



Institutionen för skoglig vegetationsekologi
SLU
901 83 UMEÅ

*The effect of different disturbance treatments on tree production,
competition, shortroot presence and ectomycorrhizal colonisation in
Ericaceae- feathermoss boreal forests.*



Björn Eriksson

Examensarbete i biologi, 20p
Handledare: Marie-Charlotte Nilsson och David Wardle

Abstract

In many northern boreal stands, forest floor vegetation constitutes a considerable part of total biomass and production, and consequently is likely to be critical in determining tree seedling growth. This study was conducted in a greenhouse with seedlings grown in intact soil profiles consisting of a minimum coverage of 90% of *Pleurozium schreberi* and 30% of *Vaccinium myrtillus* vegetation. I investigated the effect of three different disturbance treatments, (I) burning using a propane flame thrower to remove all vegetation and the uppermost portion of the humus of the profile; (II) trimming of all mosses and *V. myrtillus* at the height of the interface between the brown and green parts of mosses; and (III) control left intact, on the performance of monocultures and tree seedling mixtures of *Pinus sylvestris*, *Betula pendula* and *Populus tremula* by assessing shoot and root biomass, short root occurrence and mycorrhizal colonisation.

The results of the different disturbance treatments on seedlings response variables was generally weak although *P. sylvestris* and *P. tremula* showed significantly higher values of biomass in fire treated vegetation compared to intact vegetation. *B. pendula* did not show any effects on total or root biomass across treatments but showed an increased shoot length and shoot to root ratio in intact vegetation compared to other treatments. The effect of disturbance in seedling mixtures on relative performance of the different tree species was not strong enough to influence the strength of their interactions. *P. tremula* seemed to be quite uncompetitive with other species and this was especially evident for seedlings grown in association with *B. pendula*. The production of short roots was generally higher in seedling mixtures compared to monocultures and in more intense disturbed treatments. Higher short root production in seedling mixtures possibly indicates lower nutrient availability when grown in association with different neighbours compared to monocultures.

More than 95 % of seedling short roots independent of tree species were colonised by mycorrhiza and most of the EM morphotypes found showed great host specificity. The results of this study shows that ground vegetation of *P. schreberi* interfere with performance of *P. sylvestris* and *P. tremula* seedlings while the effect on *B. pendula* is more unclear and more study on this topic and the effect of seedling mixtures is needed.

Introduction

Disturbance and stress are important factors when determining the outcome of biotic interactions including resource competition, herbivory and the role of mutualisms (Smith and Read 1997). In particular, competition intensity between different plant species may be influenced by stress and disturbance although the pattern of competition response to gradients of stress and disturbance remains hotly debated (Grime 1979, Tilman 1982, Goldberg and Novoplansky 1997). However, most of these studies have focused on grassland-dominated ecosystem and there have been few attempts to investigate this for forest ecosystems and especially interactions involving several tree species including both conifer and broad-leaved trees. Greater knowledge of this issue is important to better understand patterns of forest productivity and the mechanisms that structure forest communities.

The most important disturbance factor for structuring the boreal forest has been wildfire through lightning strike (Zackrisson 1977) as it alters vegetation composition, productivity and often exerts important rejuvenating effects on forest ecosystems, including the production of charcoal, increased decomposition of plant litter and humus, improved cation availability and enhanced pH (Viro 1974, Dyrness et al. 1986, Tamm 1991). Additionally, long fire return intervals contribute to uneven-aged and multilayered stands (Steijlen and Zackrisson 1987).

Following disturbance by fire these forests usually become dominated by *Pinus sylvestris*, *Picea abies* and ericaceous dwarf shrub species like *Vaccinium myrtillus*, *Vaccinium vitis-idea* and *Empetrum hermaphroditum*. In late postfire successions the bottom-layer vegetation is often dominated by the feathermoss *Pleurozium schreberi* (Ebeling 1978) that efficiently intercepts nutrients from precipitation, throughfall and litter decomposing on the moss surface (Brown and Bates 1990, Longton 1992). Thus mosses prevent leaching of nutrients to lower soil horizons (Weetman 1968, Weber and van Cleve 1984) and may intercept a significant amount of nutrients before they can be taken up by vascular plants (Tamm 1953, Oechel and van Cleve 1986, Chapin et al. 1987). Because of high nutrient storage capacity and slow decomposition rate (Mikola 1954, Berg 1984, Oechel and van Cleve 1986, Fyles and McGill 1987) these mosses may act as an important reservoir for mobile nutrients (Chapin et al. 1987). In addition there is proof of additive effects when the field layer constitutes of ericaceous dwarf shrubs that may further limit the establishment and growth of tree seedlings. It has been suggested that a mechanism exists in which nutrients are directly transferred from senescent feathermosses to roots of ericaceous dwarf shrubs via ericoid mycorrhiza fungi (Zackrisson et al. 1997). In many northern boreal stands, forest floor vegetation constitutes a considerable part of total biomass and production and therefore strongly affects ecosystem nutrient dynamics (Bonan and Kurzuhin 1989). Consequently, field- and bottomlayer vegetation are likely to be critical in determining regeneration and tree seedling growth. Alteration of disturbance regimes may indirectly have important consequences for tree seedlings through affecting other biotic components both above and below ground, including mycorrhizal communities. Different ectomycorrhizal (EM) fungal species differ in their effects on tree growth (Smith and Read 1997, Herrmann et

al 1998, van der Heijden et al. 1998, Jones et al. 1998) and several studies also supports the view that a feedback may exist between plant community structure and mycorrhizal community structure (Allen et al. 1995, Herrmann et al. 1998, Jonsson et al. 2000). Considering these factors it is also important to determine mycorrhiza colonisation when examining the effect of different disturbance treatments on tree seedling performance.

