UNIVERSITY OF EASTERN FINLAND

Luonnontieteiden ja metsätieteiden tiedekunta

Faculty of Science and Forestry

Effect of boron fertilization on fiber properties and branchiness of Norway spruce

Vijay Dev Bhatt

Master's Thesis Forestry (CBU)

JOENSUU 2021

TABLE OF CONTENTS

LIST OF FIGURE AND TABLE

ACKNOWLEDGEMENT

I thank Tarja Lehto for her supervision and generous support throughout the writing process. Her guidance and insightful suggestions were great learning for me.

I thank Jouni Kilpeläinen for his help in the data analysis and guidance on SPSS.

I thank Arttu Vartiainen and Risto Ikonen for their support during the field work that taught me many new things. I thank Jarmo Pennala and Maini Mononen for their help in laboratory.

I thank Leena Kuusisto for conducting the laboratory work of nutrition analysis, I used data produced by her in this research.

I thank Antti Haapala for his support in the wood material science laboratory and logistics management.

I thank Nikolaos Papmatthaiakis for being in the laboratory as a friend and brother the whole time and motivating me.

Special thanks to School of Forestry Sciences for being very considerate and tuition fee waive for extended period.

Feb, 2021

Vijay Bhatt

ABSTRACT

Boron (B) is an essential micro-nutrient for plants and its deficiency negatively affects the yield and quality of the timber as the tree loses apical dominance. B is an essential element of the cell wall structure and involved in number of physiological processes of trees. This study examines the long-term effect of B fertilization on the element concentration on the foliage, fiber properties and the branchiness of the fertilized and non-fertilized trees. This research was carried out in a Norway spruce forest stand in Joensuu, Finland. It is a single tree fertilization study and boron was applied at 2 kg/ha in the circular plot of 2.5 radius around the trees in the year 2000. The foliage samples of the current growth were collected from 80 live trees for the nutrient analysis. The wood core samples for the fiber analysis were collected 15 boron fertilized and 15 non boron fertilized samples. Three sample types, foliage sample of the current year needle from the canopy for nutrient analysis, core sample from the height at the time of fertilization for fiber analysis and 80 cm bole samples from three different heights (1.5 m (A), height at the time of fertilization (B), two meter above B (C)) for branch study were collected.

The concentration of B, aluminum (Al), sulfur (S) and copper (Cu) elements was significantly higher in the boron fertilized trees whereas lower concentration of silicon (Si) was recorded. The fiber dimensions of the tree were not affected by the boron fertilization. However, significant within tree variation in the fiber dimensions (fiber length and fiber width) was observed. The fiber width and fiber length decreased towards the pith of the trunk. The maximum value of the fiber length and width averaged at 2.43 mm and 31.20 µm in the tree year rings 1 and 2 from the bark and the minimum value of 1.50 mm and 25.94 µm respectively in the year 13 and 14 near the pith. There was no effect of treatment and bole in the number of branches, but there was significantly higher number of branches in the bole C of the boron fertilized trees compared to controls. The median diameter significantly differed among the boles at different height. It can be inferred from the results that boron has a long retention time in the plant and soil in the study area. The effect is manifested in the branches of the sample trees with significantly higher number of branches in the boron fertilized trees. There was no significant effect of B fertilization on the fiber dimensions. However, correlation of this data with other timber properties would give insightful information.

Keywords: Boron fertilization; Branchiness; Element analysis; Fiber dimensions

1.0 INTRODUCTION

The macro and micro nutrients in soil play an important role in maintaining the vitality and productivity of plants. The biotic (pest status, species competition etc.), abiotic (climate variables, soil nutrients etc.) factors play key role in the wellbeing of the forests and also influence the quality of the wood biomass (Cregg et al. 1988; Setiawan et al. 2014). The balanced nutrient condition of soil enhances the resistance capacity to the biotic and abiotic disturbance factors contributing to quality timber supply (Saarsalmi & Mälkönen 2001).

The soil conditions, environmental factors, tree species and genetic makeup of the tree influences the physical and physiological condition of the plant cells which ultimately manifests on the wood properties (Wodzicki 2001). Thus, there is a large variation in wood properties which making it a versatile product with multiple applications. Furthermore, the advent of different wood modification and treatment technologies support the diverse use of wood. The understanding of physical and mechanical properties of wood from different growing conditions provides information for the purpose specific and efficient use of wood biomass (Barnett & Jeronimidis 2009).

Boron (B) is an important soil micronutrient and its deficiency is frequently observed around the world, it forms the essential component of the cell walls and a constant supply of B is required for the growth of the shoot and root apical meristem and buds (Kilpeläinen et al. 2013). The effect of B deficiency is visible on the cellular level. The cell, wood and mechanical properties of wood are interlinked (Barnett & Jeronimidis 2009) hence, deficiency of B may affect the wood properties (Lehto et al. 2010).

In this research, the effect of boron fertilization on the fiber properties and branchiness of the Norway spruce (*Picea abies* L.) tree is studied. Norway spruce is an important commercial tree in Finland, different aspects such as mechanical stability (Peltola et al. 2000), fiber properties suitability for pulping (Tyrväinen 1995), wood production potential (Bergh et al. 2005), wood properties of different provenances (Molteberg & Høibø 2006) of this tree have been studied but, the studies on the effect of individual nutrients on the anatomical features such as fiber properties of the tree are limited (Brändström 2001; Lindström 1996).

1.1 Forest fertilization

The forest fertilization research dates back to late 18th century but the systematic and sophisticated studies begin only after the Second World War (Binkley et al. 1995). Forest fertilization now is considered as a standard silvicultural operation especially in the plantation forestry with short rotation period. It plays an important role in maintaining a balanced soil nutrient state to increase production (Fox et al. 2007). However, there are concerns on the possible environmental tradeoffs such as water resource contamination (Van Miegroet et al. 1994).

In Finland, slash and burn agriculture prevalent until the beginning of 20th century is one of the primitive practices to manipulate the soil nutrients. The last known fertilization of forest in boron was in practice in 1940s (Kaskien väistyminen…). The major growth in the forest fertilization started in the 1960s, this coincides the high timber demand in the world market and government subsidies. However, this growth ceased in the 1980s when government stopped financial subsidization (Saarsalmi & Mälkönen 2001). Since last decade the forest fertilization has increased, it corresponds the growing interest in finding new products and services from the existing resources through expansion of bioeconomy (Hedwall et al. 2014). The severe nutrition deficiency symptoms in Finnish forests are not frequent. The rate of nutrient cycling reduces along south to north gradient and boron deficiency is more prevalent in northern Finland. B deficiency is known to show growth disturbance symptoms even in fertile stands (Saarsalmi & Mälkönen 2001).

B deficiency is a common occurrence in Finland in the nitrogen-rich sites and peatlands (Riikonen et al. 2013). The B availability in Finland is spatially variable and related to soil type, topography, soil water mobility and immobilization by microbes and fungi (Lehto et al. 2010). The phosphorus and potassium fertilization in peatlands and nitrogen fertilization and drainage in mineral soils intensifies the B deficiency (Riikonen et al. 2013).

1.2 Boron as a plant nutrient

B is established as an essential micronutrient for plants, humans, animals and some microbial community (Camacho-Cristóbal et al. 2018; Khaliq et al. 2018). The B deficiency is one of the most prevalent micronutrient deficiencies in the world (Gupta 1979), it is one of the limiting factors on growth in the nitrogen rich soils. The requirement of B in plants varies in different species and its deficiency can directly affect the productivity and tree health by affecting the physiological functions and indirectly affecting the symbiotic bacterial and fungal communities in soil (Bolaños et al. 2004; Lehto et al. 2010). The trees show visible symptoms of deficiencies like falling of buds, small and deformed fruits (Wojcik & Wojcik 2003). B deficiency in plants is linked with the poor defense mechanism against herbivores and pathogens and it shows adverse effects on the growth by affecting the root and shoot apical meristem (Lehto et al. 2010; Stone 1990).

The B deficiency prevalent in agriculture and forestry and frequently observed in sandy, alkaline (Nadeem et al. 2019) and acidic soils (Saarsalmi & Mälkönen 2001; Wang et al., 2015). B deficiency is often underdiagnosed in forest ecosystems around the world as the diagnosis standards from foliar analysis is limited to major tree species. The underdiagnoses is one of the reasons of limited B fertilization even though small amount of B is required for optimizing the adequate supply (Lehto et al. 2010). The amount as low as 2-4 kg/ha is enough to retain B in the ecosystem for a long duration of time (Kilpeläinen et al. 2013). The boron deficiency causes deposition of phenolic compounds in the meristem cells, this impedes the cell division process in the apical meristem of plants, the roots are more sensitive to stress compared to the shoot (Möttönen et al. 2001). B fertilization abates the negative effects of external stresses like drought in Norway spruce seedlings. The drought limits the movement of the nutrients in the transpiration stream of the tree caused by closure of stomata and possible damage to the vascular tissue of the trees (Choat et al. 2018; Lehto et al. 2010).

