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Burial of downed logs from vegetation covering and its effect on wood decomposition

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Acknowledgments

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Abstract

As dead trees fall to the ground and becomes woody debris (WD) it gradually buries by ground vegetation growing on the forest floor. The rate of the burial process can affect the decomposition of the WD, and thereby affect the release rate of the C stored in the wood. Here, I used a large-scale field experiment on dead wood logs in northern Sweden to examine which environmental factors that had an influence in burying wood, and if this burial had an effect on the density, C and N concentration in the wood. After being decomposing for 15 years, 32% of the studied logs were buried (more than 50% of the log surface covered by ground vegetation). Environmental factors like peat depth, soil moisture, sun exposure and altitude affected the vegetation covering. Log attributes such as tree species and diameter also affected, and so did longitudinal ground contact. Buried logs with a high cover percentage were expected to be less decomposed than exposed logs, resulting in a higher basic density in the buried wood. Nevertheless, cover of log surfaces showed no significant effect on basic density in the examined logs. Instead, peat depth showed a significant effect here, resulting in higher basic density with increasing peat depth. While logs located in deep peat had a mean density loss of only 28% in 15 years, the corresponding density loss for logs in shallow peat was 47%. Both C and N concentration increased with decreasing basic density. The slow decomposition of dead logs in forests with a thick humus layer indicates that dead logs can function as a small, but long-term nutrient pool on the forest floor, and that decaying logs can retain C for a long time. Buried wood should therefore be accounted for in future carbon budgets.

Sammendrag

Ettersom døde trær faller overende og blir liggende på skogbunnen blir de gradvis overvokst av bunnvegetasjon. Overveksthastigheten kan påvirke nedbrytingen av trevirket, og dermed hvor raskt karbonet som er lagret i trevirket slippes ut. I denne studien benyttet jeg et storskalaforsøk på døde trestammer i nord-Sverige til å undersøke hvilke miljøfaktorer som påvirker overvekst, og om denne overveksten hadde en effekt på densiteten og konsentrasjonen av karbon og nitrogen i de døde stammene. 32% av de undersøkte stammene var mer enn 50% overvokst av moser og annen bunnvegetasjon etter å ha ligget på skogbunnen i 15 år. Miljøfaktorer som torvdybde, jordfuktighet, soleksponering og høyde over havet påvirket overveksten. Treslag, diameter og markkontakt hadde også en effekt. Stammer som hadde en høy overvekstprosent var forventet å være mindre nedbrutt enn de som hadde lav overvekstprosent, noe som ville resultere i høyere basisdensitet hos de overgrodde stammene. Overvekstprosenten viste likevel ingen signifikant effekt på basisdensitet i de undersøkte stammene. Derimot viste torvdybde en signifikant effekt, der økende torvdybde ga økende basisdensitet. Stammer som hadde ligget i dyp torv hadde et gjennomsnittlig densitetstap på kun 28% i løpet av 15 år, sammenlignet med stammer liggende i grunn torv som hadde et densitetstap på 47%. Både karbon- og nitrogenkonsentrasjonen i de døde stammene økte med synkende basisdensitet. Den trege nedbrytingen av døde trestammer i skoger med tykt humuslag indikerer at døde stammer kan fungere som et lite, men langsiktig nitrogenlager på skogbunnen, og at de kan fortsette å lagre karbon over lang tid. Overvokste trestammer burde derfor regnes med som karbonlagre i framtidige karbonbudsjetter.

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1. Introduction

Decomposition of dead wood in forest ecosystems is a natural part of the carbon cycle (Koster et al. 2015). As dead wood falls and becomes woody debris (WD) it is gradually overgrown and buried by ground vegetation and litter deposition (Moroni et al. 2015). The rate of the burial process is dependent on the size of the WD, amount of ground contact and environmental factors like temperature and moisture (Dynesius et al. 2010; Jacobs et al. 2015; Koster et al. 2015). Woody debris is defined as buried wood (BW) when more than 50% of its surface is covered by soil, litter or ground vegetation (Moroni et al. 2015). In a large-scale experiment in northern Sweden, wood burial via surface covering from ground vegetation was examined by Dynesius et al. (2010). After 5 growing seasons they found that longitudinal ground contact, peat depth, soil moisture, slope and canopy shade had an effect in burying downed logs. They also examined if the size of the log and the log species had an effect on the surface covering. After 5 growing seasons the mean surface cover of the logs was 23%, meaning that many of the logs not yet could be referred to as buried wood. In this study, I visited the same logs after 15 growing seasons to examine the change in surface covering and look at which factors that affected overgrowth in the long run.

Earlier research shows that the burial rate is faster in moist forests with a thicker humus layer than in dryer environments (Dynesius et al. 2010; Jacobs et al. 2015; Moroni et al. 2015). As the WD becomes a part of the humus layer in moist forests, the decomposition rate decreases due to lower temperatures, higher moisture in the wood and anaerobic conditions caused by moist or waterlogged soils (Moroni et al. 2015). Thus, moist forest with high accumulation of soil organic matter and thereby a thick humus layer, can also accumulate and preserve large amounts of partly decomposed buried wood.

Through the IPCC Guidelines for National Greenhouse Gas Inventories, which Norway has signed, the nations "*are obliged to quantify C pools and fluxes in their forests, including its proportions occurring as dead wood*" (IPCC 2006). Even though it has been found that downed deadwood can account for approximately 20% of total ecosystem carbon (C) in forests, BW is typically not accounted for in forest C stock estimates (Stokland et al. 2016). When estimating C pools in forest soil the dominating method is to estimate C content based on the bulk density of the organic material in a soil sample (Moroni et al. 2015). Most BW pieces have a density greater than 0.13 g/cm^3, which is way higher than the density of the soil organic matter. This means that the BW has a higher C content than the surrounding humus layer. When sampling, points with BW is often avoided because the hard structure of the WD prevent the equipment from getting a complete soil sample. This leads to an underestimation of soil as a C pool, because the C stored in BW is not accounted for. In this way, BW can represent a large C pool but it is not yet recognized in forest C accounting. Stokland et al. (2016) used data from the Swedish National Forest Inventory (NFI) to document the frequency of buried wood across a wide range of forest conditions and quantify the amount of C in buried wood. The C content in the buried wood was not measured directly, but calculated on the basis of which decay class it belonged to, based on values found by Sandström et al. (2007). In this way, Stokland et al. (2016) had no direct link between wood burial processes and C content in the buried wood in their study. Here, I look into the burial process via vegetation covering, and examine the effect of the cover on density, C and nitrogen (N) concentration in the buried wood.

The density of dead wood is found to decrease with increasing decomposition stage (Di Cosmo et al. 2013; Koster et al. 2015; Sandström et al. 2007). The quality, structure and dimensions of the dead wood as well as environmental factors like temperature, moisture and aeration influences the decomposition rate, but the relative importance of these factors varies between geographic regions (Koster et al. 2015). The array of different factors makes it difficult to detect which ones are the most important for dead wood decomposition.

The decomposition of dead wood also affects the content of C, N and other components (Koster et al. 2015). C makes up about 50% of the dry matter content in fresh wood (Treteknisk 2009). The rest is oxygen (43%), hydrogen (6%), nitrogen (0.1%) and ash (0.1-1%). Different studies have shown a slight increase in C concentration with increasing decomposition level (Di Cosmo et al. 2013; Koster et al. 2015; Sandström et al. 2007). A corresponding increase is also found for N concentration (Koster et al. 2015; Krankina et al. 1999; Palviainen et al. 2008). N is known to be a growth-limiting nutrient in boreal forests, but few studies have examined which factors influence nutrient dynamics in dead wood as the slow decomposition process makes the research methodologically problematic (Palviainen et al. 2008). Due to small nutrient concentrations, WD is not a large contributor to aboveground N input, but it can function as a long term nutrient pool because of the slow decomposition (Laiho & Prescott 2004). In a nutrient study conducted in Finland, Palviainen et al. (2008) found that N was slowly released from dead stems, with about 60% of the initial N content retained in the stems after 30 years.

The objective of this research was to study which factors that had an influence in burying dead wood via vegetation covering, and to examine the effect of covering on the dead wood properties. I wanted to study the rate of the burial process in different forest environments, and to quantify the C and N concentration of dead wood at different covering rates. This is a topic that has been little studied (Moroni et al. 2015), but it is highly relevant to the climate changes the world experiences today, as forest carbon dynamics form a central part of the C cycle. As mentioned above, moist forests can function as a large C pool trough accumulation and preservation of BW. I hypothesized that dead wood located in moist forests have a faster burial rate than dead wood located in dryer environments, and that the density of BW in moist forests will be higher because of the slower decomposition rate in moist environments. N and C concentration are probably lower in buried wood with a high density, but the total N and C content are larger here than in highly decomposed wood.

