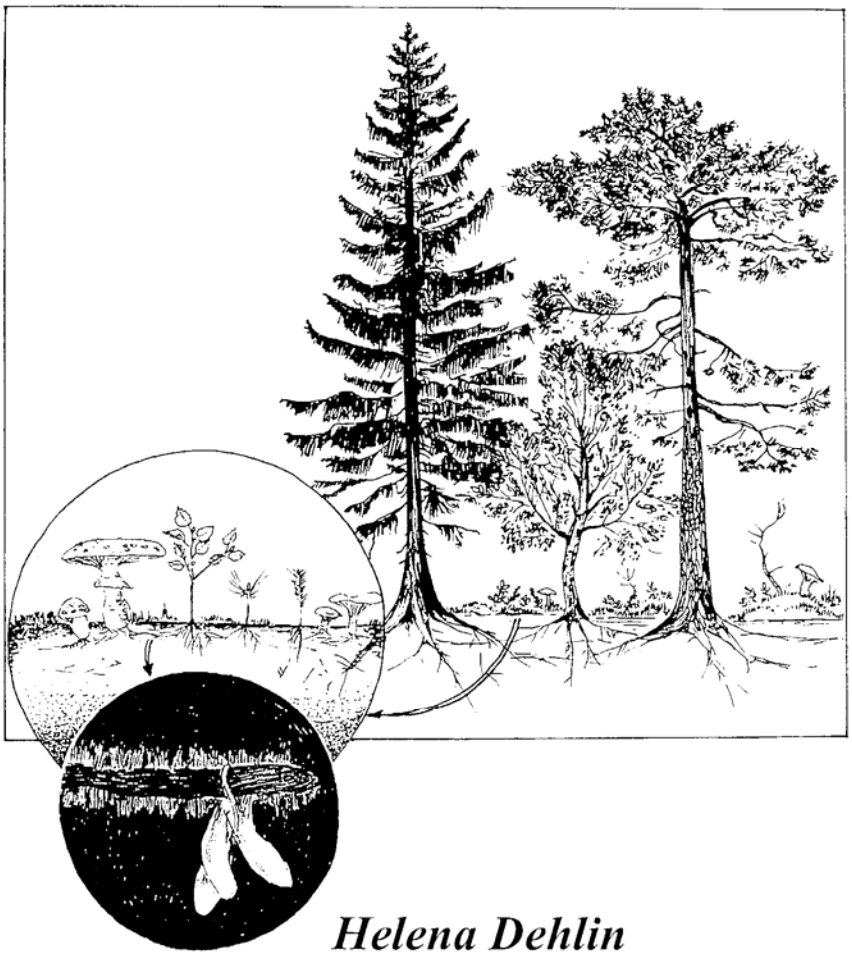
Institutionen för skoglig vegetationsekologi
SLU
901 83 UMEÅ

Effects of shade and humus fertility on boreal forest tree seedling growth, competition and mycorrhizal colonisation



Helena Dehlin

Examensarbete i skoglig vegetationsekologi, 20p.
Handledare: Marie-Charlotte Nilsson och David Wardle
September 2001

Printed by: SLU, Grafiska Enheten, Umeå, Sweden, 2001
Front page illustration by Anna Shevtsova

Preface

This degree project was conducted at the Department of Forest Vegetation Ecology at the Swedish University of Agricultural Sciences (SLU) in Umeå, as part of the Bachelor of Forestry programme. My supervisors have been Marie-Charlotte Nilsson and David Wardle.

First, I would like to thank my supervisors, Marie-Charlotte and David, for their support, involvement and for always finding time for a discussion. I also want to give a special thanks to Anna Shevtsova for her statistical advice, for her other comments on the project and for drawing the illustration on the front page!

I want to thank Greg Day and Åsa Lundberg, for their valuable assistance and for keeping me company in the lab! I also want to thank Olle Zackrisson for collecting the humus I used in the project, and Björn Eriksson for his help with the identification of the mycorrhizal morphotypes. Finally, I want to thank Lena Jonsson for her advice via e-mail, Séverine Delorme and Oskar Eriksson for watering the seedlings, and the people at the Department of Forest Vegetation Ecology for the nice coffee breaks.

Helena Dehlin
Umeå, September 2001

Abstract

In boreal forest ecosystems, growth of tree seedlings is limited by resources both aboveground (through shading) and belowground (through nutrient limitation), and the ability to tolerate or avoid these conditions is important in determining the relative performance of different tree species. Two of the means to compete for these resources, are through increasing stem-elongation to escape shading by neighbours (shade avoidance), and through mycorrhizal symbiosis that may increase the nutrient- and water up-take. This experiment studies the effects of humus fertility and vegetation shade on the shade avoidance response, productivity, competitive ability and ectomycorrhizal (EM) colonisation of seedlings of the three major boreal tree species [*Pinus sylvestris* L., *Picea abies* (L.) Karst. and *Betula pendula* Roth]. The seedlings were grown in monocultures and in all possible two-species mixtures in pots containing humus collected from low- and high fertility sites in the boreal forest. They were then placed under light filters that were intended to simulate daylight (control) and two levels of partial shade by neighbouring plants by reducing light intensity (PAR) plus reducing light quality; i.e. the red: far-red ratio (R: FR). Three species of ectomycorrhizal (EM) fungi [(*Paxillus involutus* (Batch) Fr., *Amanita muscaria* (L.) Hooker and *Laccaria bicolor* (Maire) Orton] were added to each seedling, in order to assess the effects of the humus, shade, and seedling combinations on the relative EM root colonisation of the seedlings.

The seedlings responded to shade by increasing seedling height, but occasional changes in biomass were also observed. The greatest shade avoidance response was induced in *Betula pendula* seedlings, which were tallest under the most shaded conditions (i.e. the largest reduction in R: FR) and shortest under the non-shaded conditions. However, shade avoidance of *B. pendula* seedlings was only significantly induced in the high fertility substrate. Shade avoidance was induced in *P. sylvestris* seedlings in both the low and high fertility substrate, but was not affected by the level of R: FR. The shade tolerant *P. abies* did not show any shade avoidance responses. Interspecific competition between seedlings was generally not significantly affected by humus and shade treatments.

Ectomycorrhizal colonisation was unaffected by shade treatments, but was generally higher in the low than in the high fertility substrate. For *P. sylvestris* seedlings, EM colonisation was stimulated in low fertility when grown in mixture, but not when grown in monoculture. The relative abundance of EM species differed significantly between tree species in the low fertility substrate, and also between *B. pendula* seedlings grown in the low fertility and *B. pendula* seedlings grown in the high fertility substrate. *Paxillus involutus* was the dominant root colonist in all treatments, but its dominance was reduced on *B. pendula* seedlings in the low fertility substrate, through a relative increase of colonisation by *A. muscaria*. The results provide evidence that the shade avoidance response is species-specific corresponding to the light- and nutrient strategies of the different tree species, and indicates a higher ecological importance of the EM symbiosis in the low than in the high fertility conditions.

Introduction

Competition for limited resources such as water, light and nutrients is important for determining the composition of plant communities (Keddy 1989). Competitive interactions between plants have led to an evolution of a range of life history traits and strategies that enable plants to more effectively compete for limited resources, and which are essential for plant growth and survival. Two possible means of achieving competitive success are by physiological or morphological adaptation of growth or development to competitive situations (plasticity) (Ballaré 1999, Aphalo *et al.* 1999), and by investing resources into ectomycorrizal (EM) associations to increase nutrient uptake (Smith *et al.* 1999, Tuomi *et al.* 2001). To escape shading by neighbours, many plant species allocate resources to stem elongation to locate leaves or needles at a higher position than that of their neighbours. This shade avoidance response is triggered by a reduced red: far-red (R: FR ratio) caused by selective filtering of red light by chlorophyll from neighbour and overstory plants (Schmitt and Wulff 1993, Ballaré 1999). Many plant species respond to low R: FR by promoting apical dominance, often manifested in decreased branching, reduced leaf: stem ratio, increased stem extension and internode elongation and reduced photosynthetic capacity (reviewed by Smith 1982, 1994). However, the magnitude of this response depends on the light competition strategy (shade-intolerant or shade tolerant) of the species and on the nutrient availability of the substrate in relation to the requirements of the species (Sharew *et al.* 1996, de la Rosa *et al.* 1999). Most studies on the shade avoidance responses of plants have been conducted on grasses and vascular plants, but recently there has been an increasing focus on tree species. However, few studies have been performed on the shade avoidance of boreal tree species (but see Aphalo and Letho 1997, de la Rosa *et al.* 1998, 1999, Gilbert *et al.* 2001).

The boreal forest is characterised by thick humus layers in which N is mainly conserved in organic forms, and where EM associations are common and have a role in mobilising nutrients and enhancing overall ecosystem productivity and functioning (Smith and Read 1997, Jonsson *et al.* 2001). Ectomycorrhizal associations are believed to play a more significant role in conditions of lower soil fertility (Nylund 1988, Jonsson *et al.* 2001). Our knowledge of the importance of EM in regulating the outcome of competitive interactions between plant species is still very limited. However, it has been demonstrated that the mycorrhizal symbiosis can increase intensity of competition by favouring plants with higher mycorrhizal responsiveness (Moora and Zobel 1996, Smith *et al.* 1999), or alternatively that it can reduce competition by resource sharing among plants via common mycelia (Grime *et al.* 1987, Simard *et al.* 1997).

