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D.A. Wardle · O. Zackrisson · M.-C. Nilsson

The charcoal effect in Boreal forests: mechanisms and ecological consequences

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Abstract Wildfire is the principal disturbance regime in northern Boreal forests, where it has important rejuvenating effects on soil properties and encourages tree seedling regeneration and growth. One possible agent of this rejuvenation is fire-produced charcoal, which adsorbs secondary metabolites such as humus phenolics produced by ericaceous vegetation in the absence of fire, which retard nutrient cycling and tree seedling growth. We investigated short-term ecological effects of charcoal on the Boreal forest plant-soil system in a glasshouse experiment by planting seedlings of *Betula pendula* and *Pinus sylvestris* in each of three humus substrates with and without charcoal, and with and without phenol-rich *Vaccinium myrtillus* litter. These three substrates were from: (1) a high-productivity site with herbaceous ground vegetation; (2) a site of intermediate productivity dominated by ericaceous ground vegetation; and (3) an unproductive site dominated by *Cladina* spp. Growth of *B. pendula* was stimulated by charcoal addition and retarded by litter addition in the ericaceous substrate (but not in the other two), presumably because of the high levels of phenolics present in that substrate. Growth of *P. sylvestris*, which was less sensitive to substrate origin than was *B. pendula*, was unresponsive to charcoal. Charcoal addition enhanced seedling shoot to root ratios of both tree species, but again only for the ericaceous substrate. This response is indicative of greater N uptake and greater efficiency of nutrient uptake (and presumably less binding of nutrients by phenolics) in the presence of charcoal. These effects were especially pronounced for *B. pendula*, which took up 6.22 times more nitrogen when charcoal was added. Charcoal had no effect on the competitive balance between *B. pendula* and *P. sylvestris*, probably due to the low intensity of competition present. Juvenile mosses and ferns growing in the pots were extremely responsive to charcoal for all sites; fern prothalli were entirely absent in the ericaceous substrate unless charcoal was also present. Charcoal stimulated active soil microbial biomass in some instances, and also exerted significant although idiosyncratic effects on decomposition of the added litter. Our results provide clear evidence that immediately after wildfire fresh charcoal can have important effects in Boreal forest ecosystems dominated by ericaceous dwarf shrubs, and this is likely to provide a major contribution to the rejuvenating effects of wildfire on forest ecosystems.

Key words Activated carbon · Boreal forest charcoal · Ericaceous shrubs · Wildfire

Introduction

Wildfire through lightning strike is the principal agent of disturbance in the northern Boreal forests of Fennoscandia, where it has a natural return period of 50–100 years (Zackrisson 1977). Following disturbance by fire, these forests usually initially become dominated by *Pinus sylvestris* L. (Scots pine), and in the prolonged absence of fire there is an increasing domination by *Picea abies* (L.) Karst. (Norway spruce) and ericaceous dwarf shrub species, most notably *Empetrum hermaphroditum* Hagerup (crowberry) (Sirén 1955; Haapasaari 1988). Anthropogenic suppression of wildfire over the past century has led to increased domination of forests by *P. abies* and dwarf shrub species (Bradshaw and Zackrisson 1990). Plant species which dominate in late-successional Boreal forests often contain very high levels of secondary metabolites, principally phenolics (Odén et al. 1992; Gallet and Lebreton 1995; Wallstedt et al. 1997) which can have detrimental effects on plant

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D.A. Wardle (✉)[1] · O. Zackrisson · M.-C. Nilsson
Department of Forest Vegetation Ecology,
Swedish University of Agricultural Sciences, Faculty of Forestry,
S-901 83 Umeå, Sweden

Present address:
[1] Landcare Research, P.O. Box 69,
Lincoln 8152, New Zealand
Fax: (64)(3)325-2418; e-mail: wardled@landcare.cri.nz

growth and nutrient acquisition (Zackrisson et al. 1997), mycorrhizal functioning (Nilsson et al. 1993) and soil biological properties (Wardle and Lavelle 1997), leading to considerable locking of nutrients and formation of deep mor humus layers with low biological activity (Edvardsen et al. 1988; Tamm 1991; Wardle et al. 1997).

It is well recognised that wildfire often exerts important rejuvenating effects on forest ecosystems, including increased decomposition of plant litter and humus, improved cation availability and enhanced pH (Viro 1974; Dyrness et al. 1986; Tamm 1991; Whelan 1995). In an earlier investigation we showed that charcoal produced by wildfire could make a significant contribution to this rejuvenation effect (Zackrisson et al. 1996; see also Moore 1996). In that study, we demonstrated that the sorptive surface created by newly produced charcoal was able to adsorb significant amounts of phenolics produced by *E. hermaphroditum*, resulting in their deactivation through microbial activity. These effects are characteristic of the sorptive properties of activated carbon, and operate in much the same way as commercially produced activated carbon through selectively removing certain organic compounds from the soil (Coffey and Warren 1969; Chereminisoff and Ellerbusch 1978; Nilsson 1994). Further, we were able to show that charcoal maintained a high sorptive capacity for about a century after wildfire, and that these sorptive effects were potentially capable of reversing negative effects of plant species which produced high levels of phenolics, contributing to greater success of plant species which were susceptible to phenolics.

