Conifer Regeneration Problems in Boreal and Temperate Forests with Ericaceous Understory: Role of Disturbance, Seedbed Limitation, and Keystone Species Change

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ABSTRACT: Conifer regeneration failure in the presence of dense ericaceous cover resulting from the removal of canopy trees by forest harvesting observed in boreal and temperate forest has been attributed to allelopathy, competition, and soil nutrient imbalance. Ecosystem-level allelopathic effect has been argued as a cause for conifer regeneration failure by citing examples from a species-poor boreal forest in northern Sweden with ground vegetation dominated by crowberry (Empetrum hermaphroditum, Ericales) and New Zealand dairy pastures invaded by nodding or musk thistle (Carduus nutans). This article aims to explain the phenomenon of vegetation shift from conifer forest to ericaceous heath by extending the argument of ecosystem-level impact of ericaceous plants and linking the disturbance-mediated regeneration strategies of the dominant conifer species and the understory ericaceous species with the quality of seedbed substrate that influence the direction of secondary succession. It has been argued that fire severity plays a pivotal role in controlling seedbed quality and the regeneration mechanisms of conifers, which in turn determines the direction of post-disturbance succession. The post-fire-dominated ericaceous plants and their habitat-modifying effects have been explained from the point of view of keystone species concept and their role as ecosystem engineers. In the absence of high severity natural fires the canopy keystone species (conifer) fails to regenerate successfully mainly due to limitation of favorable seedbed. On the other hand, the understory ericaceous plants regenerate vigorously by vegetative methods from the belowground components that survived the fire. Forest harvesting by clearcutting or selective cutting also create similar vigorous vegetative regrowth of ericaceous plants, but conifer regeneration suffers from the lack of a suitable seedbed. Thus in the absence of successful conifer regeneration, the vigorously growing understory ericaceous plants become the new keystone species. The new keystone ericaceous species bring about a significant long-term habitat change by rapid accumulation of phenol-rich humus. Ericaceous phenolic compounds have been found to inhibit seed germination and seedling growth of conifers. By forming protein-phenol complexes they cause a further reduction of available nitrogen of the already nutrient-stressed habitat. A low pH condition in the presence of phenolic compounds causes the leaching of metallic ions and forms hard iron pans that impair soil water movement. The phenolic allelochemicals of ericaceous humus are also inhibitory to many conifer ectomycorrhizae.

On the other hand, ericaceous plants perpetuate in the community by their stress-tolerating strategies as well as their ability to acquire nutrients through ericoid mycorrhizae. Three mechanisms working at the ecosystem level can be suggested as the cause of vegetation shift from forest to ericaceous heath. These are (1) the absence of high severity natural fire and the limitation of suitable conifer seedbed in the presence of thick humus, (2) increased competition resulting from the rapid vegetative regeneration of understory ericaceous plants after forest canopy opening by harvesting or nonsevere fire, and (3) habitat degradation by phenolic allelochemicals of ericaceous plants causing a soil nutrient imbalance and iron pan formation. Thus, a shift in keystone species from conifer to ericaceous plant in the post-disturbance habitat may induce a retrogressive succession due to ecosystem-level engineering effects of the new keystone species.
Vegetation management in conifer-ericaceous communities depends on land management objectives. If the objective is to produce timber and other forest products then the control of ericaceous plants and site preparation is necessary after forest harvesting. Ploughing and liming followed by conifer planting and repeated N fertilization has been applied successfully to promote afforestation of Calluna heathlands in Britain. However, such practice has not been proven successful in the reforestation of Kalmia-dominated sites in eastern Canada. If, on the other hand, the land management objective is to maintain heathlands for herbivore production or conservation of cultural landscape, as in the case of certain Calluna-dominated heathland in Western Europe, then moderately hot prescribed burning is useful as a management tool.

KEY WORDS: keystone species, ecosystem engineer, alternate stable states, ericaceous plants, allelopathy, phenolics, fire, harvesting, regeneration, succession, mycorrhizae, growth check.

I. INTRODUCTION

Allelopathy, competition, soil nutrient imbalance, and poor ectomycorrhization have been implicated in conifer regeneration failure in the presence of dense ericaceous understory resulting from forest harvesting and fire in boreal forests and sub-alpine spruce forests (Mallik, 1999). Pellissier and Souto (1999) have reviewed the role of allelopathy in northern temperate and seminatural boreal forests. The growth inhibition of Sitka spruce (Picea sitchensis (Bong.) Carriere) in the presence of heather [Calluna vulgaris (L.) Hull, hereafter referred to as Calluna] has been reported by several authors from Britain as early as 1953 (Wheatherell, 1953; Leyton, 1954, 1955). Similarly, the failure of natural regeneration and growth inhibition of planted conifers such as black spruce in the presence of sheep laurel (Kalmia angustifolia L., hereafter referred to as Kalmia) and Labrador tea (Ledum groenlandicum L.) has been reported by several authors (Mallik, 1987, 1992; Yamasaki, et al., 1998; Inderjit and Mallik, 1996a). Likewise, growth inhibition of jack pine (Pinus banksiana Lamb.) in the presence of Kalmia has been reported from New Brunswick, Canada, by Krause (1986). From the west coast of Canada and the Pacific Northwest of USA other ericaceous shrubs such as salal (Gaultheria shallon Pursh.) in coastal oceanic temperate rainforests and several Vaccinium species (e.g., Vaccinium alaskaense L.) in high elevation forests have been reported to cause growth stagnation of conifers such as western red cedar (Tsuga plicata Donn), western hemlock (Thuja heterophylla (Raf. Sarge)), Sitka spruce (Picea sitchensis), and Amabilis fir (Abies amabilis Doug.) (Bunnell, 1990; Messier, 1993; Prescott et al., 1996; Fraser, 1994; Fraser et al., 1993, 1995). Belowground competition for space, available N and P and to some extent condensed tannin allelopathy of salal litter have been suggested as the principal causes of growth check in these conifers (Taylor and Tabbush, 1990; Weetman et al., 1990; Messier, 1993; Prescott et al., 1996; Xiao, 1994; Xiao and Berch, 1993; de Montigny et al., 1991; de Montigny, 1992; Mallik and Prescott, 2001). In sub-alpine spruce forests in France another understory ericaceous plant, bilberry (Vaccinium myrtillus L.), has been reported to cause the regeneration failure of Norway spruce (Picea abies (L) Karst.) (Andre et al., 1986; Jaderlund et al., 1986; Jaderlund et al., 1996a,b). Phenolic allelochemicals of forest floor humus and seed predation have been implicated for this regeneration failure (Pellissier, 1993, 1994; Gallet and Lebreton, 1995; Gallet et al., 1999). In northern Sweden cowberry, another member of Ericales (Empetrum hermaphroditum Hagerup) forms by far the predominant ground cover and interferes with Norway spruce regeneration (Steijlen and Zackrisson, 1987; Wallstedt, 1998; Zackrisson and Nilsson, 1992; Nilsson, 1994). Nilsen et al. (1999) have shown that diversity and composition of plant litter have differential effects on boreal plant-soil system.

