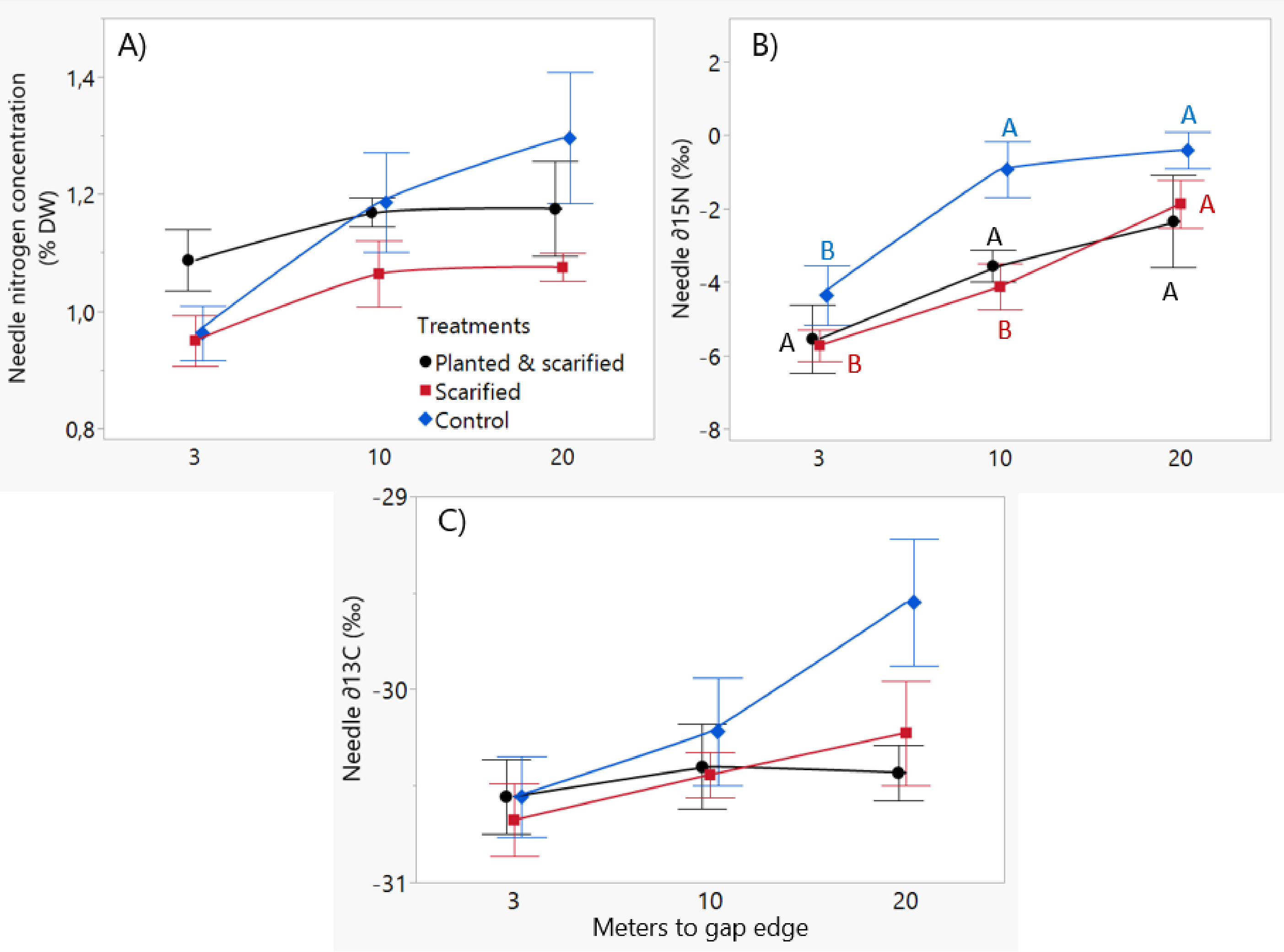

Figure 9. Isotope data at distances 3 m, 10 m and 20 m from gap edge. Data from treatments planting & scarification, only scarification and control are showed in separate lines. No data from under the forest canopy is included in the graphs since soil scarification and planting are not made outside the gap. North and south transects are combined. A) Needle nitrogen concentration by meters to gap edge. The highest increase was seen at the control gaps. B) Isotopic $^{15}N/^{14}N$ ratio, $\delta^{15}N$, of seedling foliage by meters from gap edge. $\delta^{15}N$ increased with increasing distance from edge. C) Isotopic $^{13}C/^{12}C$ ratio, $\delta^{13}C$, of seedling foliage by meters from gap edge. Control gaps increased more than the other two treatments.

