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## Allelopathic potential of peatland plant species on germination and early seedling growth of Scots pine, silver birch and downy birch

Jyrki Hytönen

TIIVISTELMÄ: SUOKASVIEN ALLELOPAATTISISTA VAIKUTUKSISTA MÄNNYN SEKÄ RAUDUS- JA HIESKOIVUN SIEMENTEN ITÄMISEEN JA TAIMIEN ENSIKEHITYKSEEN

Hytönen, J. 1992. Allelopathic potential of peatland plant species on germination and early seedling growth of Scots pine, silver birch and downy birch. Tiivistelmä: Suokasvien allelopaattisista vaikutuksista männyn sekä raudus- ja hieskoivun siementen itämiseen ja taimien ensikehitykseen. Silva Fennica 26(2): 63–73.

The potential allelopathic inhibitive effects of aqueous extracts of 13 peatland plant species on germination, radicle and seedling growth of Scots pine (*Pinus sylvestris* L.), silver and downy birch (*Betula pendula* Roth, *B. pubescens* Ehrh.) were studied. Freshly cut plant parts were finely ground, mixed with distilled water and agitated. The proportions of fresh plant mass in the mass-based extracts varied within the range of 1, 5, 10 and 20 % (w/w). The seeds were germinated in petri dishes moistened with the plant extracts. In a separate experiment growth of birch seedlings irrigated with the extracts was studied.

*Ledum palustre*, *Vaccinium uliginosum* and *Empetrum nigrum* extracts, and in certain experiments extracts from other species, inhibited the germination of pine and birch seeds. Results from the different experiments were not, however, fully consistent. None of the low (1 % w/w) extract concentrations had any effect on germination. Strong extract concentrations (20 w/w) inhibited germination of pine seedlings significantly. The extracts affected only slightly the growth of potted birch seedlings.

Eräiden suokasvien vesiutoksien potentiaalista allelopaattista vaikutusta männyn, hies- ja rauduskoivun siementen itämiseen ja taimien alkukehitykseen tutkittiin kasvihuonekokein. Tuoreet kasvinosat jauhettiin hienoksi ja kasvimassan ja tislattun veden seosta ravisteltiin. Uutosvahuuden vaikutusta tutkittiin yhdessä kokeessa. Siemeniä idätettiin petriäljoissa suodatetuilla uutoksilla kastelluilla suodatinpapereilla. Lisäksi tutkittiin uutteilla kasteltujen koivun taimien kasvua.

Potentiaalisesti allelopaattisiksi kasvilajeiksi idätyskokeiden perusteella osoittautuivat erityisesti juolukka, suopursu ja variksenmarja. Kuitenkaan useiden kasvilajien osalta eri kokeista saadut tulokset eivät olleet täysin yhdenmukaisia. Uutosvahuuden vaikutus oli erittäin merkitsevä. Laimeina uutoksina mikään kasvilaji ei ehkäissyt itämistä, mutta uutosvahuuden väkyyden kasvaessa kaikkien tutkittujen kasvilajien vaikutus oli erittäin merkitsevä. Uutoksilla oli vain vähäinen vaikutus ruukuissa kasvatettujen taimien kasvuun.

Keywords: allelopathy, *Betula*, *Pinus*, seed germination, seedling growth. FDC 181.4

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## 1 Introduction

Natural regeneration occurs readily on virgin and newly drained peatlands (Heikurainen 1954). Especially the white mosses (*Sphagnum* spp.) present in the bottom layer offer a congenial substrate for germination (Sarasto and Seppälä 1964). On pine bogs, there are seedlings considerably more on flat surfaces than on hummocks (Heikurainen 1954). On the other hand natural regeneration is more uncertain in plant communities dominated by the dwarf shrubs (Sarasto 1964). Sarasto (1964) found in his sowing experiments that shrubless plots were more advantageous for germination than plots with shrub cover. Even though the presence of the dwarf shrubs did not totally inhibit the germination of pine seeds and their development into seedlings, it considerably reduced the number of seedlings when compared to shrubless plots (Sarasto 1964). Natural regeneration or sowing on unprepared transformed peatlands may also lead to poor results (Kaunisto 1984, Moilanen and Issakainen 1984).