1.2.1 B in the cell wall

B plays important role in the stabilization of the cis-diol group, B forms stable complex with these compounds (Cakmak & Römheld 1997). In plant cell membranes Rhamnogalacturonan II (RG-II) is an important polysaccharide molecule, this and other polysaccharides contribute to physical properties and provide mechanical strength to cell membrane. B connects the monomers of RG-II by a borate bridge stabilizing the cell wall (Goldbach & Wimmer 2007). B supports the ion flux across the membranes facilitating the movement of ions and stabilizes the membrane structures (Cakmak & Römheld 1997). It is proposed that B plays important role in the cell structure and helps in the formation of cytoplasmic strands and cell to wall adhesion (Bassil et al. 2004). B works as a linkage between the glycosylinositol phosphorylceramides (GIPCs) and RG-II. GIPCs are important lipid of sphinglolipid family in the plasma membrane of plant cell (Voxeur & Fry 2014). The role of B in the cell wall signifies its importance in the cell division and growth process, the deficiency of B is thus visible as growth disorders in vegetative and reproductive cells.

1.2.2 Boron mobility in plants

B is taken up in the form of boric acid ($B(OH)_3$) from soil, it is a weak acid and an uncharged molecule that can pass through the cell wall (Brdar-Jokanović 2020; Yoshinari & Takano 2017). Plants absorb B from soil through passive uptake in adequate supply by the process of diffusion driven by transpiration. In the limited supply conditions, there are other known mechanisms (1) facilitated transport by major intrinsic proteins (MIPs) and NIP5;1 which belongs to nobulin 26-like protein and active transport by transporters genes BOR1 in the low B condition (Miwa & Fujiwara 2010; Tanaka & Fujiwara 2008). The mobility of B from the root to the shoot tissues is termed as translocation, in vascular plants water acts as a medium of transportation of nutrients. The translocation of the B in the trees is reduced when the transpiration is low (Lehto et al. 2004).

B movement within the tree is response to B deficiency and excess to avoid deficiency and toxicity (Brown & Shelp 1997). The movement of the nutrients from the old parts and storage organs to and from the growing tissues between the dormancy and growth period is called retranslocation (Lehto et al. 2004). B stored in the apoplast is available in mobile form readily available for the growing tissues whereas B in the cell wall is not available for the retranslocation (Wang et al. 2015). The retranslocation is rapid and significant in the plants with polyol compounds like mannitol, sorbitol these compounds form diester compounds with B facilitating the process (Liakopoulos et al. 2005). The formation of these B-polyol compounds enables long distance transport of the B within the tree. The extent of B mobilization varies among different plant species, suggesting no clear categorization of plants on the basis of B mobility (Brown & Shelp 1997; Lehto et al. 2010). In Norway spruce, the B concentration is maximum in the current year needles and decrease in subsequent older needles this phenomenon of retranslocation of nutrients is often observed in mobile nutrients (Lehto et al. 2010). Norway spruce shows high tolerance to B toxicity and does not show toxicity symptoms up to 400 mg/kg in seedlings and 60 mg/kg in the needles of mature trees (Riikonen et al. 2013).

1.3 Foliage analysis for nutrient concentration

The foliage element analysis is a standard method of nutrient assessment in plants introduced in early 1930s (Brække & Salih 2002). It is widely used to study the nutrient dynamics between plants and soil, nutrients mobility in the plant tissues and serves as a diagnosis tool to nutrient deficiencies (Van den Driessche 1974). The variability of nutrients in foliage is usually less compared to that of in soil in natural vegetation making it a reliable diagnosis tool to nutrient deficiencies (Foulds 1993). The foliar analysis helps in the assessment and early detection of the nutrients imbalances and provides time to correct before it affects the yield and health of the forest stand. In the long-term fertilization experiments it supports to better understand the connection between the nutrients and the forest yield, it also helps to trace the possible cause of the disorders in the tree health (Linder 1995).

1.4 Cell anatomy, fiber and wood properties

The cell anatomical features, fiber and wood properties are interrelated and affect each other. The Norway spruce is a softwood conifer tree, softwoods have less complex wood anatomy in comparison to hardwoods (Table 1). The hardwoods have variety of cell types with specialized functions whereas softwoods have uniform structure and the tracheids form the major portion of the wood (Le Guen et al. 2016).

Table 1. Differences between hard and softwood in Scandinavia

Particulars	Hardwood	Softwood	References
Cellulose	40-45%	40-45%	(Alen 2011)
Hemicellulose	30-35%	25-30%	(Alen 2011)
Lignin	20-25%	25-30%	(Alen 2011)
Fiber length	0.7-1.2 mm	2-4 mm	(Fahlén 2005)
Fiber width	10-30 µm	20-40 µm	(Fahlén 2005; Kellomäki 2009)

Softwood like Norway spruce is primarily composed of tracheid cells (up to 95% in Norway spruce), tracheids provide support and conduction function to the tree (Barnett & Jeronimidis 2009; Kekäläinen 2016). They are uniform non-living cells with tapering ends and thick secondary cell walls. The secondary wall consists of three sub-layers named as S1, S2 and S3 (Figure 1). The S2 layer is important in determining physical and mechanical properties of timber and the thickest layer with width of about 1-5 µm (Barnett & Jeronimidis 2009; Shmulsky & Jones 2019). The fiber cell wall is primarily composed of cellulose (40-50%) other polymers are hemicellulose (25-35%) and lignin (20-30% by weight) (Kekäläinen 2016). The cellulose structures called microfibrils are the major constituents of the cell wall, they lie parallel to each other and arranged in the S-helix (>90°) structure towards inner S1 layer and

Z helix (<90°) structure in the S2 layer. The orientation of the microfibrils is defined by the microfibril angle (MFA) which largely determines the timber properties. The MFA is the angle between the helical winding of microfibrils with the longitudinal axis of tracheids and it changes gradually between sub layers (Barnett & Bonham 2004). There is demonstrated evidence that MFA affects the mechanical and fiber properties significantly affecting paper properties (Barnett & Bonham 2004; Courchene et al. 2007). The low MFA is a desirable timber property as high MFA reduces the stiffness of wood (Andersson et al. 2000).

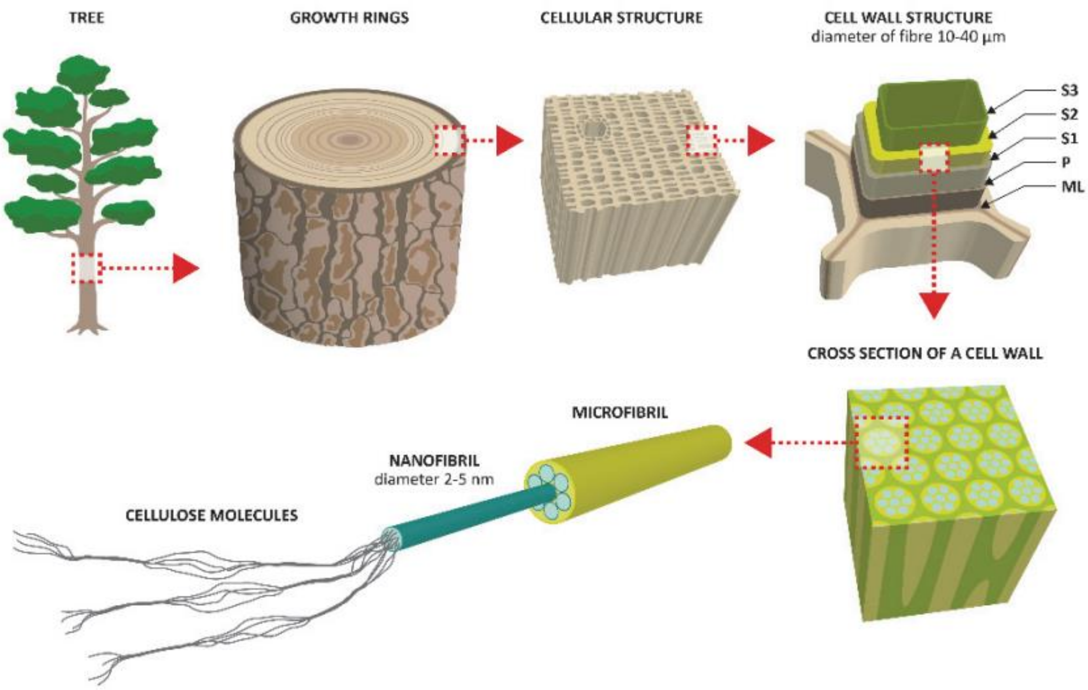

Figure 1. Position of the wood fiber and structural details in tree (Kekäläinen 2016)

The wood fiber is used in manufacturing of composite construction materials, thermoplastics are used for different purposes but primarily it is used in paper and pulp industry (Kekäläinen 2016; Stark & Rowlands 2003). The anatomical features of trees such as fiber dimensions are dependent on the genetics, age and growth conditions (soil nutrition, water, weather conditions etc.) (Zobel & Van Buijtenen 2012).

