# The role of common mycorrhizal networks for forest regeneration near clear-cut edges
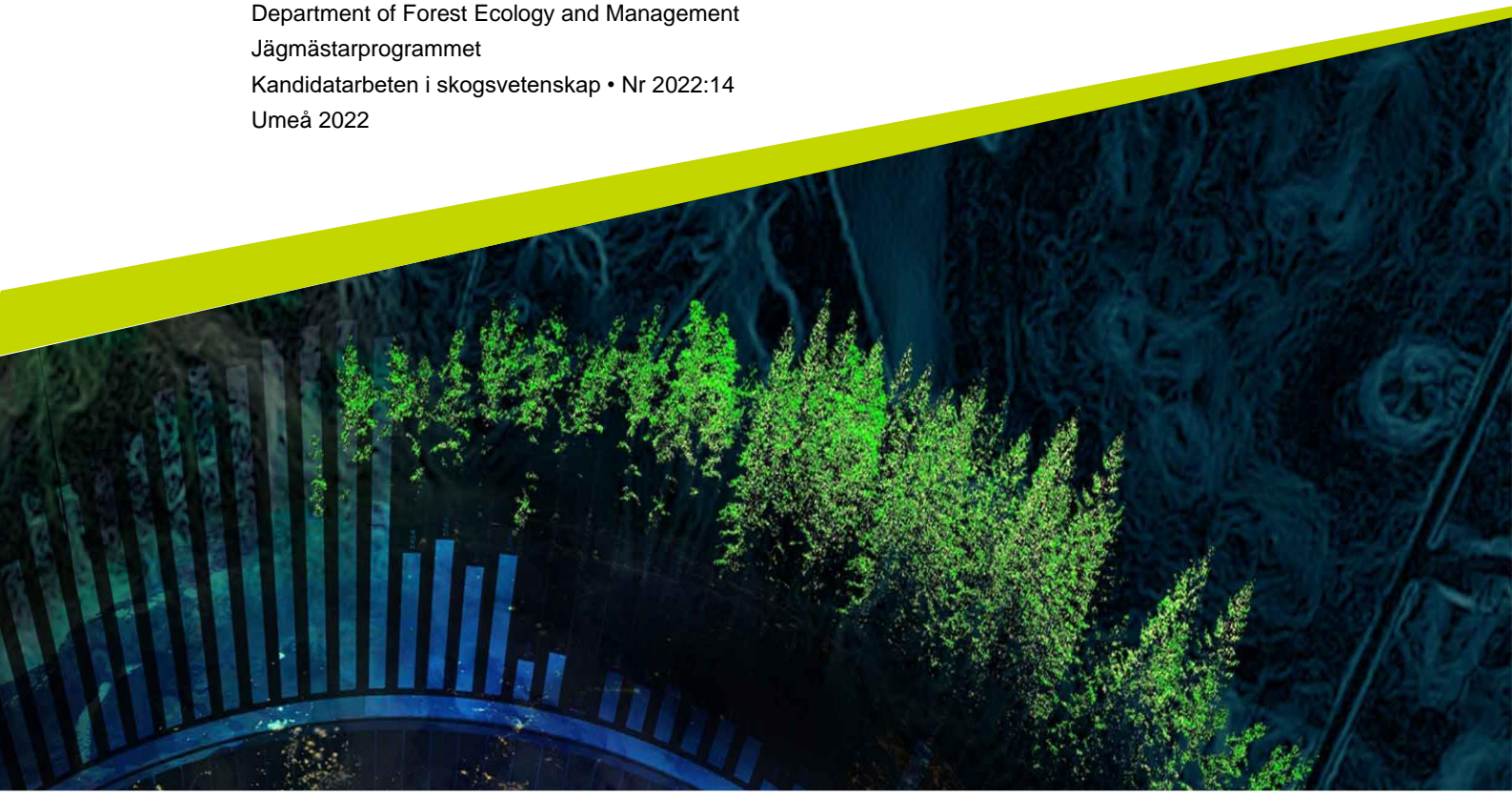# – Implications for management

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# The role of common mycorrhizal networks for forest regeneration near clear-cut edges – Implications for management