In undisturbed forests all the above-mentioned ericaceous plants form the main understory or ground cover vegetation often regenerating well in forest canopy gaps and in depapurated condition under mature conifers. Following canopy disturbance by forest harvesting and fire these ericaceous plants grow vigorously by vegetative methods and accumulate a large quantity of litter on the forest floor (Mallik, 1993, 1994; Damman, 1971, 1975; Evardsen et al., 1988). The ericaceous litter contains an array of phenolic com-
pounds that are inhibitory to conifer seed germination, primary root growth, and ectomycorrhizal growth (Pellissier, 1993, 1994; Mallik, 1987, 1992; Zhu and Mallik, 1994; Mallik and Zhu, 1995; Mallik et al., 1998). Many of these phenolic compounds can create soil nutrient imbalance by reducing the available N (by forming protein-phenol complex) and increasing the amounts of Fe, Zn, K, Ca, Mg, and Mn leading to long-term site degradation (Bending and Read, 1996a,b; Damman, 1971; Meades, 1983, 1986; Inderjit and Mallik, 1996b, 1997a,b). Wollenweber and Kohorst (1994) have extracted epicuticular leaf flavonoids from Kalmia and salal and speculated that these compounds may have growth inhibitory effects on conifers. Differential nutrient uptake of ericoid mycorrhizae that favor the host plant but have antagonistic effect on conifer mycorrhizae has been suggested as yet another cause of poor conifer growth in the presence of ericaceous plants (Read, 1982). Recently, limitation of favorable seedbed for conifers seed regeneration in the presence of thick layer of forest humus, which, in addition to its chemical effect (allelopathy), acts a physical barrier of seedling establishment has been shown to be one of the primary reasons for conifer regeneration failure after forest disturbance in eastern Canada (Bloom, 2001). In general the mechanism of ericaceous induced conifer regeneration failure is currently explained by the combined effects of competition, allelopathy, soil nutrient deficiency and imbalance, increased acidity, differential mycorrhizal activities of the ericaceous shrubs, and tree species as well as the physical barrier of the humus acting as unsuitable conifer seedbed (Mallik, 1999; Inderjit and Mallik, 1996a,b; Nilsen et al., 1999).

In almost all the above examples the conifer-ericaceous communities are characterized by one dominant canopy species (conifer) and one dominant understory species (ericaceous) that control the community structure and composition and biogeochemistry of the habitat. Wardle et al. (1998) have argued that in such a species-poor community allelopathy can have a stronger landscape-level impact, particularly where the dominant species is competitive and allelopathic compared with a species-rich community. Forest disturbance by harvesting of the canopy species often results in prolific vegetative growth of the understory ericaceous plant that preclude conifer regeneration, creating a vegetation shift from forest to heath (Mallik, 1995). In this instance one can argue that the controlling effects of one species on another species and that on the ecosystem in relation to disturbance can be articulated further by extending the suggestion of ecosystem-level allelopathic effects of dominant species (Wardle et al., 1998) to the concept of keystone species (defined below) and organisms as ecosystem engineers (Jones et al., 1994). In other words, it is worthy of attempting to explain the disturbance-mediated vegetation change from forest to ericaceous heath in light of the concept of keystone species and their ecosystem engineering role where allelopathic effect of the understory species is one of the multifaceted chain of events that follow due to the change of keystone species. One can argue that keystone species change from conifer to ericaceous (causing in the absence of appropriate disturbance regime) is the principal cause of ecosystem-level allelopathic effect and subsequent habitat degradation and forest regeneration failure. In the present review the causes and consequences of natural regeneration failure and growth inhibition of conifers following ecosystem disturbance are explored by linking the regeneration response of the dominant (keystone) species to disturbance severity and their role as ecosystem engineers.

II. PLANT SUCCESSION AFTER DISTURBANCE

Predicting vegetation change over time has been a major preoccupation in ecology. Clements (1916) and later Odum (1969) presented milestone conceptual models of succession that described communities as increasing complexity and efficiency of resource use over successional time. However, such unidirectional model of plant succession suffered from three major shortcomings: (1) unrealistic generalization of species-by-species and community-by-community replacement, that is, relay floristics (Egler, 1954), (2) lack of recognition of retrogressive succession where habitat degradation effects of certain species impede...
rather than facilitate the subsequent community organization (Connell, 1972; Drury and Nisbet, 1973), and (3) lack of recognition of frequent disturbance. The first two concerns were addressed by Connell and Slatyers’ (1977) three-pathway model of succession: (1) Facilitation pathway, in which the presence of early occupants facilitates the entry and establishment of the successive suits of species, (2) Tolerance pathway, in which earlier species will be those that are able to tolerate the lower level of resources than the earlier ones, and (3) Inhibition pathway, in which the existing species resist the invasion of later colonists. Species richness and succession vary over the course of succession (Odum, 1969), and periodic disturbance allows for this variation primarily through the prevention of competitive exclusion. Based on this theme, Connell (1978) proposed the Intermediate Disturbance Hypothesis, which states that an ecosystem maintains its highest species diversity under conditions of moderate disturbance. A direct link between species traits and probable pathways of succession was forged with the development of the vital attributes model of Noble and Slatyer (1980). This model is useful in predicting the successional sequence of fire-prone Australian ecosystems and regularly burned Scottish heathland ecosystems (Hobbs et al., 1984). While this theory takes into account the role of disturbance frequency on species diversity, it fails to appreciate the effect of habitat heterogeneity created by each disturbance such as fire. Post-fire habitat heterogeneity created by differential fire severity and species regeneration strategies play a significant role in determining species diversity as well as the rate and direction of succession. The vital attribute approach also does not differentiate between the species that determine the progress and direction of succession from subdominant species that are ‘along for the ride’ or functionally redundant. White (1979) emphasized that the basic natural history characteristics of species and their reproductive strategies are of fundamental importance in understanding succession. Rowe (1983) compared the vital attributes of the boreal species according to the groupings of Noble and Slatyer (1980) and cautioned that complexity rather than simplicity would be the nature of plant adaptations to periodically disturbed ecosystems.

Presently there is a need to unify the concept of ‘species functional groups’ (Tilman, 1996; Diaz and Cabido, 1997; Noble and Gitay, 1996) to build a predictive and realistic model of succession that focuses on ecosystem function rather than superficial measures of species composition following disturbance. We need to understand whether species replacement is controlled biotically through stress or facilitation amendments to the habitat or by competitive abilities of plants within the inherent nutrient status of the habitat. We need to link ecosystem disturbance patterns with regeneration, competition, and habitat modification traits of the persisting species that are sufficiently abundant to facilitate or inhibit succession. Although it is generally accepted that species act individualistically (Gleason, 1926) “after-life effects” (Wardle et al., 1997; Wardle and Lavelle, 1997) of abscised tissues (especially leaves and roots) is a subtle but a chronic way in which species influence their habitats. The concentrations of secondary compounds, available nitrogen, and simple carbon compounds in the tissues of various functional groups may be an important indicator of biogeochemical cycling as abundance of species within functional groups change over time (Silver et al., 1996).

The fire-prone Kalmia-black spruce communities of eastern Canada are simple in species composition and provide an excellent opportunity to test some of these contemporary theories and concepts of ecology in explaining the mechanism of secondary succession. Following disturbance plant succession in some of these communities tend to follow the inhibition pathway by converting the forests into Kalmia dominated heaths (Meades, 1983, 1986; Mallik 1995). Two factors seem to play important roles in this regressive succession from forest to heath, (1) dramatic increase in Kalmia cover after forest canopy removal (Mallik, 1994) that restricts colonization of early and late successional species, and (2) habitat-modifying ability of Kalmia litter that is unfavorable for the reestablishment of the key-stone species (black spruce) once the shrub is established. Damman (1971) suggested that long-term occupancy of Kalmia in a site changes the nutrient status of soil so much that it can no longer support tree growth. Indeed, there are ex-
amples of 15- to 40-year-old burns in central Newfoundland ranging from 3 to 1000 ha that are completely dominated by *Kalmia* without much tree cover. However, recent field visits in *Kalmia*-black spruce sites burned 30 to 50 years previously showed sporadic tree colonization often in groups mimicking island regeneration (Nyland, 1998) among *Kalmia*. In some older burns *Kalmia*-dominated retrogressive succession seems to follow a slow but progressive succession toward open canopy forest development. It seems that post-fire habitat heterogeneity created by each fire plays a significant role in determining the rate as well as direction of succession. Shifting dominance of species along the successional sequence may modify the habitat quite dramatically by increasing soil acidity (Grubb et al., 1969), iron pan formation (Damman, 1964, 1971), allelopathy (Mallik, 1987; Mallik and Roberts, 1994), and nutrient imbalance (Inderjit and Mallik 1996b, 1997a).