2. Materials and methods

2.1 Study area

The study was conducted in the middle and north boreal zone (Ahti et al. 1968) in Västerbotten and Västernorrland county, northern Sweden (63°37’ - 64°17’ N). The study sites were in forests dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus Sylvestris*) with elements of broadleaved species like birch *(Betula pubescens* and *B. pendula*) and aspen (*Populus tremula*).

2.2 Study design

A large-scale field experiment on dead wood initiated in 2001 formed the basis of my study. This experiment was used by Dynesius et al. (2010) to study vegetation covering of downed logs in 2006. A part of my study was to replicate their work, and the following description of the study design and data collection is partly taken from Dynesius et al. (2010). The experiment was originally designed to assess the colonization of logs by wood-inhibiting organisms. The study set up consists of ten different study areas (localities), five in Västerbotten county and five in Västernorrland county (Figure 1). Each locality includes three sites; a clear-cut, an old forest in a reserve or national park and an unprotected mature forest.

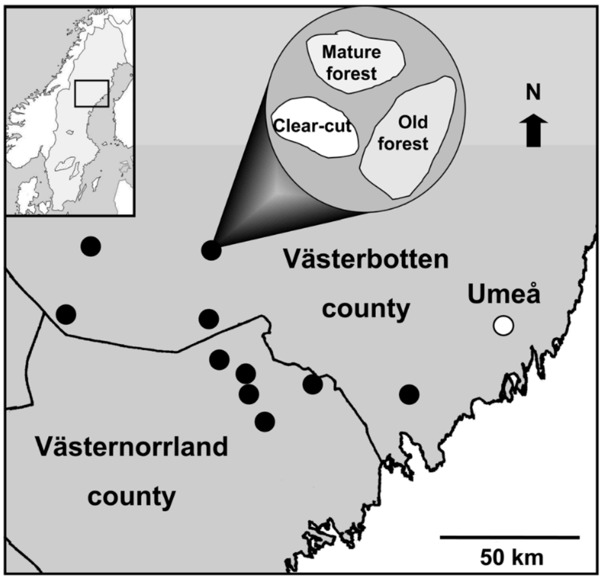

Figure 1: The ten different localities in the study (Dynesius et al. 2010).

The clear-cuts were logged between 1999 and 2001. Within each site, ten experimental blocks with a size of 20x20 metres were established (except one locality were only 5 spruce blocks were established). In each block, seven branchless logs of four metres in length were distributed. The logs originated from two logging operations, both performed in 2001. In five of the ten blocks the species of the distributed logs was birch (*Betula spp.*), while spruce (*Picea abies*) logs was distributed in the remaining five blocks. Six of the seven logs in each block were randomly distributed, while the last one deliberately was placed in the shade under a tree. In addition to the seven logs in a block, one spruce tree was cut *in situ* at a height of three metres creating a log with branches and top retained. This was only done in the spruce blocks in the forested sites (not in clear-cuts).

In the original experiment, 1995 logs were distributed in 285 blocks. About half of the logs was disturbed by different kinds of treatments or by sampling in connection with other studies, and was therefore not fitted to use in the vegetation covering study. Dynesius et al. (2010) ended up using 921 logs in their study. I used only 644 of these in my study because the rest were either not found or were disturbed due to logging operations etc. 31 of the 644 logs had braches and top retained.

2.3 Data collection

The field data were collected in august 2016. The data collection was divided into two parts, where the first part was a replicate of the study performed by Dynesius et al. (2010) in 2006 ("Cover of log surfaces"). The second part was a collection of stem discs from a selection of the logs to use in density, C and N analyses ("Stem discs").

2.3.1 Cover of log surfaces

The cover of the log surface is in this context defined as direct soil contact and cover by lateral overgrowth of dense mats of ground vegetation. To measure the cover of the log surface, seven evenly distributed points were located on the log (one point per 0.5 m from the end and up to 3.5 m). The first measure point was located at that end of the log that was marked with the log ID. For the logs with branches and top retained, seven points were similarly distributed along the four metres from the point where the log had been cut. At each of the seven points, stem diameter was measured using a caliper. This was used to calculate the circumference of the log (assuming circular form). At each point we also recorded if the log had direct ground contact and, if so, measured the length of the circumference that was not covered by soil contact or ground vegetation using measuring tape. The extent of cover was then calculated as the difference between the calculated total circumference and the measured portion of it that was not covered. Percentage cover was calculated from covered circumference and total circumference for each point of measurement. At points without ground contact, percentage cover was set to 0.

Dynesius et al. (2010) collected data on environmental conditions and log properties in the field in 2006 and we did not replicate this as we assumed that these variables have not changed greatly in the last ten years. The data include mean diameter, altitude, PADIR (Potential Annual Direct Incident Radiation), estimated soil moisture, estimated peat depth, log species and canopy shade for each log (Table 1). Dynesius et al. (2010) estimated soil conditions under each log using indicator values of understory vascular plants growing within 0.5 m of the log as surrogates for soil moisture and peat depth. The indicator values were based on values from a Swedish National Forest Inventory (NFI) data set where soil and plant data were collected from the same plots. The indicator values were a calculated mean value of the measured peat depth/estimated soil moisture class from all the NFI plots where the plants were present. The Swedish NFI divides the soil moisture into 5 classes (class 1 denotes dry soils, class 5 denotes wet soils) based on the average depth to ground water table during the vegetation period (Dynesius et al. 2010). My data set included soil moisture values in the range of 2.23-3.05 (Table 1), which corresponds to the soil moisture classes “mesic”, and “mesic to moist” in the Swedish NFI. PADIR was calculated for each log from slope inclination, slope aspect and latitude using the second equation in McCune and Keon (2002). Canopy shade was recorded using classes 1-7, where “1 and 2” represents logs placed in more or less exposed parts of clear-cuts, “3 and 4” in clear-cuts, but <20 m from forest edges, “5” in forests, but <10 m from a clear-cut edge, “6” in forests >10 m from clear-cut regardless of proximity of a shading tree, and “7” in a heavily shaded position under a spruce tree in forest. Canopy shade may have changed for the logs in the clear-cuts the past 10 years, but we did not record this in field. In the data analyses I used the mean diameter recorded in 2006 instead of the mean diameter recorded in 2016 because I thought the first recorded diameter gave a better picture of the original size of the log.

Table 1: Predictors and response variable of the 613 logs used in the study. Dynesius et al. (2010) measured all the predictors in 2006 (except longitudinal ground contact, which was measured again in 2016).

	Mean	Median	Range	Explanations
Predictors				
Diameter of log (cm)	20.2	20	9.7-43.3	Mean of seven measurements per log.
Estimated soil moisture	2.68	2.86	2.23-3.05	Highest indicator value among plant taxa recorded <0.5 m from the log.
Estimated peat depth (cm)	24.4	26.6	4.6-70.7	Highest indicator value among plant taxa recorded <0.5 m from the log.
Longitudinal ground contact (#)	5.2	6	0-7	Number out of seven sampling points along the log that had direct ground contact.
Altitude (m above sea level)	371.8	365	100-510	Taken from maps.
PADIR (MJ/cm^2/year)	0.51	0.53	0.25-0.74	Potential Annual Direct Incident Radiation, calculated from ground slope, slope aspect and latitude.
Canopy shade	4.84	6	1-7	Seven classes representing increasing shade from open clear-cut far from forest edges (1) to shaded position under a spruce tree in closed forest (7).
Site	-	-	-	Clear-cut, unprotected mature forest or old forest in a reserve or national park.
Log species	-	-	-	Birch (*Betula spp.*) or spruce (*Picea abies*).
Response variable				
Total cover (%)	41.8	37.2	0-100	Mean percentage of circumference covered (soil contact + ground vegetation cover), calculated from seven measurement points.

2.3.2 Stem discs

We collected stem discs from a selection of 25 logs of the 644 logs used in this study. The selection was based on the surface cover Dynesius et al. (2010) measured in 2006. Logs with a high cover percentage in 2006 were prioritized, but some logs with a low cover percentage were also collected to observe the differences between them. Stem discs were only collected from 4 m spruce logs in forested sites (not from clear-cuts). The stem discs were collected from the first and the last measurement point on the logs using a chainsaw, making a total of two stem discs from each log. From one log an additional 5 stem discs were collected, making a total of 7 stem discs from this log (the 5 extra stem discs were not used in the statistical analyses). The stem discs had a width of about 5-10 cm. The discs were marked with which side pointing up, and then wrapped in plastic to prevent desiccation.

