Growth Inhibitory Effects of Salal on Western Hemlock and Western Red Cedar

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ABSTRACT

Salal (*Gaultheria shallon* Pursh) regenerates vigorously after harvesting in the cedar–hemlock (CH) forests of coastal British Columbia, Canada. Eight years after harvesting, regenerating conifers on salal-dominated sites exhibited stunted growth and chlorotic foliage. The potential inhibitory effect of salal on hemlock was tested by germinating and measuring the primary growth of seedlings in the presence of salal litter and different concentrations of the litter leachate. Effects of aboveground and belowground competition of salal and its presumed growth inhibitory effects on western hemlock [*Tsuga heterophylla* (Raf.) Sarg.] and western red cedar (*Thuja plicata* Donn ex D. Don) were tested with pot experiments under greenhouse conditions. Seed germination and primary growth of hemlock seedlings were not significantly affected by water leachates of salal leaf or litter, nor were they affected when grown directly on partially decomposed salal litter. The primary root growth of hemlock seedlings was significantly increased in CH humus. Salal litter had no significant effect on hemlock and cedar seedlings. Combined aboveground and belowground competition from salal had the strongest negative effects on both hemlock and cedar, causing significant reductions in stem height, basal diameter, and biomass. Belowground competition from salal affected the conifers more than aboveground competition. The results suggest that the growth inhibitory effect of salal on conifers is primarily due to competition for nutrients rather than allelopathic effects of litter.

Salal is an evergreen ericaceous shrub that forms a dense understory in the CH forests of coastal British Columbia (Fraser et al., 1993). After forest harvesting on these sites, salal regenerates rapidly by vegetative means, and 6 to 8 yr later, both naturally regenerated and planted conifers such as western hemlock, Sitka spruce [*Picea sitchensis* (Bong.) Carr.], and to a lesser degree, western red cedar experience severe growth inhibition (Fraser, 1993, p. 166; Weetman et al., 1989a,b). Foliar analysis showed that the affected conifers suffer from low levels of N and P (Prescott et al., 1993). Trees that are established on adjacent hemlock–amabilis fir [*Abies amabilis* (Dougl.) Forbes] (HA) sites that are free of salal do not exhibit these symptoms (Weetman et al., 1989a,b). Significant improvement in conifer growth has been achieved through the N fertilization of sites that exhibited conifer growth inhibition (Prescott and Weetman, 1996, p. 85).

Inadequate natural regeneration and poor growth of planted black spruce [*Picea mariana* (Miller) B.S.P.] in the presence of another ericaceous plant, sheep laurel (*Kalmia angustifolia* L. var. *angustifolia*), has been reported from nutrient poor sites of eastern Canada (Page, 1970, p. 7; Richardson, 1975, p. 34; Richardson and Hall, 1973a, p. 63; Richardson and Hall, 1973b, p. 46; English and Hackett, 1994, p. 12). The regeneration failure of black spruce in the presence of sheep laurel was attributed to the combined effects of allelopathy, competition, and soil nutrient imbalance (Mallik, 1995, 1998). It was found that the humus and leaf leachate of sheep laurel inhibits the primary root elongation of black spruce, balsam fir [*Abies balsania* (L.) P. Mill], and red pine (*Pinus resinosa* Ait.) (Mallik, 1987; Thompson and Mallik, 1989; Mallik and Roberts, 1994). Inderjit and Mallik (1996a,b, 1997) reported that water soluble phenolic compounds released from the leaves of sheep laurel and labrador tea (*Ledum groenlandicum* Oeder) create nutrient imbalances in soil by reducing the amount of available N and increasing the amount of Fe, K, Ca, Mg, and Mn.

Poor natural regeneration of Norway spruce [*Picea abies* (L.) Karst.] in the presence of bilberry (*Vaccinium myrtillus* L.) has been reported by several authors from the subalpine spruce forests of France (Pellissier, 1993). Pellissier (1993) suggested that the potential causes of the regeneration failure of Norway spruce in these habitats are the seed predation and reduced seed germination and seedling growth due to allelopathy and competition from bilberry. A low-growing member of the Empetraceae, crowberry (*Empetrum hermaphorditum* Hagerup), was found to be responsible for the inhibition of the germination and seedling growth of Scots pine (*Pinus sylvestris* L.) in northern Sweden (Nilsson and Zackrisson, 1992; Zackrisson and Nilsson, 1992). Using these plants, Nilsson (1994) was able to separate the allelopathic effects of *E. hermaphorditum* from the effects of competition.

The autecology of salal is similar to that of the other ericaceous shrubs described above, and all of these shrubs have growth inhibitory effects on conifers. The water soluble organic substances from the fresh leaves and partially decomposed litter and humus of salal might interfere with the seed germination and seedling growth of hemlock, as occurs with the germination of Norway spruce in the presence of bilberry leaf leachate and humus (Jäderlund et al., 1996; Pellissier, 1993). Therefore, the objectives of the present study were to determine (i) if salal leaf leachate and CH humus affect the seed germination and seedling growth of hemlock, (ii) whether conifer growth inhibition in the presence of salal is due to competition or allelopathy from its litter, and (iii) whether aboveground or belowground competition is most important in the conifer growth inhibition process.

MATERIALS AND METHODS

Two sets of experiments were conducted to test (i) the seed germination and seedling growth response of western hemlock

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Abbreviations: ANOVA, analysis of variance; CH, cedar–hemlock; HA, hemlock–amabilis fir.

in the presence of salal leaf leachate and CH humus and (ii) the aboveground and belowground competition and allelopathic effects of salal on western hemlock and western red cedar in pot cultures.

