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DIRECT AND INDIRECT EFFECTS OF POST-FIRE CONDITIONS ON SUCCESSIONAL PATHWAYS AND ECOLOGICAL PROCESSES IN BLACK SPRUCE-*KALMIA* FORESTS

By

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A thesis submitted to the Department of Biology,
Lakehead University, in partial fulfillment
of the requirements for the degree
of Master of Science

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Abstract

The goal of this thesis was to estimate the relative importance of the mechanisms by which forest stands of east-central Newfoundland are replaced by unproductive dwarf-shrub communities following wildfire. Sheep laurel (*Kalmia angustifolia* L.) is the dominant species of these heath communities and its proliferation after forest fires may initiate a retrogressive pathway rather than forest stand replacement.

This problem is addressed in four chapters that evaluate the roles of differential plant establishment success (Chapters I & II), availability of limiting resources (Chapter III) and the availability of canopy cover (Chapter IV) as factors affecting vegetation dynamics following catastrophic fire. The main findings of the research are (1) that at least part of the inhibition pathway is caused by physical limitations on regeneration niches for black spruce and that the biotic process of competition from *Kalmia* is a less proximate cause of forest regeneration failure; (2) plant functional diversity and black spruce productivity are restricted spatially and physiologically by patterns in fire severity; (3) burned habitats dominated by *Kalmia* have suppressed species richness and functional diversity irrespective of low and high concentrations of limiting resources; (4) failure of black spruce to re-colonize these sites and provide cover to *Kalmia* is associated with measurable reductions in soil microbial activity and herb abundance.

A recurring theme among these chapters is the inconsistency between the pattern of stand retrogression observed in eastern Newfoundland and general theoretical models of succession as they have developed in the ecological literature. As a result of these comparisons, this thesis supports the view that the prevailing models of succession fail to be generalizable across geographic and environmental gradients. In the eastern boreal forest, the factors of fire severity and restriction of regeneration niches for successional species are the critical aspects of disturbance ecology which are not explicitly accounted for in existing successional models. Until general theories account for forces other than competition that potentially affect community structure, a unified theory of plant succession will remain elusive.

Keywords: retrogressive, succession, fire severity, black spruce, *Kalmia angustifolia*, establishment, competition, Newfoundland

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Terra Nova National Park was also a source of great personal enrichment because it is where I met my fiancée, Barbara Bahnmann. Barbara has encouraged me in all aspects of my life. Her expertise as an interpreter and interest in ecology has continually helped me to clarify my work (for both myself and for those with whom I am compelled to share my findings). Her willingness to work 24 hour shifts in the soils lab supplied the data for two of these chapters. A "Thank you" for what you bring to my life falls embarrassingly short.

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General Introduction

The comparative ecology of sheep laurel and black spruce:

This thesis is primarily concerned with the relationship between black spruce (a circumpolar conifer of the Pinaceae) and sheep laurel (a new world dwarf shrub of the Ericaceae). Sheep laurel (*Kalmia angustifolia* var. *angustifolia*, hereafter referred to as *Kalmia*) is a broad-leaved evergreen dwarf shrub found throughout eastern Canada and the northeastern United States (Figure 1). This plant has a wide ecological amplitude with respect to nutrient and moisture requirements and is a major component of both productive forest and treed bog vegetation associations (La Roi, 1967). The westward limits of its dominance are associated with increasing restriction to less productive habitats such as black spruce bogs (Jeglum and He, 1995). This distribution suggests that as alkalinity increases away from the acid oceanic and granitic soils of eastern Canada and toward the clay belt of northern Ontario, *Kalmia* becomes competitively displaced by more productive species. As a consequence, like other members of the Ericaceae, *Kalmia* is most prolific in coastal regions (Mallik, 1995) where cool temperatures and heavy precipitation tend to accelerate podzolization and produce nutrient poor, acid soils (Aber and Melillo, 1991). However, high degrees of variability in soil productivity persist and at the stand level, it remains unclear whether the nutrient-poor soils associated with *Kalmia* are a cause or consequence of its dominance in these sites (Damman, 1971; Inderjit and Mallik, 1999).

Unlike other heath-forming ericaceous plants (such as *Calluna vulgaris* and *Vaccinium angustifolium*), *Kalmia* is of little value as a food source to herbivores due to its stem and foliage toxin content (Jaynes, 1975). Similarly, *Kalmia* does not produce fruits of value to wildlife as do *Vaccinium myrtillus*, *V. myrtilloides* and *Gaultheria shallon* making its net contribution to trophic structure neutral at best. Furthermore, the same chemical compounds which make

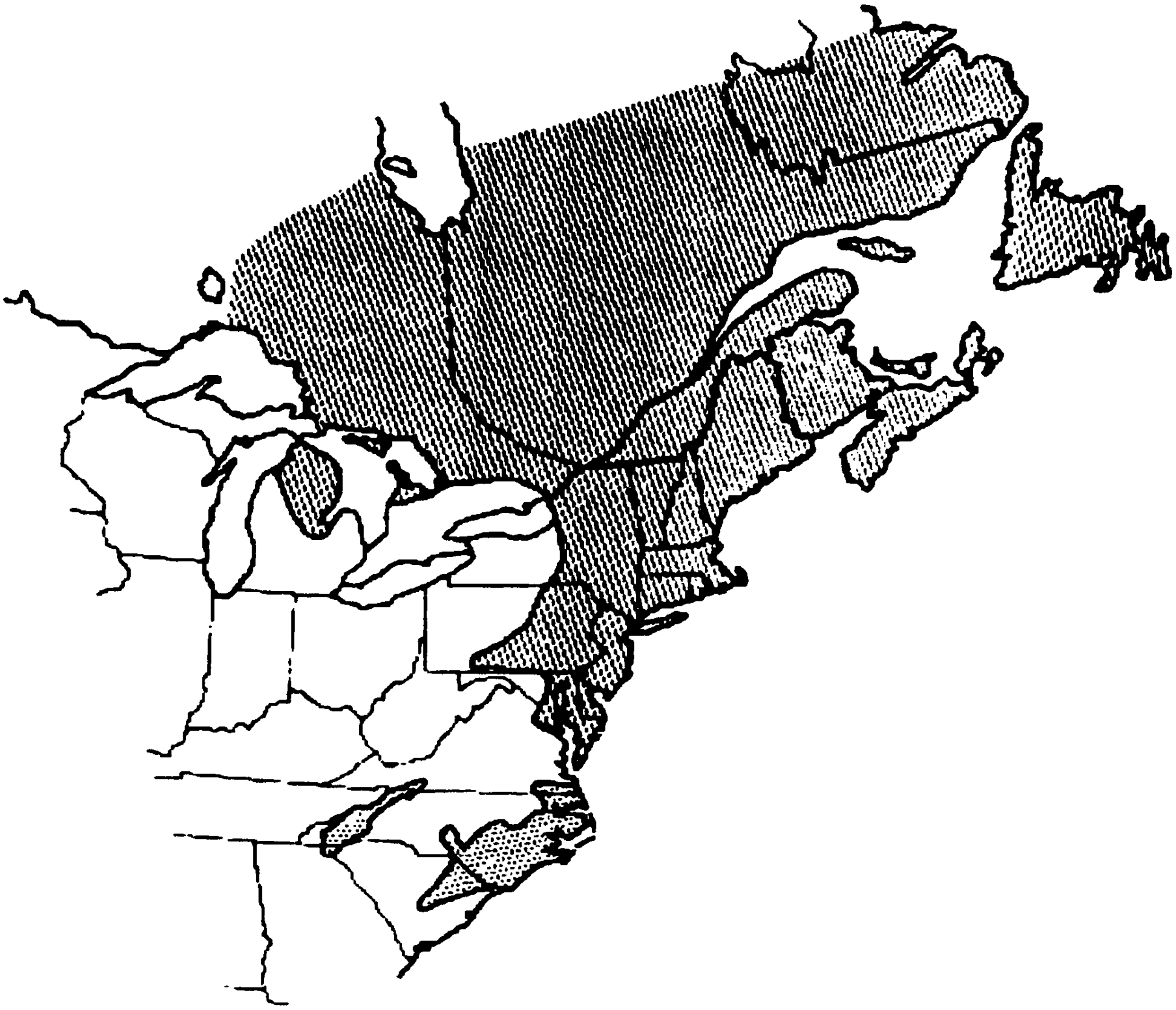

Figure 1. Distribution of *K. angustifolia*. (source: Titus et al. 1995).

leaves unpalatable to herbivores reduce the rate at which leaves can be decomposed and recycled by microbial activity (Hattenschwiler and Vitousek, 2000).

Black spruce is also unpalatable (Arnup *et al.*, 1995) but browsing of very young seedlings has been observed in Newfoundland in peak years of the snowshoe hare (*Lepus americanus*) cycle (L. Hermanutz, pers. comm.). Browsing of black spruce by moose in nitrogen-rich stands dominated by *Alnus rugosa* has also been observed in the region (Richardson, 1979). Such observations indicate that while both species are generally classed as resistant to herbivory, black spruce is less so than *Kalmia*. Furthermore, black spruce seeds are important sources of food for red squirrel (*Tamiasciurus husonicus*) and overwintering songbirds. *Kalmia* offers no such trophic services - - even its nectar is toxic (Jaynes, 1975).

Both black spruce and *Kalmia*'s conservative life history strategy can be described as competitive and stress tolerant (*sensu* Grime, 1979). Like many C-S species, *Kalmia* invests relatively little in reproductive effort and propagates most efficiently by vegetative expansion and resprouting (Mallik, 1993). Black spruce is also capable of vegetative propagation through adventitious rooting of burred lower branches (layering). Unlike *Kalmia*, black spruce appears to be able to use this vegetative strategy only as a mode of maintaining itself in harsh environments (Legere and Payette, 1981) rather than as a strategy for colonization.

Kalmia is an efficient colonizer of canopy-free organic soils but its ability to spread into more dense mineral soils is restricted. Black spruce on the other hand is known to be more successful in regenerating by seed on mineral soils than on thick organic soils which may be predisposed to desiccation (Haavisto *et al.* 1995). Although the dependency of black spruce regeneration on mineral soils in wet, maritime soils may not be as critical as it is in drier regions of the boreal forest, occasional prolonged dry spells in summer may cause seedling mortality.

Successful colonization of *Kalmia* by seed is rarely observed probably due to the lack of vigour and competitive ability conferred to these seedlings by the small seed size (Titus *et al.*, 1995). In comparison to more r-selected species of the regional species pool, such as fire weed (*Epilobium angustifolium*), goldenrod (*Solidago* spp.) and pearly everlasting (*Anaphalis margaritacea*) which specialize on exploiting these mineral soil regeneration niches, *Kalmia* is a poor competitor in its seedling phase (Titus *et al.*, 1995).

Kalmia's root foraging occurs primarily in the O horizon and makes use of mineral soil horizons only in the early stages of establishment on bare mineral soils (Titus *et al.*, 1995). After organic soil accumulates, fine roots growing from secondary and tertiary rhizomes appear to be the primary organs of lateral spread and nutrient uptake (Mallik, 1993). Black spruce shares the lower O horizon rooting niche with *Kalmia* but in well-drained sites will also make use of soil resources in the upper A/Ae horizons (Arnup *et al.*, 1995)

In the established phase, *Kalmia* stem density may exceed 200 stems/m^2 in cutover and burned habitats (Mallik, 1994). As a result of its dominance, many other species are displaced from these habitats. Poor regeneration of black spruce (*Picea mariana* (Mill) B.S.P.) has been a particular economic concern while the regeneration of forest cover in general is a concern for the conservation of landscape-level functional diversity.

The negative relationship between *Kalmia* abundance and conifer regeneration in Atlantic Canada has been studied by several authors (Candy, 1951; Wall, 1977; Richardson, 1979; English and Hackett, 1994; Mallik, 1993, 1994, 2001) but the specific mechanisms driving the relationship have been difficult to isolate. Competition for limiting nutrients (Mallik, 1996) and allelopathic mechanisms (Peterson, 1965; Mallik, 1987) have both been the subject of experimentation but methodological impasses (Weidenhamer *et al.*, 1989) have precluded the determination of the relative importance of these factors. Irrespective of the particular mechanism, disturbed sites dominated by *Kalmia* generally follow a retrogressive successional pathway (whereby standing biomass, species richness and vertical structure decline over time) as opposed to adhering to the classical models of progressive forest succession as described in popular ecological theory (Odum, 1969; Drury and Nisbet, 1973; Bazazz, 1979; Huston and Smith, 1987; Tilman, 1985; Gleeson and Tilman, 1990).

Plant community dynamics: internal and external perspectives

The structure of forest vegetation at any particular point in time is the result of the interactions of biotic forces within communities (such as competition, allelopathy, commensalisms and mutualism) and external forces such as predation, climate and soil quality. At the stand level, abiotic factors are generally homogenous enough to be negligible among similar communities (Krebs, 1985) and the relative importance of biotic factors can be expected to vary according to the stage of stand development. For example, in habitats recently disturbed by fire, competition is reduced and the environment is in some ways harsh for plant growth due to reduced moisture content and increasing temperatures at the surface of the charred soil (Lamont *et al.* 1993; Schupp, 1995). Under such conditions, plant interactions may tend to be commensal since fast growing plants provide shade to germinating seeds of other species (Thomas and Wein, 1984; Callaway and Walker, 1997). In later stages of succession, soil nutrients become more limited as the niche space becomes saturated and plant strategies shift from competing for space to competing for soil resources (Tilman, 1985; Gleeson and Tilman, 1990).

One could argue that since competition and stress tolerance are the ultimate determinants of community dynamics, they are the most important parameters for modeling and predicting community development. This seems to be an implicit assumption among investigations of competition as the primary cause of succession and community structure (e.g. Tilman, 1982; Tilman, 1985; Gleeson and Tilman, 1990; Huston and Smith, 1987). Throughout the 1970's the perspective that members of a plant community were on a trajectory toward dominance of a single superior competitor for limiting resources was the conventional wisdom (Begon *et al.*, 1996). Competition was assumed to be the primary structuring force of communities and the future 'equilibrium' community membership could be predicted from measurements of the competitive abilities of the initial community (i.e. Tilman 1982, 1985, 1994). There are at least two problems with this line of reasoning. First, regeneration patterns of the initial species composition may be governed in part by facilitative interactions. Consequently, ignoring regeneration and dispersal constraints in predictive models based exclusively on competition, will result in poor predictive power (Hacker and Gaines, 1997). Second, general competition theory (Tilman, 1982, 1985, 1994) is based on the principle of rates of withdrawal of limiting nutrients and does not incorporate annual plant inputs which may cause a net increase or decrease in the pool of limiting resources (Berendse, 1994). An intensive review of published papers found that as studies on competition increased in scope from pairs to multi-species assemblages, the number of studies detecting competitive interactions reduced from over 90% to less than 50% (Connell, 1983). Multi-species interactions are complex and there is growing recognition that there are factors other than competition, such as facilitation, that give rise to observed patterns of community structure. Such positive interactions should be parameterized for inclusion in predictive models (Hacker and Gaines, 1997).

Rivaling the conventional wisdom that plant communities are on a trajectory toward domination by a single species which reduces limiting resources to the lowest concentration (Tilman's R* rule, 1982) is a newer model explaining community dynamics as a function of disturbance. Disturbance theory is an extension of competition theory which recognizes that species interaction within communities are rarely in equilibrium and are the result of interspecific interactions since the last disturbance. As with competition theory, disturbance theory, as it has been tested and described to date, is not without its imperfections. Simplifying assumptions have been used to test the 'intermediate disturbance hypothesis' of species diversity (Connell, 1978) in natural communities and these assumptions are rarely tested. In particular, it is often implicitly assumed that the three dimensions of disturbance regimes (frequency, severity and size) are so strongly correlated within disturbance events that frequency alone is a sufficient measure of particular disturbances. The problem was reviewed by Malanson (1984) but examples of this problem continue to be pervasive in the literature. The importance of fire severity (defined here as the degree to which dominance in the community is reduced following disturbance) is of particular concern in boreal forests which accumulate organic matter but is rarely accounted for in tests of disturbance theory which focus on frequency of disturbance as a controlling factor of community composition in these northern forests. Examples include Suffling *et al.* (1988) and Johnson *et al.* (1998).

Reviews of patterns and processes of community assembly (Keddy, 1992; Belyea and Lancaster, 1999) imply that the evolution of a general predictive model of succession will need to combine the paradigms of species interactions and disturbance theory in order to be free of climatic and geographical biases. Progress in predictive ecology could be achieved through a combination of these two central paradigms in ecology. 'Assembly rules' may be a suitable basis for a framework that reconciles these previously segregated perspectives on community development (Keddy, 1992). Keddy (1992) recognized that assembly theory could be expanded to predict plant community assembly on the basis of such environmental filters on regeneration. Disturbance-induced environmental filters such seedbed quality (affected by fire severity) and dispersal limitations (affected by the size of the disturbance) could be quantified and used to more accurately describe the external processes of community assembly before using competitive ability of the local successional candidates to predict successional outcomes.

Phytogeographic setting and scope of the study:

The sampling for this study was concentrated on the greater Terra Nova ecosystem (GTNE) which is located in the east-central boreal forest eco-region of Newfoundland (Power, 2000). The dominance of black spruce stands on well drained soils across the landscape indicates that canopy species diversity is low. This low diversity translates into a single dominant stand type in the region which supports an important assumption made in the study: that independent stands burned at different times have floristic and soil properties that arise primarily due to differences between sites caused by their age rather than other sources of variability (such as site-specific differences in soil quality, nutrient status and pre-disturbance vegetation). This assumption has been widely applied to successional studies which have used such ‘chronosequence’ approaches (Brown, 1992). However critics have argued that succession on any particular site is based on unique circumstances and the assumption that a single climax community exists is unrealistic (Gleason, 1927). However, such criticisms have been borne out of old field studies in which chance establishment of a wide variety of tree species is a factor. I employed the chronosequence approach in this study because the phytosociological system is much simpler and the complications arising from species other than black spruce dominating these habitats was very unlikely.

In spite of limitations to soil fertility and the isolation of Newfoundland from the continental boreal forest, the regional pool of dominant species is similar to the mainland boreal forest of Canada and includes *Picea mariana*, *Abies balsamea* (L.) Mill., and, on the richer sites: *Betula papyrifera* Marsh. and *Populus tremuloides* Michx. These stand types occupy 52, 14 and 3% of the forest cover respectively (Power, 2000). Stand types in the region are predominantly black spruce-feathermoss communities with understories dominated by *Kalmia* and to a lesser extent *Rhododendron canadense* (L.) Torr. and *Vaccinium angustifolium* Aiton. (Day, 1982; Damman, 1971). These forests have been deemed unstable in relation to wildfire disturbances since regeneration of tree species is minimal when *Kalmia* is locally dominant (Damman, 1971; Meades, 1983; Mallik, 1994).

Objectives

The purpose of this thesis was to determine the following: (1) how the occurrence of large-scale fire affects site diversity of plant species, (2) to measure the top-down effects of the various dominant species on nutrient status and species richness following disturbance, (3) to test whether successional pathways could be predicted by degree of fire severity (defined as the amount of reduction of dominance of the pre-fire stand conditions) and (4) whether different successional pathways would cause measurable differences in community structure and function.

In response to these objectives, the first chapter of this thesis discusses regional-level species composition in pyrogenic *Kalmia* heath stands ranging from 1 to 73 years since fire. These findings indicated that the initial floristic composition (Egler, 1954) of the heath controls the post-fire successional pathway. Consequently, the remaining chapters investigate the first 38 years of post fire succession in detail. Selected sites were aged 1 to 38 years since fire (Figure 2) and were all burned by fires which were artificially suppressed (D. Hewitt, personal communication).

Due to the small sample size and geographic concentration of data in the GTNE, interpretation of the data is conservative and the statistical methods are primarily correlative. However, the widespread occurrence of *Kalmia* in eastern Canada and the dominance of coastal areas by other ericaceous plants throughout the world suggests that implications for the research may extend beyond the area of study

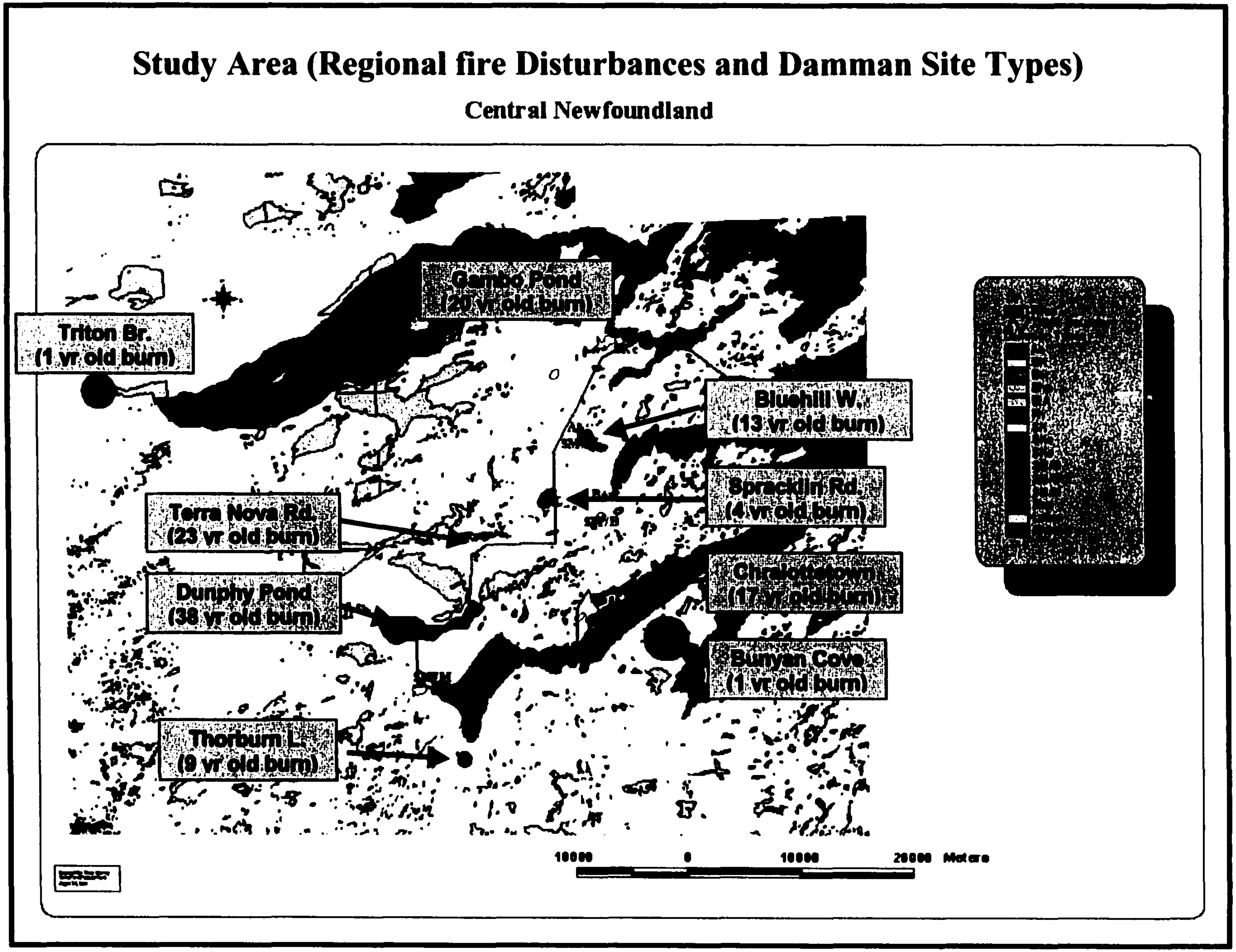

Figure 2. Distribution of study sites in and around Terra Nova National Park.

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Chapter I.

Post-fire dynamics of dominant species in coastal boreal forests: patterns and processes.

Abstract

Fire has been cited as a de-stabilizing disturbance of forest structure and species composition in the Atlantic coastal boreal forest. Using a chronosequence, I collected species cover data from twenty stands aged 1 to 73 years in Newfoundland, Canada with the objective of modeling changes in dominance of the locally important species in progressively older stands. Black spruce (*Picea mariana*, Mill. Pinaceae) cover, seedling recruitment and vegetative expansion data were used to determine the hierarchy of causes that destabilize the community structure and composition in black spruce sites with understories dominated by *Kalmia angustifolia* L. (Ericaceae).

Ordination scores describing unimodal patterns of species cover were significantly related to burn age ($r = 0.94$) and were modeled over time. There was an inverse relationship between the cornerstone species (*Picea mariana* and *Kalmia*) which were further studied since their impacts as dominant species influence community structure and stand biogeochemistry.

Results of experimental seeding showed that mineral soil seedbeds were favourable for *P. mariana* germination. However, the post-fire seedbed surface is dominated by scorched pleurocarpous moss and *Kalmia* organic matter which is unsupportive of germination. Seedbed conditions for black spruce did not improve with time since fire over this 38 year chronosequence. Our findings indicate that layering is the primary mode of propagation in absence of sexual reproduction but that without sufficient establishment conditions for individual trees, layering cannot achieve forest canopy closure. Consequently, our chronosequence model of progressive black spruce regeneration over time was not supported by observed regeneration conditions. An alternative hypothesis of historical variability in fire severity is discussed in relation to past and present climax community structure.

Keywords: chronosequence, retrogression, seedbed filters, regeneration niche

Introduction

In spite of the general acceptance of secondary succession being a progressive process driven by the abilities of plants to exploit environmental resources and create structure in vegetaton as nutrients accumulate in biomass (Clements, 1916; Odum, 1969; Whittaker, 1970;), there are important exceptional cases in which secondary succession leads to reduced standing biomass and structural diversity (Cowles, 1911; Watt, 1931; Woodwell, 1970; Rapport *et al.*, 1985; Pickett *et al.* 1987a). These phenomena are inconsistent with competition-based models of succession (*sensu* Tilman, 1985; Huston and Smith, 1987) and represent an autogenic pathway which frequently degrades site productivity in Europe and North America. Examples include the Atlantic coastal boreal forest (Damman, 1971), Pacific Northwest coastal hemlock forests (de Montigny and Weetman, 1990) and forests in the coastal United States (Latham *et al.* 1996).

Retrogressive succession is typically placed in a class separate from general successional theory since the cause is often a chronic anthropogenic induction of stress on the community (Pickett *et al.* 1987a; Kimmins, 1997). Under such conditions, the inapplicability of competition mechanisms to these cases is considered trivial because the operation of assembly rules (*sensu* Diamond, 1975; Keddy, 1992) expected to govern community development are artificially pre-empted. The implicit reason for this seems to be that such high levels of stress, usually in the form of air borne pollutants (Pickett *et al.* 1987a), are beyond the evolutionary experience of these systems. Consequently, 'normal' patterns of vegetation dynamics should not necessarily prevail when the ecological context of these communities is changed swiftly and dramatically. The qualification of 'normal' patterns of ecosystem development (*sensu* Odum, 1969; Whittaker, 1970) with the presence or absence of potentially de-stabilizing external constraints, such as stress (Gray, 1989) and seedbed filters (Keddy, 1992, Grime, 1998, Xiong and Nilsson, 1999), is a matter of increasing interest in the ecological literature (Belyea and Lancaster, 1999).

Biotic processes causing succession

In progressive succession, competitive selection in successional habitats is a force that counters the occurrence of retrogression among communities. At the stand level, competitive selection forces plants to adopt one of two strategies: persist in the local assemblage by acquiring resources faster and/or growing larger than competitors (Tilman, 1985) or persist by reducing direct competition by niche separation/resource compartmentalization (Hardin, 1960; Diamond, 1975; Wisheu and Keddy, 1992). The evolution and operation of these mechanisms prevents the initiation of a retrogressive pathway in natural systems since it is generally assumed that slow-growing, less productive plants are at risk of competitive displacement by faster-growing or larger invaders (Hardin, 1960; Odum, 1969; Tilman, 1985). In general, if principles of niche saturation and competitive selection are universal in natural systems, retrogression should not occur since members of a given community should be able to exploit much of the available resources and convert them to standing biomass at rates limited extrinsically by climate and growing conditions (Whittaker, 1970). Consequently, it is widely accepted that succession is a process whereby species with high maximal growth rates are replaced by larger, slower growing plants as resource pools are diminished (Odum, 1969; Whittaker, 1978; Drury and Nisbet, 1973; Bazazz, 1979; Pickett *et al.* 1987b; Brown, 1992; Huston and Smith, 1987).

While several reviews have described the sequence/hierarchy of processes that lead to plant community establishment (see Collins and Glenn, 1991; Pickett *et al.* 1987b), empirical studies of successional mechanisms have focused on biotic interactions as causes of species composition and successional species replacement. Community richness, and therefore composition, of a recently disturbed site is the result of dispersal of plants from the regional pool countered by "scramble" competition from other invading plants (Collins and Glenn, 1991). This theoretical approach is attributed to the classic work of Clements (1916) and Gleason (1926) and seems to have developed into an implicit assumption in many contemporary studies. For example, recent approaches have been taken to assess the mechanisms of species replacement that drive the process of succession. Of these, the most influential studies (e.g. Tilman, 1985; Grime *et al.*, 1997) are often studied in experimental systems of plants in the "established" phase of their life cycles. Both natural (Tilman, 1985) and artificial systems (Grime *et al.*, 1997) have been manipulated to document the role of interspecific competition and plant fitness in controlling community composition. Such approaches allow detailed evaluation of resource-based theories of succession (Tilman, 1985) and plant strategy/trait based theories of community assembly (Grime, 1979; Keddy, 1992). This mechanistic paradigm has resulted in a focus on "the intervals between disturbances rather than on the disturbances themselves" (Huston and Smith, 1987, p. 168). While these studies provide insight into detailed mechanisms of succession in established communities, they risk overlooking more fundamental processes of colonization and establishment limitation which also structure communities (Grubb, 1977; Harper, 1977; Facelli and Pickett, 1991). Consequently, the role of variability in disturbances and the types of habitats and seedbeds they create is under studied (Xiong and Nilsson, 1999). The evidence that physical conditions may pre-empt the influence of competition during succession has been anecdotal (Grime, 1998) but should be carefully and explicitly considered prior to singularly attributing community structure to biotic causes such as facilitation and competition.

This chapter describes post-fire succession in the coastal boreal forests in eastern Canada. Previous authors (Damman, 1971; Richardson, 1973; Meades, 1983; Mallik, 1994) have described fire as an agent of retrogression in this region since it frequently leads to the destruction of mature forest stands and the creation of unproductive heath barrens dominated by *Kalmia* in sites formerly supporting conifer forests. Despite the acceptance of this retrogressive phenomenon, no study has yet modeled the successional sequence or predicted the probability of forest regeneration under the contemporary fire regime. This study was designed (1) to model the post-fire behaviour of the dominant plants and (2) to determine the potential for site recovery to a closed canopy state based on seed and vegetative regeneration behaviour of plants.

Methods

I used a chronosequence approach to studying post-fire succession (Pickett, Brown, 1992) and made the assumption that the vegetation of spatially independent, well-drained black spruce-*Kalmia* stands disturbed by fire at various times in the past represent snapshots of succession as it progresses in a single site. Study sites ranged in age from 1 to 76 years since fire. Stands were selected on the basis of knowledge of burn age, presence of *Kalmia* and accessibility. Soil profiles were examined to ensure that all sites were characterized by similar podzolic sandy-loam mineral soils. Sampling on slopes greater than 10% was avoided. Edges of historic fire boundaries were also avoided since these interfaces may act as ecotones between the intact forest and successional habitat. Within these constraints on randomization, sampling units were distributed randomly. Sites ranged in age from 1 to 80 years since fire as determined from fire records or on-site tree-coring of mature stands.

The hierarchical research process used in this study required three distinct data sets spanning from the ecological scales of individual black spruce recruitment and growth to the multi-species scales of the greater plant community. This data included: 1) plant community cover from stands of various ages, 2) black spruce seedling establishment rates from stands of various ages and 3) rates of black spruce cover expansion via vegetative propagation. Plant community and habitat data (including species cover, species composition, organic matter depth and non-destructive estimates of biomass of community dominants) were used to evaluate the relative importance of time since fire as a factor affecting community structure and to estimate community dynamics over time. Black spruce reproductive data were used as an empirical indication of whether the forest regeneration pattern can be explained on the basis of a reproductive mechanism. Black spruce is also capable of layering as a mechanism of persistence in undisturbed habitats. The latter mode of persistence was described to estimate the potential for spruce regeneration in absence of successful seedling recruitment.

Collection and analysis of community data

In the summers of 1988 and 1999, twenty burned sites were sampled using 10 randomly placed 1 x 1m quadrats. Preliminary assessments of intra site species-area curves from 4 sites of different ages revealed that all of the dominant species and most subordinate plants were captured in a total area of 10 m^2 (Bloom and Mallik, unpublished data). This finding reflects the extremely homogenous and species-poor nature of *Kalmia* heaths.

Percent cover of all species was recorded and organic matter depth was measured at each corner of the quadrats. Sampling sites were restricted to moderate and well-drained sites with at least A-horizon mineral soil development. Sampling areas had uniform slope, aspect and soil development such that it was assumed that time since fire was a greater factor in structuring species composition and abundance than other between or within site sources of variability (Brown, 1992).

In order to quantify the relationship of the variability between sampling units and time since fire, species percent cover data was analysed in a species x plot matrix using Canonical Correspondence Analysis using PC-Ord (McCune and Mefford, 1997). Species with fewer than 5% frequency of occurrence in the 200 quadrats were removed from the analysis to reduce the influence of outliers (Gauch, 1982). The resulting ordination scores were averaged for each site and regressed against time since fire using least squares regression (SPSS, 1998). This preliminary analysis was used to test the hypothesis that between-site variability attributable to time was greater than within-site variability as a test for the validity of the chronosequence assumption. Subsequently, univariate curvilinear regressions were used to model the functional responses of species cover (averaged by site) against time since fire. Habitat parameters of organic matter depth, species richness, stem height, density and vigour (ratio of dead to live stems) of *Kalmia* were measured in 110 plots surveyed in 1988. These parameters were used simultaneously with the cover data in the CCA to explore relationships between successional trends and changes in the abiotic and biotic habitat. Unconstrained CCA was used and the analysis correlated habitat variables with axes of variability after the fact (McCune and Mefford, 1997).

Seedling regeneration

Nine of the 20 sites aged 1,1, 4, 9, 13, 17, 20, 22 and 38 years since burning were used to investigate seedbed quality for black spruce seedling establishment in the area of Terra Nova National Park, Newfoundland. Although this time span is relatively short in comparison to the length of the fire cycle described by Power (2000) to be approximately 150 years, it was believed to be sufficient to predict the future state of the stands since previous studies suggested that forest re-establishment was critically dependent on immediate regeneration when a seed source was still present in the cones of scorched trees (Day, 1982). After this point re-invasion of large burned areas by black spruce is seed-limited since its average dispersal range is 40 - 80 m (Sims *et al.*, 1990). Meades (1983) found that when black spruce seed sources within dispersal range were destroyed by fire, the resulting climax stand type became *Kalmia-Cladina* lichen. This climax community is represented in the present study by sites aged 20 –38 years since fire. This study implicitly tests the hypothesis that after a brief 4-9 year window of opportunity for black spruce establishment (Foster, 1985; Thomas and Wein, 1984) site invasion by tree species would depend on long-distance dispersal into sites which were increasingly resistant to seedling invasion with age (Day, 1982).

Due to practical restrictions imposed on the distribution of sites, only the one year old stands could be replicated since these were the only two sites with origins in the same fire year in the known fire history of the study area that were near enough for efficient monitoring. Each stand in the chronosequence was sampled using three 20 x 10 m plots. Plots were semi-randomly established in each site so that the predominant vegetation and ground cover patterns were represented. Within each plot, six permanent 30 x 30 cm seeding quadrats were established. Three quadrats were established in unshaded "safe sites" (Harper, 1977) in the vegetation and three were established under canopy of *Kalmia* dominated heath vegetation. A total of 162 plots were established. Seven were trampled by moose (Alces alces) which caused a reduction in the number of usable plots to 155.

All sites were within 100 km of each other near Terra Nova National Park, Newfoundland and were assumed to have experienced the same general weather conditions over the course of the year. The distribution within the landscape of the sites used was such that similarly aged stands were not closer than 40 km apart. This broad spatial distribution reduces the potential for spatial autocorrelation as a confounding factor in the comparisons of recruitment results of independent, similarly aged sites.

Ground cover was described and classified into one of seven substrate types which reflect the available seedbeds at various stages of succession: exposed mineral soil, charred duff, mixed pleuro/acrocarpous mosses, ericaceous leaf litter, crustose lichen, *Cladonia spp.* (club lichen), and *Cladina spp.* (shrub lichen). Thirty seeds of local seed stock (98% viable) were randomly scattered within each quadrat in early July, 1999. Plots were monitored for germination after six and fourteen weeks and establishment success at the end of the second growing season (August, 2000). No unseeded control plots were used since the objective of this component of the study was to test for the random effect of substrate type on germination and establishment of black spruce. In theory, control plots would be useful for obtaining an estimate of natural seed dispersal and establishment to the plots. However, due to a lack of natural black spruce seed sources within dispersal range (~ 100 m) the use of unseeded plots to test for dispersal limitation was unnecessary.

Statistical analysis

Germination and establishment data were correlated with percent ericaceous canopy cover and were also averaged by substrate type in independent analyses. The test for the effect of canopy cover was analyzed in using a two-tailed test of Spearman's rho. The test for the random effect of substrate type was not balanced but each substrate type was replicated by chance at least eleven times. Replication and sample sizes for this analysis are summarized in Table 5. Data did not meet the requirements of homogeneity of variance needed to analyse the results using analysis of variance. The Kruskal-Wallis non-parametric test was used instead to analyze these data in relation to seedbed classes. *Post-hoc* Mann-Whitney U tests were used to locate significant differences between substrate types detected by the Kruskal-Wallis analysis. Since there was a total of seven substrate types yielding 21 *post-hoc* comparisons, the critical P value was adjusted with a sequential Bonferroni procedure to control for the inflated experiment-wise error rate (Sokal and Rohlf, 1995).