It is not well established which processes that regulate the formation of EM on plants. It has been suggested that EM colonisation is controlled by carbohydrate concentrations in the roots, and that these are strongly influenced by both nutrient availability and light conditions (Björkman 1942, 1970 in Nylund 1988). Marx *et al.* (1977) showed that the sucrose content in short roots of *Pinus taeda* L. was significantly positively correlated with EM development of *Pisolithus tinctorius (*Pers.) Coker and Couch. Therefore, factors such as shading (i.e. reduced light intensity and quality), which regulate carbohydrate production by plants, can be

expected to strongly influence EM colonisation of tree seedlings, although this issue has been seldom considered (Skàlovà and Vosàtka 1998).

The objective of this study was to examine the role of resource availability on growth, species-interactions and EM symbiosis of three common boreal tree species; *Betula pendula* Roth (silver birch), *Pinus sylvestris* L. (Scots pine) and *Picea abies* (L.) Karst. (Norway spruce). This was investigated through a pot experiment looking at the effects of manipulating resources both aboveground (light regime) and belowground (substrate fertility) on tree seedling growth, interspecific competition and EM colonisation. The ultimate goal of this experiment was to contribute to a better understanding of the role of interspecific interactions and resource availability in influencing the relative performance of EM and seedlings of different tree species in boreal forest ecosystems.

Materials and methods

Sites and substrate

The growth substrate used for this experiment consisted of humus collected from six pairs of low fertility and high fertility forest sites in the northern boreal zone of Sweden (64°49' N to 66°01'N; 18°44'E to 19°51'E). The high fertility sites represented closed canopy stands of *B. pendula*, *P. sylvestris* and *P. abies,* with herbs and grasses dominating in the field layer. The stands have not been harvested following development after wildfires in the early 19th century. The soil type is sandy-clayey glacifluvial moraine. The mean total N of the humus of the six sites was 1.48 %, and the range was 1.00-2.03 %. The low fertility sites represented late post-fire successional forests with a naturally sparse canopy of *P. sylvestris* (and some scattered *P. abies*) and with a ground cover dominated by dwarf shrubs (*Vaccinium myrtillus* L. and *Empetrum hermaphroditum* Hagerup) and the feather moss *Pleurozium schreberi* (Bird) Mitt. The soil type is sandy-clayey moraine. The mean total N was 0.99%, and the range was 0.80-1.16%. These sites have a significantly lower total N than the high fertility sites ($F_{1,5}$= 7.71, P= 0.020). It is expected that N-availability and productivity should be lower in the low fertility sites because of a lower pH, and because of the production of secondary metabolites by dwarf shrubs that impedes mineralization through the formation of N-phenolic complexes (Kuiters 1990, Northup *et al.* 1995, Nilsson *et al.* 1999).

The humus from each site was air-dried in room temperature for 4-7 days and sieved to 4 mm. About 24 g of air-dried humus was placed in each of 18 PVC tubes (inner diameter= 50 mm; height= 120 mm) on top of a layer of 10-20 mm of medium coarse sand (Silversand 90 μm). The pots had plastic perforated lids at the bottom and were sealed at the top with a soft plug and Para film, placed in air-sealed plastic bags and then beta sterilised to kill resident micro organisms (25kGy, Gammaster Sweden AB, Kopparberg).

Organisms

Three common boreal tree species with differing nutritional requirements and light strategies were selected for use in the experiment, i.e. *P. sylvestris, P. abies* and *B.*

pendula. Seeds of each species were surface sterilised to remove adhering fungi and were left to germinate under sterile conditions. For surface sterilisation, *B. pendula* seeds were dewinged and placed in H_2O_2 for 10-15 minutes while the *P. sylvestris* and *P. abies* seeds were sterilised in $HgCl_3$ for 15 minutes. The seeds were then placed in autoclaved glass pots with lids, on top of sterilised (150°C, 12 h) quartz sand (Silversand 90 μm) that was saturated with distilled water. They were left to grow in a climate chamber (Termak 6395 F/FL, 22 °C, photoperiod 20 h) for 2-8 weeks, until secondary needles and leaves had developed on the seedlings. As the growing medium did not contain any nutrients, the *B. pendula* seedlings were given 10 ml of full nutrient solution (142 mg l^{-1} N, 30 mg l^{-1} P and 118 K mg l^{-1}) at one occasion when leaves showed signs of initial deficiency.

Three fungal species were selected, i.e. *Paxillus involutus* (Fr.) Fr., *Amanita muscaria* (L.) Hooker and *Laccaria bicolor* (Maire) Orton; all three are common in the boreal forest and are known to form EM with all selected tree species. They also form different distinctive mycorrhizal morphotypes that can be identified under a stereomicroscope with low magnification (16-40 times). For each species, fungal mycelia originating from sporocarps collected in the boreal forest of Sweden, were maintained in cultures on ½ MMN agar (Marx 1969). The cultures were kept in darkness at room temperature prior to experimentation.

Shade treatments

In order to manipulate light conditions for seedlings, three different shade treatments were used. Each treatment aimed to simulate possible light conditions in the boreal forest, i.e. two levels of vegetation shade (high or low) and a non-shaded control. The light conditions were obtained by using plastic filters (Lee Colortran International). The non-shaded control (NS) treatment was provided by transparent filters (Lee No. 130 Clear) with unaltered light intensity (PAR) and light quality (R: FR). The low shade (LS) treatment, implemented using a black filter (Lee No. 210 Neutral Density), reduced PAR and R: FR by 67% and 58%, respectively, compared to the control. The high shade (HS) treatment, implemented using a green filter (combination of Lee No. 140 Summer Blue and Lee No. 101 Yellow), gave a similar reduction to the LS treatment in PAR, but a larger reduction of R: FR (73%). Details of PAR, R: FR and temperature conditions under the different shade treatments are shown in Table 1. In comparison, the range of observed R: FR values for canopy shade is typically 0.05-1.15, with a range of 0.15-0.76 for coniferous forests and 0.36-0.97 for deciduous forest (Smith 1982). The R: FR values for open spaces are 1.05 to 1.25 (Smith 1982, 1994). The high R: FR ratio under the control filters should not significantly affect plant growth, as R: FR values which are greater than that of open spaces have little or no effect on the photoequilibrium of phytochrome (Smith 1994, Aphalo and Letho 1997). The light filters were attached to steel frames (height 220 mm; length 350 mm; and width 170 mm) and placed above the pots with seedlings. Each filter was placed on a trolley, and surrounded by aluminium foil above the height of the frames to prevent reflected light from the filters from affecting the other treatments.

Table 1. Growth conditions under the shade treatments; the non-shaded control (NS), the low level of shade (LS) and the high level of shade (HS) during the experimental period[1].

	Shade treatment		
Parameter	NS	LS	HS
Photosynthetically active radiation[2] (PAR) (μmol $m^{-2}s^{-1}$)	476a	158b	141b
Red: far-red (R: FR) ratio[3]	2.06a	0.87b	0.56c
Day temperature (°C) [4]	19.4a	18.2ab	17.5b
Night temperature (°C) [4]	17.1a	16.9b	17.0ab

[1] Numbers in the same row followed by the same letter do not differ significantly at $P \leq 0.05$ (Tukey's test).
[2] Measured in 12 minute intervals for two hours by PAR sensor (400-700 nm) (Skye Instruments, Ltd).
[3] Measured at one occasion by R: FR sensor (660/730 nm light sensor, Skye Instruments Ltd).
[4] Derived from means of the temperature in 12 minute intervals during 24 h (18h day, 6 h night).

Experimental design and set up

The experiment was set up according to a randomised nested block design consisting of a full-factorial of two humus treatments (high and low fertility), three shade treatments (HS, LS and NS), and six seedling combinations. The seedling combinations consisted of *P. sylvestris* in monoculture, *P. abies* in monoculture, *B. pendula* in monoculture and the three possible two-way combinations of these species. The six pairs of forest humus sites (true replicates) each represented a separate block.

The seedlings were planted according to an additive competition design (Snaydon 1991), and the tubes containing two tree species were used for assessing interspecific interactions. Two seedlings were planted in each monoculture pot, and two seedlings of each species were planted in each mixture pot; all seedlings were placed 1.5 cm from the centre of each pot as to maximise the distance between seedlings of the same species. At the time of planting, all seedlings were inoculated with the three EM fungal species. Inoculation was performed under sterile conditions, by placing one agar plug with growing mycelium (diameter = 3mm) of each fungal species in contact with the roots of each seedling. Thus, there were in total six fungal plugs added to seedling monoculture pots and 12 agar plugs to seedling mixture pots, so that each seedling had the same amount of total fungal inoculum at the start of the experiment. A thin layer of sterilized (160°C, 12 h) coarse aquarium sand was put on top of the pots, to reduce contamination and evaporation.

After set-up the seedlings were grown in a climate chamber under artificial light (light intensity = 580 μmol m^{-2} s^{-1}), with a relative humidity of 75%, a temperature of 16° C (day) and 17° (night) and a photoperiod of 20 h for the first 59 days and 18 h thereafter to adjust for the natural shorter day length in late summer/autumn (but see Table 1 for measured conditions under the light filters). The pots were watered twice a day the first week and thereafter every two to three days.

Harvesting and measurements

The plants were harvested sequentially depending on replicate block after 155-190 days. The roots were carefully washed and untangled under running water to remove the soil. The shoots and roots were then separated, and the height of each stem was measured from the soil surface to the apical bud. Each root was cut into 1-2 cm pieces, of which 10 random sub-samples were examined under 36-40 times magnification. The number of short roots that were colonised by *P. involutus, A.*

muscaria and *L. bicolor* was recorded separately for each sub-sample. The dry weight of the shoots and the roots were determined after oven drying at 70°C for 48 h. The biomass of the root sub-samples was determined separately.

