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THE IMPACT OF LITTER ON SOIL QUALITY AND REGENERATION OF NORWAY SPRUCE (*PICEA ABIES* [L.] H.Karst) AND EUROPEAN BEECH (*FAGUS SYLVATICA* [L.])- AN EXPERIMENTAL APPROACH

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Management of Natural Resources

PREFACE

This thesis has been written as part of a Masters degree in Management of Natural Resources at the Norwegian University of Life Sciences. It is a part of "From spruce to beech forests-fundamental ecosystem transformation driven by climate change" (the Beech-project). This project is run by a larger group of international researchers, with Line Nybakken as the project manager.

ABSTRACT

During the next decades, the climate in Scandinavia is predicted to become wetter and warmer. This change will alter the ecosystems, and implies a possible transformation from Norway spruce (*Picea abies*) to European beech (*Fagus sylvatica*) forests in the Southeast of Norway. Several factors will affect the success of these two species, and among these are the impacts of litter on soil quality and regeneration.

This study represents a litter moving and seed sowing experiment conducted at Brånakollene Nature Reserve, an area where spruce - and beech forest meet. The experiment consisted of 20 research plots; 10 in beech forest and 10 in spruce forest. Each research plot consisted of four 50 x 150 cm subplots with assigned treatments *litter removed*, *control*, *transplanted spruce litter* and *transplanted beech litter*. The treatment plots were sown with beech seeds and spruce seeds. Samples from both plant tissue and soil were collected four months later. Due to a total predation of beech seeds, the results on plant tissue contain only material from spruce plants. The collected samples were used to make a suggestion to the impact of litter on different response variables. The response variables in plant tissue were: number of recruited plants, average plant weight, carbon (C), nitrogen (N) and C:N ratio. The response variables we looked at in soil were: pH, C, N and C:N ratio.

I found that forest type had an effect on all response variables, in both plant tissue and soil. Litter treatment showed an impact on regeneration through a significant effect on the number of recruited plants, but no influences on the other response variables in plant tissue were discovered. The results also suggest that soil chemistry is not significantly affected by litter in the short-term perspective provided in this study.

In this research, I show how different litter manipulations can affect regeneration of spruce, and how this might affect interspecific competition.

SAMMENDRAG

Man regner med at det blir våtere og varmere i Skandinavia over de neste tiårene. Dette vil endre økosystemene, og innebærer en mulig transformasjon av skogdominansen fra Norsk gran (*Picea abies*) til Europeisk bøk (*Fagus sylvatica*) i sør-øst Norge. Flere faktorer vil påvirke suksessen til de to artene, og blant disse er påvirkninger fra strøfall på jordkvalitet og regenerasjon.

Dette studiet presenterer et eksperiment med flytting av strø og såing av frø utført ved Brånakollene naturreservat, et område hvor gran- og bøkeskog møtes. Her samlet vi inn prøver fra både plantemateriale og jord for å kunne framlegge et forslag om strøfallets påvirkning på ulike responsvariabler.

Eksperimentet besto av 20 plots; 10 i bøkeskogen og 10 i granskogen. Hver plot bestod av fire 50 x 150 cm subplots med tilhørende behandlinger *strø fjernet, kontroll, granstrøbehandling* og *bøkestrøbehandling*. Subplotsene ble sådd med bøkefrø og granfrø. Prøver fra både plantemateriale og jord ble samlet inn fire måneder seinere. Grunnet totalpredasjon av bøkefrøene, inneholder resultatene fra plantene kun materiale fra gran. Prøvematerialet ble brukt til å si noe om strøfallets påvirkning på de ulike responsvariablene. Responsvariablene i plantematerialet var: antall spirede planter, gjennomsnittlig plantevekt, karbon (C), nitrogen (N) og C:N ratio. I jordmaterialet så vi på pH, C, N og C:N ratio.

Jeg fant at skogtype hadde en påvirkning på alle responsvariablene, i både planter og jord. Strøbehandling hadde påvirkning på regenerering gjennom en signifikant effekt på antall spirede planter, men ingen påvirkninger av strøfall ble funnet på noen av de andre planteresponsvariablene. Resultatene fra studiet foreslår også at jordkjemien ikke blir påvirket i signifikant grad av strøfall i et korttidsperspektiv.

I dette studiet viser jeg hvordan ulike manipuleringer med strøfall kan påvirke regenerering av gran, og hvordan dette muligens kan påvirke interspesifikke konkurranseforhold.

TABLE OF CONTENT

Preface

Abstract

Sammendrag

References

1. INTRODUCTION

Climate change will affect nature profoundly in the centuries to come - both habitats, biodiversity and the distribution of species (Fischlin *et al.* 2007; Oddou-Muratorio *et al.* 2010). According to current research, the climate in northern Europe will continue to get warmer and wetter (Hickler *et al.* 2012). Since trees are long living and immobile, it is very likely they will be more affected by climate change than other taxa (Schall *et al.* 2012). To be able to predict future species distribution under given climate change scenarios, there is now an increased interest in past rates and patterns (Brown *et al*. 2012).

The hemiboreal forests in Southeast of Norway are dominated by coniferous trees, but has also a significant number of deciduous species. Norway spruce (*Picea abies* [L.] H.Karst) and European beech (*Fagus sylvatica* [L.]) (nomenclature follows Lid & Lid 2005; hereafter referred to as spruce and beech) are important tree species in Europe, and their northern borders meet in these forests. According to Sykes *et al.* (1996), the range of beech is expected to expand northwards into the spruce dominated forests because of a more favorable climate. The competition between the two species is expected to increase since a larger geographical area will fulfill the requirements of beech, and the areas where the two species can coexist will be greater. Grundmann *et al.* (2011) assume changes in competitiveness among regenerating trees of the two species, due to different coping abilities to limited resource availability.

Since beech and spruce forests only have very few species in common (Ammer *et al.* 2002, 2008; Schall *et al.* 2012), a distribution shift in these forests implies a fundamental ecosystem transformation. Potential transformations like changes in soil structure and soil acidity alter the ecosystem function, biodiversity, establishment and keystone species composition. These possible substantial changes call for more research about outcome and consequences.

The evergreen spruce forests are prevalent in both hemiboreal, boreal and temperate areas and spruce is an economically important tree species in Norway. It is not very heat tolerant, and it needs adequate, but not large amounts of water to thrive - especially the younger trees. It is a shade tolerant tree, but prefers sunlight and disperses through wind. Litter from spruce is known for being resistant, having a well-protected foliage with a reduced surface area for water loss, and slow decomposition. This result in a buildup of forest floor humus leading to acidification of the top soil (pH ranging from 3.7 to 4.5) and low nutrient-availability (Klotzbücher *et al.* 2012). Spruce prefer well-drained, moist and acidic soils, but through its

dense and not so deep root system, it easily adapts to less than ideal soil conditions. Its canopy opening allows more light to come through, compared to a beech forest.

The beech forest is recognized by its low species diversity in the field and ground layer. This is due to its closed canopy, creating a shady environment that few species tolerate. Beech is a late successional species, its regeneration potential is good, and it has a broad ecological tolerance (Ellenberg 1988). The seeds can disperse over long distances through rodents (Jensen 1985) and jays (*Garrulus glandarius*) (Wagner *et al.* 2010), but primarily beech has a short mean dispersal range (Kunstler *et al.* 2007). Seedlings and juvenile plants are able to regenerate and establish in dark forests, which makes it able to grow under the spruce canopy and thus is a strong competitor in this area. Beech is a more demanding species than spruce, and will most likely not establish in areas with low quality soil or drought. Though; in a climate favourable for beech, it is a very tough competitor (Ellenberg 1988; Bolte *et al.* 2007). Its soil pH is higher than that of soil under a spruce stand; ranging between four and five. In a short term perspective, beech forests decompose litter faster than spruce forests and this counteract soil degradation (Albers *et al.* 2004).

Several factors affect the interspecific competition between the two tree species. Some of them are site and stand conditions due to light availability (Barna 2008), dispersal (Bradshaw *et al.* 2000), phenology (Bolte & Villanueva 2006) and nutrient availability (Reiter *et al.* 2005). If these are limited due to neighboring plants, they will have a constraining effect on the possibilities for establishment. Resource investment into seedling establishment through the above-mentioned factors is a prerequisite for a species success. In addition to these factors, there are other important influences to the establishment of seedlings. Gross (1984) emphasizes seed size and growth form, others study the effects from germinative capacity (Melzack & Watts 1982), predation (Jensen 1985; Wagner *et al.* 2010) and individual species performance (Madsen & Larsen 1997). In this thesis, three important topics are considered when examining influences on the regeneration potential of spruce and beech. These are light, soil type and litter, with the main emphasis on the latter.

Studies have emphasized that light is usually the most limiting resource for seedling growth and survival (Chazdon & Kaufmann 1988; Pearcy & Sims 1994; Barna 2008; Wagner *et al.* 2009). Frost is limiting for the regeneration of beech seedlings. They are therefore dependent on overstory protection, and are very tolerant of both lateral and vertical shade. Spruce

seedlings grow better in environments that are more open. Their canopy allows more light to access than the canopy of the beech forest.