Furthermore, it is reported that under the nutrient (Mäkinen et al. 2002a) stress conditions and in slow grown trees (Sarén et al. 2004), the cell wall is thicker suggesting the effect of the variation of the nutrients and growth parameters on fiber properties. The wood fiber properties change when they are subject to physical and chemical processes in paper and pulp processing industry. These processes are believed to alter the surface chemistry of the fibers. A better understanding of the fiber properties helps to identify economical procurement of the pulp source. The pulp yield depends on the density of the wood the higher density yields greater amount of fiber per unit volume. The pulp from higher wood density produces paper with higher resistance to tearing. Higher tracheid length is preferred to pulping industry and improves the tearing, tensile and burst strength of paper (Macdonald & Hubert 2002).

1.5 Branchiness and wood quality

The branchiness refers to the number, size, position and quality of branches in the tree (Kantola et al. 2007). The branches are studied to investigate the genetics, wood quality, growth and yield etc., the models are used to find relationships between the parameters of interest. Branch size, numbers and proportional area coverage provides important information about the forest stand. The diameter of branches significantly affects the lumber quality for veneer in Douglas-fir and a small increment in the average diameter of the branches negatively affects the lumber quality (Maguire et al. 1999).

The hormones regulate and determine the growth properties of the branches. There are primarily two group of compounds regulating the growth of plant tissues (1) referred as plant hormones e.g., auxin, cytokinin, gibberellins, abscisic acid etc. (2) Growth regulators (polyamines, salicylates sterols etc.,) are responsible for the growth (radial and longitudinal) of branches (Gaspar et al., 1996). The nutrient condition of soil controls the hormonal signaling ultimately controlling the regulation of the hormones in the plants (Krouk et al. 2011). Boron is known to affect the ethylene, auxin, abscisic acid and cytokinin regulation in roots is affected by boron deficiency (Camacho-Cristóbal et al., 2018). Boron deprivation in plants cause alternations in auxin transport channels and promoting catabolism (Matthes et al. 2020).

The cell structure and anatomy of branch wood is different compared to normal wood (Buksnowitz et al. 2010). The branches when cede to grow, the intersection of branch and main trunk closes-in to form knots, it is the region of broken, dead or cut branch (Duchateau et al. 2015). The knots give unique physico-mechanical properties and provide variability in the wood which is an important part of the artistic use of wood, however it reduces the wood strength. The variability in the knot types and size provides important information for the categorization of timber (Hanhijarvi et al. 2005). The knot properties are the outcomes of the spatiotemporal interaction of the tree with the external environment (Duchateau et al. 2015). The number and size of branches are used as grading parameters in Norway spruce (Mäkinen & Hein, 2006).

The knots of Norway spruce contain about 6-24% of lignin (Holmbom et al. 2003). The branches below the canopy are particularly important and significantly affect the harvested wood quality (Larson 1969). The branches also referred to as limb wood is being increasingly used in producing chips for bioenergy and fibers affecting the quality of the end products (Zobel & Van Buijtenen 2012). The crown properties influence the physiological processes like photosynthesis and transpiration (Mäkinen & Hein 2006). The trees with less or no branches are known to minimize knots and taper effect (Barnett & Bonham 2004). The branch diameter is closely associated with distance from stem top, crown length (good crowns possess thicker branches). The pipe model is used to explain the relationship between foliage and wood (Berninger et al. 2005).

1.6 Hypothesis

It is hypothesized that the boron fertilization affects the nutrient status, fiber properties and branchiness of Norway spruce.

1.7 Objectives

The major objective of this research is to examine the effect of boron fertilization on the foliage nutrient status, fiber properties and branchiness in boreal ecosystem.

The specific objectives are;

1. To study the effect of boron fertilization on the fiber properties of wood samples.
2. To study the effect of boron fertilization on the branchiness of the trees.
3. To assess the effect of boron fertilization on different nutrient status in current year needles.

2.0 MATERIALS AND METHODS

2.1 Study Area

The study area is situated in Hammaslahti, Joensuu of Eastern Finland. The forest site is the herb rich forest, the most productive forest site classification in the region. The forest stand was planted in the year 1979. The forest stand was heterogeneous as the survival rate of the plantation was poor because of competition and complementary plantation was done two times since the plantation. It is a single tree fertilization study and boron was applied as borax ($Na_2[B_4O_5(OH)_4]\cdot 8H_2O$) at 2 kg/ha and nitrogen as urea (CH_4N_2O) at 180 kg/ha in the circular plot of 2.5 radius around the trees in the year 2000. Four different treatment combinations control (0), Boron (B), Nitrogen (N) and Boron Nitrogen (BN) were studied. The fertilization of the sites was done in the June, 2000 at the time of the budburst, altogether 148 trees were fertilized and minimum distance between the experimental trees was maintained at 7m.

In this research 30 trees, 15 B fertilized and 15 control trees were selected. The fiber properties of the samples were studied in 14 boron fertilized tree samples and 14 control tree samples. The needle samples for the nutrient analysis were taken from all the remaining trees in the study area with B, N, NB fertilizations and 0 (control) (n=79). The samples from the field were collected in the month of April and May 2019. The experimental trees were located, marked and felled to collect the samples.

2.2 Sampling

2.2.1 Wood samples

The stem samples were collected by felling the trees, the tree dimensions diameter at breast height (dbh) and height were collected before felling of trees. The trees were marked for the direction north and south and felled by using a chainsaw. The disk and core samples were collected on the harvest day and stored in the freezer at the temperature -18°C until the processing of the samples was done. Two types of stem samples (core samples and bole samples of 80cm length) were collected from each of the 30 trees felled. The sample types were collected from tree places in the main trunk, first at 1.3m height (bole A), second from the height of the tree when it was fertilized (bole B), and third 2m above of the upper end of the bole sample (bole C). The bole samples were de-branched such that 1cm of the branch is left on the bole for the branch indexing. All the samples were marked north and south and collected samples were stored in the air proof plastic bag at temperature -18°C. The bole samples were stored on site and procured later to the University facility once the tree felling work completed.

2.2.2 Core samples

The core samples through the trees yielding from bark to bark were collected using 1cm corer in the north-south direction. The collected core samples from the field were placed in air tight plastic tubes of same diameter sealed air tight on both ends and stored at -18°C on the same day of the collection of the samples. The core samples were used for the fiber analysis.

2.2.3 Needle samples for nutrient analysis

The shoots were collected from the live upper canopy using scissors, the shoots of different year class were collected in separate bags and marked with tree number and year class. The B treated and control samples were kept separately to avoid contamination. The current year needle samples were clipped and kept in paper bag in oven for drying at 40°C for 48 hours. The concentration of different elements and heavy metals in the needles was analyzed using ICP.

2.2.4 Measurement of fiber dimensions

The samples were taken out of the laboratory storage and thawed at the room temperature for 2 hours prior further processing. The samples were then taken out and soaked in the deionized water for 20 mins and the year rings of year 1 and 2, 5 and 6, 9 and 10 and 13 and 14 from cambium to pith were separated using scalpel, a microscope is used for the precise cutting of the year ring samples. Each of these samples were placed in the test tubes, concentrated solution of acetic acid and hydrogen peroxide in 1:1 w/w ratio was used for the maceration of the samples. For the maceration the samples were placed in the incubator at 60°C for 48 hours. The well macerated annual ring samples were washed and 400ml of deionized water was added to the sample, the individual fibers were separated using the blender with blunt blades for 15 seconds to make the suspension. About 20-30 ml of suspension was taken in the measurement beakers and the fiber dimensions were measured in FS5 UHD Fiber Image Analyzer (Valmet, Kajaani, Finland). The complete procedure of the experiment was optimized by running experiments with number of trial samples prior running actual samples. The fiber analysis was done from the core sample from lower end of bole B, it is the height of the tree when it was fertilized in the year 2000. The average height of the sampling point in the trunk was 5.76 m which was roughly 30% of the total height at the time of sample collection.

2.2.5 Branchiness

The number and the diameter of branches were counted from boles of 80 cm length collected from three different heights of the trunk as explained in 2.2.1. The boles were marked A, B and C towards the top of the trunk. The bole A was collected at the breast height upwards, bole B was taken from height when the tree was treated with fertilizers and the bole C was collected two meters above the bole B.

2.3 Statistical methods

The data were analyzed in SPSS and Microsoft Excel. The SPSS was used to develop linear mixed models and Microsoft excel was used to prepare graphs. The general linear model univariate analysis was used for the analysis of elements data. The fiber dimensions (fiber length and fiber width) and branches were analyzed using linear mixed model. In the model, fertilization, year class and tree side were taken as the fixed factors, tree side and year as the repeated factor and tree as the random factor. The tree diameter at breast height (dbh) and tree height was taken as covariates. And for the branch analysis, treatment and bole were the fixed factors and height as the covariate.

