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Growth limitation of trees and carbon balance of the vegetation in the treeline zone in north eastern Lapland

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The aim of the thesis was to study the factors limiting tree growth at treeline in Värriö and to investigate how reindeer grazing affects the vegetation and carbon balance of the treeline environment.

The factors limiting tree growth in the treeline ecotone were studied based on two hypotheses, the sink limitation hypothesis and the resource limitation hypothesis. Resource limitation included both carbon and nitrogen limitation. Three different manipulation treatments; debudding, defoliation and fertilization; were performed on treeline trees in Värriö to test the hypotheses. According to the results tree growth in Värriö is clearly restricted by resources. The factors supporting the resource limitation hypothesis were increased growth due to fertilization and debudding treatments and decreased stem diameter growth due to the defoliation treatment. Also, sapflow was not down-regulated due to debudding treatment. There was some increase (p=0.054) due to fertilization treatment in carbon isotope ratio, which furthermore supports the resource limitation hypothesis.

Grazing did have an effect on the amount of carbon bind to vegetation, as the biomass of lichens was decreased due to grazing by 85 %. There were also changes in species composition due to grazing. Net carbon exchange correlated with the dwarf shrub cover, but the dwarf shrub cover did not change due to grazing. Overall, grazing did not affect the carbon fluxes on the area.

Overall, the results showed that the tree growth in the study site is restricted by resources. Grazing affects the species composition and vegetation carbon stocks, but not on productivity or soil carbon stocks. Both treeline rise and increase in the abundance of the trees in the treeline would affect significantly on the carbons stocks of these ecosystems. Since reindeers might affect the regeneration of treeline, future research on the interactions between grazing and treeline progression would be important.

Keywords: sink, source, resource, reindeer, grazing

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To my grandmother, who also felt that the days were too short to learn and experience all the things you wanted in life.

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Espoo,

Sanna Susiluoto

LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, which are referred to by their Roman numerals I-III. The articles are reprinted with the kind permission of the publishers.

I	Susiluoto, S., Perämäki, M., Nikinmaa, E. & Berninger, F. 2007. Effects of sink removal on transpiration at the treeline: Implications of the growth limitation hypothesis. Environmental and Experimental Botany 60 (3): 334-339. doi: 10.1016/j.envexpbot.2006.12.015
II	Susiluoto, S., Hilasvuori, E. & Berninger, F. 2010. Testing the growth limitation hypothesis for subarctic scots pine. Journal of Ecology 98: 1186-1195. doi: 10.1111/j.1365-2745.2010.01684.x
III	Susiluoto, S. Rasilo, T., Pumpanen, J. & Berninger, F. 2008. Effects of grazing on the vegetation structure and carbon dioxide exchange of a Fennoscandian fell ecosystem. Arctic, Antarctic and Alpine Research 40 (2): 422-431. doi: 10.1657/1523-0430(07-035)[SUSILUOTO]2.0.CO;2

Sannamaija Susiluoto participated in planning the research in a following manner:

Article I: I was responsible for data collection, data analysis, modeling, literature searches and was the main author the article. Martti Perämäki, Eero Nikinmaa and Frank Berninger advised in modeling, participated in planning the research and in discussions and commented on the manuscript. Martti Perämäki also helped me with the analyses. Carbohydrate analyses were done in University of Basel, Switzerland by Dr. Günter Hoch.

Article II: I was responsible for data collection, data analysis (except for the isotope data and measuring the tree ring data that was done by Emmi Hilasvuori), modeling, literature searches and was the main author the article. Frank Berninger advised in modeling, participated in planning the research and he and Emmi Hilasvuori participated in discussions and commented on the manuscript. Carbohydrate analyses were done in University of Basel, Switzerland by Dr. Günter Hoch.

Article III: I was responsible for the collection of all the other data, except for the soil biomass data and the data for analyzing soil autotrophic and heterotrophic respiration that was collected and analyzed by Terhi Rasilo. I was responsible for modeling, literature searches and was the main author the article. Jukka Pumpanen and Frank Berninger advised in modeling, participated in planning the research and in discussions and commented on the manuscript.

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DEFINITIONS

ER = Ecosystem respiration

GPP = Gross primary production

H = Transpiration

NEE = Net ecosystem exchange

NSC = Non-structural carbohydrates

P_R = relative change in respiration rate R

Q_{10} = The relative increase in photosynthetic rate when temperature is increased by 10 °C

α = The capacity of photosynthesis

τ = The time constant of photosynthetic capacity changes relative to temperature

$\delta^{13}C$ = Carbon isotope ratio

A tree is defined as a woody plant that grows height at least two (Kullman 2003) or three meters (Körner 1999) and has a clear main stem (Körner 1999). Actual treeline is considered to start where the closed forest ends (Körner 1999). The upper limit of treeline is the line connecting the highest growing individuals of trees that fulfill the definition of a tree (Kullman 2003). Some individuals of trees can occur above treeline, but there they do not grow tall enough or have a straight growth form and occur as Krummholz trees. The upper limit of the occurrence of certain tree species, regardless of the growth form of the individuals, is called tree species limit (Körner 1999). Arctic treeline includes large areas around the northern hemisphere, whereas alpine treeline can occur anywhere in the world where land formations are high enough to limit tree growth.

1 INTRODUCTION

Temperature rise near the poles due to human activities is expected to be 1.1 to 5.5 degrees during next hundreds of years (scenarios A2, B1 and B2; ACIA 2007) and increases in the temperature will be larger during winter than during summer (ACIA 2007; IPCC 2007). Arctic and boreal ecosystems cover about 40 % of the Earth's vegetated surface and contain about one third of the carbon (C) stored in terrestrial ecosystems. Around 11 % of this C is stored in tundra ecosystems (McGuire et al. 1995). Rising temperatures will affect the vegetation composition, nutrient mineralization rates and biomass of the arctic and boreal zones (ACIA 2007). In addition, rising CO_2 concentrations and deposition of reactive forms of nitrogen can affect vegetation growth and nutrient mineralization rates in cases where trees in the cold climate are carbon or nitrogen limited (Schulze et al. 1994; Weih & Karlsson 1999; Mack et al. 2004). These processes have a substantial effect on the amount of carbon stored in soil and in the above ground biomass. Shifts in treeline position are especially important since they increase considerably the total living biomass of the zone (ACIA 2007). Grazing at the interface of the taiga and tundra by large ungulates, especially reindeers and their wild relative, the caribous, has a large local economic and spiritual importance for the local inhabitants. Reindeer grazing can strongly influence the vegetation composition (e .g. Olofsson et al. 2001) and nutrient mineralization rates (e.g. Stark et al. 2000; Stark et al. 2002) of arctic ecosystems.

Carbon dioxide concentrations in the air have risen from pre-industrial value of 280 ppm to over 390 ppm in 2012, and are continuing to rise (current results from Mauna Loa can be found from: http://www.esrl.noaa.gov/gmd/ccgg/trends/ and similar trends worldwide). Arctic tundra ecosystems were thought to be net sinks of carbon (Aurela et al. 2001; Aurela et al. 2004), though at least locally some ecosystems seem to be carbon sources (Grulke et al. 1990; Oechel et al. 1993; Ciais et al. 1995). Increasing temperature is expected to increase the loss of carbon from these ecosystems due to higher respiration rates and it is probable, that due to the effects of climate change, some areas that have previously acted as sinks of carbon, will turn into (or have already become) sources of C (Billings et al. 1982; Oechel et al. 1993).

Apart from temperature, nitrogen is said to limit the productivity of arctic boreal ecosystems. Humans have affected the global nitrogen cycle by using fossil fuels and fertilizers (e.g. Galloway & Cowling 2002). Over one third of the nitrous oxide emissions come from anthropogenic sources, primarily from agriculture (IPCC 2007). Increased atmospheric N depositions can affect species composition (Vitousek et al. 1997; Press et al. 1998), carbon uptake and storage in plants (Shaver et al. 1992) and plant productivity in ecosystems (Vitousek & Howarth 1991; Vitousek et al. 1997; Rustad et al. 2001). Climate warming is expected to stimulate N mineralization (Nadelhoffer et al. 1991; Rustad et al. 2001) by improving substrate quality for decomposers and by increasing the decomposition rate (Chapin & Bledshoe 1991).