Regeneration can also depend on soil properties. In their study, Quideau *et al.* (2001) found that there is a direct link between forest type and soil organic matter composition, and that vegetation was the factor controlling this, not climate. The species create a soil environment well arranged for their own specific regeneration preferences, through amongst other things litter fall. Both pH, N and C content in the soil will differ from forest type to forest type, due to their distinctive ecosystem construction and function. Considering the different requirements for successful establishment between species, soil type will therefore possibly influence the interspecific competition.

To determine soil pH, litter plays an important role through its contribution to soil organic matter (Sayer 2006). Brady (1974) explains this through the concentration of cations in the soil water, mainly aluminum, while Wilke *et al.* (1993) mention the regulative nature of humic acids on pH. Denslow *et al.* (1991) emphasize the capability of litter to kill or damage plants, while Shaw (1968) talks about litter as a protector from predators. According to Sayer (2006) the two major roles of litter in forest ecosystems are as an important participant in nutrient cycling, and as a regulator of the microclimatic environment due to its protective layer. Litter can affect regeneration in several different ways. Facelli & Picket (1991a) argue that litter suppress or facilitate seedling germination, emergence and survival by altering the humidity, light and nutrient availability, and will therefore affect patterns of interactions. For seedlings to grow, they need amongst other things N from the soil as a source of protein, while creating C through photosynthesis, which give the plants energy. Nutrients like N are driving forces in litter decomposition (Albers *et al.* 2004).

In this thesis, I will study the regeneration of beech in both spruce and beech litter, and the regeneration of spruce in both beech and spruce litter, and what happens to the regeneration when litter is removed. Possible effects from litter on the soil quality in the two forests will be examined and discussed. The study is designed to look at litter from both species, and in both forests. Other studies have looked at different effects from litter in the forest (Facelli & Pickett 1991a, 1991b; Molofsky & Augspurger 1992; Peterson & Facelli 1992), but then without taking the light parameter into account. Although challenging, I have through the represented research design managed to study litter disengaged from the natural light in the forest. Ammer *et al.* (2002) emphasize that very few studies have been conducted on the

effects of stand density on germination success. My study design reflects that variations in light and soil are taken into account.

Assuming that litter is one of the factors that affect the interspecific competition between beech and spruce, I expect to find that litter from beech and spruce influence the seedling establishment and the soil of the two tree species, under equal light conditions. Based on this information, I seek to test the following four hypotheses: (i) litter manipulation influence seedling establishment and biomass. As such, seedling establishment and growth will be highest when litter is removed and lowest when placed in the foreign litter, (ii) litter manipulation will have impact on soil conditions in the short term, expressed by differences in pH, C and N levels in the soil between treatments, (iii) seedling establishment, seedling biomass and content of C and N in seedlings and in soil will be influenced by forest type, (iv) effects of litter manipulation will not be independent of forest type, ie. negative or positive effects of litter will be amplified by light availability.

2. MATERIALS/METHODS

2.1 Area

The present northwestern distribution limit for beech is in South-East Norway (Fig.1). The study area is Brånakollene Nature Reserve, located about 20 km North of Larvik in South-East Norway (Fig. 2), N 59° 11' E 10° 2', just above the highest coastline. In the months May to September between the years 1961-1990, mean monthly precipitation was 90.8 mm and mean monthly temperature was 13.6 °C. The equivalent numbers for 2015 were 205.1 mm and 10.2 °C (eKlima 2016).

In these landscapes spruce forest meet beech forest, with a clear border between the two. They have established on equal monzonite bedrock and soils, but forest type have affected these over time. The spruce forest is planted and contains establishing beech trees, while the beech forest is a natural forest with beech out-competing spruce. The spruce forest surrounds the 19 ha beech dominated nature reserve in a hilly environment with large rocks (NGU 2016). The forest stands are composed of 20-30 m tall beech trees. There were some individual-tree selection cuts done here in 1905-1910, but since then no harvest has been done here. Due to its protection by law in 1980, the nature reserve is almost undisturbed and well developed (Bjune *et al*. 2013).
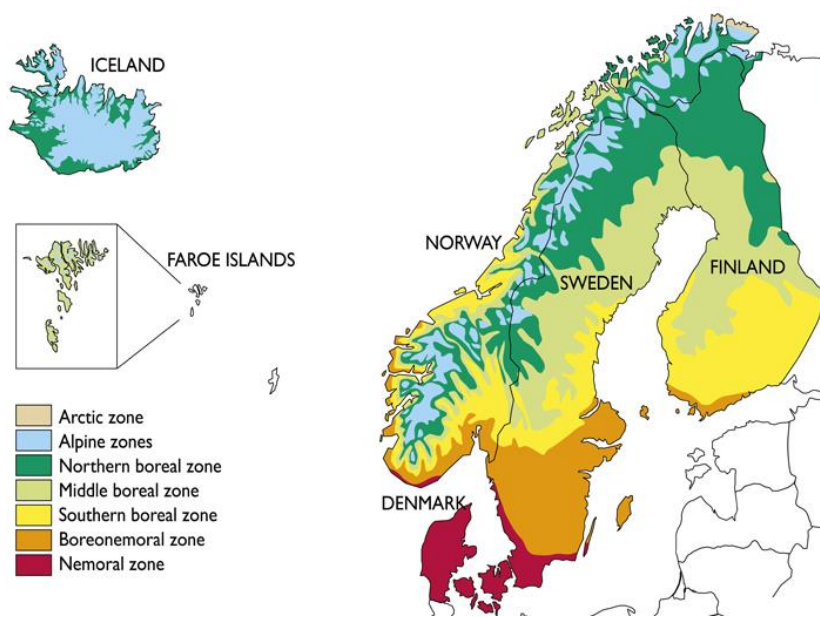
Figure 1: The distribution of main vegetation zones in Scandinavia and surrounding areas. From Moen (1999).
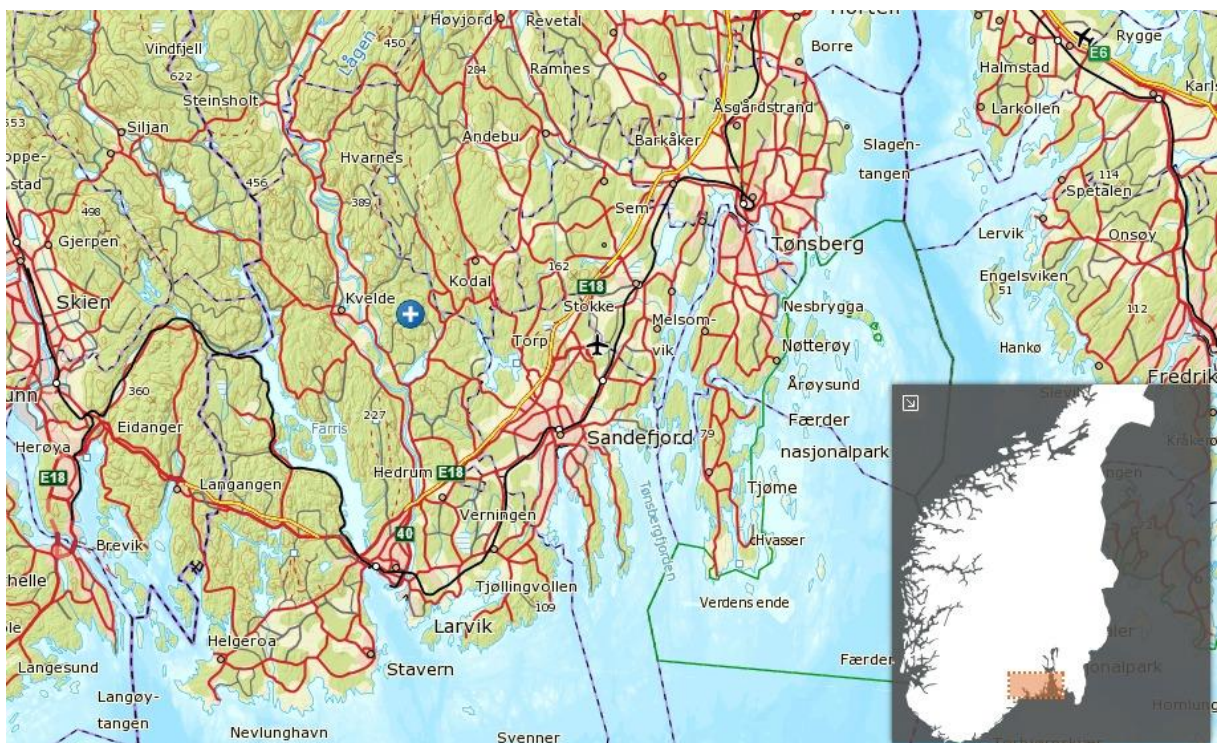

Figure 2: Map from Southeast Norway. Brånakollene is marked with a white cross in a blue dot. From Norgeskart (2016).

The soil here has developed from washouts and is dominated by rough weathering soil. According to the future climate predictions (Hickler *et al.* 2012), beech will continue to outcompete spruce in this area.