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# Abstract

Poor regeneration close to edges on clear-cuts and around seed trees in the Swedish boreal zone is well-known to foresters. With an intensifying national and European discussion concerning forestry, the prominence of edge effects is likely to increase. However, little is known of the drivers behind these edge effects. Recent developments in the research surrounding ectomycorrhizal fungi and their ability to form common mycorrhizal networks may be able to explain some of these patterns. In this study, I have analysed growth data of Scots pine seedlings planted in a Chequered-Gap-Shelterwood-System trial located in Jämtland, Sweden. I found that growth is significantly higher in the centre of a clear-cut gap than in the edge zone, defined as within five metres from the clear-cut edge. Which side of the gap the plants were exposed to was also partially significant. The results correlate well with the expected outcomes of below-ground competition described in literature. These edge effects may have long term implications for management due to lower growth, but the usage of new management methods may bring positive social benefits.

*Keywords:* ectomycorrhizal fungi, common mycorrhizal network, regeneration, boreal, scots pine

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# 1.  Introduction

Poor regeneration close to edges of clear-cuts and surrounding seed trees has been known to foresters in Sweden for over 100 years (Hagner 1963). However, the governing factors behind these edge effects remain largely unknown. Instead, large clear-cuts have been used along with planting to minimise edges and negate the need for seed trees (Hagner 1963).

Lately, discussions concerning the management methods used in Swedish forests have intensified along with a new strategy for forestry within the European Union (European Commission 2021). Systems such as continuous cover forestry and chequered-gap-shelterwood-systems are introduced, and the size of clear-cuts are decreasing (Skogsstyrelsen 2021). These changes lead to longer edges between clear-cuts and intact forests, leading to more areas where regeneration may be affected. Getting an understanding of the regeneration problem near edges is thus essential.

Adverse edge effects, influencing height and volume growth in seedlings and young trees, have been studied and documented at the currently studied site in Jämtland, Sweden (Fernemar 2019), and other sites (Hagner 1963; Elfving & Jakobsson 2006; Ruuska et al. 2008; Zdors & Donis 2017). This has been attributed to competition from overstory trees by shading (Zdors & Donis 2017), although other studies have concluded that below-ground nutrient competition might be a more critical factor (Axelsson et al. 2014).

## 1.1  Chequered-Gap-Shelterwood-System

New management methods are being introduced to Swedish forests. One of these is Chequered-Gap-Shelterwood-System (CGSS), a method in which 50% of the stand is harvested at a time in small gaps, leaving a stand that resembles a chequerboard. The remaining trees are harvested when sufficient regeneration and growth has occurred in the gaps.

Few studies have been conducted on the efficacy of CGSS, but recent results shows a higher cost coupled with higher social values. Although costs were higher when harvesting using CGSS, costs were lower than other methods of continuous cover forestry (Eliasson 2018). Other studies have suggested that CGSS provides higher recreational values (Pershagen & Westerlund 2020) and better grazing

opportunities for reindeer husbandry, and potentially decreasing conflicts between reindeer husbandry and the forestry sector (Gunnarsson 2022). Further, CGSS appears to give sufficient regeneration according to regulatory requirements following several different soil scarification and regeneration methods in the gaps of CGSS stands, however plant growth and establishment was lower closer to the edge (Fernemar 2019).

## 1.2  Plant establishment

Above- and belowground competition both affect plant growth. Aboveground competition is caused by direct interference by other plants, such as mechanical interference and shading from surrounding vegetation and nearby overstory trees. Shading leads to altered growth responses in plants. Seedlings of Scots pine (*Pinus sylvestris* L.) respond to shading by increasing height growth (Dehlin 2005). Belowground competition can be divided into two; direct competition and indirect competition. Methods of direct competition include allelopathy by which plants release exudates that harm nearby vegetation, whereas indirect competition includes primary resource capture whereby one plant uses a resource, thus preventing another plant from using that resource. Lately, belowground competition has been shown to have a greater impact on stand regeneration in nutrient-poor Scots pine forests (Axelsson et al. 2014).

## 1.3  Ectomycorrhizal fungi

Ectomycorrhizal fungi (EMF), heavily influence belowground resource competition. EMF are fungi that collectively can form symbiotic associations with the roots of ~6000 plants (Martin et al. 2016), among which are species such as *P. sylvestris* and *Picea abies* (L.) Karst. commonly used in Swedish forestry. EMF form a web of hyphae called the Hartig net around root cells through which the fungus receives photosynthetic carbon and in return provides water and nutrients. EMF colonises the fine roots of trees by releasing chemical signals from either spores or hyphae of already established mycelia that allow the EMF to bypass the tree's defences. This establishment method is likely a product of an evolutionary past as saprophytic fungi (Martin et al. 2016).

