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Bilberry *(Vaccinium myrtillus L.)* in a Boreal Forest Ecosystem

-effects on tree seedling emergence and growth

Anders Jäderlund

SWEDISH UNIVERSITY OF AGRICULTURAL SCIENCES

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Akademisk avhandling som för vinnande av filosofie doktorsexamen kommer att offentligen försvaras i hörsal Björken, SLU, Umeå den 1 juni 2001, kl. 13.00.

Abstract

The interference effects of bilberry (*Vaccinium myrtillus*) on tree seedling emergence and growth was studied in a series of indoor bioassays and in three field experiments in a bilberry dominated clear-cut in northern Sweden. Water extracts of senescent bilberry leaves reduced aspen (*Populus tremula*) seed germination and growth in bioassays aimed to test phytotoxicity. Those inhibition effects were removed by the addition of activated carbon. When senescent leaves were used as a seedbed, Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and silver birch (*Betula pendula*) seed germination was significantly reduced, but water rinsing of seeds reversed the inhibition in pine and spruce. Establishment and growth of pine and spruce seedlings were negatively affected by senescent and decomposed bilberry leaves, when applied as surface litter. These results suggests that the inhibitory compounds are water soluble and are released during decomposition. Under field conditions phytotoxic effects from bilberry reduced pine seed germination, while growth and nutrient acquisition of pine and spruce seedlings were greatly unaffected.

Pine and spruce seedlings were planted in exclusion tubes to study below ground competition by bilberry. Reduced below ground competition strongly increased biomass growth and nutrition of pine and spruce seedlings, also mycorrhizal colonisation was increased. Water addition had a small positive, but mostly non-significant effect on pine and spruce seedling biomass growth and nutrition. Reduction of above ground competition by folding back bilberry shoots actually reduced spruce seedling survival, shoot length and shoot to root ratio, but increased root biomass. The results clearly show that below ground nutrient competition is the main reason for reduced tree seedling growth and nutrition.

I also tested the effectiveness of steam treatment in reducing bilberry competition with pine and spruce as a site preparation technique. Steam treatment effectively killed bilberry vegetation and re-colonisation was slow. Pine seed germination was enhanced in the first year after treatment, especially when activated carbon were added to steamed plots. Pine seedling growth and nutrient content were also strongly increased when grown in steam treated vegetation compared to intact vegetation. I conclude that bilberry has the capacity to influence on establishment and growth of conifer seedlings in boreal forest ecosystems.

Keywords: tree regeneration, ground vegetation, plant-plant interaction, resource competition, nitrogen, soil moisture, light, rooting ability.

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Contents

Appendix

Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

I. Jäderlund A, Zackrisson O, Nilsson MC. 1996. Effects of bilberry (*Vaccinium myrtillus* L) litter on seed germination and early seedling growth of four boreal tree species. *Journal of Chemical Ecology* 22: (5) 973-986.

II. Jäderlund A, Zackrisson O, Dahlberg A, Nilsson M-C. 1997. Interference of *Vaccinium myrtillus* on establishment, growth, and nutrition of *Picea abies* seedlings in a northern boreal site. *Canadian Journal of Forest Research* 27: (12) 2017-2025.

III. Jäderlund A, 2001. Influence of soil moisture and below ground competition by *Vaccinium myrtillus* on *Picea abies* and *Pinus sylvestris* seedlings in a northern boreal forest site. Manuscript

IV. Jäderlund A, Norberg G, Zackrisson O, Dahlberg A, Teketay D, Dolling A, and Nilsson M-C. 1998. Control of bilberry vegetation by steam treatment - effects on seeded Scots pine and associated mycorrhizal fungi. *Forest Ecology and Management.* 108: (3) 275-285.

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Introduction

Background

The boreal forest covers a broad circumpolar belt across the Northern hemisphere, south of the arctic zone and north of the nemoral zone, between the latitudes 50°N and 70°N (Sjörs 1956; Walter and Breckle 1989). Conifer trees dominate the forest in the boreal zone, which accounts for 29% of the worlds total forested area (Kuusela 1992). The bilberry spruce forest is the most widespread forest-type in the Eurasian boreal forest (Sjörs 1965; Walter and Breckle 1989). In Sweden bilberry forest types covers about 33% of forest ground (data 1996-2001 from Swedish National Forest Survey). Poor regeneration of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) seedlings has frequently been associated with late succession in this forest type, especially in the northern boreal zone (Arnborg 1943; 1947; Sirén 1955; Ahti et al. 1968; Lundquist 1989; Kuuluvainen 1994). Bilberry (*Vaccinium myrtillus* L.) is the most abundant non-tree forming vascular plant in this boreal community and is also known to produce large concentrations of phenolic compounds (Sjörs 1989; Gallet and Libreton 1995). It is therefore reasonable to expect that biotic factors associated with dominance of bilberry may contribute to the slow regeneration of conifers found in these sites.

The biology of bilberry

Distribution

Bilberry is a long-lived, deciduous, ericaceous dwarf shrub with green, tree-angled aerial shoots and small ovate serrated leaves (Ritchie 1956). The rhizome system is widespread, irregular and mainly located in the humus layer (Flower-Ellis 1971; Havas and Kubin 1983). The rhizome of a single individual can cover an area of at least 5.5 m^2 (Ritchie 1956; Flower-Ellis 1971). Bilberry has a wide Eurasian geographic distribution, from its western extremities of Iceland, Ireland and Spain, east through central and northern Europe all the way to central Asia, and the Lena valley and northern Mongolia (Hultén and Fries 1986; Figure 1). In its most southern distribution, bilberry is generally found in higher elevations as in the mountainous portions of Spain, Italy, Greece, Turkey and in the Caucasus.

Bilberry occurs throughout Sweden from the southern coast up through the low alpine heath (Sjörs 1956; Hultén 1971). On average, bilberry covers 17% (3.9 million ha) of the productive forest land in Sweden, accounting for 23% in the north and 16% in the south (Eriksson et al. 1979; Sjörs 1989, Johansson 1993). Besides its common occurrence on productive forest land, bilberry also has a high abundance in vegetation of the mountain forests and in the low alpine heath (Sjörs 1956; 1989; Eriksson et al. 1979).

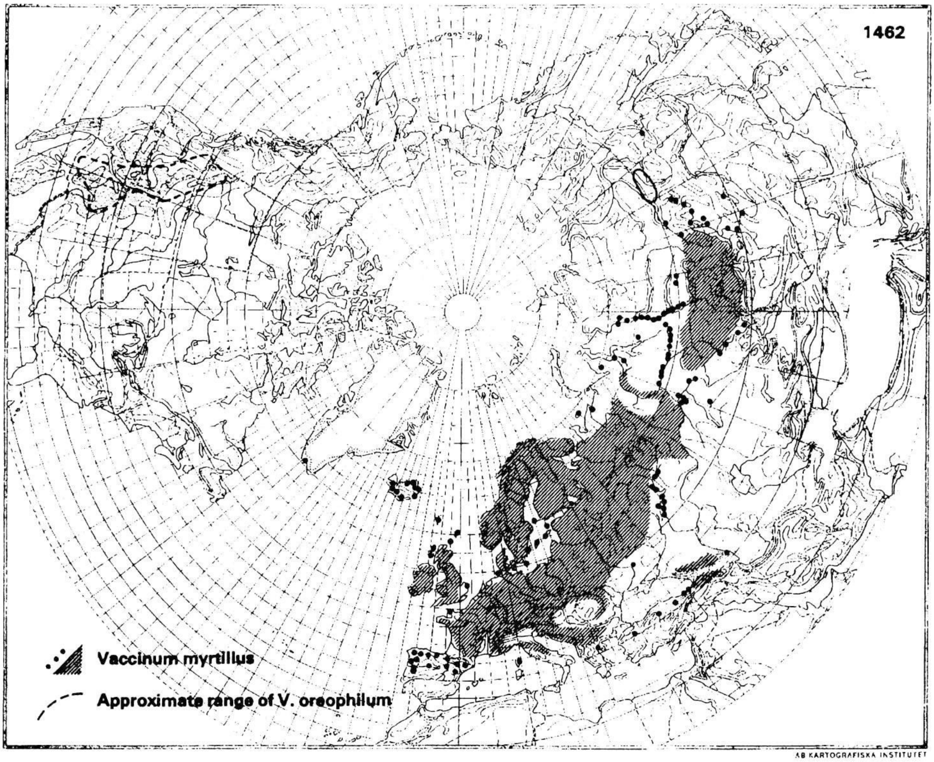

Figure 1. World distribution of bilberry (*Vaccinium myrtillus*). The species *Vaccinium oreophilum* Rydb. in western North American mountains show many similarities to and are sometimes considered synonymous to the European *V. myrtillus,* (Vander Kloet and Dickinson 1999). From Hultén and Fries (1986) with permission from Koeltz Scientific Books.

Bilberry is found across a wide range of sites, but it appears to be most well adapted to mesic, intermediate nutrient rich open boreal forests (Eriksson et al. 1979; Mäkipää 1999). The cover of bilberry increases with stand age and ground covers of more than 40% are common in old growth northern forests (Ericsson 1977; Eriksson et al. 1979; Granström 1986). Bilberry is not found on ground with a consistently high water table or sites commonly subject to flooding (Grime et al. 1988; Sjörs 1989). Snow cover is also an important factor for the spatial distribution of bilberry (Havas and Kubin 1983; Sjörs 1989). The aerial shoots of bilberry lack outer bark and are sensitive to frost (Sjörs 1989), therefore a thick insulating layer of snow favors bilberry survival. The shoots become frost-hardened during autumn. When embedded in snow, the shoot water content increases gradually in spring (Havas 1971). Higher water contents increase respiration rate followed by decreased concentrations of cryoprotective sugars and thus decreased hardiness (Havas 1971; Ögren 1996). Cold surface temperatures associated with thin snow cover can cause wide spread bilberry shoot damage (Sjörs 1989; Ögren 1996). The rhizomes will, however, usually survive this kind of damage unless exposed to such conditions each year.

Biomass and chemical composition

The average aerial biomass of bilberry in boreal forests ranges between 150 to 420 g/m^2 with about 25% of the biomass being produced during the current year (Mork 1946; Havas and Kubin 1983). Leaves comprise approximately half of the current year biomass with the other half as current year stems (Mork 1946; Havas and Kubin 1983). The above ground biomass of bilberry is small compared to the below ground portion which contributes up to nearly 90% of the total biomass (Havas and Kubin 1983). About 50% of the below ground biomass consists of fine roots and rhizomes with a diameter of less than 0.5 mm. The amount of ericaceous "hair roots" in soils of bilberry forests is very high. Hair roots are thin (c. 20-200 µm dia.) and have a rapid turnover rate, but accounted for a small portion of the standing biomass (Persson 1978; Bonfante-Fasolo et al. 1981; Read 1983, 1996; Allaway and Ashford 1996).