Data analysis

All growth variable data was analysed using ANOVA testing for effects of humus, shade and seedling combinations, blocking and all possible interactions. All data sets were tested before analyses to verify that it conformed to the assumptions of ANOVA, such as normality (Shapiro-Wilk test) and homogeneity of variances (Levene test); data was arsine square root transformed to satisfy the assumptions when necessary. Significant differences between treatment means were determined with Tukey's test ($P \leq 0.05$). All mycorrhizal variables were analysed with the Kruskal-Wallis non-parametric test, as the data in some cases did not meet the assumptions of ANOVA. The mycorrhizal data was tested for effects of humus, shade, and tree seedling combinations. All statistical analyses were done in the statistical software package SPSS (version 10.0).

For each treatment combination, measures of interspecific competition were derived for each replicate block using two-species mixtures and the corresponding monocultures from that block. The intensity of competition was determined as the combined response of each species in the mixture to the presence of the other species in each pot. The following relationship was used (Wilson 1988): Competitive intensity = [(Species A mass in monoculture + Species B mass in monoculture)/(Species A mass in mixture + Species B in mixture)]-1. The index has a value of 0 if no competition occurs, and it becomes increasingly positive as the competition becomes more intense. The relative competitive abilities of the two species in each mixture pot were determined using the following index (Wilson 1988): Competitive balance = $\log_e$ [(Species A mass in mixture/Species B mass in mixture)/(Species A mass in monoculture/species B mass in monoculture)]. A value of 0 indicates that no species has a competitive advantage over the other, whereas positive or negative value indicates that one species has a higher competitive ability.

To be able to detect competition effects on the response to humus and shade treatments, the seedlings in mixtures were analysed in ANOVA using indices describing the difference in growth between seedlings in a mixture compared to the corresponding monoculture of that species. The model for the indices, with *P. sylvestris* as an example, is as follows: Mix index 1 = [(*P. sylvestris* $_{\text{mix with } P.\ abies}$ − *P. sylvestris* $_{\text{monoculture}}$)/*P. sylvestris* $_{\text{monoculture}}$] and Mix index 2 = [(*P. sylvestris* $_{\text{mix with } B.\ pendula}$ − *P. sylvestris* $_{\text{monoculture}}$)/*P. sylvestris* $_{\text{monoculture}}$].

Results

Seedling growth response

Humus fertility had significant effects on most growth parameters for all tree species, whereas the effects of shade were mainly on seedling height (Table 2). The responses were species specific for both humus and shade (Table 3). Shoot and root growth in monocultures was significantly greater in the high fertility than low

Table 2. Effects of humus fertility (H) and shade treatment (L) on tree seedling growth in monocultures, and on the growth response of seedlings in two-species mixtures, shown as *F*-values from ANOVA[1]. Significant *F*-values for seedlings in a mixture indicates competition responses to treatments, i.e. the response to treatments for the seedlings in the mixture differs to that of seedlings in monoculture of the same species.

Tree species	Seedling combination	Response variable	H	L	HxL	Blocking
P. sylvestris	Monoculture	Seedling height	7.30*	10.61**	2.97	0.33
		Total weight	97.50***	4.49*	1.06	15.13
		Shoot weight	170.79***	4.24*	0.35	23.55
		Root weight	14.62*	2.94	2.40	8.05
		Shoot: root ratio[2]	164.65***	4.18*	2.32	n.d.[3]
	Mixture with *P. abies*	Seedling height	0.02	1.57	0.37	1.75
		Total weight	0.19	3.34	0.16	1.52
		Shoot weight	1.47	7.16**	0.29	1.63
		Root weight	0.01	1.46	0.24	1.84
		Shoot: root ratio	0.03	0.38	0.51	66.17
	Mixture with *B. pendula*	Seedling height	4.81	0.592	1.21	0.37
		Total weight	8.53*	2.55	5.45	0.38
		Shoot weight	9.67*	1.74	9.95*	0.44
		Root weight	9.30*	3.51	2.86	0.37
		Shoot: root ratio	0.25	2.80	8.10	1.22
P. abies	Monoculture	Seedling height	13.50*	1.36	1.27	1.04
		Total weight	31.14**	2.77	2.23	2.62
		Shoot weight	31.89**	1.84	1.89	2.68
		Root weight	18.05**	3.81	1.90	2.28
		Shoot: root ratio[2]	2.21	0.78	0.78	2.21
	Mixture with *P. sylvestris*	Seedling height	0.00	3.48	0.63	1.70
		Total weight	0.69	1.71	1.81	0.16
		Shoot weight	0.55	2.66	1.19	0.36
		Root weight	0.05	0.97	3.28	0.05
		Shoot: root ratio	2.37	3.53	0.48	0.76
	Mixture with *B. pendula*	Seedling height	8.36*	0.82	n.d.	1.64
		Total weight	4.44	0.58	n.d.	0.60
		Shoot weight	4.66	0.49	n.d.	0.64
		Root weight	3.93	0.76	n.d.	0.57
		Shoot: root ratio	2.56	0.11	n.d.	0.48
B. pendula	Monoculture	Seedling height	18.69**	21.98***	4.69*	1.58
		Total weight	14.98*	1.47	1.19	2.26
		Shoot weight	57.26***	0.47	2.03	3.04
		Root weight	0.49	4.74*	0.16	0.79
		Shoot: root ratio[2]	0.01	0.10	1.02	3.78
	Mixture with *P. sylvestris*	Seedling height	0.44	0.33	1.90	1.30
		Total weight	0.55	1.29	2.66	2.26
		Shoot weight	0.43	1.05	4.25	1.29
		Root weight	0.38	2.02	1.02	n.d.
		Shoot: root ratio	2.67	0.91	1.29	1.22
	Mixture with *P. sylvestris*	Seedling height	0.78	0.97	0.00	3.61
		Total weight	2.72	0.98	0.21	2.09
		Shoot weight	2.74	1.03	0.09	53.12
		Root weight	1.57	0.88	0.40	1.25
		Shoot: root ratio	0.03	0.39	0.67	0.06
	All seedlings	Monoculture pots	155.46***	2.62	0.08	6.83
		Mixture pots	49.85***	7.54**	0.80	1.68

[1] Degrees of freedom for *F* are: 1 for H, 2 for L, 2 for HxL and 5 for block. *$P \leq 0.05$, **$P \leq 0.01$, *** $P \leq 0.001$
[2] Data arcsine square root transformed.
[3] *F*-values could not be determined in cells with missing values.

fertility humus, except for the roots of *B. pendula*, which were not responsive to fertility (Table 2, Figures 1-3). Both *B. pendula* and *P. sylvestris* seedlings grew significantly taller under both shade treatments, but the shoot weight of *B. pendula* and root weight of *P. sylvestris* was slightly negatively affected by shading (Figures

Table 3. Effects of humus type (H), shade treatment (L) and tree species (S) on seedling growth in monoculture pots, shown as *F*-values from ANOVA[1].

Response variable	H	L	S	HxL	HxS	LxS	HxLxS	Blocking
All tree species								
Seedling height	57.88***	22.05***	53.50***	4.64*	8.21***	5.71***	1.64	3.14*
Total weight	73.62***	6.69**	36.74***	0.34	1.97	0.36	1.34	6.70***
Shoot weight	114.45***	4.23*	43.14***	0.88	6.47**	0.08	1.66	6.47***
Root weight	17.91***	8.59***	19.43***	0.71	1.92	0.95	0.64	5.52***
Shoot: root ratio[2]	0.19	0.59	1.76	0.32	2.92	1.04	1.00	2.72*

[1] Degrees of freedom for *F* are: 1 for H, 2 for L, 2 for S, 2 for HxL, 2 for HxS, 4 for LxS, 4 for SxLxS and 5 for block. *$P \leq 0.05$, **$P \leq 0.01$, ***$P \leq 0.001$

[2] Data arcsine square root transformed.

1 and 3). *Picea abies* showed no response to shade treatments (Table 2, Figure 2). The overall strongest shade avoidance response among species was found for seedling height of *B. pendula* seedlings growing under the HS treatment in the high fertility humus (Table 4, Figure 3). In contrast, seedling height of *B. pendula* seedlings growing in low fertility did not differ significantly between shade treatments and control. *Pinus sylvestris* seedlings showed no significant difference in seedling height between HS or LS treatments (Table 4, Figure 1). The shade treatments did not affect the shoot: root ratio of any of the species, but the humus treatment had a significant effect on the shoot: root ratio of *P. sylvestris*, which was greater in the high fertility substrate (Table 2, Figure 1).

The response of seedlings to treatments did not generally differ when grown in mixture compared to monoculture. However, there were some differences in individual tree species responses caused by the presence of neighbours (Table 2). In particular *P. sylvestris* seedlings grown in mixtures with *P. abies* had a significantly lower shoot weight under the NS treatment compared to that under the LS and HS treatments (Table 2, Figure 1). *Pinus sylvestris* and *P. abies* seedlings were generally suppressed when grown in mixtures with *B. pendula*, particularly in the nutrient-rich substrates (Table 2, Figures 1 and 2). *Betula pendula* seedlings grown in mixture with *P. sylvestris* or *P. abies* were not significantly affected by competition from neighbours, showing that *B. pendula* seedlings in general were strong competitors for nutrients and light (Table 2, Figure 3).