2.2 Field study design

The experiment site consisted of 20 research-plots; 10 in the beech forest and 10 in the spruce forest. They were established, and litter was moved between them, in 2014. Litter was also moved within each plot, to be able to separate the effect of moving from the effects of litter itself. The research plots were in close vicinity, selected within a radius of 300 meters in diameters. The plots were chosen due to similar bedrock, but different forest types. Each plot consisted of four 50 x 150 cm subplots with assigned treatments *litter removed*, *control*, *transplanted spruce litter* and *transplanted beech litter* (Fig.3). The subplots were divided into three 50 x 50 cm treatment plots; one was sown with beech, the other with spruce. Both sown treatment plots were covered with 30 x 30 cm cages to avoid predation. The middle treatment plot was not sown, and therefore not caged (Fig.4).

Measurements of diffuse light index (DLI) were estimated for each research plot in September 2015 using hemispherical photographs analyzed in the program Hemisfer v. 2.12 (Schleppi *et al.* 2007; Thimonier *et al.* 2010) to be able to say something about the effects of light availability.
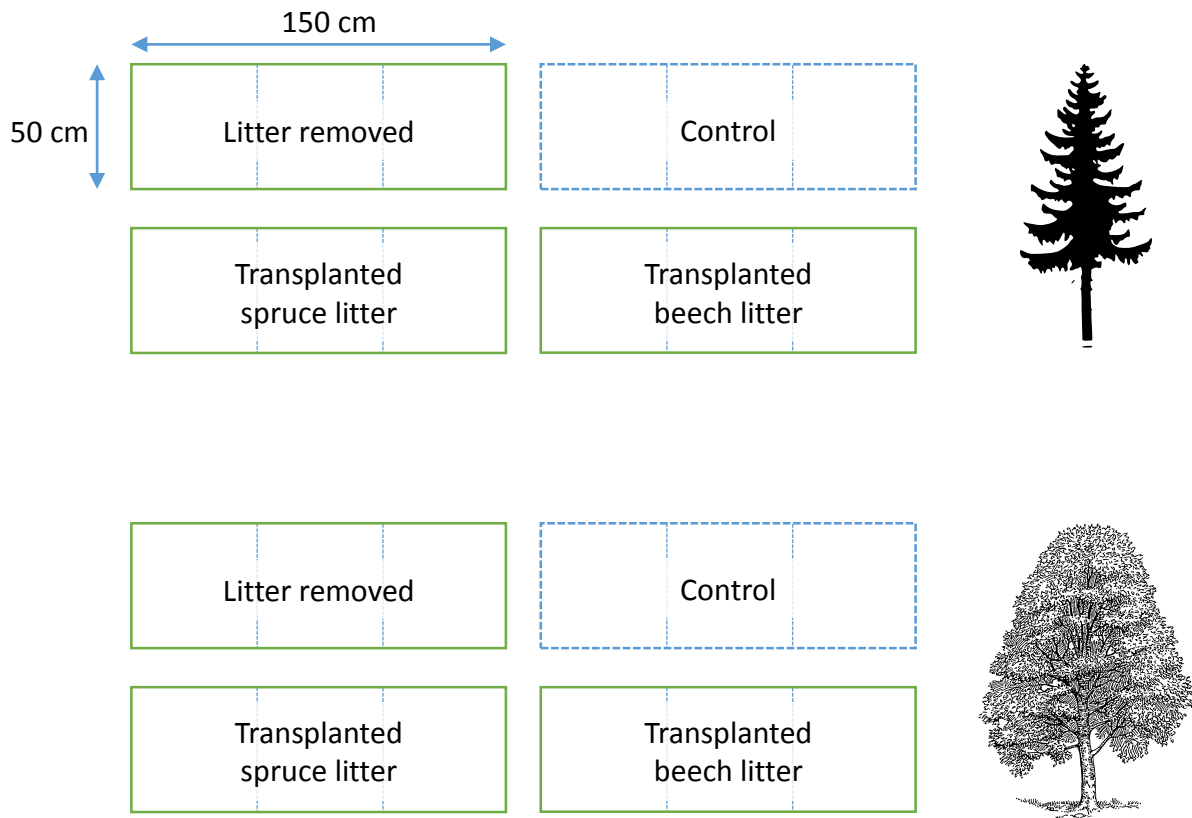
Figure 3: The design of the experiment area, showing two research plots and their subplots; one plot in spruce forest and one in beech forest (Figure made by Johan Asplund)

Figure 4: One of the subplots; spruce litter in beech forest (Photo: Eva Hustoft 2015)

2.3 Lab design and chemical analysis

2.3.1 Plant Material

In May 2015; one year after moving the litter, the treatment plots were sown with seeds already prepared. The spruce seeds were collected in Rakkestad, Østfold by Skogfrøverket, and their germinative capacity was 97 %. For the beech seeds, germinative capacity is unknown. These seeds were collected by Sagaplant in Stokke, Vestfold, and dormancy was broken as a part of this project. The seeds were first kept in moist turf for 10-12 weeks at 4 °C. Then they were stored in a freezer at -2-0 °C until they were sown. Since there was a seed size difference, the beech seeds were counted to 30 seeds per plot, while the spruce seeds were weighed to 0.49- 0.51 gram per plot. The weighed spruce seeds were counted to correspond to approximately 100 seeds.

Due to beech seed predation after sowing, only materials from spruce were available for analysis. The materials for analysis of regeneration, weight, C, N and C:N were collected in early September 2015. These samples contained the results from what was sown in May; the aboveground biomass, roots excluded.

The number of plants were counted per treatment plot, and weighed with a Starto Connect machine. For the rest of the lab analysis grinded biomass was used. The process of grinding into fine powder was conducted in a Retsch MM400 ball mill (Retsch, Haag, Germany), at 30 revolutions per sec. for 90 seconds. The biomass was then put into micro centrifuge tubes marked with the associated subplot, and stored in a freezer (-20°C). To measure C and N, 5-6 mg of the fine powder biomass from each square was weighed with a Mettle Toledo weigh, and put in small packs. The total C and N content was then determined using a Elementar Vario MICRO cube (Elementar Analysensysteme GmbH, Hanu, Germany) which burns the material and uses the gas for measuring. These numbers were then used further in finding the C:N ratio.

2.3.2 Soil material

The soil material was collected in September 2015, one sample from each treatment plot; 40 from the spruce forest and 40 from the beech forest. This procedure was done after collecting the seedlings, to avoid harming them. The soil was sampled with a 5.8 cm in diameters soil

corer, collecting approximately 5 cm of the top soil (humus), then put in paper bags and put to dry for three days in a drying cabinet at 40°C.

The dry soil was weighed and then sieved in a 2 mm sieve (Retsch, Haag, Germany). This soil was further pulverized in a ball mill and run through a C, N and further C:N ratio analysis in a process similar to the one conducted on the plant material. The total amount of C:N was not to be accounted for, due to the use of only a sieved fraction of the soil.

The remaining soil was stored in falcon tubes, and further used to measure pH according to standard pH measurement methodic. 10 ml of the dried and sieved soil from each subplot was thoroughly mixed with 25 ml deionized water and then left to rest overnight. It was shaken again the next day before pH was measured with a inoLab pH 720 (WTW GmbH, Weilheim, Germany).

2.4 Statistical analyses

All statistical tests were performed in R-commander (R version 3.0.2). Figures were made in Excel.

Data were analyzed by Analysis of variance (ANOVA). Response variables analyzed for the plant materials were number of recruited plants, average plant weight, C, N and C:N. For the soil materials the response variables analyzed were C, N, C:N and pH. The ANOVA tests were conducted to see if forest type and treatment had an effect on the response variables. To validate the use of these tests, a Shapiro-Wilk normality test was carried out for all the response variables.

To be able to say something about any possible effects of the moving of litter itself on soil and recruitment, paired T-tests were conducted for both forest types. For these tests, the results from the 20 *control* subplots were used.

Correlation analyzes were performed through Kendall´s tau rank correlation test, to look for associations between various compositions of response variables and explanatory variables.

3. RESULTS

Due to an almost total predation of beech seeds in both forest types, plants collected in this experiment contained only biomass from spruce seedlings. The soil material equally represented both forest types and treatments.

The performed paired T-tests showed that the moving of litter itself did not affect my results. Due to this, my data from the *control* treatments were excluded from the rest of the tests.

Diffuse light index (DLI) was approximately twice as high in the spruce forest (23.1 +- 2.2%), compared to the shadier beech stand (11.5 +- 0.43%).

3.1 Plant material

In both forests treatment showed a significant effect on the establishment of spruce seedlings through a higher number of recruited plants in the removal plots (Table 1; Fig.5). Differences in recruitment in spruce litter and beech litter in the spruce forest were rather small (Fig.5). There was a significant interaction between forest type and treatment on the number of plants (Table 1), and it seemed that the relative effects of the treatments beech litter and removal were strengthened by forest type (Fig. 5). There were no significant differences in recruitment as a function of litter type between the two forests.