Nitrogen is the most abundant mineral nutrient in bilberry leaves (followed by K and Ca and then P and Mg; Romell 1939; Mork 1946; Flower-Ellis 1971; Ingestad 1973; Kubin 1983; Jonasson et al. 1986; Johansson 1993). The mineral nutrient and sugar content in bilberry leaves are high compared to most other ericaceous species and to conifers, while the amount of lignin is low (Mork 1946; Jonasson et al. 1986; Johansson 1993). Bilberry, as all ericaceous species, contain high concentrations and a wide range of phenolic compounds (Jonasson et al. 1986; Pellissier 1993; Gallet 1994; Gallet and Libreton 1995).

Ericoid mycorrhizae and nutrient acquisition

Almost all ericaceous hair roots, which form a dense web in the upper humus layer, are colonized by ericoid mycorrhizal fungi (Read 1991; Smith and Read 1997). In contrast to ecto- and arbuscular mycorrhizae, ericoid mycorrhiza form less extensive mycelium. The ericaceous hair roots are already widespread, and the mycelium extends only a few mm out from the hair root (Read 1991). Ericoid mycorrhizal fungi appear to be well adapted to soils with high phenolic content (Bending and Read 1997; Souto et al. 2000). Ericoid mycorrhizal fungi can emit enzymes promoting decomposition of recalcitrant organic matter including chitin, lignin and tannin and acquire associated organic N compounds (Read 1991; Bending and Read 1996a; 1996b; Bending and Read 1997). The increased N acquisition favors the fungal colonized ericaceous plants success. Ericaceous species with ericoid mycorrhiza have higher biomass production and nutrient uptake than plants without mycorrhiza (Bajwa and Read 1985; Read 1996; Smith and Read 1997). In experiments under field conditions, bilberry (with ericoid mycorrhiza), have been shown to take up N in the form of glycine (Näsholm et al. 1998). Bilberry was also shown to be more efficient at glycine uptake than *Pinus sylvestris* and *Deschampsia flexuosa*, species which are associated with ecto- and arbuscular mycorrhiza (Nordin 1998; Näsholm et al. 1998). It has been indicated that bilberry can acquire organic N when NH_4^+-N is present at equal concentrations (Nordin 1998). In acidic soils, metal ions (i.e. Fe, Cu, Zn) can occur in toxic concentrations. Ericoid mycorrhizal fungi have the possibility to accumulate these metal ions in the fungal biomass, and thus protect the host plant from metal toxicity (Read 1991). These decomposition-, acquisition- and detoxification abilities of ericoid symbionts may give ericaceous plant species competitive advantages over other species and make ericaceous plant species more tolerant to environmental stresses (Read 1991; Bending and Read 1997; Souto et al. 2000).

Dispersal and regeneration

Bilberry flowers in early spring and is pollinated by insects, mostly bees and bumble-bees (Sjörs 1989). Cold rainy weather and night frost during the flowering period can spoil the reproduction success (Sjörs 1989). Pollen production and dispersal are not considered to be a limiting factor for berry and seed production during normal conditions (Fröborg 1996; Jacquemart 1997). Berries ripen in late July or early August, about 50 days after flowering (Vänninen et al. 1988). Seeds are conditionally dormant directly after maturity in late summer and some seeds germinate immediately if temperature is high enough (Baskin at al 2000). However, the large cohort of seeds germinate in spring and early summer when seeds are non-dormant and temperatures become satisfactory for germination (Baskin at al 2000). Some seedlings establish in parent populations, but survival is low (Ericsson 1977; Granström 1986; Eriksson and Fröborg 1996). Despite high production rate and easily dispersed seeds (by birds and animals), seed availability in combination with microhabitat availability are factors that may limit seedling establishment in parent populations (Eriksson and Ehrlén 1992; Eriksson and Fröborg 1996). Seedlings in parent populations most probably originated from seeds dispersed over the last few preceeding years (Eriksson and Fröborg 1996). Bilberry can form a persistent seedbank, but it is of little significance for seedling recruitment in parent populations (Granström 1986). Bilberry seedlings from newly dispersed seeds are well adapted to colonizing severely disturbed ground, such as ditch sides along new built forest roads. Vegetative reproduction by aerial shoots from rhizomes predominate in intact and moderately disturbed vegetation (Flower-Ellis 1971; Moubon et al. 1995; Schimmel and Granström 1996).

Berry production

On average, about 250 million kg of bilberries are produced on productive forest ground in Sweden every year, which is equal to c. 10 kg of berries/ha (Kardell 1980). Forests with a pre-dominance of bilberry have much greater berry production than average, and it can produce more than 160 kg/ha (Sjörs 1989; Salo 1995). Only c. 2-8% of the total berry production is gathered by humans (Eriksson et al. 1979; Hultman 1983; Salo 1995). Berry picking for household use is common in Sweden, but it is also a source of seasonal income, especially in northern provinces.

Bilberry spruce forest

Historically, the main large scale disturbance factor in boreal conifer forests of northern Sweden is fire (Östlund et al. 1997; Hörnberg et al. 1998; Niklasson and Granström 2000). Fire frequency ranges from 50 years on dry sites to 150 years on mesic to moist bilberry sites (Zackrisson 1977; Engelmark 1984). Early postfire succession in these forests is characterized by even aged stands of pioneer tree species birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.), aspen (*Populus tremula* L.) and pine (Kuusela 1990). In late succession the more shade-tolerant Norway spruce takes over and forms multi-aged sparse forest stands. Field and bottom layer vegetation are mostly sparse in young successions and grow more densely with age, especially when the tree layer becomes more open in late succession (Sirén 1955). Bilberry co-dominates together with lingonberry (*Vaccinium vitis-idaea* L.) in early succession and with crowberry (*Empetrum hermaphroditum* Hagerup) in late succession (Sirén 1955; Nilsson 1992; Wardle et al. 1997; Økland 2000). Moss cover in bilberry communities increases during secondary succession and feathermosses (mostly *Pleurozium schreberi* (Bird) Mitt. and *Hylocomium splendens* (Hedw.) B.S.G.) often become totally dominant. Clear-cutting increases light penetration and humus mineralisation that normally favors more nitriphilic and light demanding plant species, most commonly Wavy hair-grass (*Deschampsia flexuosa* (L.) Trin.). However, forest floor vegetation in high altitude bilberry forests within the northern boreal zone deviate from this pattern and change little after clear cutting (Ingelög 1974). This difference may depend on lower mineralisation and evapotranspiration at northern latitudes. Today fire is greatly limited by active suppression, causing logging to be the main large disturbance factor in the Swedish boreal forest (Östlund et al. 1997; Axelsson 2001). Small scale disturbance by wind, snow, herbivory, insect or fungal attack may be important factors locally and in late successional boreal forests (Siren 1955; Kuuluvainen 1994; Engelmark 1999).

Biomass production of ground layer vegetation is highest in late successional bilberry spruce forests and can exceed that of the tree layer (Romell 1939; Mork 1946; André 1947; Havas and Kubin 1983). Litter and humus produced by ericaceous dwarf shrubs and feathermosses have high C:N ratios and high contents of phenolic compounds that form protein-phenolic complexes (Hagerman 1989; Gallet and Lebreton 1995) which are notoriously resistant to microbial attack (Swift et al. 1979; Wardle and Lavelle 1997). Besides the recalcitrant litter, the dense moss layer also lower soil temperature, which may contribute to slow decomposition rates (Sirén 1955; van Cleve et al. 1986). Thick humus layers, therefore typically characterize late successional bilberry-spruce forests (Kubin 1983; Tamm 1991; Wardle et al. 1997). These organic soil horizons represent a large reservoir of nutrients, including N, however, slow N mineralisation strongly reduces the amount of N readily available for plant uptake (Tamm 1991).

Tree regeneration

Tree regeneration is known to be poor in northern boreal bilberry spruce forests (Arnborg 1943; 1947; Sirén 1955; Lundquist 1989; Kuuluvainen 1994). Seedling recruitment is dependent on seed source and suitable microhabitat for seed germination and seedling establishment. Production of viable seeds in northern boreal areas are highly variable depending on climatic conditions. Spruce has particularly long intervals between mast seed years which may negatively effect seedling recruitment (Hagner 1965). Phenol-rich litter and leaching of phytotoxic compounds from dwarf shrubs and mosses, and abiotic factors such as low moisture content and temperature in soil can negatively influence germination of tree seeds (**I**; Zackrisson and Nilsson 1992; Winsa 1995; Dolling 1996; Zackrisson et al. 1998; Mallik and Pellissier 2000). After germination, seedling roots must grow through the litter and upper humus layer to reach more stable moisture conditions. So, a fast initial growth are important for successful establishment (Winsa 1995). Predation of seeds and seedlings by slugs, voles and birds can also strongly affect seedling survival (Ericsson 1977; Nystrand 1998). However, once established, seedling growth also depends on the supply of above and below ground resources. Seedling symbiosis with mycorrhizal fungi plays an important role in improving seedling growth (Smith and Read 1997), however, limiting resources by competition from surrounding plants may be the most important factor for seedling performance (**II**; **III**; **IV**; Sirén 1955; Walter and Breckle 1989; Titus et al 1995; Zackrisson et al. 1995).

Objectives

Many factors, both biotic and abiotic can affect tree regeneration in the boreal forests. The dense cover of bilberry found in many boreal forest ecosystems can be expected to negatively interfere with tree seedling recruitment. However, the mechanisms that restrict tree regeneration are poorly understood. Alternative forestry methods based on less destructive techniques are urgently needed. The main aim of this thesis was to:

1. Investigate the mechanisms and relative impact of phytotoxicity and above- and below ground resource competition by which bilberry interferes with tree seedling establishment (e.g. seed germination and seedling survival, growth and nutrition).

2. Investigate the influence of soil water availability on seedling growth in boreal bilberry sites under normal summer conditions.

3. Test how site preparation by steam treatment of bilberry vegetation can improve Scots pine seed germination, seedling establishment, nutrition and mycorrhizal colonization.

Results and discussion

Major findings

Water soluble phenolic compounds in bilberry leaves have been claimed to reduce tree seed germination and seedling growth (André et al. 1987; Pellissier 1993; 1994; Gallet 1994). I studied the phytotoxic effects of senescent bilberry leaves under controlled conditions, in a series of water extract and seedbed experiments. Water extracts of bilberry leaves strongly reduced aspen seed germination (**I**; Figure 2). Root growth, number of fresh roots and number of upright grown seedlings were also negatively affected by bilberry leaf water extracts. Activated carbon (used as a sorbent to inactivate phenolic compounds) added to extracts reduced the negative effects of leaf extracts on seeds and seedlings.