In addition to the stem discs collected from the logs used in the study, we collected 10 fresh stem discs from five trees growing in the same site that the logs in the study originated from. The five trees were cut using a chainsaw and two stem discs were collected from each stem.

Laboratory work was performed at the Norwegian Institute of Bioeconomy Research (NIBIO) and the Norwegian University of Life Science (NMBU) during September 2016 and January 2017. First, five blocks with a size of about 2x2x2 cm were cut out of each stem disc using a band saw. The distribution of the blocks within the stem disc is shown in Figure 2. Stem wood containing small twigs was avoided during the extraction. In cases where the stem discs were so fragmented that correct block collection according to the block design in figure 2 was not possible, small pieces of stem wood were collected as close to the block design as possible.

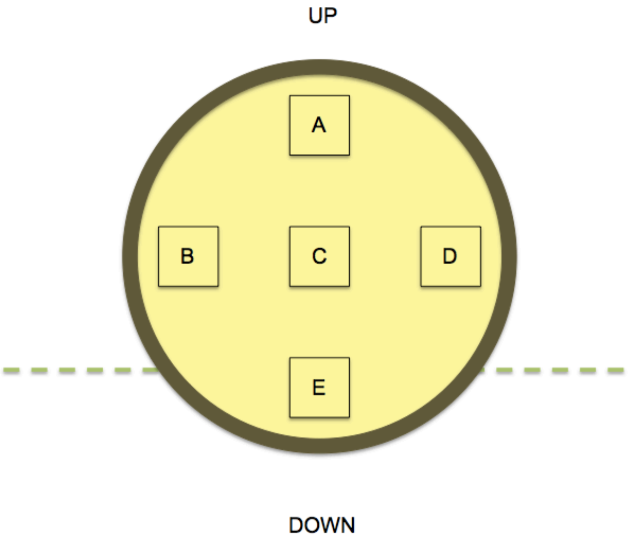

Figure 2: The distribution of the five blocks within each stem disc.

The five stem blocks from one stem disc were wrapped in plastic in the longitudinal direction leaving the lateral section uncovered. The blocks were then kept in deionized water in a cooling room. After three days in the water, basic density of the stem blocks was measured. Basic density is measured by dividing oven dry weight by green volume (Osazuwa-Peters & Zanne 2011). To measure the green volume the water displacement method was used. Each stem block was attached to a needle that was attached to a stand. The needle with the block was then immersed into a flask containing deionized water placed on an electronic balance set to 0. The block was immersed to the point where the whole block was beneath water, while as much of the needle as possible were left out. By using this method, the weight gain in grams read from the electronic balance was equivalent to the green volume in cm^3 (assuming the density of the water to be 1 g/cm^3). Some of the stem blocks were so fragmented making it impossible to attach them to the needle. These blocks were put into a tea strainer and then immersed into the water. The weight of the tea strainer was deducted from the total weight to find the green volume of the fragmented stem block.

After the measurement of green volume the blocks were put in to separate paper bags, and put into a drying oven at 103 ° C for 20 hours. The dry weight of the stem blocks were measured directly after taken out of the drying oven while they where still in the paper bags.

The stem blocks were stored in the paper bags in a dry and dark room until January 2017. They were then ground to powder using an impact mill. The powder was kept inn closed sample glasses. After this, the powder from the stem blocks was used to measure C and N concentration in the stem blocks. About 5 mg of the powder was balanced on a Mettler Toledo XP6 scale, wrapped in tin foil and analysed in an elemental analyser (Elementar Micro Cube, Hanau, Germany).

The 10 fresh stem discs collected from the living trees were left at the Swedish University of Agricultural Science (SLU) in Umeå. There, basic density measurements were performed in the same way I performed it for the 55 stem discs collected from the logs in the study.

2.4 Data analysis

All analyses were run in the statistical program R (R Development Core Team 2016). I ran four different analyses; one for total cover, one for basic density, one for N concentration and one for C concentration.

The effects of the log properties and environmental factors on the total cover (mean percentage of circumference covered) were examined using a quasibinomial generalized linear model (GLM). Quasibinomial GLM was chosen due to underdispersion. I used a dataset containing 613 logs in this analysis. The 31 logs with branches and tops retained were left out of the analysis because of the low number of observations compared to the logs without branches and tops. When examining the effects, I first fitted a full model using all predictor variables. To determine whether multicollinearity amongst predictor variables had an influence, I used the VIF-function (variance inflation factor) in the "car" package in R. The predictor "site" had a VIF-value>4 due to high correlation with canopy shade, and was taken out of the analysis. I then checked for interactions among predictor variables. The interaction was kept in the model if the P-value<0.05, using the drop1-function. I used this function until the model only consisted of significant predictor variables (P<0.05). This model is referred to as the final model.

The same procedure was used in the density, N concentration and C concentration analyses. The dataset used in these analyses contained 50 observations (2 stem discs per 25 logs). The response variables basic density, N concentration and C concentration were a mean calculated from the five stem blocks from each stem disc.

In the density-analysis I started with fitting a linear mixed model (LME) since the response variable basic density (g/cm^3) was not proportional. Locality was used as a random factor. I used an ANOVA-test to examine if this was a better model than a regular GLM. It was not, so I continued using GLM also here. Total cover measured in 2006 had a VIF-value>4, due to high correlation with cover measured in 2016 (Figure 8). In the full model, total cover in 2006 was significant, while disc cover in 2016 was not. I therefore excluded disc cover in 2016 from further analysis instead of total cover in 2006. Nevertheless, total cover in 2006 was not significant in the final model.

In the density, N concentration and C concentration analyses I excluded some of the predictor variables used in the total cover analysis. Canopy shade was left out because there was low variation in this variable since all the stem discs was collected only from forested sites. Some of the logs that I collected stem discs from were injected with fungus (the brown rot fungus *Fomitopsis pinicola* or the white rot fungus *Resinicium bicolor*) when they were placed in the sites in 2001. To check if the injection had an effect on basic density, N concentration and C concentration I created a predictor variable where 0=no injection, and 1=injection. An overview of the predictors and response variables used in the basic density, N concentration and C concentration analyses is found in Table 2.

Table 2: Predictors and response variables for the 50 stem discs in the study. Dynesius et al. (2010) measured all the predictors in 2006, except disc cover that was measured again in 2016.

	Mean	Median	Range	Explanations
Predictors				
Diameter of log (cm)	21.2	21.4	11.0-30.6	Mean of seven measurements per log.
Estimated soil moisture	2.72	2.88	2.31-3.00	Highest indicator value among plant taxa recorded <0.5 m from the log.
Estimated peat depth (cm)	29.3	26.6	7.8-54.9	Highest indicator value among plant taxa recorded <0.5 m from the log.
Altitude (m above sea level)	363.8	405	125-510	Taken from maps.
Injected with fungus	-	-	-	Not injected with fungus=0, injected with fungus=1.
Disc cover (%)	54.3	65.7	0-100	Percentage of circumference covered (soil contact + ground vegetation cover) at the measure point the disc was collected from.
Total cover (%)	28.5	19.3	2-67	Mean percentage of circumference covered (soil contact + ground vegetation cover), calculated from seven measurement points (measured in 2006).
Response variables				
Basic density (g/cm^3)	0.25	0.25	0.15-0.40	Mean of five stem blocks per stem disc.
C concentration (%)	50.6	50.7	46.4-55.4	Mean of five stem blocks per stem disc.
N concentration (%)	0.06	0.04	0.02-0.22	Mean of five stem blocks per stem disc.

3. Results

3.1 Cover of log surfaces

The mean total cover was 41.8% for the 613 logs studied (Table 1). In 2006 the mean total cover for the same logs was 24% (Dynesius et al. 2010). While only 10% of the logs were buried according to the definition in Moroni et al. (2015) after 5 growing seasons, the number had increased to 32% after 15 growing seasons.

Table 3: Parameter estimates, SE and t-value for predictors in the generalized linear model used to test effects of environmental factors and log properties on total cover (N=613).