1.1 Carbon balance in the treeline zone

Carbon stocks in any ecosystem can be divided into living biomass and dead organic material derived from the living biomass. Carbon accumulation into an ecosystem is determined primarily by the difference between ecosystem photosynthesis and respiration rates although small additional losses may often occur as dissolved organic carbon in the drainage water. There are several different ecosystem types in arctic and alpine environments and so the C stocks in vegetation may vary considerably. Vegetation in these ecosystems is usually very heterogeneous, forming as a mosaic of vegetation patches (Fletcher et al. 2010), which makes the estimations of carbon pools and fluxes more complicated. Main environmental factors affecting on the vegetation composition are temperature, humidity, slope, soil detritus and texture, but impacts due to human and animal activity can also have an important role. According to the IPCC report (IPCC 2007), about 11.6 x 10^6 km^2 of the global land area is alpine tundra. Plants of the alpine tundra contain 5.9 Pg C carbon, which is 1 % of the total carbon contained in the vegetation as a whole (IPCC 2007). The estimate of the amount of organic carbon in the northern tundra soils varies between 134 Pg and over 1600 Pg, the largest pools being in the permafrost region, which is about 50 % of the carbon in the soils in the world (IPCC 2007; Tarnocai et al. 2009).

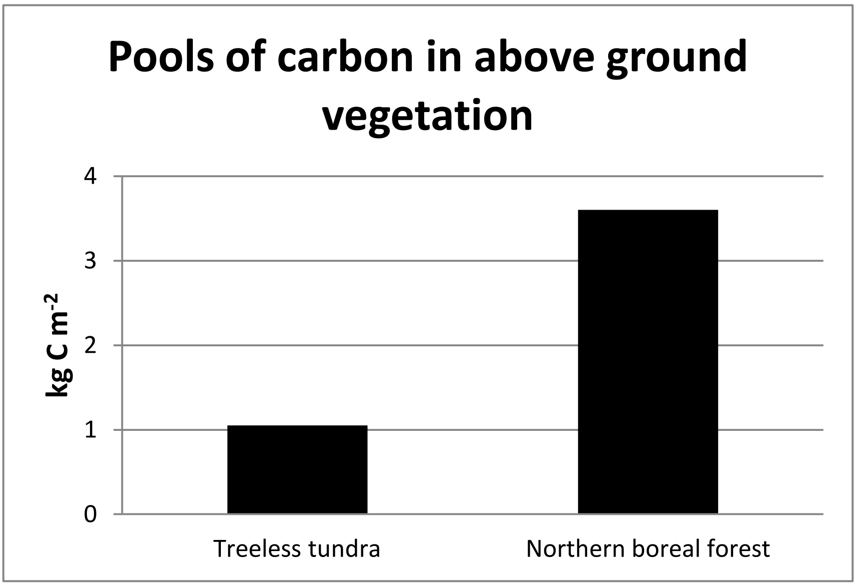

Figure 1. Carbon pools in above ground vegetation according to Miller et al. (1983).

In this thesis, I have concentrated in the ecosystems that occur on mineral soil, which can be found in and near the treeline around arctic and also in northern alpine sites (Lescop-Sinclair & Payette 1995; Heikkinen et al. 2004). Vegetation of these ecosystems is typically dominated by dwarf shrubs like Betulaceae (*B. glandulosa, B. nana, Alnus crispa*), Salicaceae (*Salix* sp.) and Ericaceae (*Cassiope* sp., *Vaccinium* sp., *Arctostaphylos* sp., *Rhododendron* sp. and *Loiseleuria* sp.), Empetraceae (*Empetrum* sp.) and Rosaceae (*Dryas* sp., *Rosa* sp.). Also mosses (e.g. *Dicranum* sp., *Polytrichum* sp., *Hylocomnium* sp., *Aulacomnium* sp. and *Pleurozium* sp.), lichens (e.g. *Cladina* sp., *Cladonia* sp. and *Cetraria* sp.) and graminoids (Poeaceae, Cyperaceae) are common (e.g. Lescop-Sinclair & Payette 1995; Sveinbjörnsson et al. 1995; Christensen et al. 1997; Hobbie & Chapin 1998; Jones et al. 1998; Illeris & Jonasson 1999). Carbon bound in ground vegetation varies in these ecosystems between 90-1100 g C m^{-2} (Norin & Ignatenko 1975; Østbye et al. 1975; Vassiljevskaya et al. 1975; Christensen et al. 1997; Stark et al. 2000; Stark & Grellmann 2002; Heikkinen et al. 2004; Olofsson et al. 2004) and in soils between 2-24 kg m^{-2} (Stark et al. 2000; Heikkinen et al. 2004; Loomis et al. 2006). The absence or presence of trees does not seem to affect the amount of carbon in the soil (Berninger et al. Manuscript).

Arctic and alpine treelines are usually formed by spruces (*Picea* sp.), pines (*Pinus* sp.), birches (*Betula* sp.), larches (*Larix* sp.), Chosenia (*Chosenia* sp.) or poplars (*Populus* sp.) (Sveinbjörnsson 1992). Sparse Krummholz forming trees and willows (*Salix* sp.) can grow above the treeline. As treeline is a transition zone, the carbon stocks bound in tree biomass varies greatly. Values between 56 and 1500 g C m^{-2} are reported (Kallio 1975; Norin & Ignatenko 1975; Østbye et al. 1975).

Basically the photosynthetic capacity of alpine and arctic plants may often be as high as that of lowland plants (Körner 1999). The reason for this is that the rate of photosynthesis is not very sensitive to temperature during growing season and it acclimates rapidly to changing temperatures (Häsler 1982; Grace et al. 2002). The main environmental factor leading to a lower net carbon gain of arctic plants is the short duration the growing season and to a lesser degree the low temperatures during the growing season. James et al. (1994) noted that even though the photosynthetic rates of treeline trees in the middle of the growing season were similar to valley trees, their rates of photosynthesis were only half of the valley trees in June both in old and newly formed needles. In the arctic environments CO_2 fluxes have a strong seasonal cycle (e.g. Laurila et al. 2001). It seems that in the early spring and late autumn, when temperatures are low, photoinhibition can decrease photosynthetic performance significantly (Öquist & Huner 1991; James et al. 1994). The length of the photosynthetically active period is extremely important at the treeline (Öquist & Huner 1991; Grace et al. 2002). As the growing season is short at the treeline, just a few extra warm or cold days in spring or autumn can affect the annual photosynthetic performance substantially (Grace et al. 2002). Also, increased supply of available nitrogen could enhance the effect of temperature on tree growth (Weih & Karlsson 1999), as the biomass productivity / leaf nitrogen of high altitude seedlings is improved in higher temperatures. Respiration is much more temperature sensitive than photosynthesis (e.g. Higgins & Spomer 1976; Atkin & Tjoelker 2003) and so warming might still reduce the net uptake of carbon by the plant. Respiration costs during winter are also suggested to be one possible factor restricting at least seedling survival at treeline, as the temperatures under snow can stay close to zero and tissues continue respiring albeit at a low rate (Karlsson & Weih 2001).

Mosses and lichens contain relatively large amount of carbon and nutrients in arctic ecosystems (Wielgolaski et al. 1981; Shaver & Chapin 1991). In contrast to other plants, mosses and lichens do not have living biomass below ground and they are able to survive without water for a long time. Lichens and mosses are poikilohydric life forms, which dry out rapidly when air humidity is low and their rate of photosynthesis depends mostly on their water content. Even when the water content of lichens is optimal for photosynthesis, their photosynthetic rate is low compared to vascular plants. Maximal rates of lichen photosynthesis have found to be less than 1 mg CO_2 g^{-1} s^{-1} (Kärenlampi 1970; Groulx & Lechowicz 1987). However, as lichen biomass in northern Fennoscandia can be as high as 500 g m^{-2} (Eriksson & Raunistola 1993), lichens can have an important effect on the carbon exchange rate of these ecosystems. Also Kallio (1975) stated that the most important plant group responsible for atmospheric nitrogen fixation in dry arctic ecosystems in Kevo in Finland, are lichens. Lichens (*Nephroma arcticum* and *Stereocaulon paschale*) were able to fix nitrogen at rates between 5-168 mg m^{-2} yr^{-1} (of land area, when lichen coverage is 100 %) in low alpine ecosystems in Kevo (Kallio 1975). Lichen biomass has been found to decrease due to experimental warming as a consequence of increased shrub coverage (Press et al. 1998; Cornelissen et al. 2001; Hollister et al. 2005; Walker et al. 2006; Hudson & Henry 2010), which might have an important effect on the nitrogen fixation of these ecosystems. They also respond negatively to increased nutritional status of soil since they are progressively outcompeted by other, more rapidly growing, plants (Press et al. 1998).