The aim of the present study was to investigate the responses on tree productivity, competition, shortroot occurrence and EM-colonisation under different disturbance intensities and through this gain a better understanding of the interactions that exist between coniferous and broad-leaved trees in a changing environment.

Materials and methods

Study area

The fieldwork for this study was conducted within the northern boreal zone (*sensu* Ahti et al. 1968) near Norsjö, N Sweden (65° 00' N; 19° 20' E, 302 m above sea level). Three late multi-layered, mixed stands with *P. sylvestris*, *P. abies*, *B. pendula* and *Populus tremula* were selected within an area of 10 km². Very few traces of previous cutting were found within the study areas and the age of the oldest *P. sylvestris* trees found are over 300 years. The most recent fire occurred in 1812. The three areas, hereafter referred to as site A, B and C (Table 1.), were found on slightly undulating fine textured bottom moraines with low boulder contents and the mean humus depth was 37 mm (Table 1). The forest floor vegetation falls within the *V. myrtillus* type (Påhlsson 1994). The bottom layer of the vegetation is almost exclusively dominated by the feathermoss *P. schreberi*, while the field-layer is mainly composed of *V. myrtillus* and *V. vitis-idaea* with patches of *Deschampsia flexuosa* and *E. hermaphroditum* (Table 1.).

Table 1. Site and humus characteristics for site A, B and C (mean values \pm SE within brackets).

	Site A	Site B	Site C
Tree basal area (m ² ha ⁻¹ , n=5)			
<i>Pinus sylvestris</i>	17.4 (\pm 3.6)	16 (\pm 3.7)	22.8 (\pm 2.8)
<i>Picea abies</i>	7.6 (\pm 2.7)	6 (\pm 3.2)	0.8 (\pm 0.4)
<i>Betula pendula</i>	0.4 (\pm 0.9)	2 (\pm 0.0)	1.6 (\pm 1.5)
<i>Populus tremula</i>	0.6 (\pm 0.9)	0.6 (\pm 0.9)	0.2 (\pm 0.4)
Vegetation cover (% , n=15)			
Field layer species:			
<i>Vaccinium myrtillus</i>	47 (\pm 17)	41 (\pm 14)	40 (\pm 17)
<i>Vaccinium vitis-idaea</i>	18 (\pm 13)	25 (\pm 11)	23 (\pm 9.5)
<i>Empetrum hermaphroditum</i>	<1 (\pm 3.0)	8 (\pm 5.3)	10 (\pm 11)
<i>Calluna vulgaris</i>	<1 (\pm 5.1)	<1 (\pm 2.3)	3 (\pm 6.4)
<i>Linnaea borealis</i>	<1 (\pm 4.4)	2 (\pm 3.4)	<1 (\pm 3.1)
<i>Deschampsia flexuosa</i>	7 (\pm 9.3)	5 (\pm 5.2)	2 (\pm 3.6)
<i>Luzula pilosa</i>	5 (\pm 5.6)	<1 (\pm 2.3)	
<i>Trientalis europaea</i>	<1 (\pm 2.1)	<1 (\pm 6.1)	<1 (\pm 2.4)
<i>Lycopodium annotinum</i>	<1 (\pm 2.2)	5 (\pm 6.8)	
<i>Lycopodium complanatum</i>		<1 (\pm 2.2)	
Bottom layer species:			
<i>Pleurozium schreberi</i>	55 (\pm 27)	54 (\pm 25)	72 (\pm 12)
<i>Hylocomium splendens</i>	27 (\pm 17)	17 (\pm 16)	7 (\pm 13)
<i>Dicranum sp.</i>	3 (\pm 2.2)	5 (\pm 3.1)	5 (\pm 8.2)
<i>Ptilium crista-castrensis</i>	6 (\pm 6.1)	5 (\pm 3.1)	<1 (\pm 3.6)
<i>Polytrichum sp.</i>	<1 (\pm 2.1)	<1 (\pm 2.1)	<1 (\pm 2.1)
<i>Cladina sp.</i>	<1 (\pm 3.4)	<1 (\pm 2.1)	3 (\pm 4.3)
Humus depth (mm, n=3)	36 (\pm 7.4)	40 (\pm 9.3)	34 (\pm 9.7)
Humus pH (n=3)	3.9 (\pm 0.1)	4.1 (\pm 0.2)	4.1 (\pm 0.1)

Experimental design

Within each site, 5 blocks (approximately 10 x 10 m) were established 50 m apart from each other in September 1999. From each block 18 intact soil profiles (20 x 20 x 20 cm) consisting of a minimum coverage of 90 % of *P. schreberi* and 30 % of *V. myrtillus* vegetation with the underlying humus and mineral soil were selected. In total 270 profiles (18 profiles x 5 blocks x 3 sites) were collected and transferred into plastic containers with holes in the bottom for drainage and left outside the greenhouse for 3 months. Before they were taken into the greenhouse they were initially left inside a storage room at 0-5° C for two weeks, so as to slowly adapt to higher temperatures.