Growth was significantly better in the spruce forest with a higher average plant weight, regardless of treatment. Here, the average plant weight was similar in spruce litter and beech litter. This indicated that forest type had an effect on growth, regardless of litter in the spruce forest (Table 1; Fig. 6).

Table 1. ANOVA (X^2 and P-values) testing the effect of forest type (beech *vs* spruce forest) and litter type (beech litter, spruce litter and litter removal) as well as the interaction term Forest type × Treatment response variables in spruce seedlings. Degrees of freedom are given in subscript. Bold letters indicate significant effects at P <0.05.
Weight per plant per spot was not normally distributed according to the regular Shapiro-Wilk normality (P<0.001). Normally distributed when log-transformed.

*For C tissue, N tissue and C:N tissue beech litter was removed, and spruce litter vs removal was tested.

Response variable	Forest type X^2 (P)	Treatment X^2 (P)	Forest type × Treatment X^2 (P)
No of recruited plants	**20.38 (<0.001)** $_1$	**81.67 (<0.001)** $_3$	**17.44 (<0.001)** $_3$
Average weight per plant per subplot (log)	**17.49 (<0.001)** $_1$	2.31 (0.511) $_3$	4.49 (0.213) $_3$
C tissue*	**23.335 (<0.001)** $_1$	1.601 (0.2057) $_1$	0.220 (0.639) $_1$
N tissue*	**44.615 (<0.001)** $_1$	0.135 (0.714) $_1$	0.0308 (0.579) $_1$
C:N tissue*	**36.170 (<0.001)** $_1$	0.419 (0.518) $_1$	0.381 (0.537) $_1$

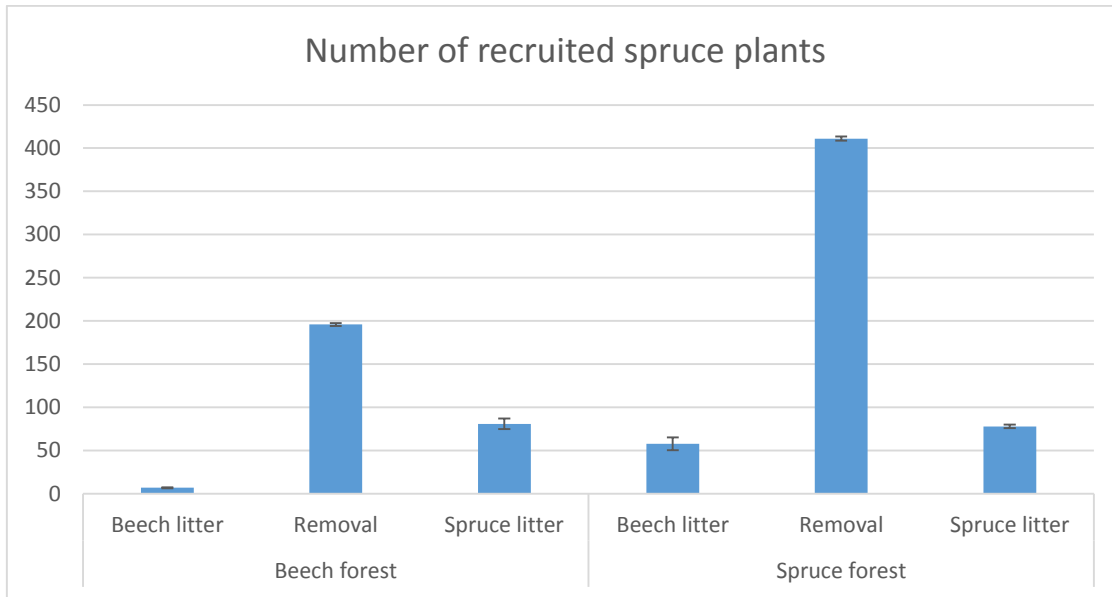Figure 5: Depicts the number of recruited plants in two different forests; beech (*Fagus sylvatica*) and spruce (*Picea abies*), after being exposed to three different treatments (beech litter/removal/spruce litter).
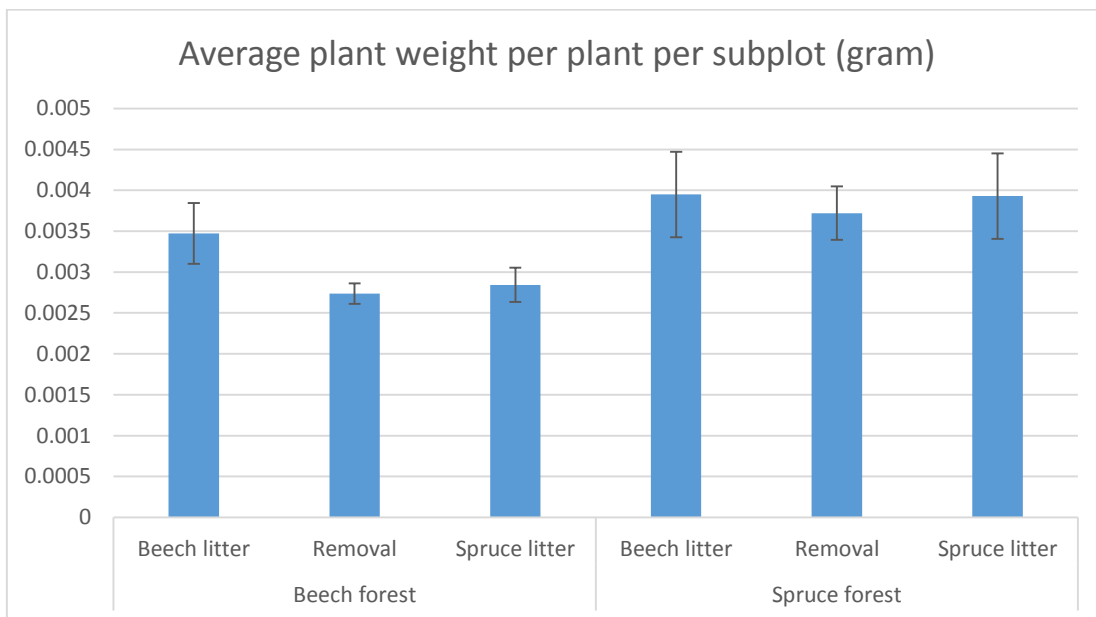

Figure 6: Bar graph portraying different average plant weights (gram) in the two forests; beech (*Fagus Sylavtica*) and spruce (*Picea Abies*) after three different treatments (beech litter/removal/spruce litter).

