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Competitive Ability and Allelopathy of Ericaceous Plants as Potential Causes of Conifer Regeneration Failures[1*]

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Ericaceous식물의 allelopathy와 경쟁력에 의한 침엽수 갱신 저해[1*]

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ABSTRACT

Certain ericaceous understory plants of temperate forests proliferate following forest clearcutting and fire. Rapid vegetative growth of these plants may affect conifer regeneration due to their strong competitive abilities and allelopathic properties. Planted conifers in these shrub - dominated habitats experience "growth check" which may result in a loss of productivity or in extreme cases total failure of forest regeneration. This growth check phenomenon is exemplified in *Calluna* - Sitca spruce - Scots pine ecosystems of western Europe, *Kalmia* - black spruce ecosystem of eastern Canada and *Gaultheria* - cedar/hemlock ecosystem of the Pacific Northwest of the United States.

Dynamics of *Kalmia* - black spruce ecosystem following disturbance was used to explain the mechanism of conifer growth inhibition and their regeneration failure. It is argued that in addition to competition for nutrients, *Kalmia* allelopathy plays a major role in growth inhibition of black spruce. This conclusion is supported by the results of various field, laboratory and greenhouse experiments. Eight phenolic compounds were isolated and identified from the leaves of *Kalmia angustifolia*, four of which are known to be highly phytotoxic to black spruce.

Methods of overcoming the allelopathic effects of *Kalmia* in order to enhance black spruce regeneration in *Kalmia* - dominated sites are discussed.

Key words : Allelopathy, Ericaceous, Conifer regeneration, Kalmia, Calluna, Phytotoxic Substances.

要 約

온대 삼림지대에서 산화 적지나 개벌 적지에 왕성하게 번성하는 것이 ericaceous속이다. ericaceous 속의 식물들은 성장이 빨라서 다른 종과의 경쟁에서 유리하고 또한 allelopathy 효과 때문에 침엽수 갱신에 영향을 미친다. *Kalmia*가 번성하는 지역에서는 삼림 갱신이 잘 되지 않거나 조림한 침엽수의 생장이 저조하였다. 이러한 생장 저해 현상은 서유럽의 *Calluna* - Stica spruce - Scot pine 생태계와 미국의 북서 태평양 지역의 *Gaultheria* - cedar/hemlock 생태계에서도 나타나고 있다. 삼림이 파괴된 다음에 *Kalmia* - black spruce 생태계의 다양한 변화는 침엽수 생장을 저해하거나 갱신을 방해하는 원인으로 생각되어지고 있다. 양분경쟁에 대한 논쟁의 여지는 있으나 *Kalmia*는 black spruce 생장을 억지하는 주원인으로 작용한다. 여러 곳의 야외, 실내 및 온실에서 한 실험 결과는 이러한 결론을 뒷

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받침해 주고 있다. 본 논문에서는 *Kalmia* 잎으로부터 8가지의 페놀물질을 분리동정해 냈으며 이들 중 4가지는 black spruce에 고도의 독성을 나타냈다. *Kalmia* 우점지역에서 allelopathic 영향을 적게 하므로써 black spruce의 갱신을 증진시키기 위한 여러 가지 방법에 대한 고찰을 하였다.