Values not connected by the same letter (A, B) are significantly different. No significant difference between the distances was found in graph A) and C). Error bars show standard error.

3.3.2 Carbon

Carbon concentration (% of DW) was related to both distance and direction ($p < 0.001$ and $p = 0.013$). Carbon content was highest at -10 m and 3 m to decrease towards the center. At the north transect, C concentration was 0.31 ± 0.12 % higher than at the south transect. C/N ratio was related to distance, but not direction ($p < 0.001$ and $p = 0.37$). Values for C/N ratio decreased with increasing distance from edge. All distances except for 10 m and 20 m were significantly different from each other. The difference from under the forest canopy (-10 m) to the center of the gap (20 m) was 15.9 ± 2.5. C/N ratio was significant to regeneration method at 3 m ($p = 0.04$). No significant effect of soil scarification on C/N ratio was found ($p > 0.08$ for all distances).

Carbon isotopic ratio, $\delta^{13}C$, was significantly increasing with increasing distance from edge for all treatments combined ($p = 0.02$). For treatments separately, a slight increase was detected, but neither isotopic ratio nor needle C content was significantly affected by soil scarification or regeneration method (Fig. 9c). Whether the seedlings were located to the north or south, had no effect.

4. Discussion

4.1 Growth and edge zone

The study shows a clear result of negative edge effects on seedlings (Fig. 4 & 5). Characteristics connected to production such as seedling size, density and biomass were all lower in the edge zone close to retained trees, which confirms the first hypothesis and correlates with results from earlier studies (de Chantal *et al*. 2003; York *et al*. 2003; Erefur *et al*. 2011). Both physical and physiological characteristics are affected by the edge. There was no effect of soil scarification with or without planting on overall seedling production, meaning that the negative effect from edge-trees is larger than the intended positive effect of treatments.

Seedlings at the gap edge were fewer and smaller compared to those further away. Despite this, the total number of seedlings in the edge zone does exceed the recommended number (1900-2500) of seedlings when planting (Skogskunskap 2022), indicating that seed fall from surrounding trees is sufficient and that seeds do germinate. However, the proportion of large seedlings is significantly reduced at the edge, compared to the center (Fig. 4). Assuming that planting was done in the whole gap area, this indicates that seeds and seedlings can germinate in the edge zone, but then either die or stop growing. The same result is identified by Hughes & Bechtel (1997) where after harvest, a positive effect from overstory trees was seen. After 8 years the result was reversed, and highest seedling density was further away from overstory trees. A larger proportion of seedlings was also found to have greater diameter with increasing distance from trees. It is identified that plants receive nitrogen from mycorrhizal fungi in proportion to how much carbon they provide (Henriksson et al. 2021a). The amount can alter but the proportion is determined, meaning that seedlings could have a hard time matching bigger trees and therefore die in the edge zone. Soil scarification could possibly alleviate this problem by cutting bigger trees’ roots, making the seedlings the main hosts for mycorrhizal fungi.

The edge zone covered an area of approximately 8.2 m width around the periphery of the gaps, which is reasonable compared to earlier studies that reported distances around 6-10 m (Ruuska *et al*. 2002; Elfving & Jakobsson 2006; Axelsson *et al.* 2014). The size of the competitive edge zone is also reasonable based on estimates of the lateral extent of tree nutrient uptake (Henriksson et al. 2021b). As 54% of the total gap area had 93% lower growth rate, it is interesting to discuss the shape of gaps. With continuous cover forestry comes suggestions of harvest areas in different shapes, for example corridors or checkered pattern (Swedish Forest Agency 2021), leading to edge zones of different proportions. Some suggest elongated shapes (such as corridors) in north-south direction to maximize incoming radiation (de Chantal *et al*. 2003), but depending on the gap-width, the edge zone would cover a considerable amount of the gap. The effect of retained trees in other forms, such as shelterwood, could also be considered with information from the results of this thesis.

