The Influences of Site Conditions, Age and Disturbance by Wildfire or Winter Logging on the Species Composition of Naturally Regenerating Boreal Plant Communities and Some Implications for Community Resilience

By

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A Thesis
Submitted to the Faculty of Graduate Studies
in Partial Fulfillment of the Requirements for the Degree of

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Abstract

Few boreal studies have assessed the sustainability of logging by directly comparing post-fire and post-logging vegetation dynamics beyond the first 15 years. This study compared the species composition of naturally regenerating plant communities grouped by site type, age (13, 37 and 65 years) and disturbance type (wildfire or winter logging). Differences in species composition were used to assess the relative influence of these grouping variables and community resilience to wildfire and logging.

Replicate burns or cutovers were randomly selected in eastern Manitoba and plots located within them using probabilistic methods. Data relating to understory cover, trees, soils and topography were collected. Each plot was classified into a site type category. Criteria were developed to identify species which had a substantial site type, age or disturbance type difference in performance. Community resilience was measured by calculating the percent dissimilarity of the species composition of 13 and 37 year old post-fire and post-logging communities with that of mature (65 year old) post-fire communities.

The strongest influence on species composition was site type followed by fire. Communities exhibited greater short-term resilience to logging than to fire but this situation reversed itself over the medium-term. Post-fire recovery between 13 and 37 years was rapid, while in post logging communities several species tolerant of moderate to high light intensity and low nutrients maintained or expanded their cover. By 37 years most of the species which performed more poorly in one disturbance type did so in post-logging communities. Most of the poorer performers were herbs or shade intolerants which typically require a moderate to rich nutrient regime.

The poorer performance of herbs in 37 year old post-logging communities could not be attributed to differences in the initial direct effects of fire and logging. Based on the species which had performance differences, it appears that logging may have had negative medium-term impacts on site fertility. Also, a number of species seem to require some of the fire's effects to maintain their abundance and distribution on the landscape. This has important implications for the conservation of ecosystem diversity.

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Chapter 1

Introduction

1.1 Introduction

The proportion of the Canadian boreal forest subjected to management has steadily increased over the past 100 years. Past management has focused largely on logging, fire suppression and selected animal species. Management priorities are now changing due to heightened concern that logging could have substantial negative impacts on the many benefits produced by forest ecosystems. The focus is shifting from selected outputs to the ecological patterns and processes that support a wide array of human values as well as the ecological functions critical to the support of human life on earth (cf. KPMG 1995).

As part of this trend, the Canadian Council of Forest Ministers (CCFM) has defined sustainable forest management as management which, among other things, conserves biological diversity, maintains forest ecosystem condition and productivity and maintains contributions to global ecological cycles (CCFM 1995). These objectives require considerable knowledge about the dynamics of natural ecosystems[1]. Such knowledge should go beyond description to understanding which are the key factors driving ecosystem dynamics and how they do so (MacLean *et al.* 1983). With this information, it may be possible to manage human activities in such a way that they best mimic key effects on ecological patterns and processes so that goals such as biodiversity conservation and the maintenance of ecological functions can be achieved.

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[1] Spatial patterns are viewed as a snapshot of temporal patterns on a collection of sites.

Research and theory indicate that some of the key factors driving boreal ecosystem dynamics are site conditions, pre-disturbance vegetation, disturbance type and characteristics, population dynamics manifested as age (i.e. time since disturbance), climate and the species found in a region (Pickett *et al.* 1987; Bonan and Shugart 1989; Payette 1992). The influence of climate and regional floristics on dynamics are minimal within ecoregions of the boreal forest since by definition (CCELC 1989) these factors are relatively homogenous at this scale. Vegetation patterns have been linked to site conditions (Carleton *et al.* 1985; Kenkel 1986, 1987; Brumelis and Carleton 1988, 1989; Bergeron and Dubuc 1989; Harvey and Bergeron 1989; Harvey *et al.* 1995; Jeglum and He 1995), age (Dix and Swan 1971; Black and Bliss 1978; Carleton and Maycock 1978, 1980, 1981; Bergeron and Bouchard 1983; Clayden and Bouchard 1983; Foster 1985; Brumelis and Carleton 1988, 1989; Bergeron and Dubuc 1989; Zoladeski and Maycock 1990; De Grandpré *et al.* 1993; Frelich and Reich 1995; Stelfox 1995) and disturbance type (Ellis and Mattice 1974; Jeglum 1983; Brumelis and Carleton 1988, 1989; Johnston and Elliott 1996). However, thus far, only one published research program (van Cleve *et al.* 1986) has studied a boreal ecoregion in enough detail to sketch out the mechanics of its post-fire ecosystem dynamics. Consequently, post-fire ecosystem dynamics are only partially understood (MacLean *et al.* 1983; Bonan and Shugart 1989; Thompson and Welsh 1993; Zoladeski and Maycock 1990). With respect to nutrient cycling, MacLean *et al.* (1983) state that we know the most about where and in what quantities the minerals are found and somewhat about the pathways of transfer between different compartments. However, very little is known about what controls transfers despite the fact that this level of understanding is key to most practical and theoretical problems.

Even less information is available on post-logging ecosystem dynamics in the boreal forest. Past research on vegetation dynamics has tended to focus on the regeneration of commercial trees (Yang and Fry 1971; Jeglum 1983) or time periods too short to assess post-logging resilience (Ellis and Mattice 1974; Noble *et al.* 1977; Abrams and Dickman 1982; Harvey and Bergeron 1989; Walsh and Krishka 1991; Harvey *et al.* 1995; Johnston and Elliott 1995). Only one study (Brumelis and Carleton 1988, 1989) directly compared the post-fire and post-logging recovery of all growth forms beyond the first 15 years and it was confined to peatlands.

The need for research which furthers our understanding of boreal ecosystem dynamics has been frequently cited as a high priority prerequisite to sustainable forest management (cf. Booth *et al.* 1993; FEMAT 1993; Maini 1993; Thompson and Welsh 1993; Grumbine 1994; Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995; KPMG 1995; Kershaw *et al.* 1996). In this context, the objectives of this project were to:

1) Compare the influences of site conditions, age and disturbance by wildfire or winter logging on the species composition of naturally regenerating plant communities in eastern Manitoba, Canada;
2) Determine how well these communities were recovering from the effects of logging using post-fire vegetation as the benchmark for recovery.