Vegetative expansion

Black spruce frequently exhibits layering behaviour under nutritional stress (Black and Bliss, 1978). Field observations suggested that black spruce canopy expansion was an important mechanism of regeneration. Forty trees aged 10 to 120 years were examined in an uneven-aged, well-drained stand representative of black spruce-*Kalmia* forest. Trees were aged by counting rings at the root collar or from increment core samples when root collars were inaccessible. Black spruce expansion was quantified by measuring the surface area enclosed by layered stems and regressing this measurement against tree age. The resulting linear model was used as an estimate of the rate of horizontal expansion.

Results

Multivariate analyses of habitat variables and species cover

Ericaceous plants dominated burned landscapes across the chronosequence. Of these dominant plants, *Kalmia* is by far the most prolific, having the highest cover and importance values of any species across the chronosequence (Table 1). Importance values of non-ericaceous plants are low indicating that most species are either rare or comprise little cover (Table 1). Pearson correlation of mean axis scores for each site and time since fire (n=20) showed a strong and highly significant relationship (r = 0.94, p = 0.01) and the hypothesis that the primary ordination axis represented a chronosequence was accepted. This relationship indicates that species abundances following disturbance are strongly unimodal since the CCA algorithm is based on Gaussian responses of species to primary gradients in the data.

CCA extracted three axes which respectively explained more variability than was expected by chance (Table 2). The analysis explained a total of 21.2% of the variability in species (Table 2). Correlation coefficients for all habitat variables in relation to the CCA axes are summarized in Table 3. The first axis was strongly inversely related to the descriptive variables of stand age (r = -0.85) and tree cover (r = - 0.82) and was moderately related to *Kalmia* height (r = - 0.40) and species diversity (r = - 0.37). The second axis was weakly correlated with total shrub cover.

Scatter plots of habitat variables against time since fire for each stand (Figure 1) revealed that responses of two habitat variables were non linear and show distinct unimodal tendencies for species richness (Figure 1 A) and ericaceous stem vigour (Figure 1 B). Ericaceous stem density declined monotonically (Figure 1 C) and ericaceous height tended to increase monotonically with time since fire (Figure 1 D).

Table 1. Percent cover and frequency of occurrence of species used in the CCA species community analysis following removal of species with < 5% frequency.

Species	Average % cover	Min. % cover	Max. % cover	Frequency of occurrence (*f*)	Importance index (average cover x *f*)
Trees					
Picea mariana	18	0	100	0.46	8.28
Shrubs					
Kalmia angustifolia	49	0	95	0.99	48.08
Vaccinium angustifolium	9	0	50	0.88	7.87
Rhododendron canadense	5	0	35	0.35	1.61
Ledum groenlandicum	1	0	30	0.19	0.22
Prunus pensylvanica	0.2	0	12	0.06	0.01
Herbs					
Cornus canadensis	7	0	80	0.54	3.67
Carex spp.	0.4	0	25	0.05	0.02
Linnaea borealis	0.5	0	15	0.10	0.05
Gaultheria hispidula	0.4	0	20	0.06	0.03
Bryophytes					
Pleurozium schreberi	16	0	100	0.51	8.32
Hylocomnium splendens	2	0	60	0.12	0.23
Ptillium crista-castrensis	3	0	80	0.16	0.54
Sphagnum spp.	1	0	25	0.06	0.04
Polytrichum juniperinum	3	0	60	0.25	0.65
Dicranum spp.	5	0	40	0.62	3.05
Lichens					
Cladonia spp.	4	0	75	0.50	1.86
Cladina spp.	9	0	95	0.52	1.86
Nephroma arcticum	0.1	0	2	0.06	<0.01
Stereoclaulon paschale	1	0	20	0.17	0.17
Hypogymnia physoides	1	0	10	0.54	0.57

Table 2. Eigenvalues and percent variance explained by the first two axes extracted by CCA, $n = 200$. Correlation co-efficients show the degree of relationship between each axis and the linear combination of habitat variables.

	Axis 1	Axis 2	Axis 3
Eigenvalue	.39	.10	.06
Variance in species data			
% of variance explained	15.1	3.8	2.2
Cumulative % explained	15.1	19.0	21.2
Pearson axis-habitat variable			
Correlations	.91	.60	.64

Table 3. Pearson correlations between habitat variables and axes extracted by CCA.

Variable	Axis 1	Axis 2	Axis 3
Time since fire	-.85	-.14	.00
Organic matter depth	-.16	-.24	-.18
Species richness	-.14	-.23	.15
Species diversity	-.37	-.09	.39
Total ericaceous stem density	.11	.20	-.20
Average ericaceous stem height	-.40	.22	-.57
Ratio of dead:live ericaceous stems	-.19	-.07	-.07
Total tree cover	-.82	.17	-.05
Total shrub cover	.17	.30	-.16

Table 4. Summary of relationships between the time since fire and species cover used in the analysis. The best measure of model fit is presented for each species as a description of the relationships irrespective of *p* values.

Species	R^2	*p*
Trees		
Picea mariana	0.862 (cubic)*	<0.001
Shrubs		
Prunus pensylvanica	.220 (linear)*	0.037
Kalmia angustifolia	0.893 (cubic)*	<0.001
Vaccinium angustifolium	0.560 (cubic)*	0.004
Rhododendron canadense	0.721 (cubic)*	<0.001
Ledum groenlandicum	0.497 (cubic)*	0.010
Herbs		
Cornus canadensis	0.394 (cubic)*	0.041
Gaultheria hispidula	0.365 (quadratic)*	0.021
Linnaea borealis	0.428 (cubic)*	0.027
Carex spp.	0.335 (cubic)	0.081
Mosses		
Pleurozium schreberi	0.773 (cubic)*	<0.001
Hylocomnium splendens	0.597 (cubic)*	0.002
Ptillium crista-cristensis	(quadratic)	<0.001
Polytrichum commune	0.452 (cubic)*	0.019
Dicranum sp.	0.704 (quadratic)*	<0.001
Sphagnum sp.		
Polytrichum juniperinum	0.352 (cubic)	0.091
Lichens		
Cladonia spp.	0.358 (quadratic)*	0.023
Cladina spp.	0.492 (cubic)*	0.011
Thyloid spp.	0.192 (linear)	0.163
Sereocaulon paschale	0.141 (linear)	0.274
Hyogymnia physodes	0.708 (cubic)*	<0.001

* indicates significant correlations at $\alpha = 0.05$.

Organic soil depth did not vary linearly (Figure 1 E) or curvilinearly over time ($r = 0.21$, $n=20$, $p = \text{n.s.}$, $\alpha = 0.05$) nor did it appear to be related to variability in the species data vai correlations with CCA axis (Table 3).

Univariate analyses of floristic dynamics over time

The results of curvilinear regression models used to fit species cover with time since fire are summarized in Table 4. Seventeen of the 21 species demonstrated significant relationships. The trends for significantly related species are presented graphically in Figures 2 and 3. Species were aggregated into growth form classes of dominant species (trees and shrubs) (Figure 2 A), herbs (Figure 2 B), bryophytes (Figure 3A) and lichens (Figure 3B) to simplify the representation of community dynamics over time.

Black spruce seed germination and seedling establishment

Analysis of experimental seeding of black spruce showed that mineral soil microsites have the highest probability of supporting seed germination and seedling establishment followed by mossy substrates which occupy mineral soil microsites 4-20 years after fire (Figure 4). Mineral soil seedbeds had higher germination and establishment rates (8% and 5% respectively) than any other substrate (Table 5). In total 42 % of germination and 63% of total seedling establishment occurred in severely burned, mineral soil microsites. Germination and establishment decline when algal crust, lichen and moss cryptogam associations of later successional stages are dominant (Figure 4).

The relative proportion of area occupied by these substrate types summarized from the quadrat data indicates that the best seedbeds (mineral soil and mosses) each occupy only ~ 10%

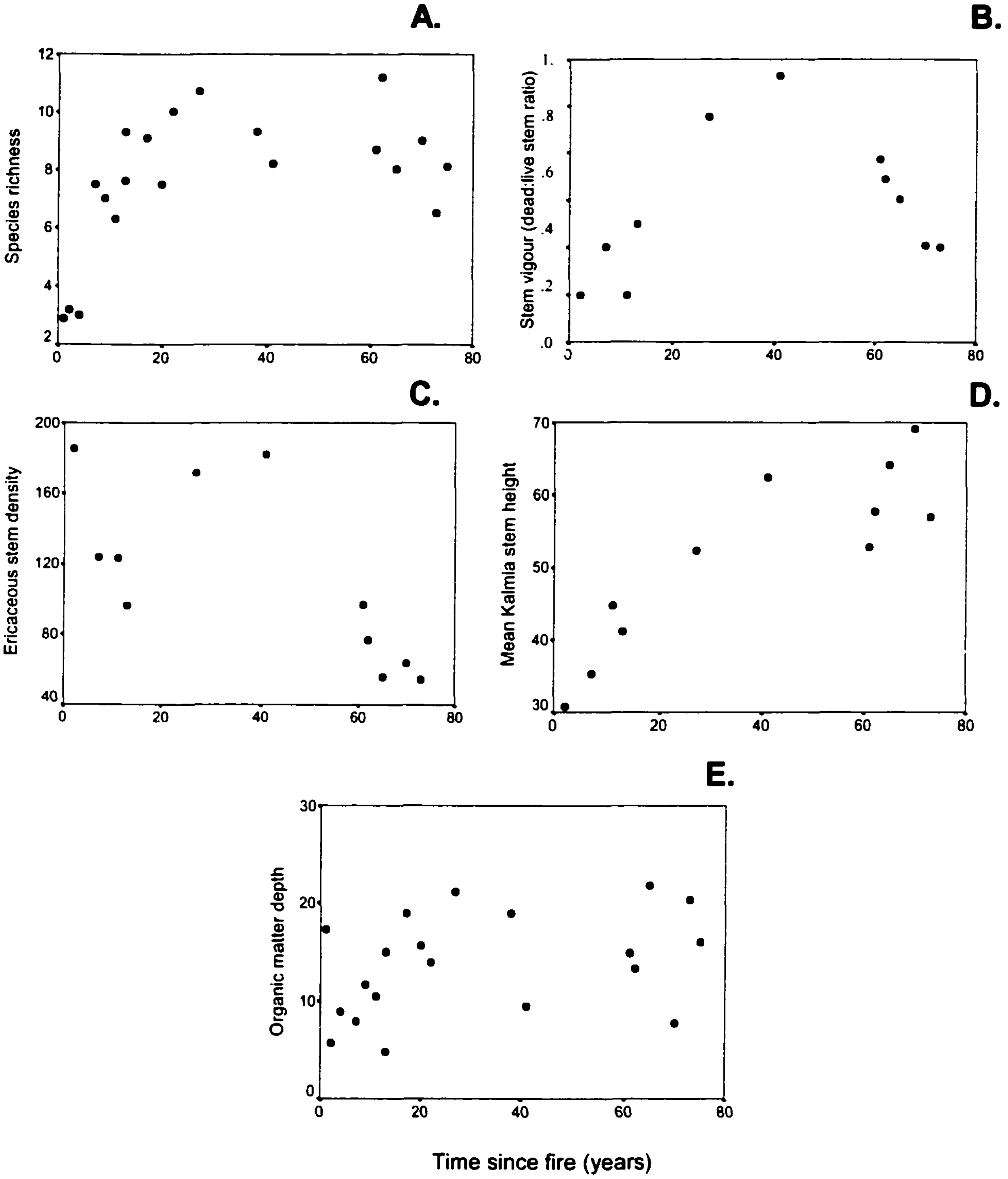

Figure 1. Scatter plots of *Kalmia* habitat parameters against time since fire of burned stands. Species richness was more strongly correlated with time using a cubic function (r = 0.38, n = 200) than a linear model, although the change over time appears to be subtle (A). The ratio of dead: live *Kalmia* stems as an index of vigour was strongly unimodal r = 0.40, n = 110 (B). Total ericaceous stem density also follows a unimodal pattern (r = 0.57, n = 110) (C). Increasing stand age is strongly associated with an increase in *Kalmia* height (r = 0.69, n = 110) (D.) Modeling of organic matter depth with both linear and non-linear models yielded weak correlations with time since fire (r = 0.26, n = 200) (E).

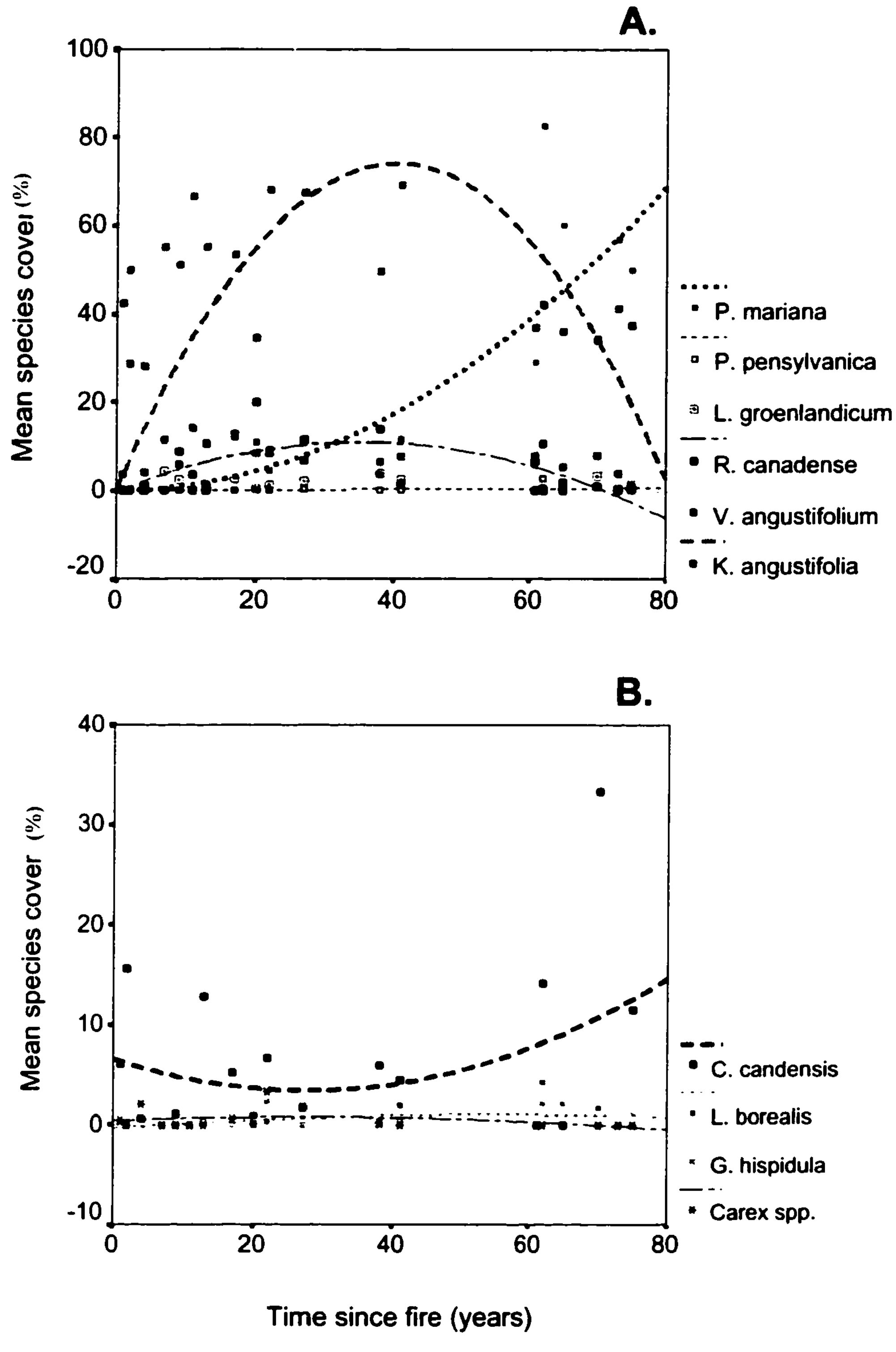

Figure 2. Mean cover of dominant plants and subordinant vascular plants in each stand plotted against time since fire. *Kalmia* is clearly the dominant plant until approximately 40 years. *P. mariana* (black spruce) has low initial cover in recently burned stands in comparison to older mature forests (A). Dynamics of subordinant plants over time show the herb guild at low proportions of cover throughout the chronosequence although *Cornus canadensis* cover shows a tendency to increase after 40 years (B). Other plants have less than 5% average cover.

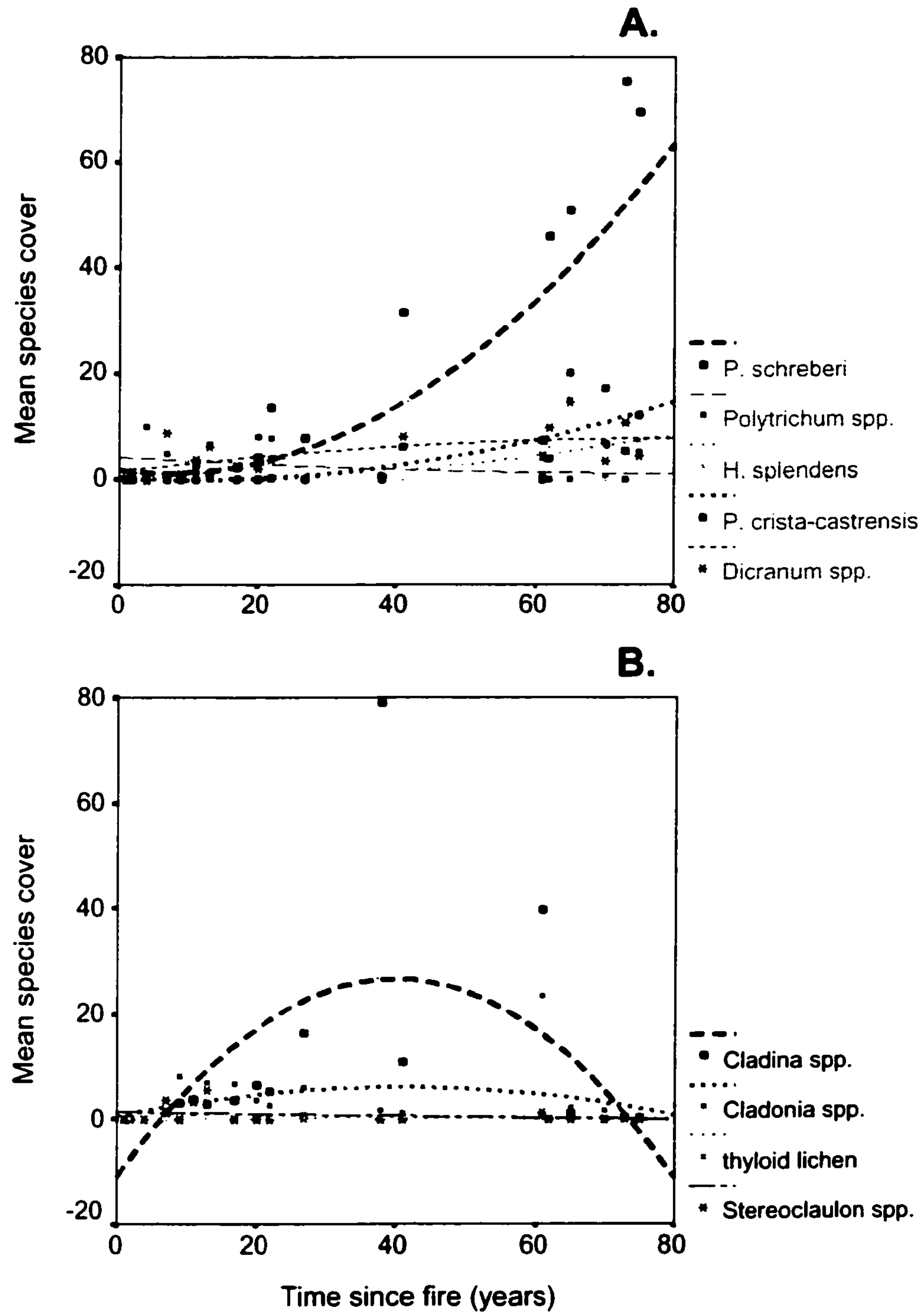

Figure 3. Trends in soil surface dominance plotted against time since fire. Cover of pleurocarpous mosses (*P. schreberi, H. splendens and P. crista-castrensis*) increase in successively older stands (A). Acrocarpous mosses (*Polytrichum spp.* and *Dicranum spp.*) have low abundance irrespective of time since fire (A). Lichens are represented across the chronosequence but shrub lichens (*Cladina spp.*) show the greatest abundance ranging from 15 to 80 % cover between 20 and 40 years since fire (B).

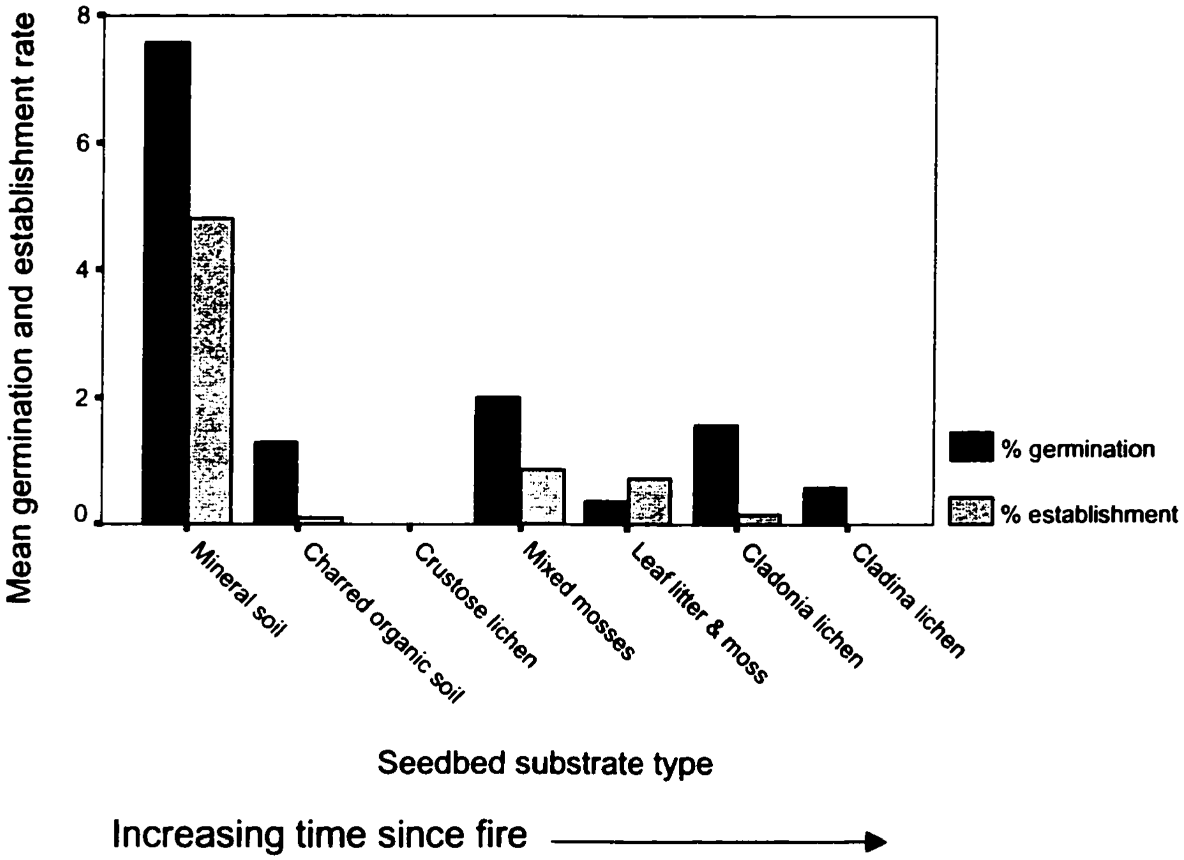

Figure 4. Black spruce seed germination and seedling establishment in various seedbeds from 1 to 38 years after fire. Changes in seedbed types are reflective of the soil surface succession described in the text.

Table 5. Results of Mann-Whitney U tests for seedbed effects on germination. Significant differences are indicated by bolded p values. Tests marked with asterisks were self-evident since no seedling establishment was observed in one of the seedbeds pairs rendering *p* values trivial.

Post-hoc comparisons of germination	Post-hoc tests for differences in establishment						
	Mineral soil (*n*=18)	Charred organic soil (*n*=28)	Litter& moss (*n*=9)	Crustose lichen (*n*=11)	Mosses (*n*=38)	*Cladonia* lichen (*n*=40)	*Cladina* lichen (*n*=11)
Mineral soil (*n*=18)	-	U= 131 **p< 0.001**	U= 92.5 **p= .002**	U= 40.5 **p=0.007***	U=181.5 **p= 0.004***	U= 194.5 **p < 0.001**	U= 47.5 **p=.007***
Charred organic soil (*n*=28)	U= 105 **p < 0.001**	-	U= 261 p=0.757	U=121.5 p = .571	U=408 p = 0.13	U= 566.5 p = 0.795	U= 148.5 p=0.531
Leaf litter & Moss(*n*=9)	U= 51 **p < 0.001**	U=221.5 p=0.119	-	U=99 p = 0.447	U=234 p = 0.231	U= 378 p = 0.932	U=99 p = 0.447
Crustose lichen (*n*=11)	U= 22.5 **p < 0.001**	U=99 p = 0.136	U= 99 p = 0.447	-	U= 126.5 p = 0.139	U=209 p = 0.454	U=60.5 p = 1.00
Mosses (*n*=38)	U= 136 **p < 0.001**	U= 436.5 p= 0.625	U= 192.5 p = 0.026	U=108 p =0.083	-	U=606 p = 0.131	U= 126.5 p = 0.139
Cladonia lichen (*n*=40)	U= 162 **p< 0.001**	U =526 p = 0.454	U=275 p = 0.022	U= 126 p = 0.054	U=660 p = 0.823	-	U= 209 p = 0.454
Cladina lichen (*n*=11)	U= 34.5 **p = 0.002**	U= 146 p = 0.723	U= 91 p = 0.264	U= 49.5 p = 0.147	U= 128.5 p =0.314	U= 185 p = 0.322	-

of the burned habitat (Figure 5). In spite of the paucity of mineral soil seedbeds, mean germination and establishment rates weighted by micro-site cover in the habitat show that mineral soil is the greatest contributor to spruce recruitment (Figure 6). For example, *Cladonia* lichens dominate the soil surface after 9 years since fire which elevates the probability of germination (Figure 6) above the rarer mineral soil microsites. However, very few of the seeds germinating on the club lichen (*Cladonia*) surface were able to establish. The main effect of the degree of ericaceous canopy cover on germination and establishment was negative but weak ($r = -.27$, $n = 161$, $p < 0.01$ and $r = -.31$, $n = 161$, $P < 0.01$ respectively).

Vegetative regeneration of black spruce

Rates of vegetative propagation by layering in individuals of *P. mariana* show a strong, linear relationship with estimates of tree age on a Log_{10} scale ($R^2 = 0.69$, $p < .001$) (Figure 7). Transformation of the rate back to original units showed an average annual spread increment of approximately 0.2 m^2 of ground area per year.

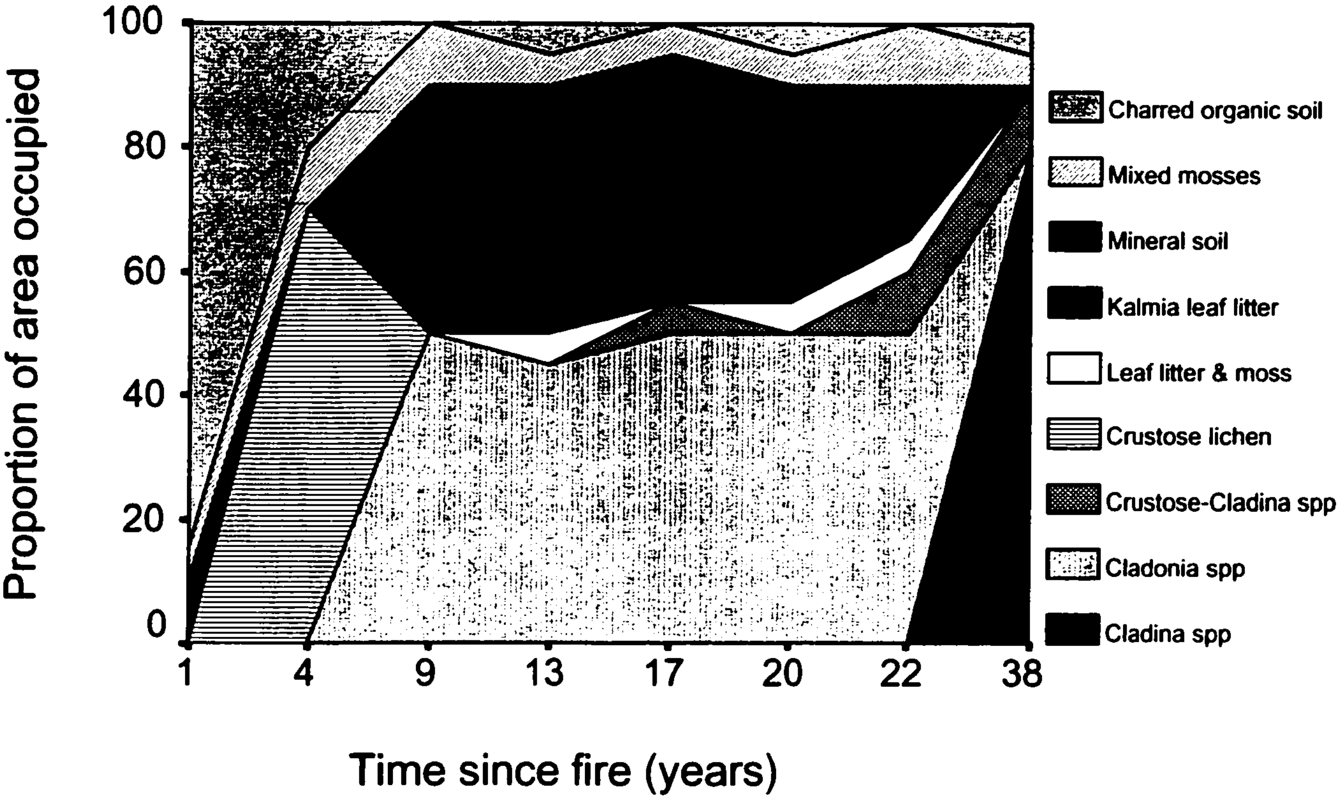

Figure 5. Proportion of area occupied by each seedbed type from 1 to 38 years after fire. The vertical axis is a relative scale and the proportion of area is indicated by subtracting low from high values rather than in relation to zero.

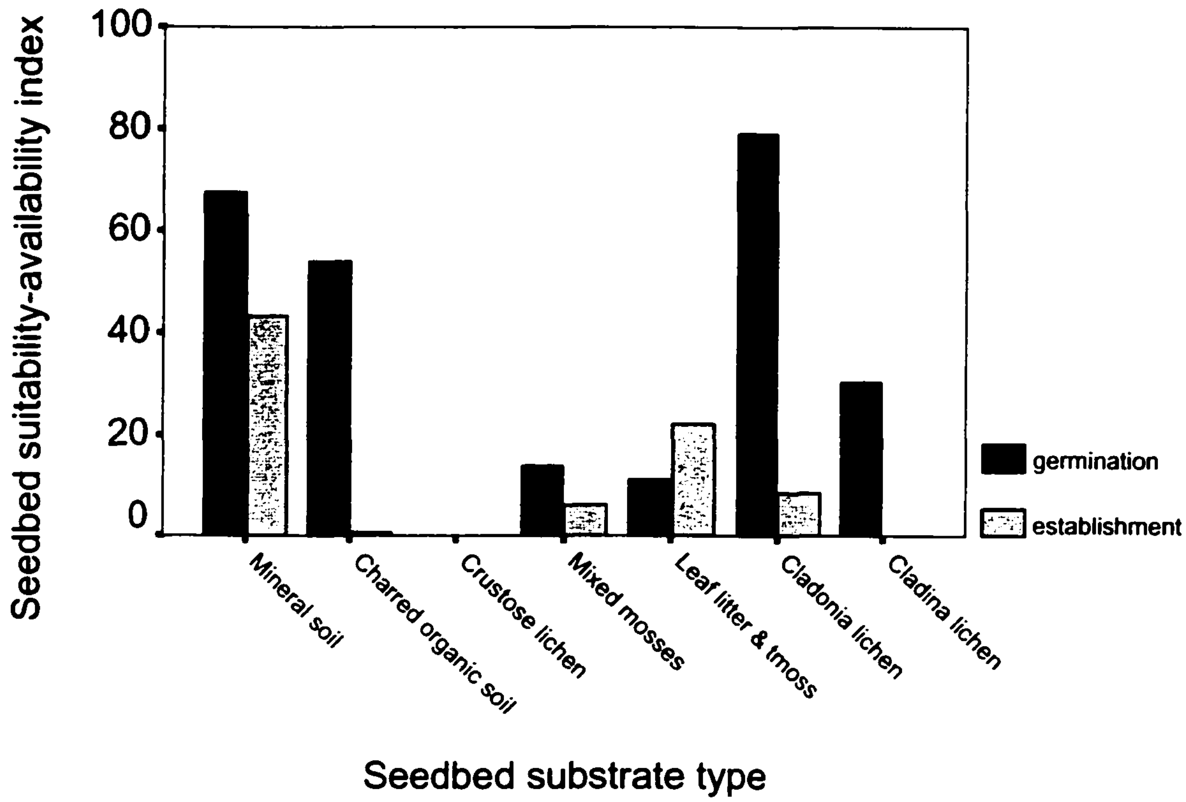

Figure 6. Black spruce germination and establishment rates multiplied by proportion of area occupied by each seedbed type. Mineral soil patches and *Cladonia* substrates support the highest germination rates per surface area but mineral soil patches facilitate highest establishment rates in spite of their scarcity in the landscape.

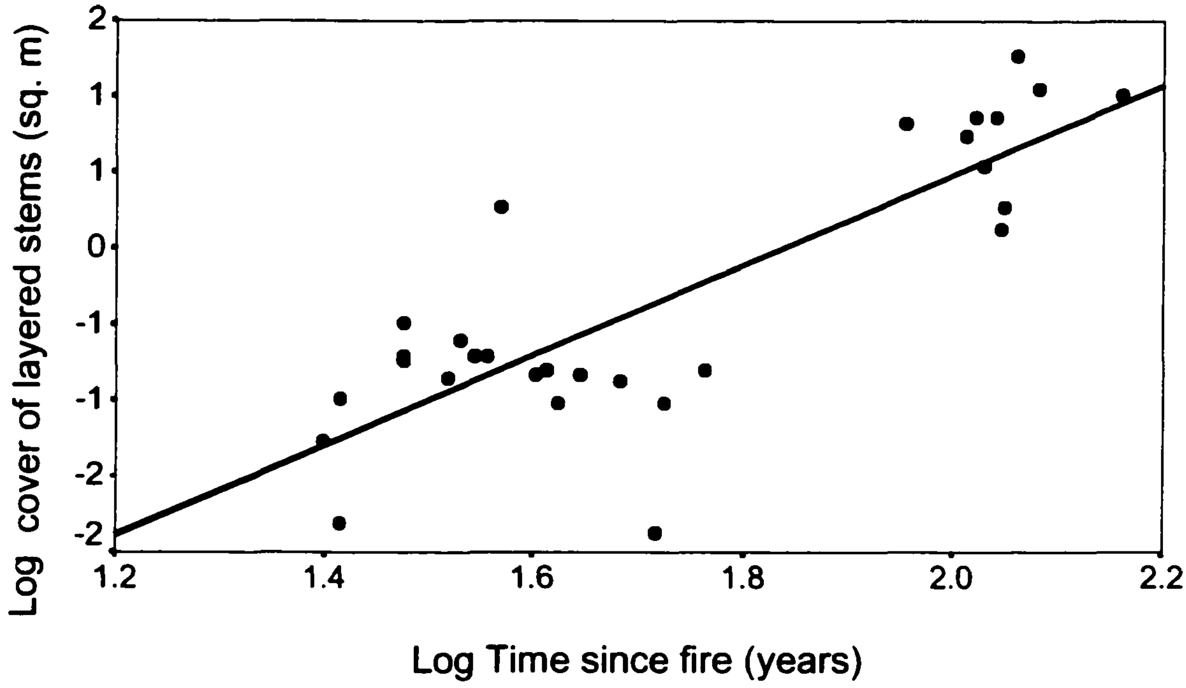

Figure 7. Rate of black spruce layering as a function of tree age. Least squares regression indicates that cover increases monotonically with black spruce age in trees that showed evidence of layering.

Discussion

Dynamics of the dominant species

Black spruce growth rates under normal growing conditions generally follow convex growth curves (Carmean, 1996) rather than the concave pattern observed over time in this study. The potential of *Kalmia* interference with expected patterns of black spruce growth has been document previously. Studies comparing post-fire black spruce growth in presence and absence of *Kalmia* indicate that in the first 20 years since fire *Kalmia* is associated with a decrease in black spruce cover from 58.5% in absence and 0.7% in presence of *Kalmia* (Mallik, unpublished). Findings from the chronosequence of the present study suggest that *Kalmia* at first inhibits black spruce invasion but the inhibition potential declines with the decline of ericaceous stem density after 30 years. Results of the present study show a strong inverse relationship between the dominance of *Kalmia* and black spruce.