### III. ECOSYSTEM DISTURBANCE AND MULTIPLE STABLE STATES

One could attempt to explain the phenomenon of disturbance induced vegetation shift from conifer-ericaceous community to ericaceous heath and their persistence around the contiguous forest in light of the concept of *multiple stable states* in natural communities (Sutherland, 1974; Connell and Sousa, 1983). Multiple stable states occur ‘when more than one type of community stably persist in a single environmental regime’ (Knowlton, 1992). Based on theoretical modeling (using mathematical stability theory) and field observations, arguments have been made for the existence of alternative stable states of plant and animal communities (see reviews by May, 1977; van de Koppel et al., 1997). Physiognomic manifestation of alternative stable states can be recognized by (1) the presence of a relatively stable vegetation mosaic in a previously uniform environment, and (2) intensification of a vegetational gradient leading to sharp boundaries (Wilson and Agnew, 1992). Examples of multiple/alternate stable states have been reported from herbivore controlled density and growth regulation of plants (Noy-Meir, 1975; May, 1977 but see Connell and Sousa, 1983; Sousa and Connell, 1985; Peterson, 1984; Sutherland, 1990). Rietkerk and van de Koppel (1997) reported alternate stable states and threshold effects in semiarid grassing systems where they found that plant-soil interaction plays a more important role than herbivore feeding behavior. They suggested that a positive feedback between plant density and reduced resource availability (soil water and nutrients) under increased grassing pressure maintains a two-phase alternate stable grassland mosaic. Latham et al. (1996) reported the contiguous occurrence of several different plant community types on similar parent material and soil type that can potentially favor forest community in Pocono barren, Pennsylvania. These are (1) *Scrub oak barrens* containing at least 50% cover of *Quercus ilicifolia* Wang., with widely spaced *Pinus rigida* P.Mill., (2) *Heath barrens* consisting of at least 50% cover of mainly *Kalmia angustifolia*, *Vaccinium angustifolium* Ait., *V. pallidum* Ait, with sparse *Pinus rigida*, (3) *Rhodora barrans* with at least 50% cover of *Rhododendron canadense* (L) Torr., with scattered *Pinus rigida*, and (4) *Forests* that have at least 90% tree cover dominated by either northern hardwoods species (such as *Fagus grandifolia* Ehrh., *Prunus serotina* Ehrh., *Betula alleghaniensis* Britt., *B. lenta* L., *Acer rubrum* L., and *A. saccharum* Marshall) or red maple-oak dominated by *Acer rubrum*, *Quercus alba* L., and *Q. coccinea* Munchn. Following further study on surficial geology, soil type, soil moisture, and plant species composition, Eberhardt and Latham (2000) concluded that the *alternative stable state hypothesis* can explain the side by side existence of such communities. They suggested that the origin and perpetuation of these communities on a similar soil environment might be related to disturbance (fire) history and biotic influence of the dominant plants. They emphasized the particular importance of the positive feedback driven by plant traits that encourage the spread of wild fire and restrict the soil nitrogen availability that allow the heath species to dominate (Petraitis and Latham, 1999). The potential significance of the biotic control of alternative stable states of vegetation can be determined by a comparative study of the autecological properties of the dominant plants.
and their ecological engineering effects on the habitat (Lawton and Jones, 1995; Nilsen et al., 1999). One can assess the role of chemical feedback mechanisms in sustaining the alternate stable states by a comparative study of ericaceous-dominated heathlands and forests that alter or sustain soil nutrient dynamics in opposite directions (Pellissier, 1993, 1994, 1998; Gallet, 1994; Gallet and Pellissier, 1997; Northup et al., 1995; Chapin, 1995). Hattenschwiler and Vitousek (2000) reviewed the role of polyphenols in nutrient cycling. This phenomenon of polyphenol-controlled nutrient release becomes even more critical under a stressed environment such as poor soil nutrient condition, low temperature, and slow decomposition in boreal and sub-alpine forests (Northup et al., 1995; Reogosa et al., 1999).

At present we do not know enough about the longevity of the altered vegetation states under the dominance of different ericaceous species. Connell and Sousa (1983) cautioned that in recognizing alternate stable states one must consider the intensity and time scale of perturbation and appropriate time and spatial scale of observations of ecosystem response. One might argue that although the treeless *Kalmia* dominated condition 40 years after a nonsevere fire in black spruce–*Kalmia* site may be considered as retrogressive succession, but the wood savannah type of *Kalmia*–black spruce community developing after a nonsevere fire may be thought of an extended seral stage of a progressive succession toward forest development.

IV. DISTURBANCE, SEEDBED QUALITY, AND REGENERATION OF KEYSTONE SPECIES

Keystone species in a habitat are ‘those species that provide the unique structure and function of the ecosystem by performing the essential ecosystem services’ (Ehrlich, 1986; Ehrlich and Wilson, 1991). The removal of keystone species from a community would cause a significant change in community structure and function (Lawton and Jones, 1995). The keystone species act as ecosystem engineers ‘by controlling directly or indirectly the availability of resources to other species and by causing state changes on biotic and abiotic materials’ (Jones et al., 1994; Lawton and Jones, 1995). In the context of allelopathy it would be relevant to examine how the different types of disturbance change the keystone species that in turn change the structure and function of the ecosystem. More specifically, it would be worthwhile to relate the disturbance-mediated change of keystone species with their functional roles that change the physical and chemical nature of the seedbed for conifer regeneration.

Forest floor allelopathy in boreal and temperate forests is regulated by the chemical nature of the humus. These forests often have one or two canopy species and a dominant ericaceous understory species that play the most predominant role in controlling above and belowground ecological functions by accumulating most of the photosynthates and by their ‘afterlife effects’ through adding leaf litter and fine roots on forest floor humus (Wardle et al., 1997, 1998). A disproportionately large amount of the humus develops from the litter of keystone species and the physical, and chemical nature of the decomposing litter forms the seedbed for newly regenerating conifers from seeds. Changes in keystone species from conifer to ericaceous following forest disturbance bring about changes in forest floor humus chemistry as well as its physical property. Forest structure and function is regulated by the disturbance mediated vegetation dynamics as well as humus chemistry of the dominant conifer and the understory species by controlling the above and belowground processes (Bradshaw and Zackrisson, 1990, Zackrisson et al., 1996; Zackrisson, 1977). The humus developing largely from the conifer and the ericaceous understory litter contains an array of allelochemicals that interfere with natural regeneration of conifers by inhibiting their seed germination and seedling growth (Gallet and Pellissier, 1995, 1997; Pellissier, 1993, 1994; Pellissier and Souto, 1999; Mallik, 1987, 1992; Inderjit and Mallik, 1996a,b; Zackrisson and Nilsson, 1992; Zackrisson et al., 1997; Prescott et al., 1996, 2000).