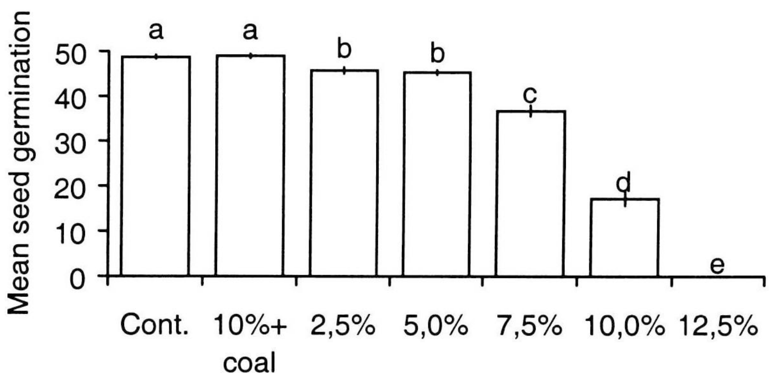

Figure 2. Seed germination of aspen (*Populus tremula*) exposed to different concentration of water extracts of bilberry (*Vaccinium myrtillus*) senesent leaves. Vertical line = standard error. Treatment with the same letter do not differ significantly in Tukey's multiple range test at $P \leq 0.05$, (**I**).

Senescent bilberry leaves, used as a seedbed, negatively effected seed germination of pine, spruce and silver birch (*Betula pendula* Roth.), but not aspen (**I**). Non-germinated seeds (after 21 days) of pine, spruce and birch were rinsed in water and placed to germinate in petri-dishes with distilled water to evaluate if they were nonviable or quiescent (**I**). Rinsing of pine and spruce seeds removed the negative effects of bilberry leaves and increased germination of pine up to the same level as the control. The increase of birch germination after rinsing was small and not significant.

In a pot experiment, sand substrate covered with senescent bilberry leaves reduced rooting ability and growth of pine and spruce seedlings (**I**). Additionally slightly decomposed leaves, used on top of sand reduced pine and spruce rooting ability and growth, but not to the same extent as senescent leaves. Repeatedly soaked and water rinsed bilberry leaves, had similar physical structure, but reduced toxicity compared to unsoaked leaves and had little or no negative effect on seedling establishment and growth.

In a field experiment with seeded Scots pine, it was found that bilberry negatively influenced seed germination and seedling survival (**IV**). There were only small phytotoxic effects on pine seedling growth and nutrient uptake. In a second field experiment with transplanted spruce seedlings, there were no phytotoxic effects found on seedling survival, growth or nutrient uptake (**II**). Under field conditions, bilberry phytotoxic compounds were concluded to more negatively influence conifer seed germination and early seedling survival than growth and nutrient acquisition of established seedlings.

Reduced below ground competition from bilberry resulted in increased spruce and pine seedling growth and nutrient uptake (**II**; **III**; Figure 3). Spruce seedling survival and mycorrhizal colonization were also positively influenced by reduced below ground competition. Reduced competition for water had only modest positive effects on spruce seedling biomass and nitrogen content, while pine seedlings were unaffected (**III**). The lack of statistically significant plant response to water addition indicates that water does not greatly limit growth in this region and may imply a more important role of nutrients in conifer growth

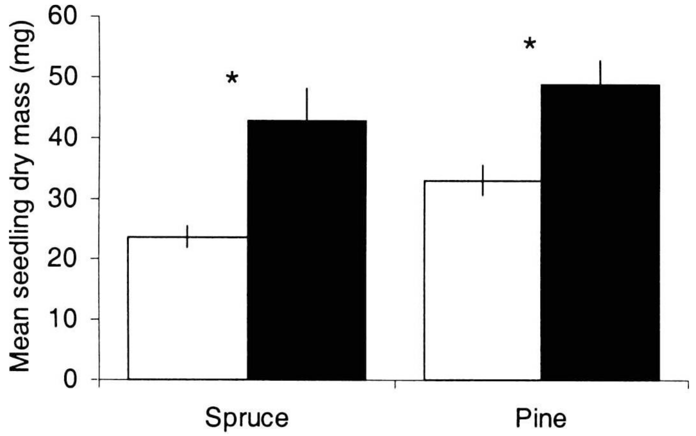

Figure 3. Mean ± SE dry mass growth of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) seedlings after two growing seasons grown in present (open) or reduced (filled) below ground competition by bilberry (*Vaccinium myrtillus*) vegetation.
* = indicate significant difference in Tukey's multiple range test at $P \leq 0.05$, (**III**).

productivity in a bilberry dominated ecosystem. Spruce seedling root growth and mycorrhizal colonization were increased by reducing above ground competition for light, however shoot length, shoot to root ratio (S:R) and seedling survival were reduced by higher light penetration (**II**).

Steam treatment effectively killed bilberry vegetation and recolonization was found to be very slow (**IV**). Scots pine seed germination was enhanced in steamed plots in the first year after treatment. When harvested after four years, Scots pine seedling biomass and nutrient content was higher in steamed than in intact vegetation. Species richness and the proportion of roots colonized by mycorrhizal fungi were not altered by steam treatment (**IV**).

Phytotoxicity of bilberry

Bilberry leaves contain a range of water soluble phenolic compounds including tannins, flavonoides, and phenolic acids (Pellissier 1993; Gallet and Lebreton 1995). Many of the phenolic compounds produced by bilberry have known phytotoxic effects on seed germination and seedling growth (Rice 1984; Einhellig 1987; Pellissier 1993; Gallet 1994). Phytotoxic compounds can be released as throughfall or leachates of water soluble compounds or following decomposition of more complex compounds (Rice 1984; Nilsson 1992; Gallet 1994; Gallet and Lebreton 1995). To separate between phytotoxic and non-phytotoxic effects of bilberry, I used activated carbon in several experiments with seeds and seedlings. Activated carbon has the capacity to adsorb and inactivate phenolic compounds without direct effects on seed germination, seedling growth and nutrition (Eliasson 1959; Mahall and Callaway 1992; Nilsson 1992; Yambe et al. 1992; Nilsson et al. 2000). In bioassays, addition of activated carbon reduced the negative effects of water extracts on aspen seed germination and growth (**I**). This suggests that the negative effects are caused by the water soluble phenolic compounds in bilberry leaves and/or their early degradation products. A seedbed of bilberry leaves inhibited pine and spruce seed germination, however, non germinated seeds (at the end of the experiment) were able to germinate after being rinsed in water (**I**). These results indicate that the compounds responsible for the inhibition were non lethal and that the inhibition is reversible.

Aspen seed germination was strongly suppressed by water extracts but less inhibited by senescent leaves when used as a seedbed (**I**). The opposite pattern was found for pine and spruce seeds where leaves inhibited seed germination more than water extracts. The results may depend on those chemical compounds present in water extracts compared to in intact leaves. Water extracts contain substances that may be easily released and are water soluble. In contrast, the compounds in leaves (used as seedbeds) may be released during the entire experimental period (7-21 days). Therefore, the seedbed leaves may contain hydrophobic compounds that are only released upon decomposition. The decomposition of leaves during the experimental period may either increase or decrease the amount and toxicity of compounds. However, seeds of different species can also vary in there sensitivity to phytotoxic compounds (Rice 1984; Nilsson 1992). The results may therefore also be explained by species specific related variations in response to compounds that originate from bilberry.

Litter and humus under bilberry are rich in phenolic compounds, mostly consisting of tannins and phenolic acids (Gallet and Lebreton 1995). The greatest amounts of phenolic compounds in soils are found in early spring before biological activity increases (Gallet 1994; Gallet and Lebreton 1995). At one field site I collected litterbags with decomposed bilberry leaves in early spring and used them as surface litter in a pot experiment with pregerminated pine and spruce seeds (**I**). Decomposed leaves reduced the number of rooted seedlings to about half of that found in the control pots with peat (Figure 4). High concentrations of phenolic compounds in bilberry litter during early spring may explain the negative effects on pine and spruce rooting ability. In the same experiment I also used senescent and water soaked bilberry leaves as surface litter in pots. Soaked leaves had similar physical structure, but reduced phytotoxic capacity compared to senescent leaves. Rooting ability of pine and spruce seedlings in senescent leaves were less than 25% of that found in treatments with soaked leaves. Seedling establishment in the treatments with soaked leaves was at the same level as found in the peat control. These results show that the chemical constitution rather than physical structure is important for seedling establishment in bilberry litter. Biomass growth of pine and spruce seedlings after seven days followed the same pattern as for rooting ability (Figure 5). Seedling biomass in treatments with senescent leaves was much lower than in peat control while seedlings in soaked leaves were only slightly affected.

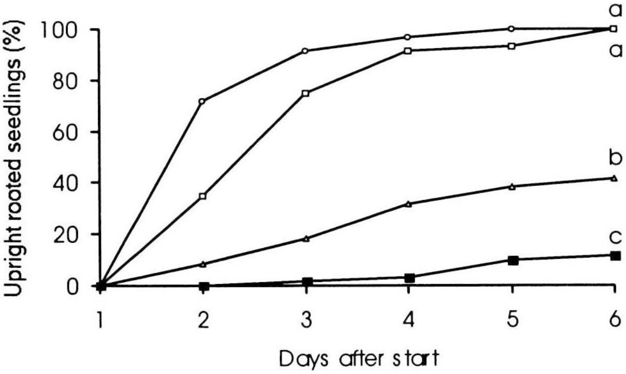

Figure 4. Proportion of upright rooted Norway spruce (*Picea abies*) seedlings in senescent (■), decomposed (△) and soaked (□) bilberry (*Vaccinium myrtillus*) leaves, and in control (○, peat). Treatment with the same letter do not differ significantly in Tukey's multiple range test at $P \leq 0.05$, (**I**).

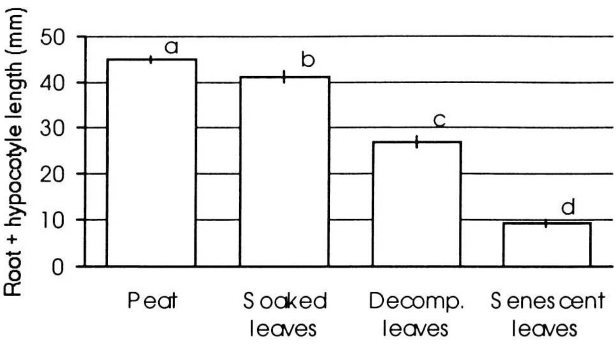

Figure 5. Root + hypocotyle length of Norway spruce (*Picea abies*) seedlings in senescent, decomposed and soaked bilberry (*Vaccinium myrtillus*) leaves, and in control (peat). Vertical line = standard error. Treatment with the same letter do not differ significantly in Tukey's multiple range test at $P \leq 0.05$, (**I**).