The focus of this dissertation is on the community level patterns generated by site scale ecosystem dynamics. Following this introduction and literature review, the two objectives are addressed in Chapters 2 and 3. Since Chapters 2 and 3 include a review of relevant literature, the literature review in this chapter is confined to general background issues. Chapter 2 compares the species composition of communities grouped by three key causal factors- site conditions, age, and disturbance by wildfire or winter logging. A relative ranking of the influence of these causal factors on the spatial and temporal patterns of species composition is provided. Chapter 3 assesses recovery after logging using community resilience as the primary criterion. A detailed examination of disturbance type related differences in species composition is used to suggest potential causes of differences in resilience. Conclusions are presented in Chapter 4.

1.2 Literature Review

1.2.1 Influence of Site Conditions, Pre-disturbance Vegetation, Disturbance Type and Age on Species Composition

1.2.2 Site Conditions

When regions with homogenous climate are examined, site conditions often exert the most substantial influence on the spatial pattern of vegetation at the landscape scale (Rowe 1956; Mueller-Dombois 1964; Swan and Dix 1965; Dix and Swan 1971; Bergeron and Bouchard 1983; Carleton *et al.* 1985; Kenkel 1986; Kenkel 1987; Harvey and Bergeron 1989; Harvey *et al.* 1995; Jeglum and He 1995). The strongest site related distinctions occur at the extremes of the moisture regime gradient. These extremes are typically represented at the xeric end by outcrops or high sand dunes and at the hydric end by peatlands or riparian areas.

In the Clay Belt of western Quebec, Bergeron and Bouchard (1983) found that soil moisture and soil type (i.e. organic or mineral) provided the strongest separation of communities at the landscape level. Both variables are indicators of moisture regime. Soil type in Bergeron and Bouchard's (1983) sense is the indirect result of the status of soil moisture over many years. A thick surface organic layer usually develops as a result of the anaerobic conditions created by wet soils (Laiho 1997).

Bergeron and Bouchard (1983) found that the first two axes of a principal components analysis arranged plots in a circle. Xeric and hydric plots were next to each other due to the bimodal distributions of several species or species groups. These included *Picea mariana*[2] and moss cover. The bimodality of the distribution of *P. mariana* declines as precipitation is reduced westwards. This shortens the fire cycle and favors *Pinus banksiana* on xeric sites (Payette 1992).

Picea mariana and *Pinus banksiana* have their ecological optima on oligotrophic sites at the extremes of the moisture regime gradient (Bergeron and Bouchard 1983). On oligotrophic hydric sites, *P. mariana* was accompanied by *Chamaedaphne calyculata*, *Kalmia polifolia*, *Ledum*

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[2] Nomenclature follows Scoggan (1978) for vascular plants, Hale (1979) for lichens and Ireland (1982) for bryophytes. Authorities for binomials are found in Appendix A.

groenlandicum, *Oxycoccus quadripetalus*, *Smilacina trifolia* and *Sphagnum* spp.. On oligotrophic xeric sites (i.e. rock outcrops) that had escaped intense fire, *P. mariana* was accompanied by *Dicranum polysetum*, *Pleurozium schreberi* and *Ptilidium ciliare*. *Pinus banksiana* communities were found on xeric and mesic sites which had experienced an intense fire that stimulated seed dispersal. *Pinus banksiana* can be replaced by *Populus tremuloides* communities where post-fire dispersal of *P. banksiana* seed is limited. *Populus tremuloides* can disperse from distant unburned areas and residual individuals sucker profusely.

Many community types were found on non-hydric sites in western Quebec (Bergeron and Bouchard 1983). Their distribution overlapped and was largely determined by fire intensity and nutrient status as indicated by soil texture and structure. *Abies balsamea* communities were widespread except on the most xeric and hydric sites. Variants of the *A. balsamea* community type reflected the ecological optima of associated species in relation to a nutrient gradient. For example, *Cornus canadensis* co-occurred on oligotrophic sites, *Clintonia borealis* on mesotrophic sites and *Circaea alpina* on eutrophic sites. The relationship between nutrient status and community type variants is also affected by other factors such as moisture regime and openings created by spruce budworm.

Several community types with restricted distribution were encountered. These were the result of uncommon site conditions created primarily by the eutrophication resulting from water movement. Examples include *Fraxinus nigra* or *Populus balsamifera* in periodically flooded areas.

Slightly further west in eastern Ontario, Kenkel (1986) also identified soil moisture as the principal determinant of vegetation composition and structure. In his study, age was controlled for by selecting a study area which had experienced a large fire about 60 years earlier. At the landscape scale, the distribution of the ecological optima of tree species along the moisture regime gradient was similar to that identified by Bergeron and Bouchard (1983). When the focus shifted to specific portions of the moisture regime gradient (Kenkel 1986, 1987), moisture status still had a substantial influence on species composition but evidence suggested that nutrient regime was also important. Sixty years after fire, sandy upland sites typically had a *Pinus banksiana* tree cover and *Pleurozium schreberi* in varying amounts on the ground (Kenkel 1986).

Two exceptions occurred. *Vaccinium angustifolium* and *Arctostaphylos uva-ursi* had the highest relative cover on the most xeric and oligotrophic sites with *Cladina rangiferina* prominent in the open communities. *Picea mariana* was the dominant tree species where the water table was near the surface.

The closest research to the study area comes from the southeastern corner of Manitoba. This area represents a transition from the Great Lakes- St. Lawrence to the Boreal forest regions (Rowe 1972). Mueller-Dombois (1964) identified soil moisture as the most obvious gradient followed by soil fertility. *Picea mariana* dominated the overstory of peatlands. As soil moisture decreased so did the proportion of *Picea mariana* in the canopy while that of *P. banksiana* increased. *Pinus banksiana* was the dominant tree species on oligotrophic sites with a very xeric to mesic moisture regime. On the xeric to mesic range of the moisture regime gradient, increases in soil fertility were associated with the gradual replacement of *P. banksiana* by *Betula papyrifera*, *Populus tremuloides* and *Populus balsamifera*. Mesic to hydric eutrophic sites were occupied by *Populus balsamifera*, *Fraxinus pennsylvanica* and *Larix laricina*. Differences in moisture and nutrient status were more accurately reflected by understory than overstory species due to their narrower ecological amplitudes. For example, on oligotrophic sites, the transition from very xeric to mesic conditions changed the species associated with *Pinus banksiana* from *Cladina* spp. to *Arctostaphylos uva-ursi* to *Linnaea borealis* to *Ledum groenlandicum*.