3.0 RESULTS

3.1 Nutrients

The conditions of homogeneity were tested using Levene's test and the data of the B and Mg was log transformed and Cu and K was inverse transformed to meet the conditions of normality and homogeneity of variances.

Table 2. Mean and standard error value of different elements

Elements	0 (n=19)		B (n=20)		N (n=17)		NB (n=23)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
B (µg/g)	1.726	0.143	4.931	0.510	1.725	0.155	4.729	0.453
Al (µg/g)	63.34	5.465	72.23	6.314	65.05	5.698	83.75	5.922
Ca (mg/g)	3.907	0.252	4.148	0.220	4.303	0.258	4.071	0.266
Cu (µg/g)	1.608	0.061	2.491	0.384	1.582	0.048	2.089	0.199
Fe (µg/g)	29.60	1.317	29.46	1.157	27.03	1.049	29.94	1.012
K (mg/g)	4.332	0.131	4.730	0.296	3.908	0.156	4.170	0.133
Mg (mg/g)	1.191	0.075	1.190	0.043	1.173	0.064	1.195	0.050
Mn (µg/g)	0.617	0.047	0.545	0.042	0.678	0.058	0.613	0.045
Ni (µg/g)	4.017	0.352	4.526	0.427	4.249	0.461	5.692	1.927
P (mg/g)	1.368	0.066	1.332	0.037	1.254	0.064	1.250	0.048
S (mg/g)	0.729	0.020	0.874	0.014	0.737	0.018	0.871	0.014
Si (µg/g)	308.5	26.90	205.9	24.47	303.4	33.91	205.3	21.73
Zn (µg/g)	27.72	2.130	27.94	3.385	30.74	2.234	27.55	1.761

There is no statistically significant interaction effect of nitrogen (N) and boron (B) fertilization in the concentration of all nutrients ($p > 0.358$). The B fertilization significantly increased the concentration of B, aluminum (Al), sulfur (S) and copper (Cu) (boron main effect $P < 0.026$) and decreased the concentration of silicon (Si) in the current growth needles (boron main effect $P < 0.001$). The Si concentration was 49% less and B, Al and Cu concentration was 64%, 18% and 30% higher respectively in the B fertilized trees (Table 1). The main effect of nitrogen fertilization shows significant reduction effect on the concentration of potassium ($p = 0.015$). The potassium concentration was found to be 12% less in the nitrogen fertilized trees (4.04 mg/g vs 4.53 mg/g).

3.2 Fiber analysis

The mean length and width of fibers decreased towards the pith in north and south direction. The fiber length of the tree rings 1 and 2 was the largest for boron fertilized and control trees and the fiber length of the year 13 and 14 the smallest (Figure 2). The fiber width also showed similar pattern with maximum width in rings 1 and 2 and minimum width at rings 13 and 14 (Figure 3).

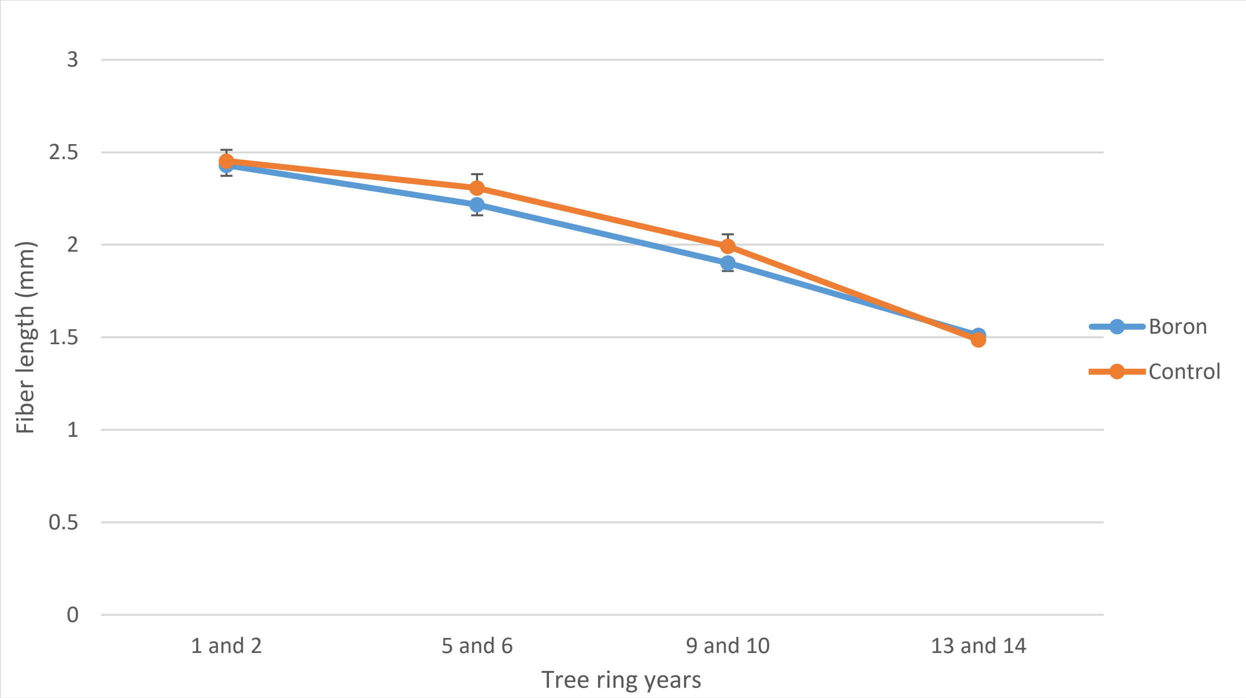

Figure 2. Fiber length of different tree ring class with error bars

There is no significant effect of the B treatment and direction (*P* > 0.136) on both fiber length and width. However, the length (*P* < 0.001) and width (*P* < 0.001) of fibers significantly differ among different age class. The probability of covariate tree height affecting the fiber dimensions is *P* > 0.073, whereas the effect of dbh is non-significant (*P* > 0.154). The fiber length of the age class 5 & 6 and 9 & 10 is slightly higher in control trees but not significant compared to B fertilized tree samples (Figure 2 and 3).

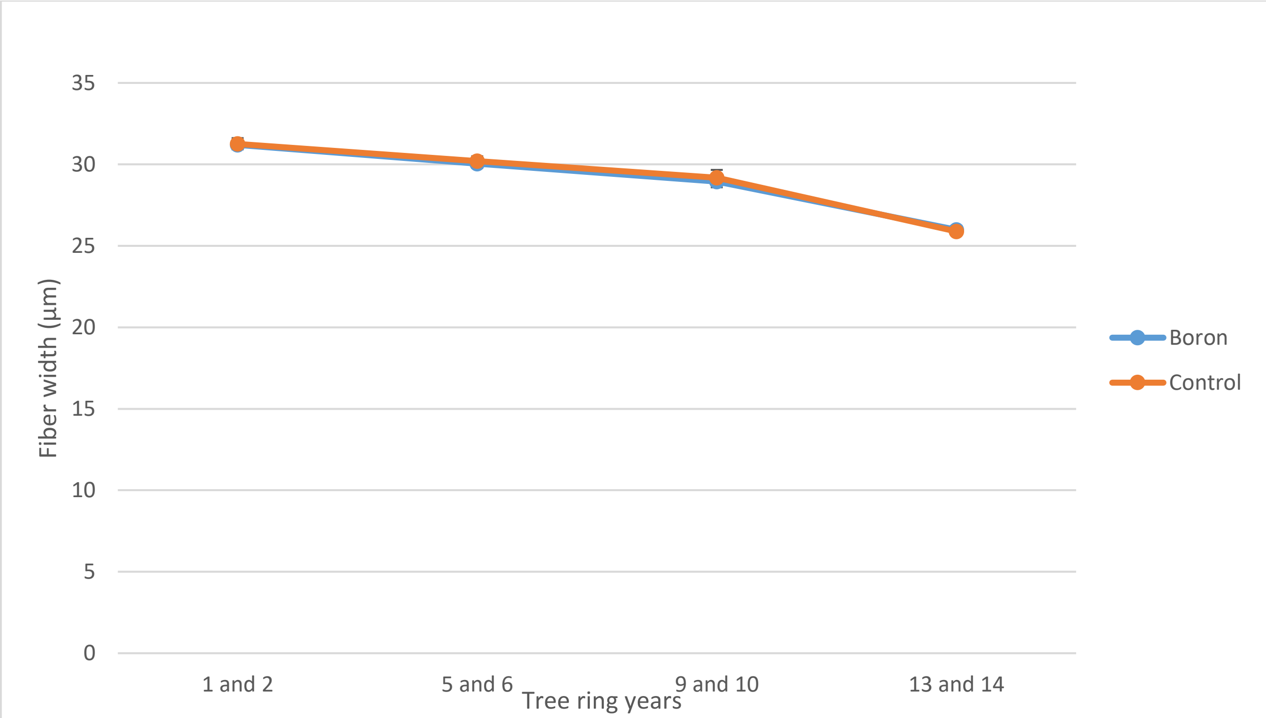

Figure 3. Fiber width with the standard error bars

3.3 Branchiness

There was no fixed effect of the treatment, bole or interaction effect of treatment*bole on the number of branches ($p > 0.148$). However, the pairwise comparison shows that the number of branches is significantly higher in the Bole C of B fertilized trees ($p = 0.032$) compared to controls. The median diameter of branches in different branches was not affected by the treatment but significantly differ among the boles ($p = 0.001$) and there was no significant interaction effect of treatment*bole.