This study aimed to investigate the effects of charcoal on aspects of the plant-soil system under controlled environmental conditions. Investigation concentrated on how charcoal affects plant growth, nutrient acquisition, competitive ability and soil biological activity; whether charcoal had greater effects when added to humus collected from under ericaceous vegetation than under other vegetation; and whether charcoal reversed negative effects caused by phenol-rich ericaceous leaf litter. The underlying goal was to better understand the role that newly produced charcoal from wildfire may have in determining vegetation and soil processes, and ultimately ecosystem function.

Materials and methods

The substrates that we used in our study were collected from Vargisån, in the northern Boreal zone of Sweden (66°01′N; 19°51′E) on 23 August 1996. We collected humus from three adjacent sites in this area which differed significantly in ground cover vegetation and soil fertility but which had near-identical climates; the humus was collected for each site over an area of approximately 30 × 30 m to the full depth of the humus layer. These sites were:

1. Herb site. This was dominated by *P. abies*, and the ground layer consisted of herbaceous species [e.g. *Melica nutans* L., *Geranium sylvaticum* L. and *Gymnocarpium dryopteris* (L.) Newm.] characteristic of highly productive, fertile areas (Hägglund and Lundmark 1977). The humus pH was 4.7 and the concentrations of the main nutrients were: N = 1.97%, mineral N = 76 μg/g (54% NH_4, 46% NO_3), Mg = 0.147%, Ca = 1.82% and P = 0.129%.
2. Ericaceous site. This was dominated by *P. sylvestris*, with a ground-layer vegetative cover of the ericaceous dwarf shrubs *Vaccinium myrtillus* L. (bilberry), *V. vitis-idaea* L. (cowberry) and *E. hermaphroditum*. In this site humus pH was 3.5 and the concentrations of the main nutrients were: N = 1.15%, mineral N = 27 μg/g (100% NH_4), Mg = 0.051%, Ca = 0.31% and P = 0.094%.
3. Cladina site. This site was dominated by slow-growing *P. sylvestris* trees, and a ground-layer vegetation of reindeer lichens [*Cladina arbuscula* (Wallr) Hale and W. Culb, *C. rangiforina* (L.) Nyl. and *C. stellaris* (Opiz) Brodo]. This vegetation is characteristic of oligotrophic sites of low nutrient availability (Hägglund and Lundmark 1977). At this site, humus pH was 3.6 and the main nutrient concentrations were: N = 1.02%, mineral N = 6 μg/g (100% NH_4), Mg = 0.038%, Ca = 0.010% and P = 0.062%.

The humus from each site was sieved to 4 mm and placed in pots (8 cm diameter × 8 cm depth), and lightly compacted. Ninety-six pots were set up for each site, i.e. six replicate blocks of 16 treatments. These treatments represented a 2 × 2 × 2 × 2 factorial design of four factors, i.e. charcoal (present or absent), litter (present or absent), *P. sylvestris* seedlings (planted or absent) and *Betula pendula* Roth. seedlings (planted or absent). The charcoal treatment consisted of adding 1 g of particles (0.5–1.6 mm) of artificially created charcoal as evenly as possible to the entire humus surface of each pot. This amount corresponds to approximately 2000 kg/ha or the amount of charcoal which is often present following wildfire (Zackrisson et al. 1996). This charcoal was prepared as described by Zackrisson et al. (1996), and involved heating twigs of *E. hermaphroditum* (collected during September 1995 at Västra Månsträsk) at 450°C for 15 min in a muffle furnace, and retaining the 0.5–1.6 mm size fraction of the charcoal formed following sieving. The litter treatment involved placing 1.5 g *V. myrtillus* litter (collected in September 1995 from Yttertavlevägen) on the surface of each pot; this level corresponds to 3000 kg/ha, which is characteristic of levels often present in the field (Havas and Kubin 1983). *V. myrtillus* was selected because this species is known to contain high levels of secondary metabolites, principally phenolics (Gallet 1994; Jäderlund et al. 1996). When charcoal and litter were placed in the same pots, the litter was always placed over the charcoal, consistent with field conditions. When pots contained *P. sylvestris* or *B. pendula* seedlings, two pre-germinated seedlings of the planted species were placed about 3 cm apart, and 2.5 cm from the edge of the pot. When both species were present in the same pot the four seedlings were arranged in the same manner with the seedlings all equal distances from the centre. The experiment thus represented an additive competition design (Snaydon 1991). The two tree species selected were chosen because of their known differential susceptibilities to secondary metabolites, with *B. pendula* being the more sensitive of the two (Jäderlund et al. 1996). The litter and charcoal treatments were imposed shortly after addition of the humus to the pots; the tree seedlings were planted 76 days later so as to allow sufficient time for the charcoal to adsorb secondary metabolites present in the humus, and for the litter to have time to partially decompose and release phenolics.