Swan and Dix (1965) failed to detect a relationship between soil moisture and species distributions on upland sites in eastern Saskatchewan. Soil moisture was measured as the difference between field and dry weights of soil samples. They did detect a relationship between species distribution and soil texture. The soil textures included ranged from loamy sands to silt loams. The combination of the narrow range of soil textures included and the method of determining soil moisture may account for the discrepancy between this study and others which have detected a strong relationship between vegetation and soil moisture. Bergeron and Bouchard (1983) found that moisture regime was related to soil texture, topographic position and drainage regime. Drainage regime reflects a soil's innate water holding characteristics and is primarily a function of soil texture. Moisture regime reflects the modification of drainage regime by

topographic position or a high water table. Mueller-Dombois (1964) recognizes this distinction by subdividing non-extreme sites on the moisture regime gradient into those which derive their favorable moisture status from groundwater or the inherent properties of the soil. In the forest ecosystem classification of northwestern Ontario (Sims *et al.* 1989, p. 146), drainage is defined as "the rapidity and extent of removal of water from soils in relation to moisture additions". Drainage regime is determined by soil texture and depth to mottling or gleying. Moisture regime is defined as "the integration of all the variations in soil moisture supply throughout the entire growing season". The moisture regime of mineral soils is determined by soil texture, soil depth, drainage regime and depth to mottling or gleying. It is suggested that the findings of Swan and Dix (1965) regarding the relationship between soil moisture and species composition do not contradict the consensus of others. The narrow range of soil textures included limited the potential effect of moisture regime. Within this narrow range, Swan and Dix (1965) found associations between species distributions and soil texture. These could be interpreted as associations with moisture regime if moisture regime is interpreted according to more recent approaches to the field measurement of moisture regime (e.g. Sims *et al.* 1989).

In eastern Saskatchewan (Swan and Dix 1965), *Pinus banksiana* and *Picea mariana* were associated with the coarsest textured soils in the area (i.e. loamy sands and sandy loams), *Populus tremuloides*, *Betula papyrifera* and *Abies balsamea* with intermediate textures and *Picea glauca* with the finest textured soils (i.e. silt loams). Strong associations between canopy and understory composition were detected. These were attributed to the effects of the canopy on light intensity rather than other canopy effects (e.g. soil pH) or soil texture.

Rowe (1956) reported on a study in the mixedwood section of Saskatchewan and Manitoba which included the area later studied by Swan and Dix (1965). He suggested that moisture regime is the principal determinant of where species are most likely to occur while overstory composition controls the stratification of the understory through its effect on light intensity. Rowe identified understory species that collectively provide an indication of the moisture regime of a stand through a weighted index. Swan and Dix (1965) note that they failed to find evidence for the relationship between moisture regime and understory composition suggested by Rowe (1956).

However, as already pointed out, their results were not directly comparable due to differences in methods.

To summarize, moisture regime seems to provide the greatest separation of community types across the landscapes that characterize the Canadian Shield. That is, it is the site factor most easily associated with the changes in species composition which parallel the pattern from outcrops through increasing mineral soil depth to organic soils. Smith and Huston (1989) provide a potential explanation for this. They argue that physiological mechanisms prevent most vascular plants from being simultaneously adapted to grow rapidly at 1) both high and low levels of light intensity or water or 2) when water and light intensity are both at low levels. Adaptations which permit a plant to cope with water or light stress generally reduce its maximum growth rate, maximum size and maximum age. These adaptations stem from tradeoffs between water loss and CO_2 uptake through stomata and between resource allocation to above and below-ground growth. Their model can include nutrients but Smith and Huston (1989) confine themselves to the influence of water and light intensity because water and light intensity encompass a fundamental physiological tradeoff and their range of variability in space and time is greater than that of nutrients. If adequate water is not available then nutrient uptake also ceases. A plant is unable to take advantage of eutrophic conditions if the site is xeric. Consequently, moisture regime contributes to variability in species composition across the landscape. Nutrient regime becomes important when variation within a particular moisture regime is examined. On mesic sites, it contributes to the potential for more than one successional pathway.

1.2.3 Pre-disturbance Vegetation

A community generally contains a large proportion of its pre-disturbance species shortly after fire (Payette 1992) because many boreal plant species are well adapted to frequent fire (Rowe 1983). Many boreal vascular plants, including all shade intolerant boreal tree species (i.e. *Pinus banksiana*, *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera* and *Larix laricina*), can regenerate immediately from within a burned area (Dix and Swan 1971; Shafi and Yarranton 1973; Archibold 1979; Ohmann and Grigal 1979; Outcalt and White 1981; van Cleve and Viereck

1981; Abrams and Dickman 1982; Brumelis and Carleton 1989). Their adaptations include the ability to resprout from underground organs or the production of fire-resistant bark and cones. *Pinus banksiana* is a good example. The bark of mature trees provides protection against light surface fires (Cayford and McRae 1983). A more intense or crown fire will stimulate release of *P. banksiana* seeds which then germinate quickly without stratification and become rapidly growing seedlings (Sims *et al.* 1990). In a study of vegetation and nutrient dynamics during the first five years following fire, Ohmann and Grigal (1979) found that all tall shrubs except *Prunus pensylvanica* and most low shrubs regenerated vegetatively.

The influence of pre-disturbance composition can be substantially reduced when the fire is severe and kills underground perennating organs (Payette 1992) or when the return interval is short and long-lived species have not produced seed (Cayford and McRae 1983).