High concentrations of phenolic compounds found in plants is often explained by abiotic factors such as high light levels, temperatures and carbon fixation, and low nitrogen availability (Rice 1984; Jonasson et al. 1986; Atlegrim and Sjöberg 1996; Koricheva et al. 1998). As these abiotic factors can vary over time it is reasonable to assume that the nature and amount of phenolic compounds in bilberry leaves also varies with season. An experiment was performed during three vegetation periods with the purpose to investigate seasonal variations in phytotoxicity of bilberry leaves. Water extracts of leaves collected approximately every second week during the vegetation season were used in bioassays with aspen seed germination (unpublished data). The experiment showed that bilberry leaves found early and late in the growing season had strong negative effects on aspen seed germination (Figure 6). Earlier studies have found higher concentrations of phenolic compounds in premature leaves than in mature leaves (Cooper-Driver et al 1977; Waterman and McKey 1989). As new leaves in spring are thin and have weakly developed cuticula, water soluble phytotoxic compounds may be easily leached out. The reason for the increased toxicity found in leaves during the autumn is unclear. However, a study in the Alps, showed that senescent bilberry leaves collected in the autumn had 80% lower flavonoid and 90% lower phenolic acid concentration while tanning capacity was 110% higher than in green leaves (Gallet and Lebreton 1995). Similar changes in the proportion of different phenolic compounds may explain the increased inhibition of seed germination found in late season leaves. Seasonal production of phytotoxic compounds and resultant effect on seed germination has also been found in *Empetrum hermaphroditum* and *Pteridium aquilinum* (Dolling et al. 1994; Nilsson et al 1998; Wallstedt et al. 2000).

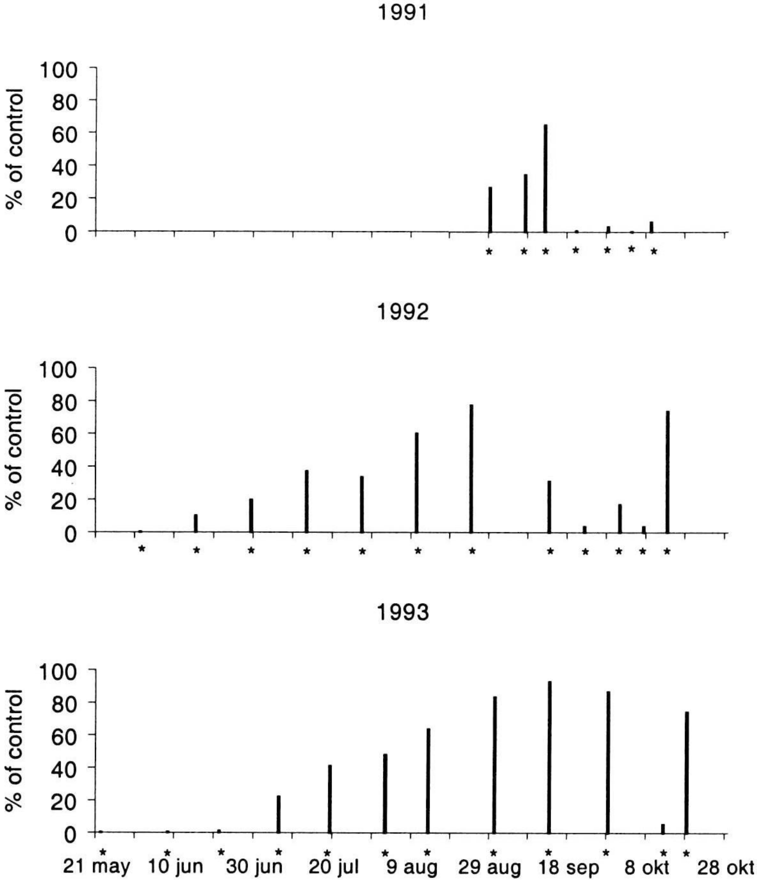

Figure 6. Mean (% of control) seed germination of aspen (*Populus tremula*) tested in water extracts of bilberry (*Vaccinium myrtillus*) leaves collected during the three growing seasons. * indicate day of collection.

In a field experiment with seeded pine, seed germination was lower in intact bilberry vegetation than in activated carbon treated bilberry vegetation (**IV**; Figure 7). Bilberry vegetation has been shown to increase the amount of phenolic compounds in throughfall compared to incident rain (Gallet and Pellissier 1995). Throughfall collected under bilberry has also been found to have inhibitory effects on spruce seed germination when tested in bioassays (Gallet 1994). The low rate of pine germination found in intact bilberry vegetation (**IV**) may be a combined effect of throughfall or leachates from bilberry shoots and high concentrations of water soluble phenolic compounds in litter when seeds imbibe in spring.

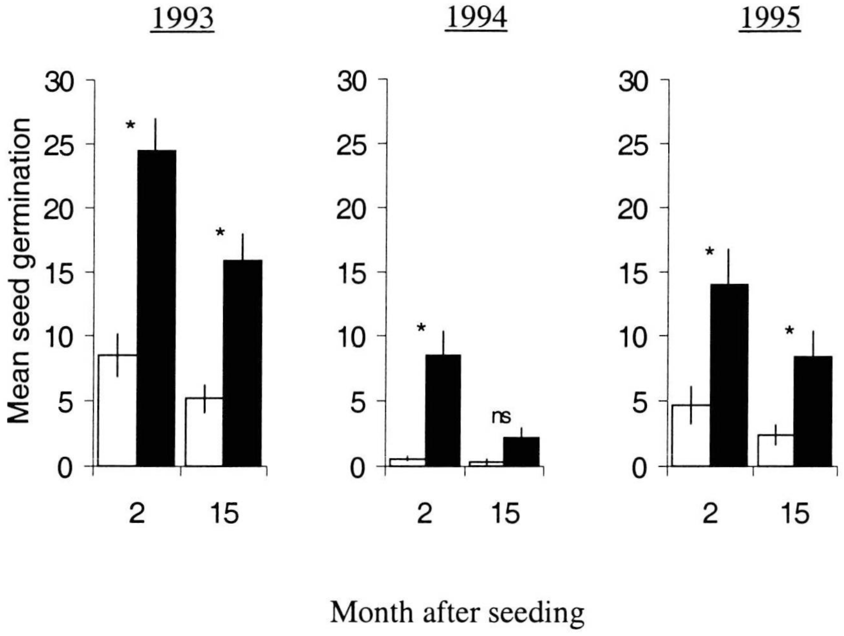

Figure 7. Mean ± SE seed germination of Scots pine (*Pinus sylvestris*) in intact (open) and in activated carbon treated (filled) vegetation 2 and 15 month after seeding in 1993, 1994 and 1995. * = indicate significant difference in Tukey's multiple range test at $P \leq 0.05$, ns = non significant, (**IV**).

These results show that bilberry can release phytotoxic compounds under field conditions that may inhibit seed germination. In contrast, the phytotoxic effects on seedling growth appear to be weak. In these studies, however, I have only focused on chemical interactions that occur in the litter layer near the soil surface. Activated carbon added to the soil surface may not reduce possible exudation products from bilberry roots. Still little is known about other effects of bilberry phytotoxicity on forest ecosystem components such as nutrient immobilization, decomposition, and microbial activity in soils (Ponge et al. 1998; Pellissier and Souto 1999).

Resource competition

Reduced above ground competition of bilberry had negative effects on spruce seedling survival at the studied clear-cut site (**II**). Clear-cut sites in northern Sweden are frequently exposed to night frost during the growing season (Lundmark 1996). Spruce seedlings are specifically known to suffer from summer night frost especially when followed by direct solar radiation (Lundmark and Hällgren 1987; Kuusela 1990). Bilberry vegetation is suggested to reduce strong temperature variations at the ground level (Bjor 1972). These shelter effects may explain the increased seedling survival observed at the clear-cut site.

Exclusion tubes and steam application were used to reduce below ground competition by bilberry. All of these treatments increased pine and spruce seedling growth and nutrition (**II**; **III**; **IV**). Spruce seedlings grown in experimental treatments with reduced below ground competition (i.e. PVC-tubes) had high nutrient concentrations in combination with high biomass growth (**II**; **III**). These results point to increased nutrient availability for spruce seedlings grown in treatments with reduced below ground competition (Chapin 1980; 1987; Neary et al. 1990; Munson and Bernier 1993). Nitrogen uptake has repeatedly been identified as an important factor controlling coniferous seedling growth in boreal sites (Tamm 1991; Timmer and Munson 1991). Therefore, increased N availability and higher N content in spruce seedlings are probably linked to the higher growth rate found in plots in which below ground competition was reduced. Ground vegetation of ericaceous dwarf shrubs in coniferous forest ecosystems can compete effectively for available N, and this may strongly restrict new tree seedling growth (Messier 1993; Nilsson 1994; Prescott et al.1995; Steijlen et al.1995; Titus et al. 1995; Zackrisson et al.1995).

Ericoid mycorrhiza colonized roots are located in the uppermost part of the humus layer, on average, they are higher up and closer to the litter layer of mosses and vascular plants than ecto-mycorrhizal fungi (Read 1991; Zackrisson et al. 1997a). Ericoid mycorrhizae also have a stronger enzymatic capacity for mobilization of nutrients from litter with complex organic compounds and a faster uptake rate of organic N than ectomycorrhizae (Haselwandter et al. 1990; Read 1991; Read 1996; Nordin 1998; Näsholm et al. 1998). A mechanism has been suggested by which nutrients are directly transferred from senescent feathermosses to roots of ericaceous dwarf shrubs via ericoid mycorrhizal fungi in a similar vegetation type as described in this thesis (Zackrisson et al. 1997a; 1998; 1999). This three part (feathermoss-ericoid mycorrhiza-ericaceous plant) biotic interaction may form a tight nutrient cycle which greatly excludes nutrient availability to coniferous species thereby reducing regeneration. The increased growth and nutrition of conifer seedlings in treatments with reduced below ground competition (PVC-tube root exclusion and steam treatment) described in this thesis may partly be a result of reduced blocking effects by this biotic mechanism.