Establishment is also dependent on dispersal, which can occur in three separate ways in EMF; through spores or sclerotia, pre-senescent mycelia, or growing hyphae (Brundrett 1991). The dispersal method is likely linked with the life-history strategy of the EMF species. Early-successional species have the most fertile spores, whereas late-successional species have spores with inferior ability to germinate and colonise seedlings (Peay et al. 2012). Direct colonisation by growing

mycelia is likely more important in late-successional species. This is supported by differing fungal community compositions across forest stand age gradients (Kyaschenko et al. 2017) and studies finding an abrupt loss of EMF in clear-cut soils (Heinonsalo et al. 2007). Early colonisation aided by dispersal of fertile spores will also yield a competitive advantage by monopolising photosynthetic carbon assimilates due to a "priority effect" (Kennedy 2010).

## 1.4 Common mycorrhizal networks

Ectomycorrhizal fungi can also form networks with many trees connected by the same mycelium. These networks have been named common mycorrhizal networks (CMN) or "The wood-wide web". By establishing into a CMN, a seedling may benefit from increased access to water and nutrients and carbon from other trees connected to the same network (reviewed by Simard & Durall 2004). Negative effects of such associations have also been shown, such as increased nitrogen immobilisation (Näsholm et al. 2013) and negative competitive effects as two or more trees compete for the same decreasing nutrient pool (Henriksson et al. 2021).

Although an apparent negative edge effect is expected in this study, other studies have pointed toward the ability of EMF-mediated carbon transport through the CMN. This might make competition between seedlings unequal if one seedling is connected with overstory trees via EMF receiving carbon while competing seedlings are not. By being part of a CMN, the seedling might be able to utilise carbon sent from overstory trees (Simard et al. 1997), lessening the effects of shading by being controlled by a "sink-source model" and giving the seedling access to an established network of nutrient and water capture (Simard & Durall 2004). Especially increased water availability may be vital to the survival of the seedlings, especially in drought-stressed environments (Booth & Hoeksema 2010). Combined, these effects may greatly influence the establishment of a new stand following harvest by preserving mother trees (Rhodes 2017).

Being part of a CMN might also negatively affect the growth of plants. By sharing a mycelium with several trees, all connected trees have been hypothesised to be competing for the same resources. This might lead to a negative feedback loop wherein each tree gets less and less nutrients for every carbon given, leading to nitrogen immobilisation in the fungus (Henriksson et al. 2021). This might have a pronounced effect on tree growth in already nutrient-poor soils (Näsholm et al. 2013). As seedlings growing at the edge of a clear-cut are likely to associate with EMF connected with the trees at the stand edge, they are likely to be in their sphere of resource capture (Lutter et al. 2021).

## 1.5  Hypotheses

Due to the presumed effects that mycorrhizae may have on the establishment of new stands, especially in the edge zone where they can form connections with established CMNs, this thesis will explore and evaluate seedling establishment and growth during six years from planting in proximity to overstory trees at the edge of clear-cut gaps in a Swedish boreal *Scots pine* L. forest. For our purposes, the edge zone is defined as being 5 meters wide, which corresponds to the documented area of belowground resource capture by pines in a boreal stand (Lutter et al. 2021). Thus I assume that seedlings growing within the edge zone can form mycorrhizal connections to the edge trees, but seedlings growing further out cannot. Seedling height will be used to predict total production, and the following hypotheses will be tested:

1. Height growth is lower in the edge zone of the clear-cut;
2. Seedling survival is higher in the edge zone of the clear-cut;
3. Light intensity has no significant effect on the growth and survival of seedlings.

Implications for management are also discussed.