Soil respiration, which is the second largest flux of carbon between an ecosystem and atmosphere after gross primary production (GPP), results from the activity of soil organisms, roots and mycorrhizae (Raich & Schlesinger 1992). According to Wohlfahrt et al. (2005) and Grogan & Jonasson (2005), 50-70 % of the total ecosystem respiration in alpine and arctic ecosystems can be attributed to the soil. Soil respiration is known to be temperature sensitive (Raich & Schlesinger 1992) and its annual gain is also strongly determined by the length of the growing season (Baptist & Choler 2008). Also, soil moisture affects the soil respiration in areas, where soils experience occasional or continuous drought (e.g. Illeris & Jonasson 1999).

Even though soil respiration during winter is only a fraction of the summer values, it can nevertheless be important to measure due to the extended winter period in the arctic areas. According to Morgner et al. (2010) and Elberling & Brandt (2003), soil respiration values during winter are highly dependent on the soil temperature and temperature under snow can be quite close to zero independent of the air temperature. Eberling & Brandt (2003) found out that soil effluxes fluctuated between 0.2-1.1 µmol CO_2 m^{-2} s^{-1} and that more than 82 % of the variation could be explained by near-surface temperatures alone. Fahnestock et al. (1998) found winter effluxes to be 0.013 µmol CO_2 m^{-2} s^{-1} on dry tundra in Alaska during winter. Also, Steenberg-Larsen et al. (2007) found substantial levels of photosynthesis under snow during winter in their study in Abisco, Sweden. During October and November they found photosynthesis fluxes of 2-8 g CO_2 (C) m^{-2} $month^{-1}$, which was 3-5 % of the total annual photosynthesis (both months combined). The photosynthetic rate on April and May accounted for 12-14 % of the annual photosynthesis. According to Wieser (1997), *Pinus cembra* growing in alpine timberline did not lose a significant amount of carbon during winter months, as the loss equaled the photosynthetic production of just one or two warm spring days. However, several studies suggest that with thick snow cover, the amount of soil respiration during winter can be as high as 15-33 % of the annual cumulative soil respiration in Arctic ecosystems (Aurela 2005; Steenberg Larsen et al. 2007; Morgner et al. 2010).

1.1.1 The role of nitrogen in the arctic and alpine ecosystems

Nitrogen supply has been found to restrict plant growth in most terrestrial ecosystems. In arctic and alpine ecosystems its role is especially important, as cold soils restrict nitrogen mineralization rates and, therefore, nitrogen is immobilized in organic matter (McKendrick et al. 1980; Moore 1984; Sveinbjörnsson et al. 1995; Grace et al. 2002). It has been found that 94-99 % of nitrogen in arctic ecosystems is bound in soil organic matter (Bunnell et al. 1975; Bunnell 1981). Also, soil organic matter quality is poorer in treeline sites than below the treeline (Nadelhoffer et al. 1991; Loomis et al. 2006). Mineralization and nitrification rates in the soil are determined by temperature, aeration, moisture, acidity and chemical and physical quality of plant litter (Lukac & Godbold 2011). Plants are able to use nitrogen in both as nitrate and ammonium, but they seem to slightly prefer NO_3^- over NH_4^- when growing in mineral soil (Schulz et al. 2011). Due to this, the production of nitrates in arctic soils can affect the species composition through the better competitive ability of the plants that can metabolize nitrate-N (Nadelhoffer et al. 1991). Though, it has been found that plants can also use organic amino acids produced by microbes (Schimel & Bennett 2004). Nitrogen is also fixed from the atmosphere by soil micro-organisms (e.g. Azotobacter, Cyanobacteria, Rhizobia and also some lichens (Chapin & Bledshoe 1991; Lukac & Godbold 2011)). As N_2 fixation rates are usually less than 10 % of the annual N uptake by plants in arctic ecosystems, release of N due to the decomposition process is the dominant source of N for plant growth (Chapin & Bledshoe 1991).

Dormann & Woodin (2002) stated in their meta-analysis that nutrient availability seems to be the main factor limiting productivity of vascular plants in arctic ecosystems, and their results are supported by various other studies (e.g. McKendrick et al. 1980; Shaver & Chapin 1986; Havström et al. 1993; Press et al. 1998; Jonasson et al. 1999; van Wijk et al. 2003; Mack et al. 2004), though locally there may be also other important factors (Havström et al. 1993). In many areas permafrost underlies arctic vegetation. It is suggested that the effect of climate warming on soil temperatures and due to this to mineralization rate would be slower in these areas, as the permafrost layers cool down the soil (Shaver & Jonasson 1999). The proportion of nitrogen bound to microbial biomass does not appear to differ between forest and treeline sites (Loomis et al. 2006), but soils in treeline environment are often colder (on average) than in forest. In addition to slowing down the mineralization rates (e.g. Sveinbjörnsson et al. 1995; Loomis et al. 2006), cold soils can also slow down the growth rates of fine roots (Tranquillini 1979). Also, in some treeline sites moisture can have an important role in the nitrogen cycle (Illeris & Jonasson 1999; Loomis et al. 2006). During early spring, N bound in soil microbial biomass is released in a large flush, apparently forming an important pool for plants (Brooks et al. 1998; Lipson et al. 1999; Lipson et al. 2000).

1.2 Theories about the factors that limit tree growth at treeline

Understanding the factors that limit tree growth at the treeline is essential to estimate the future changes in carbon stocks and the possible future threats to these ecosystems. If the tree growth is increased or the tree line moves upwards, trees will have a significant effect on the quantity of carbon bound into biomass.

Understanding future (and past) shifts of the treeline and the associated changes in carbon balance requires knowledge of the underlying causes for treeline formation. There are several different theories to explain the location of treelines. The most discussed theories are: (i) the carbon (or source, which usually includes nitrogen) limitation hypothesis (Stevens & Fox 1991; Nicolussi et al. 1995; Körner 1999; Sveinbjörnsson 2000; van Felten et al. 2007; Li et al. 2008b) and (ii) the sink limitation hypothesis (e.g. Körner 1999; Li et al. 2002; Körner

2003; Handa et al. 2006; Danby & Hik 2007). Other plausible theories include (iii) the nitrogen limitation hypothesis (Sveinbjörnsson et al. 1992; Schulze et al. 1994; Sveinbjörnsson et al. 1995), (iv) frost damages (Körner 1999; Danby & Hik 2007), (v) disturbances (Cullen et al. 2001), (vi) water stress (Barber et al. 2000; D'Arrigo et al. 2004; Li et al. 2004; Wang et al. 2006), (vii) limitations to reproduction (Black & Bliss 1980; Payette et al. 1982; Lescop-Sinclair & Payette 1995; Körner 1999) and (viii) seedling survival (Smith et al. 2003; Smith et al. 2009).

Disturbances, e.g. due to heavy biomass losses during winter can occasionally have an important effect on the carbon balance of trees that are normally limited by other factors. At least in some areas trees may lose a large proportion of their biomass during winter due to heavy snow pack (Wardle 1977; Norton & Schönenberger 1984; Körner 1999), which can certainly affect their carbon and nitrogen balance.

I concentrate here on three hypotheses, which are sink limitation, carbon limitation and nitrogen limitation hypotheses. As carbon and nitrogen limitations are closely linked, they will be discussed together as a resource limitation hypothesis.

According to the sink limitation hypothesis, tree growth is slowed down as low temperatures prevent the cell division, maturation and elongation (Körner 1999). Trees are able to produce sugars and amino acids, but they are unable to use them for growth of new tissues (Körner 1999). As a consequence an accumulation of carbohydrates occurs since the rate at which glucose is used in biosynthetic processes is slowed down more by low temperatures than the rate of net photosynthesis (Grace et al. 2002). Due to this, the growth decreases and the products of photosynthesis may accumulate in the tissues of trees as non-structural carbohydrates. In support of this hypothesis, non-structural carbohydrate concentrations in multiple functional parts of trees are often observed to be higher in trees growing at the treeline compared to lowland sites (Hoch et al. 2002; Hoch & Körner 2003; Hoch & Körner 2009). It has been suggested that there is a minimum average growing season temperature (5.5-7.5 °C), below which carbon sinks start to control the growth over carbon sources (Körner 1999; Körner 2004).

The carbon limitation hypothesis assumes that trees are not able to acquire as much photosynthates as they require for respiration, storage and growth during the short growing season (Stevens & Fox 1991). This effect is exacerbated when trees get older, as the proportion of the active biomass to the total biomass declines (Vanninen et al. 1996; Delagrange et al. 2004) and it seems that the tree size is the main factor affecting the allocation patterns on the whole tree basis (Delagrange et al. 2004). As the proportion of woody structures increases with age in trees, there is less photosynthetic tissues compared to the total biomass. Due to it the growth becomes relatively less effective with increasing plant size (Stevens & Fox 1991; Delagrange et al. 2004) and it is possible that the accumulation of woody structures limits growth and survival of trees at treeline (Stevens & Fox 1991).