Table 3 Average number of branches and median of different trunk sections

Trunk Section	Treatment	Average number of Branches	SE	Median diameter (mm)	SE
Bole A	0	22.2	0.414	14.3	0.269
Bole B	0	23.0	0.367	10.8	0.209
Bole C	0	20.0	0.404	12.9	0.364
Bole A	1	25.2	0.500	14.8	0.192
Bole B	1	23.6	0.379	10.4	0.141
Bole C	1	25.8	0.265	9.90	0.185

4.0 DISCUSSION

4.1 Nutrient concentration

The B fertilization significantly increased the concentration of B, aluminum (Al), sulfur (S) and copper (Cu) and decreased the concentration of silicon (Si) in the current growth needles. The majority of other nutrients remained unaffected by B fertilization. In a study of the tree dimensions, the height and the diameter of the tree was higher in the boron fertilized trees (Vartiainen… in preparation), it follows the trend of similar observations in the study area before (Kilpeläinen et al. 2013). The B deficiency is associated with the retarded root and height growth, lower number of root tips and mycorrhiza (Möttönen et al. 2001). B deficiency is also associated with retarded height in drought stressed Norway spruce seedlings (Möttönen et al. 2005). The optimum concentration of B in the foliage depends on the species and growing conditions (Lehto et al. 2010).

The findings of this study shows that even after 19 years of B fertilization significantly increased the concentration of B in the needles of fertilized trees. This finding continues the trend of the previous study in the same forest stand by Kilpeläinen et al. (2013). The concentration of B in the trees with B fertilizer was 4.8 µg/g compared to 8.4 µg/g in 2012, this value is still above the critical nutrient concentration for the mature spruce tree when it starts to show severe deficiency symptoms (Kilpeläinen et al. 2013; Lehto et al. 2004). The effects of fertilization were observed with increased height and volume of the B fertilized trees in the study area (Kilpeläinen et al. 2013). The previous studies show that liming and N fertilization negatively affects the B availability (Lehto & Mälkönen 1994). However, there was no dilution effect of N fertilization in this study, this might be because the site is N rich site hence, it is not the variable parameter in different trees (Kilpeläinen et al. 2013). Saarsalmi & Tamminen (2005) observed a rapid response of B fertilization in trees with growth disturbance symptoms. The higher concentration of B in the needle was recorded after one year of fertilization and deficiency symptoms were alleviated after four years of fertilization with improved height growth (Saarsalmi & Tamminen 2005) emphasizing the importance of B fertilization on recovery from growth disorders.

The Si is not an essential but a beneficial element for plants. The accumulation potential of Si greatly differs among different plant species. The annual uptake potential of Norway spruce is higher (43.5 kg/ha/year) compared to black pine or Douglas fir (Cornelis et al. 2010). Si is known to ameliorate the phytotoxic effects of different metals (Prabagar et al. 2011). The presence of Si reduces the toxic effects of Al in Norway spruce (Prabagar et al. 2011). One of the reasons of lower percentage of Si in B fertilized trees might be the competition for the transporter molecules as B and Si both partly use nodulin-like intrinsic protein (NIPs) for cellular transport (Kilpeläinen et al. 2013; Miwa & Fujiwara 2010).

In this study, B fertilization increased the Al concentration in the current year needles. The availability of Al to plants depends on the available chemical form, it usually forms complexes and not available to plants but in low pH conditions it becomes available in ionic form. Al is considered toxic to plants; it inhibits the growth of root meristem cells (Yan et al. 2018). B is known to ameliorate the negative effects of Al in acidic soil in different plants, recent studies show that borate-RG II complex promotes the adsorption of Al^{+3} in the cell wall protecting the root cells from toxic effects of Al (Li et al. 2017). Further research on the effects of Al toxicity in Norway spruce can provide further details.

According to foliage nutrient data of this forest stand in 2012, the Cu concentration was recorded higher in the B and N fertilized trees whereas NB fertilization sites were unaffected. In this study, the concentration of Cu was recorded higher (2.3 µg/g vs. 1.6 µg/g) in the B fertilized trees compared to controls. There are limited number of studies examining the interactions of B and Cu hence, it is difficult to explain the occurrence, therefore further investigation on this matter is needed (Kilpeläinen et al. 2013). Cu is an important micronutrient but with a narrow range to the toxic effects, the lethal effects are visible even in slight excess (Ivanov et al. 2016).

In addition to the interaction of different nutrients, subsidiary factors such as soil pH which is one of the most prominent soil characteristics strongly influences the availability of micronutrients in soil. The soil type of the study site is cambic podzol which is acidic in nature (Kilpeläinen et al. 2013; Tamminen & Tomppo 2008). The higher soil pH increases the adsorption of B reducing the proportion of boron in available form for the trees at the same time increasing the long term retention of the B in acidic soils (Mengel et al. 2001; Shuman, 1998).

4.2 Fiber analysis

The results on the fiber properties of this research shows generally observed trend of longer fibers near the cambium. In this study, the longest fibers (2.430 mm) were found in the tree ring 1 and 2 (the outermost rings) and the shortest in the innermost rings i.e., year ring 13 and 14 (1.510 mm). The rapid increase in the fiber length from pith in the juvenile wood and later gradual and consistent growth near cambium is reported by many research (Kučera 1992; Lindström 1997). The higher growth rate of the fiber dimensions shows transition phase of juvenile wood to the mature wood. The increment in the fiber length was gradual in this study, this might be because of the lower proportion of juvenile wood in the samples.

In this study, slightly longer fibers were recorded in the control trees of the year ring class 5 & 6 and 9 & 10 which coincides after the B fertilization. The latewood and earlywood proportion are strongly associated with the fiber dimensions, Mäkinen et al. (2002a), reported on average 11% shorter fibers in earlywood. However, the effect of the earlywood proportion can only be confirmed after the measurement of those parameters. The longer fibers might be due to the positive effect of fertilization on the growth and consequent greater proportion of the earlywood, which later faded in the year ring 1 & 2 as shown by the results of foliage analysis for nutrients concentration. However, in this study the effect of growth parameters (height and dbh) on fiber dimensions was non-significant ($P > 0.073$). Herman et al. (1998) found no statistically significant difference between the fiber length of fast grown and slow grown Norway spruce. They reported similar trend of increasing fiber length from pith to bark and the fiber lengths of the slow grown trees were slightly larger. The influence of phenotypic variation within the Norway spruce were minimum on fiber properties and wood density, whereas dbh and height varied significantly (Zubizarreta Gerendiain et al. 2009).

The width of the fibers increases with the increase in the tree ring number towards the cambium. The relatively sharp increase in the fiber width is observed between the year ring class 12-13 and 9-10 after that the growth is gradual towards the bark similar to the prior studies (Atmer & Thörnqvist 1982; Mäkinen et al. 2007). The length and width of the fibers are expressed in length-to-width ratio (L/D) or aspect ratio. The aspect ratio is used to determine wood properties such as in the manufacturing of wood composites, higher aspect ratio is a desired property for wood composites (Bouafif et al. 2009). The length and width of the fiber changes across the height and radial direction (Olesen 1982; Tyrväine 1995). The longer fiber length provides greater surface area for bonding hence increasing the chances formation of joints which increases the paper strength (Jajcinovic et al. 2016).

The majority of studies examine fiber in association with other wood properties such as density (Zubizarreta-Gerendiain et al. 2008). The past studies indicate that the fiber and wood properties are closely related (Mäkinen et al. 2002b; Wodzicki 2001). The size of the fibers significantly differed between different age classes within the tree implying the variation in wood properties. The results on the fiber dimensions concur with other similar studies on Norway spruce and other conifers with reports to the variation in other timber properties such as wood density (Herman et al. 2007; Lindström 1997; Lundqvist et al. 2005). The variation in the fiber dimensions is an indicator to the variation in the prominent wood properties such as wood density in radial direction (Mäkinen et al. 2002b). The wood properties also depend on the stand status (dominant or suppressed), water and nutrient availability, silvicultural practices (Zubizarreta-Gerendiain et al. 2009) but the manifestation of the variation is in the tracheid cells. Kučera (1992) suggest optimization of the fiber length and growth through silvicultural operation such as maintaining high competition period for 15 to 20 years and after that facilitating rapid growth by thinning.