The experiment was maintained in glasshouse conditions with a daytime temperature of 20°C and a nighttime temperature of 15°C, and with a day:night light ratio of 20 h:4 h, characteristic of growing-season conditions in the northern Boreal zone. During the course of the experiment, approximately 20 ml of distilled water was added to each pot every 2 days; after seedlings were planted all plants were misted with distilled water daily. The experiment was harvested 57 days after seedling planting, or 133 days after litter and charcoal placement. At harvest, humus was carefully separated from the plant roots, and for each plant in each pot the root and shoot material were separated, cleaned and oven-dried at 70°C for 72 h for dry weight determinations. At harvest, for each pot containing *B. pendula* seedlings, six *B. pendula* leaves were selected and their colour matched to the colour chart scale produced by the Royal Horticultural Society, London (1995 version). This scale was converted to a ten-point scale for the purposes of statistical anal-

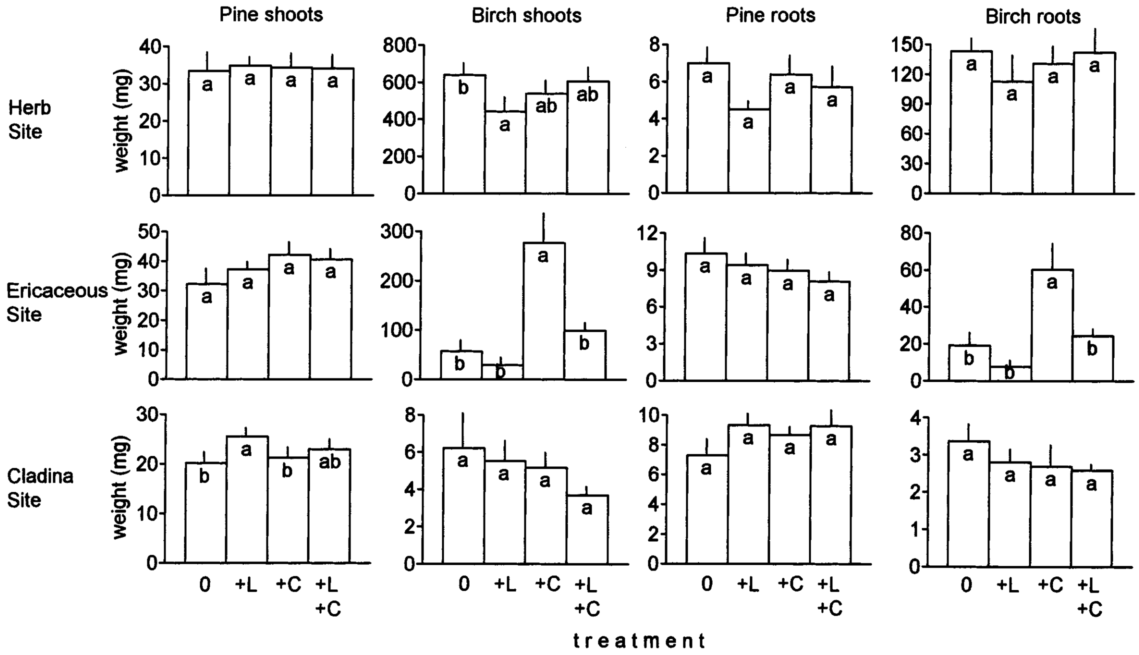

Fig. 1 Biomass of pine and birch shoots and roots in response to litter (L) and charcoal (C) addition at three sites. Vertical bars represent standard errors. Within each sub-graph, numbers accompanied by the same letter are not significantly different at $P = 0.05$ (LSD test following ANOVA on log-transformed data)