Allelopathy, the reciprocal harmful biochemical interaction between plants, does not refer to the direct competition between plants for water, nutrients or light. In a popularized form, it has been referred to as chemical warfare among plants importance of which in the Darwinian struggle for survival in nature could be significant. Examples of sectors where allelopathy can have substantial influence include plant succession, distribution, dominance, vegetational patterning and productivity in forest communities (Brown 1967, del Moral and Cates 1971, Rice 1979, 1984, Swain 1977). The potential significance of allelopathy as a reason for regeneration failures on clearcut areas and field afforestations as well as on heathlands has been reported by several authors (Fischer 1980, MacLaren 1983, Zielinska 1986, Yoder-Williams and Parker 1987, Jaworski 1988, Mallik and Newton 1988, Jobidon et al. 1989a, Zackrisson and Nilsson 1989, de Montigny and Weetman 1990). However, the effects of allelopathy are probably only secondary when com-

pared to the competition for light, water and nutrients (Norby and Kozlowski 1980, Hobbs 1980).

Allelochemicals, biochemical substances involved in allelopathic interactions, extracted from plants and soil have usually been secondary metabolites; e.g. simple phenolic acids, terpenoids, flavonoids, coumarins and alkaloids (Hennequin et al. 1967, Harborne and Williams 1969, Rice 1979, 1984, Jameson 1970, Ballesster et al. 1972, 1977, Mantilla 1975, Swain 1977, Lodhi 1978a, Fisher 1980, Patrick 1986). Allelochemicals are released from plants as volatile compounds by rain or mist leachings from foliage, by exudation from roots or other living parts or along with fruits, seeds or litter. Also, decomposition of plant residues can produce such chemicals. Many compounds can undergo chemical changes in the soil (Swain 1977, Grodzinkij 1985). Plant allelochemicals can affect, for example, seed germination, radicle elongation and growth of seedlings in a variety of ways (del Moral and Muller 1970, Swain 1977, AlSaadawi and AlRubaa 1985, McDonald 1986, Patrick 1986, de Montigny and Weetman 1990). Phytotoxic compounds of some plants, such as heather (*Calluna* spp.), raspberry (*Rubus idaeus*), reindeer lichen (*Cladina* spp.), are reported to interfere with the formation and development of mycorrhizae and affect the nutrient uptake of plants (Robinson 1972, Brown and Mikola 1974, Fisher 1979, Goldner et al. 1986, Ponder 1986, Cote and Thibault 1988). According to some researchers, allelochemicals of climax vegetation (phenolic acids and tannins) can function as chemical inhibitors of nitrification (Lodhi 1978b, Lodhi and Killinbeck 1980, Rice 1979, 1984, Jobidon et al. 1989b, see also McCarty and Bremner 1986).

The objective of this study was to find out whether aqueous extracts of 13 plant species possess potential allelopathic inhibitory effects on seed germination and radicle elongation. The effects of two extracts on the growth of potted birch seedlings were also studied.

## 2 Material and methods

### 2.1 Germination experiments

The freshly cut plant parts of 13 plant species (Table 1) collected during different times of the year (Table 2) from Kannus (63° 53' N, 23° 55' E), central Finland were finely ground. The mass based admixture of the plant material and distilled water was agitated for about 2 hours. In experiments 1, 2 and 3 extract concentration 10 % w/w was used. In experiment 4 extracts of 1 %, 5 %, 10 % and 20 % w/w concentrations were prepared. The variation in moisture content between different plant species and within the same species during the growing season may affect the comparability of the extract concentrations. After agitation, the extracts were filtered with filter paper, and then stored in a cold-room at 5 °C. New extracts were made for every experiment.

Two filter papers were placed on the bottom of petri dishes and moistened either with distilled water or with one of the extracts. Fifty Scots pine (*Pinus sylvestris* L.), silver or downy birch (*Betula pendula* Roth and *B. pubescens* Ehrh.) seeds were placed in each petri dish. The petri dishes were then placed in a greenhouse (temperature 19–23 °C). All treatments (tree species × extracts) were replicated three times using a randomized block design. Additional extract or distilled water was added to all dishes during the experiment in order to keep the filter papers constantly moist. Germination of the seeds was monitored for 11–21 days (Table 1). Birch seeds were considered to have germinated once their cotyledons opened and Scots pine seeds when the length of the emerged radicle exceeded 2 mm. Finally the length of the Scots pine radicles and hypocotyls were measured from the tip of

Table 1. Plant species whose extracts were used in germination experiments.