The response variables average weight per plant per subplot, C tissue and N tissue all showed to be significantly affected by forest type, but not by either treatment or the interaction (both p>0.05). Due to a very low *P*-value ($P= 1.808^{e-09}$) I could also say that forest type had a significant effect on C:N tissue (Table 1). The results from N tissue showed a higher amount in the spruce plants in the beech forest than in the spruce plants in the spruce forest. The analysis of C tissue showed that spruce plants in the spruce forest contain more C than spruce plants in the beech forest. There was therefore also a generally higher C:N ratio in the spruce plants in the spruce forest (Fig. 7; Fig. 8; Fig.9).
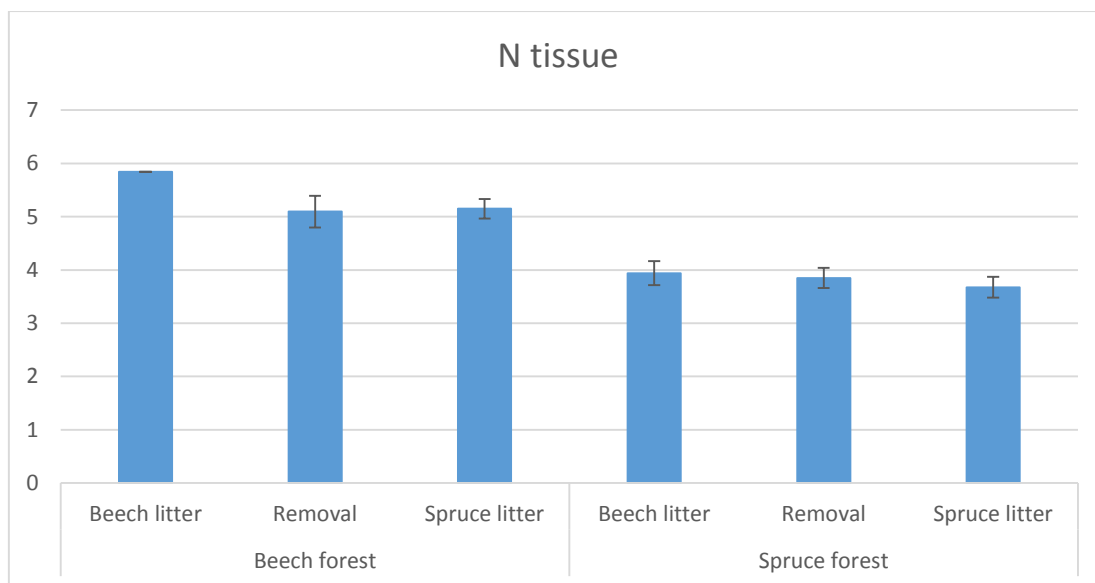
Figure 7: Illustrates the content of nitrogen in spruce plant tissue after being exposed to three different treatments (beech litter/removal/spruce litter) in two different forests; beech (*Fagus Sylvatica*) and spruce (*Picea Abies*).
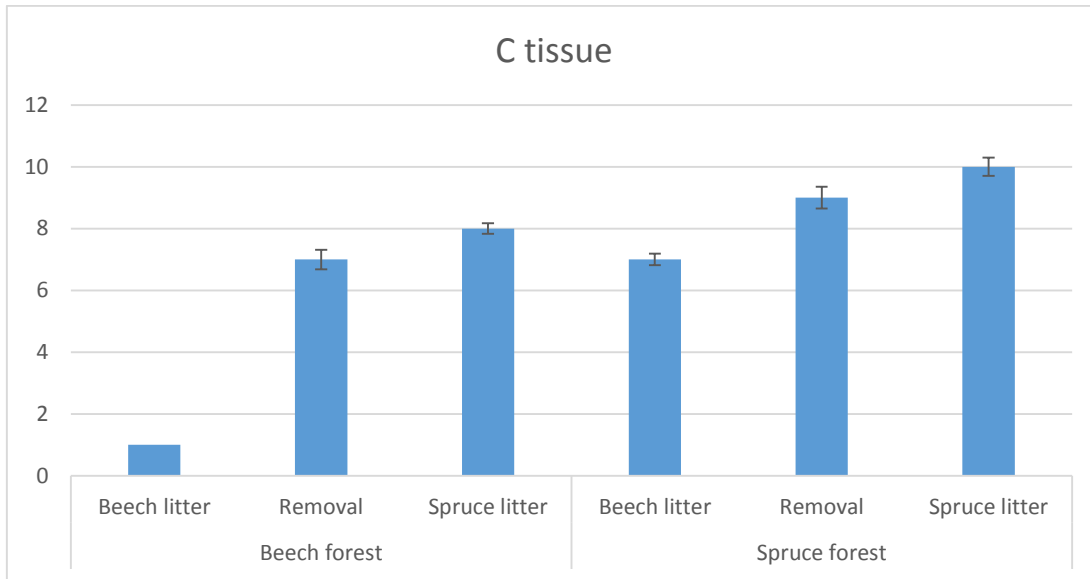
Figure 8: Depicts the carbon content in the spruce plant tissue material collected in both forests; beech (*Fagus sylvatica*) and spruce (*Picea abies*) after the exposure to three different treatments (beech litter/removal/spruce litter).
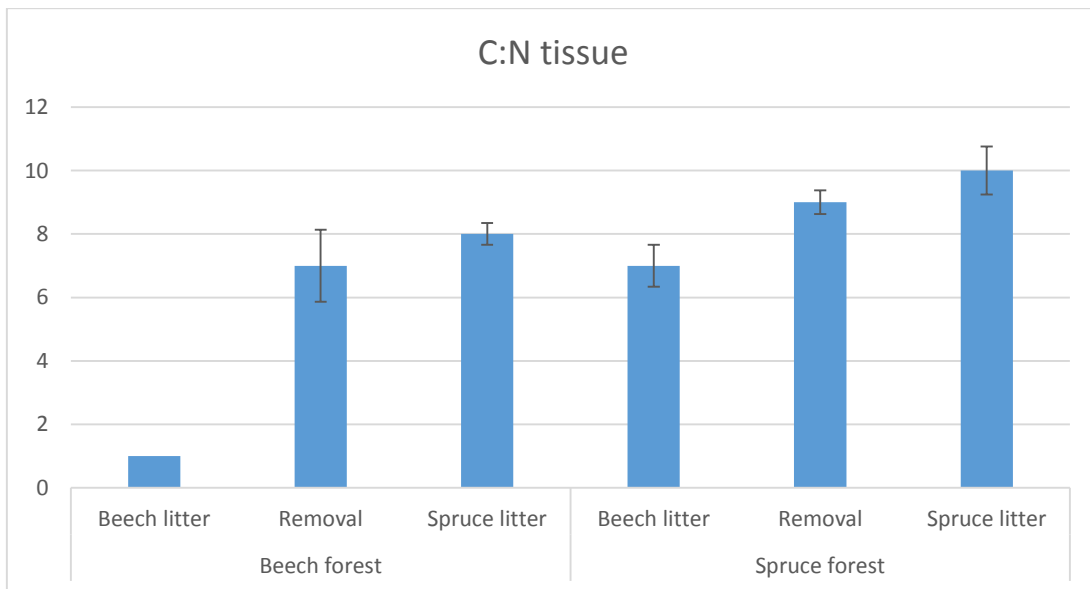
Figure 9: Bar graph of the C:N ratio in the collected spruce plants. The ratio was measured in both forests; beech (*Fagus Sylavtica*) and spruce (*Picea Abies*), and in all three treatments (beech litter/removal/spruce litter).

3.2 Soil material

The results from the ANOVA suggested that forest type had a significant effect on both pH, C and N in the soil. Neither treatment nor the interaction (both p>0.05) had any significant effect on these response variables (Table 2).

Table 2. ANOVA (X^2 and *P*-values) testing the effect of forest type (beech *vs* spruce forest) and litter type (beech litter, spruce litter and litter removal) as well as the interaction term Forest type × Treatment response variables in soil. Degrees of freedom are given in subscript. Bold letters indicate significant effects at *P* <0.05. Soil C:N was not normally distributed according to the regular Shapiro-Wilk normality (*P*<0.001), or to the log-transformed test (*P*=0.015).

Response Variable	Forest type X^2 (*P*)	Treatment X^2 (*P*)	Forest type × Treatment X^2 (*P*)
Soil pH	**8.768 (0.003)** $_1$	2.210 (0.530) $_3$	1.659 (0.646) $_3$
Soil C	**18.782 (<0.001)** $_1$	1.237 (0.539) $_2$	0.308 (0.857) $_2$
Soil N	**12.445 (<0.001)** $_1$	3.874 (0.144) $_2$	0.344 (0.842) $_2$

Soil pH was significantly lower in the spruce forest than in the beech forest. Since treatment turned out not to affect pH, this indicate that the effect on pH was from forest type, regardless of litter. There was therefore reason to say that spruce forest had increased the soil acidity over time (Fig. 10).
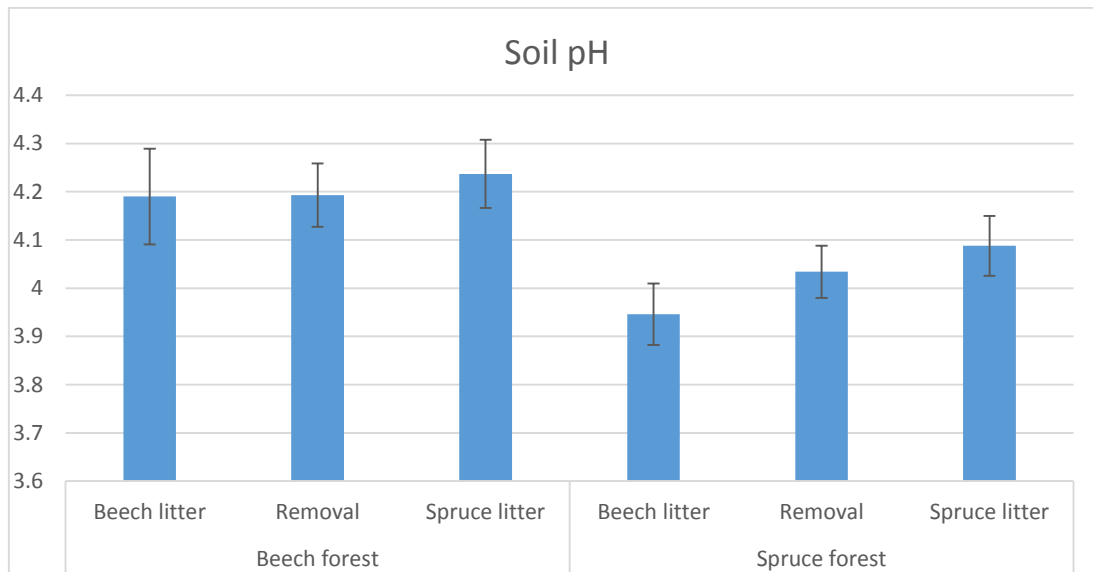
Figure 10: Illustrates the pH in soil after being exposed to three different treatments (beech litter/removal/spruce litter) in two different forests; beech (*Fagus Sylvatica*) and spruce (*Picea Abies*).