Nitrogen is known to be a limiting factor in many ecosystems, though it has rarely (though sometimes, e.g. Sveinbjörnsson et al. 1992; Weih & Karlsson 1999) been considered to limit tree growth at treeline. According to the nitrogen limitation hypothesis the acquired nitrogen per active biomass is lower than required for maximum growth. Due to this the photosynthetic capacity and leaf area are limited (Coll et al. 2011). Nitrogen and carbon limitations are linked, as nitrogen is stored in photosynthetically active parts mostly in a form of Rubisco, which catalyzes the initial step of the carbon reduction and oxidation cycles (Millard et al. 2007). It is important to note that the limitations in carbon and nitrogen are closely linked.

1.3 Vegetation changes in alpine and arctic ecosystems due to climate change

Climate warming has been found to induce plant growth in many areas (Myneni et al. 1997; Hollister et al. 2005), and especially shrub coverage has been observed to increase with increasing temperatures (Havström et al. 1993; Chapin et al. 1995; Harte & Shaw 1995; Hobbie & Chapin 1998; Sturm et al. 2001; Dormann & Woodin 2002; Jónsdóttir et al. 2005; Walker et al. 2006; Wilson & Nilsson 2009). Also biomass of graminoids is known to increase due to experimental warming in some cases (Hollister et al. 2005; Walker et al. 2006), but not in all (Wilson & Nilsson 2009). Even though plants often seem to respond to artificial temperature increase by increasing biomass production (e.g. Jonasson et al. 1999; Jónsdóttir et al. 2005), this does not occur always (e.g. Jónsdóttir et al. 2005). At least in Alaska, there seem to be tundra ecosystems where temperature rise itself does not affect the growth or nitrogen uptake (e.g. Hobbie & Chapin 1998). Also Jónsdóttir et al. (2005) pointed out that plant growth in tundra communities in Iceland seems to increase due to warming only in more nutrient rich communities, whereas in nutrient poor communities the growth does not respond to experimental warming. Often biomass increase due to increased temperature is significantly smaller than the increase due to nitrogen fertilization (van Wijk et al. 2003). This implies that growth in many cold ecosystems seems to be strongly nitrogen limited.

Nutrient addition and climate warming have somewhat parallel effects on vegetation. Nutrient addition has been often found not just to increase the total living biomass of arctic ecosystems (e.g. Shaver & Chapin 1986; Robinson et al. 1998; Shaver & Jonasson 1999) but also change the plant composition of the ecosystems, as some species are more responsive to increased nitrogen levels than others (van Wijk et al. 2003). Especially dwarf shrubs, like *Betula nana* (Shaver & Chapin 1986; Chapin et al. 1995; Shaver & Jonasson 1999; Bret-Harte et al. 2001; van Wijk et al. 2003; Mack et al. 2004) and grasses (Jonasson 1992; Parsons et al. 1995; Press et al. 1998; Graglia et al. 2001; van Wijk et al. 2003) benefit from increased amount of available nitrogen. Non-vascular plants (lichens, liverworts and mosses) seem to suffer the most from both nutrient addition and increased temperature (Jonasson 1992; Chapin et al. 1995; Press et al. 1998; Cornelissen et al. 2001; Graglia et al. 2001; van Wijk et al. 2003; Hollister et al. 2005; Walker et al. 2006). This is most likely due to increased shading by higher plants or their litter input (Cornelissen et al. 2001). This seems to occur in densely vegetated lower arctic ecosystems, but not in the more open and sparsely vegetated high arctic ecosystems (Cornelissen et al. 2001). Species diversity is also expected to decrease due to climate warming and fertilization in many arctic areas (Chapin et al. 1995; Press et al. 1998; Hollister et al. 2005; Walker et al. 2006), but not in all (Jónsdottir et al. 2005). Some results suggest that warming in the arctic results in the expansion of shrubs and leads to a short-term decline in other vascular plant diversity (Bret-Harte et al. 2001; Walker et al. 2006). The decrease in lichen and moss biomass seems to occur mostly due to increase in the biomass of other functional groups: in open canopy ecosystem, their biomass also increases (Jonasson 1992).

The effects of changes in the annual temperature differ depending on whether the rise occurs mainly as a rise in the winter temperatures (e.g. Bokhorst et al. 2008), growing season temperatures (Harte & Shaw 1995; Jonasson et al. 1999) or in the length of the growing season (e.g. Harte & Shaw 1995; Høye et al. 2007). All of these seem to have importance for the carbon balance in the arctic ecosystems. As photosynthesis acclimates rapidly to the prevailing temperatures (Körner 1999), increased growing season temperatures affect the ecosystem carbon balance mostly indirectly by increasing microbial activity and due to it, nutrient turnover (Nadelhoffer et al. 1992). Earlier onset of snow melting in spring is associated with a lengthening of the growing season (Høye et al. 2007). Temperature rise can have also a negative effect on the carbon balance of plants as increased temperatures cause higher respiration rates (Jones et al. 1998).

1.4 The role of ungulates, especially reindeers on vegetation structure in the treeline ecotone

Reindeer (*Rangifer tarandus* L.) herding is a traditional form of animal husbandry in Finnish Lapland. The numbers of reindeers were between 50 000 to 150 000 in Finland during 1840's until the 1950's (Bernes 1996) and in 2001 the numbers were around 187 000 animals (Jernsletten & Klokov 2002). Circumpolarly there are around 1,8 million reindeers in the world (Turi 2002). In northern Fennoscandia the traditional grazing system has been non-rotational system, where animals can graze freely in large areas called "paliskunta". Animal densities are low, about 1,5 animals km^{-2} in Finland (Turi 2002), but higher than most natural ungulate populations in tundra regions. Even though the numbers are low, reindeers have a large effect on the vegetation of the fjell ecosystems, as they graze there intensively during winters. Their main forage during winter time are lichens – which cover around 40 % of their food during that time and are essential to the reindeers over-winter survival (Warenberg et al. 1997). During winter, 10 000 reindeers use about 50 tons of lichens in a day (Bernes 1996).

Reindeer grazing has multiple effects on the vegetation of the fjell tops. First, they trample the vegetation while grazing. Secondly, they graze plants selectively. Also, reindeers fertilize the ground in the form of manure, which affect soil microbial activity, mineralization rates and organic matter quality (McKendrick et al. 1980; Pastor & Naiman 1992; Frank & Groffman 1998; Sirotnak & Huntly 2000). Zimov et al. (1995) has stated that trampling has also an important effect in transforming the tundra with low net primary production to more productive grassland. Also, grazing can affect the soil microclimate by increasing soil temperature (Olofsson et al. 2004) due to increased bare soil coverage (Olofsson et al. 2001) and by reductions of soil moisture (Väre et al. 1996)

2 AIMS OF THE STUDY

This study investigates components of carbon balance in treeline and tundra ecosystems in North Eastern Finland. The main aims were (i) to study factors influencing the position of the treeline and (ii) to investigate the influence of grazing on the vegetation and carbon balance.

For treeline changes I evaluate the importance of the different theories on treeline tree growth. The factors that control tree growth are discussed through two plausible theories, which are sink limitation and resource limitation theories. In my interpretation, resource limitation includes both carbon and nitrogen limitation, which are the two resources that most likely restrict the growth of treeline trees. For tundra vegetation we concentrate on the effects of reindeer grazing on the vegetation.

The main objectives of this study is to

1. Determine if tree growth at the treeline in Värriö is restricted by sink or resource limitation.

2. To estimate the amount of carbon bound in the living biomass in fjell top ecosystems in the sites

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3. To estimate the effects of reindeer grazing on the carbon balance via vegetation changes.

3 MATERIALS AND METHODS

3.1 Study sites and experiments

The experiments of the study were done in three fjells in Värriö nature park: Värriö I (67°44’24”N; 29°35’40”E) and Värriö II (67°43’37”N; 29°36’00”E) fjells are a part of a chain of five fjells in the nature park and the tops of the fjells are situated about 2 kilometers apart. Nuortti fjell (67°48’07”N; 29°39’28”E) is situated about 8 kilometers from Värriö I and is divided by a borderline between Finland and Russia. Due to this there is a reindeer fence built in the middle of the fjelltop to prevent reindeers crossing to Russian side. The Russian side of the fjell has been ungrazed since 1940’s when the reindeer fence was built (Väre et al. 1996; Stark et al. 2002), whereas the Finnish side is a traditional grazing area.