As seen in figure 6, the proportion of biomass increased towards the center for all three treatments. The untouched control gaps were flattened at 10 m, while scarification with planting was still increasing at 20 m without signs of declining. The scarified gaps seemed to have the same pattern as scarification with planting, but the variation is big at 20 m and the difference is not significant between the distances. The values will even out at distances longer than 20 m, meaning that there is still potential for increasing biomass if gaps are scarified and planted, and possibly only scarified as well.

Since no treatment with only planting was done (in absence of scarification), no full factorial analysis could be performed. It is not possible to draw separate conclusions about how planting and scarification affected the results or if there was an interaction effect between the two. Having all treatments combined and separately is a possibility for expansion of the study. Another improvement possibility concerns number of replicates. Number of sample plot replicate at each distance and treatment is quite low (six for each distance and treatment, if north and south are combined) and much data depends on how many seedlings were found in each plot. Seedlings were not found in all sample plots, giving some distances a smaller number of seedling replicates than others. A higher number of replicates would secure the quality of the results and improve the study.

4.2 Ecophysiological analysis

Explanations of why production is lower along the edge could be connected to circumstances both above and below ground. Incoming radiation was not significantly different from edge to center zones of the forest gaps (Fig. 4a), and no significant growth difference was detected between the north and south sides of the gaps, meaning that light or shading alone was not the limiting factor for growth. This is corroborated by Axelsson *et al.* (2014), where it was shown that when nutrient uptake by tree's roots was reduced because of stem-girdling, seedlings could establish while the tree canopy still was maintained. This supports idea of belowground competition being the limiting factor for seedling establishment and growth. Nevertheless, there is a possibility of the gaps being too small to create a north/south difference. Height measurements of overstory trees in combination with calculations of light angle would be needed to ensure that gap-size is not a limiting parameter. Also, proportion of large seedlings was significant to direction north/south, meaning that light can not be completely excluded.

4.2.1 Nutrient and water availability

By looking at the result from isotopic analysis of $\delta^{13}C$ (Fig. 9c), the second hypothesis, that seedlings near edge-trees having higher $^{13}C/^{12}C$ ratio, is rejected. Seedling foliage displayed higher $\delta^{13}C$ towards the center of the gap, potentially indicating a higher water use efficiency. If the transpiration of adjacent trees were causing drought stress, then closing stomata would have resulted in increased seedling water use efficiency in the edges and a higher $\delta^{13}C$. There was thereby no indication of water competition from surrounding trees being a growth-determining factor for the seedlings. These results are from measurements made in the autumn, perhaps a different result would be seen during a dry summer period. The values for soil moisture (Fig. 4b) did not correlate to those from $\delta^{13}C$. It is likely that the differences seen in soil moisture was affected by the rainy weather at the time of measurement, whereas the foliar $\delta^{13}C$ reflects the conditions during shoot elongation and needle expansion.

Regeneration treatments had no significant effect on seedling foliar nitrogen concentration (Fig. 9a), but combining all treatments, it is revealed that both nitrogen concentration and $\delta^{15}N$ was lower at the gap edge, which confirms the third hypothesis and indicates that there is belowground competition for nutrients between trees and seedlings. Some effect of treatments on nitrogen concentration and isotopic ratio could be seen, but it does not seem to be enough to explain the growth along the transects. Since C/N ratio is a common measurement of nitrogen availability in soil (Brust 2019), the results of C/N ratio being lower at the farther away from edge trees indicate higher nitrogen availability at the center of the gaps.

The increase in $\delta^{15}N$ is relatively high from edge to gap center (ca 4‰, Fig 9b), which may be due to center-seedlings having access to a different nitrogen source compared to the edge-seedlings. One possible source is decomposing mycorrhizal mycelium, since this mycelium is rich of ^{15}N. In the process of N transfer from fungi to plants, there is an isotope discrimination. The fungi are keeping a lot of ^{15}N and transferring the lighter ^{14}N to plants, resulting in high fungal $\delta^{15}N$ values (Handley *et al.* 1996; Högberg 1997; Taylor *et al.* 1997). As harvest results in reduction of mycorrhizal mycelium due to loss of transferred C from trees (Perry *et al*. 1987; Högberg *et al.* 2017), mycelium start to decompose and nitrogen is released to the soil. Uptake by plants of ^{15}N from decomposing mycelium is therefore a reasonable explanation. The difference in $\delta^{15}N$ seen in earlier studies (8-4‰) are in the same size range as in this study. Further analyses, such as adding ^{15}N tracers, are needed in order to evidently see if and which N source that affects the difference in $\delta^{15}N$. Around a year after harvest, mycorrhizal activity is heavily reduced (Harvey *et al.* 1980). These gaps were cut six years ago, raising the question of how long it takes for mycelium to decompose and for how long released nitrogen is stored in the soil. Roots from cut conifers can maintain in a somewhat living condition for several years (Harvey *et al.* 1980), which could slow the decomposition rate of mycorrhizal mycelium. Nitrogen mineralization could also affect the timeframe.