In theory, spatial heterogeneity created by stem mortality of *Kalmia* stems should improve conditions for species invasion (Tilman, 1994) and therefore open regeneration niches for black spruce seedling establishment. Such gap regeneration dynamics would explain the increasing rate of tree cover accumulation after 40 years (Figure 1) but such theories (Grubb, 1977; Tilman, 1994; Huston, 1979) assume that gap availability is the only constraint on plant invasion. In this study, canopy cover only weakly affected germination and establishment of the artificial invading species (black spruce). The results of experimental seeding (Figures 4 and 6) and the findings of previous studies (Morneau and Payette, 1989; Lavoie and Sirois, 1998) clearly demonstrate that establishment is constrained by more than simply gap availability since the seedbeds themselves might be inhospitable due to "after-life" effects of the previously dominant plants in newly created gaps (Bergelson, 1990).

While the models of black spruce cover generated from the chronosequence suggest a continual growth of black spruce cover, the observed restrictions on seedling establishment in space and time suggest that this increase in black spruce cover is not driven by recruitment from seed. Seeding data in the first 38 years since fire indicate that these stands are not sufficiently stocked with seedlings to support the hypothesized rate of forest canopy development shown in Figure 2 A. After a brief four year window of opportunity for surviving seeds held in the canopy to disperse and establish, seed dispersal limitation and seedbed inhospitability appear to place major constraints on black spruce establishment and subsequent canopy closure.

The forest-heath dynamics modeled from the community data are similar to models of forest recovery from heath shown elsewhere in Europe (Rode, 1999; Gimingham, 1972). For example, clonal break-up in *Calluna* heath in Scotland is known to facilitate invasion of tree species if the fire return interval is not maintained at artificially high frequencies (Gimingham, 1972). The patterns of tree invasion observed in the preset study appear to be similar to the Western European cases but our experimental seeding data show that the seedbed is resistant to tree invasion at the time of *Kalmia*/ericaceous stem density decline and clonal break-up (20 – 40 years since fire) (Figures 1 C and 6). Consequently, these sources of empirical and circumstantial evidence, contradict the recovery pattern predicted by the chronosequence data of this chapter.

The limitations of seedling invasibility and vegetative propagation observed in this study leave no obvious mechanism by which black spruce can regain pre-fire cover within the time scale of this chronosequence. Several authors have alluded to the ability of *Kalmia* to degrade its habitat to a lower level of limiting nutrients through chemical inputs and afterlife effects of its tissues (Damman, 1971; Mallik, 1995; Bradley *et al.*, 1997) but no study has yet determined whether the poor nutrient status of these soils is a cause or consequence of *Kalmia* invasion (Inderjit and Mallik, 1999). In the latter case, invasion by *Kalmia* may produce significant and permanent changes in site productivity (Damman, 1971).

It could be argued that as successful tree colonizers mature, they saturate the surrounding heath sufficiently with seed rain and subsequent recruitment to cause the exponential pattern over time but field observations suggest that even up to 38 years such a phenomenon would be restricted to forest edges where the effects of seedbed saturation immediately after the fire are clearly visible. Such heavy seed rain is much reduced in the *Kalmia*-dominated heath since black spruce cover is negligible in the first ten years and its seed dispersal is limited to 50-100 m from the disturbance perimeter (Greene *et al.* 1998). Even if seed dispersal throughout these habitats was sufficient, constraints on seedling establishment after 4 years since fire would probably preclude any burst of regeneration from the trees that do become established (*sensu* Nyland, 1994).

Several authors have suggested that retention of black spruce seeds in cones for several years following fire may be important for successful seedling establishment following fire (Foster, 1985; Thomas and Wein, 1984). Our results indicate that the best conditions for regeneration are within 4 years of fire when mineral soil seedbeds are devoid of plant cover. Regeneration is minimal after these ephemeral regeneration niches are colonized by cryptogams. The colonization of mineral soil niches by cryptogams 4-15 years after fire would explain the observation that spruce establishment is highest in the early successional stages (Fleming *et al.*, 1995; Haavisto *et al.*, 1995; Morneau and Payette, 1989).

Regarding patterns in the vascular flora, our data show that maximum species richness is co-incident with the peak of *Kalmia* cover (~90%) which contradicts competition-based causes of plant community structure such as centrifugal organization (Wisheu and Keddy, 1992) and the mass-ratio hypothesis of species diversity (Huston, 1979). I suggest that *Kalmia* cover provides services such as shade and shelter that compensate for the effects of asymmetric competition of established species on invaders. It has been suggested that commensalism may over ride interspecific competition as a structuring force in harsh environments when a community dominant provides services to subordinant species (Hacker and Gaines, 1997; Olofsson *et al.*, 1999). While my data support this concept, such commensalisms seem to only be temporary since the apparent self-thinning of *Kalmia* cover and stem density after 30 years resulted in a loss of species diversity (Figure 1 B).

The cause of reductions in cover, stem vigour and clonal break-up in *Kalmia* at ~ 30 years are not known but low nitrogen availability and soil autotoxicity due to heavy metal accumulaiton may be a contributing factor (Damman, 1971; Inderjit and Mallik, 1999; Mallik, 2001).

Community dynamics and species turnover over time

The low rate of species turnover also described as "exchange" by Prach *et al.* (1993), in the chronosequence strongly suggests that "initial floristic composition" (Egler, 1954) is a good predictor of species composition in these communities and is not altered significantly by fire. The hypothesized adaptions of boreal plant regeneration strategies to predominating fire regimes has been cited as a mechanism which induces stand replacement (Weber and Stocks, 1998) rather than succession in the classical sense (Clements, 1916; Gleason, 1926). With the exception of de-stabilization of black spruce cover, other vascular plants tend to show few discernible patterns of successional displacement. However, species turnover is evident among the cryptogams where a series of competitive exclusions can be explained by differences in growth strategies. With the first four years after fire, soil surface succession is initiated by algal crusts on the hydrophobic organic soil surfaces and to a lesser degree *Polytrichum juniperinum* which is an indicator of mineral soil substrates. The low growth form of crustose lichens is replaced by members of the *Cladonia* genus (the club lichens) which have a more vertical growth form. These lichens are replaced in turn by the shrub lichens (*Cladina rangiferina* and *C. mitis*) which out-compete the club lichens for light with their relatively high vertical growth habit creating a lichen mat up to 15 cm deep (Bonan and Shugart, 1989; Hollstedt and Harris, 1992). As canopy cover increases, heliophytic lichens become replaced by the shade-dependent pleurocarpous mosses. Similar successional sequences have been documented in other ericaceous communities (Foster, 1985; Morneau and Payette, 1989; Black and Bliss, 1978; Day, 1982) but in all cases, *Cladina* has been described as the successional climax.

Vegetative expansion as a mechanism of forest regeneration

The explanation of increasing spruce cover via vegetative propagation is contingent on seedling density and rates of vegetative expansion of established trees. Layering is most often observed in wet black spruce stands but is also reported as a means of propagation in mesic sites which are nutritionally limited and/or climatically stressed (Legere and Payette, 1981; Black and Bliss, 1978; Morneau and Payette, 1989; Arsenault and Payette, 1992). The growth form of these trees is reminiscent of a candle arbre of short ramets radiating outward and upward from a single, taller parent tree (R.G. Bloom and A.U. Mallik, unpublished). Estimations from our linear model indicate that canopy expansion occurs at a rate of about 0.20 m^2/year but extrapolation of this monotonic rate to estimate time needed to reach crown closure may be spurious. Legere and Payette (1981) found that clonal expansion of black spruce in forest-tundra transition forests was limited to less than three metres independent of the age of the parent tree.

Consequently there is evidence that vegetative expansion is a mechanism of maintenance of populations rather than a method of colonization (Legere and Payette, 1981; Payette and Lavoie, 1992). Interference of *Cladina spp.* with layering potential of black spruce may contribute to such observed spatial constraints on vegetative expansion (Hollstedt and Harris, 1992).

In contrast, Black and Bliss (1978) observed parental senescence in old-growth layered forests which indicates that clonal expansion may be an important mechanism sustaining a monotonic increase in forest cover but such horizontal expansion came at the cost of vertical structure. Consequently, even if the monotonic rates black spruce layering hypothesized from the data in the present study were realistic, the resulting forest would not be representative of even-aged, mature stands that characterize much of the regional landscape (Damman, 1964).

Meades and Moores (1989) define adequate restocking of disturbed black spruce sites at a rate of 2 500 stems per hectare. According to the layering rate observed here (0.20 m^2/year) and the limits on vegetative spread observed elsewhere in eastern Canada, each established tree has the potential to reach approximately 30 m^2 of circular ground cover at 150 years of age. Assuming uniform distribution, only 357 black spruce trees of this size would be needed to achieve canopy closure of a 1 ha site. If 8% of the burned habitat is comprised of favourable seedbeds, then success rates of 0.44 seedlings per m^2 of favourable habitat could theoretically facilitate black spruce canopy closure. At the observed rate of 5% establishment (Figure 4), and natural post-fire seed rain density of 50 seeds/m^2 (Zasada *et al.*, 1983), across 8% of the habitat (Figure 5), establishment rates could easily exceed the necessary threshold of 357 stems per hectare. However, the application of such liberal estimates of black spruce cover expansion are limited by the assumption of uniform distribution of seedbeds. For example, highly aggregated favourable seedbeds will cause patchiness in forest regeneration which may become permanent patterns if unfavourable *Cladina* seedbeds prevail in the remainder of the habitat (Hollstedt and Harris, 1992). Spatial patterns of seedbed availability are investigated in Chapter II.

Reconciliation of patterns and processes

A factor contributing to seedbed limitation in recently burned sites compared to the pattern of forest development between sites aged 40-70 years may be due to differences in the amount of favourable seedbed for black spruce between recent and historic fires. The historical fire regime may have been much more severe and it is likely that the even-aged stands have origins in seedbeds created by large, severe fire events. For example, Weber and Stocks (1998) reviewed fire in the boreal forest and suggested that 85-95% of boreal forest stands result from severe fire events that comprise only 1-5% of the total number of fires that occur in the region. There is a possibility that the mature stands which were used as late-successional sites in the present study have origins in extreme, stand-replacing fire conditions which differ from the *Kalmia*-dominated ericaceous stands which originated under a suppressed fire regime in which the exposure of mineral soil by severe fire is reduced.

The potential time-dependent variability in fire severity and observed restrictions on black spruce invasion weaken the realism of the chronosequence model. With this in mind, my findings indicate that burned habitats are more likely on a trajectory toward an open canopy black spruce forest type where a closed canopy forest was present previous to fire. The strong relationship between mineral soil seedbeds and spruce regeneration indicate that black spruce cover is dependent on the area of exposed mineral soil and is controlled by spatial variability in fire severity rather than by time-dependent processes. The documented reliance of black spruce stand replacement on exposed mineral soil, as is often observed following severe fire, or shallow, moist organic layers overlying mineral soils (Fleming *et al.*, 1995) is compelling evidence that recent fires are not preparing the same seedbeds as historical fires.

If the pattern of black spruce regeneration is an artifact of the juxtaposition of different fire regimes, it would be wise to consider the consequences of the differences in stand structure between the two climax types. The arrested stable state dominated by *Kalmia* is a self-perpetuating lichen heath which offers little in the way of vertical structure or community complexity. The functional roles of this ericaceous vegetation are associated with habitat degradation through allelopathic compounds, reduction of pH and accumulation of recalcitrant organic matter. Although the bulk of nutrients in open lichen forests are contained in the lichen layer, the net effect of the lichen functional group on nutrient cycling is questionable given its capacity to reduce soil temperatures and produce allelopathic compounds (Bonan and Shugart, 1989).

Conversely, the forested state is characterized by a three-dimensional habitat condition which has an increased surface area for epiphytic organisms. The provision of shade is also known to cause a shift from heliophytic lichen to shade-dependent mosses in the understory. This transition has important implications for the development of nitrogen budgets in the forest stand since plueorcarpous mosses collect and, under certain conditions, fix atmospheric nitrogen (Billington and Alexander, 1983). However, the role of pleurocarpous mosses in community functioning is unclear. Van Cleve *et al.* (1983) concluded the net effect of pleurocarpous mosses was negative since they "locked up" large amounts of ammonium. In contrast, Carleton and Read (1991) demonstrated the potential for direct uptake of organic nitrogen by black spruce from senesced moss tissue via mycorrhizae. The latter study and evidence for nitrogen budget accumulation by *P. schreberi* and other pleurocarps (Billington and Alexander, 1983) indicate that the differences in functional groups between open and closed canopy structures may strongly affect community function. However, the net effect of the functional group will depend on whether the services provided by moss outweigh their interference with tree growth (Zackrisson *et al.*, 1997).

Implications

The divergence of successional trends observed in this study is caused by the failure of the assumption that there is a tradeoff between competitive ability and stress tolerance (Huston and Smith, 1987; Tilman, 1985). In this case the slow-growing, low-productive dominant species is not under competitive stress from faster growing species due to filter effects of the seedbed which prevent invasion of competitor species. I suggest that the resulting lack of competitive selection allows the low-productive, stress-tolerant ericaceous community to dominate early in succession. Seedbed filters reduce the selective force of competition and its related selection for plant communities which approximate rates of productivity or biomass accumulation determined by local growing conditions (Whittaker, 1970; Wilson, 1997).

I speculate that contemporary practices of fire suppression may emulate the poor regeneration conditions observed in more northerly regions (for example Black and Bliss, 1978; Arsenault and Payette, 1992; Morneau and Payette, 1989) causing the replacement of closed canopy stands with ericaceous-lichen climax communities which are typical of tundra-treeline conditions. The resulting landscape is a juxtaposition of tundra heath and mature forest in a life zone and on soils which are capable of supporting mixed boreal forest.

The role of differential establishment abilities in determining species composition must be evaluated before invoking competition theory as an explanation of community dynamics in order to make existing models of community more generalizable and realistic. This is especially evident in relation to disturbances such as fire and their role in creating various regeneration niches for successional species (Bond and Migdley, 2001) . The importance of the regeneration niche for plants invading disturbed habitats is well known (Grubb, 1977; Lavorel and Chesson, 1995; Facelli and Pickett, 1991; Xiong and Nilsson, 2000) but the challenge now seems to be to explicitly evaluate whether the stage is fully set for competition to occur before applying models of how such deterministic processes are played out.

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CHAPTER II.

The effects of fire severity on successional pathways of black spruce-*Kalmia* forests of Atlantic Canada

Abstract

Fire has been cited as a natural force maintaining species richness in boreal landscapes. I tested the validity of this generalization by mapping burn severity and species cover in twenty-seven 200 m^2 plots in nine burns in the boreal forest of Newfoundland, Canada. Stands were previously conifer and mixedwood with understory dominated by *Kalmia angustifolia.*

Progressive and retrogressive successional pathways were modeled in a fire chronosequence at the scale of $200m^2$. Differences in productivity of the dominant species of each pathway indicate that ecologically significant biomass accumulation occurs only in patches of high burn severity possibly because community-level selection pressure for maximum productivity is pre-empted by the fire-enduring dominance of low-productive *Kalmia* and other ericaceous plants, in low-severity burn areas.

Burn severity increased species richness, species trait diversity, biomass production and structural diversity. Consequently, these parameters may be affected by fire suppression. These results strongly support the view that assembly rules must include or explicitly discount the importance of abiotic filters before biotic forces such as competition can be assumed to structure species composition. The interaction between plant establishment constraints and the operation of assembly rules of trait dispersion and biomass accumulation are discussed in terms of the applicability of such rules in human-modified disturbance regimes.

Keywords*: Kalmia angustifolia, fire severity, safe-sites, filter effects, species richness, stability, cornerstone species*

Introduction

Quantitative models of vegetation dynamics have developed almost exclusively from either the point of view of competition theory (e.g. Tilman, 1985; Gleason and Tilman, 1990; Tilman 1994) or disturbance theory (e.g. Grime, 1973; Connell, 1978) with little integration of the two paradigms (Begon *et al.*, 1996; Huston and Smith, 1987). Competition theory predicts that community membership is structured by the rate at which plants uptake and deplete limiting resources assuming that the system reaches competitive equilibrium and that plant communities are predicted to be dominated by successively superior competitors for these limiting resources (Tilman, 1982, 1985). Disturbance theories predict that species dynamics are controlled by periodic disturbances in space and time (such as fire, herbivory etc.) which reduce competitive exclusion and prevent many systems from reaching equilibrium (Grime, 1973; Connell, 1978; Huston, 1979). In these models, the frequency of disturbance (and its presumed correlates of severity and size) are the proximate controls of species dynamics but the process of competition is assumed to be the ultimate mechanism operating between disturbance events. A fundamental assumption of the application of these theories is that there is a tradeoff between dispersal/colonization ability and competitive ability/stress tolerance (Grime, 1979; Bazzaz, 1979; Tilman, 1994).

Tilman (1994) reviewed the simplifying assumptions of competition theory in predicting community dynamics and recognized that spatial structure was a critical, but under studied aspect of predictive theories of species dynamics and co-existence. He suggested that incorporation of spatial cycles of gap creation (due to mortality of dominant species) and concomitant gap invasion into predictive models could better explain observed community composition in natural systems. Although Tilman (1994) states several caveats to his modified model, it still fails to incorporate at least one critical mechanism (selective invasion) which was later acknowledged to potentially interfere with competition (Tilman, 1993) as a controlling force of community dynamics. In a more recent review, Grime (1998) recognized that community dynamics are the result of competition between the dominant plants but that subordinate species may have functional roles that, in some cases, control invasion of the community dominants. In particular subordinate plants may have filter effects which cause selective invasion and pre-empt the occurrence of unconstrained colonization. In such conditions, the more stress tolerant species with larger, more stress-tolerant seeds are more successful invaders than the more *r*-selected strategists with high rates of dispersal but with less robust propagules (Burke and Grime, 1997). Similarly, I argued in the previous chapter that, after fire in the boreal forest, mortality of the dominant species is not necessarily correlated with gap invasibility. The failure of this correlation means that the theoretical trade-off between competitive ability and colonization, which is fundamental to successional theory (Tilman, 1994; Huston and Smith, 1987; Grime, 1979; Grime *et al.*, 1997), may not operate universally. If such interactions are pervasive in plant communities, predictive theory will require recognition of what species do in ecosystems beside simply compete. Alternatively, the filter-effects may be reduced in cases where the interfering seedbed conditions are removed through catastrophic natural disturbances to which the regional species are adapted. Examples of such disturbances are wave action in shore-line communities (Connell, 1978) and fires in the boreal forest (Bonan and Shugart, 1989). This principle may lead to a more general hypothesis that competition models have to be nested within broader ecological models of dispersal and colonization limitation in order to produce accurate predictions of secondary succession (Keddy, 1992).

Models describing plant responses to disturbance have been developed for fire driven terrestrial systems (Noble and Slatyer, 1980) and for wetland plant communities in relation to flooding regimes (van der Valk, 1981). While these models address the species composition of disturbed habitats, their qualitative nature does not account for two important aspects of community dynamics: 1) within-disturbance variability and its potential selection for multiple plant strategies for establishment in otherwise similar habitats (Leishman and Westoby, 1992) and 2) changes in relative abundance of plants over the course of succession.

After-life effects and ecological memory

A 'complete' disturbance erases the direct competitive effect and indirect filter effects of the pre-disturbance dominant plants (Begon *et al.*, 1996) and their "afterlife" effects (Bergelson, 1990) which may endure partial disturbances (wind-throw, clearcutting, mowing etc.). Few natural disturbances cause a complete removal of ecological memory, hence the development of secondary successional theory. However, large-scale studies on the effects of disturbances often describe disturbances on categorical scales, thus making the assumption that within and between disturbance variability in the landscape is less important than the type of disturbance and time since its occurrence (Huston and Smith, 1987).

Ecological memory may affect succession when afterlife effects of the pre-disturbance species are similar to the requirements of local colonizers (e.g. forests dominated by gap-phase dynamics); all that may be required in many systems is gap creation by canopy removal. In terrestrial ecosystems this occurs in succession of insect killed stands, wind-thrown stands and human disturbances such as clear cutting.

In contrast, dominant species in the mature phase of many coniferous forests have biogeochemical feedbacks which cause an increase in concentration of secondary compounds and a concomitant decrease in plant-available soil resources (Aber and Mellilo, 1991; Pastor *et al.*, 1987). In these systems habitat stress increases due to feedbacks of the dominant species and between- and within-stand variability in fire severity become critical controls of successional pathways (Abrams *et al.*, 1985). In the boreal forest, severe fire is required to create the conditions for a successional pathway that releases recalcitrant resources allowing a successional trajectory toward mature (climax) states typical of the region (Aber and Mellilo, 1991). These conditions are: an increase in available nutrients (Huston and Smith, 1987; Aber and Melillo, 1991) and creation of regeneration niches for early successional species (Grubb, 1977). Such factors become increasingly critical in regions such as the boreal forest where nutrients become bound up in recalcitrant or standing biomass.

Two critical assumptions of disturbance-mediated theories of species dynamics (*sensu.* Grime, 1973; Connell, 1978) are (1) that the disturbance is severe enough to "knock back" the process of competitive exclusion between species and remove any interfering establishment constraints in the habitat in question (Moloney and Levin, 1996; Begon *et al.*, 1996) and (2) that frequency and severity of disturbances are correlated (Connell, 1978; Begon *et al.*, 1996). In spite of the wide spread testing of disturbance theory its power as a universal pattern is in need of qualification.

While several reviews have acknowledged the critical role of disturbance severity as a factor affecting biodiversity, empirical evidence from natural large scale disturbances are few (but see Turner *et al.*, 1997). Consequently, disturbance-based models of community dynamics, i.e. the intermediate disturbance hypothesis of species diversity (Grime, 1973; Connell, 1978), make an implicit assumption that disturbance frequency and severity are correlated (Malanson, 1984; Begon *et al.*, 1996). This simplifying assumption has led to the use of frequency (an easily quantifiable disturbance parameter) as a predictor of species dynamics and reduces the severity component to a binary variable: disturbed/undisturbed (e.g. Collins and Glenn, 1991; Suffling *et al.*, 1988). Few empirical studies have explicitly quantified the importance of severity to successional pathways that result from the denudation event (but see Van Cleve and Dyrness, 1983 and Turner *et al.*, 1997), although the role of severity has been explicitly acknowledged in reviews (see Malanson, 1984; Pickett *et al.*, 1987). The studies which have acknowledged disturbance severity have usually focused on the autecological responses of specific plants to small-scale experimental variation in severity rather than on estimating the effects of the spatial pattern over time (e.g. Skre *et al.*, 1998; Schimmel and Granstrom, 1996; Van Cleve and Dyrness, 1983; Zasada *et al.*, 1983). Empirical evidence at the landscape level have been based on the frequency of disturbance and estimates of average disturbance intensity rather than within-disturbance variability in the severity of natural disturbances (Turner *et al.*, 1997; Collins and Glenn, 1991; Huston and Smith, 1987). Consequently, the importance of severity as a landscape-level factor is poorly studied quantitatively. In part, this may be due to (1) difficulties in rigorous experimental design in natural experiments and/or difficulty in quantifying severity after-the-fact (Turner *et al.*, 1997; Whelan, 1995) and (2) the general implicit assumption that regional species are adapted to regenerating in the prevailing conditions of disturbance severity with which they co-evolved (Whelan, 1995). Under the latter case, the selective force of severity is greatly reduced in comparison to issues of frequency and patch size (e.g. Miller, 1982). With the exception of a few examples (Zasada *et al.*, 1983), the quantification of small-scale variation in seedbeds is still largely overlooked in general theory (Xiong and Nilsson, 1999) in spite of its critical role in controlling successional pathways alluded to in many post-fire studies (Abrams *et al.*, 1985; Nyland, 1998; Foster, 1985; Richardson, 1973; Thomas and Wein, 1984).

The purpose of this paper is to determine the role of variability in fire severity as a control of successional pathways and patterns of biomass accumulation following disturbance by wildfire in the eastern boreal forest of Newfoundland, Canada. The study was designed to (1) describe the various pathways of succession that may arise from variability in fire severity, (2) measure the expression of plant functional traits diversity following varying degrees of burn severity and (3) explain the mechanisms controlling these pathways on the basis of the physical and nutrient/chemical conditions which arise from varying degrees of surface soil combustion.

Methods

Mimicking fire behaviour in controlled and semi-controlled conditions, is difficult so in this study a *post-facto* approach was used to determine the effects of natural variability of fire severity on vegetation. Nine sites varying in age from 1 to 38 years since fire were used such that age was the greatest quantifiable source of between-site variability among the communities used in the chronosequence. This assumption was tested and validated with data in the previous chapter. The "controlled retrospective" approach used in this study has three components: (1) quantification of the proportion of area and cover of vegetation in each site that experienced various degrees of fire severity, (2) detection of the factors creating habitat heterogeneity in the burned habitats using historical data on the nine sites and (3) explanation of the ecological role of the observed microhabitats during succession.

Site locations and historical data for each fire were compiled from regional fire weather records (D. Hewitt, personal communication) and are summarized in Table 1.

Table 1. Locations and fire history of nine *Kalmia*-dominated sites comprising the chronosequence. Moisture contents are derived from the coastal Hemlock Canadian Fire Weather Index standard duff coefficients of Lawson *et al.* (1997).

Site	Age (years since fire)	Lat.	Long.	Pre-fire Drought Code (DC)	Estimated moisture content (%)	Duration of fire (days)	Severity Index* (DC*days)
Triton Brook	1	48°38’	54°31’	200	220	4	800
Bunyan Cove	1	48°24’	54°01’	47	310	2	94
Spracklin Rd.	4	48°38’	54°31’	233	200	2	466
Thorburn L.	9	48°38’	54°31’	100	275	2	200
Bluehill West	13	48°38’	54°31’	47	310	4	188
Charlottetown	17	48°38’	54°31’	206	210	2	412
Gambo Pond	20	48°38’	54°31’	282	180	14	3948
Terra Nova Rd.	22	48°38’	54°31’	206	210	2	412
Pitts Pond	38	48°38’	54°31’	108	280	2	216

* Severity index (DC*days) is derived form the drought code multiplied by the fire duration (days).

In each site fire severity was mapped in three 20 x 10 m relevee plots. Maps were hand drawn in the field using a 100 m tape to mark plot perimeters and a 50 m tape to subdivide the plots into more manageable 5 x 5 m units to ensure accurate representation of the ground cover and to aid in systematic sampling of species composition.

Plots were mapped using the choropleth method (Burrough, 1995) with an *a-priori* designation of the sampling classes: complete mineral soil exposure, severely burned organic matter and scorched ground. Since the middle severity class occupied very small proportions of the area and gave rise to similar species as the mineral exposure class, these microsite types were pooled. The microsite types used hereafter are 1) severe burn, defined as a microsite in which all organic soil was either consumed or transformed into a fine amorphous ash /charcoal, and 2) scorch, defined as a charred organic surface in which the pre-fire tissues are recognizable. Much of the latter microsite type is covered by charred, compacted feathermoss stems. Clear delineation of fire severity classes is shown in Figure 1.

Accuracy of fire severity classification was questionable in the oldest stand (38 years since fire) because the definitive patterns in the soil microtopography used for mapping in younger stands were concealed by a thick layer of shrub lichen and/ or mosses. Accuracy of classification was tested in the plots by randomly sampling charcoal profiles in microsites previously mapped as severe or non-severe. Core samples having charcoal residue or charcoal macrofossils from the most recent fire directly on the mineral soil horizon were classed as 'severely burned'. Samples with organic soil between the mineral soil and most recent charcoal residue/macrofossils were classed as non-severe. Cores were extracted using 7.5 cm diameter core sampler. Ninety two percent of the samples taken from microsites mapped as 'severely burned' (n= 30) were correctly classified. Similarly, sampling of charcoal depths in the non-

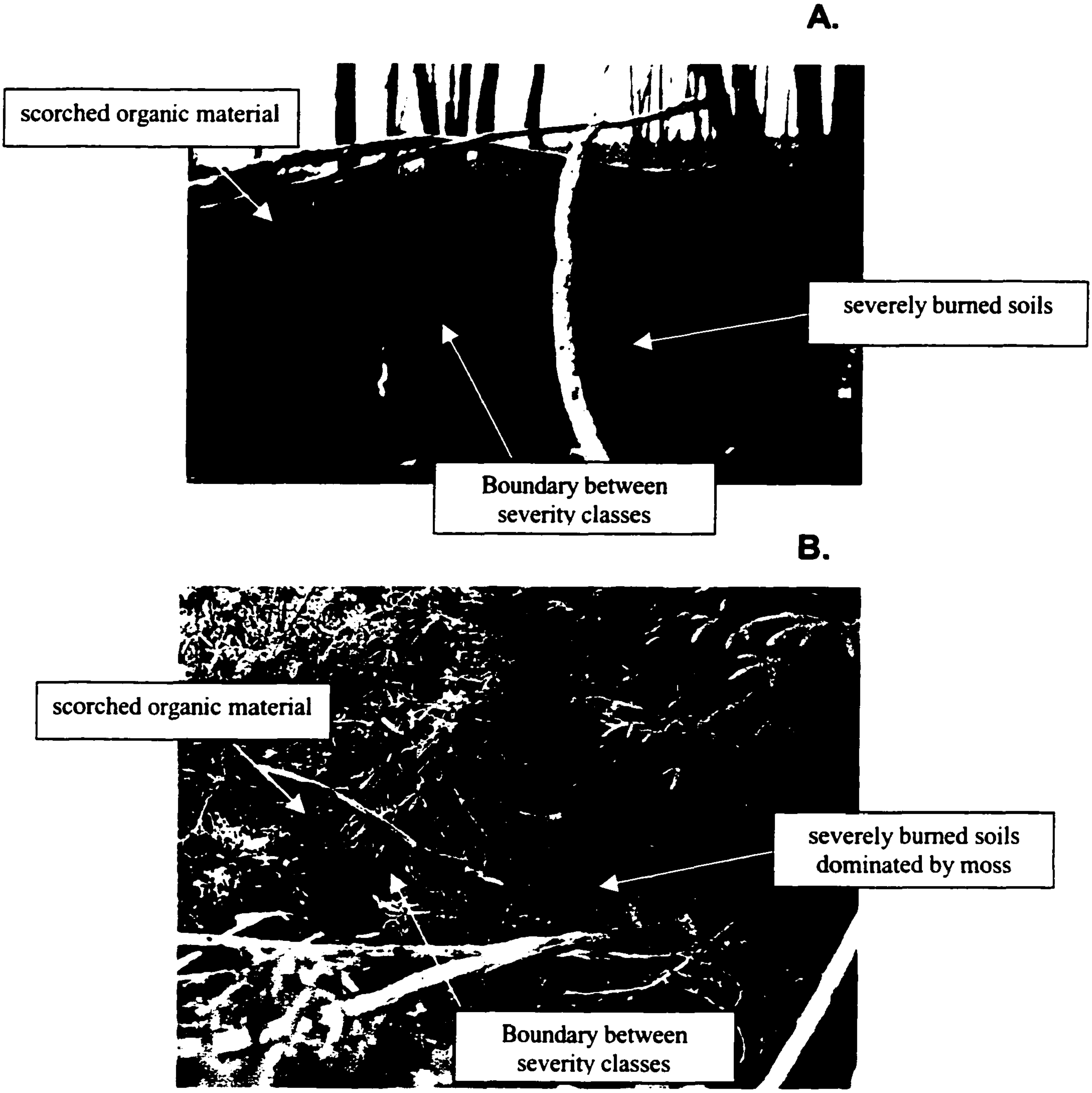

Figure 1. Delineation of fire severity patterns. A. Fire severity in a one year old burn site. Patterns in depth of burn are readily visible. B. Fire severity in a 23 year old burn site. A clear distinction between severely burned soils and adjacent scorched organic matter remains visible many years after the fire (23 years in this example).

severely burned habitat revealed charcoal residue immediately beneath the lichen layer and over at least 5 cm of unburned organic matter in 93% of the replicates. The 7.5% margin of error was derived almost exclusively from core samples taken near the edge of the mapped microsite boundary. The data from this resulting 7.5% error estimate was accepted.

Standing stems (basal diameter > 10 cm) and aerial extent of tree canopies were mapped where possible although older sites had few remaining snags due to blow-down and stem removal. Domestic use of standing dead wood for firewood occurred in four of the nine sites but an informal survey indicated that the winter harvesting methods did not cause further disturbance to the post-fire landscape even at the small spatial scale discussed here.

Species composition (presence/absence) of plants was recorded in each plot in relation to fire severity during peak periods of species richness in August. Living and recently senesced tissues were used in identification but only species with persistent above-ground structures were used in the analysis to avoid biases caused by phenological differences associated with time since fire and/or fire severity conditions. Consequently subordinate herb species with short annual cycles and rare plants which did not contribute significantly to community biomass were not used (e.g. *Maianthanem canadense*, *Cypripedium acaule*). Plants occurrences were averaged among respective microhabitats for each stand.

In order to compare patterns of succession in relation to fire severity, plants were designated to physiological functional groups on the basis of gross traits extracted from the literature (Appendix I). Allocation of plants to groups was subjective and based on the predominant method of long-term persistence in the landscape (vegetative, dispersal, seed bank) *sensu* Noble and Slatyer (1980). It is well known that classifying plants discretely to one of the above strategies is artificial since plants exhibit various strategies for persistence. However, in order to remain in the regional species pool in a dynamic landscape, the gross distinction between plants with low growth forms that require easily invasible habitats and species that specialize on persistence by tolerating shade and nutritional stresses is useful. In this sense the intolerant plants are termed '*r*-selected' and the tolerant species capable of persisting in late successional forested conditions are termed '*K*-selected' (*sensu* MacArthur and Wilson, 1967).

Plants with resprouting potential were further differentiated on the basis of evergreen versus deciduous habits. These traits strongly affect relative primary productivity of plants growing in similar habitats (Small, 1972) and are therefore gross indicators of plant strategies for persistence in the established phase. Rates of occurrence for each species in each microsite type were averaged among species in each functional group for each stand.

Determination of species composition was based on presence/absence, rather than abundance estimates, to avoid estimates of diversity from being confounded with herbivory which is known to be a regional structuring force (Power, 2000; Thompson and Mallik, 1989). Measures of species diversity and the relative cover estimations from which they are derived are expected to be influenced by browsing but presence/absence was assumed to be an unbiased determinant of composition since the important herbivores (moose, *Alces alces* and snowshoe hare, *Lepus americanus*) do not generally exhibit whole-plant browsing (Prescott, 1980). In spite of the lack of relative abundance data, the over-riding effect of seedbed was suspected to be strong enough to detect patterns in species composition in the data. Percent covers of the dominant species (*P. mariana* (black spruce) and *Kalmia*) and productivity estimates of black spruce were recorded and assumed to be unbiased since both of these species are resistant to herbivory by moose and hare (Jaynes, 1975; Arnup *et al.*, 1995; Prescott, 1980).

As a measure of forest recovery in each plot, all black spruce recruits were recorded and mapped and tree productivity data were collected from equal numbers of individuals in each microhabitat type in each plot. Number of trees sampled per microhabitat in each plot varied from 5 to 10 depending on the number of black spruce stems in the sampling area. Productivity of individual trees was estimated using stem volume per year as a non-destructive index. Stem diameter was measured at the base of selected trees. The radius, tree height and stand age were used to calculate average growth increment for each tree (m^3/yr) according to the following formula:

Average volume increase per annum = $(1/3\ \pi\ r^2 \times h)/$ tree age

where r = stem radius and h = stem height

Average black spruce productivity of microsite types was estimated by multiplying average stem volume values of individual trees by the stem density in the respective microhabitat type in each plot. The resulting biomass indices were divided by the proportion of area surveyed for each microhabitat and by stand age. The resulting productivity models were expressed in m^3/ha/yr. These values were used in a correlative bioassay to generate productivity models between microhabitats on the basis of both total stem volume accumulation per m^2 over time and average productivity of black spruce individuals between microsites.

I assumed that at this small spatial scale, seed rain for all species was randomly dispersed across all plots such that differential patterns of community development were attributable to spatial patterns of seedbed quality.

Maps were scanned and proportions of severe and scorched surface areas were calculated using SigmaScan Pro 5.0 (SPSS, 1999). Species lists were compiled for each of the sampling units (microsite types) and observations were pooled for each site to avoid pseudo replication of experimental units.

Patterns in species traits

In order to test for the effects of fire severity on plant traits, several parameters were measured in addition to plant strategies for establishment. Traits were selected which could provide insight into how the successional processes of invasion, persistence, stress tolerance and herbivory were affected by degrees of fire severity in randomly generated microhabitats which otherwise provided similar habitat conditions. A complete list of traits and references for its occurrence in each plant is provided in Appendix I.

The species data was compiled into a species x plot matrix with observations coded by fire severity class. Plants with less than 5% frequency were removed from the analysis (Gauch, 1995). A second trait x species matrix was constructed from published secondary sources on life history traits of each species and was multiplied by the species matrix using PC-Ord (McCune and Mefford, 1997) to produce a trait x site matrix coded by fire severity class. Only non-plastic traits were used to ensure that published traits for each species would be invariable across the various geographic regions and ecological contexts form which the data was compiled. Traits included mode of persistence (wind dispersal, seed bank, resprouting), growth habit (herbaceous/woody), observed mycorrhizal symbioses (ectomycorrhizae, endomycoorhzae, ericoid mycorrhizae or tendency for no mycorrhizae), primary zone of root foraging (organic soil or mineral soil horizons) and forage value (browsing and fruit value for wildlife). Species which appeared to express multiple tendencies for each trait were scored accordingly.

Patterns in soil chemistry

Since patterns of species assembly are often cited to have mechanisms related to limiting resources, chemical characteristic of the microhabitats were estimated within each microhabitat of each site. Soil samples were collected in five random pairs with each pair consisting of one scorched and one severely burned sample. In each location a 5 x 5 x 5 cm sample was taken from both the organic and mineral soil horizons. In sampling of severely burned microsites where the mass of organic soil was greatly reduced, material was collected from a larger surface area to obtain sufficient sample for analysis. Two mature black spruce – *Kalmia* stands adjacent to the 13 and 38 year old burned stands were also sampled to obtain an estimate of soil nutritional differences between successional and mature forest. These sites were even-aged and estimated to have origins in fires 90 and 100 years prior to the study (Power, 2000).