Analysis	Predictor	Coefficient	SE	t-value
Total cover	Log species (spruce)***	-0.399	0.116	-3.44
	Canopy shade	-0.343	0.197	-1.74
	Altitude***	-0.002	0.000	-5.75
	PADIR[1]***	-1.720	0.337	-5.11
	Diameter	-0.099	0.054	-1.83
	Estimated peat depth*	-0.119	0.047	-2.52
	Estimated soil moisture*	-1.004	0.469	-2.14
	Longitudinal ground contact	0.096	0.194	0.50
	Canopy shade X Estimated peat depth*	-0.005	0.002	-2.52
	Canopy shade X Estimated soil moisture*	0.205	0.086	2.37
	Estimated peat depth X Log species (spruce)*	0.009	0.004	2.29
	Longitudinal ground contact X Estimated peat depth***	0.027	0.007	3.71
	Diameter X Longitudinal ground contact	0.013	0.009	1.40
	Diameter X Estimated peat depth**	0.006	0.002	2.83
	Estimated peat depth X Longitudinal ground contact X Diameter**	-0.001	<0.001	-3.09

Significance levels: *P<0.05, **P<0.01, ***P<0.001,

[1]: Potential Annual Direct Incident Radiation

Spruce logs had lower total cover than birch logs, but as the peat depth increased this effect was weakened (significant species X peat depth interaction)(Table 3, Figure 4).

Also PADIR and altitude had a significant effect on total cover, both negative (Figure 3). These predictors were not found significant in interactions with other predictors.

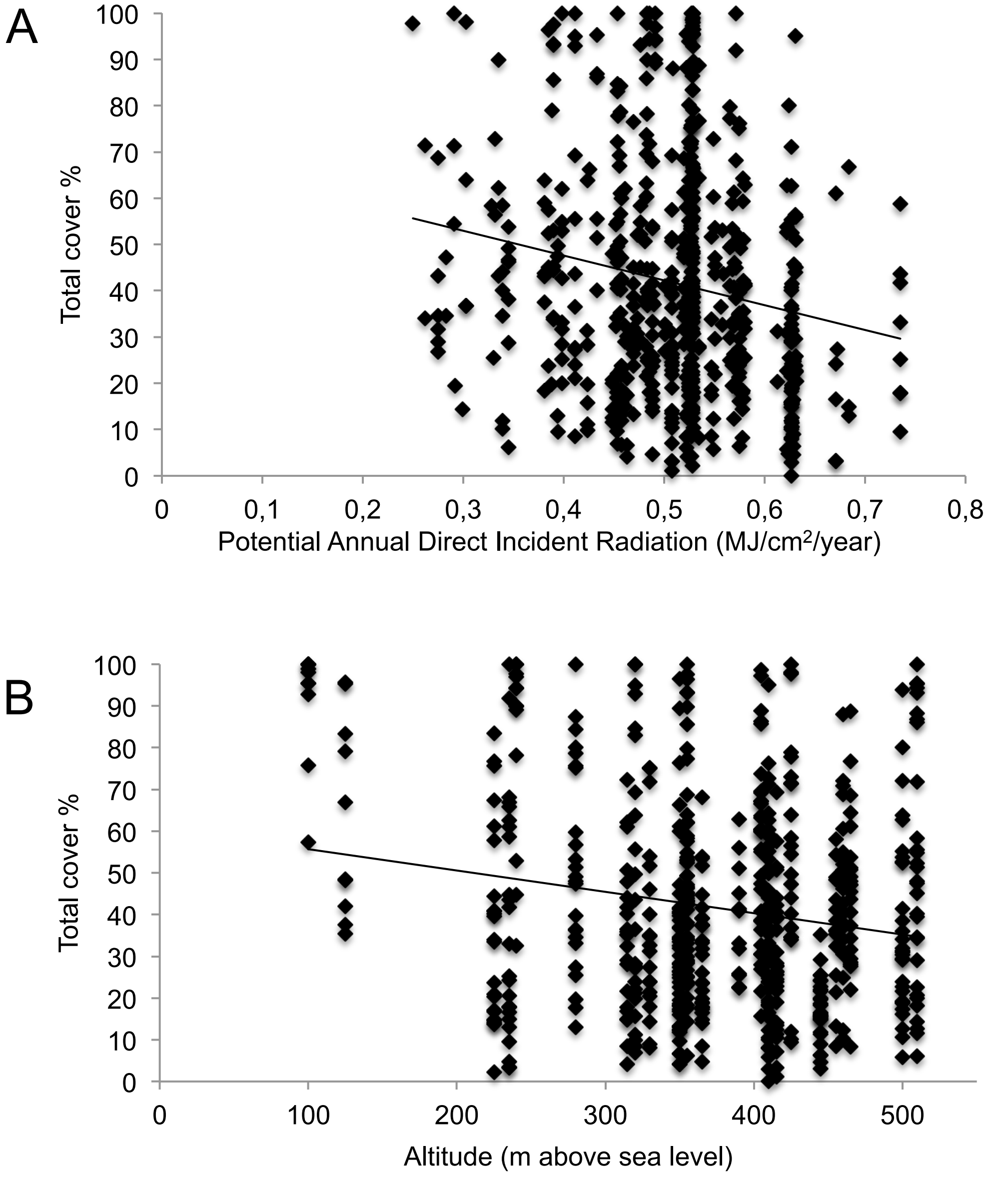

Figure 3: Total cover for the 613 studied logs plotted against (A) PADIR (Potential Annual Direct Incident Radiation) and (B) altitude. Linear trend lines are shown in black.

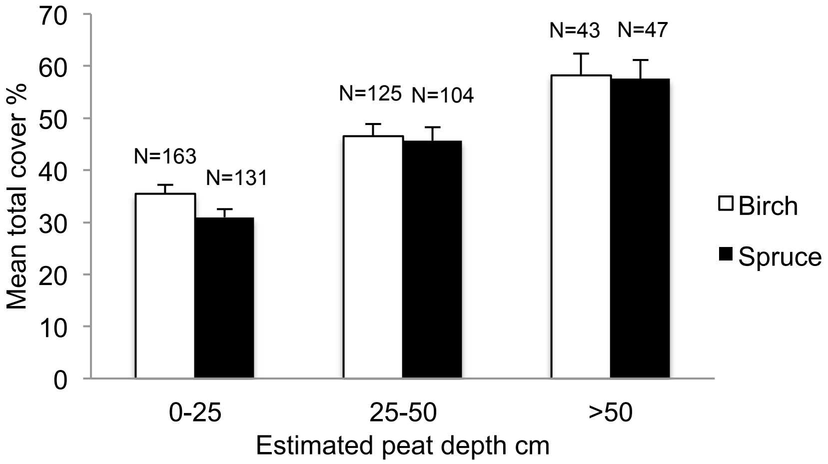

Figure 4: Mean total cover for the 613 logs studied at different estimated peat depths for birch (white) and spruce logs (black). SE and number of observations in each group shown on top of the bars.

Canopy shade had significant interactions with both estimated peat depth (P=0.012) and estimated soil moisture (P=0.018)(Figure 5). The effect of canopy shade on total cover was positive with increasing soil moisture, while it was slightly negative with increasing peat depth (Table 3).