To determine the effect on seedling response variables of different disturbance intensities the profiles were randomly subjected to three different treatments (in decreasing order of intensity): (I) burning using a propane flame thrower to remove all vegetation and the uppermost portion of the

humus of the profile; (II) trimming of all shoots of *P. schreberi* and *V. myrtillus* at the height of the interface between the brown and green parts of mosses; and (III) control left intact. The replicate profiles for each treatment was planted with each of six different combinations of tree seedlings, i.e. (I) two *P. sylvestris* seedlings; (II) two *B. pendula* seedlings; (III) two *P. tremula* seedlings; (IV-VI) each of the three pair-wise combinations of these three species (two seedlings of each species per profile). This experiment represents an additive design competition experiment (Wilson 1988) and allows determination of seedling growth, competitive balance (Cb) and competitive intensity (Ci) between species in mixtures and those in the corresponding monocultures. Measurements on Cb and Ci follow Wilson (1988). Seeds were germinated on sterilised quartz sand (120° C, 48 hours) in small closed greenhouses for seven weeks under artificial illumination with 20 hours

day and 4 hours night to reach sufficient height before planted.

The plastic containers were maintained in the greenhouse from December to May with the same light conditions described above and were watered from above with tap water every second day until harvested. Every second week the position of the blocks were randomly changed so as to avoid effects of possible heterogeneous light and growth conditions in the greenhouse.

Harvesting and measurements

The seedlings were harvested between 128 and 152 days after setup. Upon harvest all plants were carefully extracted from the soil, rinsed in tapwater and divided into shoot and root material. For seedlings in monocultures root systems were maintained in a moist condition at 4° C for EM assessment. The root system was cut up in 1.5-cm pieces and 10 fragments were randomly chosen, and for each fragment, the total number of EM colonised and non-colonised root tips were quantified per mg root dry weight under a dissecting microscope. All root tips were assessed on root systems smaller than 10 mg. For seedlings in monocultures all EM and root tips in the subsamples were quantified per mg root dry weight and divided into different classes based on morphology and colour (Agerer 1997, Smith and Read 1997). After oven drying at 70° C for 48 h the total root and shoot mass (including root subsamples from EM assessment) were determined.

Statistical analysis

Data were analysed by ANOVA followed by Tukey's honest difference test to determine whether differences existed in seedling response variables between disturbance treatments and between seedling mixtures and monocultures. All data for shoot and root growth, short roots and EM occurrence were log transformed to meet the assumptions of homogeneity and normality. Data from the three different sites were analysed together since there were no significant differences between the sites of any response variable (data not shown). All analysis was per-

formed using SPSS 7.0 statistical computer software.

Results

Seedling responses

For most of the seedling response variables measured there were surprisingly small significant differences between disturbance treatments, although *P. sylvestris* seedlings grew generally larger in monocultures and seedling mixtures when planted in fire treated and cut vegetation compared to when grown in intact vegetation (Table 2., Fig. 1).

Table 2. Effects of disturbance treatments (D) and different neighbours (N) on plant response variables as shown by F-values derived from analysis of variance.

Response variable	D	N	D x N interaction
<i>P. sylvestris</i> total weight	8.617***	3.188*	1.764
<i>B. pendula</i> total weight	2.940	0.190	1.863
<i>P. tremula</i> total weight	3.343*	5.463**	0.963
<i>P. sylvestris</i> root weight	8.635***	1.674	0.845
<i>B. pendula</i> root weight	0.430	0.392	1.815
<i>P. tremula</i> root weight	4.387*	2.554*	0.942
<i>P. sylvestris</i> shoot weight	4.483*	1.866	0.336
<i>B. pendula</i> shoot weight	2.667	0.080	2.579*
<i>P. tremula</i> shoot weight	2.624	5.938**	0.981
<i>P. sylvestris</i> shootlength	4.692*	0.908	0.940
<i>B. pendula</i> shootlength	6.620***	0.181	1.686*
<i>P. tremula</i> shootlength	0.500	6.520**	0.706
<i>P. sylvestris</i> S:R ratio	0.394	1.401	1.616
<i>B. pendula</i> S:R ratio	5.414**	1.948	1.289
<i>P. tremula</i> S:R ratio	2.852	3.691*	0.254
<i>P. sylvestris</i> shortroots	5.392**	3.495*	1.120
<i>B. pendula</i> shortroots	14.527***	8.929***	1.407
<i>P. tremula</i> shortroots	0.340	1.456	0.287
Competition intensity			
<i>P. sylvestris</i> : <i>B. pendula</i>	2.686		
<i>P. sylvestris</i> : <i>P. tremula</i>	0.773		
<i>B. pendula</i> : <i>P. tremula</i>	0.373		
Competitive balance			
<i>P. sylvestris</i> : <i>B. pendula</i>	1.690		
<i>P. sylvestris</i> : <i>P. tremula</i>	1.145		
<i>B. pendula</i> : <i>P. tremula</i>	0.570		

Note: *, **, *** = F-value significantly different to zero at P = 0.05, 0.01, 0.001 respectively.