Gallet and Lebreton (1995) studied the patterns of phenolic polymers (tannins) and monomers (phenolic acids and flavonoids) in the living leaf and root tissues, their litter and humus. They
found high abundance of tannin in bilberry leaves, whereas the spruce needles had high abundance of \( p \)-hydroxyacetophenone. Compared with the green foliage the brown foliage of bilberry exhibited greater loss of monomeric compounds, but it had high tanning activity. The amount of protocatechuic and vanillic acids (the degradation intermediates) were increased with increasing litter decomposition (Gallet and Lebreton, 1995). Spruce-dominated organic soil under bilberry had high tanning activity and a high abundance of phenolic acids. From a laboratory bioassay with natural leachates of bilberry and spruce, Gallet (1994) concluded that \( p \)-hydroxyacetophenone, a spruce tree-specific metabolite, phenolic acids and tannins associated with bilberry reduce or even often stop the natural regeneration of spruce by inhibiting primary root growth of spruce seedlings. Jaderlund et al. (1996) found that water leachate of green leaves of bilberry had more inhibitory effect on germination and root growth of Norway spruce than that of brown leaves. From a laboratory bioassay and complimentary seeding experiment in the field, Mallik and Pellissier (2000) reported only 2% and 3% germination in control plots (no Vaccinium, no litter removed) and aboveground Vaccinium removed plots, respectively. Compared with this spruce germination was 27% in plots that received humus removal treatment. Two phenolic compounds, caffeic and \( p \)-coumaric acids, were found in rather high quantities, \( 1.7 \times 10^{-3} M \) and \( 0.02 \times 10^{-3} M \), respectively, in the humus. Pure compounds of both the phenolic acids were strongly inhibitory to germination and primary root growth of Norwegian spruce (Mallik and Pellissier, 2000). A high concentration of phenolic acids in the humus layer of this forest has been suggested as a cause of Norway spruce regeneration failure.

Similarly, natural regeneration failure of Scots pine as well as Norway spruce has been reported from northern Sweden after clearcutting and the dominance of cowberry in post-harvest habitats in the absence of natural fire has been attributed to the conifer regeneration failure (Sarvas, 1950; Zackrisson et al., 1996). A phenolic derivative batatasin III (3,3-dihydroxy-5-methoxy-dihydrostilbene) has been found in high concentration in the forest floor humus and also in leaf hair glands of crowberry (Oden et al., 1992; Wallstedt, 1998). This compound has been found in water leachate of humus that inhibited seed germination and seedling growth of the conifers (Zackrisson and Nilsson, 1992; Nilsson, 1992; Gallet et al., 1999). An increase in batatasin with an increasing abundance of crowberry after clearcutting and seasonal variation in concentration of batatasin has been found to be positively correlated with the poor seedling regeneration of the conifers (Nilsson et al., 1998).

Jalal and Read (1983a,b) isolated and identified a number of phyto- and fungitoxic compounds and determined their seasonal concentrations from Calluna humus. They argued that these compounds may directly interfere with the root growth of spruce. Hobbs (1984) tested the chemical interactions among heathland ericaceous plants by using water leachates of plant shoots and plant-soil monoliths in seed germination bioassays. He used seeds of several common heathland plants as well as oat (Avena fatua L.) as a standard germination bioassay material. Growth of Descampsia flexuosa (L.) Trin. was strongly inhibited by the leachate of Calluna. However, Arctostaphylos uva-ursi (L.) Sprengel. produced the greatest number of inhibitory effects, including a strong inhibition of its own seedling. The objective of this study did not include testing the tree species response to allelopathic effects of Calluna. The standard bioassay with oat does not necessarily provide any direct evidence of chemical interaction between tree species such as Sitka spruce and Calluna (Inderjit and Dakshini, 1995). Several authors have reported on the acidifying effect of Calluna litter (Gimingham, 1960; Wilson, 1960; Grubb et al., 1969). They found strong correlations between size of Calluna bushes and soil pH underneath them as well as distance from the center of the bush and soil pH. It can be argued that vegetation changes associated with the spread of Calluna may be attributed at least partly to the increasing acidity and associated soil changes (Gimingham, 1972). Webley et al. (1952) reported marked increases in soil fungi and large reductions in soil bacteria from a fixed Ammophila sand dune to a Calluna-dominated dune.

Boreal and sub-alpine conifers such as black spruce, Norway spruce, jack pine, Scots pine, and red pine rely on seed regeneration and for that
they require appropriate seedbed. While the presence of thick humus interferes with the seedling regeneration of conifers, the ericaceous plants do just fine because their principal mode of regeneration is by resprouting and extension of vegetative organs (rhizomatous growth) that traverse through the humus layer (Mallik, 1993; Mallik and Roberts, 1994).

Seedbed quality plays a vital role in the natural regeneration of conifers. If the seedbed substrate is not conducive to seed germination and seedling establishment, then natural regeneration cannot occur. The suitability of seedbed is a function of the physical and chemical nature of the seedbed substratum (Prescott et al., 1996). Mineral soil seedbed facilitates successful natural regeneration. In boreal ecosystem severe fire creates such conditions by consuming the thick humus layer and exposing the mineral soil (Bloom, 2001; Mallik and Roberts, 1994). In the absence of such a disturbance, the seedbed remains inhospitable for conifer regeneration because of the adverse physical and chemical nature of the accumulated humus. The post-logging or lightly burned (charred humus) or insect-defoliated forest seedbed consists of thick humus originating from the partially decomposed litter of the canopy trees and understory plants that is often rich in germination and growth-inhibitory allelochemicals (Pellissier, 1993; Gallet and Pellissier, 1997; Zackrisson and Nilsson, 1992; Mallik and Newton, 1988; de Montigny 1992; Zhu and Mallik, 1994). Periodic fires remove these compounds by consuming the forest floor humus. Thermal decomposition of the humus also release nutrients, break down allelochemicals and any remaining allelochemicals get adsorbed in charcoal (Zackrisson et al., 1996). The current method of forest management by fire suppression and clearcut logging creates a shift in dominance of keystone species by restricting the creation of favorable mineral soil seedbed for conifer regeneration. On the other hand, it allows the prolific growth of understory ericaceous shrubs that regenerate vegetatively (Mallik, 1993). In nutrient-poor sites the conifer-ericaceous communities thus transform into ericaceous heath following clearcut logging and nonsevere fires (Mallik, 1994, 1995).

V. KEYSTONE SPECIES SHIFT AND RETROGRESSIVE SUCCESSION

In the absence natural regeneration of conifers such as black spruce, Norway spruce, red pine, jack pine, western hemlock, or western red cedar (the canopy keystone species), the vigorously growing understory ericaceous species such as Calluna, Vaccinium, Kalmia, Empetrum, or salal assume the role of new keystone species and the multilayered forest structure is replaced by a relatively uniform low growing heath community (Mallik, 1995; Bloom, 2001). The rapid vegetative growth of the ericaceous plants following tree canopy removal by logging and nonsevere forest fire large amounts of above- and belowground biomass (humus) that are chemically different from that of the conifers. The ‘afterlife effects’ (Wardle et al., 1997) of the ericaceous litter makes the soil even more acidic, their phenolic allelochemicals bind N in protein-phenol complexes, and thus the habitat becomes even more deficient in available N (Bending and Read, 1996a,b; Prescott et al., 1996; Mallik, 2001). In the presence of a large array of phenolic acids the metallic cations such as Fe, Al, Ca, Zn, and Mn precipitate to the lower soil horizon and form a hard iron pan and change the soil-plant-water relation. With the rapid build up of acidic humus and a high rate of paludification, occupancy of the ericaceous community brings about long-term change in the habitat that is less and less suitable for conifer regeneration (Gimingham, 1960; Wilson, 1960; Grubb et al., 1969; Damman, 1971 1975; Meades 1983, 1986; Siren, 1955; Uggl, 1958; Steijlen and Zackrisson, 1987; Zackrisson, 1977; Bradshaw and Zackrisson, 1990). Ericaceous plants such as Kalmia, Vaccinium, and Empetrum thus act as ecosystem engineers. With their autogenic properties they bring about allogenic habitat changes (Lawton and Jones, 1995).