INTRODUCTION

Certain ericaceous understory plants in temperate forests may grow vigorously and become dominant after forest disturbance such as clear-cutting and fire. In nutrient poor sites forest regeneration can be very difficult in the presence of ericoid dominance. Rapid regeneration behaviour and allelopathic properties of these ericaceous plants play important roles in a vegetation shift from forest to heathland(Mallik 1995). This is particularly the case in certain nutrient-poor, moist habitats of cool temperate oceanic ecosystems. For example *Calluna* - Sitka spruce(*Picea sitchensis*) - Norway spruce(*P. abies*) ecosystem of western Europe(Leyton 1954; Gimingham 1972), *Gaultheria* - cedar(*Tsuga plicata*) - hemlock (*Thuja heterophylla*) ecosystem of the Pacific Northwest and coastal British Columbia(Weetman *et al.* 1990), and *Kalmia* - black spruce(*Picea mariana*) ecosystem of eastern Canada(Mallik 1994). All these ecosystems have a history of past disturbance. The longer the disturbance the more wide spread seems to be the heath formation. Conifer regeneration in the ericoid dominated sites has been a challenge mainly because of aggressive regrowth of the plants that compete with conifers and perhaps more importantly because of their allelopathic property. The phyto-toxic substances released from the ericaceous plants may directly affect seed germination and growth of conifer seedlings (Pellissier 1993, 1994; Zackrisson and Nilsson 1992; Mallik 1987; Mallik and Zhu 1995) or they can indirectly affect their growth by interfering with soil nutrients availability(Inderjit and A.U. Mallik, Unpublished). Once established these ericaceous plants are very difficult to eradicate. Their occupancy in a site can bring about long-term soil changes and can create inhospitable conditions for conifer regeneration(Damman 1964, 1971, 1975; Meades 1983, 1986; de Montigny 1992).

The present paper reports on the competitive abilities and allelopathic properties of selected ericaceous plants and their effects on conifer regeneration. Landuse management of ericaceous heaths as grazing land and afforestation in ericoid dominated sites are also discussed. *Kalmia* - black spruce ecosystem was used as a model to explain the phenomenon of vegetation shift from forest to ericaceous heath. However, examples of other ecosystems were also used as appropriate.

ERICACEOUS DOMINANCE FOLLOWING FOREST DISTURBANCE

Dominance of ericaceous plants following forest disturbance by clearcutting and fire has been reported by several authors from a range of temperate ecosystems(Gimingham 1972; Page 1970; Wall 1977; Richardson 1975, 1979; Richardson and Hall 1973a,b; Meades 1983, 1986; Sabhasri and Ferrell 1960; Bunnell 1990; de Montigny 1992; de Montigny *et al.* 1991). Mallik(1994) reported that irrespective of forest type and habitat moisture regime black spruce forests with *Kalmia* understory becomes dominated by *Kalmia* after clearcutting and fire(Fig. 1). Salal-cedar-hemlock communities of the Pacific Northwest and salal-larch-fir communities of western Montana have been reported to be dominated by salal(*Gaultheria shallon*) after similar disturbance(Haeussler *et al.* 1990; Bunnell 1990; Weetman *et al.* 1990; de Montigny 1992; Miller 1977). The extensive *Calluna* heathlands of western Europe is believed to be previously occupied by productive forests. Indiscriminate clearcutting and burning during the Neolithic, Bronze and Iron age times and subsequently regular burning every 10 - 15 years converted the forests into heathlands (Dimbleby 1962; Durno 1957, 1958, 1965; Gimingham 1972).

All these ericaceous plants reproduce mainly

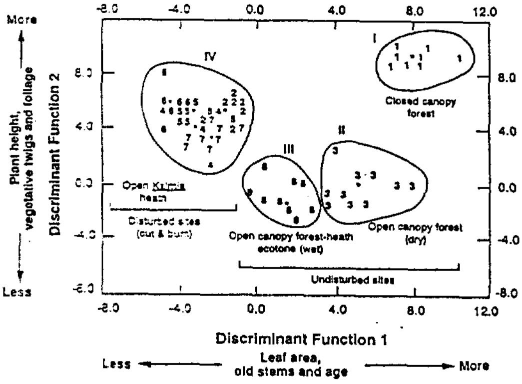

Fig. 1. Forest type and habitat moisture regime black spruce forests with *Kalmia* under story becomes dominated by *Kalmia* after clearcutting and fire.

by vegetative methods. They also produce a large number of seeds and maintain a large soil seedbank(Barclay-Estrup and Gimingham 1994; Mallik *et al.* 1984; Mallik and Roberts 1994). However, growth rate of ericaceous seedlings is much slower compared to that of vegetative shoots(Mallik *et al.* 1988). Seedling regeneration becomes prominent only when vegetative regeneration is limited which may occur due to unusually hot fires that kill the vegetative buds(Gimingham 1970, 1972; Legg 1978).