P. tremula showed the same trend as *P. sylvestris* although these differences were only statistical significant for root biomass. On the contrary, monocultures and mixtures

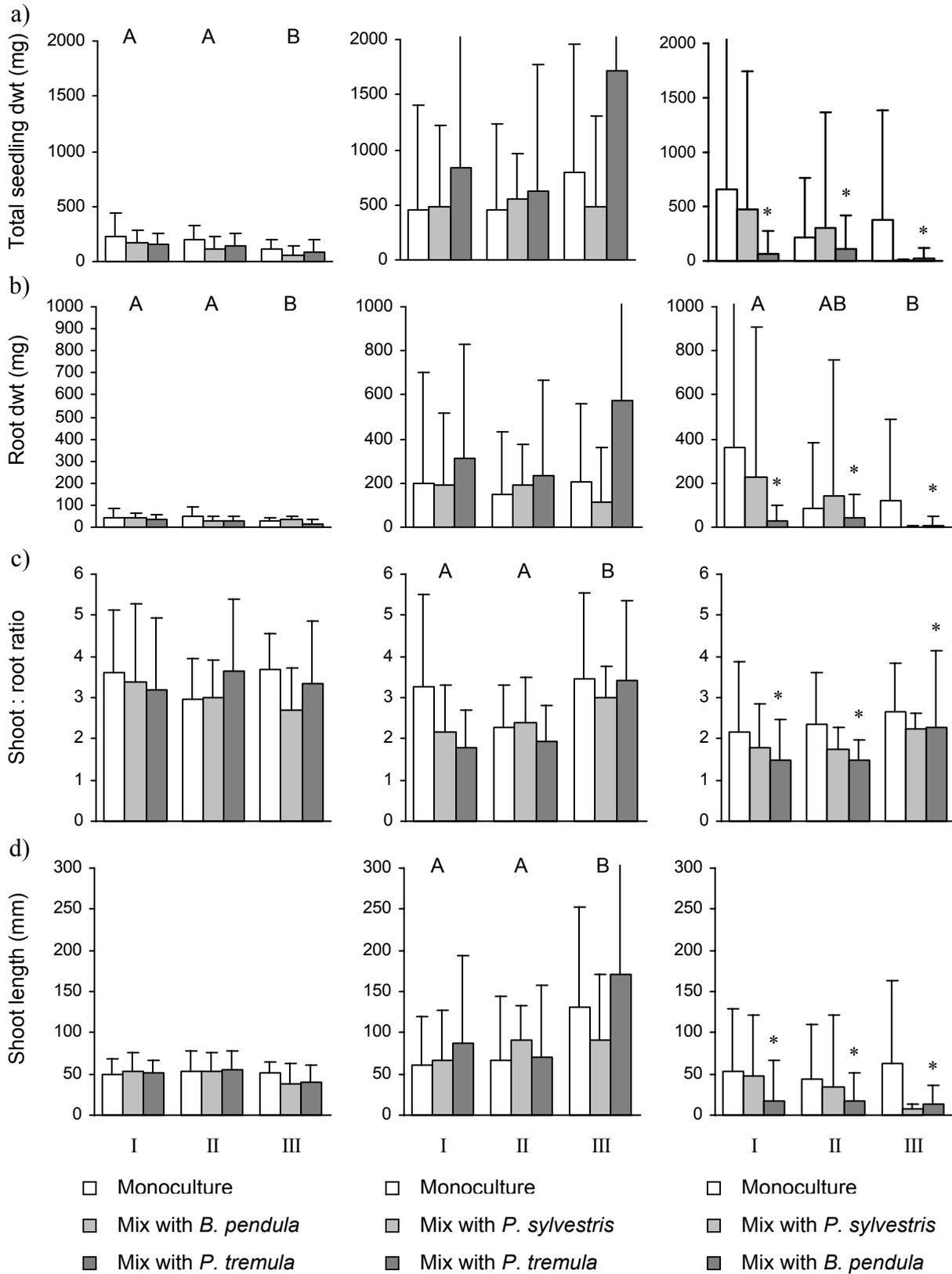


Fig. 1. Difference in (a) Total seedling dry weight, (b) Root dry weight, (c) Shoot to root ratio and (d) Shoot length between monocultures and mixtures of *P. sylvestris*, *B. pendula*, and *P. tremula* grown in substrate subjected to three different treatments (I = Burned vegetation, II = Cut vegetation and III = Control with intact vegetation). Different letters and * indicates significant differences at $P < 0.05$ between treatments and mixtures respectively. Vertical bars indicate \pm SE.

of *B. pendula* grew significantly taller in intact vegetation but biomass was equally affected by treatments (Fig. 1). *B. pendula* was generally also the most productive tree species. It grew two to four times larger biomass than *P. sylvestris* and *P. tremula* in intact vegetation and in vegetation that was cut. The mortality at harvest for the three tree species ranged between 6-13 % for seedling planted in fire treated and cut vegetation. In intact vegetation the mortality among seedlings varied between 10 and 30 %. *P. tremula* usually had higher mortality but there were no significant differences between tree species.

Irrespective of disturbance treatment, all tree species showed positive values of competition intensity indicating negative interactions between seedlings of different species. Overall there were no statistically significant differences in competitive balance or competition intensity across disturbance treatments or between any of the three different combinations of tree species (Table 2). *P. sylvestris* and *B. pendula* seedlings were generally less inhibited by neighbours than was *P. tremula* and the latter grew significantly smaller when grown in mix with *B. pendula* compared to when grown in monocultures (Fig. 1). The lower shoot to root ratio of *P. tremula* when grown in mix with *B. pendula* compared to when grown in monocultures indicates that the competition is mostly below ground.