VI. ORGANISMS AS ECOSYSTEM ENGINEERS

According to Lawton and Jones (1995), ‘ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species by physi-
cal state changes in biotic and or abiotic material. In the process the ecosystem engineers, ‘create, modify and maintain habitats’ (Lawton and Jones, 1995). The authors classified the ecosystem engineers into (1) autogenic engineers that ‘change the environment via their own physical structures’, for example, dominant plants by their living and dead tissues, and (2) allogenic engineers that ‘change the environment by transforming living or nonliving materials from one physical state to another, via mechanical or other means’, for example, beavers making dams that alter hydrology, sedimentation, decomposition, and nutrient cycling of the habitat and community composition and diversity of plants and animals (Naiman et al., 1988). Trees can be considered the autogenic equivalent of beaver in the sense that a growing forest modify hydrology, nutrient cycling, and near ground micro-climate such as humidity, temperature, wind speed, and light (Holling, 1992). These factors create conditions and habitats for other organisms, and without these engineers most of the other organisms would not survive. Lawton and Jones (1995) suggest that both auto- and allogenic engineers also modulate powerful natural forces such as fire, storms, and hurricanes that fundamentally change the distribution and abundance of resources. Using the example of plants as modifiers of fire behavior they argued that species with differential quality and quantity of living and dead tissue as fuel regulate the magnitude, duration and intensity of fire, and in turn profoundly alter the supply of resources to other species (Christensen, 1985; Dublin et al., 1990). In boreal forest high-intensity natural fires consume the thick humus layer of the forest floor, exposing the mineral soil seedbed necessary for successful conifer regeneration. The degree of thermal decomposition of the humus determines the structure and composition of the regenerating forest by modulating the creation of conifer seedbeds. The lack of mineral soil seedbed resulting from mild fires or clearcutting favor vegetatively regenerating species such as trembling aspen (Populus tremuloides Michx.), pin cherry (Prunus pensylvanica L.f.), green alder (Alnus viridis spp. Crispa (Aiton) Turril), and beaked hazel (Corylus cornuta Marsh.) (Mallik et al., 1997) instead of the dominant conifer species such a black spruce, jack pine, white pine (Pinus strobes L.), and red pine (P. resinosa Ait.), causing a dramatic change in species composition (Carleton, 2000). Changes in canopy species composition bring about changes in the understory species composition and forest floor humus property (Carleton, 2000).

VII. FIRE SUPPRESSION, LOGGING, AND KEYSTONE SPECIES SHIFT

Natural fire has been a major force in maintaining the characteristic structure and composition of boreal forest (Wein and McLean, 1983; Rowe, 1983; Haapasaari, 1988; Zackrisson et al., 1995, 1996). Periodic fires remove competition, reduce allelochemicals, and release nutrients resetting the progressive secondary succession leading to forest development (Flinn and Wein, 1977; Olson, 1981; Andrea, 1991; Schimmel and Granstrom, 1996). The main objective of the current forest management practice by fire suppression and clearcut harvesting in boreal forest is to ensure timber production. However, this form of management does not provide the ecological services necessary for resetting the characteristic secondary succession (Figure 1). The thick humus layer that develops over time from the accumulated litter of the dominant canopy and understory species is rich in germination and growth inhibitory allelochemicals that interfere with the natural regeneration of the canopy keystone species, the conifers (Mallik and Newton, 1988; Thompson and Mallik, 1989; Zackrisson and Nilsson, 1992; Mallik and Pellissier, 2000). Furthermore, the physical characteristics of the accumulated humus in the absence of periodic natural fires can act as a barrier of root establishment into the mineral soil (Bloom 2001). The delicate primary roots of the germinating seedlings in the loosely packed partially decomposed humus may become desiccated during periodic hot spells of summer (Mallik 1982). On the other hand, these conditions are favorable for the reprotuing ericaceous species such as Calluna, Kalmia, Vaccinium, and Gaultheria which survive the fire (Table 1). All the dominant understory species of the conifer-ericaceous communities mentioned above regenerate mainly by stem base sprouting and rhizoma-
FIGURE 1. Generalized pathways of keystone species change following disturbance in boreal and sub-alpine coniferous forests with ericaceous understory.
**TABLE 1**
Autecological Properties of Ericaceous Plants That Enable Them to Dominate and Inhibit Conifer Regeneration in the Post-Disturbance Habitat

<table>
<thead>
<tr>
<th>Ericaceous plants</th>
<th>Principal mode of vegetative regeneration</th>
<th>Resiliency, recovery and competitive ability after disturbance</th>
<th>Class of chemicals in humus</th>
<th>Affected conifer(s)</th>
<th>Nature of inhibition</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Kalmia angustifolia</em></td>
<td>Basal &amp; rhizomatous sprouting &amp; layering</td>
<td>High, rapid, high</td>
<td>Phenolic acids</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ledum groenlandicum</em></td>
<td>Basal sprouting &amp; layering</td>
<td>Moderate to high, rapid, high</td>
<td>Phenolic acids</td>
<td></td>
<td>Primary root growth, growth check</td>
<td></td>
</tr>
<tr>
<td><em>Rhododendron albidiflorum</em></td>
<td>Basal sprouting &amp; layering</td>
<td>Moderate to high, rapid, high</td>
<td>Phenolic acids</td>
<td>Douglas fir</td>
<td>Growth check</td>
<td>Gallet 1994</td>
</tr>
<tr>
<td><em>V. alaskaense</em></td>
<td>Basal &amp; rhizomatous sprouting &amp; layering</td>
<td>High, rapid, high</td>
<td>?</td>
<td>Western hemlock, W. red cedar, Amabilis fir</td>
<td>Growth check</td>
<td></td>
</tr>
<tr>
<td><em>Gaultheria shallon</em></td>
<td>Basal &amp; rhizomatous sprouting &amp; layering</td>
<td>High, rapid, high</td>
<td>Tannins, Phenolics</td>
<td>Sitka spruce, western hemlock, w. red cedar</td>
<td>Primary root growth, growth check</td>
<td>Sabhasri 1962; Bunnell 1990; Fraser 1993; Fraser et al. 1993; Weetman et al. 1989a,b</td>
</tr>
</tbody>
</table>
tous growth (Sabhasri and Ferrel, 1960; Sabhasri, 1961; Mallik and Gimingham, 1985; Andre et al., 1987; Mallik, 1993). Increased light at the understory and warmer summer temperature at the humus layer following forest canopy removal by logging, insect defoliation, mild surface fire, and wind throw in overmature conifer-ericaceous forests stimulate vegetative growth of the understory plants (Bunnell, 1990; Smith 1991; Messier, 1992; Messier and Kimmings, 1990, 1991; Huffman et al., 1994; Power, 2000). In the absence of adequate seed regeneration of the canopy keystone species the vegetatively regenerating understory ericaceous species, soon becomes the predominant plant in the post-disturbance habitat and assumes the role of a new keystone species, which is distinctly different in stature and chemical composition from the conifer keystone species.