The total production in the pots was on average 74 % higher in the high fertility substrate than in the low fertility substrate. Shade treatments did not affect total biomass of seedlings in monocultures, but the total biomass of seedlings grown in mixtures was 13% and 20% lower under low and high canopy shade, respectively, than under daylight. The production was equally high in the monoculture and mixture pots, except for a significantly lower production in the *P. abies* monocultures.

Interspecific competition

Overall, the intensity of competition was not significantly affected by shade treatment ($F_{1,5}$= 1.08; P= 1.367), humus fertility ($F_{1,5}$= 1.72; P= 0.242) or seedling mixtures ($F_{1,5}$= 3.29; P= 0.063) (Table 5, ANOVA data not shown). However, the competition intensity in *P. abies* and *B. pendula* seedlings mixtures was significantly lower under high canopy shade than under low canopy shade or the control, but only when grown in the low fertility substrate. The same trend was observed when *P.*

Table 4. Growth response to humus and shade treatments (as described in legend of Table 1) for seedling monocultures[1].

Humus type	Tree species	Response variable	Shade treatment		
			NS	LS	HS
High fertility	P. sylvestris	Seedling height (mm)	43.8a	81.2b	74.3b
		Total weight (mg)	615a	567a	486a
		Shoot weight (mg)	381a	369a	318a
		Root weight (mg)	234a	198ab	168b
		Shoot: root ratio	1.82a	1.98a	1.91a
	P. abies	Seedling height (mm)	34.2a	50.2a	37.3a
		Total weight (mg)	334a	308a	173a
		Shoot weight (mg)	167a	171a	98a
		Root weight (mg)	167a	137a	75a
		Shoot: root ratio	0.82a	1.13a	1.49a
	B. pendula	Seedling height (mm)	60.6a	107.8b	137.0c
		Total weight (mg)	498a	527a	441a
		Shoot weight (mg)	303a	375a	305a
		Root weight (mg)	195a	152a	136a
		Shoot: root ratio	1.82a	2.78a	2.70a
Low fertility	*P. sylvestris*	Seedling height (mm)	35.1a	52.1b	51.3ab
		Total weight (mg)	276a	346a	233a
		Shoot weight (mg)	134a	166a	104a
		Root weight (mg)	142a	179a	128a
		Shoot: root ratio	1.86a	0.88a	0.75a
	P. abies	Seedling height (mm)	25.3a	28.1a	69.8a
		Total weight (mg)	136a	123a	71a
		Shoot weight (mg)	65a	58.2a	43a
		Root weight (mg)	71a	65a	28a
		Shoot: root ratio	0.96a	9.11a	2.54a
	B. pendula	Seedling height (mm)	43.3a	54.1a	69.8a
		Total weight (mg)	414a	255a	258a
		Shoot weight (mg)	228a	137a	138a
		Root weight (mg)	186a	118a	121a
		Shoot: root ratio	3.50a	2.24a	2.46a

[1] Numbers in the same row followed by the same letter do not differ significantly at $P \leq 0.05$ (Tukey's test).

abies was grown with *P. sylvestris*. The overall intensity of competition was generally higher in the high fertility humus than in the low fertility substrate, although this was not statistically significant (Table 5). The intensity of competition was generally about two times higher in pots with *P. sylvestris* and *B. pendula* than in pots with mixtures that included *P. abies*.

The competitive balance for all seedling mixtures was not affected by shade treatment ($F_{1,5}$= 0.82; P= 0.46), but differed significantly between humus fertility treatments ($F_{1,5}$= 16.44; P= 0.005) and seedling mixtures ($F_{1,5}$= 9.88; P= 0.001) (Table 5, ANOVA data not shown). The effect of humus was particularly evident on the competitive balance between *B. pendula* and *P. abies*, resulting from the strong competitive advantage that *B. pendula* had over *P. abies* under low fertility conditions.

Table 5. Intensity of competition index (C_i) and competitive balance index (C_b) for seedling mixtures, calculated from mean total weight of seedlings[1].

Seedling mixture	Shade treatments	C_i		C_b	
		Humus fertility		Humus fertility	
		High	Low	High	Low
P. abies and *B. pendula*[2]	Non-shaded control (NS)	0.72	0.40	-2.48	-1.03
	Low level of shade (LS)	0.73	0.19	-2.97	-1.35
	High level of shade (HS)	0.18	0.45	-2.47	-0.41
P. sylvestris and *P. abies*	Non-shaded control (NS)	0.54	-0.03	0.37	0.67
	Low level of shade (LS)	0.59	0.44	-0.25	0.53
	High level of shade (HS)	0.03	0.23	0.37	0.97
P. sylvestris and *B. pendula*	Non-shaded control (NS)	0.71	0.72	-2.99	0.55
	Low level of shade (LS)	1.08	0.24	-1.57	-1.69
	High level of shade (HS)	0.73	0.18	-2.69	-2.05
P. abies and *B. pendula*	All shade treatments	0.41	0.31	-2.47 *	-0.41
P. sylvestris and *P. abies*	All shade treatments	0.37	0.23	0.19	0.74
P. sylvestris and *B. pendula*	All shade treatments	0.83	0.61	-2.45	-1.18

[1]Competitive balances are positive when the underlined species has a competitive advantage and negative when the non-underlined species has a competitive advantage. *= The humus fertility treatments differ significant from each other at $P \leq 0.05$ (Tukey's test).
[2]In the high fertility humus, the shade treatments differ significantly from each other at $P \leq 0.05$ (Tukey's test).

EM colonisation

By the end of the experiment, *P. involutus* was present on 77% of all seedlings (i.e. at least one short root was colonised), while *A. muscaria* was observed on 37%. *Paxillus involutus* established on 93% of *P. sylvestris* seedlings, on 81% of *P. abies* seedlings and on 60 % of *B. pendula* seedlings. *Amanita muscaria* established on 44% of *P. sylvestris* seedlings, 30 % of *P. abies* seedlings and 35 % of *B. pendula* seedlings. Eighteen percent of all plants were not colonised by any mycorrhizal fungal species. The percentage of *B. pendula* seedlings that had no EM colonisation was twice as high in the high fertility substrate (37 %) compared to the low fertility substrate (18%).

Table 6. Kruskal-Wallis non-parametric test results for effects of humus fertility (H), shade (L) and seedling combinations (MM) on number of root tips colonised with ectomycorrhizal (EM) species shown as Chi-Square values[1].

Tree species	Response variable	Colonisation per mg root dry weight			Colonisation per seedling[3]		
		H	L	MM	H	L	MM
P. sylvestris	*P. involutus*	20.48***	2.31	2.61	8.15**	1.04	27.01***
	A. muscaria	1.65	0.66	3.51	0.54	0.39	7.92*
	Total EM	22.46***	1.49	3.32	9.32**	1.00	30.89***
	Pi: Pi +Am ratio[2]	0.63	0.72	1.89	0.63	0.72	1.89
P. abies	*P. involutus*	3.68	0.32	4.69	0.24	1.80	3.23
	A. muscaria	1.05	0.90	12.12**	1.67	0.66	11.12**
	Total EM	3.31	1.76	4.31	0.79	4.07	6.03*
	Pi: Pi +Am ratio[2]	3.27	0.13	4.12	3.27	0.13	4.12
B. pendula	*P. involutus*	38.85***	1.42	0.17	35.66***	0.74	0.36
	A. muscaria	23.17***	0.51	1.99	22.91***	0.45	1.97
	Total EM	43.29***	0.79	0.48	39.21***	0.59	0.42
	Pi: Pi +Am ratio[2]	2.30	4.64	3.11	2.30	4.64	3.11

[1] Degrees of freedom for Chi-Square are: 1 for H, 2 for L and 2 for MM. *P ≤ 0.05, **P ≤ 0.01, *** P ≤ 0.001.
[2] Ratio of colonisation of *P. involutus* to that of colonisation of *P. involutus* and *A. muscaria*.
[3] Calculated by multiplying the recorded number of root tips colonised by EM on each root sub-sample and the total root weight of each seedling.

Laccaria bicolor generally failed to colonise the roots, and observations of this species are therefore not presented at the species level but included in the analysis for total EM. Other (contaminating) mycorrhizal morphotypes that could not be identified are also included in the analysis for total EM. These morphotypes were found on 14 % of seedlings, and they generally represented a low percentage of the total EM (data not shown). The percentage of short roots colonised by EM fungi was approximately 90-100 % for *P. sylvestris* and *B. pendula* seedlings, and was approximately 80 % for *P. abies* seedlings. The non-colonised short roots were sometimes difficult to separate from long roots (especially for *P. abies)*, and for that reason, data on percentage EM colonisation of short roots could not be obtained.

Ectomycorrhizal colonisation per mg root dry weight was strongly regulated by humus substrate, but not by light intensity or light quality (Table 6). *Betula pendula* seedlings had higher EM colonisation in the low fertility than in the high fertility substrate, and this was evident for both total EM colonisation and colonisation by individual EM species (Table 7). *Pinus sylvestris* seedlings grown in monoculture did not differ in EM colonisation between humus treatments, but when grown in mixture the EM colonisation was significantly higher in the low fertility substrate (Table 7). Ectomycorrhizal colonisation of *P. abies* seedlings was generally unaffected by treatments, except for a significantly reduced colonisation by *A. muscaria* when the seedlings were grown with *B. pendula* seedlings. There was also a tendency towards a higher number of mycorrhizal short roots in mixture than in monoculture for both *B. pendula* and *P. sylvestris* seedlings, although this was not statistically significant (Tables 6 and 7).