Seed Germination and Seedling Growth

Leachates were collected after soaking 10, 20, 40, 60, and 100 g of fresh salal leaves or an equivalent amount of partially decomposed salal litter in large glass beakers with 400 mL of distilled water for 72 h. Hemlock seeds were stratified by soaking in running water over night followed by surface drying and storing the moist seeds at 4°C for 6 wk. Eight stratified hemlock seeds were planted in a petri dish that was lined with Whatman No. 1 filter paper and received 5 mL of one of the leachates. Seeds that were sown in petri dishes on filter paper soaked with distilled water were used as the control. In addition to the leachate treatments, hemlock seeds were planted directly on salal litter and CH humus. For these treatments, the petri dishes were half filled with fresh litter and CH humus before sowing. Each treatment had five replicates. After the initial treatment, the seeds were kept moist by adding distilled water as required. The number of seeds that germinated was recorded every day for 21 d, at which time the root and shoot lengths were measured. The dry weights of the roots and shoots were determined following oven drying of the samples at 72°C for 24 h. No red cedar seeds were used in this germination experiment.

Competition and Allelopathy

This experiment was conducted with transplanted hemlock and cedar seedlings that were grown with salal in HA humus in pot cultures under greenhouse conditions. Approximately 2 m^3 of HA forest-floor humus was collected from three mature forests that are approximately 25 km west of Port McNeill, Vancouver Island (50°30′ N, 127°22′ W; 150 m above sea level). The forests were dominated by 80- to 100-yr-old western hemlock and amabilis fir, with very few understory species other than pleurocarpous mosses such as *Brachythecium frigidum*, *Kindbergia oregana*, *Rhytidiadelphus* spp., and *Hylocomium splendens*. At each of the forest sites, humus was collected from 10 random locations. After removing the living moss layer, a 15 to 20 cm thick humus sample was cut out in blocks with a knife and transported to a truck. The collections were done in small forest openings that were free from salal understory. The composite samples were transported to the University of British Columbia campus and left to air-dry for 3 wk in a greenhouse with occasional mixing. When the humus lost approximately 80% of its moisture, it was passed through a garden mulcher and thoroughly mixed to get uniform texture.

Fifteen-liter round plastic pots (29.5 cm i.d. and 23 cm deep; 5T-15, Listro Products, Vancouver, BC) were used for this experiment. First, a thin layer (2 cm) of crushed rock was put in each pot for drainage of excess water, and then the pots were filled with the thoroughly mixed HA humus. A 6-cm space was left on top for watering and adding treatment substances. A total of 104 pots were prepared, and they were divided into two sets. One set of 52 pots was used to test the effect of salal competition and allelopathy on western hemlock, and the other 52 pots were used to determine the salal effects on western red cedar. Each set of 52 pots was divided into four groups, and the following four treatments were applied: (i) no salal (Control 1), (ii) root and shoot competition from salal, (iii) shoot competition, and (iv) root competition (Fig. 1).

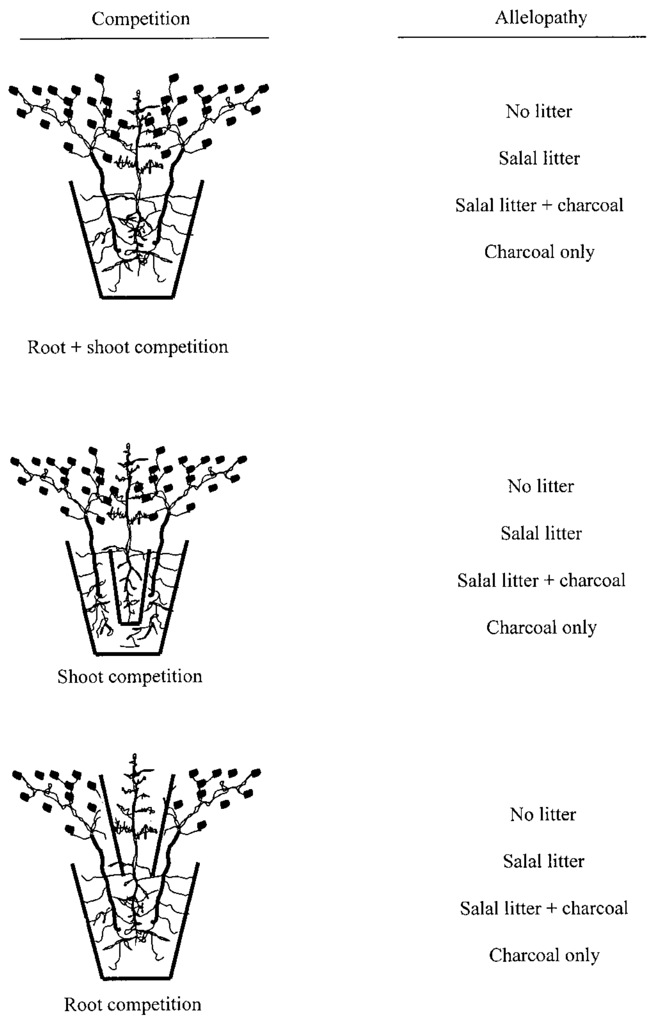

Fig. 1. Treatment structure differentiating salal root and shoot competition and allelopathic effects.

To determine the potential allelopathic effect of salal litter, each of the treatments, except the first (Control 1), received the following additional treatments: (i) no salal litter added (Control 2), (ii) salal litter (partially decomposed leaves and reproductive parts) added (70 g pot^{-1}), (iii) fine-powdered proanalysis (Labasco) activated charcoal (35 g pot^{-1}) spread on the surface followed by a salal litter amendment as in the second treatment [this treatment was intended to absorb any allelopathic compounds released from the salal litter (Nilsson, 1994)], (iv) activated charcoal (35 g pot^{-1}) to determine if charcoal alone has any adverse effect on hemlock by comparing it with the third treatment.