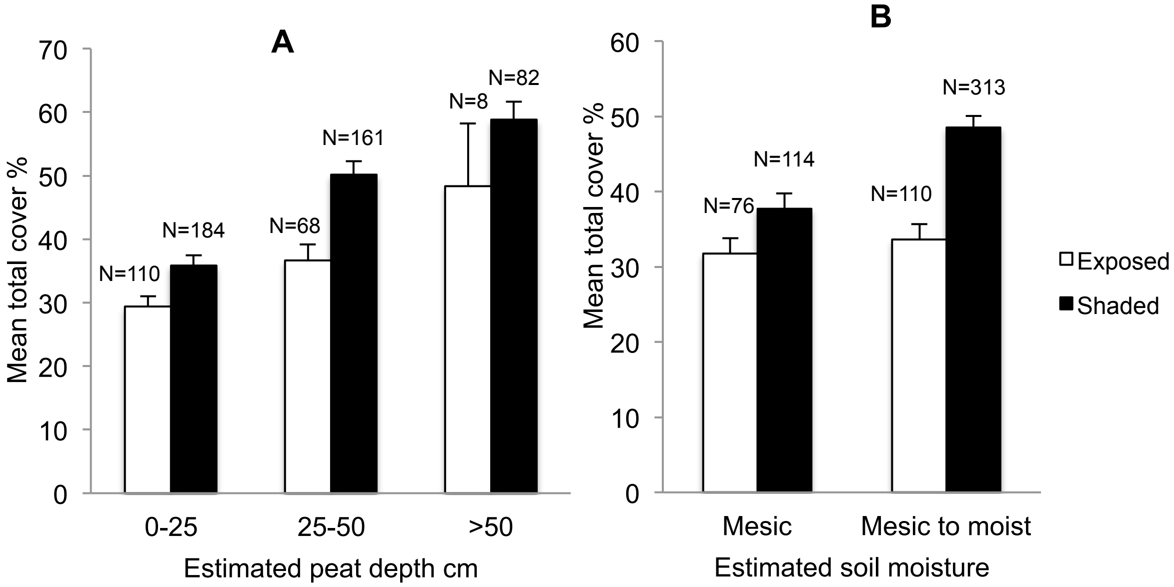

Figure 5: Mean total cover for the 613 logs studied at different (A) estimated peat depths and (B) estimated soil moisture classes. White bars shows logs in exposed positions at clear-cuts(canopy shade 1-4), while black bars shows logs in shaded positions/forested sites (canopy shade 5-7). Estimated soil moisture value<2.5 are classified as "mesic", while logs with a value >2.5 are classified as "mesic to moist" (based on the soil moisture classes used in the Swdish NFI). SE and number of observations in each group shown at the top of the bars.

Estimated peat depth had a positive effect on total cover with increasing longitudinal ground contact (P<0.001)(Figure 6). This effect was less positive for logs with larger diameter, as shown in the negative three-way-interaction (P=0.002)(Table 3, Figure 7).

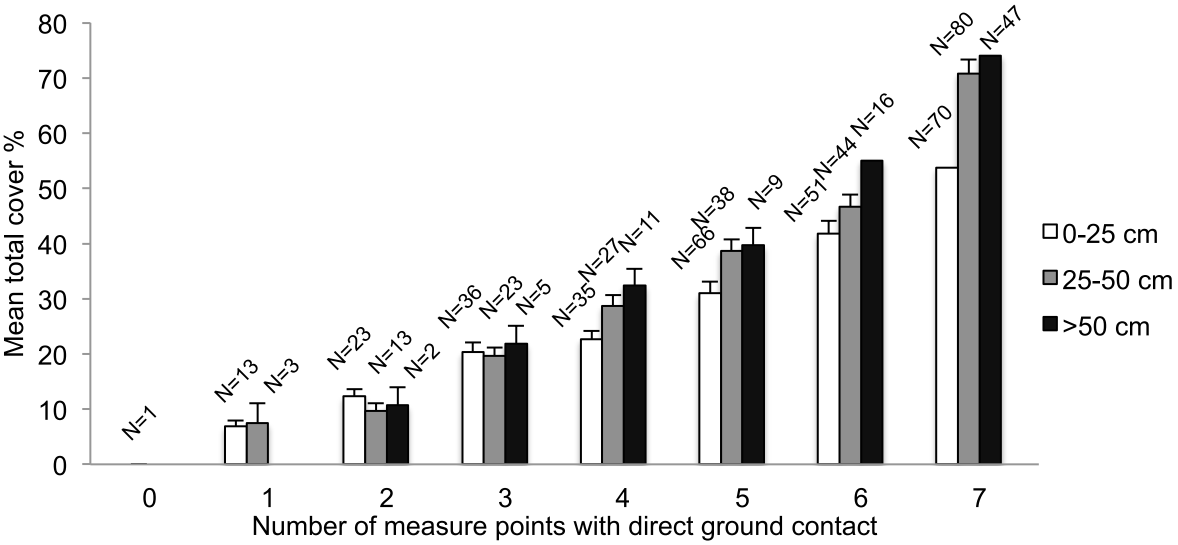

Figure 6: Mean total cover for the 613 logs studied with different number of direct ground contact points. White, grey and black bars show mean total cover in different estimated peat depth classes. SE and number of observations in each group shown on top of the bars.

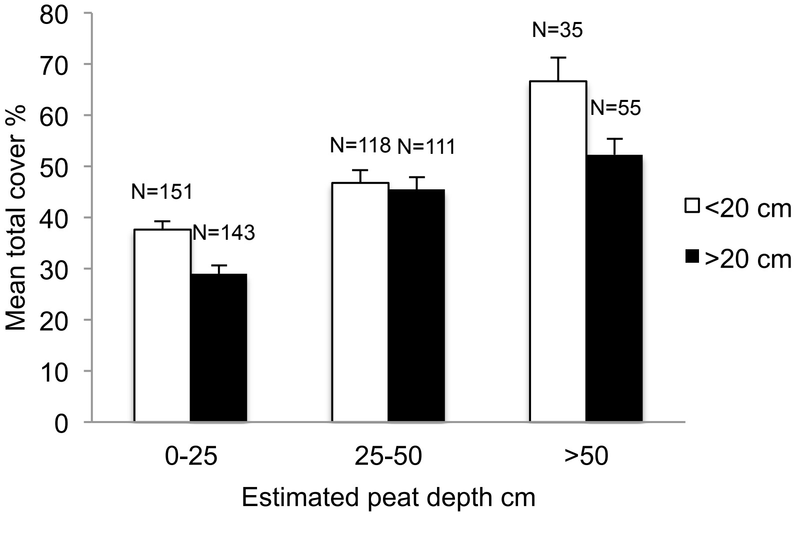

Figure 7: Mean total cover for the 613 logs studied at different estimated peat depths. White bars show logs with a mean diameter <20 cm, while logs with a mean diameter >20 cm are shown in black. SE and number of observations in each group shown on top of each bar.

Total cover in 2006 and 2016 had a strong correlation (Figure 8). To avoid problems with multicollinearity, total cover in 2006 was not used as a predictor in the analysis.

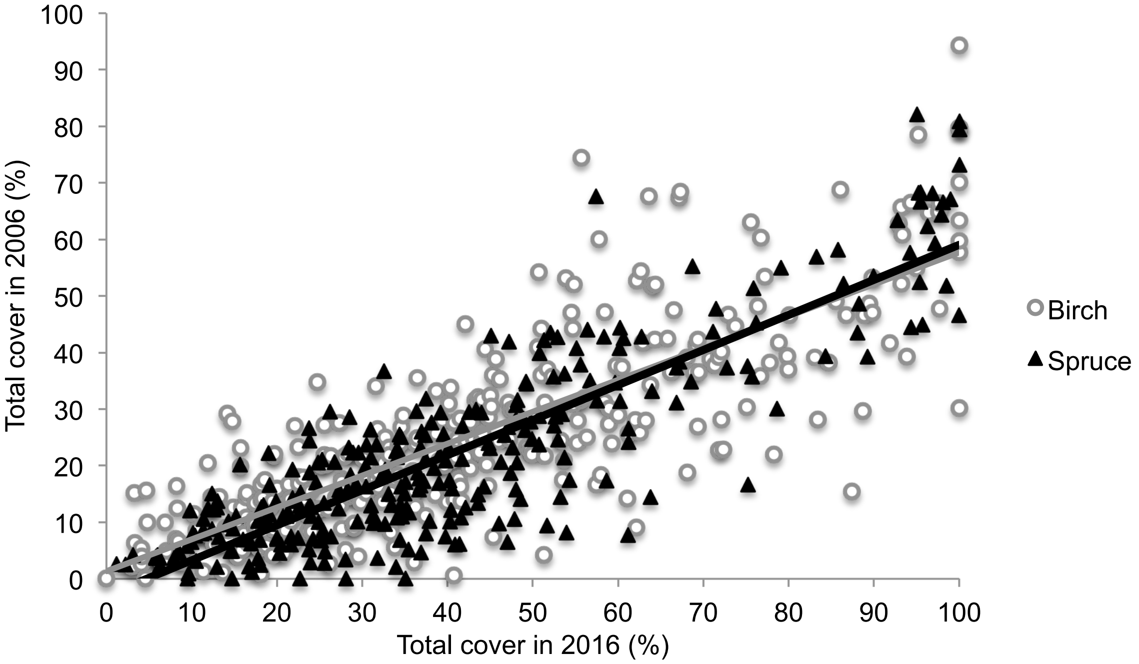

Figure 8: Total cover in 2006 plotted against total cover in 2016 for the 613 branchless logs used in the study. Linear trend lines for each log species are shown in grey (birch) and black (spruce).