Overall, the relative abundance of *P. involutus* and *A. muscaria*, measured as the ratio of colonisation of *P. involutus* to that of colonisation of *P. involutus* and *A. muscaria* (Pi: Pi+Am ratio), was not affected by humus fertility or shade treatments for any of the tree species (Table 6). However, for *B. pendula* growing in monoculture the Pi: Pi+Am ratio was significantly lower (0.29) in the low fertility substrate than in the high fertility humus (0.62) (Table 7). Further, the relative abundance of EM species differed significantly between tree species in the low fertility humus ($P \leq 0.000$), i.e. the Pi: Pi+Am ratio was highest for *P. abies* (0.89), followed by *P. sylvestris* (0.79) and then *B. pendula* (0.71).

The EM colonisation per seedling showed similar responses to humus and shade treatments as to that for EM colonisation per unit root dry weight (Table 6). However, when calculated per seedling, there were significant differences in EM colonisation between seedlings grown in monoculture and in mixture. This can be explained by reductions in growth when seedlings were grown in monocultures, since the root biomass correlated positively with number of mycorrhizal short roots for *P. sylvestris* and *P. abies* across humus treatments and for *B. pendula* in low fertility humus (Figures 1-3, correlation data not shown).

Table 7. Number of root tips colonised with ectomycorrhiza (EM) per mg root dry weight of seedlings (mean ±SE).

Fungal species	Tree species	Seedling combination	Low fertility	High fertility	K-W[1]
P. involutus	*P. sylvestris*	Monoculture	3.0 ± 0.6	2.0 ± 0.4	ns
		Mixture with *P. abies*	2.8 ± 0.6	1.1 ± 0.3	**
		Mixture with *B. pendula*	3.8 ± 0.7	0.6 ± 0.1	***
	P. abies	Monoculture	1.3 ± 0.4	0.4 ± 0.1	ns
		Mixture with *P. sylvestris*	1.3 ± 0.3	1.1 ± 0.3	ns
		Mixture with *B. pendula*	1.7 ± 0.4	0.7 ± 0.3	ns
	B. pendula	Monoculture	2.3 ± 0.5	0.1 ± 0.1	***
		Mixture with *P. sylvestris*	2.4 ± 0.6	0.1 ± 0.0	***
		Mixture with *P. abies*	2.7 ±0.9	0.2 ± 0.1	*
A. muscaria	*P. sylvestris*	Monoculture	0.7 ± 0.7	0.8 ± 0.4	ns
		Mixture with *P. abies*	0.8 ± 0.8	0.9 ± 0.3	ns
		Mixture with *B. pendula*	1.0 ± 0.3	0.1 ± 0.1	***
	P. abies	Monoculture	0.5 ± 0.3	0.1 ± 0.1	ns
		Mixture with *P. sylvestris*	0.3 ± 0.1	0.6 ± 0.1	ns
		Mixture with *B. pendula*	0.0 ± 0.0	0.2 ± 0.1	ns
	B. pendula	Monoculture	1.3 ± 0.4	0.0 ± 0.0	**
		Mixture with *P. sylvestris*	0.6 ± 0.3	0.0 ± 0.0	***
		Mixture with *P. abies*	1.4 ± 0.5	0.2 ± 0.1	*
Total EM	*P. sylvestris*	Monoculture	3.7 ± 0.6	2.9 ± 0.8	ns
		Mixture with *P. abies*	4.1 ± 0.6	2.1 ± 0.4	**
		Mixture with *B. pendula*	4.9 ± 0.9	0.7 ± 0.1	***
	P. abies	Monoculture	1.9 ± 0.5	0.6 ± 0.2	ns
		Mixture with *P. sylvestris*	1.6 ± 0.4	1.8 ± 0.4	ns
		Mixture with *B. pendula*	1.7 ± 0.4	1.0 ± 0.4	ns
	B. pendula	Monoculture	3.7 ± 0.7	0.2 ± 0.1	***
		Mixture with P. sylvestris	3.7 ± 0.7	0.1 ± 0.0	***
		Mixture with *P. abies*	4.4 ± 1.2	0.4 ± 0.1	*
Pi: Pi+Am ratio[2]	*P. sylvestris*	Monoculture	0.7 ± 0.1	0.8 ± 0.1	ns
		Mixture with *P. abies*	0.8 ± 0.1	0.6 ± 0.1	ns
		Mixture with *B. pendula*	0.8 ± 0.1	0.8 ± 0.1	*
	P. abies	Monoculture	0.8 ± 0.1	0.7 ± 0.1	ns
		Mixture with *P. sylvestris*	0.8 ± 0.1	0.6 ± 0.1	ns
		Mixture with *B. pendula*	1.0 ± 0.0	0.3 ± 0.1	ns
	B. pendula	Monoculture	0.6 ± 0.1	0.3 ± 0.1	*
		Mixture with *P. sylvestris*	0.8 ± 0.1	0.6 ± 0.1	ns
		Mixture with *P. abies*	0.5 ± 0.1	0.5 ± 0.1	ns

[1] Treatment significantly different in Kruskal-Wallis test. *$P \leq 0.05$, **$P \leq 0.01$, *** $P \leq 0.001$, ns = not significant.
[2] Ratio of colonisation of *P. involutus* to that of colonisation of *P. involutus* and *A. muscaria*.

Discussion

Tree seedling growth response

The results of this experiment demonstrate that humus fertility was a strongly limiting factor for growth of seedlings, i.e. the growth was reduced in low fertility for all growth variables. The dry weight allocation to roots was larger in the low fertility substrate for *P. sylvestris*, which a well-known adaptation to low nutrient supplies (Charles-Edwards *et al. 19*86). There were strong interspecific differences in growth response to humus fertility for seedling height and shoot weight; the fast-growing *B. pendula* seedlings showed the strongest positive response in shoot growth in high fertility compared to low fertility humus, and the slow-growing *P. abies* seedlings were the least responsive.

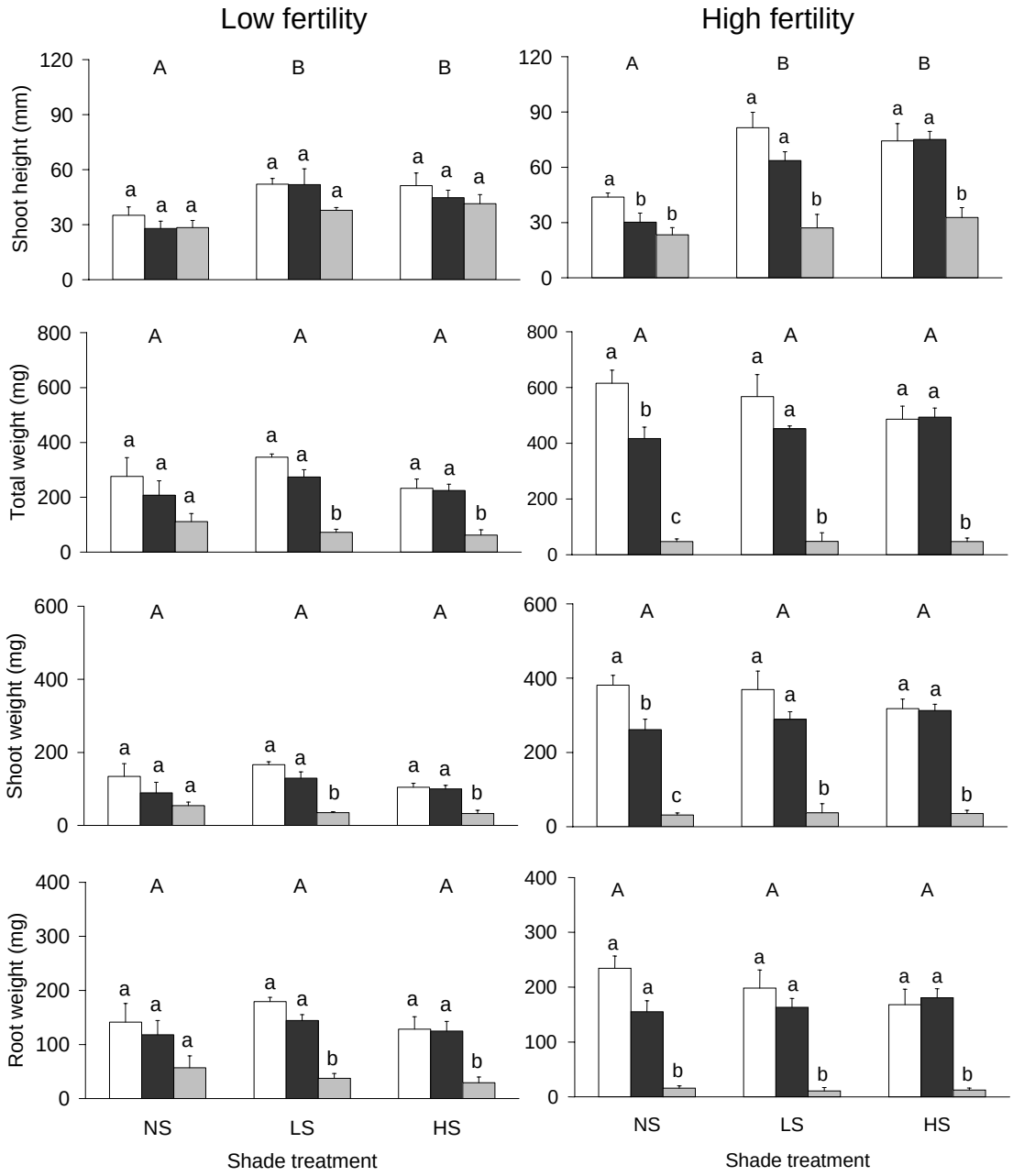


Figure 1. Growth response of seedlings of *P. sylvestris* to shade treatments. Seedling combinations: open bars = *P. sylvestris* monoculture, black bars = *P. sylvestris* grown in mixture with *P. abies*, shaded bars = *P. sylvestris* grown in mixture with *B. pendula*. Shade treatments: NS = non-shaded control, LS = low level of shade and HS = high level of shade. Capital letters indicate significant differences between shade treatments means, and small letters indicate significant differences between seedling combination means for each shade treatment (Tukey's test, $P \leq 0.05$).