# 2. Materials and Methods

## 2.1 Site description

Data has been collected from a Chequered-Gap-Shelterwood-System (CGSS) trial located in Torringsmon, Jämtlands län, at coordinates 62°42'N, 015°44'E. The forest is a 120-year old Scots pine (*Pinus sylvestris* L.) forest with site index T21. The mean height of the trees are 20 metres with a vegetation layer of bilberry (*Vaccinium myrtillus* L.) on mesic soil of sandy moraine. The stand was manually thinned in 1930-40 and later thinned again with machines in the 1990s. In 2012, the forest was harvested using the CGSS creating 16 gaps, all 30x45m in size. Two of the gaps, number 7 and 11 in Figure 1, were then studied for edge effects. These gaps were scarified with a digger in 2013, followed by manual planting of *P. sylvestris* in 2014. Complementary planting was done in late 2014, followed by fencing of the two studied gaps. The following year, seedling survival was surveyed and dead seedlings (1.9-2.2% of all planted) were replaced from a set of extra seedlings that had been planted just outside the study area. Finally, broadleaf seedlings were removed manually in the autumn of 2016.
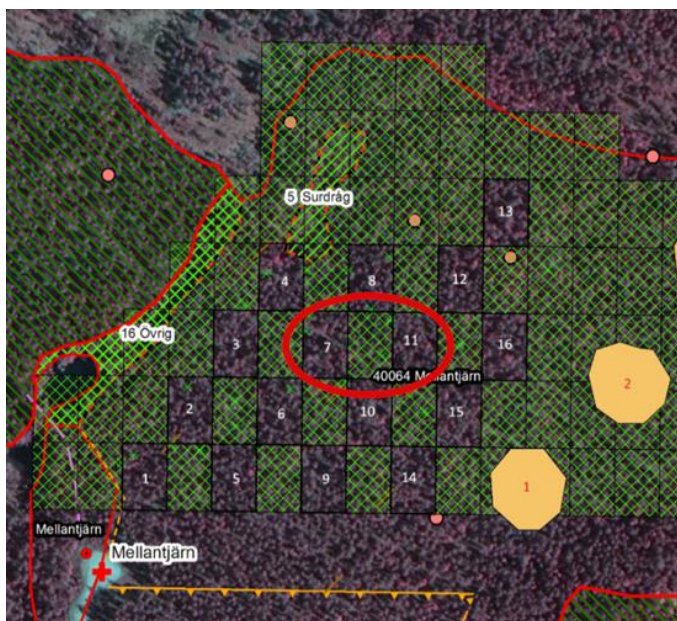


*Figure 1 Map of the trial with Chequered-Gap-Shelterwood-System. Red circle marks gaps used in this study.*

## 2.2 Experimental design

Each gap was divided into nine subplots (1-9) of equal size and eight edge zones, 5m wide (E1-8) with one centre zone (E9). A five metre edge zone corresponds to the documented area of belowground resource capture by pines in a boreal stand (Lutter et al. 2021). The nine subplots and the edge zones overlapped (figure 2). The corner edge zones E1(NW), E3(SW), E6(NE) and E8(SE) are 5x5 meters in size. Edge zones E2 and E7 (W and E, 35x5 m), E4 and E5 (N and S, 5x20 m), ran along the edges of the gaps in the cardinal directions.

| E1 | | E4 | | E6 |
|----|----|----|----|----|
| | 7 | 4 | 1 | |
| | | | | |
| E2 | 8 | E9 5 | 2 | E7 |
| | | | | |
| | 9 | 6 | 3 | |
| E3 | | E5 | | E8 |

*Figure 2 Subdivision of gaps 7 & 11. E1-9 denote edge zones with solid lines. Subplots are divided by dashed lines and numbered 1-9 with italic numbers. Edge zones and subplots overlap.*

Within the gaps, each plant was numbered and noted which edge zone and subplot it belonged to. Each plant's height and leading shoot length were measured, first in the fall of 2016 two years after planting, and then in spring of 2020 six years after planting. The vitality (marked on a subjective scale of 0=dead, 1=healthy, 2=alive but decreased growth) and any damages (1=mechanical, 2=water, 3=fungus) were also noted along with other measurements. Remarks of damages such as double leading shoots and double trunks were recorded. These plants were omitted from the data analysis due to deviating from the assumption that height growth is a predictor of total biomass.

Both gaps were subjected to the same treatment and comparing the two data sets showed no significant ($p>0.05$) differences for all pairwise T-test comparisons. Therefore, the two data sets were pooled together and treated as one in further analysis. The total edge zones for both gaps  (1300 $m^2$) were compared with the central zone (total 1400 $m^2$) using analysis of variance (ANOVA) and pairwise T-tests ($\alpha=0.05$) using R (R Core Team 2017).