Plant species extracted	Experiment	Plant part
<i>Betula nana</i> (BET NAN)	1,2,3,4	Leaves
<i>Betula pendula</i> (BET PEN)	2,3	"
<i>Betula pubescens</i> (BET PUB)	2,3	"
<i>Carex lasiocarpa</i> (CAR LAS)	1	"
<i>Cladina stellaris</i> (CLA STE)	1	Whole plant
<i>Empetrum nigrum</i> (EMP NIG)	4	Leaves
<i>Eriophorum vaginatum</i> (ERI VAG L)	1	"
<i>Eriophorum vaginatum</i> (ERI VAG R)	1	Roots
<i>Ledum palustre</i> (LED PAL)	1,2,3,4	Leaves
<i>Pinus sylvestris</i> (PIN SYL)	2,3,4	Needles
<i>Pleurozium schreberi</i> (PLE SCH)	2	Above-ground parts
<i>Polytrichum</i> sp. (POL SP.)	1	"
<i>Sphagnum cuspidatum</i> coll. (SPH CUS)	1	"
<i>Vaccinium uliginosum</i> (VAC ULI)	2,3,4	"

Table 2. Bioassay experiments and tree species used.

Experiment	Start of experiment	Germination time, days	Tree species
1	7.8.1986	11	<i>Pinus sylvestris</i> , <i>Betula pendula</i> , <i>Betula pubescens</i>
2	7.9.1986	17	<i>Pinus sylvestris</i> , <i>Betula pendula</i>
3	10.10.1986	21	<i>Pinus sylvestris</i> , <i>Betula pubescens</i>
4	14.7.1987	21	<i>Pinus sylvestris</i> , <i>Betula pendula</i>

the roots to the tip of the needles. The pH and conductivity of the extracts were measured in experiment 4. The effect of the extracts and extract concentrations on germination and radicle length was tested by means of analysis of variance using BMDP statistical programmes. The treatment means were compared with each other by the Tukey's multiple range test.

## 2.2 Seedling experiment

Three 10–15 cm long silver or downy birch (*Betula pendula* Roth, *Betula pubescens* Ehrh.) seedlings were transplanted on August 19, 1986 into each of the 24 pots filled with fertilized peat (N 150 kg/ha, P 66 kg/ha, K 125 kg/ha). Water-based extracts (5 % w/w) were prepared using fresh, ground *Ledum palustre* and *Betula nana* leaves collected between August 20 to

August 22, 1986. The extracts were filtered after being stored for three days in a cold room at 5 °C.

The seedlings grown in the greenhouse were irrigated with either distilled water (control) or with the extracts. The amount of irrigation for each pot was 3 liters of extract given in 17 separate portions and additionally 3 liters of water (in 8 separate portions) per pot. The treatments were replicated four times using randomized block design. The length of the seedlings was measured once a week. At the end of October, the stem and root mass in each pot were measured after drying to a constant weight at 105 °C. The length and dry mass of the average seedling in each pot was calculated. The effects of the treatments were tested by means of one way analysis of variance using BMDP statistical programs.

## 3 Results

*Ledum palustre* extracts were tested in all experiments. Significant inhibition of Scots pine and birch seed germination was obtained in all experiments except experiment 3 (Figs. 1 and 2). The inhibitory effect on the growth of germinants was even stronger; it was significant also in experiment 3 (Figs. 2 and 3). The inhibition of germination was very clear in experiment 1; not a single Scots pine seed out of 150 germinated.

*Vaccinium uliginosum* extracts were tested in three experiments and in all of them germination inhibition of pine and birch seeds was significant (Figs. 1 and 2). In experiment 2, not a single *Betula pendula* and only 9 Scots pine seeds out of 150 germinated during the 17 day long germination period. Even 5 % (w/w) extract concentrations proved to have an inhibitory effect (Fig. 2). *Empetrum nigrum* extract was tested only in experiment 4 where it inhibited Scots pine germination (Fig. 2). Both *Vaccinium uliginosum* and *Empetrum nigrum* extracts inhibited growth of pine germinants (Figs. 2 and 3).