Calluna regenerates vegetatively from stem base sprouting and layering. Extensive sprouting occurs following the removal of above-ground parts of the plant by grazing, burning or cutting (Mohamed and Gimingham 1970; Gimingham 1972; Hobbs and Gimingham 1987; Mallik and Gimingham 1985). Regular burning and grazing rejuvenate the plants by producing fresh vegetative shoots(Miller 1979, 1980). However, with age ability of vegetative reproduction is reduced in *Calluna*(Hobbs and Gimingham 1987) since the plant goes through cyclical phases of regeneration in absence of disturbance(Barclay-Estrup 1970, 1971; Barclay-Estrup and Gimingham 1969; Miller and Miles 1969). *Gaultheria* also reproduces vegetatively by stem-base sprouting (Sabhasri 1961). However, the plant spreads quite rapidly by underground rhizomes(Bunnell 1990). As the older parts of the plant die, extensive growth of new rhizomes keeps the plant alive and competitive. *Kalmia* has similar vegetative regeneration strategies as *Gaultheria* where all the three methods of reproduction, stem-base sprouting, rhizomatous growth and layering are common(Mallik 1993). A large number of vegetative buds ard produced around stem bases as well as on rhizomes. A six year old *Kalmia* produced 1,236 vegetative buds on it's rhizomes and 109 sprouts from the stem base(Mallik 1993). Thus the plant with it's quick and efficient vegetative regeneration strategies becomes highly competitive in the post-disturbed habitat(Mallik 1990).

HABITAT CHANGE

Long-term occupancy of ericaceous plants in a site can bring about irreversible soil changes by increased organic accumulation, allelopathy, acidity and nutrient imbalance. Rapid vegetative growth of the plants following disturbance results in the production of large amounts of above- and below-ground biomass(Chapman *et al.* 1975a,b; Damman 1971, 1975). With the slow rate of decomposition in the cool temperate climate organic accumulation occurs at a high rate(Damman 1975). The partially decomposed organic matter adds an array of organic acids causing decreased soil pH. Grubb *et al.*(1969) demonstrated a gradient of pH from the middle towards the periphery of a *Calluna* bush. Grubb and Suter(1971) explained the mechanism of acidification by *Calluna* and *Ulex* spp.. Many long chain fatty acids were reported from *Calluna* soils(Jalal and Read 1983a,b). Soil pH can be as low as 2.8 in some *Kalmia* sites in Newfoundland(A.U. Mallik, Unpublished). Addition of organic acids from ericaceous litter not only decreases the pH it also causes nutritional imbalance in soil. Conifers growing in such habitats experience nutritional imbalance and suffer stunted growth(Inderjit and A.U. Mallik, Unpublished). Nutrient analysis of planted black spruce in a *Ledum groenlandicum* dominated site showed significantly less nitrogen and higher Ca, Fe and Al in the needles compared to that grown in an adjacent non-*Ledum* site(Inderjit and A.U. Mallik, Unpublished). Weetman *et al.*(1989a,b) and Weetman and de Montigny(1990) reported nutrient deficiencies in Sitka spruce and Norway spruce planted in *Gaultheria* dominated sites in coastal British Columbia. Similar nutrient deficiencies and stunted growth of Sitka spruce and Norway spruce was reported from *Calluna* dominated sites in Britain(Leyton 1954; Handley 1963; Gimingham 1972). Meades(1986) suggested that if *Kalmia* dominates a site for a long period of time it can cause permanent change in soil and vegetation. This may bring about retrogressive succession from forest to heath(Mallik 1995).