# 3. Results

Plants established within five metres of a mature stand had a significantly lower height growth six years after planting, but not after two. In 2016, (two years after planting), the plants in the centre of the gap were 14% higher than plants in the edge zone. Centre plants were $31.7 \pm 10.4$ cm (mean ± SD) high compared to the plants within the edge zone which were $27.7 \pm 10.9$ cm high, showing no significant difference (p>0.05) (Table 1). However, in 2020 the centre plants had a mean height of $126.9 \pm 38.5$ cm, and were significantly higher than the plants growing in edge zones, which were $91.1 \pm 41.9$ cm (p < 0.05; Figure 3). A height difference of 40%.

Leading shoot length responded similarly to height growth. In the edge zone, the leading shoots were $9.4 \pm 6.6$ cm in 2016 and $18.4 \pm 9.9$ cm in 2020, whereas they were $11.7 \pm 6.8$ cm in 2016 and $27.3 \pm 8.8$ cm in 2020 in the centre zone (Table 1). This shows a significant (length difference of 48%, p<0.05) difference between the zones in 2020 but no significant difference in 2016.

Due to low mortality (1.9-2.2%), no difference in survival between edge and centre seedlings could be evaluated.

*Table 1. Height and leading shoot growth of seedlings planted in the gaps. Seedlings were planted in 2014 and measured on two subsequent occasions: two years after planting and six years after planting.*