The same experimental design was followed with red cedar and salal, except in the allelopathy test for root and shoot competition from salal, shoot competition, and root competition. For these treatments, the activated-charcoal treatment was replaced with fireweed (*Epilobium angustifolium* L.) litter (70 g pot^{-1}). We presumed that the easily decomposable fireweed litter would have little or no allelopathic effects; thus, this treatment would test the potentially positive effect of salal litter amendment on conifer growth.

One-year-old salal grown in plastic pots that were 9 cm square and 8 cm deep were purchased from Langley tree nursery in British Columbia. Each nursery container had an average of six salal seedlings with an average height of 21 cm.

At the start of the experiment, the average stem height of the hemlock seedlings was 24.2 (4.2 SD) cm, and the average

Table 1. Effect of salal fresh leaf and litter leachates, salal litter, and cedar–hemlock (CH) humus on the seedling growth of western hemlock. Values within parentheses are standard errors of the means.

Treatment	Root length	Shoot length	Root DW†	Shoot DW
	cm		g	
Control	4.08b‡	9.95b	0.25ab	0.89
	(0.56)	(0.29)	(0.03)	(0.09)
5% leachate	4.08b	11.56ab	0.18b	0.95
	(0.62)	(0.28)	(0.02)	(0.12)
10% leachate	5.00b	12.15ab	0.21ab	1.00
	(0.78)	(0.92)	(0.02)	(0.13)
20% leachate	3.58b	9.77b	0.30a	0.88
	(0.31)	(0.89)	(0.04)	(0.13)
30% leachate	3.93b	10.43b	0.19ab	0.93
	(0.22)	(0.44)	(0.03)	(0.12)
50% leachate	3.30b	11.16b	0.14b	0.92
	(0.44)	(0.70)	(0.02)	(0.03)
Salal litter	3.30b	12.68ab	0.14b	0.74
	(0.43)	(0.75)	(0.01)	(0.08)
CH humus	7.95a	14.49a	0.18b	0.96
	(0.47)	(0.98)	(0.02)	(0.08)
P-value	0.0001	0.0007	0.0014	0.7462

† DW, dry weight.
‡ Unlike letters in each column indicate that the means are significantly different between the treatments.

basal diameter was 3.0 (0.2 SD) mm. The average dry weights of the root, needle, and stem were 0.92 (0.3 SD), 1.23 (0.3 SD), and 0.55 (0.1 SD) g, respectively. For the 3-mo-old red cedar, the mean stem height and basal diameter were 8.65 (0.6 SD) cm and 0.88 (0.1 SD) mm, and the dry weights of the root and the needle plus shoot were 0.02 (0.0 SD) and 0.01 (0.2 SD) mg, respectively.

The control hemlock and red cedar seedlings were grown as a single plant in the middle of a 15-L pot. For the treatment receiving both aboveground and belowground competition from salal, two sets of container-grown salal seedlings were planted opposite each other near the margin of the pots while the hemlock or red cedar seedling was planted in the middle of each pot. At the start of the experiment, the following start values for salal in each pot were estimated: Mean height, 16.5 cm; number of stems, 36; and dry weights of the roots, leaves, and stems, 9.3, 14.3, and 4.8 g, respectively. These values were determined by destructively sampling 10 sets of salal that were contained in the nursery pots. The root competition of salal was separated from that of cedar and hemlock by growing the conifers within thin-walled (2 mm) round plastic pots with a diameter of 13.5 cm, a height of 18 cm, and 8 holes (3 cm diam.) at the bottom (Nilsson, 1994). These root exclusion containers were placed on the crushed rock in the middle of the larger pots. Root competition from salal was achieved by growing the conifer with salal in the same pot and placing a conical wire fence (mesh size 2 cm) in each pot. The fences were 29 cm high with an upper and lower diameter of 25 and 18 cm, respectively. Each fence was attached with three metal stakes that were pushed into the humus. All of the aboveground parts of salal were kept outside the fence. The experiment was conducted at the University of British Columbia Horticultural Greenhouse from April to December 1998, with a mean temperature and relative humidity of 20.5°C and 71%, respectively.

The stem height and basal diameter of hemlock and red cedar as well as the salal stem height and total number of stems per pot were determined at planting in April 1998 and at the end of the experiment in December 1998. The dry weight of the aboveground and belowground components of salal and the conifers were determined at the end of the experiment by oven-drying the samples at 72°C until they were a constant weight.

Humus samples were collected at the end of the experiment from pots containing seedlings of western hemlock and red cedar to examine the effect of belowground competition from salal on N availability. The samples were taken (i) without salal, (ii) from inside the root exclosure, and (iii) from outside the root exclosure (i.e., in the presence of salal roots). Four samples of each humus type per species were extracted with 1 *M* of KCl, and the concentrations of NH_4–N and NO_3–N in each extract were measured with an Alpken autoanalyzer (Kalra and Maynard, 1991).

Data Analysis

Data on the seed germination and seedling root and shoot growth of hemlock at the end of the germination trial were analyzed with a one-way analysis of variance (ANOVA), and significant differences among the means were determined using Tukey's HDS test. Arcsine transformation was done to normalize the percent seed germination data before the ANOVA (Zar, 1996, p. 662). Data for the allelopathy and competition experiments were also analyzed with a one-way ANOVA. All statistical analyses were done using the SPSS 7.0 software.