Figure 2. Measurement sites (green spots) in Värriö naturepark. (Source: Maastokarttarasteri 1 : 250 000 from Maanmittauslaitos, dated 18.1.2012. Map was done by ArcMap 10.1).

The treeline in the area of Värriö Nature Park is at about 470 m a.s.l. and it is formed by slow growing, scattered, Scots pines (*Pinus sylvestris*). In the treeline zone, there are no seedlings of Scots pine growing (pers. obs.) and the age of the treeline population is around 50 years. Below this zone, there is a zone of more densely growing mountain birches (*Betula pubescens* ssp. czerepanovii), with some scattered Scots pines growing between the birches.

The vegetation type in the top of the fjells in the area is dry tundra heath. The ground vegetation in the three fjells is formed mostly by lichens (e.g. *Cladina* sp. and *Cladonia* sp.), dwarf shrubs (*Empetrum nigrum, Vaccinium vitis-idaea, Vaccinium myrtillus, Arctostaphylos uva-ursi, Arctostaphylos alpinus*), mosses (e.g. *Dicranum* sp., *Polytrichum* sp., *Pleurozium schreberi*) and in lesser extent by some forbs (T*rientalis europea, Antennaria dioica, Solidago virgaurea, Hieracium alpinum, Linnaea borealis*), club mosses (*Lycopodium alpinum, Lycopodium annotinum*) and graminoids (e.g. *Deschampsia flexuosa, Juncus trifidus*).

Vegetation biomass, species coverage and carbon flux measurements were done on Nuortti and Värriö II fells; biomass and species coverage measurements on 2002 and carbon flux measurements on 2004. For the carbon flux measurements, 12 PP polypropene collars (diameter 20,3 cm) were permanently installed on soil on 2002 on each side of the reindeer fence on Nuortti and on Värriö II (36 collars in total) for the carbon flux measurements). Soil autotrophic and heterotrophic measurements were done only in Nuortti in 2004.

Tree growth experiments were performed in Värriö I fjell in 2003-2005. 25 healthy trees were randomly divided to four treatment groups, which were debudding (6 trees), defoliation (6 trees), fertilization (6 trees) and control (7 trees). From trees belonging to debudding group, ¾ of buds were removed, excluding the apical buds that were all left intact. From trees of defoliation group, all but last year needles were removed, meaning that in the end of the growing season the trees had two needle cohorts. Both manipulations were repeated for the same trees on spring 2004. The trees in the fertilization treatment group received slow-release nitrogen fertilizer in the form of pellets (Metsän kestotyppi, Kemira GrowHow, Finland; 35 % N, 1 % Mg, 0.15 % B). The fertilizer was spread within a 2 m radius of each tree. The dates of the fertilization were May 22nd 2003 (175 g N tree^{-1}), August 22nd 2003 (52.5 g N tree^{-1}), May 27th 2004 (175 g N tree^{-1}) and June 9th 2005 (35 g N tree^{-1}). As the production of “Metsän kestotyppi” was ended in 2004, we also fertilized trees (28.5 g N tree^{-1}) with another slow-release fertilizer (Metsän NP1, Kemira GrowHow, Finland; 25 % N, 2.2 % P, 5.5 % Ca, 1 % Mg, 0.15 % B, 0.15 % Zn) on June 9th 2005. Tree growth response measurements were started on May 2003.

3.2 Methodology for measuring tree growth responses

The responses of trees to the manipulations were assessed by measurements of the transpiration through sapflow density, height growth, tree ring width, branch growth, stomatal conductance through carbon stable isotopic abundances, needle nitrogen concentration and non-structural carbohydrate (NSC) concentrations.

Table 1. The timeline for the tree growth manipulations and tree measurements.

	Pre-experiment		Intensive survey + treatments							Post-experiment			
	2001	2002	Spring 2003	Summer 2003	Autumn 2003	Winter 2004	Spring 2004	Summer 2004	Autumn 2004	Winter 2005	Spring 2005	Summer 2005	Autumn 2005
Defoliation			■				■						
Debudding			■				■						
Fertilization			■	■			■				■		
NSC Sampling						■	■	■					
N Sampling			■		■	■		■					■
Isotopes	■	■	■	■	■	■	■	■	■				
Branch Increment	■	■	■	■	■	■	■	■	■				
Height Increment	■	■	■	■	■	■	■	■	■	■	■	■	■

3.2.1 Sapflow density

Sapflow measurements are often used to measure transpiration flow in trees. In this thesis, sapflow was used as a proxy for photosynthesis. The sink limitation hypothesis was tested by comparing transpiration of the debudded and the control trees. Sapflow measures the transpiration flux in trees and due to the stomatal restrictions it is closely linked also to photosynthesis. Also, we tested whether stomatal conductance of the trees acclimates to the short term temperature changes using the stomatal conductance model of Mäkelä et al. (2004).

During spring 2004, Granier-type of sapflow needles (Granier 1987) were installed on the northern side of three debudded and three control trees. The needles were installed on 50 cm height from a ground, and exactly 10 cm apart from each other. The installation was done by drilling a narrow hole in the tree and installing an aluminum tube into the hole. The hole was then filled with heat transfer compound (Electrolube, Derbyshire, UK) and the sapflow needle was installed into the aluminum tube. Needles were covered with plastic shields to prevent heating by straight solar radiation. Transpiration was measured in 1/60 s^{-1} frequency, but in the analyses, an average of 15 minutes was used.

Transpiration was then modeled using optimal stomatal conductance model (Mäkelä et al. 1996; Berninger et al. 1996).

$$H = \left(\sqrt{\frac{C_a \lambda}{1.6D}} - 1\right)\frac{I\alpha D}{I+a} \qquad (1)$$

Where, H = transpiration (mol H_2O m^{-2} sapwood s^{-1}), C_a = ambient carbon dioxide concentration (mol mol^{-1}), λ = parameter called intrinsic water use efficiency, I = light intensity, α = parameter that describes photosynthetic capacity (mol m^{-2} sapwood s^{-1}), D = water vapor deficit (mol mol^{-1}) and a = parameter describing the form the response of stomatal conductance to changes in water vapor deficit. D was calculated separately for each measurement, when α was estimated. In the final transpiration model D, I, temperature and CO_2 concentration were set as constants.

The capacity of photosynthesis (α) was used as in Mäkelä et al. (2004) and made to acclimate to temperature changes as:

$$\alpha = \alpha_0 S \quad \text{and} \quad \frac{dS}{dt} = \frac{1}{\tau}(T - S) \qquad (2)$$

where α_0 is a parameter, parameter S indicates the level of photosynthetic capacity, τ describes how rapidly α acclimates to temperature changes and T is the air temperature.

3.2.2 Carbon isotopes

For the carbon isotope analyses trees were sampled using an increment borer. From each tree, a sample from north and east side of the main stem was collected on October 12th 2004 (in the fall of the second year of experiment). The isotopic analyses were done in laboratory in University of Helsinki by Emmi Hilasvuori. The tree ring widths were first measured under a microscope. After that, the tree rings were cut into longitudinal sections about 20 µm thick with a surgical blade and α-cellulose was extracted from the wood (Loader et al. 1997). 70-100 µg cellulose samples were then combusted and CO_2 was separated in an elemental analyzer (NC 2500). Gas was then introduced to a mass spectrometer (Delta Advantage, Finnigan, Bremen, Germany) via the ConFlo II or III interface. Results of carbon isotopes are expressed using conventional δ notation. Isotope ratios are expressed relative to the VPDB (Vienna PeeDee Belemnite) standard:

$$\delta^{13}C = 1000 \times \left(\frac{R_{sample}}{R_{standard}} - 1\right) \qquad (3)$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the sample and the VPDB standard, respectively.

3.2.3 Non-structural carbohydrates

To analyze the carbohydrate concentrations in woody tissue, branch xylem samples were collected from trees every second week during growing season 2004. The samples consisted of the growth of the last year and ongoing year (one year in spring, two years in fall). The bark and phloem were peeled off during the same day when samples were collected and they were put into microwave oven on full power for 1 min to kill all living cells and to end any changes in carbohydrate composition. After this, the samples were dried at 60 °C for 3 hours and then frozen. As the sample sizes were small, two samples (from the same tree) were combined with each other. Spring samples were collected on 17 and 31 May, summer samples on 28 June and 12 July, and fall samples on 20 August and 11 October. Carbohydrate analyses were done at the Institute of Botany of the University of Basel, Switzerland, by staff of Prof. Christian Körner and Dr. Günter Hoch by using an enzymatic digest technique with subsequent spectrophotometric glucose test. The more detailed laboratory methodology is described in the Article II.