3.2 Basic density

The basic density of the 50 stem discs ranged from 0.15-0.40 g/cm^3, with a mean of 0.25 g/cm^3 (Table 2). The basic density for the 10 fresh stem discs ranged from 0.36-0.45 g/cm^3, with a mean of 0.42 g/cm^3. From the one log where I collected stem discs from each measure point (7 stem discs in total), basic density ranged from 0.17-0.39 g/cm^3 within the log.

Table 4: Parameter estimates, SE and t-value for predictors in the generalized linear models used to test environmental factors and log properties on basic density, N concentration and C concentration (N=50).

Analysis	Predictor	Coefficient	SE	t-value
Basic density				
	Estimated peat depth***	0.002	<0.001	4.69
N %				
	Basic density***	-6.949	1.130	-6.15
	Diameter**	-0.050	0.014	-3.478
C %				
	Basic density***	-0.8848	0.1359	-6.51
	Estimated soil moisture*	-0.3526	0.1359	-2.50
	Altitude*	-0.0024	0.0010	-2.50
	Estimated soil moisture X Altitude*	0.0008	0.0004	2.30

Significance levels: *P<0.05, **P<0.01, ***P<0.001

Of all the predictors tested in the analysis (Table 2), only estimated peat depth had a significant effect (P<0.001) in the best model. Basic density increased with increasing peat depth (Table 4, Figure 9). No interactions amongst remaining predictors were significant at 5% level.

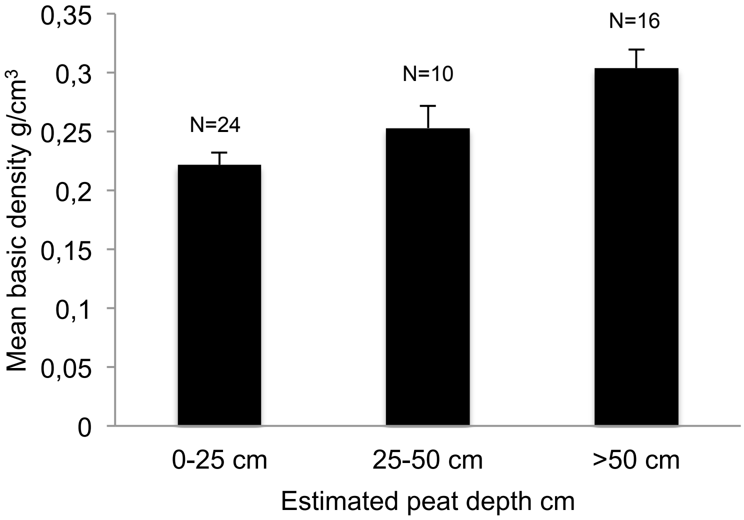

Figure 9: Mean basic density (g/cm^3) for different estimated peat depths. SE and number of observations in each group shown on top of the bars.

3.3 N concentration

The average N concentration of the 50 stem discs was 0.06% (Table 2). Basic density (P<0.001) and mean diameter of the log (P=0.001) were the only predictors that significantly affected the N concentration (Figure 10), and they both had a negative effect (Table 4). No interactions between predictor variables were significant.

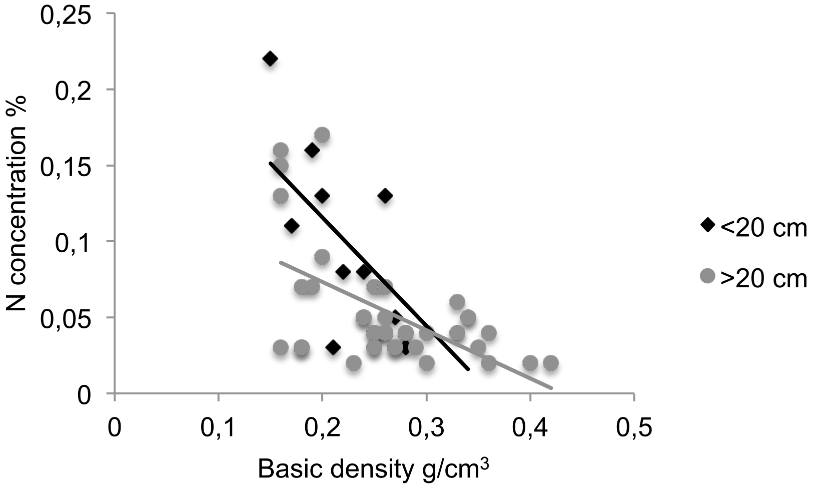

Figure 10: N concentration (%) for the 50 spruce stem discs plotted against basic density (g/cm^3). Stem discs from logs with a mean diameter <20 cm shown in black, with a black linear trend line. Stem discs from logs with a mean diameter >20 cm are shown in grey, with a grey linear trend line.

3.4 C concentration

The average C concentration was 50.6% among the 50 stem discs. Similar to the N concentration, basic density had a significant negative effect (P<0.001) on C concentration in the best model (Figure 11, Table 4). C concentration decreased with increasing soil moisture, but the effect was weaker with higher altitude (P=0.03)(Table 4, Figure 12).

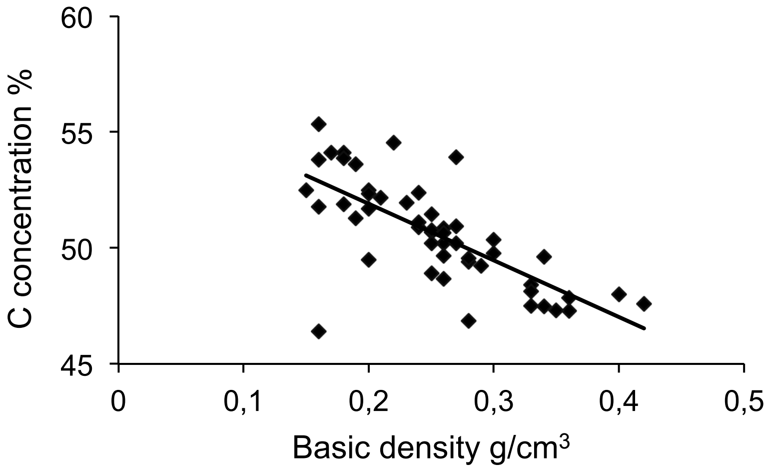

Figure 11: C concentration (%) for each of the 50 spruce stem discs plotted against basic density (g/cm^3). A linear trend line is shown in black.

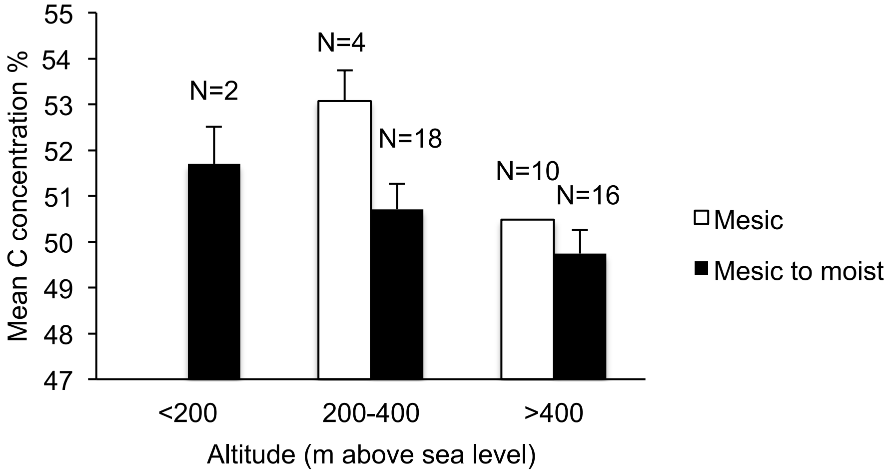

Figure 12: Mean C concentration for the 50 spruce stem discs at different altitude. Stem discs from logs in mesic soils (estimated soil moisture <2.5) shown in white, while stems discs from mesic to moist soils (estimated soil moisture >2.5) are shown in black. SE and number of observations in each group shown are shown on top of the bars.

4. Discussion

4.1 Cover of log surfaces

Cover was influenced by peat depth, soil moisture, factors related to sun exposure, altitude, longitudinal ground contact, and log properties such as diameter and tree species. The results are generally in accordance with the findings in Dynesius et al. (2010). This was expected as I used the environmental data on the logs from their experiment in 2006. However, due to some differences in the statistical tests performed my results are not directly comparable to theirs. For example, they did not examine interactions among environmental factors and log properties in their study, while I found quite many in mine (Table 3).