There were clear interspecific differences in shade avoidance responses between tree seedlings. When exposed to shade, the early-successional species (*P. sylvestris* and *B. pendula*) increased stem-elongation and showed some changes in biomass allocation, while the mid-late successional species (*P. abies*) did not show any changes in growth. These results are consistent with the two major light strategies for survival and fitness under shaded conditions; shade tolerance and shade avoidance (Smith 1994, Aphalo *et al. 19*99). Shade-avoiders like *P. sylvestris* and *B. pendula*, which usually colonise open or partially shaded areas, would benefit by being able to sense the presence of neighbours (future competition) and rapidly increase stem height as light intensity diminishes (Ballaré 1999). Shade-tolerators, like *P. abies*,

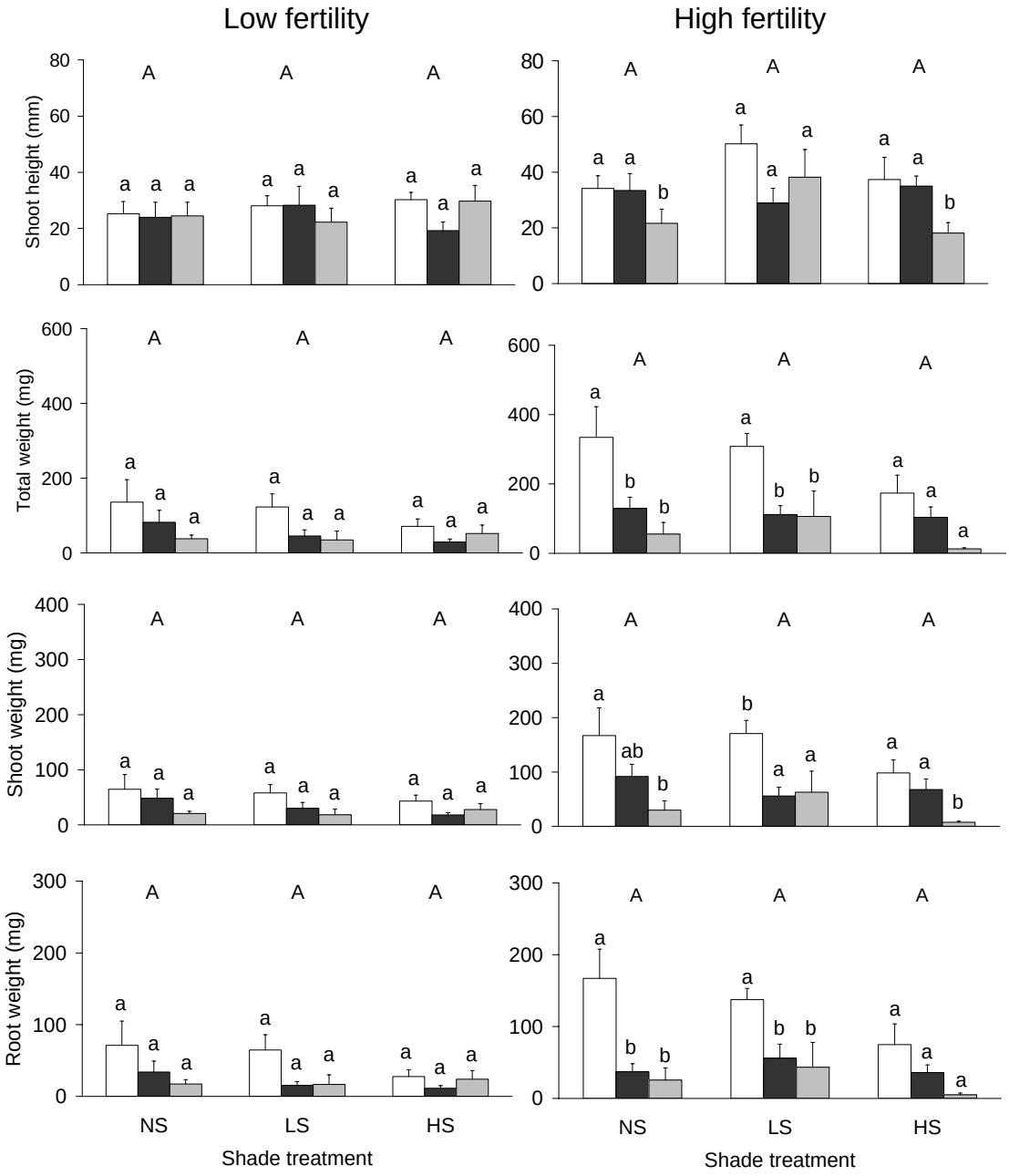


Figure 2. Growth response of seedlings of *P. abies* to shade treatments. Seedling combinations: open bars = *P. abies* monoculture, black bars = *P. abies* grown with *P. sylvestris*, shaded bars = *P. abies* grown with *B. pendula*. Legends as for Figure 1.

instead tend to allocate resources to a shade-adapted leaf physiology that maximises net carbon gain in shade and enables them to grow slowly towards the canopy (Björkman 1981). Individuals of *P. abies* can survive in shaded conditions for many years, and then develop when they receive more light following tree fall (gap formation) or after outgrowing competing trees (Kuuluvainen 1994, Drakenberg 1997). The cost of expressing a shade tolerance physiology may be so high that the seedlings are restricted to very limited growth (Henry and Aarssen 2001). Further, the shade avoidance response is not likely to be crucial for the survival of seedlings and the future abundance of individuals of *P. abies* in the canopy, as it may be for pioneer species that depend on higher light availability for growth.

De la Rosa *et al.* (1998, 1999) found that stem height of *P. sylvestris* increased only when seedlings were exposed to reduced R: FR in fertilized soil, and not when grown in natural boreal forest soil. In this experiment, a significant increase was found for stem elongation of *P. sylvestris* seedlings grown in both low and high fertility humus, even if the response appeared to be stronger under high fertility. *Betula pendula* seedlings, which are known to have higher nutrient requirements for growth (Ingestad and Ågren 1992), appeared to be highly affected by nutrient availability for maximizing shade avoidance. They responded to shade by a strong increase of stem height under high fertility, but under low fertility no significant response was found. Since *P. sylvestris* seedlings naturally establishes on nutrient poor substrates, it is likely that this species, in contrast to *B. pendula*, also can afford to induce shade avoidance responses under nutrient-poor conditions. It is also possible that the increase of stem height of *B. pendula* seedlings was restricted in the low fertility soil because they allocated more resources to support EM (de la Rosa *et al. 19*99).

The shade avoidance response requires changes in light quality (R: FR), rather than reductions in total light intensity (Smith 1994). Reductions in light quantity are instead thought to lead to typical shade tolerance responses, such as increased leaf and petiole length and reduced respiration (Smith 1982, Mitchell and Woodward 1988). Shade avoidance increased with decreasing canopy openness (i.e. decreasing R: FR) in 12 Canadian deciduous tree species (Henry and Aarssen 2001), which is consistent with previous studies (e.g. Thompson and Harper 1988, Smith 1994). *Betula pendula* seedlings grown in high fertility substrate induced stronger shade avoidance responses under high than low levels of vegetation shade, in contrast to *P. sylvestris* that did not seem to be affected by the level of R: FR. This is accordance with previous results showing that *B. pendula* is highly responsive to changes in R: FR (Gilbert *et al.* 2001).