Despite high nutrient concentrations and biomass growth, the S:R in spruce seedlings grown for three years in treatments with reduced below ground competition were low (**II**). A low S:R and associated high root growth indicates deficiency of soil nutrient resources, especially N, P and S (Wilson 1988; Hutchings and de Kroon 1994; Ericsson 1995). As the tubes have a limited soil volume, it is reasonable to assume that nutrient limitation or imbalance are the cause for the low S:R. However, the limited tube volume did not reduce total seedling biomass growth. The N concentration found in seedlings indicates that they acquired enough N needed for direct biomass growth, unless other nutrients were in short supply (Ingestad 1977; 1979; Chapin et al. 1990; Timmer 1991;

Nordin 1998; Glimskär and Ericsson 1999). Phosphorous and S are both negatively imbalanced in relation to N in tube treatments in study **II** according to balance levels described by Ingestad (1979). The decreased S:R is likely a result of high N:P in plant tissue (Timmer 1991; Ericsson 1995). Sulfur is less likely to be the reason for the imbalances as the concentration in seedlings do not differ between tube and non tube treatments. Other nutrients (i.e. Ca and K) are known to have a neutral or slightly beneficial effect on S:R (Ericsson 1995). Water limitation may also lower the S:R (Wilson 1988; Ericsson et al.1996), however low S:R are usually associated with lower total growth which is not the case here (Ericsson et al. 1996).

Water addition in study **III** had small positive, but mainly non-significant effects on pine and spruce seedling growth and nutrition. However, spruce responded more positively to water addition than pine. These results indicate that availability of soil water in northern boreal bilberry vegetation probably is adequate for seedling growth and nutrition during normal conditions, at least for pine. The high elevation, the fine textured soil and the humid climate caused by low temperature and low evapotranspiration may produce soil moisture conditions sufficient for successful conifer seedling establishment (Söderström 1976; Lundmark 1988; Eriksson and Odin 1990). However, water is also important for soil microbial activity, mineralisation and nutrient movement (Bowen 1984, Chapin 1991; Schimel et al. 1999). All these processes can increase nutrient availability following water addition and may partly explain the few positive growth responses found in spruce. Inherently different life history characteristics of the two conifer species may also play a role for the different responses (Chapin et al. 1986, 1990; Tamm 1991). Spruce is assumed to be a more N demanding species than pine, and is known to respond more rapidly to increased nutrient availability (Tamm 1991, Nikolov and Helmisaari 1992).

The sparse structure of the northern boreal forest and the long day length during summer at high latitudes will normally allow a sufficient light availability for plant growth (Siren 1955; Kuusela 1990; Kuuluvainen 1994). However, a dense cover of field layer species has the potential to decrease light intensity and thus reduce young tree seedling growth. The light levels for young spruce seedlings grown under a canopy of bilberry was c. ¼ of that for seedlings grown outside the canopy (**II**). This light reduction did not cause a significant decrease in total seedling biomass, however, biomass allocation to roots was decreased resulting in an increased S:R ratio. This allocation pattern may function to improve seedlings access to better light conditions through extended shoot growth above the field layer vegetation (Morgan 1981).

Use of steam for control of bilberry vegetation

Steam treatments effectively killed bilberry vegetation and recolonization after treatment was very slow, independent of whether steam was applied in spring or autumn (**IV**). Comparable effects of steam treatment were reported from vegetation types dominated by *Empetrum hermaphroditum* (Zackrisson et al. 1997b) and *Calluna vulgaris* (Norberg et al. 2001) in northern Sweden and *Deschampsia flexuosa* (Norberg 2000) in southwest Sweden. Comparisons four years after treatment also showed that steam is equally effective as mechanical soil scarification in controlling bilberry vegetation (Norberg et al. 1997).

The primary mechanism by which steam treatments control bilberry vegetation and improves stand regeneration is by reducing resource competition. Steam treatment has only a small positive effect on seed germination and seedling establishment (**IV**). Seed germination and initial seedling establishment are probably more dependent on phytotoxicity and abiotic factors than on resource competition (**I**; Winsa 1995). However, growth of seeded Scots pine seedlings was strongly enhanced by reduced competition from bilberry vegetation following steam treatment (**IV**; Figure 8). Seedling biomass increase in steamed plots after four years was 275% greater than seedlings grown in intact vegetation. The increase in growth is of the same magnitude as for steam treatment of *Empetrum* and somewhat higher than *Calluna* vegetation (Zackrisson et al. 1997b; Norberg et al. 2001). These results show that steam treatment, when used to reduce competition of ground vegetation and to improve seedling growth is a useful alternative to mechanical soil scarification in *Ericaceous* vegetation. To improve seed germination some additional treatments may be needed, for example addition of activated carbon. Containerized seedlings planted after steam treatment in ericaceous vegetation is also reported to have improved growth (Norberg 2000).

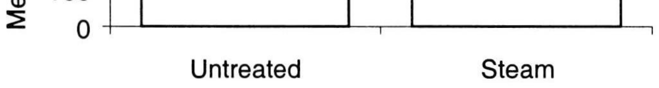

Figure 8. Mean ± SE dry mass of Scots pine (*Pinus sylvestris*) seedlings after four growing seasons grown in untreated or steam treated bilberry (*Vaccinium myrtillus*) vegetation. Treatment with the same letter do not differ significantly in Tukey's multiple range test at $P \leq 0.05$, (**IV**).

In addition to reduced competition, reduced input of phenol-rich litter from ericaceous plants after steam treatment may facilitate residue decomposition and increase seedling growth (Horner et al. 1988; Northup et al. 1995; Smith and Read 1997). Nitrate leaching which is a negative environmental effect of soil scarification, may be a less severe problem with steam treatment as the humus layer is left intact (Rosén and Lundmark-Thelin 1986; Johansson 1994). No negative long-term effects on soil microbial activity or seedling mycorrhizal colonization were found after steam treatment (**IV**; Norberg et al. 1997).

Mechanical site preparation involving patch soil scarification is performed on about 75% of all clear-cut sites in Sweden (Anon. 2000a). There are some very real and potentially long-term environmental impacts associated with such mechanical soil scarification (Rosén and Lundmark-Thelin 1986; Johansson 1994; Anon. 1995; Humphrey et al. 1995). There have also been concerns raised about the conservation of ancient archeological remains on forest ground (Anon. 2000b). Therefore there is clearly a great need to develop alternative site preparation methods that are environmentally acceptable, maintain site productivity and that allow for efficient tree regeneration. Steam treatment may be such an alternative in areas where competition from ground vegetation is the main reason for site preparation. However, there are still technical difficulties to be solved before steam can be commercially used for vegetation control in forestry (Norberg 2000).

Concluding remarks

Dense ground cover of bilberry can reduce light availability, but also shelter seedlings against low and harmful temperatures (**II**). Bilberry also produces large amounts of phenol rich litter which mediates in net immobilization of nutrients (Gallet and Lebreton 1995; Wardle et al. 1997). Below ground competition by an extensive system of thin bilberry roots greatly reduces nutrient availability by other plants (**II**; **III**,; **IV**; Persson 1978, 1980; Havas and Kubin 1983; Malmer and Wallén 1986; Read 1991). The ericoid mycorrhizal symbioses also provides a nutrient uptake advantage for bilberry over that of emerging tree seedlings (Read 1996; Smith and Read 1997; Souto et al. 2000). Altogether, these characteristics illustrate the ability of bilberry to interfere with energy and nutrient turnover in boreal forest ecosystems and to at least partially block resources for new establishing tree seedling cohorts.

The main conclusions of this thesis are:

- Bilberry has the capacity to influence on establishment and growth of conifer seedlings in boreal forest ecosystems.
- Phytotoxic compounds in leaves and litter of bilberry have the potential to inhibit tree seed germination.

- Tree seedling growth is mainly limited by below ground resource competition for nutrients.
- Competition for water is concluded to have only minor effects on tree seedling performance.
- Vegetation control by steam treatment effectively killed bilberry vegetation and strongly improved tree seedling growth and nutrition.

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III

Influence of soil moisture and below ground competition by *Vaccinium myrtillus* on *Picea abies* and *Pinus sylvestris* seedlings in a northern boreal forest site

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Abstract

Below ground competitive effects of bilberry (*Vaccinium myrtillus*) vegetation may reduce conifer seedling growth and nutrient acquisition. A field experiment was set up in a clear-cut site dominated by bilberry vegetation to determine the effects of competition for moisture and nutrients by bilberry vegetation on Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) seedling growth and nutrition over a two year period. Exclusion tubes were used to reduce total below ground competition in intact plots, and plots were amended with water two times a week in July each year to reduce competition for water. Reduced below ground competition significantly increased spruce and pine seedling biomass and nitrogen content in both years, and for spruce also increased N concentrations and reduced C to N ratios of tissues. Water addition had a small positive but mostly non-significant effect on seedling biomass and nutrition. Spruce reacted more positively to water addition than did pine. The effects of exclusion tubes gave equal results to seedling grown in intact and in water amended plots indicating that competition for nutrients rather than water are mainly responsible for limiting tree seedlings in bilberry vegetation.

Keywords: summer precipitation, seedling growth, nutrient acquisition, shoot:root ratio, tree regeneration failure, exclusion tubes, ericaceous dwarf shrub.

Introduction

Interference from ground vegetation dominated by ericaceous species, often has significant negative impacts on tree seedling recruitment in boreal forests (Sirén

1955; Messier 1993; Nilsson 1994; Zackrisson et al. 1997; Pellissier and Souto 1999; Norberg et al. 2001). Competition for below ground resources by plants have repeatedly been shown to reduce plant regeneration and growth, especially in sites with low nutrient levels (Putz and Canham 1992; Nilsson 1994; Titus et al.1995; Nilsson et al. 1996; Örlander et al. 1996; Jäderlund et al. 1997). Plant available nitrogen is usually the most limiting resource in boreal forest and has been suggested as the most important nutrient causing resource competition between plants (Chapin 1980; Tamm 1991). Lack of water has also been suggested as an important factor for reducing conifer seedling establishment and growth especially during the first years of seedling emergence (Örlander 1984; Grossnickle 1988; Nilsson and Örlander 1995; Zackrisson et al. 1998). Besides the direct negative effects of low water availability on seedling performance, soil water content also affects soil microbial activity, decomposition and mineralisation rates, and soil nutrient movement, which can in turn affect nutrient supply rates from the soil and therefore influence seedling growth (Bowen 1984; Casper and Jackson 1997; Schimel et al. 1999).