Kilpeläinen et al. (2004) studied effect of elevated temperature and CO_2 on the wood properties of Scotts pine, they observed significant increment in the radial growth, fiber length and wood density in trees with elevated temperature and CO_2. Similar growth response was documented in a simulated process-based-model for Norway spruce as well (Briceno-Elizondo et al. 2006), however, the growth was only significant in the sufficient nutrient condition (Sigurdsson et al. 2013). The increased growth rate might have negative effect on wood density as shown by Mäkinen et al. (2002) who observed 20% reduction in the wood density when the radial growth increased three times. The reduction in density limits the amount of pulp production per unit volume. The above-mentioned studies imply possible effect of elevated temperature and CO_2 conditions on fiber characteristics in temperate environment.

4.3 Branchiness

The number of branches in the apex stem depends on the site fertility, stand density and genetics of the tree. The number size and distribution of tree knots determine the quality and appearance of wood. The stand density strongly determines the death rate of branches and might also affect the self-pruning of branches (Hein et al. 2007). The branches are not homogenously distributed throughout the trunk, the young branches are situated in the upper part of the tree whereas the older branches away from the top. The young branches near the canopy take active part in the photosynthesis (Colin & Houllier 1991; Mäkinen & Hein 2006).

In this study, the average number of branches are higher in the B fertilized trees in bole A and B but the difference was not significant. The stem density is maximum at near the tree base and decreases with increasing height and again increases near the top of the trunk (Barnett & Jeronimidis 2009), similar trend was observed in this study. The number of branches in bole C (bole near to the upper canopy) was maximum. The number of branches in boron fertilized trees was significantly higher compared to the control trees in bole C. This observation is possibly due to the long-term retention of B in the soil and the tree and suggests the physiological role of boron in the branch formation in Norway spruce. The higher number of branches in the B fertilized trees highlights the role of B in the bud formation and branch development. In a study in foliage application of boron in soybean plant, the fertilized plants had higher number of branches compared to the controls (Schon & Blevins 1990). The branch density plays important role in crown and branch characteristics (Haapanen et al. 1997) and positively affects the growth as shown by the greater height and diameter in B fertilized trees. The result on the higher density of branches in B fertilized trees corresponds to the B concentration in the foliage of the sample trees as explained in 3.1.

The water availability, silvicultural practices, competition etc., are other important control factors that define crown characteristics and number of branches, the dominant trees suppress the foliage growth of the suppressed individuals (Albaugh et al. 2006; Zubizarreta Gerendiain et al. 2009). Pfister et al. (2007) found greater number of branches on the individuals grown in wider spacing with less competition.

The branch formation process and its development can be further explained by the roles of growth hormones and role of boron in regulation of these hormones, particularly auxin and cytokinin. The signaling of auxin and cytokinin through membrane receptors in *Arabidopsis* plants is inhibited in B deficit environment, particularly in the root's meristem (Abreu et al. 2014). Möttönen et al. (2001) also reported lower number of roots tips and mycorrhizal percentage in B deficit Norway spruce seedlings. This finding in Norway spruce might be related to the hormonal role of boron as auxin plays an important role in bud growth and initial initiation stage of the arbuscular mycorrhiza formation (Hanlon & Coenen 2011). The studies on hormones in the B stress environment will further elucidate the effect of B and its role on the growth hormones in trees.

The diameter of the branches closest to the breast height (bole A) was found maximum which is in accordance to previous research (Johansson 1992; Pfister et al. 2007). The median diameter of the bole C in the boron fertilized tree was greater compared to the control trees, this might be possibly due to the early death of the branches in the boron fertilized trees. The age of the branches was significantly reduced in early die back of the *Pinus taeda* fertilized with urea and six other elements including boron with irrigation, however, the diameter of the branches was higher contrary to the findings of this study. This might be due to other control factors such as supplemental other fertilizers and elements and irrigation in the study which were absent in our case (Albaugh et al. 2006).

5.0 CONCLUSION

The study shows that B fertilization increased the concentration of B in the B treated trees even after 19 years of fertilization treatment suggesting the long-term retention effect of B in the forest stand. The fertilization increased the diameter and height of the trees however, the fertilization had no significant effect on the fiber dimensions. This study is limited to the fiber length and width, the study of other dimensions and physio-mechanical properties of wood would give a clearer picture. The long-term retention of the B in the trees and its positive effect on the tree and diameter of the tree are key aspects that signify the economic importance of the boron fertilization. The fibers are considered as the primary raw material for the number of products and the information on the variables that might possibly affect the fiber dimensions provides more control over the production and manipulation.

6.0 REFERENCES

Abreu, I. Poza, L. Bonilla, I. & Bolaños, L. (2014). Boron deficiency results in early repression of a cytokinin receptor gene and abnormal cell differentiation in the apical root meristem of *Arabidopsis thaliana*. Plant Physiology and Biochemistry, 77, 117–121.

Albaugh, T. J. Allen, H. L. & Fox, T. R. (2006). Individual tree crown and stand development in *Pinus taeda* under different fertilization and irrigation regimes. Forest Ecology and Management, 234(1–3), 10–23.

Alen, R. (2011). Papermaking science and technology. Book 20, Biorefining of forest resources. Paperi Ja Puu, Helsinki.

Andersson, S. Serimaa, R. Torkkeli, M. Paakkari, T. Saranpää, P. & Pesonen, E. (2000). Microfibril angle of Norway spruce [*Picea abies* (L.) Karst.] compression wood: Comparison of measuring techniques. Journal of Wood Science, 46(5), 343–349.

Atmer, B. & Thörnqvist, T. (1982). The properties of tracheids in spruce (*Picea abies* Karst.) and pine (*Pinus sylvestris L*.). Rapport-Sveriges Lantbruksuniversitet, Institutionen Foer Virkeslaera (Sweden).

Barnett, & Bonham, V. A. (2004). Cellulose microfibril angle in the cell wall of wood fibres. Biological Reviews, 79(2), 461–472.

Barnett, & Jeronimidis, G. (2009). Wood quality and its biological basis. John Wiley & Sons.

Bassil, E. Hu, H. & Brown, P. H. (2004). Use of phenylboronic acids to investigate boron function in plants. Possible role of boron in transvacuolar cytoplasmic strands and cell-to-wall adhesion. Plant Physiology, 136(2), 3383–3395.

Bergh, J. Linder, S. & Bergström, J. (2005). Potential production of Norway spruce in Sweden. Forest Ecology and Management, 204(1), 1–10.

Berninger, F. Coll, L. Vanninen, P. Mäkelä, A. Palmroth, S. & Nikinmaa, E. (2005). Effects of tree size and position on pipe model ratios in Scots pine. Canadian Journal of Forest Research, 35(6), 1294–1304.

Binkley, D. Carter, R. & Allen, H. L. (1995). Nitrogen fertilization practices in forestry. Nitrogen Fertilization in the Environment, Marcel Dekker, New York, 421–441.

Bolaños, L. Lukaszewski, K. Bonilla, I. & Blevins, D. (2004). Why boron? Plant Physiology and Biochemistry, 42(11), 907–912.

Bouafif, H. Koubaa, A. Perré, P. & Cloutier, A. (2009). Effects of fiber characteristics on the physical and mechanical properties of wood plastic composites. Composites Part A: Applied Science and Manufacturing, 40(12), 1975–1981.

Brække, F. H. & Salih, N. (2002). Reliability of foliar analyses of Norway spruce stands in a Nordic gradient. Silva Fennica, 36(2), 489–504.

Brändström, J. (2001). Micro-and ultrastructural aspects of Norway spruce tracheids: A review. Iawa Journal, 22(4), 333–353.

Brdar-Jokanović, M. (2020). Boron Toxicity and Deficiency in Agricultural Plants. International Journal of Molecular Sciences, 21(4), 1424.

Briceno-Elizondo, E. Garcia-Gonzalo, J. Peltola, H. Matala, J. & Kellomäki, S. (2006). Sensitivity of growth of Scots pine, Norway spruce and silver birch to climate change and forest management in boreal conditions. Forest Ecology and Management, 232(1–3), 152–167.

Brown, P. H. & Shelp, B. J. (1997). Boron mobility in plants. Plant and Soil, 193(1–2), 85–101.

Buksnowitz, C. Hackspiel, C. Hofstetter, K. Müller, U. Gindl, W. Teischinger, A. & Konnerth, J. (2010). Knots in trees: Strain distribution in a naturally optimised structure. Wood Science and Technology 44(3), 389–398.

Cakmak, I. & Römheld, V. (1997). Boron deficiency-induced impairments of cellular functions in plants. Plant and Soil, 193(1–2), 71–83.