ysis, with "1" representing green (no chlorosis) and "10" representing severe yellowing or chlorosis. Total plant N concentration (roots and shoots combined) was determined by combustion and analysis of dry material using a Carlo Erba NA 1500 analyser for each *P. sylvestris* or *B. pendula* monoculture pot containing humus from the Ericaceous site, i.e. the site for which charcoal had the greatest effects (see Results). The total N content of the seedlings in each pot was determined as the product of seedling weight and nitrogen concentration. Since in some situations dominated by ericaceous dwarf shrubs the seedlings can contain less nitrogen than that initially present in the seed reserves (representing a net loss of nitrogen) (Zackrisson et al. 1997), we also evaluated the total nitrogen contents of the seeds of both species. For *B. pendula*, this was performed by measuring the nitrogen concentration (see above) and total mass of each of six batches of 150 seeds following removal of the wings, while for *P. sylvestris* this was done for seven batches of 20 seeds. The competitive balance between *P. sylvestris* and *B. pendula* seedlings was determined using the competitive balance index, C_b, of Wilson (1988); this was calculated separately for each replicate block using the monoculture and mixed species pots. This index ranges from −1 to +1 and is increasingly positive or negative as *B. pendula* or *P. sylvestris* respectively has a competitive advantage; a value of 0 indicates equitable competitive ability. Intensity of competition between the two species was determined for each replicate block using the competition intensity index, C_i, of Wilson (1988); this index ranges from 0 (no competition) to +1 (complete competition), with negative values representing growth stimulation.

Measurements were also made for other components of each pot. At harvest the total percentage cover of mosses and of fern prothalli on the humus surface was visually estimated. The humus present in each pot at harvest was analysed for microbial basal respiration and substrate-induced respiration (SIR; a relative measure of active microbial biomass) as described by Wardle (1993) and based on the approaches of Anderson and Domsch (1978) and West and Sparling (1986). Briefly, basal respiration was determined for a 1.5 g (dry weight, basis) subsample, with a moisture content adjusted to 150% (d.w. basis). This material was placed in a 169-ml sealed container and incubated at 22°C. Basal respiration was determined as the total CO_2-C released between one and four hours of incubation, measured using infra-red gas analysis. Determinations of SIR were performed in the same way, but with the sample being amended with 10 000 $\mu g\ g^{-1}$ glucose immediately prior to incubation. The ratio of basal respiration to SIR was used as a relative measure of the microbial metabolic quotient (Anderson and Domsch 1985), a measure of microbial efficiency. Finally, the *V. myrtillus* litter remaining in each pot at harvest was carefully separated from the humus, rinsed, dried at 70°C for 24 h, and weighed, so as to enable determination of the rate of litter decomposition over the course of the experiment.

The plant growth, nutrient and competition data were all analysed using ANOVA for each site, testing for effects of litter addition, charcoal addition, and litter × charcoal interactions. ANOVA was also used to analyse the soil microbial data (testing for these effects as well as the effects of presence or absence of pine and birch seedlings) and the decomposition data (testing for site and charcoal effects). All data was tested to determine whether it conformed to assumptions of normality (Wilk-Shapiro test) and homogeneity of variances (Bartlett's test), and where necessary data was log-transformed to satisfy these assumptions. For the ordinal data for the chlorosis measurements, and for the fern and moss cover data, the non-parametric Kruskall-Wallis test was used to test for effects of charcoal and of litter addition.

Results

B. pendula was highly susceptible to substrate type, with both shoot and root mass declining in the order of Herb substrate > Ericaceous substrate > *Cladina* substrate (Fig. 1). Seedlings of *P. sylvestris* were less susceptible, but generally grew larger in the Herb site and Ericaceous site substrates than in the Cladina site substrate. Both shoot and root growth of *B. pendula* were stimulated by charcoal addition and suppressed by litter addition in the Ericaceous substrate but not the other substrates (Fig. 1, Table 1). Seedling growth of *P. sylvestris* (both above- and below-ground) was unaffected by either

Table 1 Analysis of variance results (*F*-values with *P*-values in brackets) for plant responses to addition of litter (*L*) and charcoal (*C*) (*ND* not determined). Terms for ANOVA model (degrees of freedom in brackets) are C (1), L (1), C × L (1), blocking (5), error (15)