In Sweden, bilberry (*Vaccinium myrtillus* L.) is one of the most common species of ericaceous plants and is the dominant ground vegetation component in the widespread *"Picea abies - Vaccinium myrtillus"* mesic forest type (Sjörs 1965; Walter and Breckle 1989; Påhlsson 1994). However, the relative importance of soil water and nutrients for reduced tree seedling growth in this type of ericaceous vegetation is unclear. The main objective of this study was to determine; (i) if conifer seedling growth and tissue nutrient concentrations are limited by natural soil moisture availability; and (ii) the relative importance of competition by bilberry for soil moisture and for nutrients on conifer seedling growth and nutrition.

Materials and methods

Study area

The experimental area (Skavliden, 65° 35' N; 18° 38' E, 450 m above sea level), is located within the Northern boreal zone (Ahti et al., 1968) of Sweden, and was clear-cut in the winter of 1991/1992. Before harvest, the forest represented a late post fire succession dominated by Norway spruce (*Picea abies* Karst.) with scattered individuals of Scots pine (*Pinus sylvestris* L.) and birch (*Betula* spp.). The forest floor vegetation was dominated by bilberry (*Vaccinium myrtillus*) and the pleurocarpous feathermosses *Pleurozium schreberi* (Brid) Mitt. and *Hylocomium splendens* (Hedw.) B.S.G. The site was on a mor humus podzol overlaying a fine-textured mineral soil. Five years after clear-cutting the site was still dominated by bilberry in the field layer and pleurocarpous feathermosses in the bottom layer. However, the total cover of mosses had decreased to c. 50% of what was present in the uncut forest (Jäderlund et. al. 1998). Mean humus depth was 67.7 ± 2.5 mm (n=62) in the experimental plots.

Experimental design

In June 1997, 32 pairs of plots were setup, each of which was 0.5 x 0.5 m. For each pair, one plot was left intact, and the other was amended with water. The water was added in order to reduce below ground competition for soil water between tree seedlings and bilberry vegetation.

In each plot, four equivalent planting positions were chosen and two were randomly allocated to each of the two following treatments: (1) Reduction of below ground competition by bilberry and (2) no reduction of competition. Reduction of below ground competition was achieved by pressing a thin-walled PVC tube (100 mm long, 50 mm diameter) through the humus and in to mineral soil so that the upper edge of the tube was at the level of the ground surface. The tubes acted as a physical barrier between bilberry roots outside and the tree seedling roots inside the tube, reducing the total below ground resource competition of bilberry vegetation against tree seedlings.

Plantage seeds of Norway spruce (*P. abies*, Lill Pite, 65°00'N, 370 m.a.s.l, 98 % viability) and Scots pine (*P. sylvestris*, Skaholma, 66°00'N, 360 m.a.s.l, 96% viability) were germinated at 20°C on moist unfertilised quartz sand in a greenhouse. On 18 and 19 June 1997, (10-14 days after emergence), two of the four planting positions in each plot (one with reduced bilberry competition and the other without reduced competition) were planted with two pine seedlings; the other two were planted with two spruce seedlings each. Plots were watered immediately before and after planting to reduce initial mortality due to desiccation. To prevent predation of the seedlings by slugs, the slug-bait Mesurol (Bayer, Germany) was applied outside each plot.

Climatic conditions and water addition treatment

For the standard period 1961 to 1990, the mean annual precipitation in the experimental area was 626 mm, and the mean monthly precipitation for June, July and August was 57 mm, 92 mm, and 81 mm, respectively (Data from Storberg meteorological station located 10 km southeast of the study area, 453 m above sea level). For this period the mean annual air temperature was -0.7°C, and the daily mean air temperature for June, July and August was 10.8°C, 12.7°C, and 10.4°C, respectively. The highest precipitation recorded in July at Storberg meteorological station during 1944-1995 was 224 mm and lowest was 22 mm.

The growing season (June to August) in 1997 was warmer and generally drier than what is normal for the region (Anon 1997a). Precipitation was mostly from showers (thunderstorms) and unevenly distributed over the region. During July, the daily mean temperature was 3°C warmer than normal and in the middle of the month a 10 day long dry period occurred (Anon 1997b). Total precipitation in

July at the experimental site, measured 1.2 m above ground level with a electronic rain-gauge (precision ± 5%; Digi-rain, Heraco, Sweden) was 87 mm, with a dry period of 14 days in the middle of the month (10-24 July). The growing season during 1998 generally had higher precipitation than normal, although daily mean temperature in July was close to normal for the region (Anon. 1998a, 1998b). Despite the high amounts of rain in the region, the precipitation at the experimental site during July 1998 was only 50 mm, and the rain was more evenly distributed during that month than in July 1997.

For each water addition plot, four liters of tap water were added two times every week from 26 June to 31 July during 1997 and from 22 June to 30 July during 1998. This added amount of water is equivalent to a precipitation of c.180 mm. The treatment period of late June to late July was selected because this is usually the period of the year during which moisture is the most limiting. Moisture deficit are less in June because of the effects of snowmelt, and in August because of lower temperatures and hence reduced evapotranspiration. The tap water used in this experiment contains negligible amounts of nutrients (see Zackrisson et al. 1998 for details). Through this experimental setup it was possible to evaluate the effects of competition from bilberry for water from that for nutrients on the growth of spruce and pine seedlings.

Harvest, biomass and nutrient status of seedlings

About 40 seedlings from each species and each treatment were randomly harvested after one growing season on October 14, 1997. The remaining seedlings (c. 20 per species and treatment) were harvested after two growing seasons on September 30, 1998. During harvest, the seedlings were carefully excavated from the ground, brought to the laboratory, and stored at + 2°C until they were processed. Upon processing, the roots were gently rinsed in tap water and separated from the shoot. The shoots and roots of all seedlings were oven-dried (70°C, 72 h) to determine dry weights. For nutrient analysis, seedlings in each treatment were pooled together to eight independent samples per treatment. Samples were homogenised with a ball mill and analysed for concentration of the elements C and N, by combustion of dry material (Carlo Erba NA 1500).

Statistics

Data for plant dry mass and length, S:R ratio (log transformed data), C:N ratio, and nitrogen contents and nitrogen concentrations in spruce and pine seedlings were analysed using ANOVA, GLM followed by a univariate *F*-test, adjusted for split-plot design. All statistics were analysed with SPSS 10.0 statistical software.

Results

Biomass growth

Norway spruce seedling biomass and length parameters were positively and significantly affected by reduced below ground competition in both experimental years (Table 1; Figure 1; Appendix A). In 1998, total seedling biomass was 80% higher and current year shoot biomass was 214% higher when grown in reduced below ground competition from bilberry compared to seedlings grown without reduced competition. Scots pine seedlings produced significantly more biomass when competition was reduced than when competition was present; total seedling biomass was 24% greater in 1997 and 48% greater in 1998 when grown in tubes (Table 1; Figure 2). The effect of water addition on spruce seedlings biomass was generally small and non-significant (Figure 1). However, root biomass (in 1997),

Table 1. Mean ± SE current year shoot-, shoot-, and root- lenght (mm) of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) seedlings after two growing seasons grown in bilberry (*Vaccinium myrtillus*) vegetation subjected to water and below ground competition treatments.

	Water		
	added	not added	Stat[1]
Spruce			
c.y. shoot[2]	11.9 ± 1.7	10.6 ± 1.9	ns
shoot	42.5 ± 2.2	41.0 ± 2.4	ns
root	78.1 ± 3.3	67.0 ± 4.3	ns
Pine			
shoot	44.7 ± 1.3	44.7 ± 1.1	ns
root	91.8 ± 4.2	82.4 ± 4.1	ns
	Below ground competition		
	present	reduced	stat
Spruce			
c.y. shoot	6.3 ± 0.7	15.9 ± 2.0	***
shoot	35.7 ± 1.1	47.3 ± 2.5	**
root	65.0 ± 3.1	81.1 ± 3.8	***
Pine			
shoot	42.8 ± 1.0	46.2 ± 1.3	*
root	78.0 ± 4.1	94.2 ± 3.9	*

[1] Significance level within treatments *, **, *** = $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$, respectively; ns= non significant. [2] c.y. = Current year.

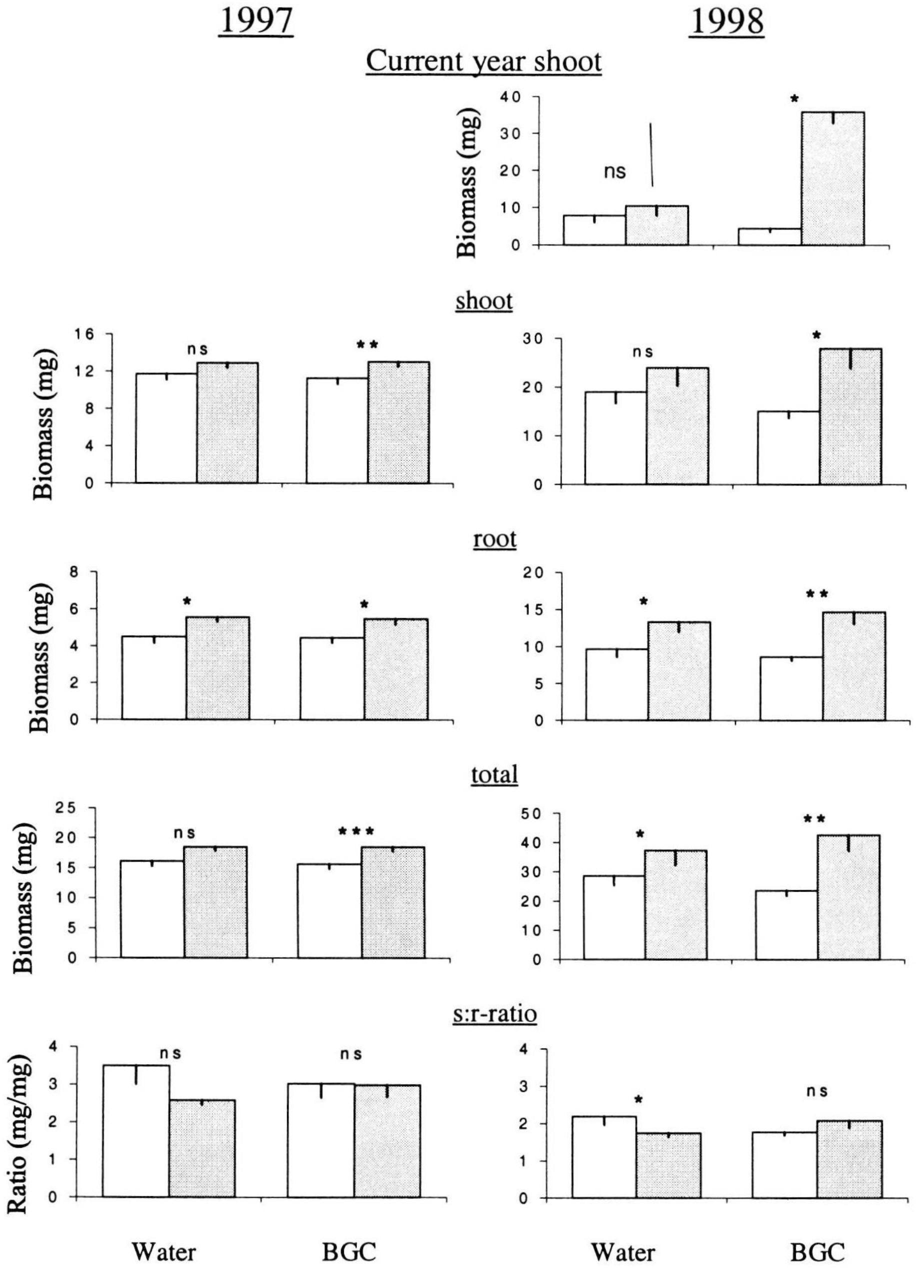

Figure 1. Mean -SE biomass parameters of Norway spruce (*Picea abies*) seedlings after one and two growing seasons grown in bilberry (*Vaccinium myrtillus*) vegetation subjected to two water levels (open = natural precipitation; filled = water addition) and two below ground competition levels (BGC; open = present BGC; filled = reduced BGC). Significance level within treatments *, **, *** = $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$, respectively; ns= non significant.