Short root and mycorrhizal occurrence

Disturbance treatments induced in general significantly higher short root production of all seedlings (Fig. 2). *P. sylvestris* seedlings produced more short roots per mg root dry weight in fire treated vegetation compared to that in other treatments. *B. pendula* showed the same trend with significantly improved short root occurrence when grown in both fire treated and cut vegetation compared to those in intact vegetation. Short root production of *P. tremula* did not differ between treatments. Occurrence of short roots on *P. sylvestris* and *B. pendula* seedlings was also significantly higher when grown in mixtures

with different neighbours compared to when grown in monocultures. The same trend was found for *P. tremula* although this was not statistically significant.

More than 95% of all short roots of all tree species were colonised by EM fungi, and there were no significant effect of disturbance on the occurrence of EM or morphotypes per root dry weight (Table 3, 4).

Table 3. Effects of disturbance treatments (D) on ectomycorrhizal morphotype abundance of each tree species as shown by F-values derived from analysis of variance.

Morphotype	<i>P. Sylvestris</i>	<i>B. Pendula</i>	<i>P. Tremula</i>
	D	D	D
1	2,135		
2	1,463	0,605	
3	0,340		
4	0,207		
5	0,290		
6	0,527		
7		2,244	
8		1,600	
9			0,774
10			1,339
11			0,409
12	1,716	0,684	
13	1,180		
14			
15	59,408		
16		0,440	

Note: None of the F-values were significantly different to zero at $P < 0.05$.

For *P. sylvestris* the number of EM colonised short roots per mg dry weight across morphotypes ranged between 0 and 5 in the three different treatments. For *B. pendula* and *P. tremula* the values ranged between 0 and 13.9 and 0 and 6.1 respectively. The highest number of morphotypes was found on *P. sylvestris* seedlings (10 morphotypes) followed by *B. pendula* (7 morphotypes) and *P. tremula* (5 morphotypes) (Table 4). Only one black monopodial mycorrhiza (probably *Cenococcum geophilum*) was clearly present on all three tree species while most of the others were either present on just one species or occurred in rather small amounts. In total ten of the fifteen morphotypes were found on one particular host species indicating the importance of the tree species present.

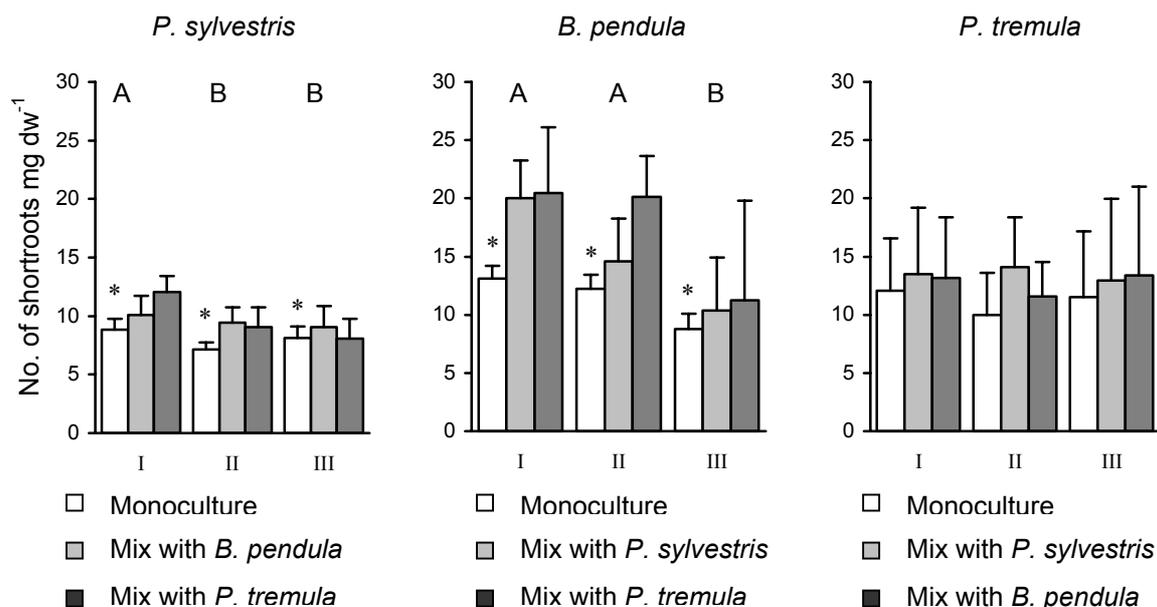


Fig. 2. Differences in amount of shortroots per mg dry weight of each tree species between treatments and between different neighbours. Letters and * indicates significantly differences at $P < 0.05$ between treatments and mixtures respectively. Vertical bars indicate \pm SE.

Table 4. Percent EM colonised root-tips and no. of EM colonised root-tips of each morphotype per mg root dw divided into *classes based on colour and morphology. *I = Burned vegetation, II = Cut vegetation and III = Control with intact vegetation.