VIII. SEEDBED ALLELOPATHY
PREEMPTION OF CONIFER
COMPETITION

Competition is believed to be the predominant force structuring plant community. In the early phase of secondary succession after wild fire successfully regenerating black spruce outcompete Kalmia in productive sites. However, in the absence of high severity wild fire, inhospitable seedbed condition created by unfavorable physical and chemical characteristics of the humus can preempt conifer competition by limiting the natural regeneration of conifers (Bloom, 2001). It is clear from the preceding discussion that logging and the absence of natural fire in conifer-ericaceous communities can stimulate the growth of understory species, which can replace the canopy keystone species by limiting their natural regeneration (Pellissier, 1993, 1994, 1998; Zackrisson and Nilsson, 1992; Mallik, 1987, 1992). In the absence of conifer regeneration the complex multilayered forest structure is replaced by simple ericaceous shrub-dominated heath which further deteriorates the habitat by inducing changes in soil chemical ecology (Mallik, 1995; Inderjit and Mallik, 1996a,b, 1997a,b). Recent studies indicate that even fire can create similar conditions of retrogressive succession from forest to heath if it is not severe enough to burn off the ericaceous humus and create a favorable seedbed for the conifers. From a seeding experiment on the manipulated seedbed of Kalmia–black spruce community Bloom (2001) concluded that the successful fire suppression program in Terra Nova National Park put out the fire before it became a large and high-intensity natural fire. Consequently, it did not produce enough high-severity burn that could consume Kalmia humus and underground vegetative organs and create the mineral soil seedbed necessary for successful black spruce regeneration.

IX. HUMUS ALLELOCHEMICALS,
DECOMPOSITION, NUTRIENT CYCLING,
AND CONIFER GROWTH

Decomposition in organic soil is mediated by litter dwelling macro- and microorganisms. These organisms can decompose humus allelochemicals and produce new allelochemicals from their decomposition products (Kaminsky, 1980; Rice, 1984; Inderjit, 1996). Microorganisms are able to metabolize large amounts of phenolic compounds rather quickly (Blum, 1998; Blum and Shafer, 1988; Lockwood and Filonow, 1981; Souto et al., 1998; Inderjit et al., 1999). The amount of available N and P in the polyphenol-rich litter is dependent on the combined effects of litter quality (Northup et al., 1995; Chapin III, 1995) and the activity of a vast array of soil organisms and their ability to influence the carbon and nitrogen cycles (Bradley et al., 1997). Postdisturbance ericaceous-dominated forests experiencing a high rate of humus accumulation and conifer regeneration failure usually exhibit a deficiency of available N in soil. Based on the results of their experimental studies, Bradley et al. (1997) hypothesized that high levels of tannins in ericaceous humus chemically immobilize and eventually control N availability. An increase in population of nitrifying bacteria such as Nitrosomonas and Nitrobacter (Smith et al., 1968), competition for ammonium between heterotrophic microbes, plants, and nitrifying bacteria (Robertson and Vitousek, 1981; Stienstra et al., 1994), allelopathic plant exudates and humus decomposition products influence
nutrient cycling (Thibault et al., 1982; Baldwin et al., 1983; Olson and Reiners, 1983; Lothi and Killingbeck, 1980; Jobidon et al., 1989a,b; see also Pellissier and Souto, 1999 for a review). Both nitrifiers as well as other groups of soil microorganisms are involved in the manifestation of allelopathic effects in forest soils (Souto et al., 1994). In low pH humus fungi play a significant role in litter decomposition. Some soil fungi are negatively affected by soil allelochemicals, whereas others show stimulatory effects (Zhang, 1997; Lindeberg et al., 1980; Souto et al., 1998).

In organic soils mycorrhizal fungi play vital roles in the functioning of higher plants of a temperate region (Malloch and Malloch, 1981, 1982). Handley (1963) and Robinson (1972) demonstrated that certain conifer ectomycorrhizae were negatively affected by Calluna root exudates. Others have found that the effect can be both inhibitory and stimulatory, depending on the ectomycorrhizae and conifer species and the type and concentration of allelochemicals involved (Rose et al., 1983; Cote and Thibault, 1988; Nilsson et al., 1993; Mallik and Zhu, 1995; Pellissier, 1998). The response of ectomycorrhizal fungi to allelochemicals is complex and often related to the chemical structure, chemical mixture, concentration, and the fungal species (Pellissier and Souto, 1999; Boufalis and Pellissier, 1994; Mallik and Zhu, 1995). Andre (1994) suggested that high phenolic contents of a Vaccinium-dominated humus layer on the forest floor restrict the development of mycorrhizae of Norway spruce seedlings in sub-alpine forests. Four forest floor humus and humic solution allelochemicals, catechol, p-hydroacetophenone, p-hydrobenzoic acid, and protocatechuic acid of sub-alpine Norway spruce-Vaccinium forest were found to cause a significant reduction in the respiration of two conifer ectomycorrhizae, Laccaria laccata and Cenococcum graniforme (Pellissier, 1993; Boufalas and Pellissier, 1994). These authors concluded that conifer regeneration failure observed in this forest can be explained at least partly by the inhibitory effects of the humus allelochemicals that threaten the symbiotic relationship between the conifer and their ectomycorrhizae.

Yamasaki et al. (1998) conducted a study in which they examined mycorrhizal symbiosis, plant height, and diameter growth and foliar N of black spruce seedlings growing in the field close to (<1 m) and away (≥1 m) from Kalmia. Black spruce seedlings close to Kalmia were found to contain significantly less mycorrhizal short roots, foliar N, plant height and diameter growth compared with those growing further away. In a separate field survey Hong and Mallik (unpublished data) observed that black spruce seedlings were relatively small and had about 50% less mycorrhizal infection in a site dominated by Kalmia compared with a contiguous non-Kalmia site.

X. ERICOID MYCORRHIZAE

Ericaceous plants are in symbiotic association with a variety of mycorrhizae that are specifically adapted to nutrient-poor habitats (Read 1982, 1991). Ericaceous plants produce large quantities of polyphenolic materials (e.g. tannins, humic acids, melanins, and quinines) that can bind soil organic N as calcitrant protein-phenol complexes (Tackechi and Tanaka, 1987; Mole and Waterman, 1987). Bending and Read (1996a) have shown that ericoid mycorrhizae are able to utilize protein N that is complexed with tannic acid by means of enzymatic degradation, whereas ectomycorrhizal fungi associated with conifers could not obtain N from the same source. They also demonstrated that ericoid mycorrhizae can utilize tannin as a carbon source, a feature other mycorrhizae do not have. Studies of these and other authors suggest that ericoid mycorrhizal associations may have resulted from the selective force of low-available nitrogen environments (Leak and Read, 1989, 1991; Bending and Read, 1996b). Largent et al. (1980) and Xiao and Berch (1992) found that roots of salal is associated with three types of mycorrhizae ericoid, arbutoid, and ectomycorrhizae making them very efficient in obtaining N and P in acidic soils as well as capturing nutrients in complex organic forms. Thus, ericaceous plants seem to be much better equipped than conifers, which are typically associated with selected ectomycorrhizae for nutrient acquisition in polyphenol-rich shrub-dominated conditions.
XI. ECOSYSTEM-LEVEL PERSPECTIVE OF ALLELOPATHY

Very few studies in allelopathy have taken an ecosystem-level perspective of the phenomenon. Citing two examples, (1) nodding thistle (Carduus nutans) containing New Zealand pasture, and (2) cowberry (E. hermaphroditum) containing Swedish boreal forest, Wardle et al. (1998) argued that secondary metabolites of these invading species can cause ecosystem-level changes by negatively influencing the regeneration of dominant plants that control the key ecological processes. They suggested that the concept of allelopathy is more applicable to ecosystem-level processes rather than population-level processes particularly in the species-poor habitats where the biogeochemical processes are controlled by one or two dominant plants with allelopathic property.