The following analyses were considered to be critical habitat quality parameters for plants: pH was determined using the 1:1 sample to distilled water method (Allen, 1989), C:N ratio was determined using a combustion gas autoanalyser. Available P and K were extracted with Mehlich solution and concentrations were determined colorimetrically. All analyses were conducted in the Forest Resources and Agrifood Laboratory in St. John's Newfoundland, Canada.

Statistical analysis

Due to the difficulty in achieving replication of burns of equal ages, the statistical design is correlative. Linear correlations (Pearson's r) were used to test for relationships between observed proportions of organic soil combustion and the historical index of fire severity. The analysis was weighted by age (SPSS, 1999) to reduce the influence of older stands in which measures of severely burned surface area were increasingly uncertain.

Severely burned microsites were considered control treatments since biotic factors and unknown historical effects would have been removed by fire. Such microsites thereby serve as natural controls against which the hypothesized reductions in species composition, trait diversity, black spruce productivity and nutrient could be tested.

Sorensen's index of difference (the inverse of Sorensen's similarity index) was used as a measure of percent dissimilarity in species composition between microhabitats (Barbour *et al.*, 1987) and was calculated for each site by pooling observations among its plots for each microsite type. The resulting observations were fitted with stand age using SPSS version 9.0.

The effect of fire severity class (high severity and low severity) on plant trait composition was determined using a non-parametric discriminant function analysis (the Multiple Response Permutation Procedure (MRPP) in PC-Ord (McCune and Mefford, 1997)), to test the hypothesis that autecological plant traits differed significantly between microhabitats. This analysis uses a measure of differences in species composition (or trait composition in this case) between the groups being tested. Euclidean distance is frequently used but the Sorensen index was used in the present analysis because it tends to reduce the influence of outliers without affecting the computation of the analysis (McCune and Mefford, 1997). In its purest form, the analysis generates a frequency distribution of expected differences in composition between groups based on calculation of all permutations of the assembly of sampling units into the groups (Zimmerman *et al.*, 1985). The observed test statistic (delta) is a combination of all the difference measures for each sampling unit between groups. In order to reduce the computational complexity of the analysis, statistical significance is determined from the Pearson type III distribution which closely approximates the results of calculating the frequency distribution of permutations (Zimmerman *et al.*, 1985). The probability of the observed difference between groups occurring by chance (the T statistic) is derived from this distribution.

Indicator species analysis (Dufrene and Legendre, 1995) was used as a *post-hoc* procedure for determining which traits acted as significant diagnostic predictors of microsite type. PC-Ord (McCune and Mefford, 1997) was used to run the analysis. The algorithm calculates indicator values for each of test units (in this case traits) in each group (high and low fire severity). Indicator values are a combined index of relative abundance and frequency of occurrence in each of the *a-priori* groups. A monte carlo simulation was used to generate a series of indicator values based on random allocation of the traits to the groups. The statistical significance of the observed indicator value was expressed as the number of time and equal or larger indicator value occurred in the 1000 randomizations of the data. Trends of selected trait frequencies in high and low severity microsites were plotted according to time since fire.

The hypothesis that fire severity class is related to black spruce productivity was analysed using a t test for independent samples. Black spruce productivity was expressed per unit area (m^2) of microhabitat to remove biases in these variables caused by comparatively large areas of low severity versus high severity microhabitats in the mapped plots. The same standardization was made for trait diversity discussed below. Data were log transformed which homogenized the data with respect to potential differences in age and the means were plotted in relation to expected levels of productivity for these sites as predicted by the Canadian Land Inventory survey (Delaney, 1974).

Trait diversity, and soil nutrient data did not meet the assumptions of homogeneity of variance in a two-way analysis of variance. Consequently, a confidence interval approach was used to test the null hypothesis that these variables were not related to fire severity class or time since fire. Organic and mineral soil data were analysed separately. Trends in the means of pH, C:N ratio, available phosphorus and available potassium were plotted with 95 % confidence intervals in relation to severity class and time since fire interpretation.

Results

Historical correlates of spatial severity patterns

The proportion of severely burned microhabitat in each plot was strongly related to the fire severity index ($r = 0.70$, $df = 8$, $p = 0.037$). Dichotomous boundaries between microhabitats are evident in recent fires but older burns show invasion of ericaceous plants into the accumulated organic matter in severely burned microsites (Figure 2). Mineral soil patches occupy an average of 8 % area (± 1.7 s.d.) of the post-fire habitat of these sites.

Responses of vegetation to fire severity conditions

Fire severity class strongly differentiated between the average frequency of plants with seed-based responses to fire (Figure 3) and vegetative responses (Figure 4). Severely burned microsites were associated with a 5-fold increase in the mean frequency of herbaceous dispersal strategists (such as *Epilobium angustifolium*, *Solidago* spp. and *Anaphalis margaritacea*) early after fire compared to the low severity condition (Figure 3A). From 1 to 13 years since fire, severity microhabitats lagged behind high severity microhabitats in the representation of late-successional (*K*-selected) tree invaders (Figure 3B) such as black spruce and eastern larch. Stands between 17 and 23 years old depict no clear trends between microhabitats in the frequency of these species. The 38 year old stand showed sustained levels of frequency of *K*-selected invaders at approximately 50% while the low severity condition has occurrence rates of less than 20%.

Seed-bank species were less frequent in high-severity microsites (peak mean frequency = 0.16) than in the low severity condition (0.21) immediately after fire but the difference declined 13 years since fire (Figure 3 C). Trends in competitive resprouters such as *Prunus*

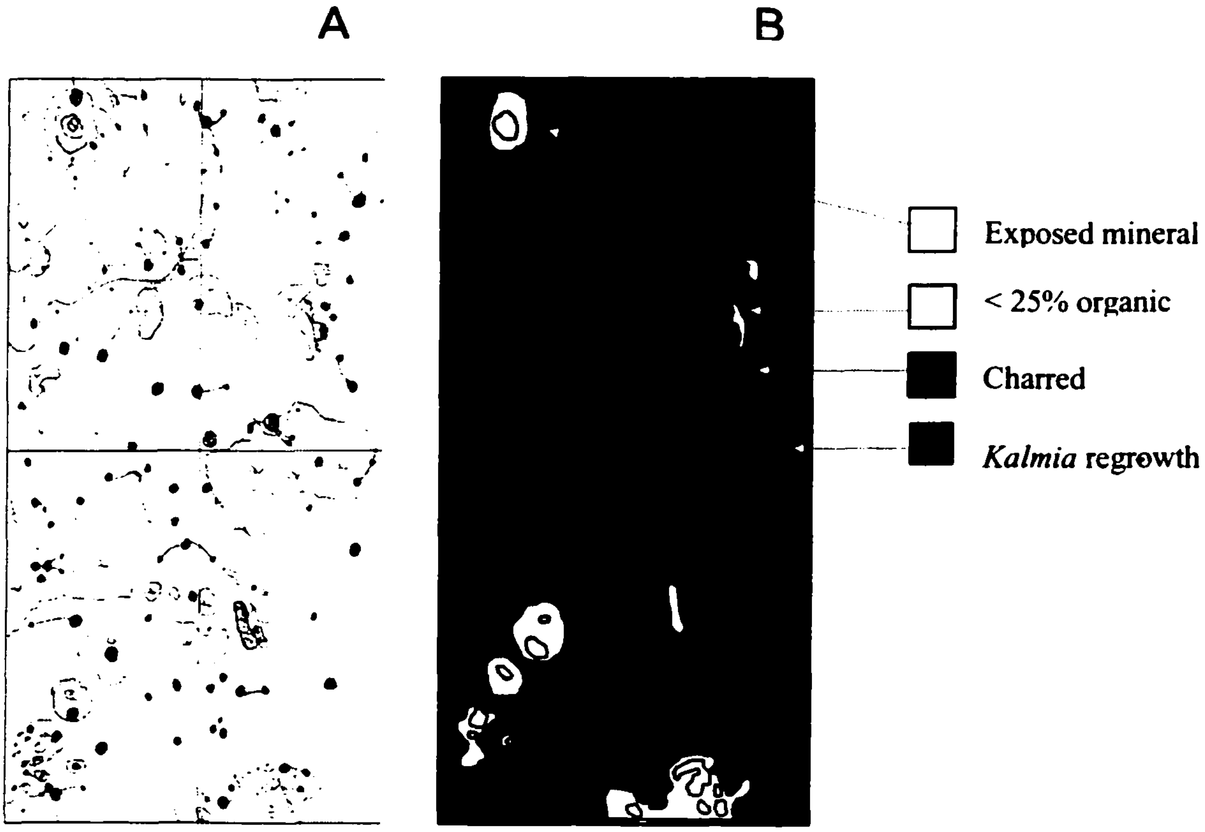

Figure 2. Example of plot maps used to quantify the areal extent of fire severity. Mineral soil exposure, black spruce stems indicated by (•) and plant cover were mapped in the field (A) and subsequently digitized for spatial analysis (B).

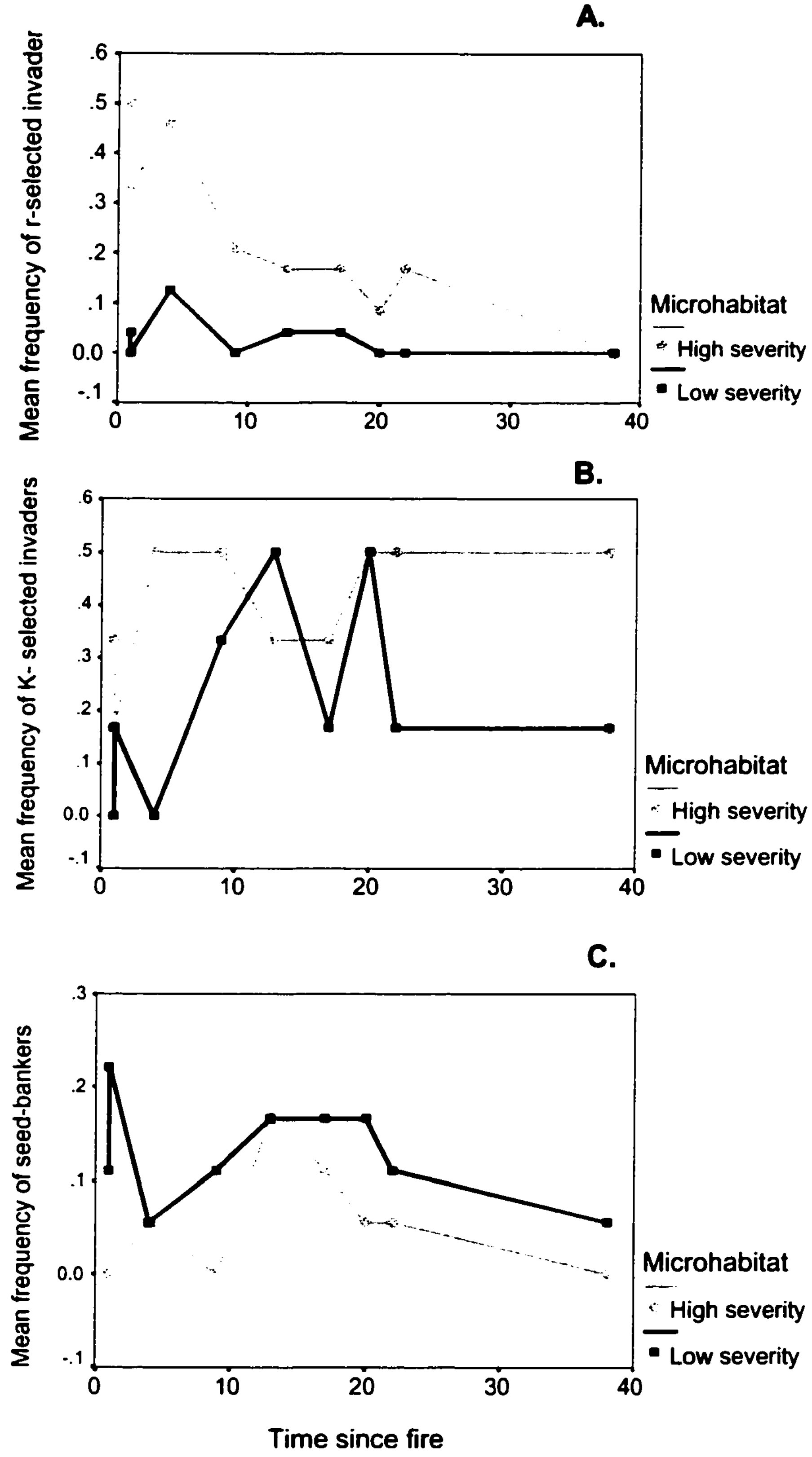

Figure 3. Trends in frequency of occurrence of invaders and seed-bankers over time since fire. Dispersal strategists (r-selected species) are present early in succession but show a reliance on patches of high burn severity compared to the low severity condition (A). Trends in the more tolerant dispersal strategists, *K*-selected species such as black spruce, larch (*Larix larcina*) show a subtle tendency for recent, severely burned microsites to have higher counts of occurrence (B). Seed-bank species exhibit a slightly higher dependency on low-severity microhabitats (C).

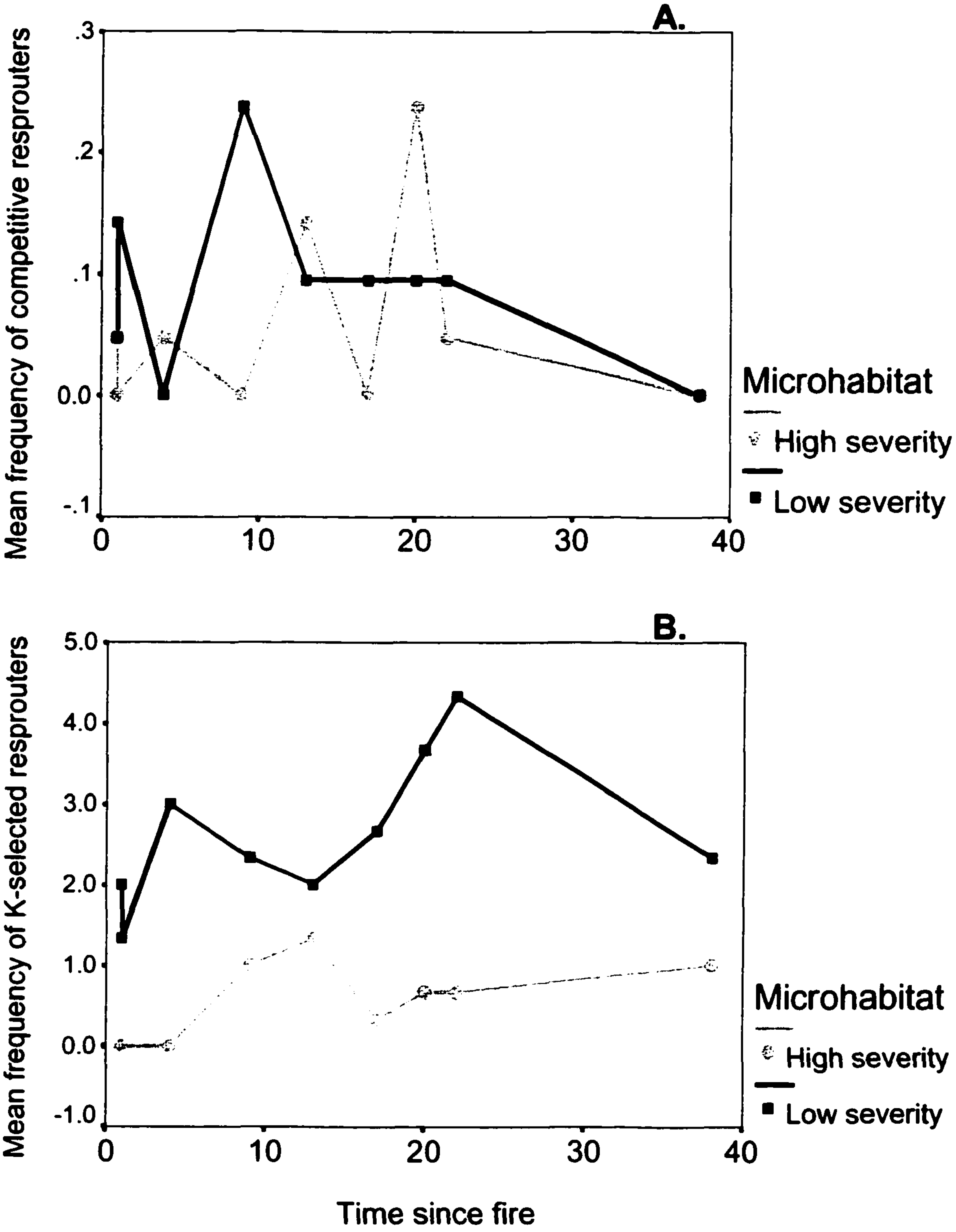

Figure 4. Frequencies of potential resprouters over time since fire. The dynamics of competitive resprouters show no systematic response to levels of fire severity (A). Stress tolerant resprouters are had higher frequencies of occurrence in low severity habitats than in high severity habitats (B).

pensylvanica, Alnus rugosa and *Betula papyrifera* (Figure 4 A) did not visibly vary between microhabitats and were on average approximately 50% less frequent than resprouting *K*-strategists (Figure 4 B). Resprouting *K*-strategists were much less frequently observed in severely burned microsites although greater incidences of occurrence of these species in severely burned microsites in older stands indicate increasing presence with age. In general patterns of r-*K* shifts in dominance are exhibited only in the severely burned portions of the habitats (Figures 3A and 3B) and low severity areas are dominated by *K*-strategists irrespective of time since fire.

The pattern of species dissimilarity between habitat types over time is characterized by an initial state of heterogeneity in species composition which recedes into a phase of homogeneity between the microhabitats between 9 and 20 years (Figure 5). After 23 years, dissimilarity rises monotonically causing a bimodal pattern over time. The cubic relationship is significant ($R^2_{(5)} = 0.87$, $p = 0.011$).

Trait diversity data failed to meet the assumption of homogeneity of variance for analysis of variance. However, visual inspection of the trends in 95% confidence intervals between microhabitats and across stand ages (time since fire) indicated significant main effects and their interaction (Figure 6). Trait diversity per unit area (m^2) was significantly higher in high severity microhabitats from 1 to 4 years since fire but fell to similar levels as the surrounding heath up to 23 years after which trait diversity increased for a second time. Trait diversity in the low severity condition was not related to time since fire and had very little variability irrespective of stand age.

The hypothesis that species trait composition of burned habitats was independent of fire severity was rejected in the MRPP analysis ($T = -16.5$, $p < 0.001$). *Post-hoc* indicator species analysis located 9 out of 13 traits in the matrix which were significantly more related to

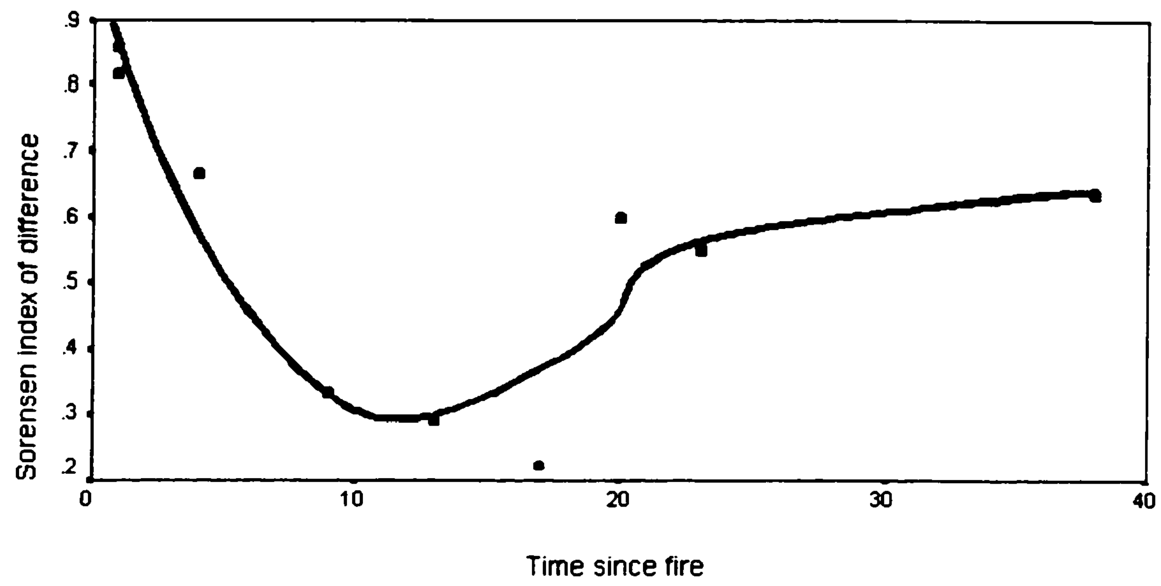

Figure 5. Curve estimation of percent dissimilarity of species composition in low and high fire severity microsites over time. The index of difference was calculated using 100 – Sorensen's index.

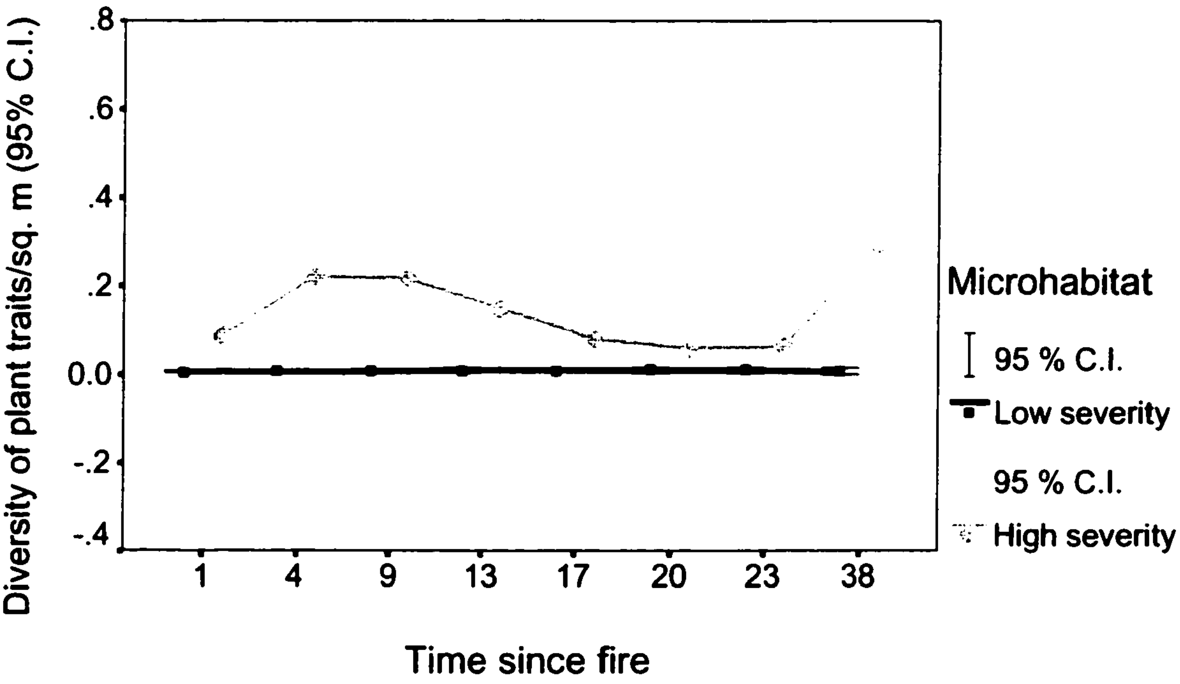

Figure 6. Diversity of species traits in relation to fire severity class and time since fire.

respective fire severity conditions than was expected by chance. These traits are summarized in Table 2.

Black spruce productivity was greatly reduced in the low-severity habitats. Log biomass in severely burned habitats (mean log productivity = 0.88 m ^{3}/ha/yr ± 0.46 s.d.) was significantly greater than that of low-severity growth conditions (mean log productivity = -2.68 m ^{3}/ha/yr ± 0.60 s.d.) ($t_{(10)} = -4.681$, p = 0.001). Total black spruce productivity per unit area (m ^{3}/ha/yr) showed an increase with increasing stand age in mineral soil microsites while biomass accumulation in the scorched condition was consistently low and apparently unrelated to time since fire (Figure 7 A). Average individual tree productivity was also consistently lower in the low fire severity condition (Figure 7 B). Transformation of these figures back to original units reveals that maximum productivity of the heath habitat is 0.3% of that estimated from the severely burned condition. Reduction in biomass due to constraints on invasion was clearly a factor since mineral soil microsites supported 210 % more establishment of individuals. Part of the pattern in total productivity difference is also related to reductions in growth of individual trees since density-corrected stem biomass in the heath was only 0.27% of that observed in severely burned conditions ($t_{(10)} = -6.09$, $p < 0.001$).

Resource dynamics and habitat pH over time

Inspection of 95% confidence intervals of pH indicated that high-severity microsites in the one year old burn sites were significantly less acidic than soils in the low severity condition for both organic and mineral soils (Figures 8 A and B). The magnitude of this difference appeared to be time-dependent and declined after 4 years (Figure 8 A). The main effect of severity class on organic appears to be increased pH in organic soils but show no consistent trend as apparent in mineral soils.

Table 2. Indicator species analysis detected 11 significant traits which contribute to the differences in plant trait composition observed between burn severity classes.

Trait	Relative abundance (%)*		% trait *f*		p
	Severity class		Severity class		
	low	high	low	high	
Mode of propagation					
resprouting	74	26	74	18	0.013
wind dispersal	31	69	23	69	0.001
seed banker	66	34	57	21	0.010
Structural habit					
herbaceous	31	69	17	67	0.001
woody	53	47			0.001
Mycorrhizal symbionts					
ectomycorrhizhal	36	64	22	51	0.034
endomycorrhizal	56	44	37	25	0.397
no mycorrhizae	0	27	0	27	0.004
ericoid mycorrhizae	82	18	88	8	0.001
Soil horizon exploitation					
mineral soil	36	64	25	57	0.017
organic soil	67	33	67	32	0.001
fibrous root system	30	70	17	62	0.003
Consumer value					
forage use	45	68	37	62	0.02

*Average abundance of a given trait in each group divided by the average abundance of that trait across all plots.

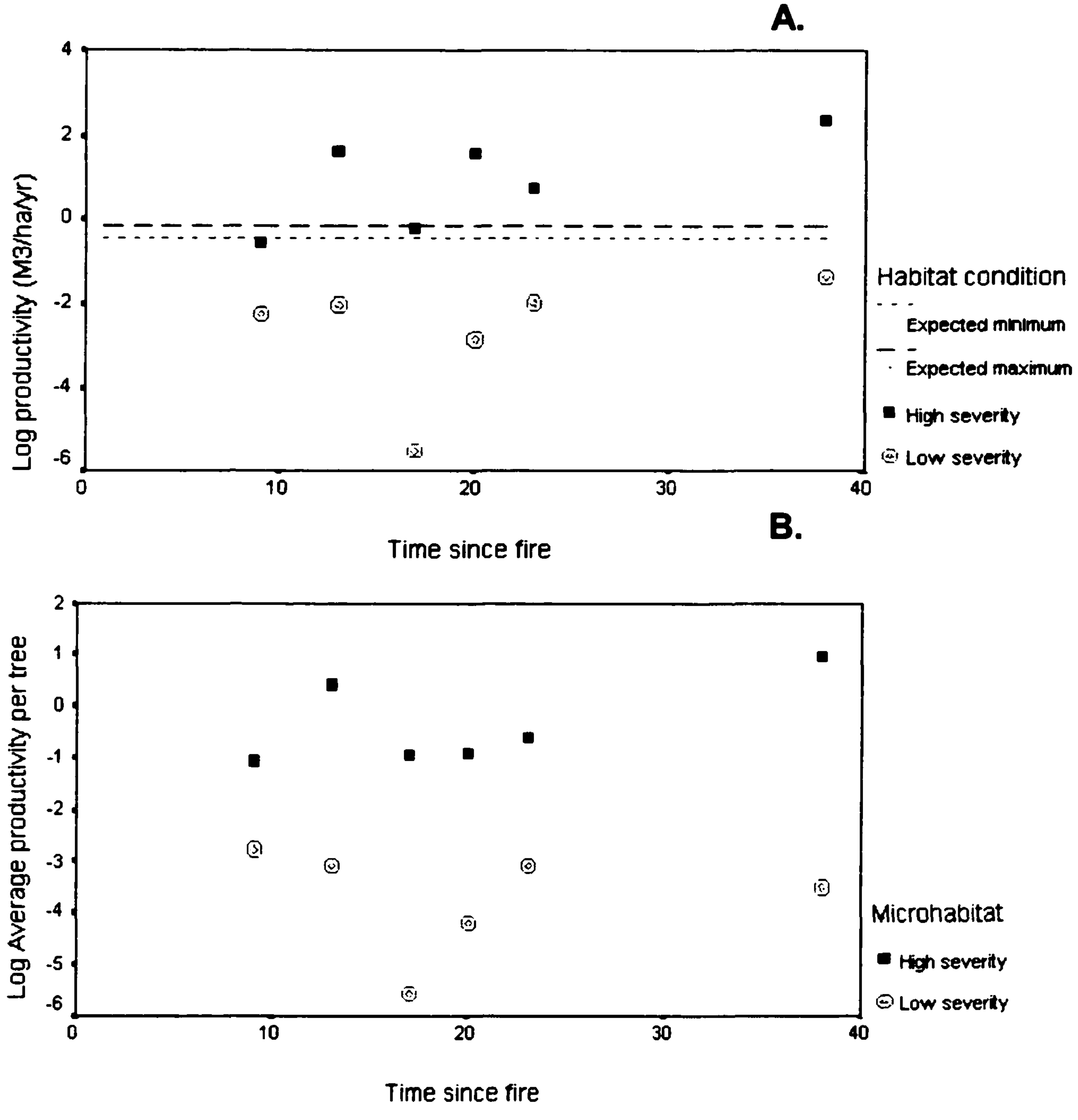

Figure 7. Patterns of black spruce productivity in relation to severity class and time since fire. Per unit area, high severity microhabitats productive than is the adjacent 'scorched' habitat (A). Individual black spruce productivity in the low severity condition is also reduced compared to patches of high fire severity.

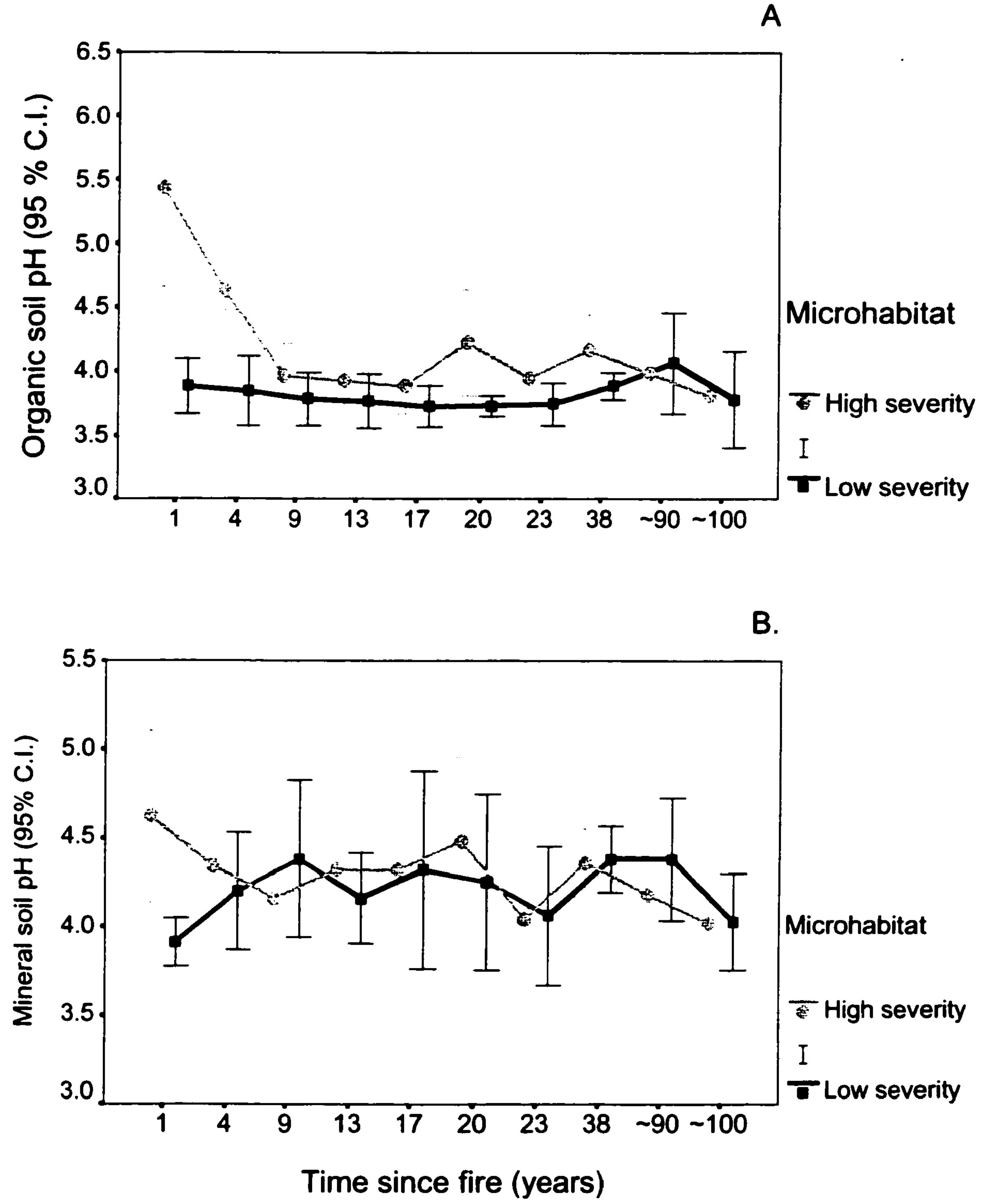

Figure 8. pH of severely burned and scorched microhabitats in a 38 year chronosequence. Organic soil pH responded was strongly related to classes of fire severity (A). Mineral soil pH did not show clear trends although there is a tendency for pH to be higher in severely burned microhabitats immediately after fire (B).

Mean C:N ratios tended to be lower in high severity microhabitats compared to low severity microhabitats except in the mature forest when the relationship is reversed (Figure 9). Comparison of confidence intervals indicates significant effects of severity class only immediately after fire. Mineral soil C:N ratio was not determined because nitrogen concentrations (mg of nitrogen per kg of soil) were below detection limits of the instrument (0.01 mg/kg) (Tom Fagner, personal communication).

The main effect of fire severity class was associated with a large increase in available phosphorus in organic soils immediately after fire (mean = 209.4 mg/kg ± 147.3 s.d.) but confidence intervals indicate that no difference occurs in stands 4 years or older (mean = 27.1mg/kg ± 16.6 s.d.) (Figure 10 A). Phosphorus in mineral soils showed a less subtle difference in concentration between microhabitats in the first year after fire (Figure 10 B). No clear trend in phosphorus dynamics is visible with respect to severity class but there is a general trend of decreasing concentration and variability in concentration in successively older stands.

Potassium concentrations in organic and mineral soils did not indicate identifiable trends in relation to levels of burn severity or time since fire (Figures 11 A and B).

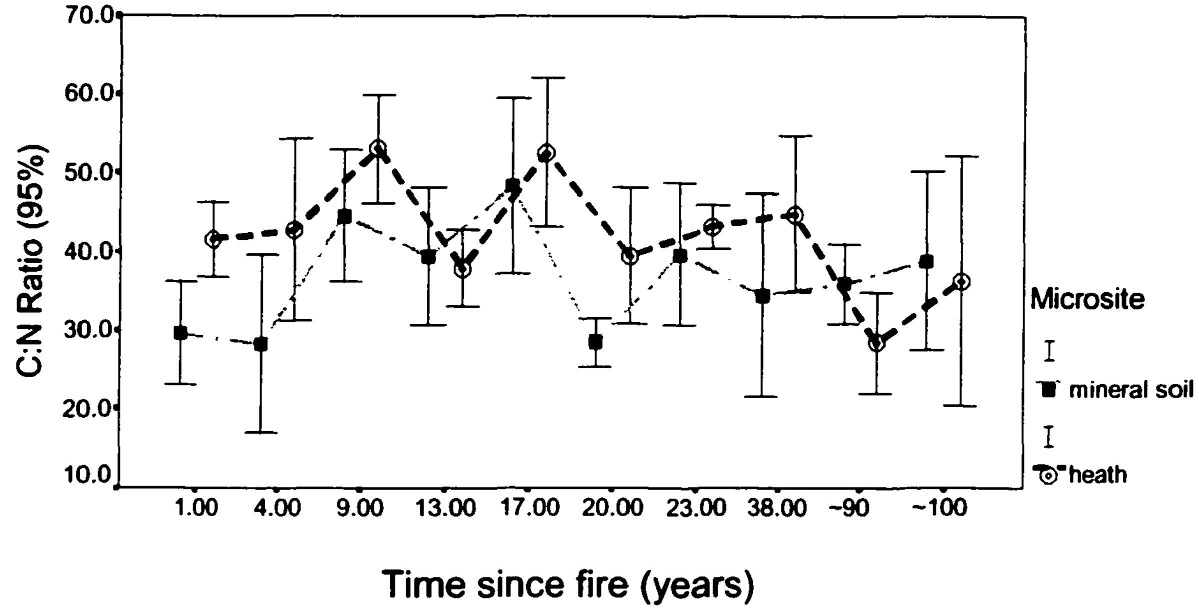

Figure 9. C:N ratio in relation to fire severity and time since fire. C:N ratio of severely burned organic soils were lower than those of organic soils of low fire severity microhabitats. Points are staggered slightly to avoid overlap of error bars.