Light and humus effects on interspecific competition between seedlings

The effect of the vegetation shade treatments on competition between seedlings was generally low, even though both the LS and HS treatments induced competition responses (i.e. shade avoidance) in *B. pendula* and *P. sylvestris*. Grime (1979) predicted that competition is more intense and has a larger effect on species composition at productive sites, i.e. in conditions of higher nutrient availability and higher level of shading (but see Tilman 1988). This prediction is consistent with the findings that mixtures of *P. abies* and *B. pendula* seedlings had lower competition intensity when grown in HS than in LS or in NS, which can be explained by the strong suppressive effects of the taller *B. pendula* seedlings in more shaded conditions. Furthermore, for *P. abies* and *P. sylvestris* seedlings grown in mixtures, interspecific competition appeared to be more intense in high fertility than in low fertility, as the differences between seedlings grown in mixtures and monocultures were greater (Figures 1 and 2). However, when estimating competition intensity by indices this was not found to be statistically significant. It has been shown that plant species naturally growing in nutrient-rich sites often have higher relative competitive abilities compared to those found in nutrient-poor or more stressed sites (Grime and Campbell 1992, Wilson and Keddy 1986). In this experiment, *B. pendula* seedlings were stronger competitors than seedlings of both coniferous species, especially in the high fertility substrate. The suppression of the other tree species by *B. pendula* is probably due to asymmetric competition for light, where taller *B. pendula* individuals

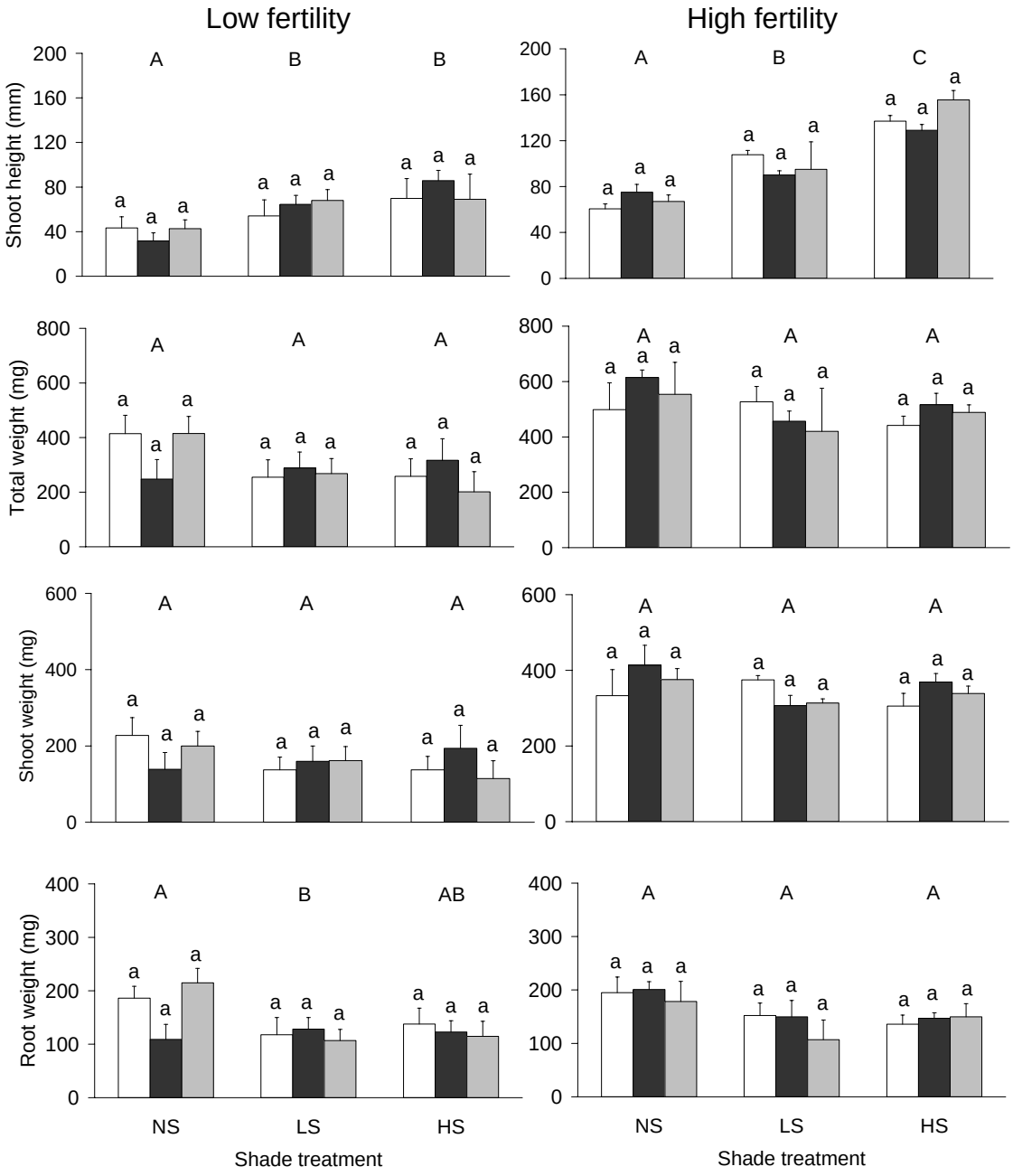


Figure 3. Growth response of seedlings of *B. pendula* to shade treatments. Seedling combinations: open bars = *B. pendula* monoculture, black bars = *B. pendula* grown with *P. sylvestris*, shaded bars = *B. pendula* grown with *P. abies*. Legends as for Figure 1.

are disproportionately successful in resource capture and thus shade and suppress smaller individuals (Schmitt and Wulff 1993).

EM colonisation

Mycorrhizal symbiosis may be an effective strategy for plants to acquire limiting nutrients, providing that carbon costs of the fungal symbiont are not too high (Grime 1987, Jones and Last 1991, Smith and Read 1997). A recent model of the cost-efficiency (i.e. the exchange ratio of carbon to mineral nutrients) of the mycorrhizal symbiosis predicts that the cost-efficiency decreases when the plant cannot respond to increased nutrient-uptake by the fungal symbiont by increasing photosynthesis. Inefficiency of, and selection against, mycorrhizal colonisation could therefore be

expected at high nutrient levels, in shade, at low temperatures or when foliage has been lost (Tuomi *et al.* 2001). Previous studies have shown varying responses of mycorrhizal colonisation to these factors. For example, defoliation can decrease EM colonisation per unit root dry weight in nutrient-poor environments (Gehring and Whitham 1994, 1995), but it has no effect on EM colonisation in more fertile soils (Gehring and Whitham 1994, 1995, Markkola 1996). In my study, lower humus fertility positively affected EM colonisation of *B. pendula* seedlings, which is consistent with previous studies that often have found positive correlations between EM colonisation and decreasing nutrient availability (reviewed by Smith and Read 1997, Jonsson *et al.* 2001). The EM associations may be very important for *B. pendula* seedlings in the low fertility sites in boreal forests of northern Sweden (dominated by dwarf shrubs), since N-uptake and growth of *B. pendula* have been shown to be severely depressed by the presence of phenolics released from dwarf shrubs (Wardle *et al. 19*98). In conditions of higher nutrient availability, the EM symbiosis probably would not be cost-efficient considering the high growth and the high percentage of non-colonised (often large) seedlings in the high fertility substrate. For *P. sylvestris* seedlings grown in monoculture and for *P. abies* in all seedling combinations, there were no differences in EM colonisation between low and high fertility. Jonsson *et al.* (2001) found a higher EM colonisation (percentage colonised short roots) for *P. sylvestris* in high fertility humus, which they suggested was a result of a greater amount of carbon exudates released from the roots, a higher fungal usage of carbon from the humus or a lower concentration of phenolics derived from dwarf shrubs. However, when *P. sylvestris* was grown in mixtures with *B. pendula* seedlings, the EM colonisation was significantly higher in the low fertility than in the high fertility substrate. This may be a cause of the stronger suppression by *B. pendula* seedlings in high fertility soil, which greatly reduced the total weight and presumably the vigour of *P. sylvestris* seedlings. In this study, EM colonisation on *P. abies* was low across treatments, most probably because of the slow growth of seedlings and the low number of short roots. This was particularly evident for the strongly reduced colonisation by *A. muscaria* when *P. abie*s was grown with *B. pendula*.

Some authors have found negative correlations between reduced light intensity and EM colonisation (e.g. Björkman 1942 in Nylund 1988, Son and Smith 1988). However, my experiment clearly showed that reduced light quality and quantity did not affect mycorrhiza colonisation, which is in accordance with other studies on EM colonisation of *P. sylvestris* seedlings (de la Rosa *et al. 19*99), and on arbuscular mycorrhizal colonisation of *Trifolium subterraneum* cv. Mt. Barker. (Facelli *et al. 19*99). My results suggest further that the light quantity under the filters was not limiting for photosynthesis and the production of carbohydrates. However, a small negative affect on production of carbohydrates might not be detected as EM fungi have been shown to able to utilise soil carbon, at least to some extent (Smith and Read 1997). In this experiment, the only effects of shading appear to be through reductions in seedling root and total biomass, which decreased the total colonisation of EM species per seedling (but not per unit root dry weight).

In previous studies, the relative abundance and diversity of EM species on plant roots have been altered by defoliation and N-fertilization (Saikkonen *et al.* 1999, Cullings *et al.* 2001, Lilleskov and Bruns 2001). These results suggest that the response of EM fungal species to decreased carbon flow from roots is species-

specific, and that this can alter their competitive abilities (Cullings *et al.* 2001). The morphotype composition of natural EM communities on *P. sylvestris* was not affected by light quality (reduced R: FR ratios) (de la Rosa *et al. 1*999). In this study, the composition of EM species was more affected by the strong dominance of *P. involutus* than by treatments and host tree species. It is difficult to draw any conclusions about competitive abilities of the fungal species, as the plants were only successfully colonised by two fungal species. However, the observed increase in the proportion of *A. muscaria* colonisation (i.e. the reduction of the Pi: Pi+Am ratio) on *B. pendula* grown in monoculture in the low fertility humus, and its higher proportion of *A. muscaria* compared to the other tree species, indicates that this symbiosis may be important for *B. pendula*.

Conclusions

The results of this study demonstrate that humus fertility and shade strongly influence the growth and relative performance of seedlings of the studied tree species, despite the absence of statistically significant effects for the effects of treatments on measures of interspecific competition. The expression of shade avoidance by the pioneer species *B. pendula* and *P. sylvestris* is likely to increase the chances for individual trees of these species to reach the canopy, which would influence the future composition of the forest stand. The shade avoidance response was also strongest in the high fertility substrate where it probably would be most important because the seedlings would be exposed to more light competition (more shaded conditions). *Betula pendula* seedlings were the strongest competitors among seedlings, and the interspecific competition appeared to be higher in the high fertility substrate. Further, the results show that humus fertility, but not vegetation shade, is an important factor for EM colonisation, and indicates that the EM symbiosis has a greater ecological importance in low fertility than high fertility substrate in the case of *B. pendula* seedlings.