Pre-disturbance composition is typically more important to establishment stage species composition after logging than after fire. Fewer species suffer aboveground mortality and fewer available sites are created for colonization. Johnston and Elliott (1996) took advantage of a fire which spread into a recent cutover to provide information on several combinations of wildfire and logging. They compared the species composition of mature forest with that of 1) burned mature forest, 2) logged and then burned mature forest and 3) logged mature forest. Detrended canonical correspondence analysis of the herb and ground layers indicated that the disturbance with the species composition most similar to the mature forest was the logged mature forest. The two disturbances which produced the most similar species composition one year later were the two which involved fire. Disturbance type similarities and differences were manifested as stability or change in the relative cover of the most abundant species in the mature forest. *Pleurozium schreberi* was the species with the highest cover in the mature forest and the second highest cover in the unburned cutover. In contrast, it was absent in the burned cutover and had a relative cover < 1% after fire. A similar pattern was observed for several of the other species with high relative abundance in the mature forest including *Dicranum polysetum*, *Cladonia cristatella* and *Maianthemum canadense*. Understory species which typically thrive after fire such as *Epilobium angustifolium*, *Polytrichum juniperinum*, *P. piliferum* and *Marchantia polymorpha* (Rowe 1983)

were the most abundant species in the burn and burned cutover. *Epilobium angustifolium* apparently does not require fire for robust regeneration since it was also the most abundant species in the unburned cutover.

In some situations, a few pre-disturbance species can generate a community with an atypical post-disturbance composition. Overstory removal can facilitate the expansion of some shade suppressed species to the extent that the re-establishment of many other pre-disturbance species is pre-empted and the community undergoes a long-term conversion to a different type. Abrams *et al.* (1985) compared the regeneration of *Pinus banksiana* on sandy soil in Michigan after wildfire, clear-cutting and clear-cutting followed by prescribed burning. Based on data from adjacent 35 year old and mature communities, they assumed that all the disturbed sites contained *Carex* spp. prior to disturbance. All the clear-cut and some of the other disturbed sites quickly converted to *Carex* meadows. The *P. banksiana* site which contained a small amount of *Populus tremuloides* prior to clear-cutting and burning was converted to a *P. tremuloides* dominated community. On all sites but one, community conversion occurred due to failure of *P. banksiana* to regenerate. Successful *P. banksiana* regeneration on the one site was attributed to a high density of standing dead trees which limited *Carex* spp. expansion and provided shade adequate for seedling development.

1.2.4 Disturbance Type and Characteristics

The results of Abrams *et al.* (1985) and Johnston and Elliott (1996) emphasize Rowe's (1983) suggestion that regeneration patterns are strongly influenced by the interaction between disturbance characteristics and life history strategies. Some species such as *Epilobium angustifolium* and *Carex pensylvanica* benefited from overstory removal while others such as *Hylocomium splendens* and *Ptilium crista-castrensis* suffered large reductions in cover when the overstory was removed (Abrams *et al.* 1985; Johnston and Elliott 1996). Other species such as *Aralia hispida*, *Equisetum arvense* and *Carex houghtoniana* seemed to require some of the effects of fire since they became relatively abundant after fire but were either virtually or completely absent in the mature forest or unburned cutover.

Rowe (1983) highlights strategies which promote persistence in the boreal forest- a biome which has historically been regulated by frequent wildfire (Payette 1992). He argues that the frequency, intensity and spatial patterns of fire are too variable to have produced boreal plant adaptations to particular levels of fire frequency and intensity. Fire adaptations should be found at the local ecosystem level. Three attributes important for survival at this level in a biome characterized by frequent fire are mode of regeneration, competitive relationships and the time scale of critical life history events. In explaining persistence, Rowe places the greatest weight on mode of regeneration because there will be limited opportunities for competitive exclusion in a system with a high disturbance frequency and long-lived species which regenerate from within burns. He classifies species primarily based on whether they survive fire by dispersal of propagules or vegetative regeneration. Disseminule based strategies include invader, evader and avoider while vegetative based strategies are resister and endurer. Invaders are pioneering fugitives while avoiders establish at later stages of recovery. Evaders have propagules that are protected from fire's heat either by serotinous cones or the forest floor. Resisters are shade intolerant species whose adult stages can survive low severity fires. Endurers are species which resprout from underground perennating buds.

These strategies summarize attributes which have allowed species to survive recurrent fire during the Holocene. They also provide an indication of how a species will respond to a different type of disturbance such as logging. Evidence suggests that a life history strategy which promotes *in situ* regeneration also promotes community resilience (Dix and Swan 1971; Shafi and Yarranton 1973; Ohmann and Grigal 1979; Outcalt and White 1981; Abrams and Dickman 1982; Halpern 1988; Brumelis and Carleton 1988, 1989; Johnston and Elliott 1996). Species which can establish immediately after disturbance are more likely to persist. The successional pathways characteristic of an area provide evidence for this. For example, Bergeron and Dubuc (1983) characterize post-fire succession in western Quebec as the successive disappearance of shade intolerant species which established shortly after fire.

When a community has a high proportion of species which regenerate quickly from within it, species composition can rapidly approximate pre-disturbance conditions. *In situ* regenerators help

the community withstand the invasion of species not found in the pre-disturbance community. In the case of fire, the rapid growth characteristic of many herbaceous invaders causes a temporary, superficial change in the community's species composition because the cover of these species overwhelms that of regenerators (Cogbill 1985). However, the invaders eventually recede in importance due either to their life history characteristics (e.g. annuals or biennials: Abrams *et al.* 1985) or changes brought about by regenerators in factors such as competition, shading, and site availability (Cogbill 1985; Peet 1992).

Since community resilience is affected by the interaction between disturbance characteristics and life history strategies, it is important to elucidate the potential differences in the direct effects of fire and logging on site conditions and pre-disturbance vegetation. The three general categories which are affected and contribute to vegetation dynamics are site availability, species availability and species performance (Pickett *et al.* 1987). Species performance is affected not only by the direct effects of disturbance but also by indirect effects mediated through soil processes.

1.2.4.1 Effects on Species Availability

Disturbance related differences in species availability (species present as plants or propagules) are expected to be minor until immediately after disturbance in areas having a long history of recurrent fire. As already discussed, most pre-disturbance vascular species regenerate *in situ* unless the fire is severe or the return interval short. The extent to which they are supplemented by invaders is a function of the distance to unburned or slightly burned patches (Flinn and Wein 1977; Archibold 1979). Invaders also arrive in post-logging communities, however, when logging occurs in the winter, the lack of available sites may limit their establishment.