The accumulation of large amounts of litter in the northern environment can be explained by the dominant plants adaptation to produce polyphenol-rich litter in a nutrient-stressed environment (del Moral, 1972; Muller et al., 1987), reduced litter decomposition due to poor litter quality, and cool and moist climatic conditions (Facelli, 1988; Facelli and Pickett, 1991; Mallik, 1995). Fire adaptation and antiherbivory can also be considered as reasons for the production of polyphenol-rich litter by the dominant plants in this ecosystem (Rice, 1979; Williamson and Black, 1981; Coley, 1988; Coley et al., 1985). The subtle changes of ecosystem are continually being brought about by the secondary compounds of living and dead remains of the dominant plants and that influence the biotic and abiotic processes of the ecosystem. However, so far, our research efforts in allelopathy have been almost exclusively directed toward the more dramatic effects of plant secondary compounds on the neighboring plants at the individual and population levels. We must focus our attention on the study of a broader landscape-level perspective of ecosystem disturbance and allelopathy. We need to study the combined effects of many subtle physical and biochemical changes involving allelochemicals at a range of temporal and spatial scales.

XII. CONSEQUENCE OF FIRE SUPPRESSION AND CLEARCUTTING

Boreal forests of the northern hemisphere have evolved in the presence of periodic natural disturbances such as fire and insect outbreaks, and coniferous stands in boreal forests owe their origin to these natural disturbances (Attiwill, 1988). It appears that the periodic removal of forest floor humus by wild fires is a precondition for rejuvenating forest communities by creating the necessary conditions for the keystone species regeneration and resetting the secondary succession. The removal of forest floor humus requires hot fire or slow but high-intensity smoldering combustion that can consume the humus along with the underground perennating structures of the ericaceous plants. This ensures the much-needed mineral soil seedbed for successful conifer regeneration as well as the relatively competition-free and allelochemical-free initial stage of progressive secondary succession. The rate and degree of biotic and abiotic changes are dependent on the type of canopy tree, the dominant understory plant, soil type, nutrient, pH, and climatic condition. For example, mild fires or clearcutting or heavy spruce budworm defoliation in nutrient-poor black spruce–Kalmia or balsam fir (Abies balsamea (L.) Mill.–Kalmia forest can convert the forest community into Kalmia heath, and it can last for a very long time. Scattered black spruce establishment may occur over a long period of time (70 to 100 years) in the patchy mineral soil-exposed seedbeds. Layering regeneration of these isolated black spruce may develop into a wood savannah community as observed in some parts of Terra Nova National Park, Newfoundland. If, on the other hand, the understory is predominantly Labrador tea (L. groenlandicum), then the growth inhibition of planted black spruce may last for only 6 to 10 years, and after that black spruce may regain the canopy dominance (Inderjit and Mallik, 1996a). Similarly, the growth inhibition of salal on Sitka spruce or western hemlock may last for 10 to 15 years (depending on the site fertility), and after that the conifers can resume growth and shade out the ericaceous understory.
XIII. A GENERALIZED MODEL OF CONIFER GROWTH INHIBITION

Figure 2 summarizes the dynamics of conifer-ericaceous interactions where competition, allelopathy, and nutrient sequestration all play a role in creating unfavorable conditions for conifer regeneration. The degree and mechanism of conifer growth inhibition often depend on the site type and the ericaceous species involved. For example, natural regeneration failure of Norway spruce in the presence of bilberry (*V. myrtillus*) is mainly due to the germination inhibition of the spruce under a *Vaccinium* canopy (Pellissier, 1993, 1994; Mallik and Pellissier, 2000), whereas black spruce regeneration in the presence of *Kalmia* is caused not so much by germination inhibition but by root growth inhibition, competition, and nutrient deficiency (Mallik, 1987, 1992; Mallik and Newton, 1988). Salal-induced conifer growth inhibition in the west coast of British Columbia is mostly due to competition for nutrients and light and allelopathy seems to play a relatively minor role (Messier and Kimmins, 1990; Messier, 1993; de Montigny, 1992; Prescott and Weetman, 1994; Weetman et al., 1989a,b, 1990; Mallik and Prescott, 2001). The time required for canopy closure after forest harvesting and fire also depends on the site type, climatic conditions, the species of ericaceous plant, and the associated conifer involved. For example, certain nutrient-poor *Kalmia*–black spruce sites in central Newfoundland may require 150 to 200 years to achieve forest canopy closure (some sites may not achieve

![Figure 2](https://example.com/figure2.png)

**FIGURE 2.** Conifer growth inhibition resulting from the combined effects aggressive vegetative regeneration strategies and competitive ability, allelopathy, and nutrient sequestration of the ericaceous plants (Modified from Mallik, 1998 and reproduced with permission from Kluwer Academic Publishers.)
canopy closure at all, instead form open canopy wood savannah vegetation), whereas a poor-quality salal-hemlock site may require less than 50 years to develop canopy closure. In the case of Kalmia-induced regeneration failure of black spruce in Newfoundland, Mallik (1995) suggested that the extent of regeneration failure is determined by the combined effects of many factors, such as climate, soil fertility, vegetation composition, type, frequency and intensity of forest disturbance, and the resiliency to disturbance, regeneration strategies, competitive abilities, and allelopathic property of Kalmia. Similarly, Messier and Kimmens (1991) and Prescott and Weetman (1996) suggested that competition for nutrients and declining site fertility after the assart flush are the major reasons for Sitka spruce, western hemlock, and western red cedar growth check in young plantations with salal. In addition to allelopathy of crowberry (Empetrum hermaphroditum) on Sitka spruce (Zackrission and Nilsson 1992; Nilsson, 1994), Zackrission et al. (1997) demonstrated a three-way interaction between conifers, ericaceous plants, and feather moss in immobilizing nutrients that may cause growth inhibition in conifers in northern Sweden.

XIV. LAND MANAGEMENT IMPLICATIONS

Depending on the land management objective, the resource manager aims to enhance the development of a desirable keystone species at the cost of another. For example, in the case of forest development with ericaceous understory the management objective would be to control the understory plants after harvesting and enhance natural regeneration or growth of planted conifers so that the conifers become the keystone species. However, if the land management objective is to maintain a productive ericaceous heathland for herbivore production, recreation, tourism, and cultural landscape as is the case of heathlands in Britain and Western Europe then the maintenance of ericaceous plants as keystone species is a vital necessity. The value of conservation of a wide range of Calluna heathlands as distinct vegetation types has been recognized by many ecologists in Western Europe (Malmer, 1965; Westhoff 1961; Froment, 1975; Gimingham et al., 1979; Gimingham, 1980, 1981; Gimingham and de Smidt, 1983). Organizations such as the Nature Conservancy Council and the Countryside Commission in Britain have been working toward the protection and maintenance of certain heathlands as natural areas (Gimingham, 1981; Hobbs and Gimingham, 1987). Uniform and productive Calluna has significant economic importance as grazing land for game birds, sheep, and cattle. Landowners in the highlands of Scotland manage Calluna heathlands by regular burning to maintain a healthy red grouse (Lagopus lagopus scoticus L. (Lath.)) population for revenue generation. This is done by prescribed burning heather every 12 to 15 years so that the heathland plants can regenerate rapidly by vegetative means, and the regular burning kills any tree seedling invasion (Gimingham, 1972; Khoon and Gimingham 1984; Mallik and Gimingham, 1985).