*Pinus sylvestris* needle extract inhibited the germination and growth of Scots pine germinants in all experiments, even the 5 % (w/w) extracts gave significant inhibition (Figs. 1 and 2). Scots

pine needle extracts inhibited germination of silver birch in experiment 2, but had no effect on the germination of downy birch in experiment 3.

The effect of birch leaf extracts on germination varied from one experiment to the other (Figs. 1 and 2). In experiment 1, significant inhibition of Scots pine and silver and downy birch germination was obtained due to the *Betula nana* extract. In experiment 2, it had no effect on germination of Scots pine and silver birch. In experiment 3, it inhibited significantly the germination of Scots pine but not that of downy birch. In experiment 4, its inhibiting influence on Scots pine germination was significant only when the concentration of the extract was 20 % (w/w) (Fig. 2). *Betula pendula* and *B. pubescens* extracts inhibited the germination of Scots pine seeds but only in experiment 3. In experiment 3, downy birch extract inhibited the germination of downy birch seeds. All birch extracts inhibited the growth of pine radicles and hypocotyls (Figs. 2 and 3).

Extracts of *Sphagnum cuspidatum*, *Polytrichum* sp., *Pleurozium schreberi*, *Cladina stellaris*, and *Carex lasiocarpa* had no inhibitory effect on the germination of seeds (Fig. 1). Leaf extract of *Eriophorum vaginatum* inhibited pine