Response variable	Herb site			Ericaceous site			Cladina site		
	L × C	L	C	L × C	L	C	L × C	L	C
Pine shoot weight[a]	0.16(0.694)	0.00(0.955)	0.27(0.610)	0.58(0.459)	3.06(0.101)	1.08(0.316)	7.30(0.016)	0.13(0.721)	1.97(0.181)
Birch shoot weight[a]	2.16(0.163)	0.05(0.828)	5.39(0.035)	9.94(0.007)	10.65(0.006)	1.14(0.304)	0.76(0.397)	1.18(0.294)	0.41(0.533)
Pine root weight[a]	3.67(0.073)	0.00(0.949)	0.70(0.416)	0.74(0.403)	1.60(0.226)	0.01(0.921)	2.55(0.131)	0.83(0.375)	1.21(0.289)
Birch root weight[a]	0.90(0.358)	0.15(0.702)	1.76(0.208)	15.62(0.001)	6.57(0.023)	2.01(0.178)	0.20(0.663)	1.65(0.219)	0.72(0.411)
Pine shoot to root ratio	3.46(0.083)	0.11(0.750)	0.56(0.466)	2.19(0.159)	10.63(0.005)	0.30(0.589)	0.02(0.883)	1.71(0.211)	0.22(0.644)
Birch shoot to root ratio	0.59(0.454)	0.19(0.672)	2.31(0.149)	0.43(0.552)	19.20(0.001)	0.10(0.758)	0.34(0.569)	0.26(0.621)	2.13(0.165)
Pine N concn.	ND	ND	ND	3.24(0.091)	8.46(0.011)	13.94(0.002)	ND	ND	ND
Birch N concn.	ND	ND	ND	2.69(0.121)	1.81(0.196)	1.01(0.331)	ND	ND	ND
Total N per pine plant[a]	ND	ND	ND	0.05(0.825)	5.90(0.028)	6.11(0.026)	ND	ND	ND
Total N per birch plant[a]	ND	ND	ND	9.20(0.009)	19.25(0.001)	2.85(0.114)	ND	ND	ND
Pine reduction by birch	0.18(0.677)	0.16(0.695)	4.16(0.060)	0.27(0.613)	0.72(0.409)	0.46(0.510)	1.29(0.273)	0.16(0.694)	6.44(0.022)
Birch reduction by pine	0.63(0.438)	0.12(0.730)	0.12(0.738)	3.30(0.091)	0.90(0.360)	0.27(0.611)	0.07(0.769)	0.11(0.746)	0.05(0.828)
Competitive balance	1.37(0.261)	0.15(0.703)	0.17(0.684)	3.13(0.098)	0.047(0.492)	0.024(0.632)	3.58(0.078)	0.01(0.914)	3.47(0.082)
Intensity of competition	1.42(0.251)	0.68(0.421)	0.86(0.357)	2.54(0.133)	0.020(0.844)	1.720(0.211)	0.22(0.645)	0.71(0.413)	2.41(0.141)

[a] Variables log-transformed

charcoal or litter for all three substrates, with the exception of a marginally significant stimulation of shoot mass by litter addition for the Cladina substrate. There was no consistent evidence of interactive effects between charcoal and litter (Table 1). Shoot to root ratios of both *P. sylvestris* and *B. pendula* were highly significantly stimulated by charcoal but only at the Ericaceous site; there were no effects of litter on shoot to root ratios at any site (Fig. 2). Chlorosis of *B. pendula* seedlings was greatest for the Cladina substrate and least for the Herb substrate and charcoal reduced chlorosis only when added to the Ericaceous substrate (Fig. 3). For the Ericaceous substrate, plant N concentration was enhanced by charcoal addition for both *P. sylvestris* and *B. pendula*, although the effect was statistically significant only for *P. sylvestris*; the high variability of the *B. pendula* data probably obscured possible trends (Table 1; Fig. 4). For both species, plants had more total N per seedling when charcoal was added, and this was especially pronounced for *B. pendula*, for which charcoal addition induced a 6.22-fold increase in the amount of N immobilised in plant tissue. All *B. pendula* plants acquired significant amounts of N following germination; each seed contained 0.015 (SD = 0.001) mg N, which was less than 3% of the mean N content of individual seedlings for any of the treatments. *P. sylvestris* seeds each contained 0.296 (SD = 0.021) mg N, which was 29% and 19% of that in control and charcoal-treatment seedlings respectively. The overall data for individual plant responses clearly indicates that the only consistent

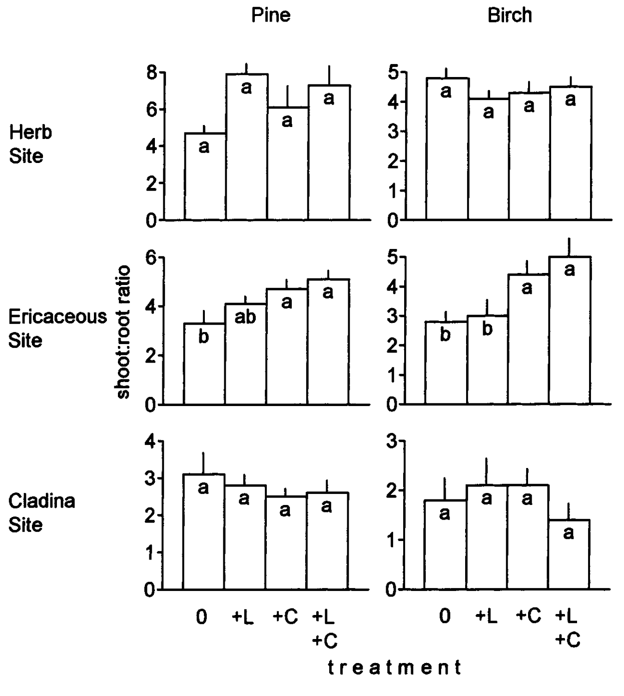

Fig. 2 Pine and birch shoot to root ratios in response to litter (L) and charcoal (C) addition at three sites. Vertical bars represent standard errors. Within each sub-graph, numbers accompanied by the same letter are not significantly different at $P = 0.05$ (LSD test following ANOVA)