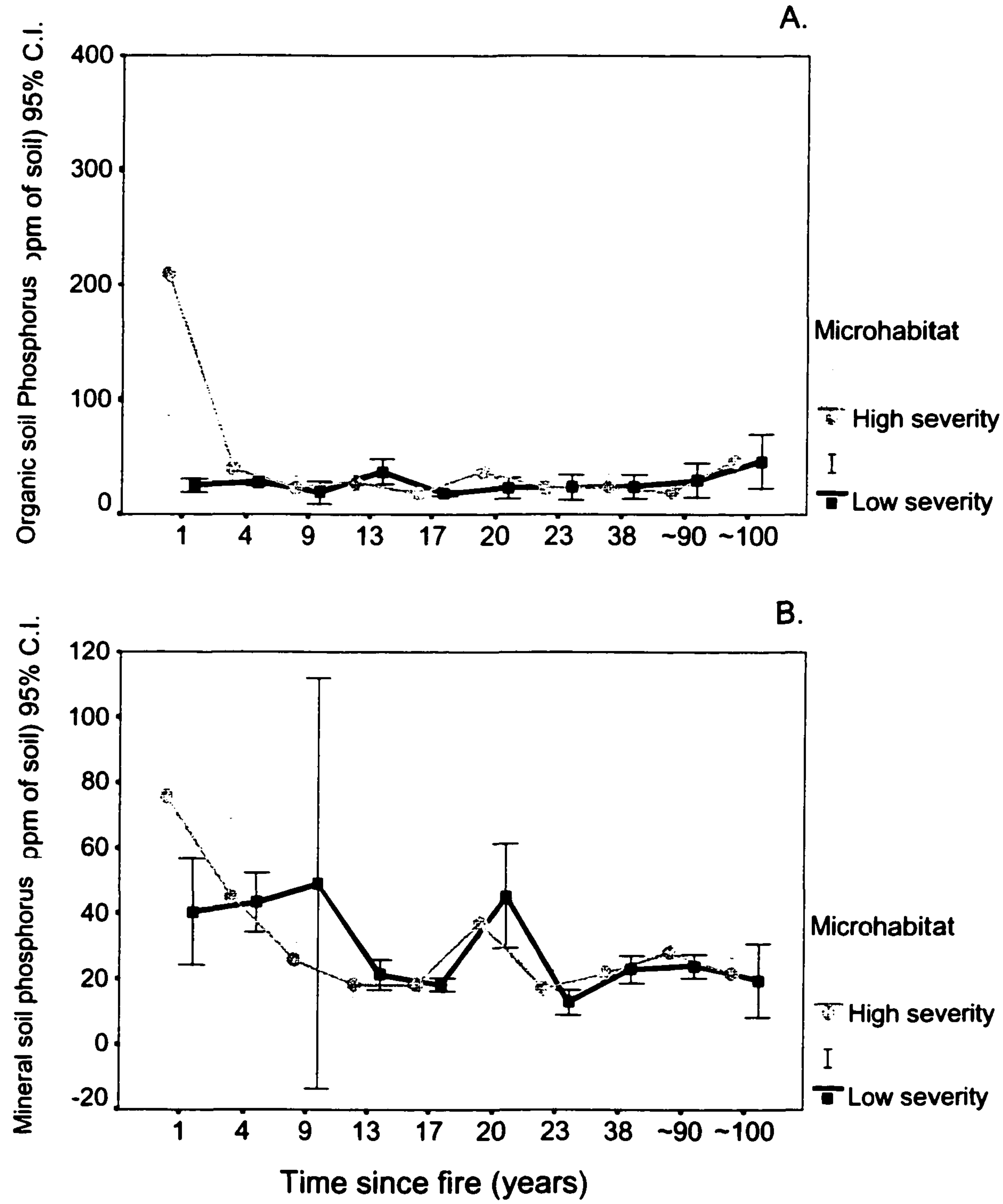

Figure 10. Concentrations of available phosphorus in relation to fire severity class and time since fire. In the first year after fire, severely burned organic soils had higher phosphorus availability than did soils of the low severity condition but older stands show no effect of fire severity (A). Mineral soil horizons showed now discernible difference in P availability between microsites but there was a general trend of decline in concentrations with increasing time since fire (B). Points are staggered around values on the x axis to prevent overlap of error bars.

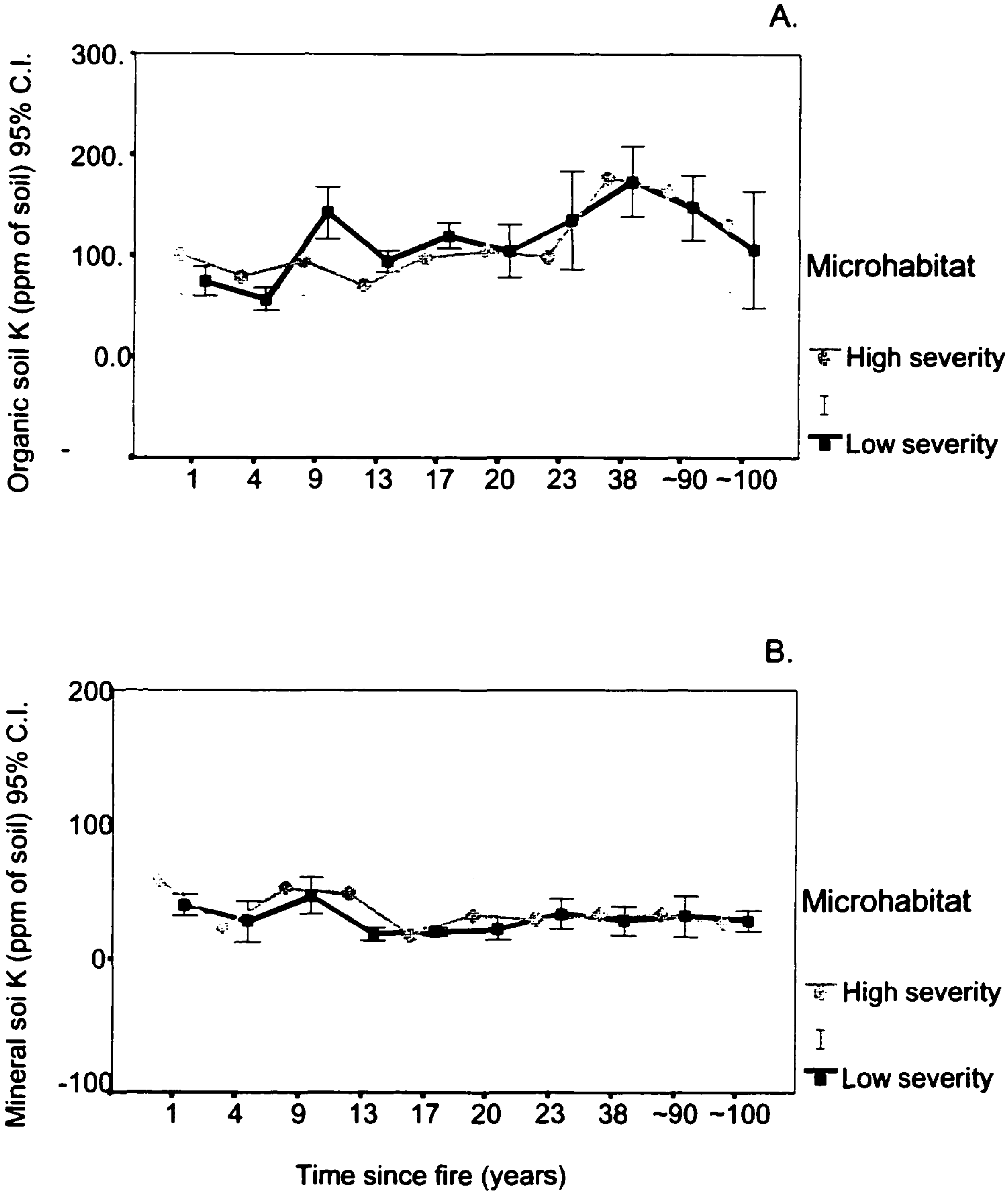

Figure 11. Concentrations of available potassium (K) in relation to fire severity class and time since fire. Potassium showed little variability with respect to fire severity classes or stand age in both organic soils (A) and mineral soils (B)

Discussion

The findings of this study suggest that fire can induce one of two pathways of succession in the eastern boreal forest which are respectively dominated by cornerstone species with different roles as ecosystem controllers (*sensu* Grime, 1998). Black spruce dominates a successional trajectory toward forest regeneration in severely burned microhabitats. Conversely, an ericaceous dwarf-shrub community dominated by *Kalmia* regenerates in scorched areas and induces a low-productive unforested stable state for at least 40 years (Chapter 1).

The two cornerstone species dominating the high and low productive pathways of post-fire recovery differ greatly in their top-down effects on community trait and species composition. Perhaps more critically, key functional traits strongly differentiate between the microhabitats. For example the "immediate" effects of black spruce cover is to offer canopy services to shade-dependent subordinates which in turn may have longer-term contributions to community nutrient budgets. The strong correlation between black spruce cover and pleurocarpous moss cover is an example of a commensal relationship driven by the microclimate engineering services of the conifer canopy (Bonan and Shugart, 1989) which leads to an increase in total system nitrogen as moss biomass accumulates over time (Billington, 1983; Van Cleve and Dyrness, 1983; Carleton and Read, 1991). I suggest that the geometric increase in black spruce productivity may be related to increased rates of direct nutrient cycling (*sensu* Went and Stark, 1968) as feathermoss biomass accumulates. Black spruce is known to have mycorrhizal relationships with *Pleurozium schreberi* which facilitate the direct allocation of nitrogen from senesced moss tissues to black spruce roots in the F-layer of the soil (Carleton and Read, 1991). The findings of this study strongly support the view of Grime (1998) that critical roles of species diversity in maintaining community function will be to facilitate community stability through re-establishment of the dominant 'engineering' species. Such a facilitative role was not detected in the *Kalmia* heath habitat probably because the shrub canopy degrades between 23 and 38 years after fire and heliotrophic lichens dominate in the unshaded condition (A.U. Mallik and R.G. Bloom, unpublished). Furthermore, this unproductive community has chemical afterlife effects which could explain the continued degradation of both the biotic and abiotic soil conditions through a cumulative retrogressive feedback (Damman, 1971).

The pattern of forest de-stabilization documented here shows important departures from patterns of post-fire regeneration observed in similar life zones but it is comparable to the findings of studies at the northern limit of the boreal forest. (e.g. Black and Bliss, 1978; Payette, 1992). Several studies in the west coast mountain forests (Halpbern, 1988, 1989; Halpbern and Franklin, 1989) and central North American fire driven forests (Abrams *et al.*, 1985) have described the floristic pathways of forest fire succession. They found that successional pathways were all characterized by similar patterns of *r-K* tradeoffs during succession in spite of the fact that fire was not always stand replacing. Halpbern (1988, 1989) found that various levels of fire "intensity" did not cause deviations from the general pattern of *r-K* tradeoffs in the first twenty years of succession. In the western taiga forests, invasive species were recorded even when the soil surface was not disturbed (i.e. canopy removal only) indicating that regeneration niches are available to fugitive invaders in this system under a wider range of disturbance conditions than observed in the present study. Halpbern (1988) reported measurable increases in successional complexity and higher degrees of departure from pre-fire community composition with increasing fire severity but the data indicate that fire severity (or lack thereof) did not destabilize the original stand composition. Conversely, the results of this study indicate that community recovery rates increase with increasing fire severity. The results of the present study support the findings of Halpern and Franklin (1989) and Abrams *et al.* (1985) in the sense that fire severity interacts with regeneration conditions to determine the degree to which various pathways deviate from the expected *r-K* models. However, the present study shows increasing forest stability with increasing severity while Halpbern and Franklin (1989) noted reduced rates of forest recovery with increasing disturbance severity. The opposing relationships between stability and severity observed in these two systems suggests that the nature of the interaction may depend on the degree of adaptedness the dominant species have to variability in the regional disturbance regime. This comparison yields the tentative conclusion that western coastal forests have a broader range of stand-replacing disturbances than do eastern coastal forests. Greater instability of eastern forests may be due to a combination of habitat factors including poorer, shallower soils, high soil acidity and a coastal climate moderated by cold Arctic currents, rather than tropical currents which influence the west coast forests of North America.

Prediction of multiple pathways following disturbances on similar sites may be difficult without detailed quantitative models (McCune and Allen, 1984; Cattelino *et al.*, 1979), but patterns of productivity seem to remain similar regardless of the initial floristic composition and the physiognomy of successional communities developing on similar sites. Even when pre-emptive competition interferes with climax development via inhibition mechanisms (*sensu* Connell and Slatyer, 1977), community selection for maximum productivity (Wilson, 1997) should ensure that the disturbed habitat is relatively productive. The operation of this assembly rule suggests that several stable community states are possible on similar sites but they should all be driven to high levels of resource use and therefore have similar net annual productivities. For example, Abrams *et al.* (1985) provided empirical evidence for multiple fire-induced states dominated by species as functionally diverse as *Carex spp.* (Cyperaceae) and *Pinus banksiana*

(Pinaceae) on similar sites. It was speculated that seedbed and dispersal limitations in some stands burned by wildfire determined the pathway of succession. In the absence of tree regeneration, the nature of competition shifted from the expected "Vertical Competition Strategy" (*sensu* Mallik *et al.*, 1997) with moderate rates of nutrient uptake and tree biomass accumulation to a "Horizontal Competition Strategy" with high nutrient uptake and annual turnover of herbaceous biomass rather than standing biomass accumulation. Independent of dispersal/establishment constraints on the expected community dominant, community productivity was maintained by the highly productive subordinate species which was shown to be a strong competitor for nitrogen. In this case, the nature of competition and the types of competition-related traits expressed in the system seem to be determined by the nature of the disturbance. This pattern implies that successful prediction of community assembly requires a knowledge of the type of competitive interactions which follow from different Initial Floristic Compositions (Egler, 1954). For example, although Abrams et al. (1985) found that the priority effects of *Carex* dominance altered the suite of deterministic competitive traits of the stable community from above- to below-ground characteristics, high levels of resource use intensity (*sensu* Loreau, 1998) appeared to be maintained. Consequently, spatial patterns of vegetation result from disturbance interactions with species traits (Cattelino *et al.*, 1979) and the indiosyncracies of local seed dispersal. In spite of a range of different successional communities and physiognomies which may follow a disturbance event, the conventional wisdom predicts that the identity of successional plants seem not to translate into differences in observed versus potential primary productivity following disturbance. The results of this study demonstrate that predictive models of succession (Odum, 1969; Bazazz, 1979; Tilman, 1985, 1994) and species co-existence (Connell, 1978; Huston, 1979) based on trade-offs are not directly applicable to this systems because, in eastern Canada, trade-offs are contingent on disturbance severity. Geographic application of these theories may a problem in regions where the species that survive non-severe disturbances have stress-tolerant properties but escape competitive displacement by the invasion of more productive plants in the regional species pool by the action of seedbed filters. Whether or not this combination of factors is esoteric to eastern Canada or is a potential phenomenon in more global ericaceous associations has not yet been determined.

In this study, the dependence of a progressive pathway on mineral soil microsites suggests that the process of species packing (a.k.a. community assembly) operate differently between the habitats measured in this study, in spite of their common mineral soil and light conditions. Different probabilities of establishment of facilitative and cornerstone species in severely burned versus scorched organic soils is an important factor determining successional pathways in this system.

The richness and frequency of plants in the *Kalmia* dominated heath community known to forage in mineral soil horizons is significantly less than in severely burned microsites. Consequently, there appears to be unexploited niche space underneath *Kalmia* humus which may be a cause of the observed reduction in biomass accumulation and vertical structure in comparison to the more "tightly packed" mineral soil communities. Failure of plants to saturate the niche space may be caused by physical/chemical barriers to seedling establishment in this thick, resource-poor organic soil. The inhospitability of these seedbeds was demonstrated by the spatial pattern of seed-invading plants observed in this study and was shown with a black spruce seeding experiment in a previous paper (Chapter 1). The fact that different establishment conditions result in significantly different pathways of community development leaves us to conclude that these forests have no redundancy within the tree functional group. Consequently, forest regeneration is de-stabilized when disturbance conditions are non-severe or are actively suppressed. Severe fire conditions are known to be infrequent but account for the majority of conditions in which boreal forests regenerate (Weber and Stock, 1998). For example, the return interval of the stand-replacing fire conditions of 1961 was estimated from fire records to be once every 100 to 200 years (Meades and Moores, 1994).

At the micro-habitat scale, severe fire has been shown to provide nutrient cycling services such as a 10-fold decrease in acidity and concomitant increases in availability of nutrients (Kimmins, 1997) such as the phosphorus levels observed here. This flush of nutrients is a characteristic of many boreal disturbances which improve conditions for the release of recalcitrant nutrients in the soil horizon (Aber and Melillo, 1991; Kimmins, 1997) but, in the present study, this transformation mechanism is limited to small and infrequent patches in the burned habitats. Since nutrient dynamics are an important predictor of plant life history strategies (Grime, 1979), failure of nutrients to be recycled in such large proportions of burned areas may select against ruderal and competitive strategists of the regional species pool. Chronically low nutrient availability and lack of regeneration niches indirectly facilitate occupancy of stress tolerant shrubs in much of the burned landscape in spite of the fact that edaphic conditions can support forests.

Management implications

It has been established that the majority of boreal forest stands are regenerated by unusually severe fire weather conditions that recur rarely but are estimated to be the regeneration agent for 80-90% of the area occupied by northern fire-driven forests (Weber and Stocks, 1998). With this in mind, I used the burned sites in this study (which were all artificially suppressed) as indicators of the future impact of fire suppression on forest regeneration. Although prevention of fires should positively feedback on the probability of severe fires in mature forests, conintued investment in technology for extinguishing fires threatens to destabilize the frequency-severity relationship which, historically, seems to have played a critical role in forest regeneration in these stands (Chapter I). At present, combinations of 'waterbombing' and 'hot spot' detection with infra red cameras are efficient respective methods for reducing the intensity and severity of fires in this region. It can only be speculated that as fire fighting technology improves, our ability to decouple the relationship between increasing fuel loads and fire severity will improve as well.

The impact of fire suppression, and perhaps the near extinction of natural fire regimes, on reductions of species diversity have largely focused on the potential loss of fugitive species which rely on landscape-level patch dynamics for their continued regional distribution. However, in the wet, maritime boreal forest, fire suppression is a force that, with increasing efficiency, could critically reduce the creation of regeneration niches on which the cornerstone species rely. The ability to predict the success of forest regeneration is of economic and conservation interest. The findings of the present paper may be useful for modifying current models of fire so the effects of fire suppression on successional pathways can be accurately forecasted by resource managers.

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Appendix 1. Ecological traits derived from published sources for each species in the dataset.

	Primary mode of persistence			Growth form		Mycorrhizal symbioses				Root concentration in soil		
Species	Dispersal	Seed bank	Vegetative	Woody	Herbaceous	ecto-mycorrhizae	endo-mycorrhizae	ericoid-mycorrhizae	no mycorrhizae	Mineral soil	Organic soil	Forage use
Trees												
Picea mariana	+a			+		+b				+a	+a	+a
Larix laricina	+a			+		+b					+e	e
*Betula papyrifera**	+a		+a	+		+b				+a		+a
Populus tremuloides	+a		+a	+		+b				+a		+a
Shrubs												
Prunus pensylvanica		+a	+a	+			+b			+a		+a
Alnus spp	+a		+a	+		+b				+a	+a	+a
Nemopanthus mucronuta			+	+								+
Sorbus decora		+a	+a	+			+b			+a	+a	+a
Amelanchier spp.	+a	-h	+a				+b			+a	+a	+a
Salix spp	+a		+a	+			+b			+a	+a	+a
Sub-shrubs												
Kalmia angustifolia			+f	+				+b			+fg	f
Vaccinium angustifolium			+a	+				+c			+g	+a
*Rhododendron canadense**			+e	+				+			+g	
*Ledum groenlandicum**			+a	+				+b			+g	a
Vaccinium vitis-idaea		g	+e	+				+c			+g	+
Gaultheria hispidula		g		+				+b			+d	
Herbs												
Cornus canadensis		?	+a		+		+b				+ag	+a
Linnaea borealis			+e	+			+b				+g	
Coptis trifoliate					+		+b				+g	
Aralia hispida					+		+(inferred from b)			+d		
Aralia nudicaulis					+		+b				+d	
Pearly everlasting	+e				+				+i	+e		
Solidago	+e				+				+i	+e		
Epilobium angustifolium	+e				+		+c			+e	+e	+a

Deschampsia spp.	+c			+	+c		+a	+d
Eriophorum spp.	+a	+a		+		+c	+d	+d
Pteridophytes and Bryophytes								
Pteridium aquilinum	+a d		+		+b			
Pluerozium schreberi	+		+					
Polytrichum spp.	+							
Dicranum spp.	+							
Ceratodon purpurea	+							
Sphagnum spp.	+		+					

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Chapter III.

Components of variability in nutrient status and its relationship to dominant vegetation of pyrogenic *Kalmia* heaths of Newfoundland, Canada

Abstract

Models of secondary succession generalize that vegetation dynamics proceed through a continuum of dominance by dispersal strategists, competitive strategists and stress tolerant strategists as resources accumulate and become stored in biomass. The occurrence of such transitions in plant strategies are contingent on increased nutrient availability in early versus late successional stages.

I tested for the effects of fire on nutrient status across a 38 year chronosequence of *Kalmia* heathland sites which were dominated by black spruce (*Picea mariana*, Pinacaea) prior to burning. Macronutrients and micronutrient concentrations in organic and mineral soils were determined for each site and the results were analyzed in relation to vegetation cover. Principal components analysis indicated that variability in soil moisture was the most important source of variability in nutrient status of both organic and mineral soil samples. Availability of metals (Ca, Na, Mg) increased with moisture content. Concentrations of limiting resources (available nitrogen and total nitrogen) were not related to time since fire. Analysis of relationships between vegetation and available N indicated that positive above-ground interactions among plants structure community composition more strongly than below-ground limitation of resources. Failure of these suppressed fires to release nitrogen bound in the raw humus layer which accumulates between disturbances may be an important factor in the creation of unproductive heathlands in the region. Implications for prediction of species composition in disturbed habitats are discussed.

Keywords: *Kalmia heathland, fire,nutrient status, succession, nitrogen limitation, percent cover*

Introduction

Causal relationships between resource availability and plant strategies during secondary succession are the basis of successional theory (Odum, 1969; Drury and Nisbet, 1973; Bazazz, 1979; Huston and Smith, 1987) and mechanistic models of vegetation responses to disturbance such as the resource-ratio hypothesis (Tilman, 1985). Disturbances have direct and indirect effects that often lead to increased available nutrient levels in early successional habitats. Nutrient pools often increase as decomposition rates accelerate in open conditions (Aber and Melillo, 1991). The reduction of biomass by disturbance also causes nutrient levels to rise since uptake is temporarily low. Such nutrient flushes are measurable within weeks, months or years depending on the type of disturbance and ecosystem (Aber and Melillo, 1991). Thereafter, declining resource availability is caused by increasing levels of resource uptake as standing biomass increases during succession. The combination of these factors during succession is related to increased standing biomass of vegetation, increased litter accumulation and reduced nutrient availability (Odum, 1969; Drury and Nisbet, 1973; Huston and Smith, 1987; Aber and Melillo, 1991). Consequently, the generalization that disturbances in mature communities create successional conditions in which species with high maximal growth rates are replaced by larger, slower growing plants as resource pools are diminished (Tilman, 1982; Huston and Smith, 1987; Odum, 1969; Drury and Nisbet, 1973; Bazazz, 1979; Pickett *et al.*, 1987; Brown, 1992) is a central assumption of models of secondary succession and species dynamics (Grime, 1979; Gleeson and Tilman, 1990; Tilman, 1994; Odum, 1969; Pickett *et al.*, 1987).

This trade-off principle has received empirical support when interactions between plants and resources are one-way but newer perspectives on soil resource availability recognize that plants add, as well as withdraw resources, into and from the soil solution (Pastor et al., 1987;

Pastor et al. 1988; Wardle *et al.* 1997). Plant modification of soil nutrient status can be caused simply by withdrawal of resources from the soil solution and through more complex processes such as differential decomposition rates of litter/rootfall inputs (Wardle *et al.*, 1997). The latter case will be especially critical in habitats which are open to colonization by dominant plants with different litter qualities whereby relatively rich litter stabilizes or increases nutrient status and productivity as observed in facilitation pathways (*sensu* Connell and Slatyer, 1977) and relatively poor litter inputs by community dominants causes measurable declines in nutrient status (Pastor *et al.* 1987; Pastor *et al.*, 1988; Wardle *et al.* 1997). The recognition of plant feedbacks on soil resource availability led to the recognition that plant tissue inputs in many habitats can be a factor structuring a wide variety of communities as physical barriers to colonization (Bergelson, 1990; Tilman, 1993; Facelli and Picket, 1991; Xiong and Nilsson, 1999) and/or chemical filters which limit rates of organic matter decomposition and nutrient availability (Northup *et al.*, 1998; Wardle *et al.*, 2000). Such feedbacks appear to be especially strong when abiotic factors of acid soils and oceanic climates coincide to create harsh habitats dominated by stress tolerant plants (often members of the Ericacaea) which have high nitrogen use efficiency and poor litter quality (Northup *et al.*, 1998; Damman, 1965, 1971). Permanent soil degradation in heathland may result when fires destabilize the recovery of forest canopy species allowing ericaceous plants to gain dominance and inhibit tree re-colonization (Gimingham, 1972; Latham *et al.*, 1996; Damman, 1971). In some cases the inhibition of succession by ericaceous plants may give way to site retrogression if the chemical after-life effects of litter on soil physical properties go unchecked by disturbance for long periods of time (Damman, 1965).

Members of the Ericaceae are among the most successful vascular plants in the northern hemisphere (de Montigny and Weetman, 1990) and there is widespread evidence for their abundance being coincident with human dominated landscapes (Owen and Marrs, 2000; Tinsley, 1975; Meades, 1983; Gimingham, 1972). Ericaceous plants such as those of the genuses *Kalmia, Calluna, Vaccinium* and *Gaultheria* are thought to achieve local dominance when disturbance events de-stabilize the persistence of the regional tree species and thereby release the understory dwarf shrubs from competition for light and nutrients (Gimingham, 1972; Mallik, 1995; de Montingy and Weetman, 1990). However, whether or not tree exclusion following disturbance in these regions is a permanent de-stabilization has been debated (Gimingham, 1972; Gong, 1976). Rode (1999) documented changes in organic soil conditions of heathland in Germany and used the improving soil conditions to explain the chemical mechanism behind heath replacement by conifer colonization which is later succeeded by broad-leaf forest re-establishment. In contrast, New World *Kalmia* heathland does not appear to support these transient dynamics over time. *Kalmia* heathland appears to encourage permanent feedbacks on both the organic and mineral soil habitat which reduce site fertility (Damman, 1971), limits tree colonization (Mallik *et al.*, unpublished) and interferes with growth rates of established trees (Mallik, 2001). The mechanism for this retrogression has been documented elsewhere and has been shown to have physical and soil nutrient components (Chapter I and II). Stand-level assessments of nutrient status of *Kalmia* heathland soils have been made in relation to forest nutrient status (Inderjit and Mallik, 1999) but such comparisons are weakened by the possibility that nutrient status is dependent on the length of *Kalmia*'s term of occupancy since site degradation is time-dependent (Damman, 1965).

The purpose of this study was to determine if patterns of post-fire vegetation cover and physiognomic development across a chronosequence could be explained by soil nutrient properties in *Kalmia* heath. Two hypotheses were tested to determine if *Kalmia* heathland exhibited conditions of improving nutrient status over time as seen in European heathland (e.g. Gimingham, 1972; Rode, 1999). I hypothesized that (1) nutrient status varied between heath communities according to identifiable habitat factors such as time since fire, moisture content, pH and organic soil depth and (2) that limiting nutrient concentrations such as available nitrogen (in the form of ammonium, NH_4^+), total nitrogen (N) and total phosphorus (P) are related to species richness, vegetation cover and to the life history traits of the dominant plant functional groups across a post-fire chronosequence.

Methods

Site descriptions

The study was conducted in the greater Terra Nova National Park ecosystem located in the east-central Newfoundland ecoregion (Damman, 1964) (48° 35' N lat. 54° 5' W long.). The area experiences an oceanic climate with high annual precipitation (1184.3 mm) and mean growing season (May-September) temperature of 12.6°C (Power, 2000).

At the landscape level, forest habitats are highly fragmented by bogs and are dominated by boreal conifers such as black spruce (*Picea. mariana*) and balsam fir (*Abies balsamea*) on well-drained soils and, to a lesser extent, conifer mixed wood stands in the richest sites (Power, 2000). Forest soils are generally podzollic with pH ranging between 3 and 5 (Meades and Moores, 1994). Large even-aged stands of black spruce with charcoal macrofossils in the soil profile indicate that fire is a historical factor influencing the present forest structure in the Park (Power, 1996, 2000). The study area contained nine ericaceous barrens dominated by *Kalmia angustifolia* (hereafter referred to as *Kalmia*) of known fire history within a 100 km radius of Terra Nova National Park. Sites were burned between the years 1961 and 1998. These fires occurred in stands growing on mineral soils of poor to good quality and are limited primarily by fertility. Black spruce stem densities on these sites generally vary between 4700 and 6800 stems/ha (Meades and Moores, 1994).

Sampling areas in the nine sites were delineated within each *Kalmia* barren to match sampling areas among sites on the basis of soil drainage, mineral soil development and distance from undisturbed edges. Based on observations of adjacent burned and unburned stands with similar black spruce stem densities (dead and live respectively), pre-fire vegetation was known to be black spruce with ericaceous understory dominated by *Kalmia*. The resulting series of sites was assumed to represent a successional chronosequence since abiotic between-site variability, other than time since fire was controlled in the sampling design as mentioned above (Brown, 1992).

Sample collection and analysis

Sampling of soils and vegetation cover were taken randomly within the selected sites but were performed independently within sites in June and August 1999 respectively. Percent cover of all plants was measured in 10 randomly placed 1 m^2 quadrats in each site late in the growing season (August) when it was assumed that most species would be identifiable. However, the presence of spring ephemerals and species with short annual cycles (such as moccasin flower, *Cypripedium acaule*) was likely not detected in the field. Soil sampling was done early in the growing season when it was assumed that plant uptake of soil resources would be relatively low. At each sampling location representative organic and mineral soil samples (dimensions: 15 cm x 15 cm x 15 cm) were excavated and placed in separate polyethylene bags. Sub-samples of approximately 200 cm^3 were collected in mid-June to measure early season soil nutrient status and the remaining soil monoliths were replaced in the soil profile and allowed to incubate for approximately 30 days in order to measure nitrogen immobilization/mineralization rates (Eno, 1960). In mid-July and mid-August, second and third 2.5 x 5 x 15 cm sub-samples were collected from each location and were analysed for available ammonium. All samples were stored frozen to reduce microbial activity until analysis in January, 2000. At all stages of sample handling care was taken to protect the samples from air drying. A total of 90 organic samples and 83 mineral soil samples were collected. Seven of the sampling locations occurred on rocky soils and did not yield mineral soil samples.

Sub-samples of the soils collected in June were analyzed to establish soil profiles consisting of 15 parameters for each sample. Ammonium nitrogen was measured during each term of incubation and concentrations were divided by the number of incubation days to calculate average changes in nitrogen over each of the two terms. Ammonium was extracted from moist soil samples using 1 M KCl and was analyzed using an autoanalyzer (see Inderjit and Mallik, 1999). Total N and P were determined using the Micro-Kjeldahl technique (Allen, 1989). Total phenols were extracted using distilled water and were analyzed using the method of Swain and Hillis (1959) with the modifications of using phenol crystal as the standard and measuring absorbance at 725 nm (Inderjit and Mallik, 1996). Metals and sulfur concentrations were determined by extraction in 0.1 M HCl and analysing the extracts with an Inductively Coupled Argon Plasma system (ICP). A blank subtraction was used to control for impurities. Results for copper were removed from further analysis since it appeared to be adsorbed onto mineral soils in high-clay samples and yielded negative concentrations following subtraction of copper concentrations in the blank extraction samples. Organic matter content was determined by loss on ignition (Allen, 1989). Results for extracted nutrients were expressed as a proportion of soil dry weight which was determined by measuring and subtracting the moisture content of subsamples prior to extraction.

Statistical analysis

Principal components analysis (PCA) was used without rotation to objectively extract the main components of variability in nutrient parameters. Tests for correlations between the axes extracted by PCA and known habitat factors such as within-site variability in moisture content, pH and organic soil depth were conducted using SPSS (1998). Analysis of between-site variability consisted of tests for correlations among site nutrient status, time since fire and percent cover of dominant plants. Tests involving time since fire were conducted separately by averaging PCA scores for samples from each stand to avoid the inflation of statistical power with non-independent sample ages (Hurlbert, 1984).

Spearman's non-parametric rank order co-efficient was used for all correlation analyses. Tests for between-site differences in concentrations of limiting nutrients (ammonium-nitrogen (NH_4^+), total nitrogen (N) and total phosphorus, (P)) and nitrogen mineralization rate were conducted using the non-parametric Kruskal-Wallis procedure (SPSS, 1998) due to non normality of the data. Organic and mineral soil profiles were treated independently in all analyses. For some variables sample size varied due to insufficient sample tissue for all analyses.

Relationships between nutrients and vascular plant richness, total vascular plant cover were tested with correlation analysis. Plant cover data was corrected for average site organic matter depth to remove biases caused by different levels of plant colonization limitation according to varying thickness of organic accumulation (Facelli and Pickett, 1991; Xiong and Nilsson, 1999). Above-ground interactions of species richness and species dominance were also analysed with correlation.

Results

The first four principal components extracted from the data accounted for 62.7% and 69.4% of the variability in organic and mineral soil nutrient status respectively (Table 1). The first organic soil principal component axis appears to be driven by micronutrient concentrations such as sodium (Na), manganese (Mn), calcium (Ca) and zinc (Zn) which had relatively high factor loadings ($\geq .60$) on this axis (Table 2). Available nitrogen (NH_4^+) and nitrogen mineralization rate appeared to be negatively correlated and were the only parameters with relatively high factor loadings on axis 2. Relative to other variables, these nutrient parameters were also influential on axis 3 but the loadings were weak. Axis 4 had no factor loadings greater than .46 and, consequently, showed no trends in its representation of the raw data.

Axes of variability in mineral soils showed clearer trends in the relationship between the axes and original nutrient variables. As in organic soils, axis one in the mineral soil data was primarily driven by the micronutrients Ca, Mg and Zn with factor loadings >.80 but explained 11% more variability in the data (Table 1). Potassium (K), total phenolics and iron (Fe) also contributed to variation in this dimension of the data (Table 3). Axis two was strongly associated with concentrations of aluminum (Al) and phosphorus and accounted for 14 % of nutrient status variability. Component three showed declining factor loadings with three moderately weak associations with Mn, Na and P. Axis 4 appears to represent a gradient in available nitrogen (ammonium) but this dimension of the data explained less than 9% of the total soil status variation.

Table 1. Summary of principal components of variability in nutrient status of organic and mineral soils across the 38 year *Kalmia* heath chronosequence.

Soil Horizon	Axis	Eigenvalue	% Variance explained	Cumulative % variance explained
Organic soils	1	3.174	22.671	22.671
	2	2.376	16.969	39.640
	3	1.693	12.090	51.731
	4	1.530	10.929	62.660
Mineral soils	1	4.757	33.981	33.981
	2	1.961	14.009	47.990
	3	1.762	12.584	60.573
	4	1.238	8.845	69.418

Table 2. Factor loadings of nutrient variables on extracted axes of variability in organic soils. Nutrient parameters are listed in order of descending importance to the principal component 1.

Nutrient parameters	Components			
	1	2	3	4
Na	.670	.399	.073	-.454
Mn	.627	-.246	-.121	.428
Ca	.606	-.531	-.261	.163
Zn	.598	-.438	-.330	.348
Mg	.586	-.171	-.154	-.347
Total phenolics	.579	.290	-.035	-.262
K	.542	.181	.307	.107
P	.499	.218	.474	.457
S	.406	.428	.188	-.429
N	.366	.047	.567	.163
NH4	.191	.606	-.588	.071
Mineralization rate	-.032	-.600	.573	-.211
Fe	-.041	.579	-.140	.383
Al	-.216	.490	.318	.423

Table 3. Factor loadings of nutrient variables on extracted axes of variability in mineral soils. Nutrient parameters are listed in order of descending importance to the principal component 1.

Nutrient parameters	Component			
	1	2	3	4
Ca	.885	-.288	-.215	-.121
Mg	.826	-.290	.132	.246
Zn	.801	-.077	-.417	-.230
K	.766	-.104	-.105	.213
Mn	.615	-.226	-.604	-.269
Total phenolics	.601	.092	.086	.233
Fe	.599	.305	.365	-.309
Total N	.513	.490	-.052	.341
Al	.464	.766	.262	-.190
Na	.410	-.270	.625	-.343
Ammonium-N	.348	-.154	.245	.735
S	.307	-.428	.622	-.177
P	.306	.714	.008	-.028
N Mineralization rate	.103	.095	-.315	-.037

Relationships of principal components to habitat variables

Organic matter depth

None of the principal components of mineral soil status were related to organic matter depth (Table 4). Organic matter depth appeared to feedback on the fourth axis of its nutrient soil status (representing available nitrogen) but the relationship was weak ($r = -0.288$, $p = 0.017$).

pH

The third and fourth principal components of mineral soils explained a total of 21% of variation and were both significantly related to pH (Table 4). Likewise, pH appeared to be an important factor in organic soils and was significantly related components 1,2, and 4.