ALLELOPATHIC PROPERTY

In addition to the increased organic accumulation; high acidity and nutritional imbalance, ericaceous plants may be responsible for releasing allelopathic substances in the soil environment(Robinson 1971; Hobbs 1984) which may directly affect seedling growth of trees(Table 1). The allelopathic substances may be excreted from the root surface(Robinson 1972) or it may be released from leaves, roots and decomposing litter(Mallik 1987) of the ericaceous plants. These substances can affect seed germination (Zackrisson & Nilsson 1992) and primary root growth of tree seedlings(Mallik 1992). Jalal and Read(1983a,b) identified several long and medium chain fatty acids and phenolic acids from *Calluna* humus. Most of these compounds are known to be fungi and phyto toxic. Zhu and Mallik(1994) reported eight phenolic acids from fresh *Kalmia* leaves. These were(in order of decreasing toxicity) *O*-hydroxyphenylacetic, *p*-hydroxybenzoic, vanillic, *p* coumaric, gentisic, syringic, ferulic, and *m*-coumaric acid. All these phenolic compounds except *m* coumaric acid were previously reported from other ericaceous plants such as *Erica scoparia*(Ballester *et al.* 1977), *E. australis*(Carballeira 1980) and *Calluna vulgaris*(Jalal *et al.* 1982). Apart from the phenolic substances other compounds such as terpenoids, sesquiterpenoids and proanthocyanins may be present in soils dominated by ericaceous plants. These can also affect tree seedling growth (Pellissuier 1993). Often growth inhibition in the affected plants is brought about by the synergistic

Table 1. Allelopathic growth inhibition of tree species by ericaceous understory plants

Ericaceous plants	Affected tree species	References
Calluna vulgaris	Sitka spruce(*Picea sitkensis*)	Leyton(1954) Handley(1965)
	Scots pine(*Pinus sylvestris*)	Robinson(1972) Miles and Kinnard(1979)
	Silver birch(*Betula pendula*)	Gimingham(1972)
	Norway spruce(*Picea abies*)	Read and Jalal(1980)
Ledum palustre *Vaccinium uliginosum* *Eupetrum nigrum*	Scots pine, Sliver birch, Downy birch(*B. pubescens*)	Hytonen(1992)
Vaccinium myrtillus	Sub-alpine spruce(*P. abies*)	Pellissier(1993, 1994)
Ledum groenulandicum	Black spruce(*P. mariana*)	Inderjit & Mallik(unpublished)
Empetrum hermaphroditum	Scots pine, Aspen(*Populus tremula*)	Zackrisson & Nilsson(1992)
Kalmia angustifolia	Black spruce	Peterson(1965), Mallik(1987)
	Jack pine(*P. banksiana*)	Krause(1986)
	Red pine(*P. resinosa*)	Mallik & Roberts(1994)
	Balsom fir(*A. balsamea*)	Thompson & Mallik(1989)
Rhododendron albiflorum	Douglas fir(*Pseudotsuga menziesii*)	Del Moral & Cates(1971)
Gaultheria shallon	Douglas fir, Western hemlock	de Montigny(1992)
G. procumbeus	Jack pine	Brown(1967)

effects of all these phytotoxic compounds. Concentrations of these compounds vary in soil depending on the season. Zackrisson and Nilsson (1992) found that early Spring run off from *Eurpetrum hermaphorditum* site have strong phytotoxic effects on seed germination and seedling growth of poplar and Scots pine. In addition to the common phenolic compounds Oden *et al.*(1992) isolated a germination inhibitor from *E. hermaphorditum*. This signifies the need for devising allelopathic experiments in such a way that the methods can capture the ecological relevance of the process(Inderjit and Dakshini 1995; Einhellig 1995). Extraction of germination or growth inhibitory substances from plant or soil leachates does not give conclusive evidence of allelopathy nor does it explain the ecological role of allelochemicals in plant to plant interactions. However, it may provide some initial clues to the presence of such a phenomenon.

IMPLICATIONS FOR LAND MANAGEMENT

Disturbance induced vegetation shift from forest to heath formations has significant land management implications. If the landuse objective is forest renewal then the ericaceous species must be controlled to ensure tree regeneration. However, if the heathlands provide other forms of landuse benefits such as grazing, recreation and nature conservation as in the case of *Calluna* heathland of Europe then maintenance of heath rather than it's eradication would be the land management objective. Thus, for over two centuries, large tracts of *Calluna* heathlands of Scotland have been managed as grazing land by regular burning(Gimingham 1972). Burning rejuvenates *Calluna* plants by the production of new shoots from the surviving stem bases (Mallik and Gimingham 1985). These new shoots are an excellent source of nutritious food for grazing animals such as red grouse(*Lagopus scoticus*) sheep and cattle(Miller 1979, 1980). In absence of grazing and fire *Calluna* plant degenerates due to old age(Barclay-Estrup 1970). Reclamation of *Calluna* dominated sites for forest regeneration is often challenging. Conifer plantation in *Calluna* dominated sites experience "growth check" where the planted seedlings remain stunted and becomes yellow. Ploughing followed by liming and nitrogen fertilization has been practised to overcome the growth inhibition effect of *Calluna* on conifers. Conservation of semi-natural heathlands with it's distinctive flora and fauna has been another land management objective in selected *Calluna* dominated heaths of Britain and other west European countries(Gimingham 1972, 1981, 1992; Gimingham *et al.* 1979).