Camacho-Cristóbal, J. J. Navarro-Gochicoa, M. T. Rexach, J. González-Fontes, A. & Herrera-Rodríguez, M. B. (2018). Plant response to boron deficiency and boron use efficiency in crop plants. In Plant Micronutrient Use Efficiency (pp. 109–121). Elsevier.

Choat, B. Brodribb, T. J. Brodersen, C. R. Duursma, R. A. López, R. & Medlyn, B. E. (2018). Triggers of tree mortality under drought. Nature 558(7711), 531–539.

Colin, F. & Houllier, F. (1991). Branchiness of Norway spruce in north-eastern France: Modelling vertical trends in maximum nodal branch size. Annales Des Sciences Forestières 48(6), 679–693.

Cornelis, J.-T. Ranger, J. Iserentant, A. & Delvaux, B. (2010). Tree species impact the terrestrial cycle of silicon through various uptakes. Biogeochemistry 97(2–3), 231–245.

Courchene, C. E. Peter, G. F. & Litvay, J. (2007). Cellulose microfibril angle as a determinant of paper strength and hygroexpansivity in Pinus taeda L. Wood and Fiber Science 38(1), 112–120.

Cregg, B. M. Dougherty, P. M. & Hennessey, T. C. (1988). Growth and wood quality of young loblolly pine trees in relation to stand density and climatic factors. Canadian Journal of Forest Research 18(7), 851–858.

Duchateau, E. Auty, D. Mothe, F. Longuetaud, F. Ung, C. H. & Achim, A. (2015). Models of knot and stem development in black spruce trees indicate a shift in allocation priority to branches when growth is limited. PeerJ 3, e873.

Fahlén, J. (2005). The cell wall ultrastructure of wood fibres: Effects of the chemical pulp fibre line. KTH.

Foulds, W. (1993). Nutrient concentrations of foliage and soil in South-western Australia. New Phytologist 125(3), 529–546.

Fox, T. R. Lee Allen, H. Albaugh, T. J. Rubilar, R. & Carlson, C. A. (2007). Tree nutrition and forest fertilization of pine plantations in the southern United States. Southern Journal of Applied Forestry 31(1), 5–11.

Gaspar, T. Kevers, C. Penel, C. Greppin, H. Reid, D. M. & Thorpe, T. A. (1996). Plant hormones and plant growth regulators in plant tissue culture. In Vitro Cellular & Developmental Biology-Plant 32(4), 272–289.

Goldbach, H. E. & Wimmer, M. A. (2007). Boron in plants and animals: Is there a role beyond cell-wall structure? Journal of Plant Nutrition and Soil Science 170(1), 39–48.

Gupta, U. C. (1979). Boron nutrition of crops. Adv. Agron 31, 273–307.

Haapanen, M. Velling, P. & Annala, M.-L. (1997). Progeny trial estimates of genetic parameters for growth and quality traits in Scots pine.

Hanhijarvi, A. Ranta-Maunus, A. & Turk, G. (2005). Potential of strength grading of timber with combined measurement techniques. Vtt Publications, 568.

Hanlon, M. T. & Coenen, C. (2011). Genetic evidence for auxin involvement in arbuscular mycorrhiza initiation. New Phytologist 189(3), 701–709.

Hedwall, P.-O. Gong, P. Ingerslev, M. & Bergh, J. (2014). Fertilization in northern forests–biological, economic and environmental constraints and possibilities. Scandinavian Journal of Forest Research 29(4), 301–311.

Hein, S. Mäkinen, H. Yue, C. & Kohnle, U. (2007). Modelling branch characteristics of Norway spruce from wide spacings in Germany. Forest Ecology and Management 242(2–3), 155–164.

Herman, M. Dutilleul, P. & Avella-Shaw, T. (2007). Growth rate effects on temporal trajectories of ring width, wood density, and mean tracheid length in Norway spruce (Picea abies (L.) Karst.). Wood and Fiber Science 30(1), 6–17.

Holmbom, B. Eckerman, C. Eklund, P. Hemming, J. Nisula, L. Reunanen, M. Sjöholm, R. Sundberg, A. Sundberg, K. & Willför, S. (2003). Knots in trees–A new rich source of lignans. Phytochemistry Reviews 2(3), 331–340.

Ivanov, Y. V. Kartashov, A. V. Ivanova, A. I. Savochkin, Y. V. & Kuznetsov, V. V. (2016). Effects of copper deficiency and copper toxicity on organogenesis and some physiological and biochemical responses of Scots pine (*Pinus sylvestris* L.) seedlings grown in hydroculture. Environmental Science and Pollution Research 23(17), 17332–17344.

Jajcinovic, M. Fischer, W. J. Hirn, U. & Bauer, W. (2016). Strength of individual hardwood fibres and fibre to fibre joints. Cellulose 23(3), 2049–2060.

Johansson, K. (1992). Effects of initial spacing on the stem and branch properties and graded quality of *Picea abies* (L.) Karst. Scandinavian Journal of Forest Research 7(1–4), 503–514.

Kantola, A. Mäkinen, H. & Mäkelä, A. (2007). Stem form and branchiness of Norway spruce as a sawn timber—Predicted by a process-based model. Forest Ecology and Management 241(1–3), 209–222.

Kaskien väistyminen. (n.d.). Retrieved February 10, 2021, from http://www.helsinki.fi/kansatiede/histmaatalous/kaskenviljely/vaistyminen.htm

Kekäläinen, K. (2016). Microfibrillation of pulp fibres. The effects of compressions hearing, oxidation and thermal drying [University of Oulu]. http://jultika.oulu.fi/files/isbn9789526213668.pdf

Kellomäki, S. (2009). Papermaking science and technology, Volume 2, Forest resources and sustainable management, Paper Engineers’ Association. Paperi Ja Puu Oy.

Khaliq, H. Juming, Z. & Ke-Mei, P. (2018). The physiological role of boron on health. Biological Trace Element Research 186(1), 31–51.

Kilpeläinen, J. Räisänen, M. Mehtätalo, L. Sutinen, S. Rummukainen, A. Repo, T. & Lehto, T. (2013). The longevity of Norway spruce responses to boron fertilisation. Forest Ecology and Management, 307, 90–100.

Krouk, G. Ruffel, S. Gutiérrez, R. A. Gojon, A. Crawford, N. M. Coruzzi, G. M. & Lacombe, B. (2011). A framework integrating plant growth with hormones and nutrients. Trends in Plant Science 16(4), 178–182.

Kučera, B. (1992). A hypothesis relating current annual height increment to juvenile wood formation in Norway spruce. Wood and Fiber Science 26(1), 152–167.

Larson, P. R. (1969). Wood formation and the concept of wood quality. Bulletin No. 74. New Haven, CT: Yale University, School of Forestry. 54 p., 1–54.

Le Guen, M.-J. Newman, R. H. Fernyhough, A. Hill, S. J. & Staiger, M. P. (2016). Correlations Between the Physiochemical Characteristics of Plant Fibres and Their Mechanical Properties. In Natural Fibres: Advances in Science and Technology Towards Industrial Applications (pp. 35–47). Springer.

Lehto, T. Lavola, A. Julkunen-Tiitto, R. & Aphalo, P. J. (2004). Boron retranslocation in Scots pine and Norway spruce. Tree Physiology 24(9), 1011-1017.

Lehto, Ruuhola, T. & Dell, B. (2010). Boron in forest trees and forest ecosystems. Forest Ecology and Management 260(12), 2053–2069.

Lehto, T. & Mälkönen, E. (1994). Effects of liming and boron fertilization on boron uptake of Picea abies. Plant and Soil 163(1), 55–64.

Li, X. W. Liu, J. Y. Fang, J. Tao, L. Shen, R. F. Li, Y. L. Xiao, H. D. Feng, Y. M. Wen, H. X. & Guan, J. H. (2017). Boron supply enhances aluminum tolerance in root border cells of pea (*Pisum sativum*) by interacting with cell wall pectins. Frontiers in Plant Science 8, 742.

Liakopoulos, G. Stavrianakou, S. Filippou, M. Fasseas, C. Tsadilas, C. Drossopoulos, I. & Karabourniotis, G. (2005). Boron remobilization at low boron supply in olive (*Olea europaea*) in relation to leaf and phloem mannitol concentrations. Tree Physiology 25(2), 157–165.

Linder, S. (1995). Foliar analysis for detecting and correcting nutrient imbalances in Norway spruce. Ecological Bulletins 178–190.

Lindström, H. (1996). Basic density in Norway spruce. Part I. A literature review. Wood and Fiber Science, 28(1), 15–27.

Lindström, H. (1997). Fiber length, tracheid diameter, and latewood percentage in Norway spruce: Development from pith outward. Wood and Fiber Science 29(1), 21–34.

Lundqvist, S.-O. Grahn, T. & Hedenberg, Ö. (2005). Models for fibre dimensions in different softwood species. Simulation and comparison of within and between tree variations for Norway and Sitka spruce, Scots and Loblolly pine. Proceedings IUFRO Conference, Auckland, New Zealand.