RESULTS

Seed Germination and Seedling Growth

Hemlock seed germination ranged from 85 to 92.5%, and there was no significant difference among the treatments (data not shown). The root length of germinated hemlock did not differ significantly among the treatments, with the exception of the CH humus treatment, where an increase in root length occurred compared with all other treatments (Table 1). The shoot length of the hemlock seedlings grown in CH humus was also significantly greater than that of the control and the 20, 30, and 50% leachate treatments (Table 1). There was no significant difference in the dry weight of shoots, but the dry weight of hemlock roots that received the 20% leachate treatment was significantly greater than that receiving 5 and 50% leachate and salal litter and CH humus treatments.

Response of Hemlock to Salal Competition and Allelopathy

The data from the various litter amendments were pooled to test for the effects of the four competition treatments. The stem height of hemlock was significantly reduced in the root and the root-plus-shoot competition treatments compared with the control (no competition from salal) (Fig. 2). The root length of hemlock was significantly reduced in the root-plus-shoot competition treatment compared with all other treatments. The dry weight of the shoot (needles and stem) was reduced by >70% in all competitive situations compared with the control (Fig. 2). There were no significant differences in the dry weights of the needles and stems of hemlock in competition with salal. The root dry weight of hemlock was most negatively affected by the root-plus-shoot competition treatment followed by the shoot and root competition (Fig. 2). The root/shoot ratios of hemlock in these treatments were 0.22, 0.41,

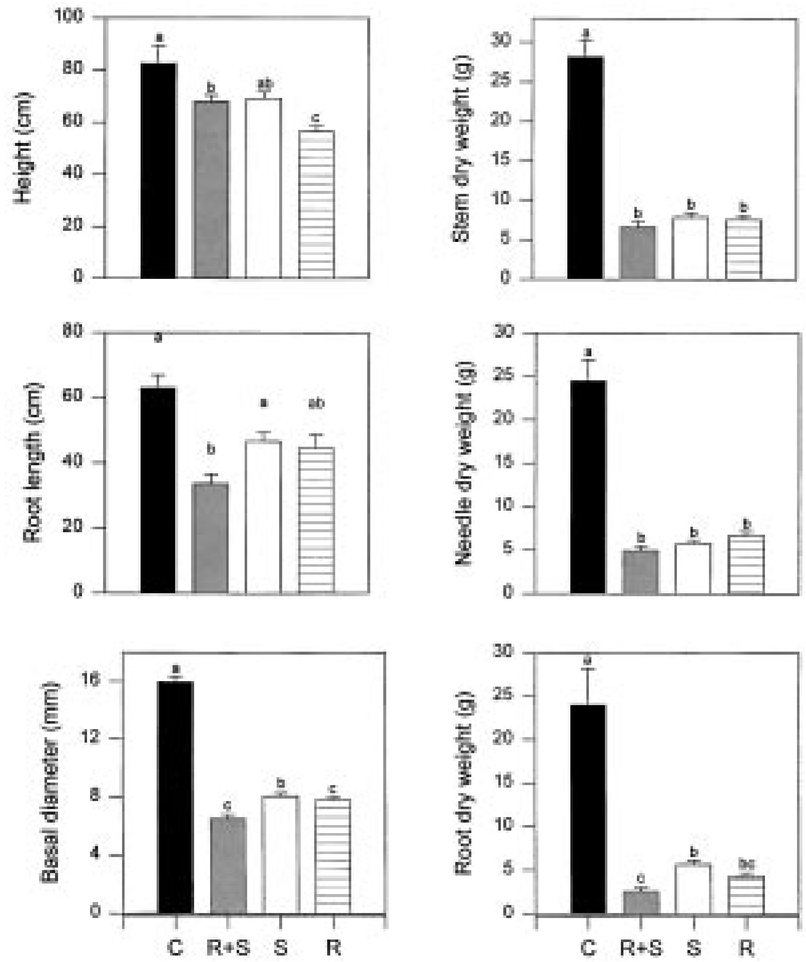

Fig. 2. Mean ± SE of height, root length, basal diameter, and stem, needle and root dry weights of western hemlock seedlings after 9 mo of receiving (C) no competition (control), (R + S) root-plus-shoot competition, (S) shoot competition, and (R) root competition from salal. Histograms in each experiment topped by different letters are significantly different at $P = 0.05$ (Tukey's multiple-range test).

and 0.30, respectively, whereas the value for the control was 0.46.

In the presence of salal root-plus-shoot competition, none of the litter-amending allelopathic treatments had a significant effect on the stem height, basal diameter, root length, and dry weights of aboveground and belowground biomass of hemlock (data not shown). There was a small, but nonsignificant, increase in the stem height, basal diameter, and biomass of the aboveground and belowground components of hemlock in the treatments receiving salal litter and salal litter plus charcoal compared with the no litter and charcoal-added treatments.

In the absence of salal root competition, salal litter

Table 2. Response of western hemlock to aboveground and belowground competition and the potential allelopathic effects of salal litter 9 mo after the treatments. Values within parentheses are standard errors of the means.

Treatment				
Competition	Allelopathy	Basal diam.	Root length	Total DW†
		mm	cm	g
Control (no salal)	N/A	15.95 (0.39)	63.00 (3.91)	24.00 (4.19)
Shoot competition	No litter	9.01a‡ (0.27)	45.53 (6.11)	6.64 (1.33)
	Salal litter	7.48b (0.50)	46.55 (1.36)	5.01 (0.59)
	Salal litter + charcoal	7.40b (0.33)	38.85 (4.66)	4.78 (1.40)
	Only charcoal	8.31ab (0.32)	55.60 (5.48)	6.44 (0.38)
P-value		0.026	0.156	0.387
Root competition	No litter	8.23 (0.30)	54.33a (9.65)	5.97a (0.38)
	Salal litter	7.98 (0.47)	51.38ab (6.28)	4.49ab (0.86)
	Salal litter + charcoal	7.38 (0.13)	27.38b (5.48)	2.67b (0.73)
	Only charcoal	7.59 (0.47)	45.65ab (1.17)	4.03ab (0.46)
P-value		0.402	0.047	0.024

† DW, dry weight.
‡ Unlike letters in each column indicate that the means are significantly different between the treatments.