	Treatment*	% myc.	Morphotype class*														
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>P. sylvestris</i>	I	99	2.3	0.7	3.7	2.0	4.7	1.0	0	0	0	0	0.3	2.3	0	0.7	0
	II	99	1.4	1.3	2.1	1.3	4.3	0.8	0	0	0	0	1.1	2.0	0	0.4	0
	III	98	2.0	0.4	1.9	1.3	5.0	1.1	0	0	0	0	0	3.5	0.8	0	0
<i>B. pendula</i>	I	98	0	2.8	0	0	0	0	4.1	7.4	0	0	3.9	0	0	0	13.9
	II	99	0	3.9	0.6	0	0	0	4.1	4.5	0	0	4.9	0	0	0	0.1
	III	98	0	2.3	0	0	0	1.1	2.1	4.3	0	0	3.0	0	0	0	4.8
<i>P. tremula</i>	I	100	0	3.6	0	0.2	0	0	0	0	6.0	6.0	1.8	0	0	0	0
	II	95	0	3.9	0	0	0	0	0	0	2.6	4.4	0	0	0	0	0
	III	98	0	6.1	0	0	0	0	0	0	4.2	5.6	0	0	0	0	0

Discussion

The effects of the three different disturbance treatments on seedlings response variables were surprisingly weak. *P. sylvestris* was the only tree species that showed a clear pattern where disturbance had a positive effect on both shoot and total dry weight (Fig. 1). This result combined with slightly but not significantly higher mortality for seedlings in intact vegetation indicates that *P. schreberi* and *V. myrtillus* interfere with *P. sylvestris* seedling performance, and that disturbance is necessary for successful tree establishment and growth. Both of these species are known to release secondary metabolites (Gallet 1994,

Jäderlund et al. 1996, Erikson and Miksche 1974, Wardle et al. 1998) that possibly could interfere with root cell membrane activity (Vaughan and Ord 1991) and limit seedling growth. Ericoid mycorrhiza may also function as pathogens tapping nutrients from poorly growing seedlings (Zackrisson et al. 1997). At least one species of ericoid mycorrhiza, *Phialocephala fortinii*, has been implicated as a weak pathogen of coniferous seedlings (Wilcox and Wang 1987). However, there is uncertainty as to whether this and other dematiaceous fungi are parasitic or mutualistic in their relationships with roots of trees and ericaceous plants (Wilcox 1983, Read 1993). It has also been suggested that

there is a direct transfer of nutrients between senescent feathermosses to roots of ericaceous dwarf shrubs via ericoid mycorrhiza fungi which may further limit establishment and seedling growth (Zackrisson et al. 1997). However, there were no significant effects on shoot to root ratio for this species that could indicate differences in nutrient availability depending on treatment. *P. tremula* was the other species that showed a response across treatments on root dry weight with significantly higher biomass in burned vegetation compared to intact vegetation. This is in accordance with earlier studies of positive effects of wildfire on establishment and seedling growth through increased decomposition of plant litter and humus, improved cation availability and enhanced pH (Viro 1974, Dyrness et al. 1986, Tamm 1991). In addition, the study of Wardle et al. (1998) showed that addition of charcoal had effects on seedling biomass production in substrate that originated from an ericaceous dwarf shrub site, indicating that charcoal was capable of partially reversing whatever factor was responsible for inhibiting seedling production for the ericaceous substrate. They proposed that the primary agents of inhibition of seedling growth in this substrate were phenolics originating from the ericaceous plant species contributing to humus formation at that site. *B. pendula* did not show any effects on total or root dry weight across treatments but showed an increased shoot length and shoot to root ratio in intact vegetation compared to other treatments. This result is somewhat confusing but indicates that biomass production of *B. pendula* is not affected by disturbance treatments. A few individuals in the intact treatment did reach extreme shoot lengths, which probably interfered with the overall result for this species. Even though the seedlings were watered every second day, one can not fully exclude the possibility that differences in moisture content depending on vegetation cover might play an important role, possibly resulting in lower biomass production due to water stress in seedlings grown in cut and burned vegetation.

Focusing on seedling mixtures the competitive balance and competitive intensity data did not show any significant trends. This means that the effect of disturbance on relative performance of the different species was not strong enough to influence the strength of their interactions. *P. sylvestris* and *B. pendula* seedlings were unaffected by seedling mixture treatments. On the contrary *P. tremula* seemed to be quite uncompetitive with other species and showed generally lower response variable values when grown in seedling mixtures compared to monocultures (Fig 1, Table 2). This was especially evident for seedlings grown in association with *B. pendula* indicating that these seedlings interfere most intense with *P. tremula* seedling performance. Further the reduced shoot to root ratio of *P. tremula* when grown with other species (Fig 1, Table 2) suggests that the other two species reduce nutrient availability for *P. tremula*, reducing shoot weight, but with competition occurring most intensely in the soil. This is in accordance with earlier studies of the importance of root competition (Donald 1958, Snaydon and Harris 1981, Wilson and Newman 1987).

The production of short roots across species was generally higher in seedling mixtures compared to monocultures and in more intense disturbed treatments (Fig 2). One important external factor that influences short root growth and function is nutrient availability. Nitrogen affects the carbon allocation pattern of trees, and there is a negative relationship between nitrogen supply and short root biomass (Alexander and Fairley 1983, Vogt et al. 1990). *P. sylvestris* and *B. pendula* did show higher short root production in burned and both burned and cut vegetation respectively, possibly indicating lower nutrient availability in these treatments. However, there was also a significant difference in short root production for both of these species when grown in seedling mixtures compared to monocultures. This implies that the effect of seedling mixtures is greater compared to disturbance treatment on nutrient availability since *P. sylvestris*, despite higher short root production in

burned vegetation, shows higher total and root biomass (Fig 1).