and root- and total seedling biomass (in 1998) were statistically higher for seedlings grown in water-amended plots than for those grown in non-amended plots (Figure 1). Scots pine also showed small positive responses of water addition, although none of these were statistically significant (Figure 2). S:R ratios were lower for both spruce and pine seedlings in water amended plots than in intact plots, but this effect was only statistically significant for spruce during 1998 (Figures 1 and 2).

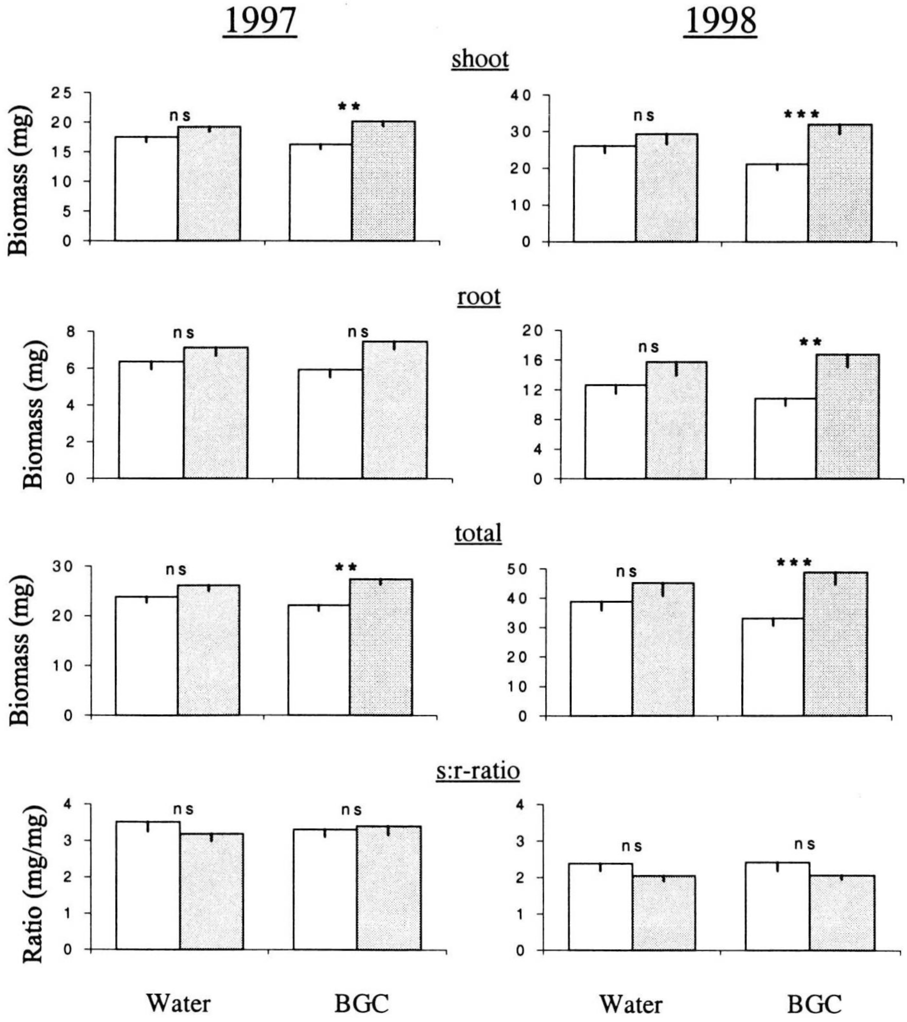

Figure 2. Mean -SE biomass parameters of Scots pine (*Pinus sylvestris*) seedlings after one and two growing seasons grown in bilberry (*Vaccinium myrtillus*) vegetation subjected to two water levels (open = natural precipitation; filled = water addition) and two below ground competition levels (BGC; open = present BGC; filled = reduced BGC). Significance level within treatments *, **, *** = $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$, respectively; ns= non significant.

Nutrients

For both years, nitrogen contents and concentrations of Norway spruce seedlings grown in plots where below ground competition from bilberry was reduced were significantly higher than for seedlings grown in plots with below ground competition present (Figure 3). For Scots pine seedlings, nitrogen contents were significantly higher when grown in reduced below ground competition from bilberry than when competition was not reduced, during both 1997 and 1998 (Figure 4). The C:N ratio for spruce seedling tissues was significantly lower in plots with reduced below ground competition, compared to seedlings grown in plots with below ground competition present (Figure 3). Scots pine tissue C:N ratios were lower in 1998 when competition was reduced, although this effect was not statistically significant (Figure 4). Water addition increased nitrogen

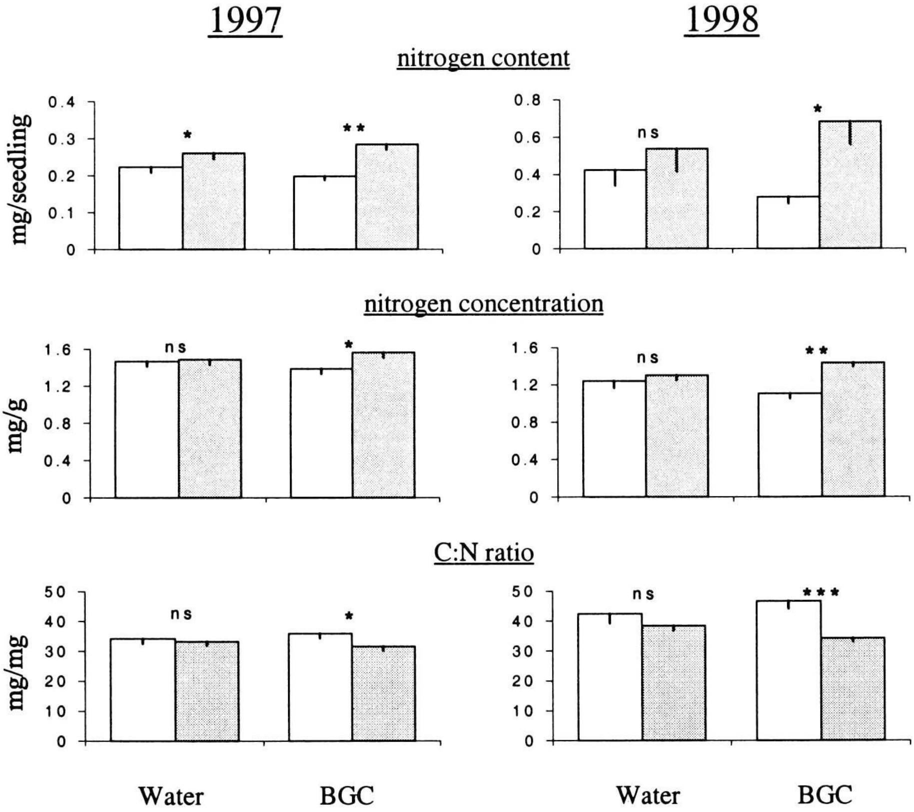

Figure 3. Mean -SE nitrogen content and concentration, and C:N ratio of Norway spruce (*Picea abies*) seedlings after one and two growing seasons grown in bilberry (*Vaccinium myrtillus*) vegetation subjected to two water levels (open = natural precipitation; filled = water addition) and two below ground competition levels (BGC; open = present BGC; filled = reduced BGC). Significance level within treatments *, **, *** = $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$, respectively; ns= non significant.

contents of spruce seedlings in 1997, but otherwise the nitrogen parameters of both spruce and pine seedlings were not significantly affected by water addition (Figure 3 and 4).

Species differences

Norway spruce generally responded more strongly to treatments than did Scots pine. This was particularly evident for seedlings grown with reduced below ground competition during 1998 (Figure 1 and 2). The relative biomass increment (tube vs. non-tube treatment) of spruce seedlings was 80%, meanwhile it was only 48% for pine seedlings in 1998. The increase in nitrogen content for Norway spruce seedlings were twice that for Scots pine seedlings in response to competition reduction, for both the first and the second season (Figure 3 and 4).