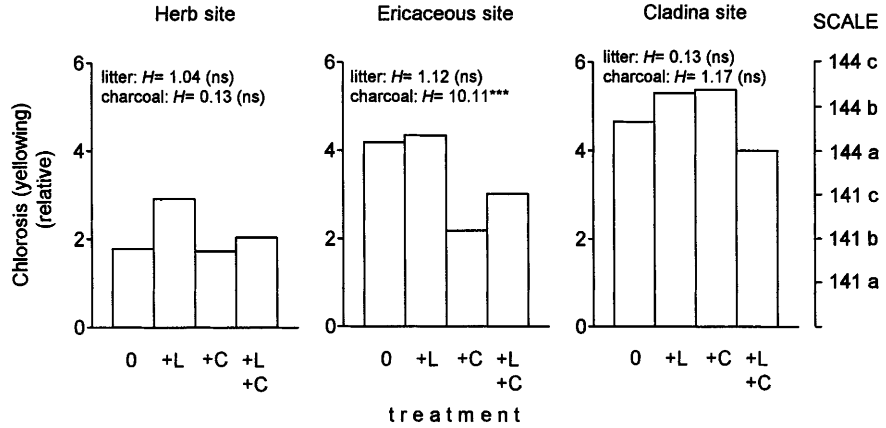

Fig. 3 Chlorosis (yellowing) of birch foliage in response to litter (L) and charcoal (C) addition at three sites. Data analysed using Kruskall-Wallis statistic (H); NS = effect not significant at $P = 0.05$; *** = effect significant at $P = 0.001$. The scale on the right corresponds to the Royal Horticulture Society colour chart

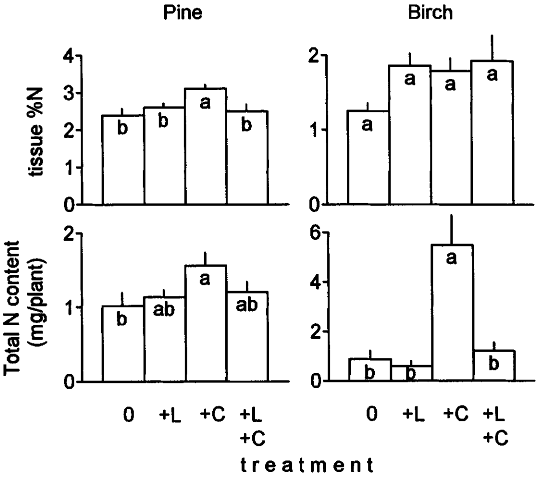

Fig. 4 Pine and birch seedling nitrogen concentrations and total seedling nitrogen contents in response to litter (L) and charcoal (C) addition at the Ericaceous site. Vertical bars represent standard errors. Within each sub-graph, numbers accompanied by the same letter are not significantly different at $P = 0.05$ (LSD test following ANOVA; analyses for total N data performed on log-transformed data)

effects of charcoal addition were for the Ericaceous substrate, and that *B. pendula* was clearly more responsive than *P. sylvestris* to charcoal addition; these effects were often large. We also found some litter effects, but these were generally not reversed by charcoal.

Neither *P. sylvestris* nor *B. pendula* had a consistent competitive advantage, as determined by the C_b values (data not presented). Competition intensity (C_i) indices were usually positive, and in the majority of cases mutual inhibition of growth of the two species was detected, although some mutual growth stimulation was also detected for the Ericaceous substrate (data not presented). There was consistently no significant effects of either charcoal or litter addition on either C_b or C_i for any of the three substrates (Table 1).

The main moss species present in the pots were *Ceratodon purpureus* (Hedw.) Brid. and *Polytrichum* spp. Fern species present could not be identified at this early stage of establishment. Moss and fern cover were both inhibited by litter addition, and for both the Herb and Ericaceous substrates there were clear positive effects of charcoal addition (Fig. 5). This was especially apparent for ferns in the Ericaceous substrate, which were only present when charcoal was also present. There were also instances for both the Herb and Ericaceous substrates in which charcoal addition appeared to partially reverse the negative effects of litter (Fig. 5). Values of SIR were greatly enhanced by the presence of tree seedlings (data not presented), and there was also a significant effect of litter addition for the Herb site ($F_{1,80} = 8.96$, $P = 0.004$) and almost significant for the Ericaceous site ($F_{1,80} = 3.28$, $P = 0.073$) (Table 2). Charcoal stimulated SIR only in the Cladina substrate, but for the other two sites there were significant birch × charcoal interactive effects [$F_{1,80} = 3.82$ ($P = 0.050$) for the Herb site and 6.55 ($P = 0.012$) for the Ericaceous site] (Table 2). There were no significant effects of either litter or charcoal on either basal respiration or the basal respiration to SIR ratio (and thus microbial efficiency) (data not presented). Decomposition of litter of *V. myrtillus* was accelerated by the presence of both *P. sylvestris* and *B. pendula* seedlings (data not presented); charcoal caused a statistically significant reduction of litter decomposition for the Herb substrate but enhanced litter decomposition for the other substrates (Table 3). There were no significant interactions between tree seedling and charcoal effects on decomposition.