Peat depth is a factor that is proved to have an effect in burying downed wood in several ways (Hagemann et al. 2010; Moroni et al. 2015; Stokland et al. 2016). The peat in the humus layer consists of living and dead organic matter, especially from bryophytes, which form a continuous mat on the forest floor in boreal forests (Hagemann et al. 2010; Moroni et al. 2010). Bryophytes have a high growth rate, but they decay slowly and are therefore effective in burying downed WD (Moroni et al. 2015). Also, the low bulk density makes it possible for heavy objects sinking into it. In the model, as the diameter of the log increases, so does the positive effect of peat depth on cover of the log. This is probably because of the higher weight related to diameter increase. Denser soils will not give the same sinking effect as peat, and a log that is located in a forest with dense soil will probably have less ground contact than a log that is located in a forest with a thick humus layer. This can explain the positive significant effect longitudinal ground contact has on total cover in interaction with estimated peat depth in the model. Still, this effect was less positive for larger logs.

Dynesius et al. (2010) found increasing diameter to have a negative effect on covering on the logs. They explained this with larger logs having a larger surface to be covered by growing vegetation. Contradictory results was found by Stokland et al. (2016). Here, the authors were critical to their own findings as they suspected that many small logs went unnoticed during sampling, and they concluded that the relationship found by Dynesius et al. (2010) probably was the true one. Based on my own findings, I suggest that the effect of diameter on covering of downed logs is dependent on the structure of the forest floor.

Sun exposure also had an effect on covering of log surfaces. With increasing potential solar radiation (PADIR), the covering decreased, meaning that logs located in north facing slopes had higher percentage cover. This matches the results found ten years earlier by Dynesius et al. (2010), who explained this with peat forming more rapidly in cold and wet conditions which usually are found in north facing slopes. As PADIR was calculated using the log location, and the logs not having been moved since then, one can assume that the relationship between PADIR and cover of log surfaces is stable and realistic. PADIR only shows the potential solar radiation, and does not account for shading structures like canopy, which is why canopy shade is a separate factor in my model. Logs located in shaded positions generally had a higher total cover than exposed logs (Figure 5), probably for the same reasons as for PADIR. Even though plants need light to grow, bryophytes benefit from moist and cool environments on forest floors. This is probably why canopy shade had less effect on cover with increasing peat depth (Table 3). Nevertheless, canopy shade enhanced the positive effect of increased soil moisture on total cover. Constant shading, like the one from tree crowns, prevent the ground from drying up. This facilitates a stable moist environment for the vegetation on the ground, which again facilitates bryophyte growth and covering of log surfaces.

Total cover of the log surfaces declined with increasing altitude (Figure 3B). Moroni et al. (2015) stated that the burial process of WD "*is primarily determined by the productivity, turnover and decay rates of the burying vegetation*". Productivity is known to decrease with increasing altitude, most likely due to decreasing temperature (Raich et al. 1997). Dynesius et al. (2010) did also find this negative relationship between altitude and covering of log surfaces in their study, but it was not significant and not a part of their best fit model. One can therefore assume that the altitude effect on cover not was as clear in the short term as it is in the long term.

Birch logs seemed to be more overgrown than spruce logs, which is in accordance with the results in Dynesius et al. (2010). They explained this relationship by birch wood being denser, and thereby heavier, than spruce wood, leading it to sink faster into the ground. In my final model, there was a significant interaction between log species and peat depth, showing that the tree species effect was less clear with increasing peat depth (Figure 4). This effect can possibly be explained with the weight of the object being less important if the peat depth is high. All heavy objects will sink into deep peat because of the low bulk density, meaning that more of its surface will be covered with ground vegetation.

4.2 Basic density

There were large differences in basic density among the 50 stem discs (Table 2). While some of them had a basic density close to the density of the fresh stem discs, others were highly decomposed and fragmented. The density of a tree varies with many factors. Tree species, geographical location, site quality, the tree position, age, size, growth rate and genetics are some of the factors that affect the wood density of a stem, but the density can also vary within the stem (Repola 2006). This makes it difficult to find a start-value for wood density when looking into decomposition rate. Here, I use the basic density for the fresh stem discs as a reference value for the start density of the 50 stem discs collected from the logs. As the logs that I sampled stem discs from originated from the same site as the fresh logs, a lot of the factors influencing tree density are the same among the logs (geographical location, site quality etc.). The basic density of the fresh stem disc were in the range of 0.36-0.45 g/cm^3, which is in accordance with earlier findings of basic density of spruce (Johansson 1999). If I use the mean basic density for the fresh stem discs as the start density (0.42 g/cm^3), the 50 stem discs had a basic density loss of 5-64% in 15 years, with a mean loss of 40%. The large difference in basic density among the 50 stem discs indicates that environmental factors have an influence in the decomposition process.

From the one log where 7 stem discs were collected, the differences in basic density (0.17-0.39 g/cm^3) was almost as big as the differences between all the 50 stem discs analysed (0.15-0.40 g/cm^3). This log had a mean total cover of 98% in 2016, which means that total cover measured this year cannot explain the large variation in basic density within this log. Nevertheless, the reason why this log was examined in detail was because there was a clear visible variation in moisture and degree of cover from the one log end to the other. One end was buried deeply into the peat and was covered with a thick bryophyte layer, while the other side was covered more recently and some parts were still slightly exposed. The total cover in 2006 was 67%, showing that the one end of the log had been covered with bryophytes for a long time. This log shows that a fast burial rate combined with a stable and thick cover probably have an effect on decomposition. Unfortunately, I did not have data on cover at each measure point from 2006; I only had data on total cover of the log from this year. Total cover in 2006 does probably not have much value as a predictor in the basic density model as it is a mean value for the whole log, and not a specific value for the points the stem discs were collected from in 2016. The cover history of the detailed examined log can therefore explain why neither total cover in 2006 nor disc cover in 2016 was significant in the final basic density model for the 50 stem discs.

When analysing the stem discs, only estimated peat depth had a significant effect on basic density. As the peat depth increased, so did the basic density (Figure 9). While the logs located on peat depth<25 cm had a density loss of 47%, the corresponding density loss in the deepest peat class (peat depth>50cm) was only 28%. As mentioned earlier, the low density of the peat facilitates objects sinking into it and more of the objects surface will be in contact with the bryophytes growing in the humus layer. Bryophytes are known to lower the temperature and increase humidity in both the soil environment and in BW, which are mechanisms that decrease the decomposition rate (Hagemann et al. 2010; Moroni et al. 2015). Consequently, as the peat depth increases and more of the log is incorporated into the wet humus layer, the decomposition rate of the log decreases and the basic density loss is slowed down.

I hypothesized that logs located in moist forests would have a slower decomposition rate, and thereby a higher basic density than logs located in dryer environments. Nevertheless, estimated soil moisture was not significant in the basic density model. There can be several reasons to this. First of all, the soil moisture was not measured directly, it was estimated. This means that it could be somewhat imprecise. Secondly, the soil moisture values ranged from 2.31-3.00, which indicates “mesic” and “mesic to moist” soil types, which are moderately wet. Earlier research has shown that the relationship between decomposition rate and moisture is non-linear (Shorohova &

Kapitsa 2014). Both very dry and very wet sites slow down decomposition, while moderately wet sites do not. This is because decomposing organisms such as fungi and insects are not metabolically active if the humidity is too low or too high (Zhou et al. 2007). As all of my samples were collected from moderately wet sites (with suitable moisture for decomposers), this can explain why the soil moisture factor did not have an effect in the model. Also, the soil moisture of the site probably has little effect on the basic density of the log unless the log is in contact with a wet medium (e.g. humus layer). It therefore makes sense that it is the peat depth (which clearly affects the incorporation of the log in the humus layer) that impacts the most on basic density of the log, and not the soil moisture of the site.

Surprisingly, injection with fungi did not have an effect in the basic density model. The injected fungi are both wood decomposers, and one should expect these logs to be more decomposed than the ones that were not injected, as the decomposition process got a head start in the injected logs. Nevertheless, during the sampling in the field we were not quite aware of the fact that we sampled discs from some logs that had this treatment, and the dataset therefore have to much variation compared to the number of observations. Ideally, we should not have sampled discs from the logs with the fungus treatment, or if we had, we should have sampled discs from a larger number of logs. It is generally difficult to detect patterns in a dataset that contains a low number of observations. Another reason why this factor had no clear effect in the model could be that the two injected fungi species decompose wood at a different rate and attack different parts of the wood. By gathering these two treatments in one factor, the variations in wood decomposition rate between the two species did not become visible, and looking back I realise that the two fungi treatments should have been analysed separately. This also counts in the C and N concentration models, where the differences between the fungi species probably would have an effect. While white rot fungus attack all the main components in wood, brown rot fungus stay clear of the C rich lignin component (Stokland et al. 2012). This means that the C concentration in the logs possibly could have been affected of what fungus it was injected with.