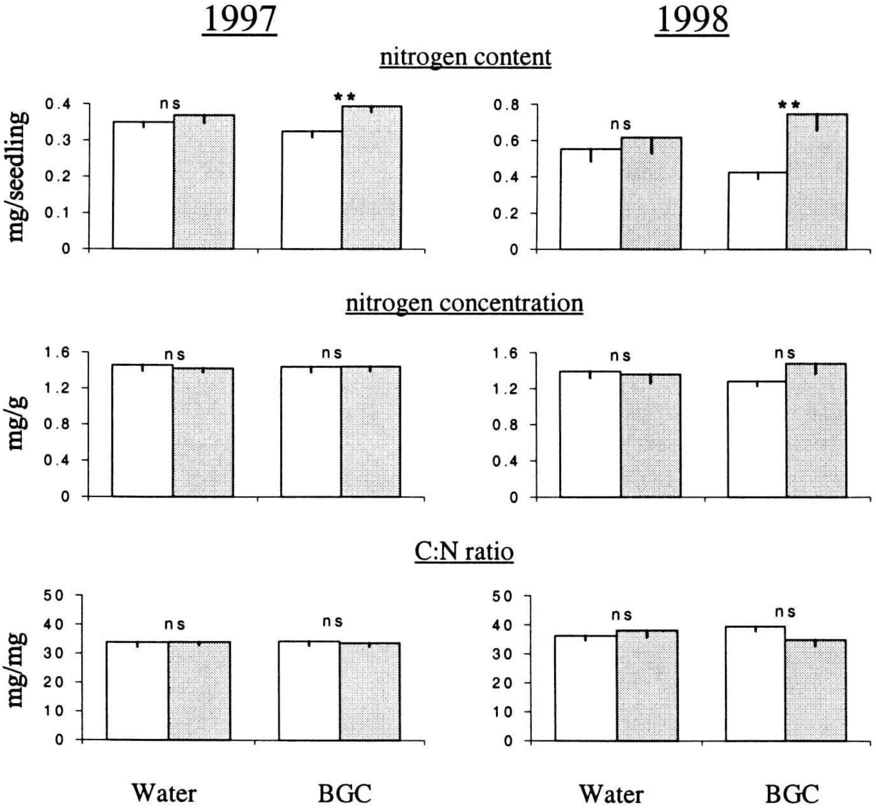

Figure 4. Mean -SE nitrogen content and concentration and C:N ratio for Scots pine (*Pinus sylvestris*) seedlings after one and two growing seasons grown in bilberry (*Vaccinium myrtillus*) vegetation subjected to two water levels (open = natural precipitation; filled = water addition) and two below ground competition levels (BGC; open = present BGC; filled = reduced BGC). Significance level within treatments *, **, *** = $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$, respectively; ns= non significant.

Discussion

Reduced below ground competition from bilberry vegetation is more important than water availability for both growth and nutrient acquisition of Norway spruce and Scots pine seedlings. Addition of water had some positive growth effects on Norway spruce, but Scots pine seedlings did not respond to additional water. These results imply that availability of soil water in bilberry vegetation is probably adequate for pine seedling growth and nutrition during normal conditions, and that below ground competition from bilberry restricts seedling growth of both pine and spruce.

In the present study, isolation of conifer seedling roots from the normal presence of bilberry roots was shown to increase early pine and spruce seedling biomass growth. This suggests that competition for below ground resources occurs and is consistent with studies showing that nitrogen availability is a key factor for growth of vascular plants in boreal forests (Chapin 1980, 1987; Tamm 1991; Munson and Bernier 1993). Soil water was not a key factor in reducing seedling growth, as the effects of water addition on seedling growth were small. The high nitrogen contents and nitrogen concentrations of pine and spruce seedlings in plots from which below ground competition from bilberry had been reduced also points to a higher availability of nitrogen in these plots than in plots where competition from bilberry occurred. Increased nitrogen concentrations and reduced C:N ratios of spruce seedlings grown in plots with reduced below ground competition from bilberry were, associated with increased concentration also of other nutrients in an earlier study in this site (i.e. P, Mg, S, K, Mn, Ca, Fe, and B; Jäderlund et al. 1997). This result suggests that in the present study, concentrations of nutrients other than nitrogen may also be higher for spruce seedlings grown in reduced below ground competition. It would appear that the reduced growth and nutrition of conifer seedlings when growing in bilberry vegetation is driven mostly by below ground competitive acquisition of bilberry for nutrients, most probably nitrogen. These results are consistent with those of other studies of below ground competition by ericaceous species on conifer seedling growth and nutrition in boreal areas (Messier 1993; Nilsson 1994; Prescott et. al. 1995; Titus et al. 1995; Zackrisson et al. 1997).

Root isolation by PVC-tubes is not likely to cause increased soil moisture availability for the seedlings compared to the situations in intact bilberry vegetation. There were no statistically significant interactions between water addition and reduced below ground competition in this study. These results also show that the effect of below ground competition is not dependent on water availability, since the effect of reduced below ground competition on seedling growth is the same in plots exposed to only natural precipitation as in plots also amended with water. Therefore, below ground competition by bilberry is primarily for nutrients, and not for water.

The water addition treatment most probably caused an excess of soil moisture since the plots which were treated with water were subjected to around double the amount of normal precipitation during July each year. The 14 days without precipitation and a 3°C higher mean temperature than normal in July 1997 (Anon. 1997b) may have reduced soil moisture availability in plots which received only natural precipitation; however, this was probably not a sufficient moisture deficit to reduce growth and nitrogen uptake by pine seedlings. It has previously been shown that growth of pine seedlings is sensitive to drought during the first years of emergence (Örlander 1984; Kuusela 1990; Zackrisson et al. 1998). The generally small effects of water addition on pine seedling growth and nutrient acquisition even during dry conditions indicates that soil water availability is generally sufficient for pine seedling growth and nutrition during normal climatic conditions in northern mesic sites dominated by bilberry. In July 1998 was the precipitation at the experimental site low, only 50 mm. That is about half of the mean precipitation (92 mm) for the standard period 1961-1990. That unusually low precipitation may partly be a reason for the higher spruce seedling growth in water amended plots in 1998.

Norway spruce responded to water addition by increasing carbon allocation to roots both during the first and the second season, and this is shown by the low S:R ratio of spruce in water amended plots. If water was the limiting factor for spruce seedling growth, seedlings should respond with an increase in S:R ratio following water addition; if water was not the limiting factor the S:R ratio should remain unchanged (Wilson 1988; Ericsson et al. 1996). However, the lower S:R-ratio resulting from moisture addition indicates a deficiency in some other soil resource as a result of moisture addition (Schultze and Chapin 1987; Wilson 1988; Ericsson 1995). Oxygen deficiency as a consequence of water excess is an unlikely explanation because soil water saturation probably never occurred, and because oxygen deficiency is known to decrease root growth (Coutts 1982; Wilson 1988). One possible explanation for the low S:R ratio could be an increased competition for nitrogen by soil microbes after water addition (Zackrisson et al. 1998; Schimel et al. 1999).

The generally small and positive, but often not statistically significant, higher seedling growth and nutrition of pine and spruce after water addition might be explained by an higher nutrient mobility as a result of greater moisture availability. Only a small decrease from the optimum soil water content may reduce nutrient mobility and therefore nutrient availability for seedling roots; this may occur while the soil water content is otherwise adequate for maintaining plant growth (Bowen 1984; Chapin 1991).

Inherently different life history characteristics of the two conifer species may be responsible for the different responses to reduced below ground competition by bilberry (Chapin et al. 1986, 1990; Tamm 1991). Spruce is assumed to be a more nitrogen demanding species than is pine, and is known to respond rapidly to increased nutrient availability (Tamm 1991; Nikolov and Helmisaari 1992).

In this study of a mesic boreal site, reduced below ground competition of bilberry had an overall significant positive effect on Norway spruce and Scots pine seedling growth and nutrition, while addition of water had an overall small positive but mainly not significant effect on Norway spruce and Scots pine seedlings. In conclusion, soil moisture status is generally not limiting for seedling growth and nutrition, at least for Scots pine. Further below ground competition for nutrients (mainly nitrogen) is the main limiting factor for the seedlings growth and nutrition of both Norway spruce and Scots pine.

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Appendix A.

Effects of reduced below ground competition (BGC) and water addition (W) on seedling response variables as shown by *F*-values derived from analysis of variance[1].

Response variable[2]	BGC	W	BGC x W	Block	df	W x Block	df	BGC x Block	df
Picea abies 1997									
dw shoot,	9,50**	1,86	0,97	1,61	30	1,69	23	0,58	21
dw root	4,92*	5,43*	1,94	1,12	30	2,48**	23	0,83	20
dw total	11,64***	3,66	1,39	1,70	30	1,67	23	0,52	21
s:r ratio	0,27	3,58	0,13	0,83	30	4,95***	23	0,76	20
N content	16,77**	5,51*	0,09	1,00	7	0,41	7	0,82	7
N concentration	6,04*	0,13	0,02	8,52	7	0,66	7	0,46	7
C:N ratio	8,40*	0,34	0,01	15,75	7	0,70	7	0,38	7
Picea abies 1998									
dw c.y. shoot	5,92*	2,51	0,02	1,22	17	0,61	15	1,85	15
dw shoot	6,32*	3,92	0,04	1,47	17	0,48	15	1,55	15
dw root	12,21**	6,96*	0,08	1,48	17	0,69	15	0,89	15
dw total	7,99**	5,21*	0,05	1,50	17	0,52	15	1,34	15
s:r ratio	0,22	4,80*	0,30	1,01	17	1,69	15	0,78	15
length c.y. shoot	14,25***	1,02	1,27	0,72	17	3,34	15	5,28*	15
length shoot	11,85**	1,03	1,20	1,22	17	0,77	15	1,86	15
length root	14,85***	3,75	0,41	0,82	17	1,47	15	0,83	15
N content	5,48*	2,43	0,08	0,92	7	0,66	7	3,67*	7
N concentration	24,14**	0,64	0,30	0,94	7	1,10	7	0,83	7
C:N ratio	33,76***	1,39	0,78	0,99	7	1,14	7	0,47	7
Pinus sylvestris 1997									
dw shoot	10,13**	1,04	1,43	1,58	30	1,08	26	0,84	26
dw root	3,86	1,33	1,20	1,09	30	1,58	25	1,94*	26
dw total	8,90**	1,40	0,33	1,17	30	1,33	26	1,18	26
s:r ratio	0,24	1,53	0,70	2,17*	30	1,41	25	1,50	26
N content	17,41**	0,74	0,24	--	7	0,65	7	0,34	7
N concentration	0,00	0,20	1,46	0,48	7	0,93	7	1,38	7
C:N ratio	0,05	0,01	1,11	0,50	7	0,96	7	1,49	7
Pinus sylvestris 1998									
dw shoot	15,56***	0,72	1,32	1,80	17	1,35	15	1,67	14
dw root	10,99**	0,33	0,94	2,08	17	1,56	15	1,10	14
dw total	15,11***	0,63	1,27	1,98	17	1,31	15	1,41	14
s:r ratio	0,55	0,07	0,76	1,35	17	2,94*	15	1,93	14
length shoot	6,85*	0,05	0,03	4,70	17	0,70	15	0,57	14
length root	5,06*	0,72	0,07	1,06	17	1,27	15	1,40	14
N content	10,97**	0,53	0,07	1,44	7	1,48	7	1,80	7
N concentration	2,10	0,13	0,23	1,45	7	1,93	7	4,96*	7
C:N ratio	3,56	0,50	0,02	1,70	7	2,17	7	1,81	7

[1] Degree of freedom for *F* are 1 for C, W and CxW; for block and block interactions see table. Significans for *F*-value *, **, *** = $P \le 0.05$, $P \le 0.01$, $P \le 0.001$, respectively. [2] Year of harvest, dw = dry weight, c.y. = current year.