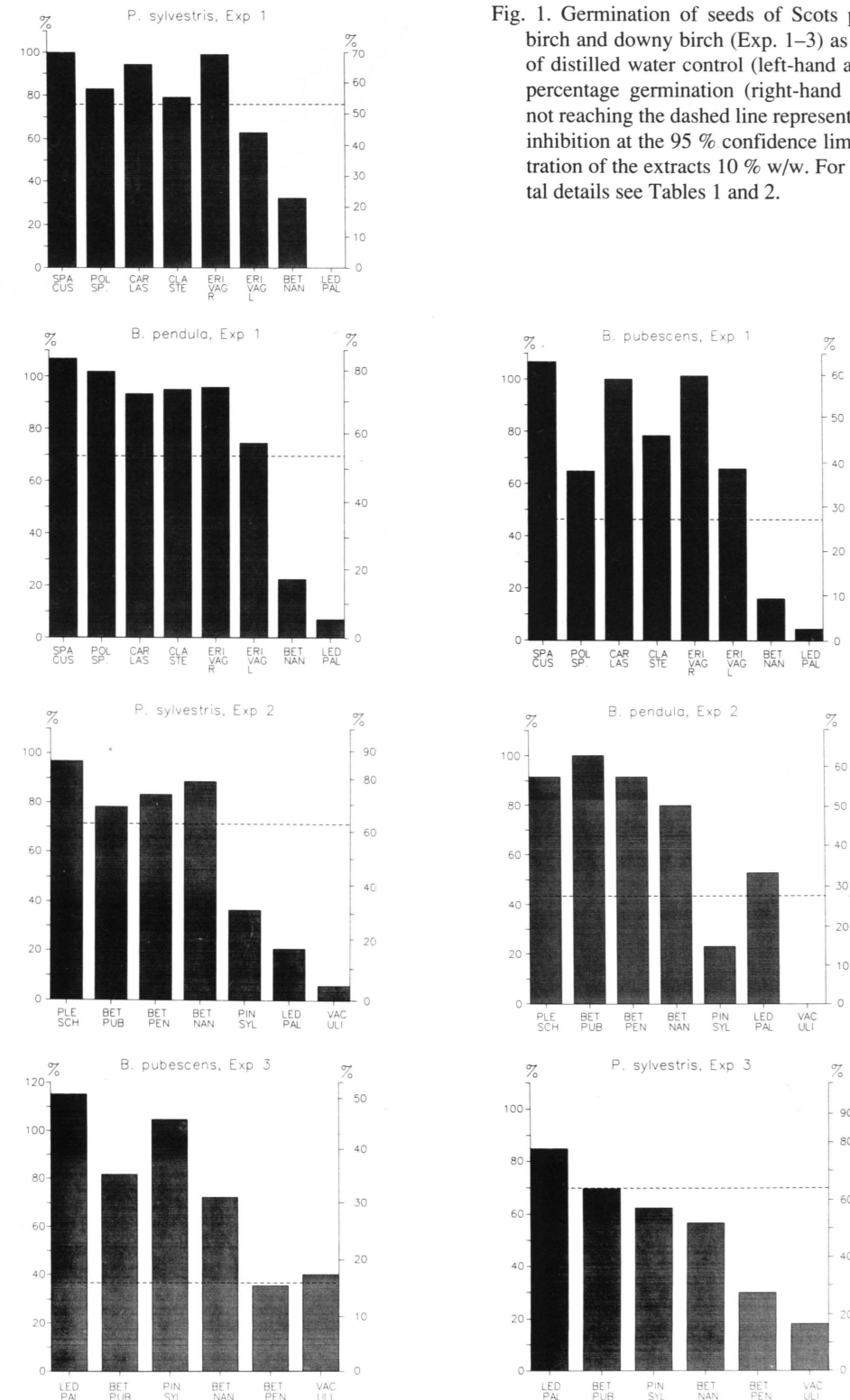


Fig. 1. Germination of seeds of Scots pine, silver birch and downy birch (Exp. 1–3) as percentage of distilled water control (left-hand axis) and as percentage germination (right-hand axis). Bars not reaching the dashed line represent significant inhibition at the 95 % confidence limit. Concentration of the extracts 10 % w/w. For experimental details see Tables 1 and 2.

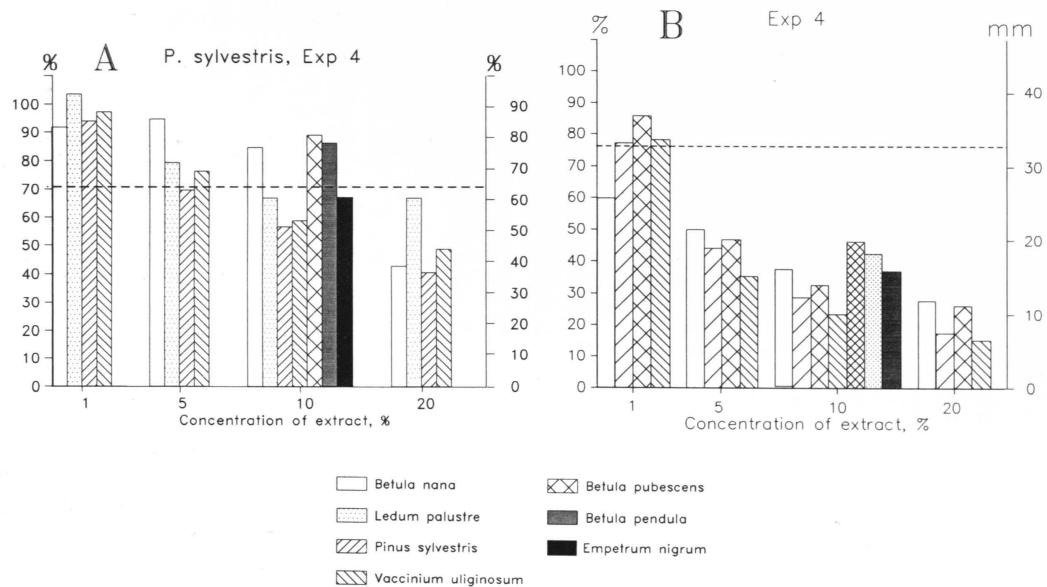


Fig. 2. Germination of Scots pine seeds (A) and length of pine radicles and hypocotyls (B) (Exp. 4) as percentage of distilled water control (left-hand axis) and as percentage germination or as mean length of germinated seedlings (right-hand axis). Bars not reaching the dashed line represent significant inhibition at the 95 % confidence limit.