In the pacific Northwest reforestation has been the main emphasis in post-harvest *Gaultheria* dominated sites. Although *Gaultheria* has some use for wildlife as winter forage, it's growth inhibition effect on conifer seedlings is a concern in raising new plantations(Bunnell 1990; Weetman and de Montigny 1990). Therefore, reclamation of *Gaultheria* dominated lands for forest regeneration is a priority. Unlike *Calluna* and *Gaultheria* that have grazing values, *Kalmia* leaves are unpalatable to animals and insects. According to Jaynes(1975) "nothing feeds on *Kalmia*" because their leaves are poisonous. Therefore, *Kalmia* dominated sites are unproductive from the forestry and wildlife point of view. Raising plantation is the primary landuse objective in *Kalmia* dominated sites.

KALMIA CONTROL

Since *Kalmia* is equipped with many efficient regeneration strategies it is very difficult to eradicate the plant by traditional vegetation control methods. Several greenhouse experiments were performed to control *Kalmia*. Mallik(1991) reported that cutting and cutting followed by burning did not affect *Kalmia* regrowth significantly. The plant resprouted profusely from stem bases following these treatments. The number of new sprouts were more than that of the control plants eight months after the treatments. Mulching treatments on the other hand, were found to be effective in controlling vegetative growth of *Kalmia*. Perhaps mulching treatments destroyed vegetative buds and sprouting centres of the plant by physical damage.

Several herbicides were tested on potted *Kalmia* under greenhouse conditions. The most commonly used forest herbicide, Vision(Glyphosate or Roundup) was not effective against *Kalmia* even when applied at a relatively high dose, 7L/ha (a.i. 356g/L). Vision in combination with surfactants such as Tween 20 or Triton XR were not effective either. However, the treatments temporarity stopped new foliar growth and sprouting of *Kalmia*. Krenite(Fosamine ammonium) applied at the rate of 11.2L/ha(a.i. 480g/L) caused some damage to *Kalmia* six weeks following the treatment. But subsequently, new shoots appeared from the plant and the plant regained its vigour. Velpar(Hexazinone or Pronone, 5kg/ha, a.i. 4.9kg/ha) treatment caused defoliation of *Kalmia* 2 3 weeks after treatment. However, since the treated plants were not killed new leaves appeared in large numbers within 4 6 months following the treatment.` Unlike all the above herbicides, Garlon 3A (Trichlopyr, 7L/ha, a.i. 360g/L) caused significant lethal effects on *Kalmia* killing most of it's above - and below - ground components. This herbicide also selectively killed *Kalmia* without adverse effects on some desirable understory plants such as blueberry(*Vaccinium angustifolium* and *V. myrtilloides*) and bunchberry (*Cornus canadensis*). A subsequent experiment with the commercial brand of Garlon called Garlon 4 was found to be equally effective against *Kalmia*. The product has potential as a tending herbicide since it did not have any significant damaging effect on planted black spruce seedlings(A.U. Mallik, Unpublished).

N, P and K fertilization was applied in a factorial experiment with potted *Kalmia* in the hope that added fertilizer(s) would cause damage to the ericoid mycorrhizae and thus reduce *Kalmia* vigour. Ploughing, liming and nitrogen fertilization has been used successfully in *Calluna* dominated sites of Scotland to raise conifer plantation(Gimingham 1972). Reduced growth of *Gaultheria* following nitrogen fertilization was reported by Prescott *et al.*(1993). However, *Kalmia* responded with significant increase in above - and below ground biomass and increased number and length of sprouts and rhizomes following application of N alone or in combination with P and /or K(A.U. Mallik, Unpublished). Therefore N, P or K fertilization can not be used as an option to control *Kalmia*.