| Torringsmon | | | | | | | |
|---|---|---|---|---|---|---|---|
| Edge zone | Location | Number of plants | Mean height 2016 ± SD (cm) | Mean height 2020 ± SD (cm) | Mean leading shoot 2016 ± SD (cm) | Mean leading shoot 2020 ± SD (cm) | Relative growth |
| E1 | NW Edge | 11 | 29 ± 14.3 | 96.6 ± 53.5 | 10.9 ± 7.7 | 19 ± 10.8 | 1.43 |
| E2 | W Edge | 66 | 27.7 ± 11.2 | 95.2 ± 45.3 | 9 ± 6.6 | 19.7 ± 10.4 | 1.41 |
| E3 | SW Edge | 10 | 23.2 ± 12.3 | 87.8 ± 53.4 | 7.7 ± 7.2 | 19.3 ± 12.6 | 1.36 |
| E4 | N Edge | 44 | 29.2 ± 10.9 | 100.7 ± 39.4 | 10.9 ± 7.1 | 20.5 ± 8.9 | 1.41 |
| E5 | S Edge | 41 | 26 ± 9.9 | 85.1 ± 37.9 | 8.2 ± 5.5 | 17.6 ± 8.7 | 1.44 |
| E6 | NE Edge | 10 | 33.4 ± 7.1 | 115.2 ± 26.7 | 12.6 ± 6.5 | 24.6 ± 8.1 | 1.41 |
| E7 | E Edge | 67 | 27.3 ± 10.1 | 79.4 ± 38.2 | 8.7 ± 6.7 | 15.2 ± 9.8 | 1.53 |
| E8 | SE Edge | 11 | 28.9 ± 15.1 | 93.9 ± 41.2 | 10.5 ± 6.6 | 17.9 ± 9.5 | 1.44 |
| E9 | Centre | 282 | 31.7 ± 10.4 | 126.9 ± 38.5 | 11.7 ± 6.8 | 27.3 ± 8.8 | 1.33 |
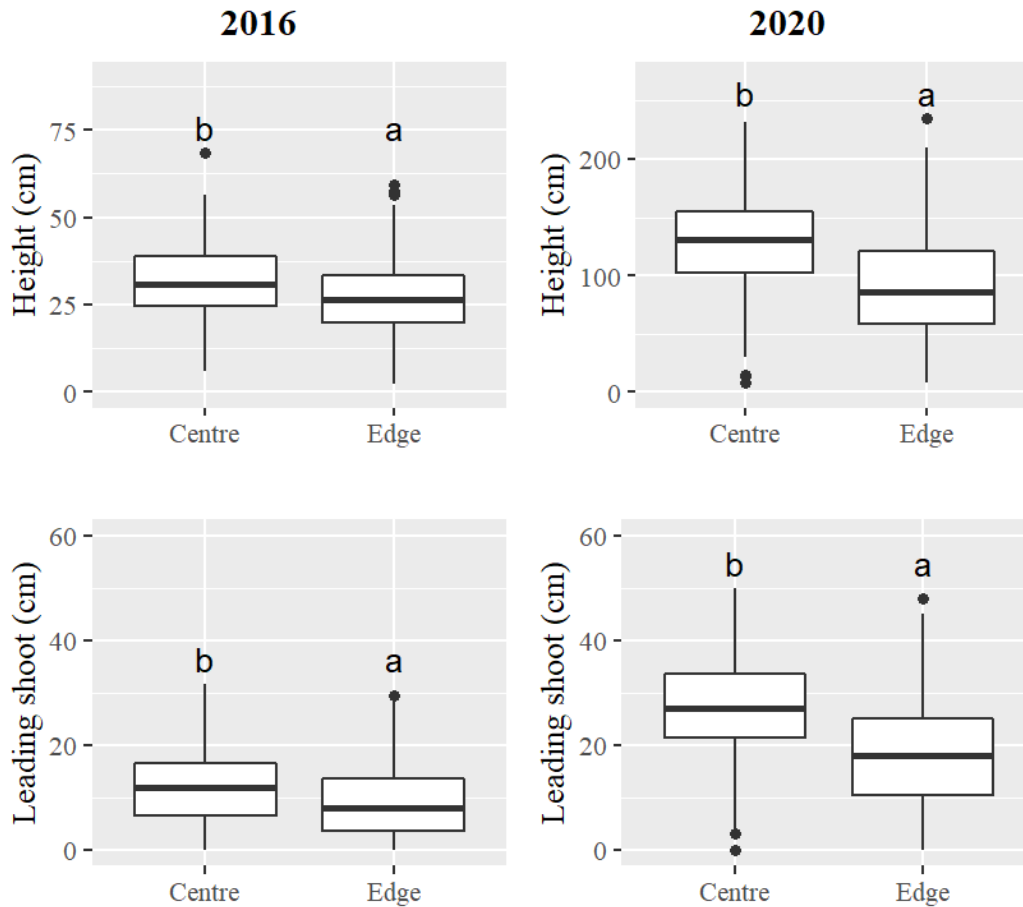
*Figure 3 Height and leading shoot differences two and six years after planting in the gaps. Plants on the edge are those planted within five metres from the existing stand. Different letters show significant differences using pairwise T-tests (α=0.05).*