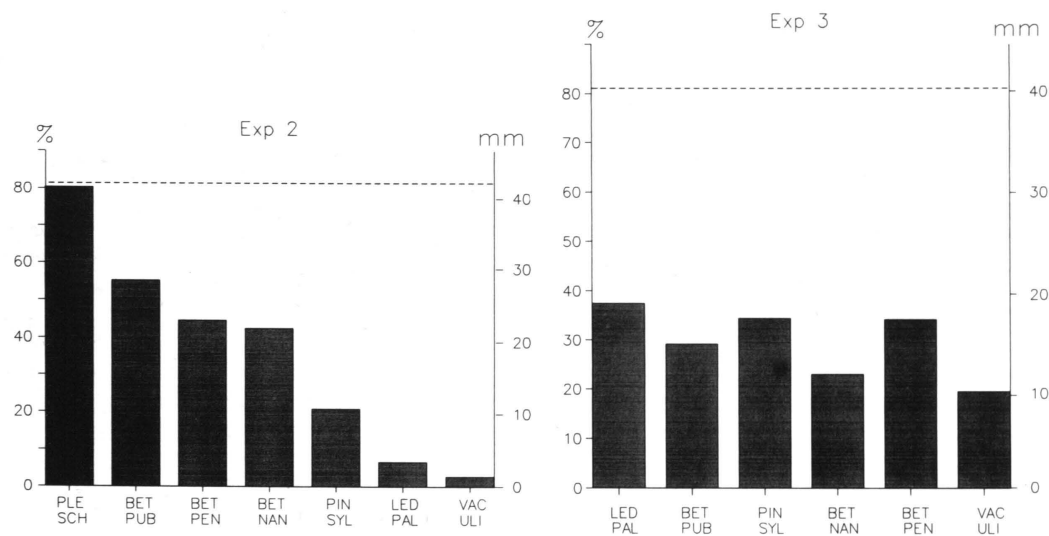


Fig. 3. Length of Scots pine radicles and hypocotyls (Exps. 2 and 3) as percentage of distilled water control (left-hand axis) and as mean length of germinated seedlings (right-hand axis). Bars not reaching the dashed line represent significant inhibition at the 95 % confidence limit. Concentration of the extracts 10 % w/w. For experimental details see Tables 1 and 2.

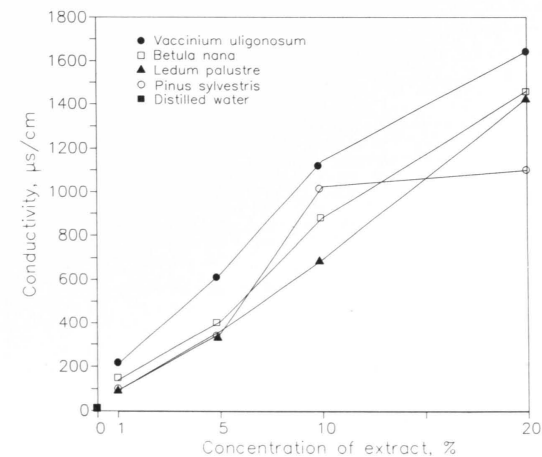


Fig. 4. Conductivity of extracts of varying concentrations.

seed germination, whereas its root extract had no effect (Fig. 1).

The effect of different concentrations of freshly ground leaf extracts on the germination of Scots pine seeds was tested in one experiment. The effect of concentration on pine seed germination ( $F = 28.40^{***}$ ) and growth of germinants ( $F = 158.84^{***}$ ) was highly significant. The high-

her the concentration, the smaller the number of germinated Scots pine seeds and the shorter the germinants (Fig. 2). All studied extracts inhibited germination when the concentration was 20 % (w/w) and none when the concentration was 1 % (w/w). The effect of extracts on germination was significant ( $F = 3.23^*$ ) at 0.05 level and on the growth of germinants ( $F = 4.47^{**}$ ) at 0.01 level.

The conductivity of the extracts increased with an increase in the extract concentration (Fig. 4). The highest conductivity (1647  $\mu\text{S}/\text{cm}$ ) was measured in the strongest *Vaccinium uliginosum* extract. The concentration of the extracts did not, however, have much effect on their pH-value. The highest pH values were recorded for *Ledum palustre* (4.0) and *Pinus sylvestris* (4.2) extracts and the lowest for the *Vaccinium uliginosum* extract (3.5).