3.2.4 Nitrogen concentration in needles

Nitrogen concentration in needles was measured from samples collected from each tree on 24 May 2003, 27 August 2003, 31 May 2004, 11 October 2004 and 2 October 2005. For the samples, healthy side branches were chosen from the northern side of the tree. Each sample consisted of the growth of the previous and ongoing year (one year in spring, two years in fall). The samples were dried at 60 °C for 12 hours. Needle nitrogen concentrations were analyzed by Leco elemental analyzer (model CNS-1000; LECO Corporation, St. Joseph, MI, USA).

3.2.5 Growth response

Height growth of the trees was measured on 29 September 2005 by measuring the length of internodes of the main axis of the branch during last 5 years.

Branch extension was measured from branch samples collected in April 2005. The measurements were done from 3-8 samples of side branches from each tree. The growth of the last four years was measured from the internodes.

The cell growth in stem was measured in the laboratory from the same samples that were used in the isotope analyses. The annual tree ring width was measured for years 2000 – 2004.

3.3 Ground vegetation measurements

3.3.1 Biomass

Vegetation biomass and species coverage of ground vegetation was measured in Nuortti and Värriö II fjell during mid-July in 2002. Species coverage was measured from 50 cm x 50 cm plots, from where percentual coverage of each species was estimated. There were 20 plots in each side of the fence in Nuortti, and 80 plots in Värriö II fjell.

Biomass was measured from 30 cm x 30 cm plots during summer 2002. In Värriö II fjell the measurements were done three times to estimate also the growth rate during summer. The dates were 5-9 June, 1-7 July and 7-11 August in Värriö (ten plots each time), and 12-16 July on Nuortti (10 plots in each side of the fence). The biomass was stratified into functional groups, which were mosses, lichens, herbaceous plants, grasses, the new (ongoing year) and old growth of dwarf shrubs. The samples were dried for 20 hours in 60 °C and weighed after that.

3.3.2 Carbon flux

Carbon flux measurements (NEE = net ecosystem exchange and ER = ecosystem respiration) were performed in Nuortti and Värriö II during the growing season on year 2004 using chamber method. Chambers measured CO_2 flux from ground and / or vegetation from a strictly defined area in semi-controlled conditions. NEE was measured with a transparent cuvette, whereas ER was measured using dark cuvette. The measurements were always done during the same day with short time interval. Respiration and NEE were measured in both sites (Värriö II and Nuortti) in ten day interval.

The measurements of soil autotrophic and heterotrophic respiration in Article III were done by Terhi Rasilo during summer 2004. On June, four measurement plots were established on both sides of the fence on Nuortti. Root respiration was measured using trenching method. For this, the above ground vegetation was removed from the collars by clipping the vegetation. The roots growing into the collar were cut by digging a 15-20 cm deep trench around the collar. Four control plots were also established without plant and root exclusion. The relative change in respiration rate was calculated as:

$$P_R = \frac{(C_1 \times T_2)}{(C_2 \times T_1)} \qquad (4)$$

where

P_R = relative change in respiration rate, C_1 = respiration in control plots before trenching, C_2 = respiration of the control plots at a given measurement time, T_1 = respiration in the trenched plots before trenching and T_2 = respiration in the trenched plots at a given measurement time.

Q_{10} values were calculated as

$$R = a \times Q_{10}^{(T/10)} \qquad (5)$$

where a is constant (µmol m^{-2} s^{-1}), R = respiration (µmol m^{-2} s^{-1}) and T = soil temperature (°C) at 2 cm at a given moment.

4 RESULTS

4.1 Growth responses of trees due to manipulation experiments

Debudded trees did not have lower sapflow rates than the control trees and the sapflow rate of the trees was not sensitive to changes in daily mean temperature (Article I). Trees were able to compensate the loss of buds by increasing the growth of the remaining shoots (Articles I and III). In accordance to this, height growth was also increased by 35 % due to the debudding treatment, but the results were not statistically significant, as the *p*-value was 0.069 (Article II). There were no changes in tree ring width due to the treatment (Article II). Debudding did not affect sugar or starch concentrations of the branch xylem during spring, summer or fall (Article II). Needle nitrogen concentrations were not changed due to the debudding treatment (Article II).

Defoliation of the trees did not affect the height or shoot growth of the trees, but tree ring width was significantly decreased (Article II). The $\delta^{13}C$ values did not differ significantly between control and defoliated trees (Article II). Defoliation did have a slight effect on the amount of non-structural carbohydrates, as concentration was significantly lower in spring Though, when the concentrations of NSC were measured for sugars and starch separately, there were no significant differences. The results were not statistically significant during summer or fall measurements (Article II). There were no changes in needle nitrogen concentration due to this treatment (Article II).

Nitrogen fertilization treatment doubled the height growth and also the shoot growth was increased according to the results in 2004 (Article II). Nitrogen fertilization did not have an effect on the tree ring width (Article II). Carbon isotope ratio showed somewhat increasing trend due to the fertilization treatment, *p*-value being close to significant (0.054; Article II). There were no statistically significant differences in the sugar or starch concentrations of the branch xylem due to the fertilization treatment during any measured time (Article II). Needle nitrogen concentrations increased significantly due to the fertilization treatment (Article II).

4.2 Responses of ecosystem carbon balance on reindeer grazing

The total above ground biomass (without trees) in Nuortti was about 50 % lower in the grazed side of the fjell than in the ungrazed side (Article III). The difference was caused by a lower biomass of lichens in the grazed area. The lichen biomass on the grazed side was only 15 % of the values on the ungrazed side. On the other hand, grazing favored deciduous shrub species (e.g. *Arctostaphylos alpinus* and *Vaccinum uliginosum*), but opposite to these evergreen shrubs like *Arctostaphylos uva-ursi* and *Empetrum nigrum* were more common on ungrazed side of the fjell. Grazing increased the biomass of mosses but not biomass of grasses.

Average ecosystem respiration in the sites was 0.8-0.9 µmol CO_2 m^{-2} s^{-1} and average photosynthesis in the sites was between -0.4 and -0.5 µmol CO_2 m^{-2} s^{-1}. Average NEE was slightly positive with values between 0.2-0.5 µmol CO_2 m^{-2} s^{-1}. Measurements included forest floor but not fluxes from the treeline trees. According to the results of soil respiration, about half of the respiration originated below ground, and it was strongly controlled by soil temperature, but soil moisture did not have an effect on the carbon exchange. Grazing did not have an effect on the CO_2 exchange in the site. In our site fluxes correlated strongly with the total biomass of dwarf shrub coverage (NEE negatively and respiration positively). Grazing did not affect on the rate of fluxes despite the changes in the species composition. Also, fluxes had weak correlations with lichen coverage (Article III).

5 DISCUSSION

5.1 Tree growth restrictions

I hypothesized that trees were sink limited. According to sink limitation hypothesis, the following would be expected due to the treatments: (i) Tree growth of neither shoots nor stems will increase as a response to debudding; (ii) growth of stems and shoots will not change as a response to fertilization or defoliation; (iii) carbohydrate concentrations in the branches will increase as a response to debudding, but will remain unchanged as a response to the other treatments; (iv) stomatal restrictions ($\delta^{13}C$ values) can stay on the same level or decrease slightly due to defoliation, as the growth of sink limited trees do not change but the total photosynthesis stays in the same level than before manipulation. Fertilization should not affect the $\delta^{13}C$ values; (v) transpiration measured by sapflow will be depressed in debudded trees; and (vi) temperature sensitivity of photosynthesis will be depressed in debudded trees since the trees are carbon saturated and variations in sink activity should not affect sink limitation much.

According to the results in the Articles I and II, it seems clear that the trees in the treeline study site are restricted by availability of nitrogen and to a lesser amount by availability of carbon. The growth responses were overall the strongest in fertilized trees, as was assumed according to the nitrogen limitation hypothesis. Fertilization significantly increased growth of the stem and branches. Interestingly the tree ring width did not increase. It seems that the increased amount of available nitrogen changed the allocation pattern so that the trees started to increase the growth of the photosynthetizing organs. The growth responses of the debudded trees were very modest, with the only statistically significant result being the increased branch growth. But, debudded trees were able to increase growth of the remaining buds, which – together with the growth results from fertilizer addition – speaks against the sink limitation hypothesis.