Another potential N source could be decomposing harvest residues, although this would not explain the observed shift in foliar $\delta\ ^{15}N$. Studies of residues impact on regeneration has been made, showing that seedling survival was significantly lower when residues were removed after harvest due to reduction of N pools (Olsson *et al*. 1996; Jacobson *et al*. 2017). Seedlings also have an ability to store and remobilize N (Millard & Grelet 2010). These storage and remobilization processes are could also be possible factors affecting the difference in $\delta^{15}N$. If so, seedlings closer to the center are reusing more N from earlier years needles compared to those at the edge. Due to isotope discrimination (Zhang et al. 2016), the heavier ^{15}N would be kept in the seedling, while lighter ^{14}N is released from needles as ammonia. To be able to draw any conclusion, samples of earlier years foliage need to be analyzed to make a comparison, which is a possibility for further studies. In terms of nitrogen fixation, where bacteria connected to plants are fixing atmospheric N_2 into nitrogenous compounds such as NH_3, isotope discrimination has been seen as well (Yoneyama et al. 1986; Unkovich 2013). Results indicate that there is a slight preference for the lighter isotope, meaning that availability of N_2 could affect $\delta^{15}N$ values so that more of $^{15}N_2$ is fixed by bacteria at the center for uptake by seedlings.

5. Conclusion

The negative effect of edge-trees on seedlings growth is extensive. The most reasonable explanation is belowground competition for nutrients, mainly nitrogen. The extent of the edge effect is important if forest management is shifting towards smaller harvest areas and alternative management methods, since a considerable amount of productive area is lost and establishment of new stands are uncertain. The results also provide indications about the effect of retained trees in other forms, such as seed trees and shelterwood which are relevant in times of changing forest management. Neither of the regeneration interventions tested in the study (soil scarification with and without subsequent planting) could alleviate the negative edge effect on seedling production in the forest gaps. This is also interesting when developing and testing new management measures, both for economic and environmental reasons.

It is possible to reject water competition and light availability as limiting factors for growth, leading to competition of nutrients as remaining explanation, which is supported by isotope analyses of N. Since the difference in $\delta^{15}N$ between seedlings at the edge and seedlings closer to the center was quite high, some other factor is probably affecting the result. Most likely a nitrogen source that the center-seedlings have access to, such as decomposing mycorrhizal mycelium. After harvest, mycelium start to decompose and release nitrogen, which is a reasonable source of nitrogen to the seedlings.

This study should not detract from the importance of benefits in alternative forest management, such as gentleness for biodiversity, but it provides information about potential issues that are important. More research is needed, and interesting aspects to test in upcoming projects would be to trace from which source seedlings get their ^{15}N after harvest. Tests of foliage from time close after harvest and following years are interesting to trace and clearly define the competition from trees. Treatments of other kinds could make it possible to see whether other treatments could eliminate or reduce the edge effect. Analyzing seedlings at different points in time also provide important information, to test when the edge effect is significant and if it changes upcoming years, both the areal extent of edge zone and the effect from edge-trees.