With the possible exception of logged species, immediately after logging, post-logging communities will have the same species available as post-fire plus three other types of species. The first type of species favored by logging are exotics that are transported into post-logging communities on logging or other equipment. The second type includes species which can survive logging but not fire and re-invade slowly after fire (i.e. Rowe's {1983} avoiders; e.g. *Abies*

balsamea). This disturbance type difference in species availability is eliminated over time as the additional species endemic to the region disperse into post-fire communities also. The third type of species to distinguish post-logging from post-fire communities does so by its absence or poor performance in post-logging communities because fire is required either to trigger dispersal or germination (e.g. *Geranium bicknellii*: Abrams *et al.* 1985) or to create conditions favorable for growth (e.g. *Polytrichum juniperinum*). *Pinus banksiana* requires both of these fire effects in regions where most individuals have serotinous cones (Cayford and McRae 1983). If it is one of the species cut then the cones contained in logging slash may open if they are on the ground and exposed to the sun. However, even when this occurs, the number of seedlings produced is lower than after fire because seedling survival on mineral soil decreases with increasing organic layer thickness (Ellis and Mattice 1974; Bell 1991).

1.2.4.2 Effects on Site Availability

Site availability following fire and logging differs greatly. Mosses and lichens usually constitute a large proportion of the ground cover in the mature post-fire communities typical of forests adjacent to the study area (Sims *et al.* 1989). By removing most of the living ground cover, fire creates a large area available for colonization. Fire also reduces the thickness of the surface organic layer. In some areas, fire exposes the mineral soil or bedrock and thereby creates a greater variety of site characteristics than found in the pre-disturbance community (MacLean *et al.* 1983). The overall effect on site availability varies in accordance with the intensity, severity and patchiness of the fire.

Logging creates available sites when it disturbs the ground layer or when plants are killed by logging equipment, slash deposition or the subsequent increase in light intensity. Taking into consideration both the proportion of the area disturbed and the effects on the organic layer, site availability is generally expected to be altered much less by logging than by fire (Zasada 1986). Consequently, the number and variability of colonization opportunities is lower in post-logging than in post-fire communities. Zasada (1986) found that 80% of the surface was undisturbed or slightly disturbed in a summer logged clearcut and in a shelterwood cut on mineral soils. Only 9% of the

area had mineral soil exposed. Surface disturbance was virtually absent on a winter logged flood plain.

Post-logging site preparation and some logging methods can alter site availability greatly if substantial ground disturbance occurs. Brumelis and Carleton (1989) found that mechanical skidding in the winter caused deep rutting in peatlands if the frozen layer was not thick enough to support the weight of a skidder. Rutting created two new microhabitats: exposed bare peat and water-filled depressions. Exposed peat remained bare except for a few bryophytes due to the harsh conditions associated with it. Water filled ruts were invaded by atypical species such as *Typha latifolia*.

1.2.4.3 Effects on Species Performance

Disturbance type differences in species performance (i.e. how well a species establishes, grows, persists and reproduces at a site) are expected to result from differential effects on direct and indirect factors. Direct effects include altered competitive relations and reductions in biomass (Flinn and Wein 1977); indirect effects occur through site factors such as changes in light intensity, nutrient cycling, soil temperature and soil chemistry (MacLean *et al.* 1983). Fire eliminates some species and kills the above-ground parts of others. Plant cover is not replaced until stems sprout from propagules or under-ground parts. Provided they are able to tolerate the drastic increase in light intensity and wind exposure, the established root systems of regenerators in post-fire communities may provide them with a competitive advantage relative to invaders (Ahlgren 1960).

Winter logging generally results in limited direct mortality of foliage and stem tissue in non-commercial species (Rowe 1983; Zasada 1986; Brumelis and Carleton 1989). Logging indirectly reduces the cover of a few species (e.g. *Hylocomium splendens*, *Ptilium crista-castrensis*: Johnston and Elliott 1996) which become desiccated in the more exposed microenvironment present after canopy removal (Crites and Dale 1995). However, these species are the exceptions. Most other species are shade suppressed (Viro 1974; Sims *et al.* 1990; Bell 1991) and the net effect of canopy removal for many is an increase in cover even though they may need to replace

shade leaves with sun leaves (Bell 1991; Brumelis and Carleton 1989). Species which can tolerate or benefit from the direct impacts of logging will have a substantial head start in cover compared with their conspecifics in post-fire communities because they do not need to replace stem tissue and, in some cases, photosynthetic tissue. The cover head start conferred by logging is especially important for slow growing species which are eliminated by fire (e.g. *Cladina mitis, C. rangiferina* and *C. stellaris*).

Competition is not expected to have a major effect on species performance immediately after logging because shade suppression generally limits total cover in the herb or shrub layers except in some deciduous vegetation types (Rowe 1956; Sims *et al.* 1989). Any competition that existed in these layers prior to logging will be lessened in the short- term by tree mortality. Only the ground layer is expected to experience competition prior to disturbance since the cover of its living components often approaches 100%. Ground cover is dominated by feather mosses in closed, coniferous communities. The proportion of reindeer lichen cover increases as the canopy opens and soils become more xeric (Payette 1992). At least over the short-term, logging can reduce competition in the ground layer. Removal of a closed overstory reduces the cover of feather mosses intolerant of high light intensity (Ellis and Mattice 1974; Crites and Dale 1995).

Altering light intensity generally has a substantial effect on species performance. Light intensity in post-fire communities increases all the way to the ground layer since foliage in all other overstory layers is removed. Standing boles provide some shade which can be important for the survival of tree seedlings (Cayford and McRae 1983). In post-logging communities, residual understory cover affects light intensity by intercepting light and acting as an overstory for the layers below it. Light intensity at lower layers will decrease as a direct function of the degree to which the tallest layer containing residual vegetation is closed (Rowe 1956). Residual cover in the shrub and herb layers provides some shade for the ground layer and this may facilitate the persistence of species intolerant of high light. This is expected to contribute to the maintenance of pre-disturbance floristics and species richness in post-logging communities. A general increase in light intensity in all layers will occur if none has a dense layer of foliage.