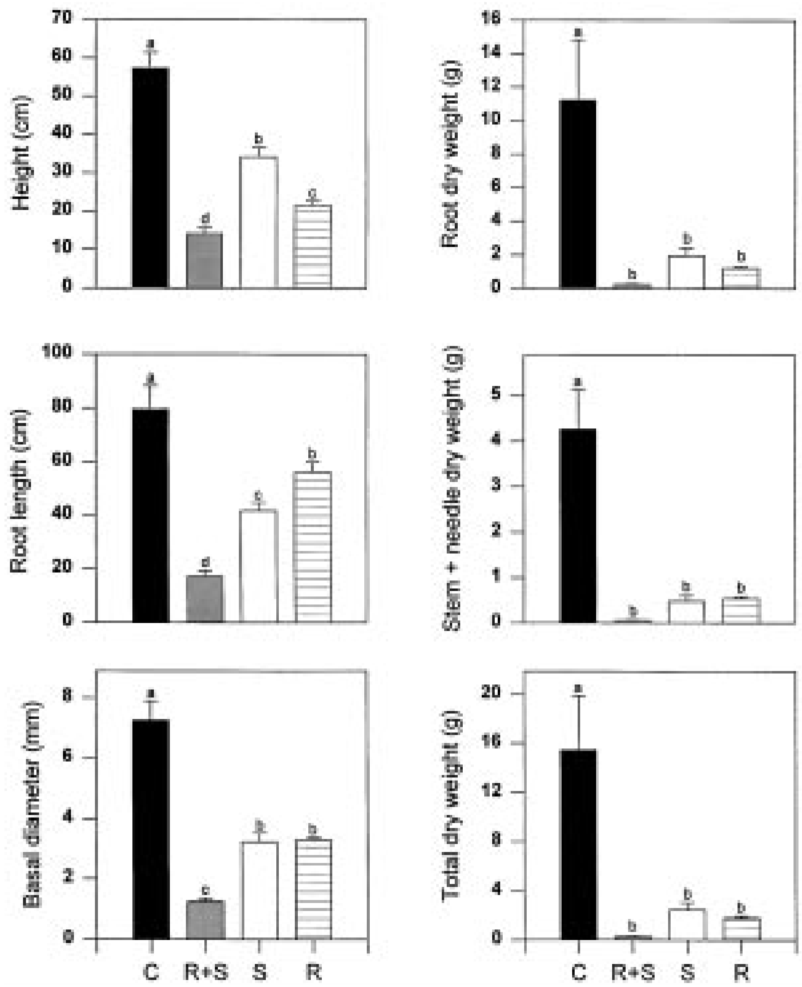

Fig. 3. Mean ± SE of height, root length, basal diameter, root, stem plus needle, and total dry weights of cedar seedlings after 9 mo of receiving (C) no competition (control), (R + S) root-plus-shoot competition, (S) shoot competition, and (R) root competition from salal. Histograms in each experiment topped by different letters are significantly different at P = 0.05 (Tukey's multiple-range test).

and salal litter plus charcoal caused a significant reduction in the basal diameter of hemlock compared with the no litter and charcoal-added treatments (Table 2). In the presence of root competition, hemlock had a significantly smaller root length and total biomass compared with no litter, salal litter, and charcoal-added treatments. No significant difference was found in the

Table 3. Response of salal to the removal of aboveground and belowground competition from western hemlock 9 mo after the treatments. Values within parentheses are standard errors of the means.

Treatment	Number of salal stems	Salal height	Total salal DW†
		cm	g
Root + shoot competition	85.06	35.28	106.70a‡
	(4.62)	(0.93)	(2.76)
Shoot competition	75.63	33.63	89.97b
	(2.72)	(0.84)	(2.30)
Root competition	85.56	34.66	88.57b
	(3.99)	(0.60)	(2.18)
P-value	0.1334	0.3445	0.0001

† DW, dry weight.
‡ Unlike letters in each column indicate that the means are significantly different between the treatments.

other parameters of hemlock following the litter and charcoal amending treatments (data not shown).

Response of Salal to Allelopathy and Competition Treatments

No significant differences in the stem height, aboveground biomass, or number of salal stems per pot were observed among the litter amending treatments. Among the different competition treatments, there were no significant differences in the salal height or number of stems per pot, but the aboveground biomass of salal was significantly lower in separate root and shoot competition treatments (Table 3).

Response of Red Cedar to Salal Allelopathy and Competition

Significant reductions in the stem height, basal diameter, and root length of cedar were observed in the treatments under competition compared with the control (Fig. 3). The dry weight of cedar roots was reduced >80% under competitive situations compared with the control (no salal). Reductions in the shoot dry weight were similarly high in the same treatments (Fig. 3). There were no significant differences in the height, basal diameter, or biomass of cedar seedlings among the litter amendment treatments, except for a slight increase in the height and basal diameter in the salal litter, fireweed litter, and salal litter-plus-charcoal treatments compared with the no litter treatment (when both root and shoot competition of salal was allowed).