The response variables C soil, N soil and C:N soil all showed to be significantly affected by forest type, but not by the interaction nor by treatment. There was significantly more C and N in the soil in the spruce forest than in the beech forest, regardless of litter (Fig. 11; Fig.12; Fig.13).
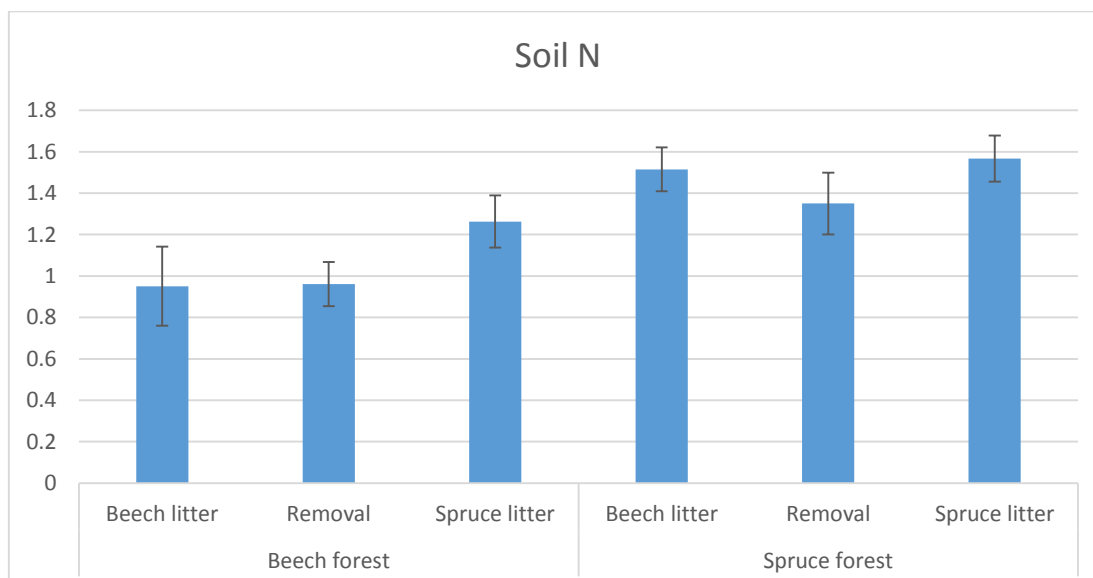
Figure 11: Illustrates the content of nitrogen in soil after being exposed to three different treatments (beech litter/removal/spruce litter) in two different forests; beech (*Fagus Sylvatica*) and spruce (*Picea Abies*).
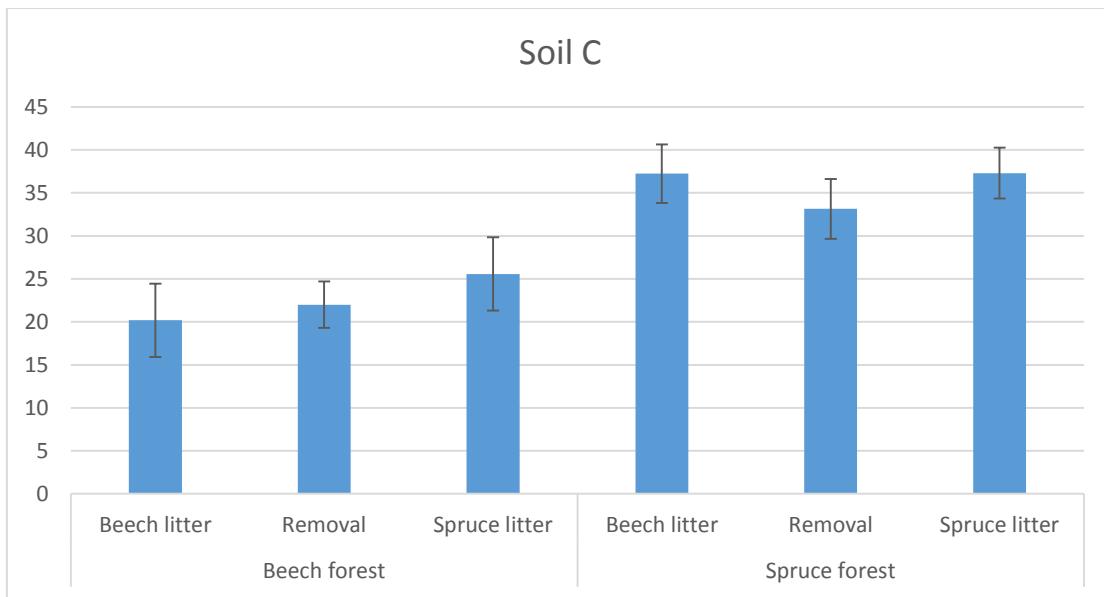
Figure 12: Depicts the carbon content in the soil samples collected in both forests; beech (*Fagus sylvatica*) and spruce (*Picea abies*) after the exposure to three different treatments (beech litter/removal/spruce litter).

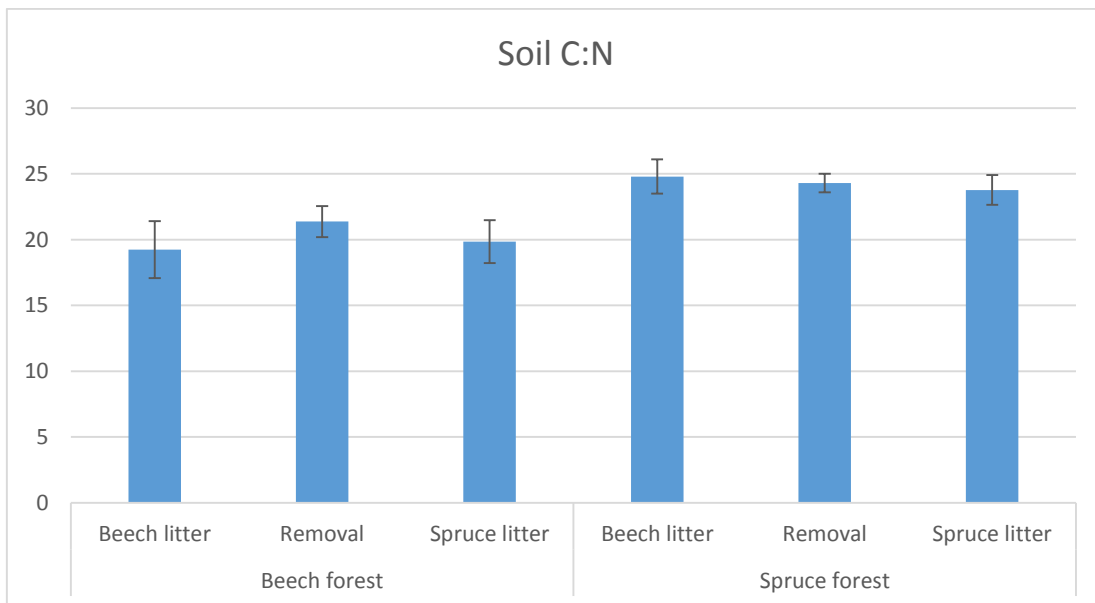Figure 13: Bar graph of soil C:N ratio in the collected soil samples. The ratio was measured in both forests; beech (*Fagus Sylavtica*) and spruce (*Picea Abies*), and in all three treatments (beech litter/removal/spruce litter).

3.3 Correlation test

The correlation analyzes showed significant positive associations between DLI vs Recruited number of spruce plants (tau=0.217, p=0.018), DLI vs Weight per plant per subplot (tau=0.421, p=2.23e^{-05}), C plant tissue vs DLI (tau=0.284, p= 0.004) and C plant tissue vs Weight per plant per subplot (tau=0.500, p=2.289e^{-07}) (Table 3). In addition, N plant tissue vs Weight per plant per subplot (tau=-0.672, p=0.0004) came out with significant negative correlation (Table 3).

Table 3: Kendall´s tau rank correlations for associations between various compositions of response variables and explanatory variables. Bold letters indicate significant correlations at *P* <0.05.

Correlation	tau-values
DLI vs Recruited number of spruce plants	**0.217**
DLI vs Weight per plant per subplot	**0.421**
pH vs Recruited number of spruce plants	-0.110
pH vs Weight per plant per subplot	-0.070
N soil vs Recruited number of spruce plants	0.118
N soil vs Weight per plant per subplot	0.120
C soil vs Recruited number of spruce plants	0.161
C soil vs Weight per plant per subplot	0.165
C plant tissue vs DLI	**0.284**
C plant tissue vs C soil	0.046
N plant tissue vs DLI	0.080
N plant tissue vs N soil	-0.125
C plant tissue vs N soil	0.261
N plant tissue vs C soil	-0.198
N plant tissue vs Weight per plant per subplot	**-0.672**
C plant tissue vs Weight per plant per subplot	**0.500**

4. DISCUSSION

4.1 Beech seeds and predation

An overall predation of beech seeds happened in both forests with empty and in some cases devastated, beechnut shells. According to Wagner *et al.* (2010), beech has a seedling sensitivity to animal predation. Both deer, birds, rodents and other granivores are potential predators (Madsen 1995; Olesen & Madsen 2008). The seeds are rich in both nitrogen and energy, and are preferred due to their large size (Jensen 1985). Since all the sown squares were covered with cages, and there were some signs of hazards on these, predation in this experiment could possibly have been done by mice. They could possibly have accessed the cages by crawling under them. For my experiment, a predation like this says something about a potential challenge for beech seeds when establishing in this particular area. A high risk of beech seed predation can be a possible disadvantage for beech establishment, and can therefore be an important factor when considering the interspecific competition between the two tree species. In my research, due to the small sized nature of spruce seeds, it was not possible to quantify if predation also did occur here. According to Shaw (1968), litter can function as a predation cover. This makes it reasonable to suggest that the majority of a spruce seed predation in my research would most likely have occurred in the removal treatment plots. Côté & Gagnon (2003) support this speculation by arguing that small rodents like squirrels predate seeds and seedlings of black spruce after a burn, and that this affects its early regeneration establishment. My results from recruited number of plants (Fig. 5) show that the removal plots had the highest recruitment. Derived from this, there are no indications of spruce seed predation of quantitative importance in my research.