Moisture content

All four components of mineral soil nutrient status were significantly related. Of these, component 1, representing metal concentrations had the second strongest correlation ($r = 0.54$). Al and P in mineral soils (component 2) also appeared to be positively related to moisture although the relationship was weak. The association of moisture with component three (Mn, Na and S was the strongest correlation observed among all the relationships ($r = 0.6$). Ammonium nitrogen (the most important factor in component 4) appeared to be weakly negatively correlated with moisture content ($r = - .33$) (Table 4).

Time since fire

Time since fire showed equally strong correlations to component one in both soil types ($r = \sim.5$) but neither of these relationships were statistically significant. No relationships of stand age to other components were detected in either soil type (Table 4).

Table 4. Correlations between variability in nutrient concentration (principal components) and *Kalmia* heath habitat factors.

Soil horizon	Habitat factors		Components			
			1	2	3	4
Mineral soil	Organic matter depth	$r_{(s)}$	-.078	.013	.095	.128
		p	.553	.924	.472	.328
		n	60	60	60	60
	pH	$r_{(s)}$	.116	.074	.320	-.389
		p	.365	.562	.011	.002
		n	63	63	63	63
	Moisture content	$r_{(s)}$	.540	.274	.604	-.331
		p	.000	.029	.000	.008
		n	64	64	64	64
	Time since fire (years)	$r_{(s)}$	-.552	.075	-.050	-.176
		p	.123	.847	.898	.651
		n	9	9	9	9
Organic soil	Organic matter depth (cm)	$r_{(s)}$	.181	.149	-.081	-.288
		p	.140	.226	.513	.017
		n	68	68	68	68
	pH	$r_{(s)}$	.280	.229	-.012	.325
		p	.016	.051	.919	.005
		n	73	73	73	73
	Moisture content %	$r_{(s)}$	.263	.392	-.110	-.330
		p	.024	.001	.352	.004
		n	74	74	74	74
	Time since fire (years)	$r_{(s)}$	.539	-.270	-.234	-.330
		p	.134	.482	.576	.386
		n	9	9	9	9

Concentrations of limiting nutrients: nitrogen, phosphorus

Concentrations of nutrients limiting plant growth in these habitats, such as ammonium nitrogen, nitrogen mineralization, total N and total P, were not associated with the primary components of variability in either mineral or organic soils (Table 2). They were, however, marginally important (factor loading ~ 0.6) in subsequent components.

The null hypothesis that sites did not differ in content of limiting nutrients was accepted since total nitrogen in organic and mineral soils did not differ significantly between sites (Table 5). Ammonium levels and mineral soil phosphorus showed a weak tendency to decline over time but the relationship was not significant (Table 6). Organic soil phosphorus, however showed a strong tendency to decline over time ($r = -.93$, $p < 0.001$).

Total net nitrogen mineralization over the 60 day term was negligible in all sites in organic soils (mean = -1.40 mg/kg/d ± 3.5 s.d.) and mineral soils (mean = - 0.20 ± 1.0) and was not related to time since fire ($r < 0.35$, p = n.s.).

Variability in ammonium concentrations among samples was correlated with total nitrogen in mineral soils ($r = 0.26$, $n = 76$, $p = 0.025$) and with the ratio of organic matter (loss on ignition) to total N in organic soils ($r = 0.39$, $n = 77$, $p < 0.001$). Ammonium levels increased slightly with increasing concentrations of total phenols in organic soils ($r = 0.26$, $n = 82$, $p = 0.02$). Mean values of soil chemical properties are summarized for each site in Table 7.

Table 5. Results of Kruskal-Wallis non-parametric tests for differences in limiting nutrients among the nine heathland habitats.

Soil horizon		Nitrogen mineralization rate	Ammonium-N	Total N	Total P
mineral	Chi-Square	9.88	24.32	12.43	11.63
	df	8	8	8	8
	Sig.	.274	.002	.133	.169
organic	Chi-Square	11.20	20.27	10.06	19.67
	df	8	8	8	8
	Sig.	.191	.009	.261	.012

Table 6. Relationships between limiting nutrients and time since fire in *Kalmia* heath barrens.

Soil horizon	Limiting nutrients		Time since fire (years)
Mineral soil	Ammonium-N	$r_{(s)}$	-.418
		p	.262
		n	9
	Total N	$r_{(s)}$	.000
		p	1.000
		n	9
	Total P	$r_{(s)}$	-.561
		p	.116
		n	9
Organic soil	Ammonium-N	$r_{(s)}$	-.527
		p	.145
		n	9
	Total N	$r_{(s)}$	.109
		p	.781
		n	9
	Total P	$r_{(s)}$	-.929
		p	.000
		n	9

Table 7. Mean values of physical habitat and nutrient status parameters in a *Kalmia* heath fire chronosequence. Values in brackets indicate standard deviation.

Chemical characteristics	Soil Horizon	Time since fire (years)								
		1•	1 ‡	4	9	13	17	20	23	38
Organic soil depth (cm)		12.9 (7.1)	13.5 (4.4)	11.0 (7.4)	10.2 (6.3)	10.3 (4.7)	13.9 (5.3)	11.8 (2.9)	8.2 (2.2)	15.5 (6.7)
Moisture content (%)	O	.73 (.05)	.77 (.04)	.74 (.99)	.71 (.05)	.62 (.07)	.76 (.02)	.69 (.07)	.74 (.05)	.79 (.02)
	Ae	.27 (.06)	.35 (.13)	.29 (.05)	.26 (.05)	.26 (.19)	.28 (.04)	.28 (.11)	.25 (.04)	.31 (.08)
pH	O	3.0 (.2)	3.3 (.3)	3.2 (.4)	2.9 (.3)	2.9 (.2)	3.1 (.2)	3.1 (.1)	3.2 (.2)	3.0 (.2)
	Ae	3.5 (.4)	3.3 (.3)	3.3 (.5)	3.7 (.2)	3.0 (.3)	3.6 (.4)	3.4 (.4)	3.2 (.3)	3.4 (.3)
Organic matter (%)	O	77.7 (8.2)	89.6 (8.9)	86.7 (14.6)	88.7 (7.2)	72.5 (32.8)	89.9 (6.7)	83.4 (29.6)	86.7 (9.5)	92.2 (7.4)
	Ae	4.6 (2.5)	7.7 (6.8)	5.6 (4.0)	7.2 (2.1	15.2 (30.3)	5.2 (2.5)	8.0 (5.9)	3.8 (1.9)	6.5 (4.4)
Total phenolics mg/kg	O	96.0 (56.2)	101.6 (28.6)	76.6 (29.6)	57.9 (20.4)	41.1 (15.4)	76.1 (19.9)	54.8 (18.7)	59.5 (22.6)	66.5 (22.1)
	Ae	3.1 (1.4)	6.3 (4.6)	4.8 (2.6)	4.8 (2.0)	5.5 (3.5)	3.9 (2.0)	3.2 (1.3)	3.4 (2.1)	4.7 (1.2)
Ammonium-N mg/kg	O	103.0 (107.1)	169.6 (91.4)	73.2 (119.4)	16.1 (5.7)	100.7 (124.6)	21.8 (15.9)	74.4 (135.0)	36.0 (58.7)	43.6 (73.8)
	Ae	6.6 (4.5)	21.4 (31.1)	3.6 (2.3)	3.3 (1.2)	2.8 (4.8)	2.3 (1.1)	18.8 (40.7)	2.0 (2.0)	5.2 (5.6)
N mineralization rate mg/kg/day	O	-4.1 (3.9)	-1.3 (3.3)	1.5 (3.0)	-.4 (.3)	-2.2 (4.2)	-.6 (.8)	-2.9 (5.3)	-.54 (2.1)	-1.4 (3.1)
	Ae	-.19 (.1)	-.7 (1.5)	-.5 (1.4)	.3 (.9)	.2 (.3)	-.0 (.1)	-.2 (.3)	-.4 (1.7)	-.1 (.4)
Total N g/kg	O	7.3 (2.7)	5.1 (2.8)	4.8 (2.4)	5.3 (2.6)	7.4 (2.5)	4.7 (2.6)	6.0 (4.8)	5.6 (2.0)	5.3 (3.0)
	Ae	.6 (.3)	.6 (.3)	.6 (.5)	1.1 (1.1)	.8 (.4)	.6 (.3)	.9 (.7)	.4 (.3)	.7 (.2)
Total P g/kg	O	.9 (.3)	.7 (.2)	.6 (.2)	.6 (.4)	.6 (.2)	.5 (.2)	.5 (.3)	.6 (.2)	.4 (.2)

• denotes site near Bunyan Cove; ‡ indicates site near Triton Brook

Table 7 cont'd

K g/kg	O	745.6 (210.8)	549.0 (207.8)	274.8 (100.0)	456.4 (142.6)	355.1 (123.4)	326.8 (108.4)	381.6 (156.7)	560.7 (279.6)	495.1 (278.7)
	Ae	22.9 (14.7)	41.2 (27.9)	21.4 (12.6)	36.8 (27.8)	34.3 (25.9)	9.6 (7.7)	25.1 (22.1)	21.2 (24.3)	27.2 (22.5)
Ca g/kg	O	2 663.9 (1 601.8)	4 340.2 (5 026.2)	3 309.0 (2 370.3)	2 745.3 (1 747.0)	2 214.2 (1 192.5)	2 428.7 (1 280.2)	2 699.0 (1 407.2)	2 921.8 (1 247.9)	2 131.2 (995.9)
	Ae	58.5 (48.9)	131.3 (141.0)	37.8 (46.0)	44.1 (39.5)	136.6 (219.4)	407.7 (17.3)	60.0 (102.9)	37.8 (17.1)	51.8 (26.3)
Na g/kg	O	253.2 (155.3)	236.5 (91.0)	196.7 (97.3)	48.8 (21.9)	60.1 (44.1)	148.2 (32.2)	81.8 (34.8)	155.4 (39.6)	148.2 (55.3)
	Ae	12.4 (4.1)	20.4 (7.8)	9.3 (9.4)	.1 (.2)	2.5 (4.8)	12.3 (3.9)	1.0 (2.3)	12.1 (3.5)	13.7 (4.5)
Mg g/kg	O	996.2 (505.1)	1 028.9 (479.1)	930.6 (326.0)	754.8 (324.1)	578.9 (351.5)	772.7 (468.9)	755.4 (269.8)	720.0 (197.7)	760.0 (327.4)
	Ae	21.1 (12.9)	38.5 (39.0)	13.1 (16.5)	21.2 (16.4)	22.8 (18.8)	10.3 (3.4)	28.4 (36.0)	14.4 (5.8)	16.6 (5.5)
S g/kg	O	48.3 (34.8)	48.1 (22.5)	39.6 (28.3)	10.5 (11.7)	25.3 (20.2)	34.8 (20.9)	23.1 (14.6)	46.0 (25.7)	44.6 (29.8)
	Ae	3.6 (3.8)	4.1 (3.7)	3.0 (1.9)	.6 (1.3)	.6 (1.0)	3.3 (3.4)	1.8 (2.6)	3.6 (2.1)	3.9 (3.8)
Fe g/kg	O	56.4 (54.0)	276.2 (355.9)	27.2 (38.9)	22.7 (16.4)	38.8 (86.0)	31.8 (40.0)	52.0 (67.9)	15.9 (13.4)	73.8 (198.4)
	Ae	32.5 (40.6)	62.9 (61.8)	44.6 (39.5)	39.8 (32.2)	40.7 (76.5)	45.9 (29.2)	18.0 (16.4)	32.4 (42.4)	34.5 (23.7)
Al g/kg	O	1 3057.9 (1658.6)	855.9 (604.5)	450.6 (216.7)	615.7 (380.7)	681.2 (1 428.3)	842.2 (970.4)	576.0 (510.2)	319.6 (149.4)	549.5 (631.7)
	Ae	268.4 (197.3)	489.2 (218.3)	639.8 (470.4)	481.7 (351.8)	428.6 (541.3)	362.8 (257.8)	267.6 (172.8)	185.9 (181.1)	423.1 (269.4)
Mn g/kg	O	342.9 (359.2)	272.0 (191.8)	136.5 (124.5)	168.6 (164.6)	254.2 (314.9)	152.1 (184.5)	98.0 (84.7)	196.0 (180.8)	24.9 (16.7)
	Ae	4.8 (7.0)	6.6 (6.4)	.8 (1.0)	3.3 (2.4)	22.5 (37.3)	1.2 (1.4)	2.0 (1.5)	.8 (.7)	.6 (.8)
Zn g/kg	O	30.9 (18.0)	43.2 (41.0)	25.9 (25.3)	28.0 (13.6)	30.5 (17.3)	18.9 (11.8)	27.5 (13.9)	31.0 (13.1)	14.5 (6.7)
	Ae	.6 (.8)	1.1 (1.2)	.5 (.4)	.7 (.2)	2.5 (3.6)	.2 (.2)	.8 (.8)	.5 (.5)	.3 (.2)

Nutrient status and relationships among vegetation

Total vascular plant cover (corrected for organic matter depth) was strongly inversely related to available nitrogen in mineral soils (r = -.72, n = 9, p = 0.03) but was not related to that of organic soil (r = - .37, n = 9, p = n.s.) not related to nitrogen availability in either horizon (Figure 1). Species richness declined monotonically with increasing levels of ammonium (corrected for organic matter depth) in organic soils (r = -.67, n= 9, p = 0.05) as well as mineral soils (r =-.78, n= 9, p = 0.013 (Figure 2 A,B). In contrast, increasing cover of *Kalmia* was positively associated with species richness (r = .70, n = 9, p = 0.030) (Figure 2 C). Similarly, total cover of shade tolerant herbaceous plants was also strongly correlated with *Kalmia* cover (r = .76, n = 9, p = 0.04) (Figure 3 A). *Kalmia* cover did not appear to significantly influence the cover of shade intolerant species (r = - .25, n= 9, p = n.s.) (Figure 3 B.).

Cover of black spruce (max. cover = 10.9%) increased significantly with stand age (r = .70, n =9, p = .029) but was not related to nitrogen availability in either soil horizon and remained at low cover values (mean cover < 3% ± 3.7 s.d.). The habitat is dominated by ericaceous dwarf shrubs across all stages of the chronosequence (mean cover = 95% ± 0.06 s.d.) (Figure 4 A). Over this period, *Kalmia* exhibits a tendency to decline over time but the pattern is not statistically significant (r = - .47, n = 9, p = n.s.) (Figure 4 B).

Moisture content was an important correlate of several variables in both organic (Table 2) and mineral soils (Table 3). Metal and trace element concentrations, especially Al and Mg, were significantly correlated with moisture content (Table 4).

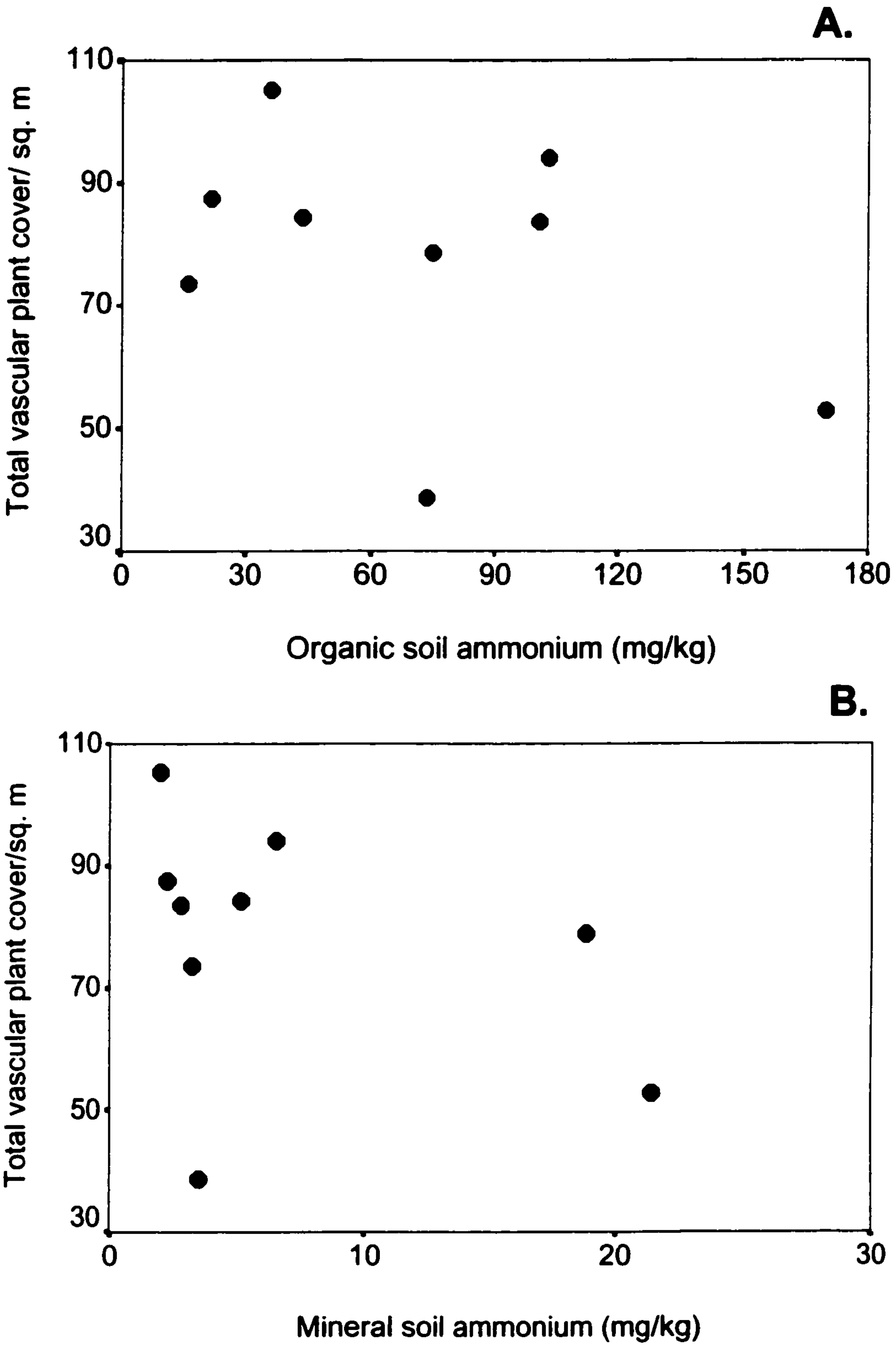

Figure 1. Total cover of vascular plants plotted against concentrations of available nitrogen (ammonium) in organic soils (A) and mineral soils (B).

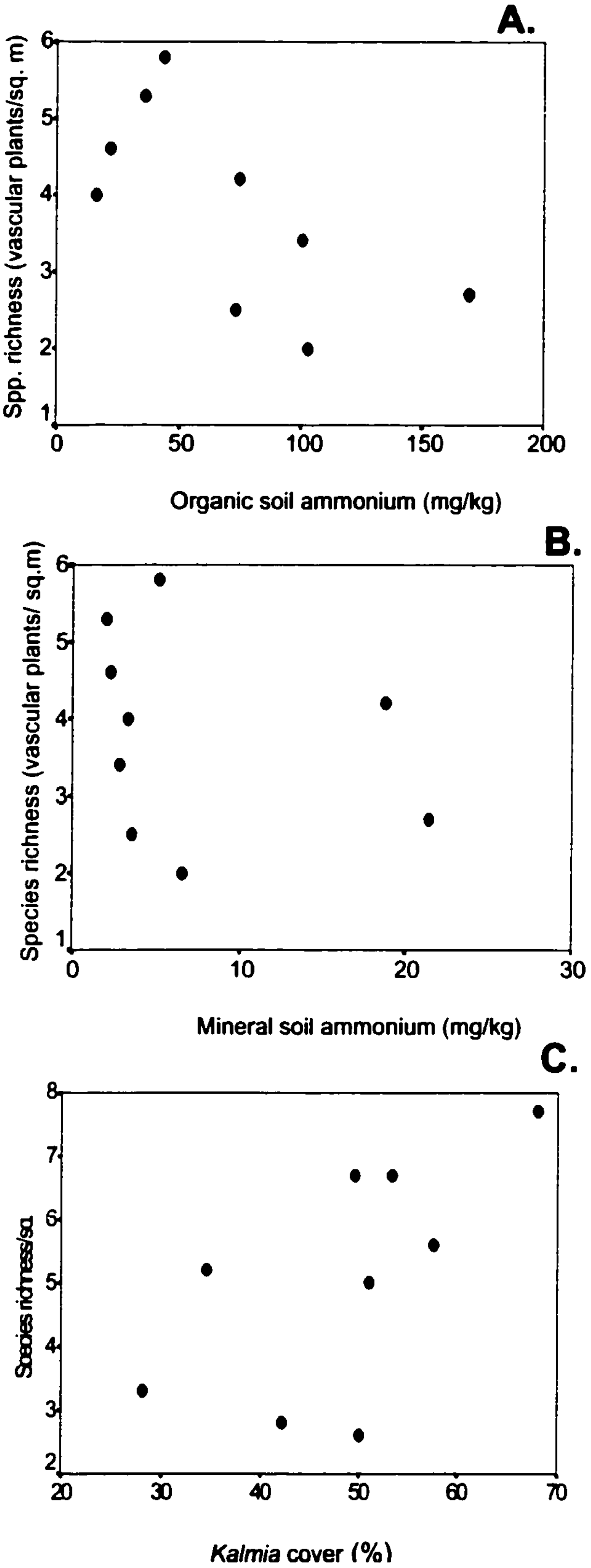

Figure 2. Fertility and dominance as variables affecting vascular plant richness in *Kalmia* heath. Richness is inversely related to soil fertility in organic soils (A) but is not significantly related to mineral soil fertility (B). Richness also appears to be related to above-ground interactions since species richness responds positively to increasing proportions of *Kalmia* cover (C). Values are means of 10 samples in each site

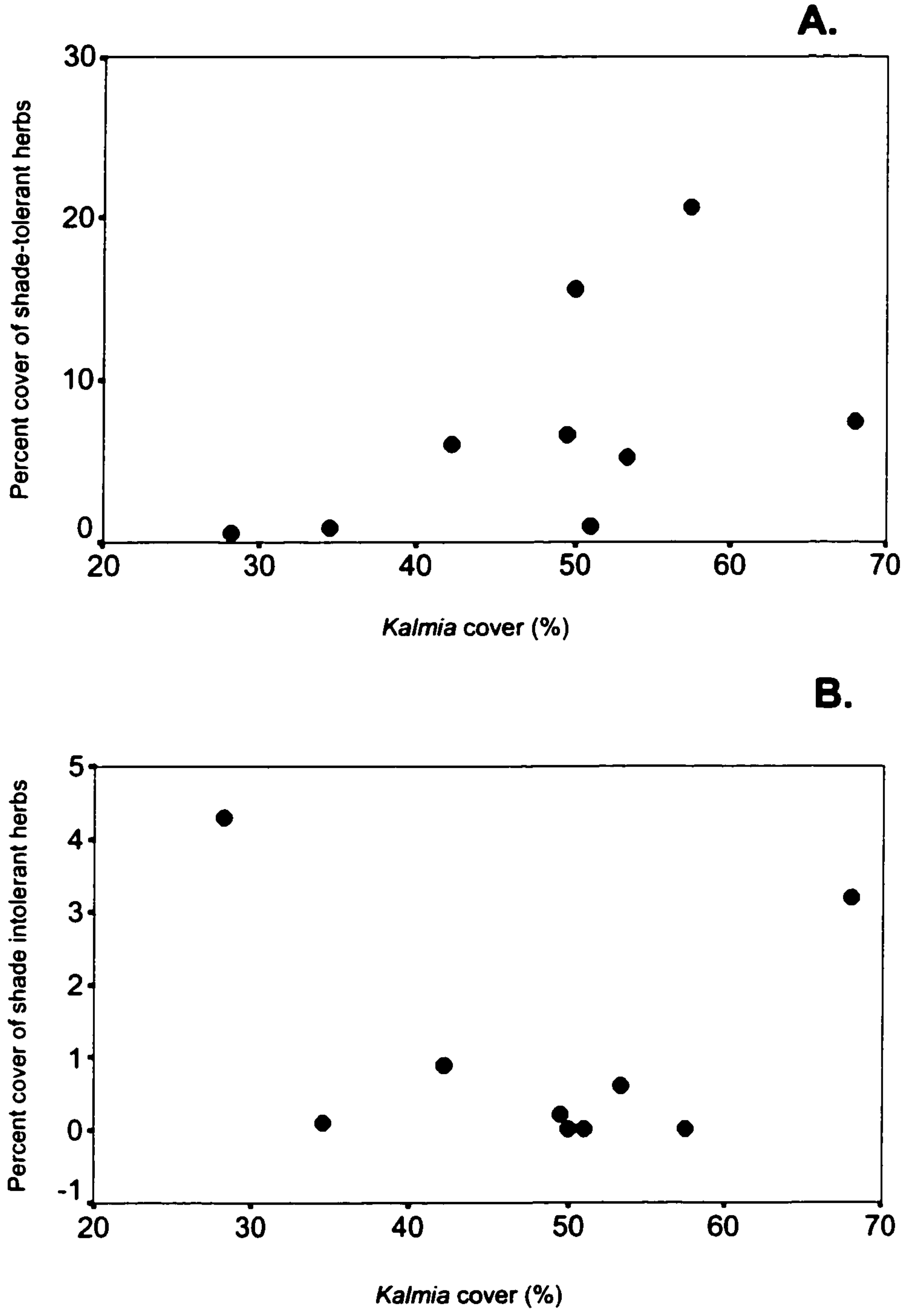

Figure 3. Relationships of shade tolerant and shade in-tolerant herb functional groups to levels of *Kalmia* dominance. Total cover of shade tolerant herbaceous plants was strongly correlated with *Kalmia* cover (A). Shade intolerant plants were inversely related to *Kalmia* cover but the relationship is not significant (B).

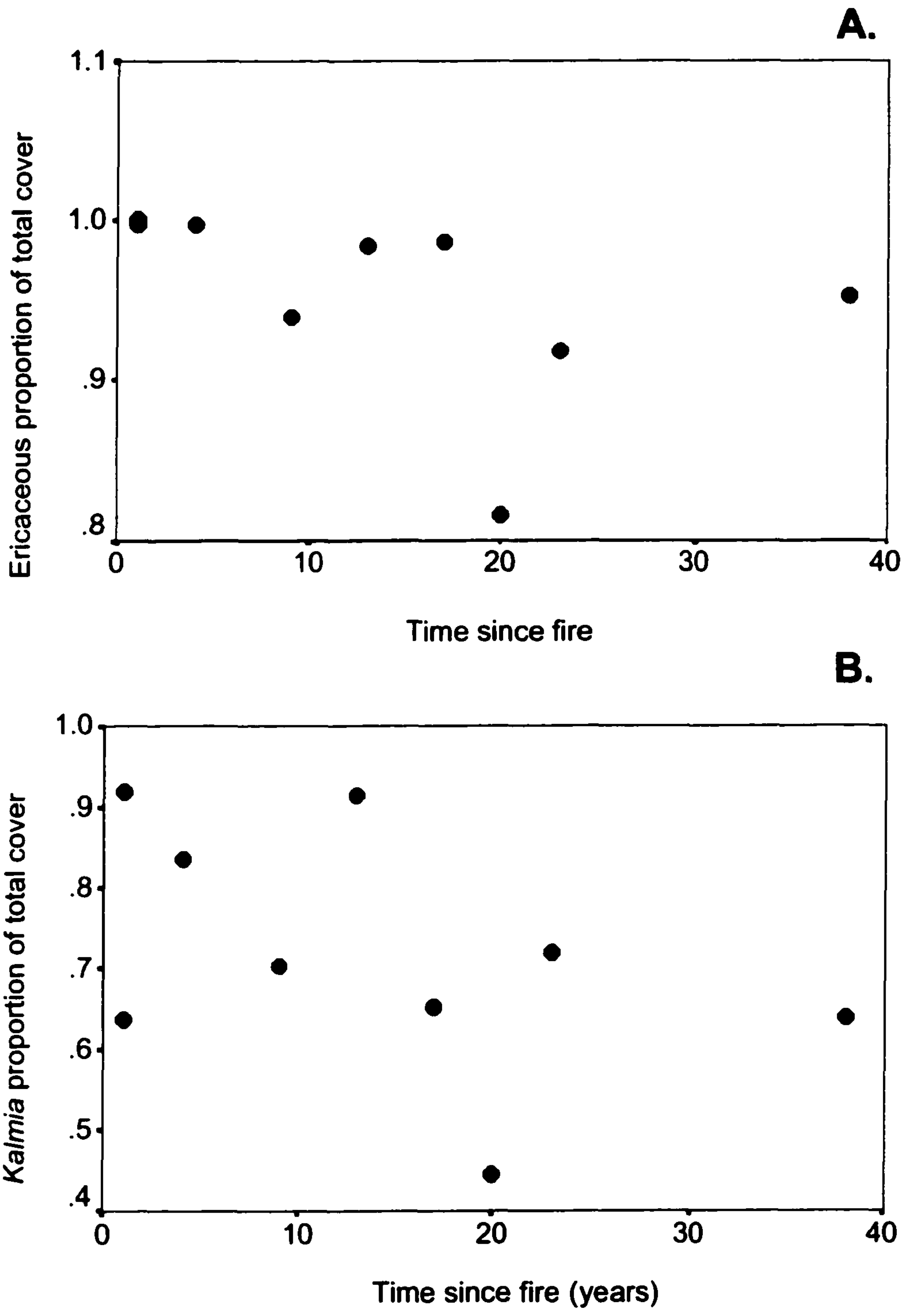

Figure 4. Patterns of dominance in the shrub canopy across the chronosequence. Ericaceous plants (primarily *Kalmia angustifolia, Vaccinium angustifolium, Rhododendron canadense*) demonstrate a stable pattern of dominance over the chronosquence (A). The proportion of *Kalmia* in the community in these sites showed a tendency to decline but the pattern is not statistically significant (B).

Discussion

Increased nutrient availability and reduction of interspecific competition in post-fire habitats are pre-requisites to the stages of invasion and competition on which the general models of secondary succession are based. This is especially evident in boreal forest stands in which resources accumulate in the forest floor and are dependent on repeated fire to release recalcitrant nutrients (Van Cleve *et al.*, 1983; Schimmel and Granstrom, 1996; Wardle *et al.*, 1997). Otherwise growth conditions may become inhospitable, even to stress-tolerant climax species such as black spruce (Pastor *et al.*, 1987).

The lack of relationship between organic matter depth and time since fire suggests that organic soil depth is not reduced after fire and that post-fire nutrient flushes are suppressed by continued nutrient "holdover" from the previous mature forest condition. The expected flush of nutrients into the soil solution within the first few years of burning documented in many regions of the boreal forest (Van Cleve *et al.*, 1983; Schimmel and Granstrom, 1996) appears to be retarded in the pyrogenic *Kalmia* heaths investigated here. Neither of total nitrogen or available nitrogen showed significant trends over time. Phosphorus, however, declined monotonically in mineral soils suggesting time-dependent losses from the system since data indicate a lack of uptake since vegetation cover declined over time. In spite of significant between-site concentrations of some of ammonium it was not related to plant cover indices nor with the relative importance of life history strategies of dominant plants. In contrast, patches of high fire severity in these sites are associated with relatively high levels of nitrogen and phosphorus accompanied by dominance of black spruce rather than heath species (Chapter II).

Soil decomposition and nutrient cycling in boreal stands are frequently limited by the cool, damp condition of the forest floor (Bonan and Shugart, 1989; Kimmins, 1997). Large-scale disturbances are generally known to lead to increased decomposition rates, reduction of organic matter depth and increased nutrient availability in the boreal forest due to the increased activity of micro-organisms under warmer, unforested conditions (Kimmins, 1997). Such periodic episodes of nutrient release are an important factor in sustaining site productivity for new forest stands (Pastor *et al.*, 1987; Kimmins, 1997). The failure for significant nutrient flushes to occur in this chronosequence indicates that factors other than canopy removal and increased insolation are proximate constraints on nutrient release. The persistence of high volumes of recalcitrant organic matter in these burned habitats compared to other disturbed systems (Kimmins, 1997) may be related to litter quality of the dominant plants. Ericaceous vegetation is well known to resist decomposition (Berendse, *et al.* 1989; Cornelison, 1996). Consequently, occurrence of these non-severe fires may cause gradual reductions in forest productivity and habitat quality rather than pulses of increased productivity generally observed after fire.

Of further interest is that the inverse relationship between nitrogen availability in the organic horizon and species richness observed here is inconsistent with patterns predicted from existing theories of species diversity. In saturated niche space with limited resources, inverse relationships of species richness with increasing nutrient availability are classically explained on the basis of the displacement of a group of poor competitors by a single successful dominant plant which reduces limiting resources to levels below the tolerance of other species in the local assemblage (Tilman, 1982, Gleeson and Tilman, 1990). In the present study, both plant cover and species richness are low at high levels of resource availability (Figure 1), meaning that competitive exclusion cannot explain the observed pattern. Although the sample size for these correlations are small and confidence in the pattern may be tentative, it is wise to consider that colonization limitation may be an important factor in these habitats which prevents plants from exploiting soil resources maximally. This is particularly so in the underlying mineral soil horizons which have been previously hypothesized to be under exploited (Chapter II).

This hypothesis, coupled with the observation of peak species richness under peak levels of *Kalmia* cover suggest that species composition is structured by colonization limitation in the early stages and by above-ground facilitative interactions such as the availability of shade/shelter created by the forest canopy in older stands (Figure 3). Consequently, species dynamics in these habitats appear to operate with a high degree of independence from soil nutrient status and cannot be predicted from resource-based models (Tilman, 1982, 1985) as they presently exist.

Effects of moisture variability on soil nutrients

Ammonium nitrogen is a volatile compound which will evaporate from the soil during drying (Brady, 1974). Therefore, moderate moisture contents tend to conserve ammonium in the soil solution. High moisture contents were positively correlated with microbial rates of immobilization which indicates that although ammonium is held in solution, its concentration declines at rates proportional to initial ammonium concentrations and moisture content. Moisture-dependent concentrations of heavy metals are likely the result of long-term local paludification which facilitates leaching of Al and Fe ions into the soil solution (Damman, 1965; Glebov and Korzuhkin, 1992).

Mineralization relationships to total phenols

Soluble carbon in the form of phenols may be an important source of energy in this system in which microbial activity is largely carbon-limited (Bradley *et al.*, 1997). Consequently, the relationship between ammonium immobilization rates and the concentration of total phenolic acids may indicate that these light weight phenolics are a carbon source for soil microbes (Blum, 1998; Hattenschwiler and Vitousek, 2000) and that high concentrations of both carbon and ammonium lead to microbial population growth until available resources from the soil solution are consumed. This pattern of immobilization is often encountered in acidic soils which are dominated by fungi (Binkley and Vitousek, 1989) causing immobilization of available N rather than mineralizing it directly through nitrification as seen in more basic and nutrient-rich soils. Exhaustion of ammonium after 30 days may cause a shift in the population size or life history strategy of the immobilizing microbes (Blum, 1998) causing the observed release of ammonium observed during the second term of incubation.

High rates of immobilization and slow rates of mineralization indicate that nutrient retention following disturbance is high and N losses from the system are minimized. However, ammonium concentrations declined in the first month of incubation in spite of the removal of root uptake in the samples during incubation indicating that plants and microbes probably compete intensely for ammonium-N.

The slow release of ammonium over the course of the second term of incubation resulted in very little mineralized N since final concentrations showed little deviation from pre-incubation concentrations. Damman (1971) found ammonium mineralization rates to be negligible in a 65 year old *Kalmia* heath which may be an indication that future N status will not improve in the sites of the present study. However, several studies indicate that a variety of plant functional groups ranging from grasses to trees can directly access organic nitrogen via mycorrhizal symbioses (Carleton and Read, 1991; Nassholm *et al.*, 1998). Consequently, available nitrogen may not be a robust predictor of site productivity in communities dominated by plants that have the capacity for direct nutrient uptake such as ericaceous plants (Bending and Read, 1995;

Bradley *et al.*, 1997) and black spruce (Carleton and Read, 1991). Ericoid mycorrhizae may be an important adaptive mechanism allowing ericaceous communities to persist under this chronically stressed condition through resistance to low pH and heavy metal toxicity (Bending and Read, 1995).

Total Nitrogen capital

Site-specific vegetation and disturbance factors may interact and be responsible for the high degree of variability in nitrogen capital between sites. In the sites investigated in this study, the dominant species complex, composed primarily of *Kalmia* with other ericaceous dwarf shrubs, was stable irrespective of available nutrient levels and time since fire. This demonstrates the capacity for *Kalmia* create a homogenous heath complex irrespective of local heterogeneity in available nitrogen. Consequently the nutrient heterogeneity hypothesis of stand-level species richness (Tilman, 1994) appears to be inapplicable to these habitats.

In spite of a decline in total vascular cover in the oldest stand, degradatory soil changes speculated to occur in *Kalmia* heath were not observed in the first 38 years of heath dominance but this is not surprising since chemical site retrogression is thought to operate over the course of hundreds of years (Damman, 1965). Furthermore, dominance of heathland is known to be the result of non-severe fires which encourage heath expansion due to failure of fire to remove organic soil (Meades, 1983; Day, 1982; Mallik, 1993; Chapter II). Surviving underground plant organs are accompanied by ecological memory in the soil which extends from the last severe fire event to the next. Site-to-site differences in this ecological memory may be an important aspect of organic soil nutrient status which could be estimated using carbon dating analysis (e.g. Wardle *et al.*, 1997) but were beyond the scope of this study.