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Popular science summary

Forest debates often include change of mindset from the classic forest management with clear-cuts, towards reduced harvest area and continuous cover forestry. In Sweden, there are laws directing management with different purposes. In 1800, a law concerning which size of trees allowed to harvest was implemented (Kardell 2004). Only trees larger than a certain diameter could be harvested in order to spare both trees with growth potential and the environment. It did not go as expected, and difficulties with things like regeneration resulted in our management approach today, where clear-cut, scarification and planting/sowing are the common practices. Some laws today concern retaining trees, size-limits of harvest areas, consideration of sensitive biotopes and so on. As in 1800s, retention of trees still affect regeneration. Continuous cover forestry is a collective term of management methods, where retention of trees is essential in some form in order to avoid a clear-cut (Pommerening & Murphy 2004). One continuous cover forestry method is gap-cutting, where smaller gaps are cut instead of a whole stand (Bengtsson & Rosell 2010). Gaps allow seedlings to grow and create an uneven stand in both size and age. Gaps-size is an important factor, determining interaction with surrounding trees which influence regeneration with seed fall and frost protection, but also nutrient and water competition, shading and interception of precipitation. Studies have shown negative effects of retained trees on seedling production at distances around 6-10 m (Elfving & Jakobsson 2007, Örlander & Karlsson 2000, Erefur *et al.* 2011, Tishler *et al.* 2019). The zone where the effect is strongest is called the edge zone. Seedling growth is lower in the edge zone compared to farther away from overstory trees. Both biomass and size are affected.

Seedlings could be affected by not only environmental factors as light, but also competition of nutrients and water. By analyzing isotopes is possible to further analyze seedlings physiology and draw conclusions about their growth conditions (Fry 2006). Isotopes react at different speed, meaning that depending on the content in the seedling’s needles, it will provide information about what processes seedlings have gone through. This thesis work will investigate what influence edge trees have regeneration of pine seedlings after gap-cutting. Seedling density and production will be linked to isotopic measurements of water use efficiency and nitrogen status.

Measurements were done in a pine forest where gaps were cut in 2016. Three treatments were included, scarification with and without subsequent planting and untouched gaps (control gaps). In the gaps, seedlings were calculated and measured in sample plots at different distances from gap-edge; -10 m (outside the gap), 3 m, 10 m and 20 m. Two transects with sample plots were laid out in each gap, at north and south respectively. Seedlings were weighed and needles were saved for further analysis. Isotope analyses of the needles were made in lab, giving information about isotopic ratio ($^{15}N/^{14}N$ and $^{13}C/^{12}C$) as well as N and C concentrations.

Results showed a clear negative effect on seedlings from edge-trees. Seedling growth (biomass and density) was significantly lower at the gap edge compared to the center. Proportion of large plants (>31 cm height) was highest at the gap center and lowest at the edge. The edge zone was estimated to 8.2 ± 0.6 m, thus 55 ± 1.8 % of the gaps were defined as edge zone. Biomass was 94% lower in the edge zone compared to the center. Scarification with or without planting had no significant effect on neither biomass nor number of seedlings. No difference was seen between the north and south transects, and there was also no significant effect of incoming radiation or soil moisture on growth. The isotopic analyses showed that nitrogen concentration (% of dry weight) and $^{15}N/^{14}N$ ($\delta^{15}N$) was lowest near edge-trees compared to farther away. $^{13}C/^{12}C$ ($\delta^{13}C$) was also lower at the edge compared to the center. Overall, none of the isotope values were affected by the treatments.

The negative effect of edge-trees on seedlings is extensive, and results indicate that seeds can germinate, but then either die or stop growing. Since there was no difference from north and south transects, shading is not the limiting factor for seedlings growth. The $\delta^{13}C$ values makes it possible to reject water availability as limiting factor as well. What is left is competition of nutrients (nitrogen) by edge-trees, which is confirmed by looking at the low values near edge and higher values near center. The difference is high and can be influence by some other factor as well. Since there is an isotope discrimination when mycorrhiza absorb nitrogen (Handley *et al.* 1996; Högberg 1997; Taylor *et al.* 1997), it contains of a high amount of ^{15}N. When trees are harvested, mycelium die and ^{15}N is released to be absorbed by seedlings.

It is interesting to discuss the extent of the edge effect. With continuous cover forestry comes retention of trees in many forms and reduction of harvest area. Since the edge effect covered a lot of the gap-area, shape of harvested gaps and shelterwood-systems are important to have in mind. A lot of productive area is lost, and a new stand may be unable to establish. The effect of the edge-trees inhibits the intended positive effect of scarification with or without planting, which could not affect seedling production.

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Appendix 1

Figure 7. Gentle soil scarification made with metal balls connected to a tractor (Skogsstyrelsen).

Figure 8. Example of distance from edge to established regeneration at one of the gaps in Rånddalen (Tyra Tornberg).

Publishing and archiving

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