4.2 Litter manipulation and influence on seedling establishment and biomass

The results from my research revealed that litter manipulation influence spruce seedling establishment through a higher recruitment in the removal subplots in both forests (Fig. 5).

When altering litter content through removal or addition, several of the cues seeds need for germination are changed. This can be temperature, light and moisture. The observed differences in recruitment can be an increase due to removal of litter, a decrease because of the litter addition, or a combination of these. In their meta-analysis, Xiong & Nilsson (1999) are trying to find general patterns in current existing studies on the effects of plant litter.

Studies that are according to them, characterized by huge variations. They put emphasis on the duration of the studies; that short-term effects of litter on establishment in a forest ecosystem are mostly negative outweighing the positive effects, in studies that lasted for less than 3-4 years. This could be a part of the explanation for the differences in recruitment between the removal subplots and the subplots treated with litter in my research (Fig. 5). According to Xiong & Nilsson (1999) the strongest effect from litter was on germination, and these negative effects first turn positive after 3-4 years. This indicate that removing litter early in the growth season can possibly remove these negative effects on establishment. Xiong & Nilsson´s (1999) findings are supported by the results of Carson & Peterson (1990) where litter removal increased plant densities, while adding litter led to a reduction. Facelli & Pickett (1991a) explain a possible reduced germination due to litter functioning as a physical barrier for seeds to reach the soil. This highlights the importance of disturbances like for instance animal trampling and flooding early in the growing season, participating in moving and removing litter. Considering my results, these theories are in support of my findings. In the events of for instance drought or other extremes, we might have found that removal could have negative effects on establishment. This was not the case here, and removal of litter seemed to have a positive impact on early establishment. The seeds were placed under the canopies in both forest, and this gives protection from the sun and from drought.

To regard soil moisture as an aspect of interest, Ammer *et al.* (2002) found that the coverage of beech seeds with spruce leaf litter resulted in a distinct increase in seedlings. They give no solid explanation for this, but speculate on possible effects of a reduction in soil evaporation due to leaf coverage. Goldberg & Werner (1983) discovered that soil moisture tended to be lower when litter was removed. In accordance with my results, they too had a lower recruitment under litter cover. Several of their explanations for this can also count for my results, such as the low light levels. The levels can possibly inhibit emergence, but the light conditions in their study does not completely explain the emergence patterns, indicating that the influences can be complex and many. The effects from light will be considered further down in this thesis.

Carson *et al.* (1990) concluded in their study that short-term litter removal and addition had no significant impact on total plant biomass. In my study too, litter treatment did not affect average plant weight (Fig. 6), whether you look at effects either from litter type or from removal. These results are contradictory to the findings of Nyland *et al.* (1979) in their research on spruce. According to them, the removal of litter negatively affected the shoot

weights, nine growing seasons after a clearcutting. My research was done beneath the canopy, not in an open clear-cut. One likely explanation for my deviant result can therefore be drought as a consequence of clearcutting in Nyland *et al.*´s (1979) study. For their plants, litter would have helped moisture stay in the soil and litter removal could possibly create a very dry environment. The canopies removed in the clearcutting, would have intercepted sunlight and reduced water run-off. Differences in time scale can also be a part of the divergent results. When researching the effects from litter, one could argue that a single growing season is too little to see any positive or negative effects on biomass, although some studies contradict this (Sayer 2006, Xiong & Nilsson 1999).

4.3 Soil conditions and C and N content in plants

Litter did not significantly affect the soil parameters in the short-term perspective that my research provide (Table 2). Gou *et al.* (2013) argue in their research that leaf-litter derived N from beech stabilized rapidly in the mineral soil 5-10 cm deep, only after 21 days. There was still N in the 0-5 cm soil, but it showed a rapid translocation of N from litter to the deeper layers of the soil. They explain this with the mycorrhiza taking up nutrients and transporting it to the hyphae in the mineral soil. Another explanation from their research is the contribution from earthworms transferring N to the deeper soil layers around 10 cm. This is supported by Schaefer (1990) who found that approximately half the litter fall disappears from the surface after one year, as a result of earthworms. This would not have occurred in the spruce forest since the soil pH here is too low for earthworms. These might well be parts of the explanation for my result that litter does not affect the N in soil 0-5 cm deep in the beech forest, and that the soil in the spruce forest has a higher N content (Table 2; Fig.11). According to Gou *et al.*´s (2013) findings, N seem to transfer vertically at a rapid pace. Zeller *et al.* (2000) too found that parts of the ^{15}N from beech litter mineralized immediately after litterfall and then went straight to the mineral soil. They went a bit further in their research, to see where the litter ^{15}N was located after 3 years of litter decomposition. Most of the ^{15}N was then recovered in the top 2 cm of the humus, and only 12 per cent was located below 2 cm depth. For the competition between beech and spruce, this might be a factor to consider due to the more shallow root system of spruce, as a rapid vertical transfer can possibly make the nutrients harder for spruce to reach in the early stages of regeneration.

Klotzbücher *et al.* (2012) examined how fluxes of dissolved organic matter in the forest floor of a spruce stand was affected by litter input. They concluded that when it comes to changes in fluxes of dissolved organic matter, recent litter is not an important source. When litter input was increased over a six-year period though, they found that fluxes was affected through a change in the decomposition of organic matter. Their study also brings results regarding fluxes of dissolved organic carbon within the forest floor, and that these fluxes were not directly related to C input from litter fall. This corroborate my studies, where litter did not affect C content in the top 5 cm of the soil (Table 2).

Forest type showed a significant influence on all soil variables (Table 2). It was found that the C, N and C:N content was higher in spruce forest soil than in beech forest soil (Fig. 11; Fig. 12; Fig. 13). Corroborating this, Quideau *et al.* (2001) found a clear link between forest type and soil chemistry, indicating that a forest´s specific vegetation is a part of what controls the composition of its soil organic matter. Berger *et al.* (2002) reported more C and N under spruce stands than under beech as a total of the upper 50 cm of the soil, and might possibly corroborate my results (Fig.11; Fig.12). An explanation for the effects of forest type on soil is according to them through its regulation of the microclimate. Temperature and water are the two main components controlling C turnover and these are both affected by each species distinctive forest floor microclimate (Berger *et al*. 2002). Vesterdal *et al.* (2008) saw significant differences in soil C, N and C:N ratios under six different European tree species after 30 years, but only in the forest floor and in some of the mineral soil layers. Amongst the trees were beech and spruce. In their research they found that species generally affect C and N content and C:N ratio strongly, but in the 0-5 cm top layer of the soil, they found no significant species differences in C and N. For my study, this is interesting because I did find differences in the top 5 cm of the soil that could not be explained through the treatments (Fig.11; Fig.12). Vesterdal *et al.* (2008) showed that spruce generally had a tendency to higher forest floor influence than beech, with a higher C and N content, and explain this with the slow turnover rates of C and N in spruce. This tendency can be an explanation for the significant influence of forest type in my study (Table 2). Quideau *et al.* (1996) on the other hand found higher soil nutrient levels under oak (*Quercus*) than pine (*Pinus*) in their long-term research. The evolved mechanisms of coniferous trees is to retain nutrients in standing biomass, through for instance low leaf turnover, unlike broadleaf forest strategies with a more rapid nutrient cycling. They argue that this is what is leading to increased nutrient retention in the soil of broadleaf species, supported by studies conducted by Cole & Rapp (1981). My

results came out opposite with higher C and N levels in the spruce forest soil. Vesterdal *et al.* (2008) emphasize that species differences in forest floor C and N cannot be explained by species differences in litter fall, but argue that they were offset by differences in mineral soil C and N. They explain this through the tendency of spruce to accumulate C and N in the forest floor, not in the mineral soil. In an earlier study, it was clarified that also soil nutrient status of tree species have an effect on the forest floor (Vesterdal & Raulund-Rasmussen 1998). Guo *et al.* (2013) looked at the importance of N nutrition for beech seedlings. Their study showed only a minor contribution of leaf litter N to beech seedlings, and a rapid stabilization of N in the mineral soil. A possible explanation for the differences is that N is more easily available in the soil in the beech forest.