If enriching deciduous species (such as *Betula papyrifera, Populus tremuloides, Acer rubrum*) from the regional species pool could invade, increases in nutrient capital would probably occur in *Kalmia* heath as it does in *Calluna* habitats in Germany following beech invasion (Rode, 1999) and in Scotland following *Betula* invasion into gaps during the degenerate phase of the *Calluna* cycle (Gimingham, 1972). However, due to physical filter effects of the thick organic mantle, the seedbed appears to be resistant to invasion after the establishment of algal crusts and dense lichen cover (Chapter II). The large difference in thickness of *Kalmia* raw humus (mean = 11.3 cm ± 2.6 s.d.) and the *Calluna* organic layer (mean = ~ 3 cm) (Rode, 1999; Mallik *et al.* 1983) may be an important factor causing the observed differences in successional pathways between *Calluna* and *Kalmia* communities.

Lack of trends across this series of low severity fires indicates that nutrient accumulation observed in *Calluna* heath (Rode, 1999) do not occur in *Kalmia* heath of eastern Newfoundland. Habitats remain nutrient poor with high concentrations of heavy metals irrespective of time since fire. This indicates that both early (1-9 years) and late theoretical stages of habitat recovery (20-38 years) from disturbance are characterized by inhospitable conditions for black spruce colonization and growth. In contrast Rode (1999) documented significant forest regeneration in the same time line. Fire suppression in the present study may have played a role in preventing fires from becoming severe enough to "re-set" the ecological memory of these sites and appears to facilitate pre-emption of relatively productive forest habitat by unproductive *Kalmia* heath.

The inhospitability of the organic soils of these unforested sites indicates that post-fire forest regeneration critically relies on chemical and physical transformations that occur in severe fires such as increases in pH and exposure of mineral soil seedbeds. If forest regeneration is to occur in these sites human intervention may be required to mimic the effects of severe fire.

Aforestation methods involving herbicides and ercicaceous canopy removal may help to reduce direct, pre-emptive competition of *Kalmia* on regenerating forest species but will not address the need for purging of the chemical after-life effects which are present in the organic layer of the ericaceous community. These accumulations may have feedbacks which permanently reduce the capacity for the site to support a forested state in the future (Damman, 1971).

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Chapter IV.

Direct and indirect effects of black spruce cover on community structure and function in *Kalmia* dominated heath of eastern Canada

Abstract

Studies addressing the inter-relationship between biodiversity and stability of community processes have used species, or combinations thereof, as units of analysis. Implicit in this approach is that variability of the relevant species traits is greater between species than within species. However, recent studies on phenotypic plasticity of plant traits indicate that within-species variation in litter quality may be a significant factor affecting stand level decomposition and nutrient cycling.

In the present study, I document the effect of a natural shade gradient on species composition and on the phenotypic diversity of the ericaceous dwarf shrub *Kalmia angustifolia* L. which dominates much of the forest understory and unforested heathlands in Atlantic Canada. The vegetation of the study area regenerated after a fire 39 years prior to the study and is primarily unforested. Black spruce invasion was limited to the disturbance edges where seed dispersal and establishment was assumed to be the cause of the present gradient in black spruce cover. Thirty-two 50 x 50 cm quadrats were randomly distributed among five transects in the study area. Light levels, species composition, vascular plant cover and soil respiration rate were determined for each plot. Tissue samples of litter, mature and current year leaves of *Kalmia* were collected and analysed for nutrient status.

Kalmia foliar N concentrations and above ground biomass increased with increasing shade. Soil respiration rates were strongly related to the light gradient and increased monotonically with increasing quality of *Kalmia* litter inputs. Herb species richness and cover peaked at intermediate light levels. Our data indicate that *Kalmia*'s fitness is greater under black spruce canopy as opposed to open heath conditions and that the unstressed phenotype has relatively benign feedbacks on soil productivity compared to the open-habitat phenotype. In absence of functional diversity at the species level in these species-poor habitats, phenotypic plasticity in *Kalmia* appears to be an important component of the biodiversity-stability relationship in these communities. The role of forest regeneration as an indirect control of boreal forest soil processes is discussed.

Introduction

Compelling evidence from old-field and grassland systems has led to testing specific hypotheses of competition as a primary structuring force in plant communities (Egler, 1954; Tilman, 1982, 1985, 1994). However, reviews of studies on competition among a broad range of ecosystem types have revealed that competition may be accompanied by facilitation or may not be detectable at all (Callaway and Walker, 1997; Schlapfer and Schmid, 1999).

Recent studies provide evidence in favour of communities as non-random, "functionally organized units" (Wilson, 1997) in which species have net positive interactions which increase the fitness of the larger community. In turn, the improved state of the community positively feeds back on the member species. Evidence for such organizational feedbacks (Hobbie, 1992; Van Breeman and Finzi, 1998; Vitousek and Hooper, 1993) has led to the entitlement of ecosystems as "complex adaptive systems" (CAS's) (Brown, 1995). Under this conceptual framework communities have a tendency to maintain themselves at maximal rates of biological work (i.e. productivity) within external constraints of the habitat such as climate, precipitation and soil quality. Implicit in this conceptualization is that members perform roles in the maintenance of energy flow through the larger system and in return, receive direct or indirect benefits from community membership. Benefits to individual organisms are generally thought to come in the form of increased fitness of community members, reduction of predation or shelter from physical stress (Brown, 1995).

Evidence for forests as functionally organized units/CAS's is found in the positive effects of various plant functional groups on the availability of limiting resources in soils. Wardle *et al.* (1997) documented the indirect effect of forest fire on a cascade of community parameters ranging from the identity of the dominant species to soil microbial biomass. This study demonstrated strong top-down linkages among a wide variety of community characteristics. Similar inter-relationships have been documented in other terrestrial systems where plant functional groups have been disturbed (Pastor *et al.*, 1988). Such studies cumulatively comprise a literature in which the effects of antagonistic interspecific relationships (such as competition and allelopathy) are outweighed by the benefits of species co-existence (Olofosson *et al.*, 1999).

The potential for species to have critical roles in ecosystem processes, such as nutrient cycling, has raised questions about the degree to which natural systems can be altered in their species composition and richness without losing functionality (Erhlich and Mooney, 1983; Silver *et al.*, 1996; Naeem *et al.*, 1994; Wardle *et al.*, 2000; Tilman and Downing, 1994; Walker, 1992). It has recently been argued that the identity of species is less critical to ecosystem function than are the persistence and richness of functional groups which control cycling of limiting nutrients (Wardle *et al.* 2000; Grime, 1997; Silver *et al.*, 1996). Implicit in this argument is that greater species richness within each functional group should increase the stability of community processes when species composition is altered by stress or disturbance (Frost *et al.*, 1995; Vitousek, 1990). From this perspective, it would seem that depauperate communities may be at greatest risk of de-stabilization following disturbances or stresses to which the dominant species are not optimally adapted.

The relationship between species richness and the stability of ecological processes within communities has recently been addressed primarily from the perspectives of species effects on the stability of community-level processes which control productivity (Wardle *et al.*, 1997; Wardle *et al.*, 2000; Holland *et al.*, 1992; Tilman and Downing, 1994). However, over the course of the evolution of the diversity-stability hypothesis, several fundamental recognitions have only recently been made. First, there is growing acceptance that diversity *per se* lacks a mechanism through which higher levels of diversity confer greater stability to communities (Silver *et al.*, 1996; Grime, 1997; Wardle *et al.*, 2000). The relationship between diversity and stability is instead observed as an artefact of causal relationships between functional diversity and ecosystem processes (Vitousek and Hooper, 1993; Wardle *et al.*, 2000). Species richness is a hit-and-miss cause of ecosystem stability (Schlapfer and Schmid, 1999) which only works when the addition of species is made without overlap in functional roles and fundamental niches (Vitousek and Hooper, 1993).

This perspective has led to the simple but effective axiom that the organisms which matter most to ecosystem stability, belong to functional groups which have controlling effects on the rate at which limiting nutrients are transferred through the system (Silver *et al.*, 1996). A corollary of this principle is that the character of the dominant species controls ecosystem processes (Wardle *et al.*, 1997). Recent reviews on the subjects of positive species interactions (Callaway and Walker, 1997) and the diversity-stability hypothesis (Schlappfer and Schmid, 1999) have demonstrated a need for empirical studies of the dependency of ecosystem function on the stability of dominant species or functional groups with critical "engineering roles" (*sensu* Lawton, 1996). Forested ecosystems are particularly understudied in this respect (Wardle *et al.*, 1997; Bauhus *et al.*, 1998; Schlappfer and Schmid, 1999)

A well-known example of community de-stabilization is the large-scale conversion of forest to heathland in areas of Scotland, Finland, Germany and coastal regions of North America (Gimingham, 1972; de Montigny and Weetman, 1990; Mallik, 1995). These species-poor communities provide an opportunity to test the null model of species redundancy/ complimentarity (*sensu* Frost *et al.*, 1995) following changes in community composition. The replacement of forests by low-productive ericaceous plants has led to the general conclusion that forest regeneration failure after disturbance is the result of competitive or allelopathic interactions which favour the dominance of heath species. However, in *Calluna* heath, these conclusions come from systems which are artificially maintained at relatively high levels of productivity by repeated burning. In *Kalmia* heath of Atlantic Canada, which is not actively managed, fitness of the community dominant declines after an early post-fire peak (Mallik, 1994; Chapter III). I previously provided evidence that the inverse relationship between the dominance of these species could be explained simply by seedbed resistance to invasion rather than by interspecific competition among community dominants (Chapters II and III).

I present this study as a re-evaluation of the conventional wisdom that conifer-ericaceous relationships are inherently antagonistic. Previous observations that *Kalmia* above-ground productivity and seed viability are favoured by partial shade from black spruce canopy cover in mature forests (Mallik, 1994) raise fundamental questions of the evolutionary relationship between these cornerstone species.

Recent experiments with light regimes in controlled conditions have documented evidence for phenotypic modification of litter quality and life history characteristics in heathland plants. Moody *et al.* (1996) observed that shelter from UV stress strongly modifies the life history traits of *Vaccinium myrtillus* in Europe. Similarly, *Kalmia* has been observed to have larger, more pliable leaves under shade and to be grazed by moose and snowshoe hare under deep shade conditions (R.G. Bloom and A.U. Mallik, unpublished data). It has been speculated that increased litter quality of ericaceous plants sheltered from UV may have effects on soil productivity (Moody *et al.*, 1996). Similarly, Gehrke *et al.* (1995) noted that increased exposure of *V. uliginosum* to UV caused a decline in litter quality that was speculated to affect soil fertility. However, the occurrence of these indirect effects of solar radiation on stand-level processes in forest-heath ecosystems have not been verified in natural communities.

The purpose of this study was to test the null hypothesis that the dominant species of the ecosystem have non-interactive life history traits relevant to ecosystem function across a gradient of co-existence. This study tested for: (1) significant direct feedbacks of black spruce canopy cover on the nitrogen use efficiency of the subordinate dwarf shrub (*Kalmia*) and (2) significant indirect effects of canopy cover on soil biological/microbial activity due to differential litter quality of *Kalmia* across the light gradient. Soil respiration rate was used as a measure of the biological activity occurring in the organic soil horizon. Although the field method of measuring soil respiration does not differentiate between soil and root respiration, it has been cited as a general index of biological activity in soil. In particular, soil respiration has been used as a surrogate for productivity (Medina *et al.*, 1980; Lieth and Ouellette, 1962) since it is a composite measure of root activity, microbial uptake and microbial mineralization of nutrients (Tewary *et al.*, 1982; Gordon *et al.*, 1987). Taken together, these sources of variability of soil respiration rate were assumed to act as a robust indicator of the rate of carbon cycling and the concomitant moblization of associated nutrients from detritus to plant and microfaunal components of the community (*sensu* Silver *et al.*, 1996).

Methods

Study site description

Non-severe fires are a natural cause of conversion of closed-canopy forests to ericaceous heathland in the Atlantic boreal forest (Richardson, 1973; Damman, 1971; Mallik, 1994). These heath barrens are dominated by *Kalmia* and have been speculated to be resistant to black spruce re-colonization irrespective of time since disturbance (Damman, 1971; Richardson, 1973). The success of black spruce invasion in these sites has previously been shown to depend on high fire severity (Chapter II). The site used in the present study was created by a fire in 1961 which burned an area of approximately 200 ha over the course of two days prior to artificial fire suppression (Power, 1996). Adjacent unburned forests are assumed to be pyrogenic and to have origins in a stand replacing fire approximately 60-70 years prior to the non-severe fire of 1961 (Power, 1996). The vegetation is representative of the *Kalmia-Cladina* climax vegetation which was previously described by Damman (1971) and Bloom (Chapter III) as highly acid (pH = 3), nutrient poor (since less than 1% of total nitrogen is available) and having negligible rates of N mineralization (< 0.1 mg/kg/day). Persistence of *Kalmia* in nutrient poor habitats has been attributed to its high nitrogen use efficiency and evergreen habit (Titus *et al.*, 1995).

The present study took advantage of a natural gradient of black spruce cover that created a "natural experiment" (*sensu* Diamond, 1986) suitable for testing hypotheses of the relationships between dominant species and (1) understory plant composition and (2) soil productivity. Patterns of black spruce regeneration following fire have been previously shown to depend on the distribution of mineral soil microsites which are created by patches of high burn severity where mineral soil is exposed (Chapters I and II) (Figure 1 A). These patches act as regeneration niches where black spruce can establish and grow relatively free of interspecific competition for 17-20 years when patches become colonized by the rhizomes of the surrounding *Kalmia* (Chapter II). Increased seed rain at the perimeter of these burned habitats saturates these regeneration niches and causes a progressive increase in black spruce density along transects from the burned habitat to the forest edge (Figure 1 B). The relationship between black spruce establishment and organic soil removal was confirmed in the present study by the presence of the most shallow, and therefore most recent, charcoal macrofossils at the mineral soil surface underneath each of ten randomly selected trees (data not shown). Outside of the high severity microsites, vegetation and nutrient status were extremely homogenous and species poor which creates a natural bioassay for the effect of tree cover on small-scale species composition and soil processes (Figure 1 C).

Sampling design and data collection

Sampling stations were established using a stratified random method. Five areas (each approximately 1 ha) of heath-forest ecotone were randomly selected from ten areas identified and numbered using aerial photographs. In the field, transects were laid out with a 50 m measuring tape from the forest edge toward the center of the barren. Between 5 and 7 points were randomly marked with survey flags and numbered for identification along each transect starting at a point of complete open condition and progressing toward forest closure as tree density increased near the forest edge (Figure 1 C).

Photosynthetically active radiation (PAR) was measured using a Quantum light sensor beam on a uniformly overcast day in early July, 2000 between the hours of 10 a.m. and 2 p.m. These conditions were required for stabilized measurements over the course of the sampling

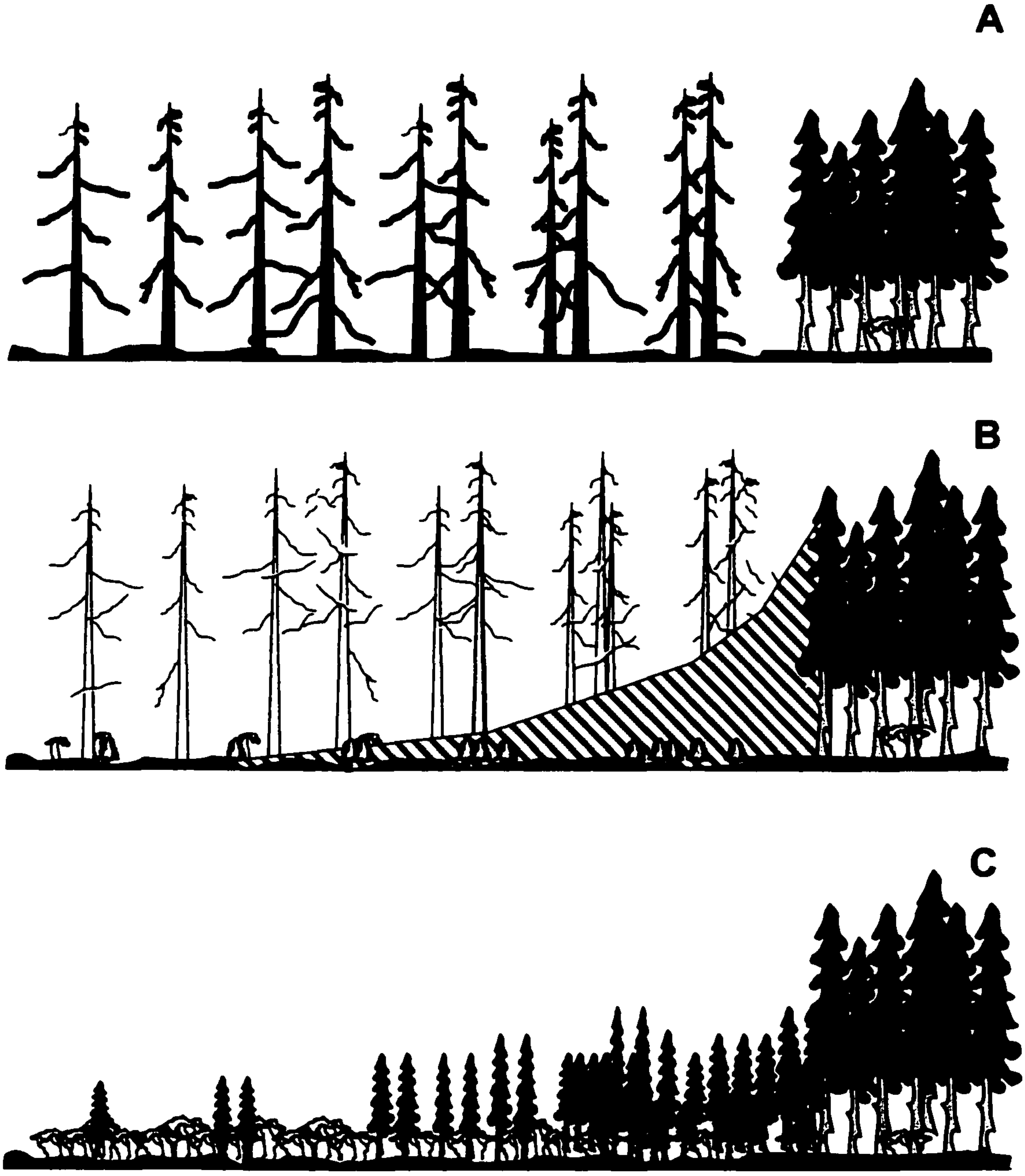

Figure 1. Phases of black spruce colonization explaining the present pattern of tree cover observed in the study site. Post-fire habitats (A) are characterized by poor seedbeds which consist of charred organic matter over 85-95% of the area (Chapter II), while favourable seedbeds of exposed mineral soil are limited to 5-10%. *Kalmia* resprouts and spreads vegetatively creating a homogenous community of dwarf-shrubs and shade tolerant herbs. Black spruce seeds are dispersed from semi-serotinous cones in the burned canopy and also invade from intact forest edges according to distance-dependent dispersal curves (indicated by shading) resulting in safe-site saturation in the forest-heath boundary (B). The resulting pattern of black spruce establishment is a function of seed rain density and suitable microsites fore regeneration (C).

period. To quantify the amount of shade provided by the black spruce canopy along each transect of the shade gradient, PAR was measured above the understory canopy of *Kalmia* at a height of 1 m above ground at each station. Measurements were taken with the instrument beam leveled and oriented to 180 degrees in the horizontal plane. Measurements were repeated in reverse order within each transect to estimate sampling error and provide representative measurements. Measures of within-transect sampling with greater than 10% error were re-sampled due to the possibility of variability in cloud cover between transects. Completely exposed stations were used as a 100% exposure standard and all other measurements for each transect were taken as a proportion of these measurements as an index of shade cover by the forest canopy.

Soil respiration rate was recorded at each site using a portable infra-red gas analyser (IRGA, Nortech, Ottawa, Ontario) (Parkinson, 1981). A 78.5 cm^2 surface area of soil was measured by pressing the sampling chamber 1 cm into the organic layer, following removal of the dry litter layer, to create a seal and allowing the rate of partial CO_2 pressure in the chamber to stabilize. Due to time constraints there was no replication of sampling stations on the date of data collection although the stations were re-surveyed at a later date under similar weather conditions to confirm the reproducibility of the data. At the time of repeated sampling, several sampling stations showed signs of disturbance by moose as indicated by fecal pellets and trampling. To avoid contamination of samples with increased N from fecal pellets or other related disturbances, these sampling stations were not used. A fourth random transect with ten sampling stations was added to maintain the sample size above 30 for the purposes of statistical inference (Sokal and Rohlf, 1998).

At each station soil temperature and organic matter depth were measured simultaneously with respiration at a depth of 2.5 cm below the top of the F horizon. Moisture content at the various stations were assumed to be homogenized by a period of heavy rain three days prior to sampling. Qualitative observations indicated that soils were near field capacity across the gradient.

Vegetation sampling

Foliage collection followed the method of Small (1972). First year leaves, mature leaves and leaf litter of *Kalmia* and 5x5x5 cm humus samples were collected respectively from stems, soil surface and from deeper soils 5 – 10 cm below the litter surface within the measured 78.5 cm^2 area. Litter types for each location were identified to species and *Kalmia* tissue samples were placed in plastic zip lock bags and stored in a refrigerator for four days prior to air-drying. All tissues and humus samples were analysed for % C and N using a LECO gas analyzer (LECO Instruments, Mississaga, Ontario). Perecent nitrogen retranslocation from mature to new leaves was estimated as the difference between new and mature leaf N concentrations corrected for initial leaf N in new leaves using the following formula:

(first year leaf N – mature leaf N)/ first year leaf N.

Similarly, percent N retention was estimated by calculating the relative difference in N concentrations of mature and litter leaf tissue:

(mature leaf N – litter leaf N)/ mature leaf N.

Percent cover of all plants was estimated in 50 x 50 cm plots at the edge of each station and mean height, stem density and stem diameter of *Kalmia* were recorded. These parameters were used to calculate a biomass index based of stem volume:

$$\text{stem volume} = (\pi\,(d/2)^2 \times h)/3 \times n$$

where : d = mean stem diameter
h = mean stem height
n = stem density

Statistical analysis

An a-priori path model was constructed based on known factors controlling soil respiration and nutrient cycling in heath and forest ecosystems (Berendse *et al.*, 1989; Gehrke *et al.*, 1995) (Figure 2). The model was tested using a path-analysis approach to quantify the components of variability in soil respiration rates. Light intensity (PAR) was expressed on a scale of proportion of available light from 0 (complete shade) to 1.0 (unshaded condition).

Quadrat data from the five transects were pooled. Soil respiration rates were used as a response variable to the factors of PAR, litter type, *Kalmia* litter C:N ratio and deep organic litter C:N ratio. Four classes of litter type were derived from the ground cover data on the basis of dominant vegetation. Ordered by association with decreasing PAR they are: *Cladina* lichen-*Kalmia* litter, *Kalmia* litter - feather moss litter, pure *Kalmia litter* and *Kalmia* litter – with hardwood litter (such as red maple, *Acer rubrum*, and white birch, *Betula papyrifera*). As reviewed elsewhere (Bonan and Shugart, 1989) black spruce needles were not a major component of the litter in comparison to broadleaf and bryophyte tissue of the boreal forest floor.

A one-way ANOVA was used to estimate and statistically remove the effects of differences in vegetation and litter types from rates of soil respiration. PAR, litter C:N ratio and soil respiration residuals (controlled for litter type) were analysed for relationships with each of the following variables: *Kalmia* N retranslocation, *Kalmia* litter C:N ratio, species richness and percent herb cover using Pearson's *r*. Correlations were also used to test for relationships between soil respiration and organic soil depth and soil temperature variation.

Nitrogen dynamics of *Kalmia* were analyzed using a general linear model composed of three levels of *Kalmia* leaf age (first year, mature and litter) with PAR as a covariate. Relationships between PAR and each of *Kalmia* biomass, richness of herbaceous species and cover of herbaceous plants were analysed using curvi-linear regression (SPSS, 1998).

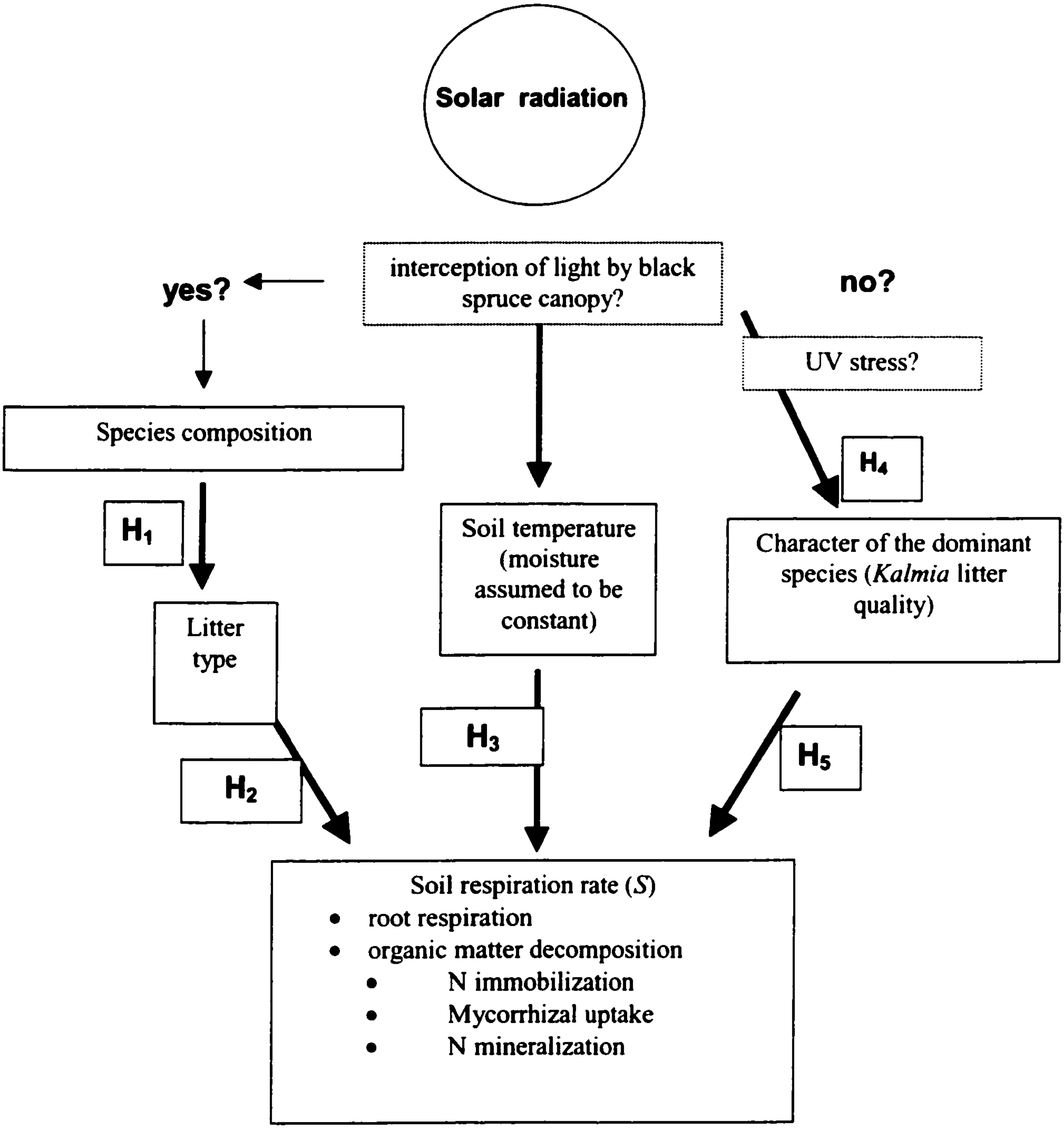

Figure 2. Summary of the major factors affecting soil respiration. Hypotheses tested are bolded; remaining causal links are drawn from the literature as indicated. (1) **H_1**: vascular plant richness and abundance is correlated with light intensity. (2) **H_2** : plant species richness can affect decomposition and soil respiration rates (Wardle *et al.*, 2000). (3) **H_3** : soil temperature is positively correlated with soil respiration (Singh and Gupta, 1977); (4) unshaded conditions expose ericaceous plants (*Kalmia*) to UV stress (Gehrke *et al.* 1995); (5) **H_4**: *Kalmia* litter quality is modified by shade; (6) **H_5**: quality (C:N ratio) of litter input of *Kalmia* across the shade gradient is correlated with soil respiration rate.

Results

Understory responses to light exposure

Nitrogen content of all age classes of *Kalmia* leaves declined with increasing age and with increasing levels of photosynthetically active radiation (Figure 3). First year leaves had the highest nitrogen content per unit of carbon (Figure 3) and were only weakly affected by PAR (Figure 3). Mature and abscissed leaves showed successive declines in N content but the magnitude of the difference declined significantly at low levels of PAR (Figure 3). *Kalmia* leaves demonstrated uniform rates of nitrogen retranslocation from mature to new tissues across the light gradient (r= 0.07, n=32, p= n.s., mean = .53% ± .01 s.d.) but had progressively higher rates of N retention prior to abscission under increasing light exposure (r = 0.32, n =32, p= 0.038). Consequently the hypothesis that *Kalmia*'s physiology and litterfall are altered under black spruce canopy cover was accepted.

Kalmia biomass index and height increased with increasing shade to a unimodal peak at approximately PAR = 0.6 after which biomass declined (Figure 4 A). Herb richness and cover were related to PAR and therefore black spruce cover (Figure 4 B & C). Herb richness peaked under partial shade of black spruce (PAR = 0.5) along a cubic response curve ($F_{(3,28)}$ = 3.33, p = 0.033) (Figure 4 B). Total herb cover (maximum = 67%) peaked at intermediate levels of black spruce cover (PAR = 0.4) but the curvilinear relationship is not statistically significant (Figure 4 C). Data indicate that partial shade of black spruce facilitates peak understory richness, plant, biomass and plant cover. Based on these findings, the hypothesis that understory species composition and abundance are associated with black spruce canopy cover was accepted.

Relationships between light, litter quality and soil respiration

The average soil respiration rate of pooled samples was 1.10 g/m/hr ± 0.35 s.d. PAR was negatively related to soil respiration rates ($r = -0.69$, $n = 32$, $p < 0.001$). Closed-canopy forest-heath conditions (25-35 % PAR) had soil respiration rates approximately 100 % greater than the adjacent unshaded heath conditions (Figure 4 D). Analysis of the hypothesized path linking canopy cover to soil respiation via understory litter composition revealed no significant difference between the litter classes ($F_{(3,28)} = 1.197$, p = n.s.). Further analysis of the extreme differences observed between soil respiration rates associated with *Cladina-Kalmia* litter and *Kalmia*-hardwood litter (Table 1, Figure 5 A) showed a significant difference ($t_{(28)} = 2.78$, $p = 0.01$).

When the variability due to the random effect of litter type was removed in the one-way analysis, the residuals (representing *Kalmia* litter quality since this litter source was constant) were still significantly related to soil respiration rates ($r = -.50$, $n = 32$, $p = .002$) (Figure B). C:N ratio of the deep organic layer corrected for soil depth was less strongly related to soil respiration ($r = -.33$, $n = 32$, $p = .031$) (Figure 5 C) than were recent litter inputs by *Kalmia*.

Soil temperature ranged from 9° to 15° C and was positively related to light exposure ($r = 0.416$, $n = 32$, $p = 0.009$) but was inversely related to soil respiration ($r = -0.337$,$n = 32$, $p = 0.03$) (Figure 5 D). The hypothesis that increasing soil temperature under increasing levels of PAR would positively affect soil respiration was rejected. Partial correlation controlling for litter C:N ratio in the relationship between soil respiration and temperature was not significant ($r = -0.20$, $n = 29$, p = n.s.) indicating that the negative relationship between temperature and respiration was driven in part by the indirect association of temperature with litter quality.

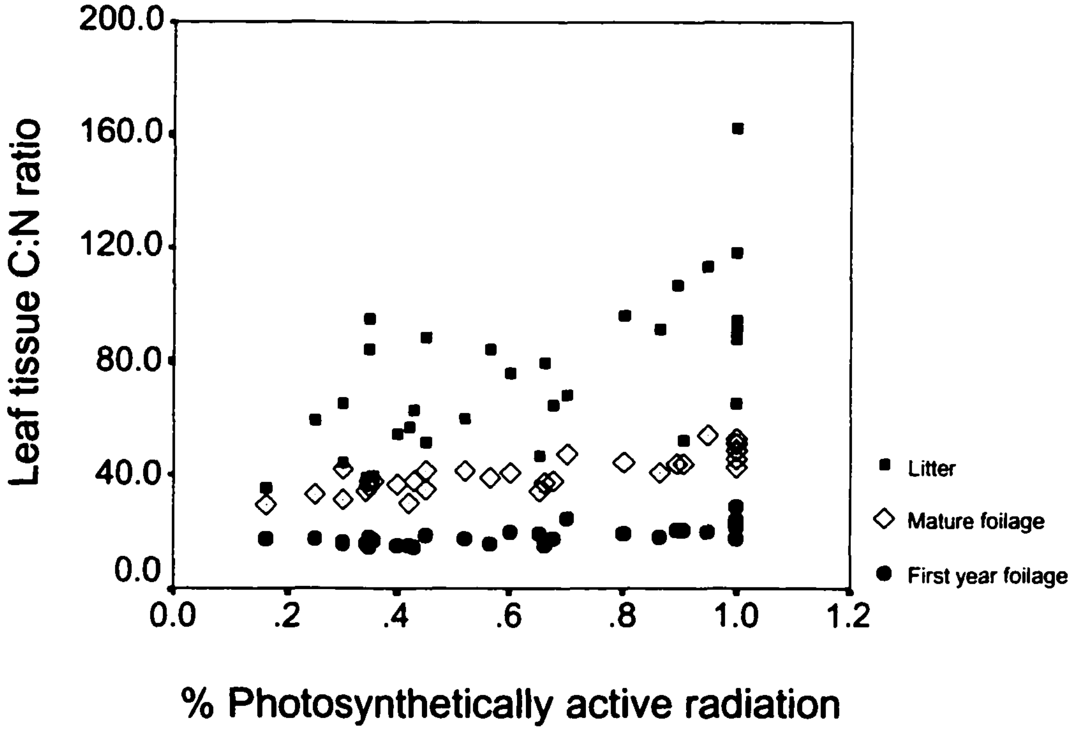

Figure 3. *Kalmia* foliar C:N ratios in relation to leaf maturity and light exposure. Low light conditions show little difference in C:N ratio of leaves irrespective of stage of development. In contrast, litter produced in full sunlight undergoes stepwise increases in C:N ratio with increasing tissue age.

Table 1. Mean habitat, vegetation and Kalmia foliar nitrogen parameters associated with groundcover classes across a gradient of black spruce canopy cover in *Kalmia* heathland.

	Cladina-Kalmia litter	*Kalmia*-feather moss litter	pure *Kalmia* litter	*Kalmia*-hardwood litter
PAR (%)	.72 ± .10	.65 ± .07	.64 ± .12	.39 ± .02
Herb richness	.63 ± .26	1.3 ± .29	2.8 ± .80	2.8 ± .85
Herb cover (%)	1.5 ± .7	9.2 ± 2.9	14.2 ± .7	35.8 ± 12.8
First year *Kalmia* leaves C:N	19.8 ± 2.9	18.6 ± 2.7	18.6 ± 5.8	15.8 ± 1.8
Mature *Kalmia* leaves C:N	44.4 ± 5.4	40.2 ± 8.0	40.0 ± 3.2	35.7 ± 1.7
Litter C:N *	94.7 ± 11.4	70.0 ± 6.4	68.5 ± 9.2	69.2 ± 13.5
Kalmia foliar N retranslocation (%)	53.0 ± 5	52.0 ± 6	53.0 ± 10	54 ± 6
Kalmia foliar N retention (%)	51 ± 14	39 ± 14	37 ± 20	41 ± 22
Soil respiration rate ($g/m^2/hr$)	0.96 ± .15	1.07 ± .07	1.32 ±.11	1.45 ± .19

* refers to *Kalmia* litter only

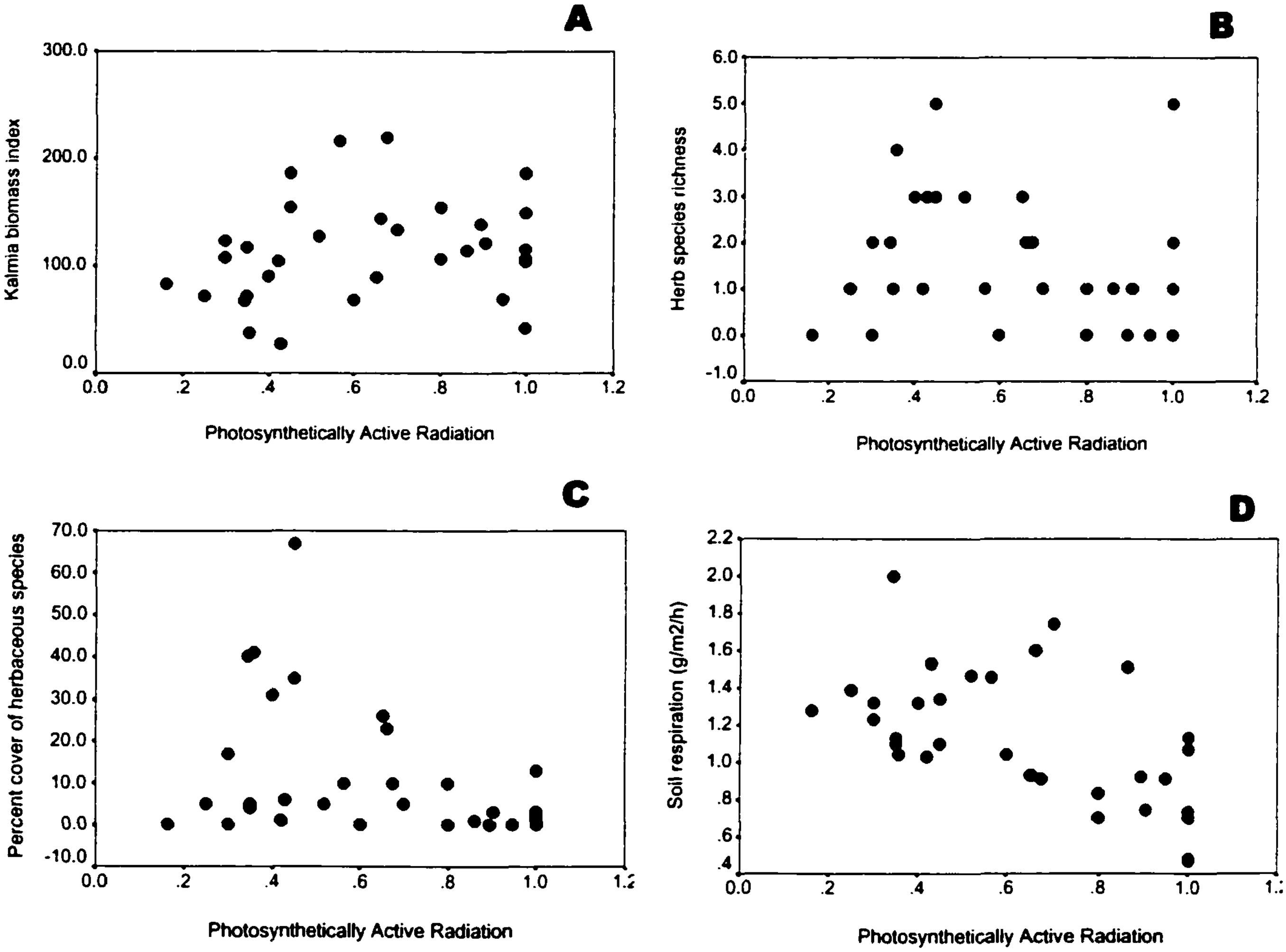

Figure 4. Effects of photosynthetically active radiation, as moderate by black spruce cover, on the forest understory. *Kalmia* biomass index responded curvilinearly to the gradient (A). Herb richness showed a tendency to peak under partial black spruce cover (B). Cover of herb species was also favoured by partial cover (C). Soil respiration rate declined monotomically with increasing light exposure (D).