The major forest management objective after harvesting boreal and sub-alpine spruce forest is to control the spread of ericaceous plants and enhance natural regeneration or growth of planted conifers so that the conifers remain the keystone species. It is clear that forest harvesting by clearcutting as well as selective cutting enhance ericaceous dominance in the post-harvest habitat if such plants are present in the understorey and they affect forest productivity (de Montigny and Weetman, 1989). Logging in stands that have potential for converting the forest into ericaceous heath should be avoided unless practical methods are in place for (1) controlling the spread of ericaceous plants, and (2) enhancing the regeneration of conifers. In medium- to poor-quality site types infested with Kalmia successful conifer regeneration is not possible without the removal of ericaceous dominance. In nutrient-rich sites, however, healthy growth of conifers may outcompete the ericaceous plants. The reclamation of Calluna heathland for forest regeneration is done by plowing, liming, and repeated fertilization, which reduce Calluna growth and enhance the growth of planted conifers (Gimingham, 1972). However, so far, the success of controlling Kalmia growth in post-harvest/post-burn habitats in eastern Canada has been limited. None of the commonly used silvicultural methods, such as scarification,
ploughing, herbicide treatment, or prescribed burning, proved to be successful (Richardson, 1979; Mallik and Inderjit, 2001). A forest research report from Nova Scotia claimed that glyphosate (Vision) applied at the rate of 1.12 to 3.36 kg a.i./ha provided effective control of *Kalmia* and blueberry (*Vaccinium angustifolium*) in the first and second year after treatment, but the degree of control at the end of the third year was reduced at the lower concentration of the herbicide (Anon., 1988). In a greenhouse experiment Mallik and Inderjit (2001) tested the efficacy of glyphosate (3.36 kg/ha), triclopyre (4 kg/ha), fosamine ammonium (2.5 kg/ha), and hexazinone (2.2 and 5.0 kg/ha) on *Kalmia* control and found that of all the treatments triclopyre was the most effective in controlling the plants by killing its above- and belowground components. A field trial conducted in central Newfoundland in early July and late August with glyphosate and triclopyr (both at the rate of 2.88 kg a.i/ha) with and without Sylgard surfactant (1.5 L/ha) indicated that the August application of glyphosate with Sylgard was able to kill *Kalmia* (Titus and English, 1996). However, because Sylgard had damaging effects on black spruce, this treatment was suggested as a site preparation treatment only and not as a silvicultural conifer release treatment. Glyphosate can have a significant impact on the metabolism of phenolic and other secondary compounds (Duke and Hoagland, 1978; Hoagland et al., 1979; Lydon and Duke, 1988, 1989). More research is needed to study the levels of phenolic compounds in *Kalmia* plants treated with glyphosate. Jobidon (1991) reported that bialaphos, a microbially synthesised herbicide applied at the rate of 1 to 2.5 kg a.i./ha, gave effective control of *Kalmia*. Jobidon and Margolis (1994) reported on the differential tolerance of conifer species to bialaphos showing that August application at or below 2.0 kg ai/ha have no damaging effect on conifers. They suggested that bialaphos has a strong potential as an alternative to chemically synthesized herbicides for vegetation management. Bialaphos, however, is not registered in Canada.

An experiment with transplanted *Kalmia* showed that mulching may be effective in controlling *Kalmia* (Mallik, 1991). However, there are practical limitations in applying mulching treatments for its high costs as well as the challenge of operating mulching equipment in shallow and rocky soils. Nonetheless, it has some potential in creating forest regeneration nuclei among *Kalmia* heath, where all other techniques fail. The application of N, P, and K fertilizers to enhance the growth of black spruce planted in *Kalmia* indicated that most of the added nutrients are absorbed by *Kalmia*, which makes the plant grow even more vigorous with limited benefits to black spruce growth (Mallik, 1996). On the other hand, on a relatively dry jack pine site high doses of N application (672 and 1344 kg/ha) were reported to reduce *Kalmia* abundance and enhance jack pine growth (Prescott et al., 1995).

Preinoculation of black spruce with certain ectomycorrhiza such as *Paxillus involutus* (Bat.:Fr.), *Laccaria laccata* (Scop. : Fr.) Berk. et Br., and E-strain has potential for overcoming the conifer growth inhibition in the presence of *Kalmia* (Mallik et al., 1998). The reason for this growth stimulation in the inoculated seedlings is based on the fact that conifer ectomycorrhizae such as *P. involutus*, *L. laccata*, and *L. bicolour* has been found to degrade *Kalmia* phenolics such as o-hydroxyphenylacetlic, o-coumaric, and ferulic acid and use them as their carbon source (R.-S. Zeng and A.U. Mallik, unpublished). It is important to note, however, that in order to be effective the mycorrhizae of the preinoculated seedlings will have to compete with the existing microbial community of the *Kalmia* rhizosphere. The nutrient loading of conifer seedlings before planting may provide another opportunity to enhance conifer growth in the presence of the ericaceous plants. It is based on the premise that the high nutrient reserve of the nutrient loaded seedlings will have a head-start in the nutrient-limited environment of ericaceous heath (Timmer and Munson, 1991). Field trials with mycorrhiza (*P. involutus*)-inoculated black spruce seedlings in the presence of *Kalmia* are underway.

Bunnell (1990) suggested that prescribed burning immediately after forest harvesting may reduce salal growth and thus would enhance the growth of planted conifers. A field trial with burning and Garlon 4E herbicide treatments was able to reduce salal cover, but the plants gained dominance by vegetative regrowth in the second and
third year (J. Baker, personal communication). Messier and Kimmins (1990, 1992) reported a rapid increase of above- and below-ground biomass of competing vegetation (mainly salal) between 2 and 8 years after clearcutting and slash burning. Planted conifers in these post-disturbed salal dominated habitats experienced growth check with foliar N and P deficiencies. They found the continuous removal of salal for three growing seasons increased the availability of N and P in resin bags. Height growth of planted conifers can be temporarily improved by a single application fertilizer (300 kg/ha N and 100 kg/ha P) but to sustain the sapling growth multiple application of the fertilizer is necessary as observed in Calluna heathland afforestation (Gimingham, 1972). Operational fertilization treatments with N and P (300 and 100 kg/ha, respectively) has been found to significantly increase conifer growth in the order of Sitka spruce > western hemlock > western red cedar in the presence of salal and has been recommended to overcome the conifer growth check (Thompson and Weetman, 1992b; Prescott et al., 1996; Chang et al., 1996a,b, 1999). However, in Ontario herbicide use in forestry has been criticized by the public on the grounds of adverse effects on wildlife and human health (Wagner et al., 1998). In the case of sub-alpine spruce forest in France fertilization and herbicide use for forest management is forbidden on the grounds that villagers in the valley rely on the watershed for their drinking water (F. Pellissier, personal communication).

The above discussion signifies the challenges in controlling the ericaceous plants after forest harvesting and reestablishing the conifer keystone species. More research is needed to understand the vegetation dynamics and soil processes in the presence of ericaceous plants in order to develop ecologically sustainable and environmentally acceptable methods to regain the desirable keystone species.

XV. CONCLUSIONS

Allelopathic phenomenon can be better appreciated at the ecosystem level by taking into account the predominant biotic and abiotic processes influenced by plant litter of keystone species. Disturbance-induced vegetation shift from forest to ericaceous heath with rapid humus accumulation and subsequent habitat degradation can be articulated by linking the concept of keystone species and their role as ecosystem engineers with the concept of alternative stable states of community. The approach is described by using examples of conifer regeneration failure in the presence of ericaceous plants in boreal and sub-alpine temperate forests. The change of keystone species following ecosystem disturbance results from a combined effect of biotic processes such as competition, species regeneration strategies that influence productivity, and litter accumulation, which in turn control the rate and direction of habitat changes and succession. To understand the mechanism(s) of community structuring following disturbance, we must identify the major biotic and abiotic events and their roles in ecosystem function. In most cases a combination of factors working at the ecosystem level can be identified as the cause of such vegetation change. In the present examples these were (1) the absence of high-severity natural fire and limitation of conifer seedbed, (2) rapid vegetative regeneration of understory ericaceous plants after forest canopy disturbance, and (3) habitat degradation by phenolic allelochemicals of ericaceous plants causing allelopathy, soil nutrient imbalance, iron pan formation, and the removal of natural conifer mycorrhizal inocula.

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