Discussion

Although the three substrates we considered had vastly differing effects on seedling biomass (especially for *B. pendula*), addition of charcoal only had effects on biomass production for the substrate which supported intermediate productivity, i.e. that from the Ericaceous site. This means that charcoal addition was capable of partially reversing whatever factor was responsible for inhibiting seedling production for the Ericaceous substrate, but not for the Cladina substrate. We propose that the primary agents of inhibition of *B. pendula* seedling growth in the Ericaceous substrate were phenolics originating from the ericaceous plant species

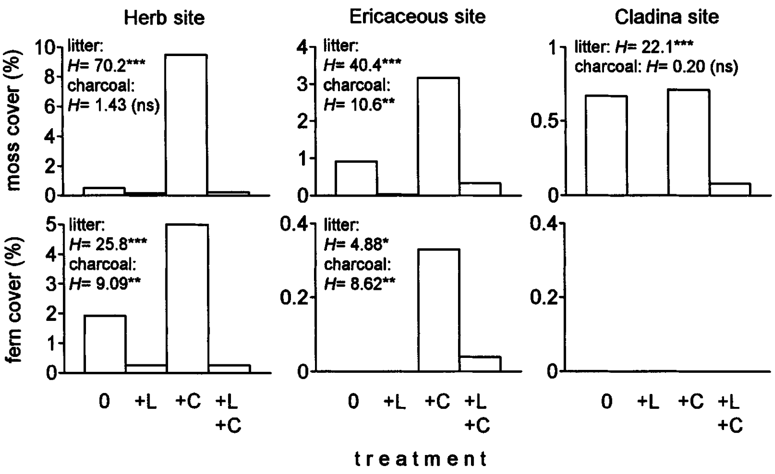

Fig. 5 Ground cover of mosses and juvenile ferns at time of harvest in response to litter (L) and charcoal (C) addition and presence of birch seedlings (B) at three sites. Data analysed using Kruskall-Wallis statistic (*H*); NS = effect not significant at $P = 0.05$; *, **, *** = effect significant at $P = 0.05$, 0.01 and 0.001 respectively

Table 2 Substrate-induced respiration of humus (μg CO_2-C g^{-1} h^{-1}), in response to addition of litter (*L*), charcoal (*C*) and birch seedlings (*B*) to the experimental units

Treatment (addition)	Herb site	Ericaceous site	Cladina site
No additions	23.7	18.7	19.3
+L	22.1	20.7	19.2
+C	25.4	17.8	21.3
+L+C	24.8	19.6	20.7
+B	29.3	19.5	20.1
+B+L	24.5	19.8	19.4
+B+C	27.4	21.2	22.0
+B+L+C	25.0	21.6	21.2
$LSD_{0.05}$	3.2	2.1	1.7

Table 3 Decomposition of *Vaccinium myrtillus* litter (%) over the course of the experiment in response to charcoal addition at each of three sites. *P*-values obtained by analysis of variance

Site	No charcoal	Charcoal	Significance (*P*)
Herb site	56.4	51.6	0.003
Ericaceous site	50.3	54.0	0.009
Cladina site	43.8	49.2	0.003
Significance (*P*)	<0.001	0.039	

contributing to humus formation at that site, while inhibition of growth in the Cladina substrate was due to other factors, probably low nutrient availability. Enhancement of shoot to root ratios for both species by charcoal addition in the Ericaceous substrate is indicative of greater nutrient availability and thus effectiveness of nutrient uptake (Chapin 1980; Ingestad and Ågren 1988), and is consistent with the enhanced plant concentrations of N caused by charcoal addition for this substrate. Secondary metabolites such as phenolics produced by Ericaceous shrubs can have important adverse effects on plant growth, both as allelopathic agents (Zackrisson and Nilsson 1992; Gallet 1994; Nilsson 1994), and through complexing N thus reducing its availability to plants (Gallet and Lebreton 1995; Wardle et al. 1997); removal of phenolics by charcoal could therefore conceivably be expected to enhance humus N availability to plants, thus explaining the trends we observed. Our findings are consistent with recent field studies in Swedish boreal forests, in which increasing densities of *E. hermaphroditum* and *P. abies* over successional time were found to contribute to higher levels of phenolics in the humus, which in turn reduced mineralisation of soil nitrogen, causing a reduction in plant nitrogen acquisition and growth (Wardle et al. 1997). In situations with high humus phenolic concentrations, plant species differ tremendously in their abilities to access different forms of nitrogen (Northup et al. 1995; Kaye and Hart 1997). In our study it is apparent that *B. pendula*, an early successional species, was less well adapted to reduced-N conditions than was *P. sylvestris*, and that it was only able to access soil N in sufficient amounts to maintain vigorous growth when humus phenolic concentrations were reduced.