Independently of tree species or treatment more than 95 % of seedling short roots were colonised by mycorrhiza. This is normal in nutrient-impooverished conditions that prevail in forests where at least 90 % of the feeding roots of the trees are colonised by ectomycorrhizal fungi (Read 1997). Flemming (1983,1984) showed that birch seedlings planted in forests supporting mature trees were colonised largely by the fungi associated with the adults. Since intact soil profiles were used in this study it is likely that most of the morphotypes present are the same as those in the forest stand. Accordingly most of the ectomycorrhizal morphotypes found showed great host specificity (Table 4) supporting earlier studies of Last et al. (1987), who suggests that this process was driven by differences in quality and quantity of the litter present, although other studies contradicts this model (Molina et al 1992).

Acknowledgements

Many thanks to Marie-Charlotte Nilsson for guidance and support and David Wardle for helpful comments on the manuscript.

References

- Agerer, R.**, 1997. Colour Atlas of Ectomycorrhizae. 8th ed. – Einhorn-Verlag, Germany.
- Ahti, T., Hämet-Ahti, L. and Jalas, J.**, 1968. Vegetation zones and their sections in northwestern Europe. – *Annales Botanici Fennici*, 5 : 169-211.
- Alexander, I. J. and Fairley, R. I.**, 1983. Effects of N fertilization on populations of fine roots and mycorrhizas in spruce humus. – *Plant and Soil*, 71 : 49-53.
- Allen, E. B., Allen, M. F., Helm, D. J., Trappe, J. M., Molina, R. and Rincon, E.**, 1995. Patterns of regulation of mycorrhizal plant and fungal diversity. – *Plant and Soil*, 170 : 47-62.
- Berg, B.**, 1984. Decomposition of moss litter in a mature Scots pine forest. – *Pedobiologia*, 26 : 301-308.
- Bonan, G. B. and Kurzuhin, M. D.**, 1989. Simulation of moss and tree dynamics in the boreal forests of interior Alaska. – *Vegetatio*, 84 : 31-44.
- Brown, D. H. and Bates, J. W.**, 1990. Bryophytes and nutrient cycling. – *Bot. J. Linn. Soc.*, 104 : 129-147.
- Chapin, F. S. III., Oechel, W. C., van Cleve, K. and Lawrence, W.**, 1987. The role of mosses in the phosphorus cycling of an Alaskan black spruce forest. – *Oecologia*, 74 : 310-315.
- Donald, C. M.**, 1958. The interaction of competition for light and for nutrients. – *Australian Journal of Agricultural Research*, 9 : 421-435.
- Dyrness, D. T., Viereck, L. A. and van Cleve, K.**, 1986. Fire in taiga communities of interior Alaska. In : van Cleve, K., Chapin, F.S., Flanagan, P.W., Viereck, L.A. and Dyrness, C.T. *Forest ecosystems in the alaskan taiga*. Springer. Berlin Heidelberg New York, pp 74-86.
- Ebeling, F.**, 1978. Nordsvenska skogstyper. – *Sver. Skogsvårdsförb. Tidskr.* 76 : 339-381.
- Erikson, M. and Miksche, G. E.**, 1974. On the occurrence of lignin or polyphenols in some mosses and liverworts. – *Phytochemistry*, 13 : 2295-2299.
- Flemming, L. V.**, 1983. Succession of mycorrhizal fungi on birch : infection of seedlings planted around mature trees. – *Plant and soil*, 71 : 998-1002.
- Flemming, L. V.**, 1984. Effects of trenching and coring on the formation of ectomycorrhizas on birch seedlings grown around mature trees. – *New Phytologist*, 98 : 143-153.
- Fyles, J. W. and McGill, W. B.**, 1987. Decomposition of boreal forest litters from central Alberta under laboratory conditions. – *Can. J. For. Res.*, 17 : 109-114.
- Gallet, C.**, 1994. Allelopathic potential in bilberry-spruce forests: influence of phenolic compounds on spruce seedlings. – *J. Chem. Ecol.*, 20 : 1009-1024.
- Goldberg, D. and Novoplansky, A.**, 1997 On the relative importance of competition in unproductive environments. – *J. Ecol.* 85 : 409-418.
- Grime, J. P.** 1979. Plant strategies and vegetation processes. – Wiley, Chichester.
- Herrmann, S., Munch, J-C. and Buscot, F.**, 1998. A gnotobiotic culture system with oak microcuttings to study specific effects of mycobionts on plant morphology before, and in early phase of, ectomycorrhiza formation by *paxillus involutus* and *Philoderma erocum*. – *New Phytol.*, 138 : 203-212.
- Jones, M. D., Duvall, D. M. and Tinker, P. B.**, 1998 Comparison of arbuscular and ectomycorrhizal *Eucalyptus coccifera* : growth response, phosphorus uptake efficiency and external hyphal production. – *New Phytol.*, 140 : 125-134.
- Jonsson, L. M., Nilsson, M.-C., Wardle, D. A. and Zackrisson, O.**, 2001. Context dependent effects