The average concentrations of KCl-extractable N (NH_4–N and NO_3–N) in humus with hemlock at the end of the experiment were greatest (16.0 mg kg^{-1}) in the pots without salal, intermediate (11.1 mg kg^{-1}) in humus from which salal roots were excluded, and least (8.6 mg kg^{-1}) in humus containing salal roots. The difference in N concentrations was significant ($F = 3.34$, $P = 0.055$) between salal-free humus and humus containing salal roots. In the pots with cedar, the concentrations of KCl-extractable N in humus followed the similar trend ($P = 0.018$). The values were 19.23 and 14.53 mg kg^{-1} in the absence of salal and salal roots (inside the exclosure) and 8.13 mg kg^{-1} in the presence of salal roots (outside the exclosure).

Response of Salal to Allelopathy and Competition Treatments

There were no significant differences in the salal height, aboveground biomass, or number of stems per pot among the different litter treatments. The stem height of salal was significantly greater in the pots that received fireweed litter compared with other treatments (in the absence of salal shoot competition) (data not shown).

When the salal response was compared among the competition treatments, a significant increase in the salal stem number per pot was observed in the root competition treatment compared with the other two treatments (data not shown). However, the salal stem height was significantly less in the root competition treatment compared with the shoot competition treatment and the control (no salal). Significantly less aboveground biomass of salal was observed in the shoot competition treatment compared with the root competition treatment and control (Table 4).

Table 4. Response of salal to removal of aboveground and belowground competition from western red cedar 9 mo after the treatments. Values within parentheses are standard errors of the means.

Treatment	Number of salal stems	Salal height	Total salal DW†
		cm	g
Root + shoot competition	87.63a‡	33.97a	120.30a
	(3.76)	(1.34)	(2.65)
Shoot competition	86.50a	32.16ab	105.85b
	(4.99)	(0.90)	(3.67)
Root competition	103.56b	29.88b	112.69ab
	(3.15)	(1.03)	(3.01)
P-value	0.0069	0.0409	0.0086

† DW, dry weight.
‡ Unlike letters in each column indicate that the means are significantly different between the treatments.

DISCUSSION

Hemlock Germination Bioassay

Our results indicate that leachates of salal leaf and litter and the direct contact of salal litter are not inhibitory to the germination and seedling growth of western hemlock. The seed germination and seedling growth of hemlock were enhanced by CH humus. These results are contrary to those obtained with several other ericaceous shrubs where the germination and seedling growth of their associated conifers were inhibited in the presence of ericaceous litter and humus (Pellissier, 1993; Mallik, 1987; Thompson and Mallik, 1989; Nilsson and Zackrisson, 1992; Mallik and Roberts, 1994; Zhu and Mallik, 1994). deMontigny (1992) reported significantly lower germination of hemlock seeds in the presence of water leachate of salal flowers and berries. She found no significant difference in hemlock seed germination in the presence of salal soil solution. However, she recognized that these results were inconclusive because of very poor hemlock germination (<30% in the control).

Response of Hemlock to Salal Allelopathy and Competition

In the presence of both root and shoot competition from salal, the addition of salal litter had no significant effect on hemlock growth. Therefore, it is concluded that salal litter had no apparent allelopathic effect on hemlock. However, in the absence of root competition from salal, the addition of salal litter and salal litter plus charcoal caused a significant decrease in the basal diameter of hemlock compared with the no litter treatment (Table 2). But in the absence of salal shoot competition, the addition of salal litter and charcoal caused a significant reduction in the root length and total biomass of hemlock. This result is contrary to the general expectation that the charcoal would absorb the soluble phenolic compounds (Nilsson, 1994) while the litter was expected to provide nutrients, and hence improve the seedling growth. It is possible that microbial decay of the litter immobilized the nutrients during the course of the experiment. Nutrient immobilization is common during the early stages of litter decomposition (Aber and Melillo, 1991). Coupled with competition for N with the extensive fine root mass of salal in these pots, this treatment may have increased the severity of N deficiency for the seedlings.

The hemlock seedling growth was most greatly affected by the combined effects of salal whole plant competition, followed by root competition and shoot competition (Fig. 2). The affected seedlings were chlorotic with very poor root development. Increased shoot growth is a common response of seedlings to N fertilization (Cormer and Jarvis, 1990; Hinckley et al., 1992). Thus, the greater seedling shoot growth in the absence of salal roots may be indicative of a greater availability of N in the humus from which salal roots were excluded. The measures of KCl-extractable N in humus at the end of the experiment corroborated this suggestion, as N levels were lower in the humus where salal roots were present.

Water was maintained at nonlimiting levels throughout the experiment. Thus, the increased seedling shoot growth in the absence of salal roots suggests that the negative influence of salal on hemlock seedling growth is primarily an effect of competition for N.

Response of Western Red Cedar to Allelopathy and Competition

There was no evidence of an allelopathic effect of salal litter on the growth of cedar seedlings. The small increase in the stem height and basal diameter of cedar amended with salal litter, fireweed litter, and salal litter plus activated charcoal is likely due to the release of nutrients from the litters. The growth of cedar seedlings was, however, even more affected by salal competition than hemlock. This may be because the cedar seedlings were smaller at the start of the experiment (only 3-mo-old compared with the 1-yr-old hemlock seedlings), and hence more sensitive to competition.

Response of Salal to Allelopathy and Competition

Generally, all allelopathy experiments test the effects of donor plants on the target plants (Mallik, 1987; Nilsson and Zackrisson, 1992; Zackrisson and Nilsson, 1992; Weidenhamer et al., 1989; Nilsson, 1994; Jaderlund et al., 1996). In this experiment, we studied the effects of allelopathy and competition treatments reciprocally on both the target plants (conifers) and the donor plant (salal). Litter-amending allelopathic treatments had no significant effect on the salal stem number or biomass, indicating no autotoxic effects of salal litter. There was some reduction in salal growth in the shoot competition treatments, likely due to the limited space for root growth in these pots.