The effects of *Betula nana* and *Ledum palustre* extracts on the growth of silver and downy birch seedlings were studied in the greenhouse. The initial lengths of seedlings in different treatments did not differ from each other. Also, the differences in the final lengths at the end of the experiment were not significant, although seedlings irrigated with plant extracts were shorter than those irrigated with water (Fig. 5). The stem mass of downy birch seedlings irrigated

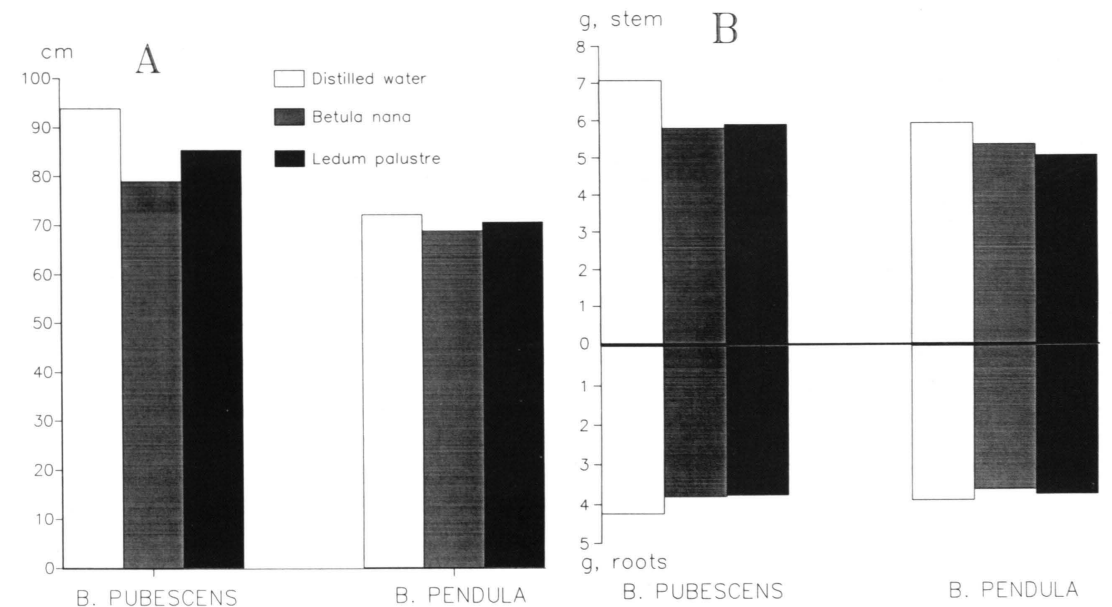


Fig. 5. Height (A) and dry mass (B) of downy birch and silver birch seedlings irrigated with distilled water or *Betula nana* or *Ledum palustre* (5 % w/w) extracts.

with plant extracts was lower at the 0.05 level ( $F = 5.81^*$ ) than that of seedlings irrigated with water (Fig. 5). With silver birch, the differences in stem mass were not significant ( $F = 3.87$ ).

The treatments influenced the root mass of silver birch significantly at the 0.05 level ( $F = 5.97^*$ ), but not that of downy birch ( $F = 0.59$ ).

## 4 Discussion

Though aqueous extracts of certain plant species inhibited the germination of birch and pine seeds and radicle and hypocotyl elongation of pine seedlings, the results of the different experiments were not fully consistent with one another. An extract of a certain plant could inhibit germination in one experiment but not in another. One reason for this may be that the plants for the different experiments were collected during different times of the year. Annual variation in the amounts of allelochemicals both in plants and in the soil can be considerable (Lodhi 1978a). The effects of leaf extracts are often stronger than those of root extracts (Leibundgut 1976). Besides allelochemicals that may have been leached from the plants, some other factors may also have affected germination of seeds. The low pH of the extracts most probably is not an inhibitor of seed germination (Brown 1967, Abouguendia and Redmann 1979, Hobbs 1984). The osmotic potential of leaf extracts is usually so low that it cannot normally affect germination (Stowe 1979, Norby and Kozłowski 1980, Hobbs 1984).

The inhibitory effect of plant extracts depended very much on their concentration (Ballester et al. 1977, Rai and Tripathi 1984). The lowest concentrations (1 % w/w) did not affect germination of Scots pine seeds, whereas all the plant species studied inhibited seed germination when the concentrations were 20 % w/w. It is almost impossible to determine what is the suitable concentration to be used in bioassay experiments (Stowe 1979). In nature, the concentrations are determined by the rate of release of phytotoxins, their solubility, microbiological and chemical processes, soil drainage, amount of precipitation, runoff and leaching and distance between plants releasing and plants receiving allelochemicals (Swain 1977, Fischer 1978, Lodhi 1978a, Stowe 1979).