5.1.1 Fit of the results to the sink limitation hypothesis

The results from the manipulation experiments did not support the sink limitation hypothesis. According to the sink limitation hypothesis, low temperatures are limiting the growth of the trees. Since growth is limited directly by temperature and not the availability of resources there should not have been any positive growth responses to our treatments. Also, trees should not have decreased growth due to defoliation at least very much, as the trees have high storages of NSC usable for growth and C availability is not directly limiting growth.

Also, according to sink limitation hypothesis, carbohydrate concentrations in tree tissues were expected to increase due to the debudding treatment as growth of the remaining buds does not increase, but this did not happen in our experiment. The sink limitation hypothesis does not make any statements on the effects of fertilization on the labile carbohydrate concentrations. Also, defoliation should not have an effect on the NSC concentrations as the growth is not restricted by the availability of resources and there is equilibrium between resource availability and their production. Defoliation had a small effect on the NSC concentration during spring, but the effect disappeared in the mid-summer.

Fertilization tended to increase the carbon isotope concentrations (*p*-value = 0.054) in 2004, which disagrees with sink limitation hypothesis. In the point of view of the sink limitation hypothesis, as the demand of carbon for growth is not increased, the carbon isotope ratio should not change due to fertilization. There is no clear hypothesis how the carbon isotope ratio would change due to defoliation treatment according to the sink limitation hypothesis. Sapflow should be down-regulated in debudded trees as the need of carbohydrates decrease and photosynthesis is inhibited by high carbohydrate concentrations, which did not happen according to our results (Table 2).

Table 2. Expected responses according to sink limitation hypothesis. “0” means that according to sink limitation hypothesis there should not be a response, “+” means that a positive response is expected and “–“ that there should be a negative response. The responses that occurred due to the manipulation experiments are presented in black bold, where as the results which did not follow the expectations, are presented in gray.

Responses of the trees according to sink limitation	Debudding	Defoliation	Fertilization
Carbon isotopes	Not measured		**0**
NSC	+	**0**	
Stem diameter growth	**0**	0	**0**
Height growth	**0**	**0**	0
Branch growth	0	**0**	0
Sapflow	-	Not measured	Not measured

5.1.2 Fit of the results to the resource limitation hypothesis

The results support the resource limitation hypothesis. Growth of the trees increased due to the debudding and fertilization treatments, which should occur according to resource limitation hypothesis. Also stem diameter growth of the defoliated trees was decreased, which also supports the resource limitation hypothesis, since there are less photosynthates for growth. Most likely trees allocate proportionally more resources to new foliage to recover the balance between different biomass compartments. According to the resource limitation hypothesis, removal of buds should increase the allocation of the carbon to other parts of the tree and due to this to increase the growth of the remaining growth buds in branches and main shoot. The branch growth was increased due to both treatments, but in the height growth was statistically significant only for the fertilized trees, though it is worth of noting that the height growth of debudded trees was increased by 35 % on 2004, even though the results were not statistically significant with a *p*-value of 0.069.

The resource limitation hypothesis suggests that NSC (non-structural carbohydrate) levels in the trees would decrease due to the defoliation treatment as the level of available carbon is already the limiting factor for growth. There was some evidence to support this, since the NSC concentration on spring was slightly decreased in defoliated trees. Since trees are limited by resources, debudding should not increase carbohydrate concentrations according to resource limitation hypothesis, since additional carbon is readily used for growth, which was also supported by the results (Table 3).

Table 3. Expected responses according to the resource limitation. “0” means that according to resource limitation hypothesis there should not be a response, “+” means there should be a positive response and “–“ that there should be a negative response. The responses that occurred due to the manipulation experiments are presented in black bold, whereas the results which did not occur are presented in gray.

Responses of the trees according to resource limitation	Debudding	Defoliation	Fertilization
Carbon isotopes	Not measured	-	**0**, +
NSC	+	-	**0**
Stem diameter growth	+	-	+
Height growth	+	-	**+**
Branch growth	**+**	-	**+**
Sapflow	**0**	Not measured	Not measured

If resources would be limiting growth, carbon isotope ratio should be increased due to fertilization, as increased concentration of nitrogen enhances the photosynthetic capacity. The carbon isotope ratio of fertilized trees tended to increase, though the *p*-value was only 0.054. Defoliation treatment should induce lower carbon isotope ratios (meaning more open stomata), as the remaining part of the needles should increase their photosynthetic performance and due to this stomatal opening. We could not find evidence to support this. There were no changes in sapflow due to debudding treatment, which support the resource limitation hypothesis, as according to the hypothesis there is no excess photosynthates do not limit carbon fixation (Table 3).

5.1.3 Comparison of different growth responses

There were no statistically significant differences in the NSC concentrations due to the treatments (Article II), except that the total NSC concentration during spring was slightly lower in defoliated trees, as compared to the control. Though, already in the mid-summer the effect had disappeared. When sugars and starch were measured separately, there were no statistically significant changes due to any of the manipulations. There is a possibility that the NSC concentrations did not change since the treatments were not strong enough to induce any changes, but more likely the NSC concentrations of the treeline trees are just very resilient against changes in resource availability and consumption. Hence, the trees adjust their storages of resources to a constant level, which does not easily change. It has been noted that carbohydrate concentrations appear to never get depleted in treeline trees (e.g. Hoch et al. 2002; Li et al. 2002; Hoch & Körner 2003; Hoch & Körner 2009) and carbohydrate concentrations seem to be higher in trees growing at the treeline than at lower altitudes (Hoch et al. 2002; Körner 2003). However, there are contradictory results (Richardson 2004; Li et al. 2008a; Li et al. 2008b). It is possible that the high carbohydrate levels in treeline trees are an adaptation to harsher and more unpredictable climatic conditions (e.g. Chapin et al. 1990). As treeline trees grow in extreme growth habitats and their life cycle lasts for almost hundreds of years, the growth strategies of trees should enable them to survive harsh years. When the growing season is short, it is essential for survival to start the growth as early in the growing season as possible. For this, trees require carbohydrate reserves. Hjelm & Ögren (2003) also emphasized the possible function of starch reserves in coniferous needles as sink that enhances growth during spring. It is well known that during spring growth utilizes mostly carbohydrate reserves, whereas summer cells are formed only with the products of current photosynthesis (Luxmoore 1991). Also, in treeline environment there is a large probability of physical damage during winter, which can be lethal if the trees have no reserves. Therefore, trees have most likely created patterns to survive through the losses and repair the structural damages affected on them with only minimal costs.

As pointed out above, trees reacted to the manipulation treatments with multiple structural changes. It is interesting that the growth responses of the trees were large, even though there were almost no changes in the NSC levels of the branches. Li et al. (2002) found in his study of complete defoliation and debudding and partial pruning experiment of treeline *Pinus cembra* trees that trees responded to defoliation and pruning by a strong reduction of NSC concentration in number of structural parts, whereas there was no statistically significant difference in the NSC concentration due to debudding. Though, part of the NSC depletion was already replaced at the end of the growing season in the expense of growth, which clearly decreased. Together with our results this indicates that the growth strategy of treeline trees is to attempt to maintain a certain level of NSC before entering winter. The evolutionary explication could be that treeline trees are required to be resilient against physical damage. NSC reserves act as buffer against possible unpredictable losses of foliage or other biomass during winter. This capacity to survive at the treeline is maintained by balancing the resource acquisition and their use. For trees living in extreme areas costly morphological adjustments to quickly fluctuating climate conditions can be fatal (Sveinbjörnsson 2000). This means that for the survival of treeline trees, the optimal strategy is to react slowly to changes that demand morphological adjustment or other cost that will burden the energy or resource budget of tree, but at the same time to acquire as much resources that they are able, even though they will not be used straight away. These non-structural carbohydrate reserves can maintain survival in the sometimes rapidly changing environment. They will also act as a potential for the morphological changes in the long run, if there would be permanent changes in the climatic conditions or resource availability.

Defoliated trees were able most likely able to maintain the same rate of photosynthesis in the remaining needles, and the decreased growth of stem was a reaction to decreased need for the water transport capacity per needle area. Also, as the photosynthetic efficiency may have increased in the fertilized trees, they were able to allocate more resources to branch and height growth compared to stem growth than the control trees, as they were able to photosynthetize with a lower level of transpiration compared to control trees. These changes occured as the manipulations caused changes in allocation of the trees as the balance of resources and structure of the trees was changed due to the manipulations (e.g. Nikinmaa 1992).