Macdonald, E. & Hubert, J. (2002). A review of the effects of silviculture on timber quality of Sitka spruce. Forestry 75(2), 107–138.

Maguire, D. A. Johnston, S. R., & Cahill, J. (1999). Predicting branch diameters on second-growth Douglas-fir from tree-level descriptors. Canadian Journal of Forest Research 29(12), 1829–1840.

Mäkinen, H. & Hein, S. (2006). Effect of wide spacing on increment and branch properties of young Norway spruce. European Journal of Forest Research 125(3), 239–248.

Mäkinen, H. Jaakkola, T. Piispanen, R. & Saranpää, P. (2007). Predicting wood and tracheid properties of Norway spruce. Forest Ecology and Management 241(1–3), 175–188.

Mäkinen, H. Saranpää, P. & Linder, S. (2002a). Effect of growth rate on fibre characteristics in Norway spruce (*Picea abies* (L.) Karst.). Holzforschung, 56(5), 449–460.

Mäkinen, H. Saranpää, P. & Linder, S. (2002b). Wood-density variation of Norway spruce in relation to nutrient optimization and fibre dimensions. Canadian Journal of Forest Research 32(2), 185–194.

Matthes, M. S. Robil, J. M. & McSteen, P. (2020). From element to development: The power of the essential micronutrient boron to shape morphological processes in plants. Journal of Experimental Botany 71(5), 1681–1693.

Mengel, K. Kirkby, E. A. Kosegarten, H. & Appel, T. (2001). Boron. In Principles of plant nutrition (pp. 621–638). Springer.

Miwa, K. & Fujiwara, T. (2010). Boron transport in plants: Co-ordinated regulation of transporters. Annals of Botany 105(7), 1103–1108.

Molteberg, D. & Høibø, O. (2006). Development and variation of wood density, kraft pulp yield and fibre dimensions in young Norway spruce (*Picea abies*). Wood Science and Technology 40(3), 173–189.

Möttönen, M. Lehto, T. & Aphalo, P. J. (2001). Growth dynamics and mycorrhizas of Norway spruce (*Picea abies*) seedlings in relation to boron supply. Trees 15(6), 319–326.

Möttönen, M. Lehto, T. Rita, H. & Aphalo, P. J. (2005). Recovery of Norway spruce (*Picea abies*) seedlings from repeated drought as affected by boron nutrition. Trees 19(2), 213–223.

Nadeem, F. Farooq, M. Nawaz, A. & Ahmad, R. (2019). Boron improves productivity and profitability of bread wheat under zero and plough tillage on alkaline calcareous soil. Field Crops Research 239, 1–9.

Olesen, P. O. (1982). The effect of cyclophysis on tracheid width and basic density in Norway spruce. For Tree Improv Arbor Horsholm 15, 1–80.

Ozanne, C. M. Anhuf, D. Boulter, S. L. Keller, M. Kitching, R. L. Körner, C. Meinzer, F. C. Mitchell, A. W. Nakashizuka, T. & Dias, P. S. (2003). Biodiversity meets the atmosphere: A global view of forest canopies. Science 301(5630), 183–186.

Peltola, H. Kellomäki, S. Hassinen, A. & Granander, M. (2000). Mechanical stability of Scots pine, Norway spruce and birch: An analysis of tree-pulling experiments in Finland. Forest Ecology and Management 135(1–3), 143–153.

Pfister, O. Wallentin, C. Nilsson, U. & Ekö, P.-M. (2007). Effects of wide spacing and thinning strategies on wood quality in Norway spruce (*Picea abies*) stands in southern Sweden. Scandinavian Journal of Forest Research 22(4), 333–343.

Prabagar, S. Hodson, M. J. & Evans, D. E. (2011). Silicon amelioration of aluminium toxicity and cell death in suspension cultures of Norway spruce (*Picea abies* (L.) Karst.). Environmental and Experimental Botany 70(2–3), 266–276.

Riikonen, J. Lehto, T. & Rikala, R. (2013). Effects of boron fertilization in the nursery or after planting on the performance of Norway spruce seedlings on boron-poor sites. New Forests 44(5), 671–685.

Saarsalmi, A. & Mälkönen, E. (2001). Forest fertilization research in Finland: A literature review. Scandinavian Journal of Forest Research 16(6), 514–535.

Saarsalmi, A. & Tamminen, P. (2005). Boron, phosporus and nitrogen fertilization in Norway spruce stands suffering from growth disturbances. Silva Fennica 39(3)

Sarén, M.-P. Serimaa, R. Andersson, S. Saranpää, P. Keckes, J. & Fratzl, P. (2004). Effect of growth rate on mean microfibril angle and cross-sectional shape of tracheids of Norway spruce. Trees 18(3), 354–362.

Schon, M. K. & Blevins, D. G. (1990). Foliar boron applications increase the final number of branches and pods on branches of field-grown soybeans. Plant Physiology 92(3), 602–607.

Setiawan, N. N. Vanhellemont, M. Baeten, L. Dillen, M. & Verheyen, K. (2014). The effects of local neighbourhood diversity on pest and disease damage of trees in a young experimental forest. Forest Ecology and Management 334, 1–9.

Shmulsky, R. & Jones, P. D. (2019). Forest products and wood science: An introduction. John Wiley & Sons.

Shuman, L. M. (1998). Micronutrient fertilizers. Journal of Crop Production, 1(2), 165–195.

Sigurdsson, B. D. Medhurst, J. L. Wallin, G. Eggertsson, O. & Linder, S. (2013). Growth of mature boreal Norway spruce was not affected by elevated [CO_2] and/or air temperature unless nutrient availability was improved. Tree Physiology 33(11), 1192–1205.

Stark, N. M. & Rowlands, R. E. (2003). Effects of wood fiber characteristics on mechanical properties of wood/polypropylene composites. Wood and Fiber Science Vol. 35, No. 2 (2003): Pages 167-174.

Stone, E. L. (1990). Boron deficiency and excess in forest trees: A review. Forest Ecology and Management 37(1–3), 49–75.

Tamminen, P. & Tomppo, E. (2008). Finnish forest soils [Working Paper]. Finnish Forest Research Institute. http://www.metla.fi/julkaisut/workingpapers/2008/mwp100.htm

Tanaka, M. & Fujiwara, T. (2008). Physiological roles and transport mechanisms of boron: Perspectives from plants. Pflügers Archiv-European Journal of Physiology 456(4), 671–677.

Tyrväinen, J. (1995). Wood and fiber properties of Norway spruce and its suitability for thermomechanical pulping.

Van den Driessche, R. (1974). Prediction of mineral nutrient status of trees by foliar analysis. The Botanical Review 40(3), 347–394.

Van Miegroet, H. Norby, R. J. & Tschaplinski, T. J. (1994). Nitrogen fertilization strategies in a short-rotation sycamore plantation. Forest Ecology and Management 64(1), 13–24.

Vartiainen, A. Effects of boron fertilization on Norway spruce growth. M.Sc. thesis, UEF, School of Forest Sciences. In preparation.

Voxeur, A. & Fry, S. C. (2014). Glycosylinositol phosphorylceramides from Rosa cell cultures are boron-bridged in the plasma membrane and form complexes with rhamnogalacturonan II. The Plant Journal 79(1), 139–149.

Wang, N. Yang, C. Pan, Z. Liu, Y. & Peng, S. (2015). Boron deficiency in woody plants: Various responses and tolerance mechanisms. Frontiers in Plant Science 6, 916.

Wodzicki, T. J. (2001). Natural factors affecting wood structure. Wood Science and Technology 35(1–2), 5–26.

Wojcik, P. & Wojcik, M. (2003). Effects of boron fertilization on Conference'pear tree vigor, nutrition, and fruit yield and storability. Plant and Soil 256(2), 413–421.

Yan, L. Riaz, M. Wu, X. Du, C. Liu, Y. Lv, B. & Jiang, C. (2018). Boron inhibits aluminum-induced toxicity to citrus by stimulating antioxidant enzyme activity. Journal of Environmental Science and Health Part C, 36(3), 145–163.

Yoshinari, A. & Takano, J. (2017). Insights into the mechanisms underlying boron homeostasis in plants. Frontiers in Plant Science 8, 1951.

Zobel, B. J. & Van Buijtenen, J. P. (2012). Wood variation: Its causes and control. Springer Science & Business Media.

Zubizarreta Gerendiain, A. Peltola, H. & Pulkkinen, P. (2009). Growth and wood property traits in narrow crowned Norway spruce (*Picea abies* f. pendula) clones grown in southern Finland. Silva Fennica 43(3), 369-382.

Zubizarreta Gerendiain, A. Peltola, H. Pulkkinen, P. Ikonen, V. P. & Jaatinen, R. (2008). Differences in growth and wood properties between narrow and normal crowned types of Norway spruce grown at narrow spacing in southern Finland. Silva Fennica 42 (2008): 3.