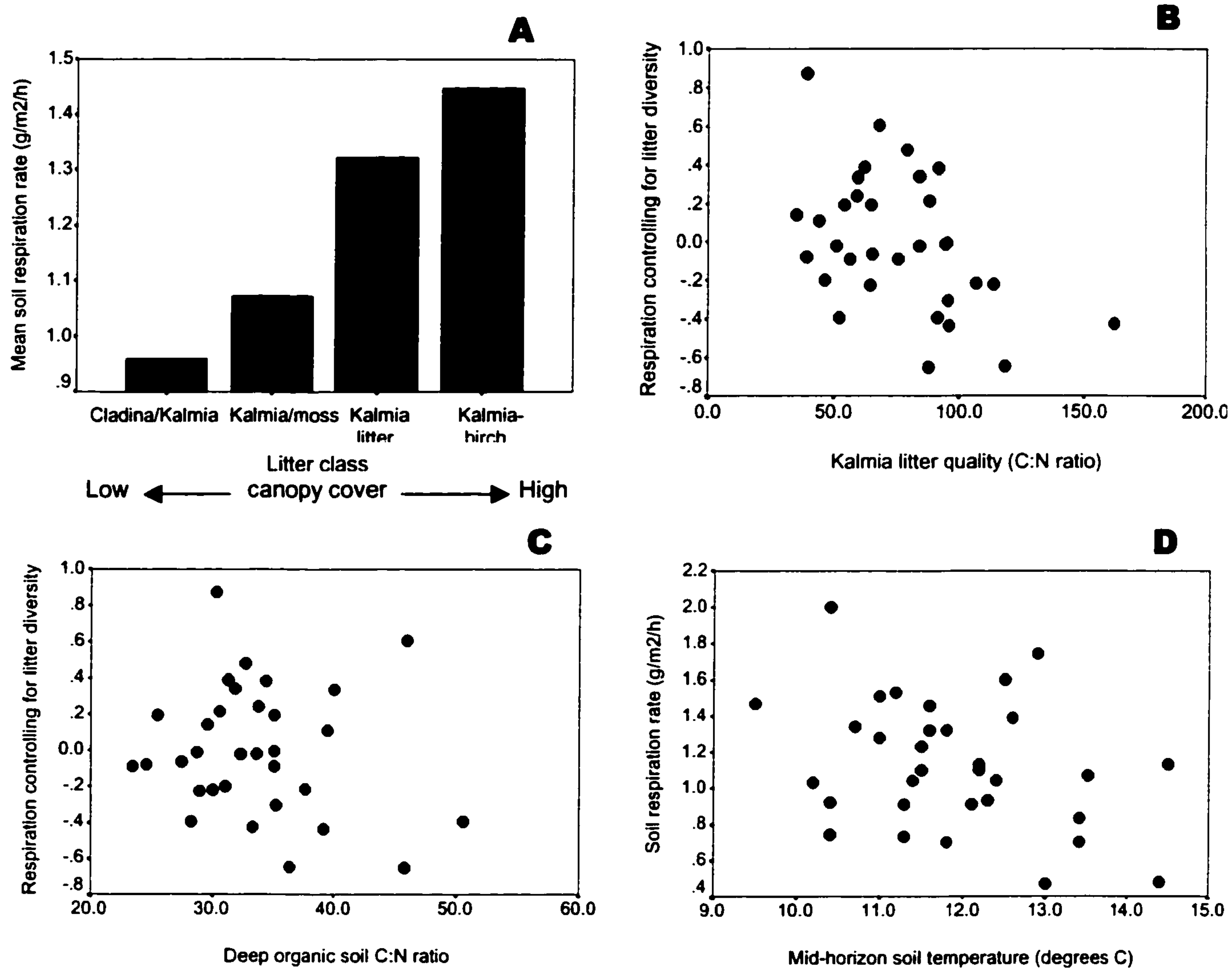

Figure 5. Relationships between soil respiration and habitat factors. Soil respiration differed among plant litter classes found at different levels of black spruce canopy cover (A). Residual soil respiration rate data left over after the effect of litter classes was removed were significantly related to the litter quality of *Kalmia* (B). Soil respiration rates were only weakly related to C:N ratios of deep organic matter underlying *Kalmia* litter across the gradient (C). Soil respiration rate was negatively related to soil temperature (D). This unexpected pattern is probably due to an indirect associations rather than cause-and-effect. (see text)

Discussion

Reduction of light levels under black spruce canopy strongly modifies phenotypic qualities of *Kalmia*. Under increasing shade, *Kalmia* exhibits less nutrient use efficiency and higher litter quality than in unshaded heath conditions. Assuming that litterfall is constant across the light gradient, this alteration of *Kalmia*'s litter quality translates into a two-fold increase of annual nitrogen inputs into the soil horizon under heavy shade compared to treeless heath. However, shade appears to the encourage above-ground productivity of *Kalmia* (Mallik, 1994; Inderjit and Mallik, 1999) which suggests that greater amounts of litter will be produced and recycled under increasing shade. Increased nitrogen inputs by *Kalmia* under shaded conditions appear to enhance soil biological activity and may account for the increase in biomass of subordinate herb species as shade and litter quality increase. The mechanism causing this association has a basis in the known direct relationships between soil respiration and soil litter quality and inputs from above-ground functional groups (Singh and Gupta, 1977; Tewary *et al.*, 1982; Read, 1992; Weber, 1985; Gordon *et al.*, 1987).

Soil respiration could have been more affected by litter quality than by deep organic soil C/N ratios probably because the latter measure incorporated ecological memory reflective of the homogeneity of the pre-fire condition of the study area. Furthermore, since disturbance, open heath conditions were associated with a three-fold increase in C:N ratio of litter inputs as compared to historical ratios (as indicated by deep organic C:N ratios) and C:N ratios of litter under shaded conditions in the present. Such high rates of C inputs in absence of high respiration rates indicates carbon sequestration by open heath communities and a concomitant decline in rates of C and N nutrient cycling compared to adjacent forests. It could be argued that the high C:N ratios observed in leaves of unshaded conditions had higher levels of C due to greater photosynthate concentrations (Boardman, 1977). However, addition of tissues with high carbohydrate:N ratios to soils are typically expected to increase soil microbial respiration through the addition of carbon as an energy source (Blum, 1998; Bradley *et al.*, 1997) and the opposite was observed. Alternatively, the additional carbon concentration may be a stress response in the form of allocation of carbon to form complex molecules associated with UV absorption.

Theoretically, high soil respiration rates are thought to cause concomitant N immobilization in the biomass of the growing microbial population (Kimmins, 1997). After the period of rapid grow is ended by disturbance or starvation, the nitrogen is released to the soil system. However, this process of nutrient immobilization and eventual mineralization may be impeded when litter substrates are composed primarily of secondary compounds such as polyphenolic acids and lignin which are resistant to microbial degradation (Berendse *et al.*, 1989; Aber and Melillo, 1991; Hättenschwiler and Vitousek, 2000).

Links between foliar phenol concentrations and UV exposure have been made in several cases (Hattenschwiler and Vitousek, 2000; Gehrke *et al.*, 1995; Rozema *et al.*, 1997). Since I generally observed highest respiration rates when the dominant plant litter had low C:N ratios, I propose that the extra carbon observed in unshaded *Kalmia* litter failed to increase soil respiration because the unshaded leaves are higher in phenolic compounds which are known to inhibit mycorrhizal communities (Yamasaki *et al.*, 1998) and N mineralization in heathland systems (Berendse *et al.*; 1989; Northup *et al.*, 1998). This is supported by the informal observations that shade was associated with greater leaf pliability, specific leaf area and palatability to herbivores which are known indices of increasing lignin content (Cornelissen, 1996). In contrast, the higher respiration rates under spruce cover may be representative of increased microbial activity following addition of labile C to heathland soils as observed by Read (1992).

In a global context, soil respiration rates are known to vary by orders of magnitude along latitudinal and altitudinal gradients with the highest rates in the tropics and lowest rates in alpine and arctic environments (Singh and Gupta, 1977). The respiration rates observed in the present study (mean = 1.2 $g/m^2/h$) are substantially higher than other observations from boreal systems (Mallik and Hu, 1997; Weber, 1985; Gordon *et al.*, 1987) but this may be a function of the especially thick organic soil (15-30 cm) found in wet, coastal environments compared with warmer and more arid interior boreal forests (0-10cm) (Mallik and Hu, 1997; Weber, 1985; Gordon *et al.*, 1987) .

In recent years, concerns regarding increased levels of UV have prompted studies on the direct and indirect effects of light on ecosystem processes of decomposition in natural systems. While generalizable patterns of the effect of UV on plants have not yet been elucidated, strong plant-specific patterns have been documented (Rozema *et al.*, 1997). In particular, the effect of high levels of solar radiation are known to increase foliar concentrations of some phenolic compounds and is hypothesized to be a phenotypic response to ultraviolet light exposure. Similarly, increases in the C:N ratio have been documented in several ericaceous plants (i.e. *Vaccinium myrtillus* (Moody *et al.*, submitted), *V. uliginosum* (Gehrke *et al.*, 1995) in response to increasing levels of UV radiation. These authors noted that such direct effects of light on plant tissues may have implications for local community processes since litter quality is known to strongly affect rates of nutrient availability and site fertility. Since it has been well established that dominant plants strongly influence soil metabolism (Holland, 1992; Wardle *et al.*, 1997; Wardle *et al.*, 2000), I conclude that the monotonic increase in *Kalmia* litter quality observed across the light gradient was the primary cause of increased soil respiration in forested versus unforested heathland.

In addition to indirect effects of canopy cover on biogeochemistry, the shade-dependent increase in 'spare' nitrogen in *Kalmia*'s internal nutrient budget is accompanied by increased above-ground biomass which supports the hypothesis that light intensity may also control the ratio of above:below ground biomass allocation of *Kalmia* (Titus *et al.*, 1995). UV stress and light exposure have been shown to induce increased root:shoot ratios in *Vaccinium myrtillus* heath (Moody *et al.*, 1996) and in *Vaccinium uliginosum* (Gehrke *et al.*, 1995) and to cause increased allocation to foliar lignin and phenol refractory compounds with concomitant reductions in litter quality (Rozema *et al.*, 1997; Gehrke *et al.*, 1995). Killingbeck (1993) observed inefficiency of N resorption in a nitrogen fixer and questioned whether this "evolutionary ineptitude" in resource use was, in some way, compensated. In the present case, the occurrence of relatively benign litter inputs coupled with potential for reduced root growth of *Kalmia* in shaded conditions may reduce the structuring force of competition between established trees and the ericaceous understory. Under this interpretation, intact black spruce-*Kalmia* forests appear to act as a functionally organized unit/adaptive system (Wilson, 1997; Brown, 1996) which provides compensation to *Kalmia* for its altruistic behaviour in the form of shelter from light stress. This sheltering service of forests is associated with both an increase in productivity and seed viability in *Kalmia* (Mallik, 1994). In response to Jones *et al.* (1997) one "ecological role of a tree in a forest" (p. 1946) in these communities appears to be the facilitation of shade-dependent interactions between plant traits, understory productivity and nutrient cycling.

It has been suggested that complimentarity of dominant species (Frost *et al.*, 1996), also termed redundancy (Walker, 1992) and substitutability (Ehrilch and Mooney, 1983), is an important aspect of community stability (Wardle *et al.*, 2000) which tends to maintain ecosystem processes when disturbance or stress cause shifts in the identities of the dominant species (Frost *et al.*, 1996). The positive effects of black spruce cover on soil activity and the association of species richness and herbs with forest, rather than with exposed heath indicate that open *Kalmia* heath and black spruce forest communities are not complimentary in the services they provide to the local plant community. The consequences of forest cover loss in these sites are summarized as a new dimension to the mechanism of retrogression in Figure 6.

In contrast to the negative feedbacks observed in *Kalmia* heath, other authors (Curtis and McIntosh, 1951; Whittaker, 1956, 1960; Chapin, 1985) have observed that shifts in the dominant vegetation in a wide variety of habitats did not significantly affect the understory species composition. Several authors have documented equivalent roles of invading dominant species, such as oak and maple, in the absence of the original community dominant (chestnut) which was removed from communities by selective disturbance in the form of disease (Woods and Shanks, 1956; McCormick and Platt, 1980). Similar substitutions, were observed following the decline of elm (*Ulmus Americana*) in response to the introduction of dutch elm disease (Parker and Leopold, 1983). In these cases, the declines of the community dominants were complimented by an increase in the abundance of apparent functional equivalents which maintained understory species composition at characteristic levels. Such redundancy is not exhibited in secondary succession of black spruce-*Kalmia* forests. This is because black spruce is nearly the solitary tree colonizer following forest fire disturbances and, despite its reputation as a fire-adapted species, its post-fire regeneration and growth is inhibited when *Kalmia* dominates the understory

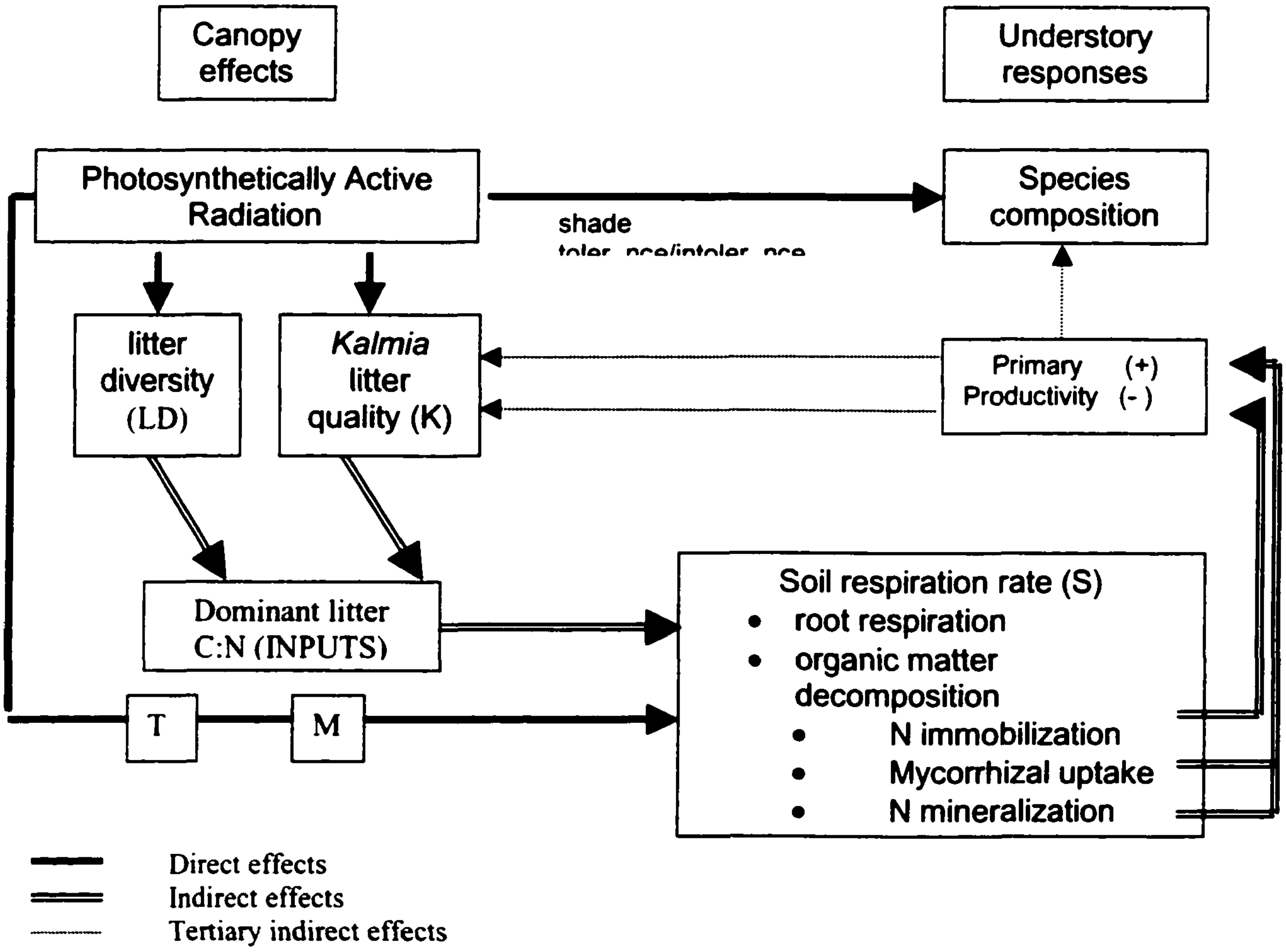

Figure 6. Summary of direct and indirect relationships between canopy cover and understory vegetation in black spruce-*Kalmia* ecosystems. INPUTS are hypothesized to be the result of (1) differences in species composition which are mediated by canopy cover (LD) and of the litter quality of the dominant plant (K) (Berendse *et al.*, 1989; Wardle *et al.*, 2000). Temperature (T) and moisture (M) effects on soil respiration are usually assumed to be direct (Singh and Gupta, 1977) and controlled by light exposure but appear to have been over-ridden by the importance of litter quality in this system. Because the quality of litter inputs of the dominant species (*Kalmia*) decline with light exposure, the nature of the INPUT and respiration will be contingent on the degree of canopy cover.

(Richardson, 1973; Day, 1982; Mallik, 1995; Mallik, 2001). Previous papers (Chapters, I,II and III) have described strong associations between long-term canopy cover and species diversity. For example, herb cover has been shown to rely on black spruce cover in otherwise treeless heathland as are pleurocarpous mosses which represent the dominant ground cover of mature forests in the region (Damman, 1964). In this context, the observed "Clementsian" relationships between dominant species and community structure and function appear to be highly dependent on the functional identity of the dominant species. Such strong inter-relationships between forest and understory species suggest that in regions with little diversity in the dominant guild of species, anthropogenic interference with stand-replacing disturbance may cause community-wide shifts in composition (Chapter II). Fire suppression is of primary concern since it is known to cause long-term declines in forest structure and function in boreal regions (Wardle *et al.*, 1997).

The findings of this study provide circumstantial evidence that reductions of site fertility reported to be caused by de-stabilization of forests to heathland (Damman, 1971; Owen and Marrs, 2000) and allelopathy (Peterson, 1965; Inderjit and Malllik, 1996) may not be evolutionarily stable strategies for *Kalmia* in the long term. The possibility that existence in unshaded habitats is beyond *Kalmia*'s evolutionary experience should be carefully studied in order to re-evaluate the relationship between *Kalmia* and black spruce under natural disturbance severity regimes. A new hypothesis should be tested which considers that *Kalmia*'s stressed phenotype and associated allelopathic potential represent a counter-evolutionary state. Under high light intensity, I suggest that *Kalmia* is forced to invest in refractory compounds as defences against UV stress and, as litter inputs accumulate, *Kalmia*'s extended phenotype creates a positive feedback on stress tolerance and nutrient use efficiency that reduces site productivity indices (Newton, 1998) and reduces its own vigour in comparison to shaded conditions (Mallik, 1994). Pastor *et al.* (1988) speculated that processes that select for stress tolerant life histories at the landscape level (such as herbivory by unchecked moose populations) could become a de-stabilizing force of forested ecosystems causing trophic cascades (*sensu* Carpenter *et al.*, 1985). However terrestrial trophic cascades have rarely been documented due to the apparent improbability of such de-stabilizing factors coinciding in natural systems (Polis, 1999).

This preliminary investigation of soil processes in the presence/absence of cornerstone forest species provides evidence that destructive stand-level positive feedbacks are occurring in the marginal conditions of the Atlantic boreal region. The dual role of anthropogenic changes to the historic fire regime and herbivory by introduced species (such as the red squirrel (*Tamiascirius hudsonicus ungavensis*), moose (*Alces alces americana*) and snowshoe hare (*Lepus americanus*) that have landscape level influences on regenerating plants appear to be a critical aspect of the destabilization of community structure and function. The findings of the present study suggest that further research is needed to understand the interrelationships between habitats and dominant vegetation to prevent permanent habitat degradation.

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General Discussion

Recent reviews on the topics of plant regeneration (Bond and Midgely, 2001), positive plant-plant interactions (Callaway and Walker, 1997) and physical barriers to plant establishment (Facelli and Pickett, 1991; Xiong and Nilsson, 1999) collectively develop the theme that predicting plant community dynamics solely from species competitive abilities is inadequate for many systems. Likewise, models for predicting community composition based on plant attributes in response to disturbance (Noble and Slayter, 1980; Van der Valk, 1981) do not parameterize the successional interactions which structure established vegetation and are limited in application to systems in which the "initial floristic composition" after disturbance (Egler, 1954) persists throughout succession.

As a result of these shortcomings, both deterministic models (Tilman, 1985, 1994) and disturbance-based models of species dynamics (Connell, 1978; Huston, 1979; Kimmins, 1997) fail to accurately explain the persistence of *Kalmia* heath on soils that are capable of supporting forests. A general model of succession appears to rely on the hybridization of disturbance and competition-based approaches.

Kimmins (1997) reviewed many of the contemporary computer models used to predict stand dynamics in various ecosystems. Of these, the FORECAST series of models are particularly detailed in quantifying the various site-related mechanisms which affect plant growth as well as regeneration probabilities and long-term feedbacks of plants on the site (Kimmins, 1997). Unlike, general predictive models (Connell, 1978; Tilman, 1982), conditions such as seedbed suitability, nutrient cycling, light regimes and forest productivity are explicit in these models. However, these otherwise holistic models focus on the complex autecology of forest stands and tend to be ecosystem-specific. Application of these models may be suitable to *Kalmia* heath, and other stand types, by factoring in the structuring forces of pre-emptive competition and/or allelopathy. At present, autogenic retrogressive succession is not explained by any general model of community development. Such models assume that competition for nutrients and light drive community development and fail to account for cases in which stress tolerant plants gain dominance by default.

The examples provided in this thesis indicate that the emphasis on competition and regeneration in generic models of plant dynamics (Tilman, 1994; Grubb, 1977) have a geographic bias toward dispersal-dominated systems. As geographic setting changes toward progressively higher altitudes and latitudes, vegetative propagation and its related strategies of stress tolerance become critical mechanisms of vegetation responses to disturbance (Grime, 1979). The suppression of fire in eastern Newfoundland mimics this geographic gradient by selecting for plants which resprout from the unburned organic soil rather than for plants which regenerate in mineral soil substrates.

A conceptual model relating species strategies to productivity gradients and disturbance severity is presented in Figure 1. In relatively productive systems, species composition may not be altered significantly by disturbances of low severity since the dominant species may have the capacity to resprout from persistent bud banks or other vegetative tissues. If the dominant species are removed, there is evidence that relatively productive systems, such as the temperate hardwood vegetation associations, are buffered from significant changes in community structure by invasion of 'ecological equivalents' from surrounding habitats. The occurrence of high severity disturbance in productive regions may cause larger deviations from pre-fire species compositions (Figure 1) but there is evidence that community selection may ensure stability of

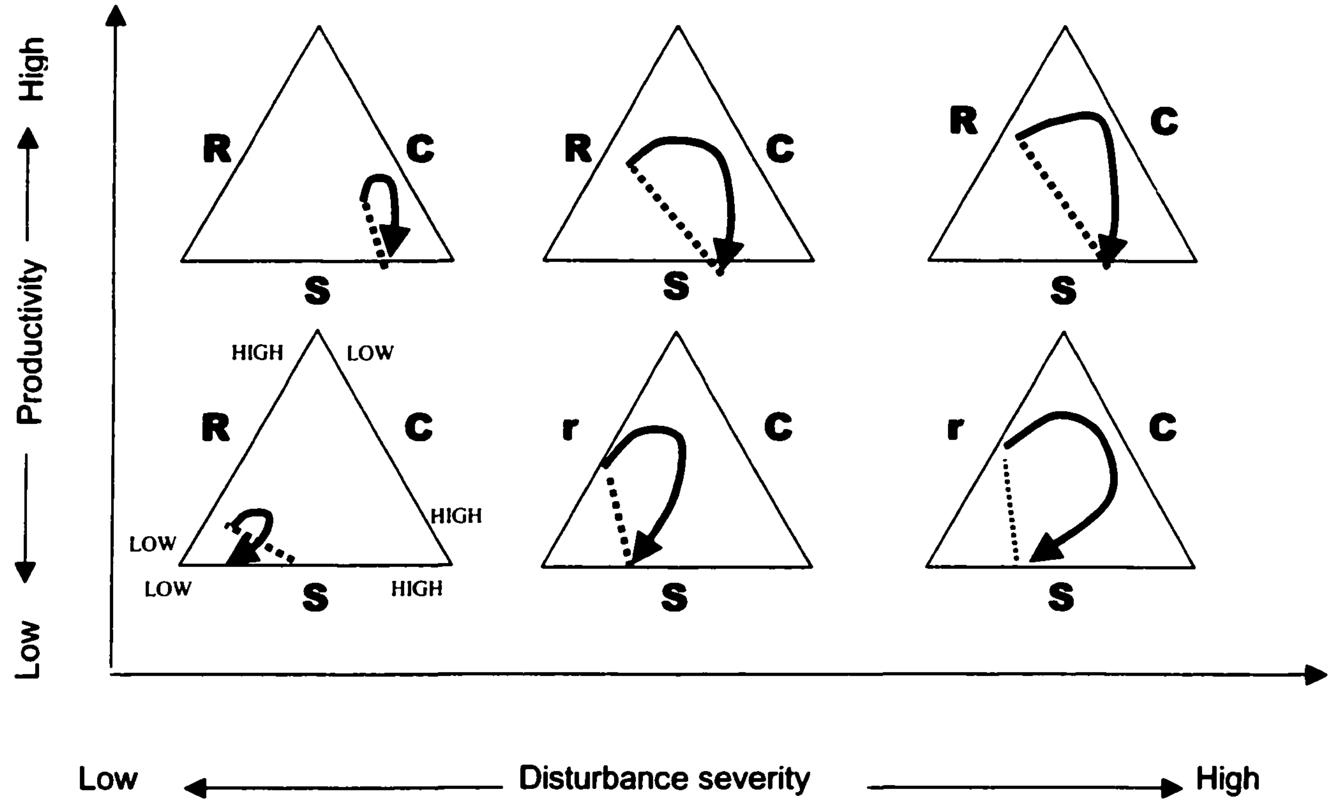

Figure 1. Plant community resilience in relation to disturbance severity and site productivity. Solid lines represent pathways of dominant vegetation recovery in Grimian space. "R" represents the relative dominance of plants with primary strategies of dispersal and rapid colonization of new sites; "C" represents relative dominance of species which tend to exhibit competitive strategies for exploiting limiting resources; "S"- represents the relative dominance of plants the specialize in tolerating stress. Dotted lines represent vectors of disturbance severity.

the community in the long term (Halpbern and Franklin, 1990). Consequently, community stability may be high in more productive habitats. Following severe fire in nutrient poor habitats, large deviations from pre-fire conditions may result and, although the rate of succession may be slower in poor soils (Bornkamm, 1981), the pattern of transitions among primary species strategies is generally similar among stands irrespective of nutrient status. However, less productive sites will select for species with greater stress tolerance (Grime, 1979). In the low fire severity scenario on poor soils, community stability may be at risk since nutrients may not be released from the raw humus layer (Chapter III). Lack of fresh nutrients immediately after fire will select for successively more stress tolerant dominant species which could cause a destructive positive feedback on site productivity (Pastor, *et al.* 1988; Damman, 1971). Furthermore, restriction on regeneration space in poorly burned habitats may be an even stronger restriction on the capacity for regional 'fugitive' species (such as fireweed, goldenrod etc.). In the low severity condition on poor soils, the range of life history traits, and therefore the range of species which persist in the region, is highly reduced from that of the high severity scenario (Figure 1).

If restriction of regeneration niches continues to be a characteristic of burned habitats in the greater Terra Nova National Park ecosystem, then many of the r-selected species in the regional species pool may be at risk of local extinction. Furthermore, the short life span of r-strategists places them at increased risk. More detailed analyses of how *Kalmia* interacts with its habitat and other species are strongly recommended to prevent loss of species diversity and the potential functional values associated with it (Vitousek and Hooper, 1993; Silver *et al.*, 1996; Wardle *et al.*, 2000).

Directions for future research

Krebs (1985) recognized that "one of the major thrusts of applied ecology must be to determine the limits of resilience with respect to specific disturbances for managed communities". In Terra Nova National Park and its greater ecosystem, these disturbances include fire suppression and the introduction of herbivores. In order to attain the goal of re-establishing historic patterns of stand structure in Terra Nova National Park (Power, 2000), the relative importance of these structuring forces must be determined. These factors are considered here in order of increasing ecological scale.

Individual level

On one hand, *Kalmia* and black spruce share the same fundamental niche in the landscape, hence allelopathy and competition for light may be the respective evolutionary mechanisms by which these species gain local dominance (Titus *et al.*, 1995). On the other hand, *Kalmia*'s fitness (defined as the combined status of above-ground biomass, seed viability and its long-term relative abundance) is greatest under partial shade of black spruce. Consequently, the evolutionary history of *Kalmia* is poorly understood and further detailed analysis of *Kalmia*'s relationship to forest cover is needed. Because shade appears to mediate all aspects of *Kalmia*'s phenotype (i.e. vegetative spread, toxicity and biogeochemical feedbacks), further understanding of *Kalmia* as a "problem species" (Titus *et al.*, 1995) can best be gained by considering the plasticity of these problematic traits. Experiments on *Kalmia* which confirm its phenotypic modification under shade cover are recommended.

Randomly located shade structures could be permanently erected in open heath conditions and the dependent variables of above-ground productivity, leaf nutrition and soil nutrient status could be monitored over time under different levels of light. *Kalmia*'s fitness in relation to shade could also be monitored in such a field experiment by including non-destructive repeated measures of reproductive effort. Such an experiment would unequivocally test the potential of canopy cover to feedback on soil processes via release of the community dominant from environmental stress. Decomposition and nutrient release studies of *Kalmia* litter produced under different levels of shade would also be important laboratory components.

The specific adaptive significance of polyphenolic acid production in plants is not yet clear but there is compelling evidence that the production of these compounds is phenotypic and stimulated by stress as discussed in chapter IV. Understanding interspecific nutrient competition in *Kalmia*-dominated systems will demand a better understanding of rates at which the insoluble polyphenol fraction, such as lignin, release nitrogen for mineralization. However, recent laboratory research has demonstrated the abilities of black spruce and *Kalmia* to bypass mineralization and take up inorganic N via mycorrhizae. The role of mycorrhizae and the potential for differential ecto- and ericoid mycorrhizal competitive ability in these phenol-rich soils must also be investigated.

Unequivocal evidence for allelopathy in this system requires determination of (1) the quantity and quality of phenols deposited in the soil environment by *Kalmia* and (2) the fate of these various compounds as they run the gauntlet of consumption by soil microbes, UV degradation and weathering before gaining allelopathic status. At present, "total phenolics" is the predominant quantitative measure of phenolics concentrations. More sophisticated measures of phenolic status are needed to trace particular compounds from production in the leaf to degradation in the environment. The use of radioisotopes in tracing the fate of carbon in *Kalmia* tissues as it cycles through the system should be considered. This aspect of the chemical ecology of phenolics is highly data-limited and has been touted to be a research priority in terrestrial communities (Hättenschwiller and Vitousek, 2000). Consequently, the return-on-investment of such research may be great for both applied and basic progress in terrestrial ecology.

Stand-level: preventative and restorative options

Prevention-oriented research

Throughout this thesis, severe fire has repeatedly been proposed as a factor separating black spruce and other obligate seed invaders from *Kalmia* in niche space. However, if *Kalmia*'s role in structuring these habitats is to be extended beyond interference with black spruce, the effects of *Kalmia* must be separated from inhospitable seedbed conditions and herbivory. Although seedbed filters were isolated from *Kalmia* dominance by stratified sampling (Papers I & II), this was achieved for black spruce only because it is herbivore-resistant (Prescott, 1980; Deichman, 1983) . However, the abundance of seedlings and/or vegetative sprouts of balsam fir, white birch, trembling aspen and successional shrubs such as alder and pin cherry may be restricted by any or all of the following factors: seedbed limitation, pre-emptive competition from *Kalmia* or moose and hare browsing. Moose and hare exclosures erected in the Terra Nova region have demonstrated the ability of these animals to alter species abundance and composition in regenerating balsam fir stands (Power, 2000). Whether or not herbivory structures the composition of *Kalmia* heath communities has yet to be determined. Preliminary observations from a discontinued study of browsing following fire in the Pitts Pond fire of 1961 were inconclusive and a renewed commitment to this issue could reveal interactions between herbivory and fire severity in structuring plant communities in these habitats.

A prescribed burning strategy for maintaining species diversity is actively being pursued within the boundaries of TNNP. At present, the prescribed burning programme is limited to activity in the uncharacteristic fire seasons of spring or fall (R. Power, personal communication). In order to overcome the potentially wet spring and autumn fire conditions, artificial fuel loading may be useful to initiate and sustain smouldering combustion in the organic horizon. This has been used successfully in both small scale studies (Schimmel and Granstrom, 1996) and in prescribed burns in La Mauricie National Park, PQ (D. Quann, personal communication) to create favourable seedbed conditions for tree regeneration.

A field experiment has been put in place to test the effects of artificial placement of coarse woody debris on mineral soil exposure following prescribed burning. Sufficient numbers of experimental units have been allocated to test for interactions between browsing and fire severity by exclosing half of the plots immediately following the fire. Findings of this preliminary study will provide insight into the specific challenges of artificially creating disturbances for the maintenance of site productivity and species diversity.

Restoration-oriented opportunities

Stands which have already been converted to heath by accidental fires or other disturbance will require a restoration approach to meeting management objectives. This occurs in sites which have already been dominated by *Kalmia* due to anthropogenic disturbance. Under these conditions, methods of regeneration must address the competition and allelopathic factors. Killing above ground parts of *Kalmia* with herbicides does not reduce the thick organic soil layer and nutrient imbalances (Mallik, 2001) which are the legacies of *Kalmia* dominance (Damman, 1971). Because these soils are nutrient poor, sustainable forest use may rely on historic mechanisms of succession to restore nutrient availability for forest growth. The increase in pH caused by severe fire and the litter deposits of pioneering species such as alder (Hudson, 1992) and birch (Roberts *et al.*, 1998) may be critical components of this mechanism. Since severe fire is presently an unacceptable option for areas outside of Terra Nova National Park, methods of simulating its effects are needed.

The potential for favourable microsites to be created artificially in previously disturbed sites is currently being addressed in a field trial in Terra Nova National Park (A.U. Mallik, personal communication). However, natural microsite creation is usually caused by severe fire which creates a flush of nutrient availability and an increase in pH as demonstrated previously (Chapter II). It is recommended that liming or some other mechanism of increasing pH be added to the trial to further emulate natural regeneration conditions. Although the buffering capacity of these highly acidic soils has been cited as a concern, Bhure (1970) noted that the low cation exchange capacities of acidic black spruce stands leave these soils poorly buffered against liming in comparison to more rich balsam fir stands. Measurable increases in pH have been observed following the addition of relatively small amounts of ash derived from *Kalmia* duff to experimentally burned plots (R.G. Bloom and A.U. Mallik, unpublished data).

Collectively these experiments will help us better understand (1) whether or not *Kalmia*-black spruce interactions are innately or circumstantially competitive and (2) how past and future disturbances can be manipulated to meet management objectives. In the event that the problematic nature of *Kalmia* is circumstantial, findings of these studies may prove useful for maintaining historical stand conditions.

Landscape level

At present, *Kalmia*'s increasing dominance appears to be commensal with human disturbance as are other heathlands in Europe and North America. In contrast to the extensive anthropogenic heathlands of Scotland (Tinsley, 1975; Gimingham, 1972), *Kalmia* heaths are not yet a landscape-scale plant association. Well-supported research and a focus on long-term, sustainable forest rotations will likely prevent ecologically and economically undesirable change following disturbance.

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