The degree to which understory light intensity changes after logging will be a function of the

species composition of the pre-disturbance tree canopy. Dix and Swan (1971) arrange trees in order of increasing shade cast by mature individuals as follows: *Pinus banksiana*, *Populus tremuloides*, *P. balsamifera*, *Betula papyrifera*, *Picea mariana* and *Abies balsamea*; *Picea glauca* varies greatly in the shade it casts. Rowe (1956) constructs an upland understory light intensity continuum based on overstory composition which moves from pure *Populus tremuloides*/ *P. balsamifera* on to mixed *Populus tremuloides*/ *P. balsamifera*/ *Picea mariana* and finally to pure *P. mariana*. Tall shrubs and herbs do not attain high cover values under a spruce canopy due to insufficient light. On the other hand, light penetration through a *Populus tremuloides*/ *P. balsamifera* canopy is adequate to permit the development of a tall shrub layer which suppresses tall herbs. An evenly mixed canopy of *Populus tremuloides*, *P. balsamifera* and *Picea mariana* simultaneously maintains some tall shrub cover and maximizes tall and medium herb cover. Medium shrubs and low herbs are relatively unaffected by the performance of the tall shrubs and medium herbs. Logging a closed *Picea mariana* community will cause a much larger change in light intensity and leave a community with less vertical structure than when a *Populus tremuloides* community is logged. This occurs because a *Populus tremuloides* lets more light through than a *Picea mariana* canopy and this facilitates the development of a shrub layer (Rowe 1956). Logging will favor species tolerant of the increase in light intensity created by overstory removal since their above-ground parts will generally suffer little mortality relative to fire (Brumelis and Carleton 1989).

Fire indirectly enhances species performance by releasing nutrients locked up in biomass and increasing soil pH (Ahlgren and Ahlgren 1960; Viro 1974; MacLean *et al.* 1983). Although fire directly leads to the loss of some nutrients, the proportion is small relative to the total found in the biomass and soils (Viro 1974). Direct nutrient losses arise as elements mineralized by the oxidation of organic matter are converted to gases or carried away as particulate matter. Volatilization losses increase directly with fire intensity and the amount of biomass consumed. Unless the fire is very hot, volatilization losses are generally substantial only for N (MacLean *et al.* 1983). Viro (1974) notes that the ecological significance of volatilization losses of N is much less than the positive effect of an increase in mineralized N. In addition, increased N fixation by N-fixing soil bacteria during the initial stage of post-fire succession partially compensates for

volatilization losses.

Increased nutrient availability is generally more important than nutrient losses for post-fire ecosystem dynamics. It results from the increase in soil pH, the mineralization and transfer of nutrients to the soil surface in ash, increased mineralization of soil organic matter and increased N fixation. The ash leached into the soil profile during the first year after fire contributes to a nutrient flush in the soil solution. Soil pH increases because high nutrient concentrations facilitate the displacement of protons from cation exchange sites (Aber and Melillo 1991). Mineralization increases because transpiration is reduced and this often increases soil moisture (MacLean *et al.* 1983), fire may break down compounds that decay slowly otherwise (Aber and Melillo 1991) and lower surface albedo increases soil temperature.

Increased soil temperature in post-fire communities often enhances species performance over the short-term (Ahlgren 1960; Ahlgren and Ahlgren 1960; Viro 1974), especially for soils undergoing paludification (Rowe and Scotter 1973) or with a thin active layer due to permafrost (MacLean *et al.* 1983). A decrease in growth rates may occur on fresh to moist soils if the increase in soil temperature is accompanied by a decrease in moisture availability. The latter effect can arise if the decrease in evapotranspiration is more than offset by increased evaporation from the soil.

Leaching is the primary source of nutrient losses from the soil profile (Cole 1995). Leaching losses are generally minimal after fire. MacLean *et al.* (1983) attribute this to the combined effect of increased soil pH, the intact cation exchange capacity and immobilization by rapidly regenerating vegetation. Rapidly growing, herbaceous post-fire thrivers such as *Epilobium angustifolium* perform an essential function by intercepting nutrients before they are lost to leaching. When shading eventually eliminates them from the community, decomposition releases the nutrients they have immobilized for use by shrubs and saplings (Viro 1974).

Post-logging nutrient dynamics differ from those after fire (Huttl and Schaaf 1995). Since there are no medium-term studies comparing post-fire and post-logging nutrient dynamics, expected patterns are derived from shorter term studies or studies which examined post-logging dynamics alone. Based on the results of a number of European and American studies on the

effects of logging on soil processes, Huttl and Schaaf (1995, pp. 33-34) conclude that:

> "Whole-tree clear-cutting is a severe ecosystem disturbance leading to (I) nitrification, (II) soil acidification, and (III) a loss of nutrients not only through the export of the harvested biomass, but also by way of leaching from the rooted soil profile stemming mainly from the forest floor."

Dahlgren and Driscoll (1994) examined the effects of whole tree clear-cutting on soil processes in hardwood and softwood ecosystems at the Hubbard Brook Experimental Forest. Clear-cutting led to increased acidification, leaching losses of nutrients and toxic levels of Al in the soil solution and stream waters. Lower soil pH was attributed to nitrification of ammonium in the forest floor. Logging increases nitrification because it raises soil temperature and provides a rich substrate for energy limited microbial populations (Bormann and Likens 1979). Fire does not have the same indirect effect on microbial populations because it oxidizes readily decomposable C and lowers the C:N ratio. Nitrification produces a nitrate ion, which is highly mobile, and a proton (Cole 1995) which either acidifies the soil or reduces nutrient availability depending on the pre-disturbance pH of the soil. The softwood sites at the Hubbard Brook Experimental Forest had the most acidic soils prior to disturbance and the highest nitrate losses due to leaching. Cation leaching losses peaked with those of nitrate (to maintain charge balance) one year after clear-cutting. Cation leaching losses were greatest for Al and K. Dahlgren and Driscoll (1994) attributed the delay in nutrient loss to temporary immobilization of mineralized nutrients in rapidly expanding microbial biomass (Vitousek and Matson 1984). As the energy rich logging residues and the forest floor were decomposed, the C:N ratio and litter quality declined. Microbial populations crashed within one year. Decomposing microbial biomass released nutrients into the soil solution where a high proportion of nutrients was permanently leached away due to low pH and limited vegetation recovery.