The plants' direction of exposure to the gap also affected their height and leading shoot growth. Six years after planting, height growth was significantly (p=0.04) lower on the eastern side of the gap than on the northern side. Leading shoot growth was significantly lower on the east side of the gap compared to the western (p=0.04) and north (p=0.03) side, but only in 2020.

Growth in the centre of the clear-cut was also significantly higher than nearly all sides of the clear-cut (Figure 4). The only discrepancy is the northern side of the gap in 2016 for both height and leading shoot length. This side has the highest expected solar radiation, but variation within the zones is large (Table 1).
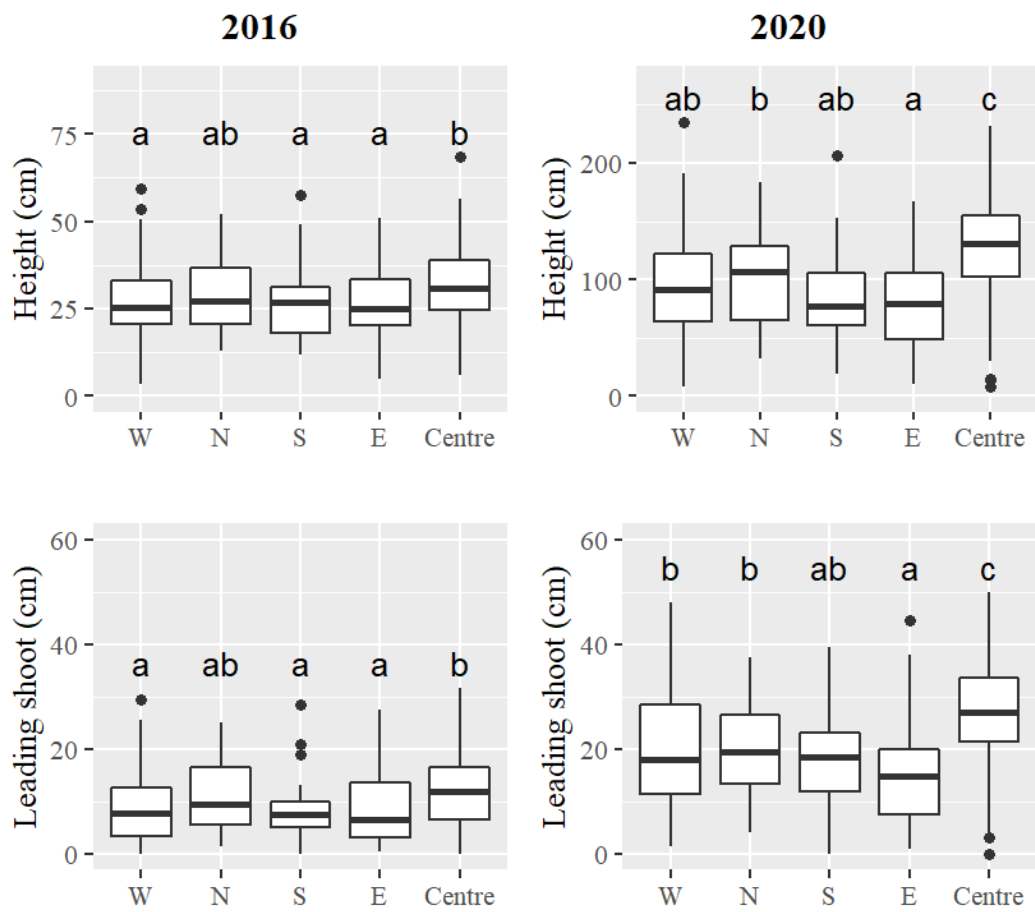
*Figure 4 Height and leading shoot of Pinus sylvestris L. located on the different sides clear-cut gaps, five metres from the edge of the existing stand. Measurements were made two and six years after planting. Different letters denote significant differences using pairwise T-tests (α=0.05).*

# 4.  Discussion

## 4.1  General results

This study clearly shows a lower height growth in plants located less than five metres from the edge of a clear-cut (figure 3a-b), supporting my first hypothesis. I also found no significant difference in growth between the northern and southern borders of the clear-cuts, which would have been expected if shading had been the limiting factor (de Chantal et al. 2003). Shading is also expected to have triggered a shade avoidance response in shaded *P. sylvestris* plants, increasing stem elongation. This response is expected in both high- and low fertility soils. Diameter of trunks were not measured in this study, so this response was not able to be tested. Due to smaller stem diameter, the plants are likely to be more susceptible to snow breakage. The low mortality would suggest that this response was also absent, however large variation is expected because of weather.

I would also expect to see higher productivity on the western edge, as temperature and humidity are better for growth in the morning (de Chantal et al. 2003). The lack of such responses likely signifies another limiting factor due to below-ground competition (Axelsson et al. 2014). This supports my third hypothesis that there would be no decrease in growth due to shading. Survival was not able to be evaluated due to low mortality.

## 4.2  Common mycorrhizal networks

In the current study, the edge zone is defined as stretching five metres from the border into the gap, which corresponds well with the observed lateral root spread of several coniferous species as well as their primary nutrient uptake area (Bishop 1962; Taskinen et al. 2003; Henriksson et al. 2021). Any plant in the edge zone would thus likely be in the nutrient capture sphere of the bordering mature trees and their associated EMF (Jonsson et al. 1999; Teste et al. 2009).

It has been suggested that plants connected to a common mycorrhizal network must compete for a shared nitrogen pool and that a seedling or a plant will have a small competitive ability due to lower total photosynthetic activity allowing it to

"trade" less carbon for nutrients (Henriksson et al., 2021). My results show that edge seedlings grew significantly less than centre seedlings during the study period (figure 3), which agrees with the expected outcome of such competition.

This is further supported by studies where girdling of the stem was used to prevent the transport of photosynthetic carbon assimilates to root structures whilst maintaining water transport. Axelsson et al. (2014) showed a substantially higher establishment and growth of *P. sylvestris* seedlings two years after stem girdling, highlighting the relative importance of below-ground nutrient competition in relation to above-ground shading. They also showed that competition for water was not a limiting factor in growth or establishment at their site. Instead, water deficiency in plants likely causes increased mortality rather than limit growth (Booth & Hoeksema 2010).