Litter is a major source of soil organic matter, which again plays an important role in determining soil pH (Sayer 2006). pH can change through the concentration of cations in the soil water, mainly aluminum (Brady 1974). Wittich (1951) explains a decrease in pH as a consequence of diminished supply of base ions, often occurring on nutrient poor soil types. According to my results, forest type had a significant effect on pH, whereas litter treatment had not (Table 2, Fig.10). Berger *et al.* (2002) explain a generally lower pH under spruce stands with an acidification starting at the top layer, due to slow litter decomposition and a subsequent buildup of forest floor. Partly due to the higher pH in beech forest, N-rich beech leaves decompose faster here (Albers *et al.* 2004; Berger *et al.* 2002). Sayer (2006) emphasize that litter removal can either increase or decrease pH in soil, and she found no uniform response in her long-term based review of several studies. Ponge *et al.´*s (1993) study showed a decrease in soil pH after long-term litter deprivation in a mixed deciduous forest, whereas natural litter accumulation has proved to increase pH in other long-term studies (Beatty & Sholes 1988; Wilke *et al.* 1993). This corroborate my results that litter showed no short term effects on the soil parameters regardless of treatment, but forest type did (Table 2). My research showed that time scale can be an important aspect when regarding soil pH, and there was an insignificant tendency of higher pH in soil transplanted with spruce litter than soil transplanted with beech litter. The effects of forest type on pH indicate a possible long-term effect, and the lack of effects from treatment indicate no significant short-term effects from litter (Table 2, Fig.10). If my research had lasted a longer time, we might have expected for instance to find more N derived from litter in the 0-5 cm top layer of the soil, according to the 3-year aspect conducted by Zeller *et al.* (2000) and also a possible effect on pH. This could bring a different result, where an effect from litter on the various soil parameters could have

been significant. In the long term, we can therefore say that litter is most probably significant for the soil properties and possibly an important aspect of what we call forest type.

Different studies have proven that beech litter decompose faster than spruce needles (Albers *et al.* 2004; Jørgensen 1991). Albers *et al.* (2004) who also looked at beech and spruce, emphasize that both types of litter decompose more rapidly in beech stands than in spruce stands, indicating an effect of forest type on decomposition rates. The studies partly corroborate the results from Prescott *et al.* ´s (2000) research who in addition discovered that during the first year broadleaf litter decomposed faster than needles, but after three years the differences were small since broadleaf litter decomposition had then slowed down and approximately met the decomposition speed of needles. The reason for the rapid decomposition of broadleaved litter was, according to them, higher N concentrations and low lignin, but they attribute greater losses through leaching in the early stages of decomposition due to greater labile content. I found that spruce tissue from the beech forest had a higher N concentration than spruce tissue from the spruce forest (Fig.7), and also an effect from forest type on N tissue (Table 1). Poorter *et al.* (1990) explain a higher content of N in fast growing species with a higher rate of photosynthesis per unit N in the leaves. When regarding the result that DLI and average plant weight correlate positively (Table 3), my study corroborate their result. This can possibly explain why the spruce seedlings in the beech forest have a higher N content than the ones in the spruce forest. A higher allocation of N to the seedlings gives a higher rate of photosynthesis, and in the dark environment of the beech forest where light is a limiting resource this can be vital for their survival and establishment. It could also be that the N concentration in fast growing plants gets lower as a thinning effect. This is supported by the results from figure 6 showing that the largest plants are in the spruce forest where there is more light available, and that these plants have a lower N concentration (Fig.7). The negative correlation between N plant tissue and weight (Table 3) corroborate these thoughts. There was more C in the plants in the spruce forest, than in the beech forest in my research (Fig. 8). One likely explanation for this is also the different light availability in the two forests, since the plants get their carbon through photosynthesis. C plant tissue vs DLI correlates positively (Table 3), and supports this. It could also be that the more a plant grows, the more C it contains, as shown by the positive correlation between C plant tissue and average plant weight (Table 3).

4.4 Light conditions

For plants to establish there are several intertwined plant characteristics contributing in the interspecific competition of capturing resources. According to Kozlowski *et al.* (1991) many environmental factors influence the rate of photosynthesis; CO_2 concentration, soil water availability, temperature, humidity and light. Photosynthesis account for approximately 90 % of a plant´s dry weight (Poorter *et al.* 1990), and is therefore important to consider when regarding recruitment. To look at possible explanations for the effect from forest type on seedling growth in the two forests (Table 1), light is an important factor to consider. My results show that the low light environment under the beech canopy can be a possible explanation for the reduced growth of spruce seedlings, supported by a positive correlation between DLI and plant weight (Table 3; Fig.6). Stenberg *et al*. (1999) looked at changes in shoot structure of four-year-old spruce seedlings due to canopy openness. They conclude that shade shoots had up to three times larger shoot silhouette area per unit needle mass than sun shoots, but did not look directly at the effects from shade. According to this, we could have expected to see a weight difference in the seedlings in my research - where the roots were excluded - with bigger plants in the shady beech environment. This is not the case, the seedlings are still bigger in the spruce forest. This can possibly be explained by other abiotic parameters like moisture, temperature or litter, which can all affect the effects from light on seedling establishment. Schall *et al.* (2012) found in their study on effects from light availability on growth, that spruce reduced total biomass in low light treatment. They regarded biomass allocation and discovered that spruce changed the allocation from belowground to aboveground biomass under decreased light availability.

There was a significant decrease in recruitment in the subplots treated with beech litter in the beech forest (Fig. 5), and the interaction between forest type and litter treatment was significant (Table 1). In other words, the recruitment was lowest when spruce seeds were placed in beech litter, in the beech forest (Fig. 5). Peterson & Facelli´s (1992) study contributes with very interesting information regarding this. When comparing two species, one with small seeds (*Betula alleghaniensis*) and one with larger seeds (*Rhus typhina* L.) and subjecting them to various types of plant litter, they found that seedling emergency was reduced from the effects of litter only in the small-sized species. *Rhus typhina* L , the species with the larger seeds, was not affected by the amount of litter above it. Gross (1984) got the same result in her research on effects of seed size on seedling establishment in monocarpic perennial plants. When placed in litter, the larger seeds had the highest relative growth rate.

Figure 5 shows a reduction in recruitment of the small-sized spruce seeds in the litter treatment subplots. Peterson & Facelli (1992) speculate if this might be explained through different dispersal strategies, and that wind-dispersed seeds – like spruce seeds - germinate primarily in response to light. To corroborate these thoughts, my correlation tests showed a significant correlation between DLI and the number of recruited plants (Table 3). A combined effect from a darker forest and litter might therefore also explain the lower recruitment in the plots treated with litter (Fig.5). Due to predation of the beech seeds, I cannot say if this would have occurred for beech seeds under spruce litter in the spruce forest. Peterson & Facelli (1992) attribute the different responses to litter, to the differences in seed size. They also propose the suggestion that the different consequences of litter on emergence due to seed characteristics, contribute to a coexistence between the two species.

Studies done by Schall *et al.* (2012) show that beech was less affected by low light than spruce. According to Sagheb-Talebi & Schütz (2002) beech seedlings can establish under a wide range of canopy openings, and have a high competitiveness in a more shady environments. Parhizkar *et al.* (2011) did a research on oriental beech (*Fagus orientalis* Lipsky) and its regeneration under different relative light intensity (RLI) values. They found that regeneration development was better with an RLI of 10-15 per cent, but the differences in number of saplings showed no significant effects across the RLI-levels. This can indicate that beech will not necessarily struggle to establish under a spruce canopy, and that an interspecific competition in this forest might not be in favor of spruce due to amount of light. Barna & Bosela (2015) on the other hand, found that the regeneration proportion for beech was dependent on light conditions, with noticeably lower regeneration in an open canopy but they too found no significant impacts from other various canopy openings. They emphasize that even in the clear cut stands, beech reached up to 44% of the regeneration. This corresponds well with its broad ecological tolerance (Ellenberg 1988), and can be a part of what makes it hard to outcompete. Knapp & Smith (1981) looked at factors influencing seedling establishment of Engelmann spruce (*Picea engelmannii*), where light was one of the parameters. They found that lack of light was not responsible for the low numbers of seedlings in the understory. According to them, other factors like seed size and root growth are more likely to explain low recruitment than light. Baldwin (1934) supports this and says that not light itself but possible effects from light on temperature and soil moisture can be important for germination.

5. CONCLUSION

Litter influenced seedling establishment through higher recruitment when litter was removed. Forest type had an impact on soil conditions and light, which again affect the growth in plants. It is therefore likely that forest type will affect the species success. In Norway it will primarily be beech spreading in the spruce forest. This study does not provide results regarding this, due to beech seed predation.

My research show that predation will most likely be a challenge for beech when establishing in this area. According to my results and the referred studies undergone, there is reason to say that direct effects from reduced light availability will be a potential disadvantage for spruce regeneration when competing with beech. Within the established beech forest, I found that a combination of light and litter could possibly affect spruce recruitment. This indicates an advantage for beech establishment compared to spruce establishment in the beech forest. To corroborate these assumptions, further studies are required.

Weaknesses of this study include that results can be hard to interpret since many variables are affected by litter at the same time. This was a short-term study. Due to slow responses in nutrient dynamics, short-term responses can therefore be absent.

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