References

Aphalo, P.J. and Letho, T. 1997. Effects of light quality on growth and N accumulation in birch seedlings. Tree Physiology 17: 125-132.

Aphalo, P.J., Ballaré, C.L. and Scopel, A.L. 1999. Plant-plant signalling, the shade avoidance response and competition. Journal of Experimental Botany 50: 1629-1634.

Ballaré, C.L. 1999. Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. Trends in Plant Science 4: 97-102.

Björkman, O. 1981. Responses to different quantum flux densities. *In* Physiological Plant Ecology. Eds. Lange, O.I., Nobel, P.S., Osmond, C.B. and Ziegler, H. Encyclopedia of Plant Physiology, New series, Vol. 12A. pp 57-107. Springer-Verlag.

Charles-Edwards, D.A., Doley, D. and Rimmington, G.M. 1986. Modelling plant growth and development. Academic Press.

Cipollini, D.F. and Schultz, J.C. 1999. Exploring cost constraints on stem elongation in plants using phenotypic manipulation. The American Naturalist 153: 236-242.

Cullings, K.W., Vogler, D.R., Parker, T.V. and Makhija, S. 2001. Defoliation effects on the ectomycorrhizal community of a mixed *Pinus contorta*/*Picea engelmannii* stand in Yellowstone Park. Oecologia 127: 533-539.

De la Rosa, T.M., Aphalo, P.J. and Letho, T. 1998. Effects of far-red light on the growth, mycorrhizas and mineral nutrition of Scots pine seedlings. Plant and Soil 201: 17-25.

De la Rosa, T.M., Letho, T. and Aphalo, P.J. 1999. Does far-red light affect growth and mycorrhizas of Scots pine seedlings grown in forest soil? Plant and Soil 211: 259-268.

Drakenberg, B. 1997. Trä- och trädbiologi. Kompendium för jägmästarutbildningen: Drömmen om det perfekta trädet- några förslag. SLU, Umeå.

Ekwelebam, S.A., Reid, C.P.P. 1983. Effect of light, nitrogen fertilization, and mycorrhizal fungi on growth and photosynthesis of lodgepole seedlings. Canadian Journal of Forest Research 13: 1099-1106.

Facelli, E., Facelli, J.M., Smith, S.E. and Mclaughlin, M.J. 1999. Interactive effects of arbuscular mycorrhizal symbiosis, intraspecific competition and resource availability of *Trifolium subterraneum* cv. Mt. Barker. New Phytologist 141: 535-547.

Gehring C.A. and Whitham, T.G. 1994. Comparison of ectmycorrhizae on pinyon pines (*Pinus edulis*; PINACEAE). American Journal of Botany 81: 1509-1516.

Gehring, C.A. and Whitham, T.G. 1995. Duration of herbivore removal and environmental - stress affect the ectomycorrhizae of pinyon pines. Ecology 76: 2118-2123.

Gilbert, I.R., Jarvis, P.G. and Smith, H. 2001. Proximity signal and shade avoidance differences between early and late successional trees. Nature 411: 792-795.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley.

Grime, J.P., Mackey, J.M.L, Hillier, S.H. and Read, D.J. 1987. Floristic diversity in a model system using experimental microcosms. Nature 328: 420-22.

Grime, J.P. and Campbell, B.D. 1992. An experimental test of plant strategy theory. Ecology 73: 15-29.

Henry, A.L. and Aarssen, W. 2001. Inter- and intraspecific relationships between shade tolerance and shade avoidance in temperate trees. Oikos 93: 477-487.

Ingestad, T. and Ågren, G.I. 1992. Theories and methods on plant nutrition and growth. Physiologia Plantarum 84: 177-184.

Jones, C.G. and Last, F.T. 1991. Ectomycorrhizae and trees: implications for aboveground herbivory. *In* Microbial mediation of plant-herbivore interactions. Eds. Barbosa, R., Krichnik, V. and Jones, C. pp. 65-103. John Wiley and Sons.

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.

Keddy, P.A. 1989. Competition. (-Population and community biology series). Chapman and Hall.

Kuiters, A.T. 1990. Role of phenolic substances from decomposing forest litter in plant-soil interactions. Acta Botanica Neerlandica. 39: 329-348.

Kuuluvainen, T. 1994. Gap disturbance, ground microtopography, and the regeneration dynamics of boreal coniferous forests in Finland: a review. Annales Zoologici Fennici 31: 35-51.

Lilleskov, E.A. and Bruns, T.D. 2001. Nitrogen and ectomycorrhizal fungal communities: what we know, what we need to know. New Phytolologist 149: 154-158.

Markkola, A.M. Effect of artificial defoliation on biomass allocation in ectomycorrhizal *Pinus sylvestris* seedlings. Canadian Journal of Forest Research 26: 899-904.

Marx, D.H. 1969. The influence of ectotrophic mycorrhizal fungi on the resistance of pine roots to pathogenic infections. I. Antagonism of mycorrhizal fungi to root pathogenic fungi and soil bacteria. Phytopathology 59: 153-163.
Marx, D.H., Hatch, A.B. and Mendicino, J.F. 1977. High soil fertility decreases sucrose content and susceptibility of loblolly pine to ectomycorrhizal infection by *Pisolithus tinctorius*. Canadian Journal of Botany 55: 1569-1574.
Mitchell, P.L. and Woodward, F.I. 1988. Responses of three woodland plants to reduced photosynthetically active radiation and low red to far-red ratio in shade. Journal of Ecology 76: 807-825.
Moora, M. and Zobel, M. 1996. Effect of arbuscular mycorrhiza on inter- and interspecific competition of two grassland species. Oecologia 108: 79-84.
Nilsson, M.-C., Högberg, P., Zackrisson, O. and Fengyou, W. 1993. Allelopathic effects by *Empetrum hermaphroditum* on development and nitrogen uptake by roots and mycorrhizae of *Pinus sylvestris*. Oikos 86: 16-26.
Nilsson, M.-C., Wardle, D.A. and Dahlberg, A. 1999. Effects of plant litter species composition and diversity on the boreal ecosystem. Oikos 86: 16-26.
Northup, R., Yu, Z., Dahlgren, R. and Vogt, K. 1995. Polyphenol control of nitrogen release from pine litter. Nature 377: 227.
Nylund, J-E. 1988. The regulation of mycorrhiza formation – carbohydrate and hormone theories reviewed. Scandinavian Journal of Forest Research 3: 465-479.
Saikkonen, K., Ahonen-Jonnarth, U., Markkola A.M., Helander, M., Tuomi, J., Roitto, M. and Ranta, H. 2001. Defoliation and mycorrhizal symbiosis: a functional balance between carbon sources and below-ground sinks. Ecology Letters 2: 19-26.
Schmitt, J. and Wulff, R.D. 1993. Light spectral quality, phytochrome and plant competition. Trends in Ecology and Evolution 8: 47-51.
Sharew, H., Grace, J., and Legg, C.J. 1996. Response of two Afromontane coniferous tree species to light and nutrient supply. Tree physiology 16: 617-626.
Simard, S.W., Perry, D.A., Jones, M.D., Myrolds, D.D., Durall, D.M. and Molina, R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature 388: 579-582.
Skàlovà, H. and Vosàtka, M. 1998. Growth response of three *Festuca rubra* clones to light quality and arbuscular mycorrhiza. Folia Geobotannica 33: 159-169.
Smith, H. 1982. Light quality, photoreception and plant strategy. Annual Review of Plant Physiology 33: 481-518.
Smith, H. 1994. Sensing the light environment: the functions of the phytochrome family. *In* Photomorphogenesis in Plants, 2nd ed. Eds. Kendrick, R.E. and Kronenberg, G.H.M. pp. 377-416. Kluwer Academic Publishers.
Smith, M.D., Hartnett, D.C. and Wilson, G.W.T. 1999. Interacting influence of mycorrhizal symbiosis and competition on plant diversity in tall grass prairie. Oecologia 121: 574-582.
Smith, S.E. and Read, D.J. 1997. Mycorrhizal symbiosis. Academic Press.
Snaydon, R.W. 1991. Replacement or additive designs for competition studies? Journal of Applied Ecology 28: 930-946.
Son, C.L. and Smith, S.E. 1988. Mycorrhizal growth responses - interactions between photon irradiance and phosphorus nutrition. New Phytolologist 108: 305-314.
Thompson, L. and Harper, J.L. 1988. The effect of grasses on the quality of transmitted radiation and its influence on the growth of the white clover *Trifolium repens*. Oecologia 75: 343-347.
Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press.
Tuomi, J., Kytöviita, M.-M. and Härdling, R. 2001. Cost efficiency of nutrient acquisition and the advantage of mycorrhizal symbiosis for the host plant. Oikos 92: 62-70.
Wardle, D.A., Zackrisson, O. and Nilsson, M.-C. 1998. The charcoal effect in Boreal forests: mechanisms and ecological consequences. Oecologia 115: 419-426.
Wilson, J.B. 1988. Shoot competition and root competition. Journal of Applied Ecology 25: 279-296.
Wilson, S.D. and Keddy, P.A. 1986. Species competitive abilities and position along a natural stress disturbance gradient. Ecology 67: 236-1242.