Vegetation performs a critical function in soil processes by intercepting nutrients in soil solution that would otherwise be leached (Marks 1974; Bormann and Likens (1979). Marks (1974) observed an overlapping succession of plant species involved in nutrient retention after clear-cutting in New Hampshire. *Rubus* spp. were the first to thrive and sequester the nutrients released by logging. *Prunus pensylvanica* established at the same time as *Rubus* spp. but did not become important in nutrient immobilization until a few years after logging. *Prunus pensylvanica* can

continue to perform the nutrient retention function for up to 25 years. It is followed by *Betula alleghaniensis* and/ or *Populus tremuloides*. Marks (1974) does not identify the mechanism for *Rubus* spp. and *Prunus pensylvanica* decline but it may be the result of changes in shade created by differential maximum growth rates and heights.

1.2.5 Age

Immediate differences in post-fire and post-logging vegetation dynamics were identified in the previous section and were related to the differential immediate effects of disturbance type. A disturbance has many longer-term and/ or indirect effects which may be manifested in species composition as community recovery occurs. In general, no attempt will be made to separate these effects from those of age since previous research has not been designed to address this.

As already noted, vascular plant recovery after fire or logging is dominated by regeneration of pre-disturbance species unless the fire is severe or logging has created substantial ground disturbance. Apparent changes in species composition are the result of the different growth rates and life spans of species rather than a sequence of species replacements (Bergeron and Dubuc 1983; Cogbill 1985; Frelich and Reich 1995). Trees have a large influence on these dynamics. They affect understory composition through their effect on light intensity and litter accumulation (Rowe 1956; Dix and Swan 1971). Litter can smother bryophytes, lichens and low growing plants, alter the chemical properties of the soil (Pastor *et al.* 1987) and increase the thickness of the organic layer (van Cleve *et al.* 1983). A thicker organic layer leads to lower soil temperatures and increased soil moisture which in turn leads to a slower rate of decomposition and then to further increases in the thickness of the organic layer. Fire arrests this process (van Cleve et. al 1983; Bonan and Shugart 1989).

Trees exert little influence in the stage immediately after fire because they regenerate more slowly than herbaceous species. Some time after 5 years of age, tree species overtake herbs and shrubs and often form a dense canopy (Ohmann and Grigal 1979). Tree sapling shade and litter then influences which species can persist and continue to establish. Density dependent self-thinning begins some time after the shrub stage in *Pinus banksianal Picea mariana* communities

(Carleton and Wannamaker 1987; Kenkel *et al.* 1997). Slower growing tree species (e.g. *P. mariana*) eventually enter the primary canopy formed by species with more rapid initial growth (e.g. *P. banksiana*, *Populus tremuloides*: Kenkel 1986; Frelich and Reich 1995).

Post-fire shrub dynamics are influenced by tree dynamics. Fire causes drastic changes in light intensity in the lower layers. Most species which resprout from underground organs are adapted to deal with both the shade characteristic of a closed spruce or fir canopy and the high light intensity present after canopy removal (Rowe 1983; Brumelis and Carleton 1989). Vegetative regeneration stimulated by the nutrient flush leads to a rapid increase in the cover of most shrub species until trees overtake them. Shrub cover is then linked to the characteristics of the canopy formed by tree species whether it be at the sapling or mature tree stages. The dynamics of fire intolerant shrubs are initially influenced by dispersal, site availability and site conditions but later become a direct function of light intensity in the shrub layer and shade tolerance.

Herbs exhibit similar dynamics to those of shrubs but may be affected by tall shrub as well as tree cover. A light permeable *Populus tremuloides* canopy may facilitate the formation of a dense tall shrub canopy (e.g. *Corylus cornuta*) leading to the same effect on the herb layer in terms of light intensity as a *Picea mariana* canopy (Rowe 1956). In general, tall shrub shading is not expected to be an important factor in herb dynamics since only a small proportion of boreal vegetation types have a well developed tall shrub layer (Rowe 1956; Sims *et al.* 1989). As with trees, shading by tall shrubs is relatively unimportant in the dynamics of herbs during the initial post-fire stage. Fire tolerant and intolerant pioneers appear shortly after fire and quickly attain a high relative abundance. Some species such as *Epilobium angustifolium* and *Agrostis scabra* reappear within a few weeks following fire (Bell 1991). The seed bank is an important source of propagules for herb regeneration (Ahlgren 1974).

Ground layer dynamics typically go through a sequential succession that is linked with tree dynamics (Black and Bliss 1978; Clayden and Bouchard 1983; Foster 1985). Succession proceeds from bare rock, mineral soil or organic material to increasing abundance of *Cladonia* spp. and pioneer mosses and lichens (e.g. *Ceratodon purpureus, Lecidea granulosa, Polytrichum* spp.) to the addition of feather mosses and *Cladina* spp.. On xeric sites, post-fire communities

typically remain open and eventually become characterized by a *Cladina* lichen ground cover (Payette 1992). Lichens re-establish and regain their pre-fire cover more slowly than other plant groups. It may be a number of years before some species even appear in post-fire communities (Foster 1985; Kershaw 1977). For instance, *C. stellaris* is thought to require particular soil conditions for establishment and these are generally not produced until about 25 years after fire (Kershaw 1977).

On sites where a coniferous closed tree canopy develops, feather moss cover increases (initially *Pleurozium schreberi* and then *Hylocomium splendens* and *Ptilium crista-castrensis*) until a ground cover is formed (Payette 1992). The moss layer of a mature forest affects ecosystem dynamics in several ways (van Cleve *et al.* 1983; Bonan and Shugart 1989). A continuous moss layer prevents the invasion of species requiring a mineral seedbed for germination or seedling survival. It is also very effective at intercepting the moisture and nutrients provided by throughfall and precipitation. Mosses accelerate the thickening of the organic layer because they decompose at 10% of the rate of herbs (Oechel and van Cleve 1983). These effects combine to lower soil temperature, raise soil moisture and retard decomposition and the cycling of nutrients. The result is a nutrient build-up in the thickening organic layer (van Cleve *et al.* 1983; Bonan and Shugart 1989). In areas where the fire return interval has been relatively long, it is thought that degradation into open woodlands or shrublands is more likely to occur than self-replacement (Dix and Swan 1971; Payette 1992).