- of ectomycorrhizal species richness on tree seedling productivity. – *Oikos*, 93: 353-364.
- Jäderlund, A., Zackrisson, O. and Nilsson, M-C.**, 1996. Effects of bilberry (*Vaccinium myrtillus L.*) litter on seed germination and early seedling growth of four boreal tree species. – *J. Chem. Ecol.*, 22 : 973-986.
- Last, F. T., Dighton, J. and Mason, P. A.**, 1987. Succession of sheathing mycorrhizal fungi. – *Tree*, 2 : 157-161.
- Longton, R. E.**, 1992. The role of bryophytes and lichens in terrestrial ecosystems. In: Bates, J.W. and Farmer, A.M. Bryophytes and lichens in a changing environment. – Clarendon, Oxford. 32-76.
- Mikola, P.**, 1954. Experiments on the role of decomposition of forest litter. – *Comm. Inst. For. Fenn.* 43 : 1-79.
- Molina, R., Massicotte, H. and Trappe, J. M.**, 1992. Specificity phenomena in mycorrhizal symbiosis : community-ecological consequences and practical implications. In : Allen, E.D. ed. Mycorrhizal functioning. – Chapman and Hall, New York. 357-423.
- Oechel, W. C. and Van Cleve, K.**, 1986. Role of bryophytes in nutrient cycling in the taiga. In : Van Cleve, K., Chapin, F.S.III., Flanagan, P.W., Viereck, L.A. and Dyrness, C.T. Forest ecosystems in the Alaskan Taiga : A synthesis of Structure and Functions. – Springer Verlag, New York. 121-137.
- Påhlsson, L.**, 1994. Vegetationstyper i Norden. – Nordiska Ministerrådet, Köpenhamn.
- Read, D. J.**, 1993. Mycorrhiza in plant communities. – *Advances in Plant Pathology*, 9 : 1-31.
- Smith, S. E. and Read, D. J.**, 1997. Mycorrhizal Symbiosis. – Academic Press, London.
- Snaydon, R. W. and Harris, P. M.**, 1981. Interactions below ground – the use of nutrients and water. – International Workshop on Intercropping, ICRISAT, Hyderabad.
- Steijlen, I. and Zackrisson, O.**, 1987. Long-term regeneration dynamics and successional trends in a northern Swedish coniferous stand. – *Canadian Journal of Botany*, 65: 839-848.
- Tamm, C. O.**, 1953. Growth, yield and nutrition in carpets of the forest moss (*Hylocomium splendens*). – *Medd. Statens Skogsforskningsinst.* 43 : 1-140.
- Tamm, C. O.**, 1991. Nitrogen in terrestrial ecosystems. – Springer, Berlin.
- Tilman, D.**, 1982. Resource Competition and Community Structure. – Princeton Univ. Press, Princeton.
- Van der Heijden, M. G. A., Boller, T., Wiemken, A. and Sanders, I. R.**, 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. – *Ecology*, 79 : 2082-2091.
- Vaughan, D. O. and Ord, B. G.**, 1991. Extraction of potential allelochemicals and their effects on root morphology and nutrient contents. In : Plant root growth. An ecological perspective. Edited by Atkinson, D. – Blackwell Scientific Publications, Ltd., Oxford, U.K. 399-421.
- Viro, P.J.**, 1974. Effects of forest fire on soils. In: Ahlgren, C.E. and Kozlowski, T.T. Fire and ecosystems. – Academic Press, New York. 7-45.
- Vougt, K. A. and Persson, H.**, 1990. Measuring growth and development of roots. In : Techniques and approaches in forest tree ecophysiology. Eds. Lassoie, J. P. and Hinkley, T. M. – CRC Press, Boca Raton. FL.
- Wardle, D. A., Zackrisson, O. and Nilsson, M-C.**, 1998. The charcoal effect in Boreal forests: mechanisms and ecological consequences. – *Oecologia*, 115: 419-426.
- Weber, M.G. and Van Cleve, K.**, 1984. Nitrogen transformations in feather moss and forest floor layers of interior Alaska black spruce ecosystems. – *Can. J. For. Res.*, 14 : 278-290.
- Weetman, G.**, 1968. The relationship between feather moss growth and the nutrition of black spruce. – Proceedings of the Third International Peat Congress. International Peat Society, Québec.
- Wilcox, H. E.**, 1983. Fungal parasitism of woody plant roots from mycorrhizal relationships to plant disease. – *Annual review of Phytopathology*, 21 : 221-242.
- Wilcox, H. E. and Wang, C. J. K.**, 1987. Mycorrhizal and pathological associations of dematiaceous fungi in roots of 7-months old tree seedlings. – *Can. J. For. Res.*, 17 : 884-899.
- Wilsson, B. J.**, 1988. A review on the control of shoot:root ratio, in relation to models. – *Ann. Bot. (London)*, 61 : 433-449.
- Wilson, J. B. and Newman, E. I.**, 1987. Competition between upland grasses : Root and shoot competition between *Deschampsia flexuosa* and *Festuca ovina*. – *Acta Oecologia, Oecologia Generalis*, 8 : 501-509.
- Zackrisson, O.**, 1977. Influence of forest fires on the north Swedish boreal forest. – *Oikos*, 29 : 22-32.
- Zackrisson, O., Nilsson, M-C., Dahlberg, A. and Jäderlund, A.**, 1997. Interference mechanisms in Conifer-*Ericaceae*-feathermoss communities. – *Oikos*, 78: 209-220.