Also, the results of the sapflow measurements do not corroborate the sink limitation hypothesis. Debudding of the trees did not affect the sapflow and both the temperature sensitivity of transpiration and variation in the transpiration capacity of the trees was unaffected by the treatments. The stomatal conductance model used has been proven to provide realistic results for modeling both transpiration and photosynthesis (e.g. Berninger et al. 1996; Mäkelä et al. 2004). We also estimated changes in stomatal conductance of fertilized and defoliated trees through changes in carbon isotope ratio, which tended to increase (with *p*-value of 0.054) fertilized trees (Article II), which acts against the sink limitation hypothesis.

Our results show that the growth of the trees in our treeline site is primarily resource limited. The growth responses were by far strongest in the fertilized trees. The trees allocated a large amount of biomass to the growth of photosynthetic machinery, whereas there was no response on the tree ring width. There is evidence that increased nutrient acquisition rate induces changes in allocation patterns by decreasing root:shoot ratio of the trees (e.g. Chapin 1980b; Hättenschwiler & Körner 1998), whereas increased CO_2 fertilization increases the root:shoot ratio (e.g. Hättenschwiler & Körner 1998). As E.g. Weih & Karlsson (1999) suggested, treeline trees seem to have adapted to maintain higher nitrogen concentrations than the trees below treeline. This increased level of nitrogen acts same time as a buffer against the environmental perturbations, but also makes photosynthesis more effective with higher water use efficiency as trees are able to keep their stomata more closed. This might be important as trees in treeline are more xeromorphic that low altitude plants (Li et al. 2002; Li et al. 2004).

The nitrogen cycle is strongly affected by both increasing temperature and increasing CO_2 level, as increased temperature increases net mineralization rates in cold soils (McKendrick et al. 1980; Press et al. 1998; Hartley et al. 1999; Grace et al. 2002) and experimental warming of arctic soils has led to increases in N mineralization (Press et al. 1998; Hartley et al. 1999). Increasing temperatures are therefore expected to increase the amount of nitrogen available for tree growth at treelines, which in turn could make the photosynthetic production of the trees more efficient as carbon transferred below ground by trees can result in greater nitrogen uptake due to increased amount of fine roots or more extensive mycorrhizal development (Lukac & Godbold 2011). Also, increased aerial nitrogen depositions from anthropogenic emissions (Pitcairn et al. 1995) might be stimulating plant growth at some treeline ecosystems (Grace et al. 2002).

5.2 Effects of reindeer grazing on the vegetation and carbon balance of the fjell ecosystems in north eastern Finland

Grazing had two main effects on the standing biomass of the fjell fields. The first on was that lichen coverage was reduced by 85 % due to grazing (Article III). This fits well with the results of Väre et al. (1996), who found out that the lichen biomass had decreased by grazing from 790 g m^{-2} to 86 g m^{-2} in four sites in Finnish Lapland. The second effect was that even though the amount of dwarf shrubs was not affected by grazing, there were clear changes in species composition. Certain species seemed to benefit from grazing (e.g. *Vaccinium uliginosum* and *V. vitis-idaea*), whereas some showed an opposite response (e.g. *Arctostaphylos uva-ursi*; Article III). According to CCA analysis (Article III) grazing favored deciduous dwarf shrub species compared to evergreen dwarf shrub species. Changes in vegetation composition can occur due to changes in the microclimatic conditions in soil (den Herder et al. 2003), due to allelopathic extracts produced by lichens (Brown & Mikola 1974) or due to direct effect of grazing and trampling (Oksanen & Virtanen 1995). Due to this, the community structure under grazing shifts usually towards species that do not decompose that easily and slow down the nutrient cycle of the ecosystem (Article III; Pastor & Naiman 1992). Graminoids are often favored by grazers, but they seem to benefit from grazing due to their investments to the roots and due to their high growth rate (Chapin 1980a; McKendrick et al. 1980; Olofsson et al. 2001; Post & Pedersen 2008). Though, Olofsson et al. (2004) noted, that the long term effects of grazing can be very different from the short term effects. Olofsson et al. (2001) has suggested that especially summer grazing by reindeers in arctic tundra changes the vegetation so that the slow growing dwarf shrubs will be decreased and graminoids will increase. This can increase the primary productivity of the area significantly (Olofsson et al. 2001). Decrease in lichen cover can have an important effect on the albedo of the soil and due to it directly on climate change (Betts 2000; Bernier et al. 2011). As the light colored lichens disappear and either bare ground cover or the area of the green vegetation increases, more of the solar radiation is transferred to soil and vegetation as heat. The changes in soil temperature were clear also in our sites, as the soil temperature measured from 2 cm depth was higher in bare ground plots than in plots with vegetation intact (Article III). Even though the changes in percentage of bare ground cover would not be very high, this can be important, as the effect lasts through the whole growing season, which is also the time, when the amount of solar radiation is at its highest.

The average NEE of the fjell field during growing season was slightly positive with values of 0.2-0.5 µmol m^{-2} s^{-1} (trees were not included in the measurements) and the fluxes were unaffected by vegetation changes or reindeer grazing. The average ecosystem respiration of 0.8-0.9 µmol m^{-2} s^{-1} during growing season in our research area is low compared to previous measurements in arctic (e.g. Christensen et al. 1997; Hobbie & Chapin 1998; Illeris & Jonasson 1999; Wohlfahrt et al. 2008), most likely due to the fact that also the productivity is very low. Though, Grogan & Jonasson (2005), who did measurements in similar ecosystem in Sweden, did also measure fluxes of 0.9 µmol m^{-2} s^{-1}. In our study site in Värriö, annual soil respiration was 58 g C m^{-2} y^{-1} (in 2002 to 2004; Bahn et al. 2008). Ecosystem respiration correlated positively and NEE negatively with dwarf shrub coverage, whereas lichen coverage had an opposite effect. The latter happened most likely due to the negative correlation between lichen and dwarf shrub coverage.

It seems that reindeer grazing do not have a substantial effect on the carbon balance of the fjell fields in the area. As the lichens are not important functional group for the carbon exchange, their decrease due to reindeer grazing does not substantially affect either the stocks or the exchange. Though, this seems to be true in more continental sites, as in more maritime and nutrient-rich areas of Fennoscandian arctic-alpine tundra heaths reindeer grazing increases the amount of graminoids, which can have a different kind of effect on the carbon balance (Stark et al. (2002). In the more continental tundra lichen heaths – like our sites in Värriö – graminoids do not replace dwarf shrubs due to grazing (Stark et al. 2002). The effect of grazing on lichen community depends on the number of grazers on the area, and grazing can decrease the lichen biomass drastically (Olofsson et al. 2001).

Both Olofsson et al. (2009) and Post & Pedersen (2008) proposed that grazing can have an important role in vegetation changes when we are facing climate change due to their multiple effects on vegetation and microbial dynamics. Post & Pedersen (2008) noted that herbivory reduced the relative biomass in response to warming in most functional groups. Olofsson et al. (2009) showed that reindeer grazing had strongest effect by reducing biomass of lichens and that reindeers diminished the positive growth effect of increased temperatures to *Betula nana* coverage, which is the most important shrub in the area. Browsing can also locally affect also on the position of treeline, if animals are using tree seedlings as forage (Miller & Cummins 1982; Motta et al. 2006).

6 CONCLUSIONS

The size of carbon stocks in the treeline ecotone depend on the other hand on the growth and survival of trees and on the other hand on the accumulation of carbon in the ground vegetation and through litter fall and decomposition to soil. The results showed that the tree growth in the experimental area is restricted by resources. The main restricting factor seems to be nitrogen, though also carbon plays a part in the limitation. Evidently the results did not support sink limitation hypothesis. Even though increase in temperature would not itself increase tree growth directly, temperature induced increases in the soil processes can increase the availability of nitrogen, which in turn affects the tree growth.

Grazing affected on the species composition and vegetation carbon stocks, but productivity, soil carbon stocks and soil respiration were not affected by grazing. Above ground carbon stocks in these fjell ecosystems are small compared to most arctic and alpine treeline ecosystems. Reindeer grazing has an effect on the vegetation biomass especially on the lichens that they forage extensively. Though, as reindeers did not have a significant effect on the carbon fluxes in the area, the total effect of reindeers to ecosystem carbon balance is not important.

At least locally grazing is known to restrict seedling establishment at treeline. Both treeline rise and increase in the abundance of the trees in the treeline would affect significantly on the carbons stocks of these ecosystems. Since reindeers might affect on the regeneration of the treeline trees, future research on the interactions between grazing and treeline progression would be needed.

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