*Ledum palustre* extracts inhibited germination in three out of the four experiments. The effect of *Vaccinium uliginosum* extract was significant

in all three experiments. The effect of birch leaf extracts was, on the other hand, quite variable. Pine needle extracts inhibited the germination of pine seeds in all three experiments. Additionally, *Empetrum nigrum* and *Eriophorum vaginatum* leaf extracts appeared to be potentially allelopathic. A considerable number of ericaceous plant species (especially genera belonging to the *Ericaceae* and *Empetraceae* families; e.g. *Arctostaphylos*, *Calluna*, *Erica*, *Kalmia*, *Ledum*, *Vaccinium*, *Rhododendron*) have been shown to be allelopathic (Braathe 1950, Pearman 1959, Harborne and Williams 1969, del Moral and Cates 1971, Robinson 1972, Mantilla et al. 1975, Ballester et al. 1977, Fisher 1980, Hobbs 1984, Tinnin and Kirkpatrick 1985, Mallik 1987, de Montigny and Weetman 1990). Also in other experiments, *Empetrum nigrum* has strongly inhibited the germination of Scots pine seeds (Zackrisson and Nilsson 1989). In Brown's (1967) experiments, water extracts of *Ledum groenlandicum*, *Vaccinium angustifolium* and *Vaccinium myrtilloides* did not inhibit the germination of *Pinus banksiana* seeds.

Autotoxicity, as shown here by pine needle extract inhibiting pine seed germination, is one of the more contradictory aspects of allelopathy. Many species seem to excrete substances that are deleterious even to seedlings of the same species (Lysikov 1987, Stowe 1979, Becker and Drapier 1985, Mallik and Newton 1988). Natural selection would presumably operate against this phenomenon if allelopathy is effective under natural conditions (Stowe 1979). Another mechanism might be avoidance or resistance. Autotoxicity has even been considered as an attractive explanation for the phenomena of tree species alternation which is classically observed to take place in forests (Becker and Drapier 1985).

*Cladina stellaris*, *Sphagnum cuspidatum*, *Polytrichum* sp., *Pleurozium schreberi*, *Carex lasiocarpa* leaf extracts and *Eriophorum vaginatum* root extracts did not have inhibitory ef-

fects on seed germination. Brown and Mikola (1974) and Fisher (1979) have, on the other hand, shown that *Cladina stellaris* interferes with the formation of tree mycorrhizae. In the experiment of Brown (1967), *Sphagnum capillaceum* and *Cladonia cristatella* inhibited the germination of *Pinus banksiana* seeds whereas *Carex pennsylvanica* and other *Cladina* species tested had no effect.

The allelopathic influences of plant extracts are often greater on seed germination than on the growth of rooted plants (Leibundgut 1976). The effects of *Ledum palustre* and *Betula nana* extracts on the growth of birch seedlings were small. The stem mass of downy birch and the root mass of silver birch were lower when watered with plant extracts than with water. Ponder (1986) has shown that *Festuca arundinacea* extracts decreased the growth of the stems but not that of the roots of *Juglans nigra*.

Results from germination tests cannot be directly applied to natural conditions and must be considered potential rather than actual. However, with bioassay experiments it is possible to identify plant species that could have allelopathic potential in nature as well. Field experiments are difficult to conduct. According to

Hobbs (1984) the determination whether chemical interactions are important in the field is almost impossible, because of the inability to separate the chemical and physical effects. Thus, comparison of bioassay results with studies dealing with the effects of different plant cover on natural regeneration or sowing (e.g. Hertz 1932, 1934, Yli-Vakkuri 1961, Sarasto 1964, Sarasto and Seppälä 1964, Kaunisto 1984) is difficult (Stowe 1979, Heilman and Stettler 1985, Heisey and Delwiche 1985, McDonald 1986). Results from these bioassay experiments indicate the potential allelopathic effects of some peatland plants, especially ericaceous dwarf shrubs. Besides root and nutrient competition, allelopathic effects may thus be one explanation for the results obtained by Sarasto (1964).

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Total of 61 references