I found no support for the claim made by Simard et al. (1997) that carbon can be transported between plants through the CMN following a "sink-source" model, as the expected outcome would be equal or higher growth in the edge seedlings compared with centre seedlings. This is likely due to shading not being a limiting factor, but nitrogen.

Novel EMF associations for plants in the centre of the stand might stop such competition, thus increasing growth. Clear-cutting alters the chemical and environmental conditions at the site and significantly reduces the amount of colonisable fine roots in the soil (Hagerman et al. 1999). Further studies have also shown an abrupt decrease in EMF abundance after clear-cutting (Hagerman et al. 1999; Heinonsalo et al. 2007; Hasby 2022). Plants in the centre of the stand would then likely form novel EMF connections from spores or pre-senescent mycelia, not with a CMN, potentially increasing nitrogen uptake per carbon "traded".

Although likely, it is impossible to state with certainty that nitrogen limitations exacerbated by CMNs is the cause. First, no mapping of EMF in the soil was done for this study so it is only assumed from the results of previous studies that they are connected coupled with this being the expected outcome following the hypothesis stated by Henriksson et al. (2021). Second, no quantification of nitrogen in plant or EMF tissues were done. Thus, any difference between plants in the centre and at the edge can only be assumed. Third, there was also no weight recorded which forces the assumption that height is a predictor for productivity. A more destructive measuring where below- and aboveground biomass was measured would likely have been a more precise measurement strategy and would at the same time have allowed for quantification of nitrogen in tissues. Taken together, these limitations give this study a narrow application and more studies should be conducted to combat these limitations.

## 4.3   Implications for forest management

From the results of this study, it is clear that increased edge zones negatively influence growth in boreal Scots pine forests, and lower growth along edges is still detectable in young stands after 25 years (Jakobsson 2005; Ruuska et al. 2008; Hughes & Bechtel 2011). As focus moves towards smaller clear-cuts and other alternative management methods such as continuous cover forestry, edge zones are set to increase in abundance, potentially making edge zones a vital focus for foresters in the future. This point is also raised by Högberg et al. (2021) where they suggest management methods that minimise nitrogen competition. This study suggests minimising the abundance of edge zones to limit the effect of below-ground competition.

However, harvesting will also expose the trees on the border of the gap, having an effect similar to thinning, whereby total productivity increases for individual trees, which is attributed to increased crown growth and increased wind stress (Valinger et al. 2000). A study by Bowering et al. (2006) investigating the growth response in Lodgepole pine (*Pinus contorta* Douglas ex Loudon) following road edges found an increased growth response in the trees within 5 metres from the edge for at least 20 years following road construction, with a maximum response 6-10 years after construction. They suggest that this response may, in part, recover timber losses due to road creation.  This response is likely also applicable to trees along edges created by clear-cutting as for the Chequered-Gap-Shelterwood-System.

Although evidence points towards minimising edge effects to prevent soil nitrogen immobilisation, other social factors should be considered when managing forests. The usage of Chequered-Gap-Shelterwood-Systems might for example have positive effects in areas important for reindeer herding (Gunnarsson 2022), an area that today is heavily conflicted (Widmark 2009). Using continuous-cover forestry systems such as Chequered-Gap-Shelterwood-Systems are also often valued higher for recreation in urban forests, with clear-cutting and associated measures being perceived as negative (Pershagen & Westerlund 2020). These factors should also be considered when deciding on management system, though it is clear that edge effects cause long-term reduced productivity in a young Scots pine stand in boreal Sweden.

# 5. Conclusions

This study has clearly shown a decrease in height growth in seedlings growing within five metres from the forest edge on a clear-cut. Further, this has been shown to likely be due to nitrogen limitations caused by the seedlings being associated with the same CMN as mature trees causing negative carbon-nutrient trade feedback loops (Henriksson et al. 2021) and nitrogen immobilisation (Näsholm et al. 2013). These effects are noticeable long-term and are likely to cause productivity losses. However, these losses may be countered by a corresponding productivity increase in the bordering overstory stand.

Due to the presumed increase in edges because of shifts in management methods in the future, the importance of edge effects is likely to increase. This puts pressure on foresters to consider these effects when managing systems whilst also managing for other social factors.

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