Forest Management Implications

We found that the negative influence of salal on conifer growth was through competition—primarily root competition for nutrients rather than allelopathic effects of litter leachates. This has implications for the management of cedar–hemlock sites to improve the productivity of conifers. If competition for nutrients is the main effect of salal, fertilization to alleviate the nutrient supply problem should be more effective than vegetation control to eliminate salal. A combination of fertilization and vegetation control would be even more effective at alleviating competition from salal.

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REFERENCES

Aber, J.D., and J.M. Melillo. 1991. Terrestrial Ecosystems. Saunders College Publ., Toronto, ON, Canada.

Cormer, R.N., and P.G. Jarvis. 1990. Growth and biomass partitioning in *Eucalyptus* seedlings in presence of nitrogen supply. Aust. J. Plant Physiol. 17:503–515.

deMontigny, L. 1992. An investigation into the factors contributing to the growth check of conifer regeneration on northern Vancouver Island. Ph.D. thesis. Univ. of Br. Columbia, Vancouver.

English, B., and R. Hackett. 1994. The impact of *Kalmia* on plantation performance in central Newfoundland. Silviculture Notebook 2. Newfoundland Forest Serv., Canada.

Fraser, L. 1993. The influence of salal on planted hemlock and cedar saplings on northern Vancouver Island. M.S. thesis. Univ. of Br. Columbia, Vancouver.

Fraser, L., R. Turkington, and C.P. Chanway. 1993. The biology of Canadian weeds. 102. *Gaultheria shallon* Pursh. Can. J. Plant Sci. 73:1233–1247.

Hinckley, T.M., A.L. Friend, and A.K. Mitchell. 1992. Response at the foliar, tree, and stand levels to nitrogen fertilization: A physiological perspective. *In* H.N. Chappell et al. (ed.) Forest fertilization and improving nutrition and growth of western forests. Inst. of Forest Resources. Contribution 73. Univ. of Washington, Seattle.

Inderjit, and A.U. Mallik. 1996a. Growth and physiological responses of black spruce (*Picea mariana*) to sites dominated by *Ledum groenlandicum*. J. Chem. Ecol. 22:575–585.

Inderjit, and A.U. Mallik. 1996b. The nature of interference potential of *Kalmia angustifolia*. Can. J. For. Res. 26:1899–1904.

Inderjit, and A.U. Mallik. 1997. Effect of *Ledum groenlandicum* amendment on soil characteristics and black spruce seedling growth. Plant Ecol. 133:29–36.

Jäderlund, A., O. Zackrisson, and M.-C. Nilsson. 1996. Effects of bilberry (*Vaccinium myrtillus* L.) litter on seed germination and early seedling growth of four boreal tree species. J. Chem. Ecol. 22:973–986.

Karla, Y.P., and D.G. Maynard. 1991. Extraction of NH_4–N and NO_3–N with 2*M* KCl. Methods manual for forest soil and plant analysis. Inf. Rep. NOR-X-319. Forestry Canada, N.W. Region, N. Forestry Cent., Edmonton, AB.

Mallik, A.U. 1987. Allelopathic potential of *Kalmia angustifolia* to black spruce. For. Ecol. Manage. 20:43–51.

Mallik, A.U. 1995. Conversion of temperate forests into heaths: Role of ecosystem disturbance and ericaceous plants. Environ. Manage. 19:675–684.

Mallik, A.U. 1998. Allelopathy and competition in coniferous forests. p. 309–315. *In* K. Sassa (ed.) Environmental forest science. Kluwer Academic Publ., London.

Mallik, A.U., and B.A. Roberts. 1994. Natural regeneration of red pine on burned and unburned sites in Newfoundland. J. Vegetation Sci. 5:179–186.

Nilsson, M.-C. 1994. Separation of allelopathy and resource competition by the boreal dwarf shrub *Empetrum hermaphroditum* Hagerup. Oecologia 98:1–7.

Nilsson, M.-C., and O. Zackrisson. 1992. Inhibition of Scots pine seedling establishment by *Empetrium hermaphroditum*. J. Chem. Ecol. 51:1857–1870.

Page, G. 1970. The development of *Kalmia angustifolia* on black spruce cutover in central Newfoundland. Forest Res. Lab. Internal Rep. N-27. St. John's, NF, Canada.

Pellissier, F. 1993. Allelopathic inhibition of spruce germination. Acta Oecol. 14:211–218.

Prescott, C.E., L.P. Coward, G.F. Weetman, and S.P. Gessel. 1993. Effects of repeated nitrogen fertilization on the ericaceous shrub, salal (*Gaultheria shallon*), in two coastal Douglas fir forests. For. Ecol. Manage. 61:45–60.

Prescott, C.E., and G.D. Weetman. (ed.) 1996. Salal-cedar hemlock integrated research program: A synthesis. Univ. of Br. Columbia Faculty of Forestry, Vancouver.

Richardson, J. 1975. Regeneration after disturbance in Newfoundland forests: Patterns, problems, and prescriptions. Inf. Rep. N-X-130 Environ. Canada, Canadian Forestry Serv., St. John's, NF.

Richardson, J., and J.P. Hall. 1973a. Natural regeneration after disturbance in the forest of central Newfoundland. Inf. Rep. N-X-86. Environ. Canada, Canadian Forestry Serv., St. John's, NF.