Although the two plant species differed in their response to litter and charcoal addition, their relative competitive abilities were unaffected by these treatments. The most probable explanation is that the intensity of competition was extremely low in the substrate for which growth responses to charcoal and litter occurred, i.e. that from the Ericaceous site. This is indicative of significant resource partitioning between the two species, and is reflective of their very different ecological strategies (Nikolov and Helmisaari 1992). In the absence of competition, any factor promoting the success of one plant species is unlikely to have a corresponding negative effect on the other.

Inhibition of *B. pendula* growth by litter addition was probably due to nutrient immobilisation in the litter rather than release of large quantities of phenolics, since adverse effects of litter were not usually reversed by charcoal. This means that whatever levels of phenolics were released from the *V. myrtillus* litter were small in relation to the total levels present in the humus. Although *V. myrtillus* litter is characteristically rich in phenols (Gallet 1994; Jäderlund et al. 1996) it is probable that these compounds are either released only gradually as the litter decomposes, or released only relatively late in the decomposition process (Swift et al. 1979) since no beneficial effects of litter addition on *B. pendula* was apparent.

Charcoal had important effects on the cover of both mosses and ferns in the pots, and this was apparent even for the Herb substrate, for which no charcoal effects on tree seedlings were noted. Establishment and early growth stages of bryophytes are highly susceptible to secondary metabolites and related stress factors (Thomas et al. 1994), and it is probable that low levels of phenolics occur at the Herb site, though not at levels that cause inhibition of *B. pendula*. The fern data from the Ericaceous substrate is particularly intriguing, since prothalli were entirely absent from pots without charcoal but had significant cover when charcoal was present. Several fern species seem to be favoured by fire, charcoal or activated carbon during their initial establishment from spores (White 1930; Oinonen 1967; Kim et al. 1996). Charcoal may thus contribute to altering forest species diversity, and fern establishment appears possible only when fresh charcoal is also present. The sensitivity of cryptogams to secondary metabolites is also consistent with the significant interactive effects that occurred between litter and charcoal; charcoal presumably reduced the comparatively small amounts of phenolics released from the decomposing litter during the experiment, stimulating the cryptogams but not the less sensitive tree seedlings. The significant stimulation of mosses by charcoal may also contribute to sustaining soil nitrogen levels; the moss species present in our study which occur only in the first few years after wildfire form a symbiotic association with cyanobacteria which have immense importance as nitrogen fixers in early successional ecosystems (Brown and Bates 1990; Longton 1992).

Our data showed some small (although significant) effects of charcoal addition on SIR (i.e. relative active microbial biomass) for the Cladina substrate, and significant birch × charcoal interactions for the other two. The generally beneficial effects on soil microflora are consistent with reductions of humus phenolics, and are in agreement with our earlier experiment showing some microbial stimulation when humus is in close contact with charcoal (Zackrisson et al. 1996). The absence of charcoal effects on microbial activity appears surprising given that charcoal probably stimulated nitrogen mineralisation in the Ericaceous substrate. However, this stimulation may have mainly occurred early in the experiment, i.e. some time before the pots were harvested. The enhancement of litter decomposition in the Ericaceous and Cladina substrates is also consistent with enhanced microbial activity, although for the Herb substrate the reverse trend was found. These sorts of idiosyncratic responses to charcoal are, however, consistent with our previous results showing unpredictable responses of decomposition to charcoal (Zackrisson et al. 1996), and are probably attributable to the complex nature of direct and indirect interactions between litter, microbial dynamics, plant roots and soil animals (Dormaar 1990; Wardle and Nicholson 1996).

Our results provide evidence that charcoal produced by wildfire may cause detectable shifts in several components of the Boreal forest plant-soil system at least in the initial phases, and that these effects are likely to be especially apparent in sites dominated by ericaceous vegetation high in phenolics. The mechanism responsible probably involves charcoal adsorbing and deactivating phenolics released from the humus, and greater availability of N (and enhanced plant N acquisition) resulting from less phenolic activity. Beneficial effects of charcoal are most likely to occur through adsorption of phenolic compounds present in ericaceous humus rather than those released from decomposing ericaceous litter, probably because the net amounts of phenolics in the humus layer is much greater. Ultimately our results support the hypothesis that wildfire is likely to have rejuvenating effects on late-successional ecosystems dominated by ericaceous dwarf shrubs, at least in part through the sorptive characteristics of the charcoal produced.

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