Since disturbance enhances *Kalmia* growth, the idea of enhancing black spruce growth in presence of *Kalmia* was tested by inoculating the black spruce seedlings with mycorrhizal fungi. In an initial screening experiment 51 black spruce mycorrhizae were tested against *Kalmia* leaf leachate toxicity in liquid culture. Nineteen mycorrhizae were able to grow in the presence of *Kalmia* leaf leachate among which biomass of three fungi, *Paxillus involutus*, *Laccaria laccata* and *E* - strain, were significantly higher compared to the control. Black spruce seedlings inoculated with these three mycorrhizae were grown in presence of *Kalmia* in pot culture. At the end of the experiment, four months after commencement the number of mycorrhizal short roots, height and diameter of black spruce seedlings and the oven - dry biomass of their root and shoot were determined. Over 90% of the mycorrhizae were attributed to the inoculated fungi although some indigenous mycorrhizae were also found in these seedlings (Mallik and Zhu 1995). Persistence of inoculated mycorrhizae was not affected by living *Kalmia*. The shoot and root biomass of inoculated black spruce seedlings were significantly higher compared to the noninoculated seedlings. The seedlings inoculated with *Paxillus involutus* isolated from Newfoundland soil produced 2 - 3 times higher root and shoot biomass compared to the control and as such, this fungus exhibited the best potential for overcoming *Kalmia* allelopathy. As Trappe(1977) suggested it is necessary to select appropriate mycorrhizal strain(s) adapted to a particular host - soil - climate combination for seedling inoculation. Therefore, *P. involutus* isolated from central Newfoundland soil would be an excellent candidate for black spruce inoculation in overcoming *Kalmia* allelopathic growth inhibition of black spruce.

SUMMARY AND CONCLUDING REMARKS

In certain nutrient poor temperate forests ericaceous plants such as *Calluna vulgaris*, *Erica cinerea*, *Kalmia angustifolia*, and *Gaultheria shallon* dominate the habitats after forest clearing by logging and fire. All these plants regrow quickly and vigorously after disturbance because of their efficient vegetative regeneration strategies. The plants also induce allelopathic growth inhibition in conifer seedlings and thus affect forest regeneration. Occupancy of these plants in a site can bring about long - term soil changes by increasing organic accumulation(paludification), nutrient sequestration, soil acidification and allelochemicals. The modified habitat becomes unsuitable for conifer regeneration. Thus some temperate forests with ericaceous plants may turn into heaths following distur - bance.

This disturbance induced vegetation shift has important landuse implications. If the heathlands have economic values for grazing, recreational hunting and nature conservation then they are maintained as productive heathlands such as the *Calluna* heaths of Europe. On the other hand if the ericaceous heaths do not have grazing or recreational values reforestation becomes the landuse objective, for example *Kalmia* heath of eastern Canada.

Reforestation of ericoid dominated sites is very difficult because of the difficulty in controlling the shrubs to make the habitat conducive to conifer growth. Ploughing, liming and nitrogen fertilization have been used successfully in *Calluna* dominated sites in Scotland. Nitrogen fertilization also seems to be effective in reducing vigour of *Gaultheria*. However, these methods are not effective in reducing *Kalmia* growth. Mulching and application of Garlon herbicide seem to be effective in controlling *Kalmia*. However, the problem being that mulching equipment can not operate in stony soils. Moreover, the operating cost of such equipment is very high. Although Garlon seems to be an effective herbicide to control *Kalmia*, it is not registered in the provinces of Canada that have *Kalmia* problems.

Inoculation of black spruce with mycorrhizal fungi such as *Paxillus involutus*, *Laccaria laccata* and *E* - strain was found to be effective in improving black spruce growth in presence of *Kalmia* under greenhouse conditions. A field trial is recommended to determine the ability of the inoculated black spruce to overcome *Kalmia* allelopathy under natural field conditions. The aspect of allelopathy - nutrient interaction in ericoid dominated sites causing long term soil changes requires further investigation.

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