Richardson, J., and J.P. Hall. 1973b. Natural regeneration after disturbance in the forest of eastern Newfoundland. Inf. Rep. N-X-90. Environ. Canada, Canadian Forestry Serv., St. John's, NF.
Thompson, I.D., and A.U. Mallik. 1989. Moose browsing and allelopathic effects of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. Can. J. For. Res. 19:524–526.
Weetman, G.F., R. Fournier, J. Baker, and E. Schnorbus-Panozzo. 1989a. Foliar analysis and response of fertilized chlorotic Sitka spruce plantations on salal dominated cedar-hemlock cutovers on Vancouver Island. Can. J. For. Res. 12:1512–1520.
Weetman, G.F., R. Fournier, J. Baker, E. Schnorbus-Panozzo, and A. Germain. 1989b. Foliar analysis and response of fertilized chlorotic Sitka spruce plantations on salal dominated cedar-hemlock cutovers on Vancouver Island. Can. J. For. Res. 12:1501–1511.
Weidenhamer, J.D., D.C. Hartnett, and J.T. Romeo. 1989. Density-dependent phytotoxicity: Distinguishing resource competition and allelopathic interference in plants. J. Appl. Ecol. 26:613–624.
Zackrisson, O., and M.-C. Nilsson. 1992. Allelopathic effects by *Empetrum hermaphroditum* on seed germination of two boreal tree species. Can. J. For. Res. 22:1310–1319.
Zar, J.H. 1996. Biostatistical analysis. (3rd ed.) Prentice-Hall, New Jersey.
Zhu, H., and A.U. Mallik. 1994. Interactions between *Kalmia* and black spruce: Isolation and identification of allelopathic compounds. J. Chem. Ecol. 20:407–421.

Black Spruce Growth and Understory Species Diversity with and without Sheep Laurel

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ABSTRACT

Growth and understory species diversity of black spruce [*Picea mariana* (Miller) B.S.P.] planted in central Newfoundland at contiguous sites with and without dense cover of sheep laurel (*Kalmia angustifolia* L.) were compared. Black spruce stem density and volume per hectare were calculated by sampling 10 circular quadrats (50 m^2), and the cover of all plant species was determined by sampling 20 quadrats (1 m^2) in each site. In addition, 10 randomly sampled planted black spruce samplings from each site were analyzed for stem height, basal diameter, and foliar chemistry. Results showed a significantly lower stem height and basal diameter (65 and 51%, respectively) at the site with dense sheep laurel cover (36%) compared with the site with sparse sheep laurel cover (<1% sheep laurel cover, and henceforth referred to as the non-sheep laurel site for simplicity). Black spruce grown at the sheep laurel dominated site contained significantly higher quantities of Ca, Al, Fe, and K in the needles than that grown at the non-sheep laurel site. The sheep laurel dominated site also had a significantly higher mean organic matter depth of 8.3 cm compared with 5.6 cm at the non-sheep laurel site. Canonical correspondence analysis (CCA) of the species cover data clearly separated the sheep laurel dominated plots from the non-sheep laurel plots. The sheep laurel dominated site had reduced species richness of vascular plants but increased species richness for lichens compared with the non-sheep laurel site. Allelopathy associated with phenol-induced soil nutrient imbalance and nutrient stress is a possible cause for black spruce growth inhibition at the sheep laurel dominated site.

RAPID GROWTH OF SHEEP LAUREL after clear cutting and fire in sheep laurel–black spruce communities has been widely observed in eastern Canada, particularly at sites with organic and coarse textured medium-quality soil types (Page, 1970, p. 7; van Nostrand, 1971, p. 68; Damman, 1975). The natural regeneration of black spruce at these sites is poor, and planted black spruce seedlings exhibit stunted growth (Candy, 1951, p. 224; Richardson and Hall, 1973a, p. 63, 1973b, p. 46; Wall, 1977, p. 55). Competition and allelopathic effects of sheep laurel have been attributed to the regeneration failure and poor growth of conifers (Mallik, 1987, 1990, 1992, 1996; Mallik and Roberts, 1994). In eastern and central Newfoundland, large areas of moderately productive black spruce forests with sheep laurel understory have been converted into sheep laurel dominated heath following forest disturbance (Mallik, 1995). A regeneration survey of 5888 plots in black spruce plantations found that 55% of them contained sheep laurel (English and Hackett, 1994, p. 12). Black spruce in sheep laurel infested sites exhibits typical symptoms: Poor plant height and diameter growth and short and chlorotic needles, as observed in other conifers in the presence of different ericaceous plants (Handley, 1963; Gimingham, 1972; de Montigny and Weetman, 1990; Fraser, 1993, p. 166; Inderjit and Mallik, 1996a; Jaderlund et al., 1997). Black spruce forests that are dominated by sheep laurel tend to have a reduced species richness and deficiency in available nutrients (Damman, 1971). Recently, Yamasaki et al. (1998) reported that black spruce seedlings in close proximity of sheep laurel (<1 m) experience lower height, biomass, root/shoot ratio, foliar N and P, and lower mycorrhizal infection than those growing farther (>1 m) away from sheep laurel.

Damman (1971, 1975) suggested that long-term occupancy of a site by sheep laurel causes irreversible soil degradation, leading to a stable heath formation by precluding forest regeneration. Apparently sheep laurel, like other ericaceous plants, is able to grow in nutrient poor conditions where black spruce growth is very much restricted. There is evidence suggesting that the ericaceous plants are able to access the N that is bound in the protein–polyphenol complex through the ericoid mycorrhizae, but this N is not available to the conifers

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Abbreviations: CCA, canonical correspondence analysis; IAA, indoleacetic acid.