4.3 N concentration

The N concentration in the 50 stem discs ranged from 0.02-0.22%. This is somewhat lower than the N concentration found in other studies examining decomposing WD (Koster et al. 2015; Krankina et al. 1999; Palviainen et al. 2008), ranging from 0.12-0.54%. All these studies found that the N concentration increased with increasing decay class. I did not collect data on decay class for my data, but these studies have also found a decrease in density for increasing decay class. One can thereby assume a similar relationship between N concentration and density as for N concentration and decay class (although with opposite signs).

In my study, I found that N concentration decreased with increasing basic density (Figure 10). Assuming the relationship commented above, this result is in line with earlier research (Koster et al. 2015; Krankina et al. 1999; Petrillo et al. 2016; Sakai et al. 2012). N concentration also decreased with increasing log diameter. In a Japanese study, Sakai et al. (2012) found a similar relationship. They explained this with smaller logs having a higher amount of nutrient rich bark compared to stem wood than larger logs. My samples only contained stem wood, so this could not be the explanation in my study. There is little literature commenting on the relationship between N concentration and log diameter, but several studies have examined nutrient concentrations in stumps and coarse roots versus fine roots (Hellsten et al. 2013; Iivonen et al. 2006). They have found a decrease in nutrient concentration for increasing root diameter. The greater proportion of older tissue in coarse roots can explain this, which also can explain the decreasing N concentration in large logs versus small ones.

The problem concerning a reference value for start basic density occurs also for the N concentration. I did not examine the N concentration for the 10 fresh stem discs, and can thereby not use them as reference. A general value for N concentration in fresh stem wood is given to be 0.1% in Treteknisk (2009). This is also in accordance with the N concentration for decay class 1 (recently dead) in Koster et al. (2015) and Krankina et al. (1999). The N concentration for the 50 stem discs examined in my study is both higher and lower than this. There are several reasons for increasing concentration of N with increasing decomposition. One reason can be that the other components in the wood are being decayed at a faster rate than those containing N. Another reason can be that the N content in the wood increases, despite the fact that the tree no longer grows. N fixation or presence of wood-decaying fungi can explain accumulation of N in dead wood (Laiho & Prescott 2004; Palviainen et al. 2008; Sakai et al. 2012). The fact that many of the stem discs had a lower N concentration than the reference value could mean that N releases at a faster rate than the other wood components, or that the actual start value of N concentration was lower than the reference value given here. Krankina et al. (1999) reported that some environmental conditions could contribute to fast loss of nutrients from dead trees. For example can abundant precipitation cause leaching, and a cool climate can slow down processes that contribute to nutrient immobilization and input.

During the laboratory analyses of N and C concentration, the elemental analyser gave a waning message concerning the N concentration for each sample it analysed because the concentration was lower than the guaranteed detection limit of the instrument. The exact values must therefore be used with caution. Still, the values are realistic and I chose to use them.

4.4 C concentration

The C concentrations found in my study (46-55%) match earlier findings of C concentrations in spruce and other conifers (Butler et al. 2007; Harmon et al. 2013; Koster et al. 2015; Krankina et al. 1999; Makinen et al. 2006; Petrillo et al. 2016; Weggler et al. 2012). 50% is a globally known default value for C concentrations in wood, and is often used in calculations of C content in dead WD (Weggler et al. 2012). Whether this is a realistic estimate or not, is somewhat discussed. Several of the above mentioned studies have found C concentrations to increase with increasing decay stage (Harmon et al. 2013; Koster et al. 2015). This is also the case in my study, as the C concentration increases with decreasing basic density (Figure 11). The increase in C concentration with increasing decomposition is probably linked to the loss of cellulose early in the decomposition stage (Sandström et al. 2007). Cellulose, hemicellulose and lignin makes up the three main components in wood (Stokland et al. 2012). Cellulose contains less C (44%) than lignin (63-72%), and decays at a much faster rate than the latter (Harmon et al. 2013). The higher lignin to cellulose ratio with increasing wood decay thereby increases the C concentration in the dead wood.

In the final model, estimated soil moisture and altitude also had a significant negative effect on C concentration (Figure 12). These effects can both be explained by having a negative effect on decomposition. Since C concentration increases with increasing decomposition, one can assume that factors that have an effect on decomposition will have the same effect on C concentration. As mentioned earlier, increasing altitude is known to decrease temperature. Generally, as the temperature decreases so does the decomposer activity, which leads to lower decomposition rate (Zhou et al. 2007). The effect of soil moisture is a bit more complicated, as mentioned when explaining the effects on basic density. I hypothesized that increasing soil moisture would have a negative effect on decomposition. As we have learned, C concentration follows the decomposition stage, and the observed relationship between soil moisture and C concentration is thereby logical according to the hypothesis. Nevertheless, in the basic density part I concluded that my samples were collected from areas with moderate soil moisture, which would not have a negative effect on decomposition. I therefore find it difficult to explain that the soil moisture factor had a significant effect in the C concentration model, but not in the basic density model. This also applies to the altitude factor.

Estimated soil moisture and altitude also had a positive significant interaction in the C concentration model. This interaction showed that as the altitude increases, soil moisture affected C concentration less than what it did in lower areas. This can be explained by the fact that decomposition is slower in colder climate (Russell et al. 2014), and other environmental factors that may influence the decomposition rate are maybe not that noticeable here.

The slow decomposition of C rich lignin compared to cellulose indicates that lignin in dead wood can be a long-term C pool in forest ecosystems (Butler et al. 2007; Manies et al. 2005). Even though the C concentration significantly increased with increasing decomposition, this increase was not very large and the mean C concentration among the 50 stem discs studied was the same as the assumed initial C concentration (50%). One can therefore assume that the decrease in C content in the logs follows approximately the same pattern as the density loss. In the 15 years the studied logs had been decomposing on the forest floor, the mean C loss from the logs was therefore 40%. This means that the logs still function as a C pool, which slowly releases C to the surroundings.

5. Conclusion

Total cover of the log surfaces increased from 24% to 41,8% in the 10 years between my study and the one conducted by Dynesius et al. (2010) in 2006. Not much had changed regarding the influencing factors on cover of log surfaces since then, as almost all of the same factors where used in both their model and mine. It is hard to point out what factor influencing the most, but estimated peat depth distinguishes itself considering all the interactions it takes part in. This also coincides with other research on the area (Hagemann et al. 2010; Moroni et al. 2015; Stokland et al. 2016), which emphasizes the importance of the overgrowing vegetation on the burial rate of WD.

Unlike what I hypothesized, neither the cover measured in 2016, nor the one measured in 2006 had a clear effect on density, N or C concentration in the studied logs. I can therefore not conclude that this factor alone can describe the decomposition rate of dead wood to a good extent. Nevertheless, estimated peat depth did explain some of the variation for basic density. While the logs located in shallow peat had a density loss of 47%, the corresponding density loss was only 28% for logs located in deep peat. This shows that the structure and microclimate of the forest floor clearly have an effect in the decomposition of dead wood. I also hypothesized that soil moisture would explain variation in basic density of the logs. Here, my results were unclear as the variation in soil moisture probably was too low to detect patterns like this. Also, this factor was only an indirect estimate and not a direct measure of the moisture in the soil at that exact point, which maybe could have given clearer results regarding this factor.

When it comes to C concentration, my results coincide largely with similar findings, while the results for N concentration are a bit different. As mentioned, the accuracy of the N concentration values can be questioned due to the warning messages during the laboratory measurements. Nevertheless, if they are correct they show that dead stem wood can function as a small but long-term nutrient pool on the forest floor. The increasing C concentration shows that decaying wood also can retain C for a long time, with about 60% of the initial C left after 15 years of decay. With the increasing amount of dead wood in Scandinavian forests, it is clear that this C pool should be accounted for in future carbon budgets. Still, more research is needed in this field to better understand which environmental factors affecting the rate of the decomposition process of dead wood. The large-scale experiment in northern Sweden has a good study design to examine these relationships, and possible future research here should focus on more accurate measures of the environmental factors. Also, a larger number of samples than what used in my study is needed to detect patterns.

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