Many of the factors leading to the dynamics observed after fire operate in a similar way after logging. However, as previously discussed, the difference in disturbance characteristics interacts with life history strategies and soil processes to produce different dynamics.

Brumelis and Carleton (1988, 1989) provide the only boreal study which directly compares the species composition of post-fire and post-logging communities at developmental stages which include canopy closure and maturity. Their study involved peatland communities of various ages in the Clay Belt of northeastern Ontario that were either burned by wildfire or logged. Logging took place year-round. Trees were winter skidded to the roadside by horse or machines. Mechanical skidding caused intense ground disturbance for the reasons mentioned above.

Brumelis and Carleton (1989) describe four general post-logging successional patterns and relate them to nutrient and ground disturbance intensity gradients. Where ground disturbance and nutrient availability were high, aggressive atypical invaders (e.g. *Typha latifolia*) became established and were expected to persist indefinitely. Where ground disturbance was high but nutrient availability was low, sites were available but conditions were too harsh for pre-disturbance species to re-establish. Overstory removal killed the feather mosses and created a droughty substrate tolerated only by a few bryophytes (i.e. *Ceratodon purpureus*, *Leptobryum pyriforme* and *Marchantia polymorpha*). Where disturbance was low and nutrient availability high, many residual understory species performed well but there was a shift in species composition from those which typically establish shortly after fire (e.g. *Picea mariana*) to fire intolerant species (e.g. *Abies balsamea*). A large proportion of the tree regeneration resulted from residual individuals. Since logging removed *P. mariana*, most of the residual individuals were *A. balsamea*. At the same time, competition from understory plants limited *P. mariana* establishment. The only situation where communities approached their pre-disturbance composition was where ground disturbance intensity and nutrient availability were both low. Low nutrient availability was associated with a relatively open pre-disturbance canopy. This reduced self-pruning by *Picea mariana* and provided branches for layering. The *Sphagnum* species characteristic of oligotrophic sites (*S. nemoreum* and *S. angustifolium*) formed a dense mat favorable for *P. mariana* seedling establishment and advance growth through layering. The eventual development of a *P. mariana* canopy facilitated the entry of species which require the specialized conditions provided by an overstory. Recovery towards the pre-disturbance composition was occurring albeit with a higher component of fire intolerant species such as *A. balsamea*.

It is unclear to what extent the successional patterns observed by Brumelis and Carleton (1988, 1989) occur on mineral soils in the boreal forest. Long-term direct comparisons of post-fire and post-logging vegetation dynamics are lacking and many of the species which characterize peatlands possess specialized adaptations to cope with hydric soils and low pH (Brumelis and Carleton 1989). In the absence of studies which have directly compared post-fire and post-logging dynamics on mineral soils beyond the shrub stage, the best information is provided by

comparative establishment stage studies and longer-term fire or logging studies.

Carleton and MacLellan (1994) compared the woody vegetation of post-fire and naturally regenerating post-logging communities in northeastern Ontario. They concluded that logging resulted in "... a massive conversion from needle-leaved, conifer-dominated ecosystems to broad-leaved, deciduous forest and shrub ecosystems ..." (Carleton and MacLellan 1994, p. 148). Such conversions are common (Ellis and Mattice 1974; Yang and Fry 1981; Jeglum 1983; Harvey and Bergeron 1989). Carleton and MacLellan (1994) found that the extent to which community conversion occurred appeared to be related to the pre-disturbance vegetation and was a direct function of site fertility and intensity of ground disturbance. Conversion from a *Picea mariana* to an *Abies balsamea* vegetation type often occurred on sites where residual *A. balsamea* seedling and sapling densities were high. Conversion to a *Populus tremuloides* and/ or *Populus balsamifera* vegetation type often occurred on clay or silt-clay sites due to suckering and seed colonization of exposed areas.

Harvey *et al.* (1995) clarify these patterns for the establishment stage of post-logging vegetation dynamics. Their data included cutovers between 1 and 8 years old on a broad range of site types in the *Abies balsamea*/ *Betula papyrifera* zone of northwestern Quebec. Regeneration patterns varied considerably. Much of the variability could be attributed to site type and its interaction with disturbance intensity and season of cut. Limits to the short-term predictability of successional pathways resulted from the potential for a number of different types of competition problems to develop. This was attributed to among site variability of pre-logging species composition and the amount of site disturbance.

In conclusion, it is clear that many factors influence vegetation dynamics and that discrete events such as disturbances can have long-term indirect effects through below-ground ecological processes. Our understanding of vegetation dynamics can be furthered by incorporating as many of these substantial influences as possible into study design. It is also clear that, although differences in the initial effects of fire and logging can have longer-term effects on vegetation recovery, we lack information on long-term post-logging recovery as well as an understanding of the mechanisms which control ecosystem dynamics.

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Chapter
2
The Relative Influence of Site Conditions, Age and Disturbance Type (Wildfire or Winter Logging) on The Species Composition of Plant Communities

2.1 Introduction

Many factors influence the distribution and abundance of species in space and time. These distributions create patterns which appear as a spatial mosaic of vegetation types at the landscape scale or temporal changes in species composition on particular sites within the mosaic. If a landscape mosaic can be regarded as a snapshot of temporal patterns on a collection of sites, then a theory of vegetation dynamics can further our understanding of how spatial as well as temporal patterns are produced. Our knowledge of vegetation dynamics has not progressed to the point where a general theoretical model has been widely accepted (Finegan 1984; Pickett *et al.* 1987; Shipley and Keddy 1987; Pickett and Kolasa 1989; Smith and Huston 1989; McCook 1994; Cook 1996). Nevertheless, there is sufficient consensus to outline a theoretical framework for a model (Pickett *et al.* 1987; Glenn-Lewin and van der Maarel 1993; Peet 1992). Such a framework provides the essential foundation for study design, interpretation of results and development of robust predictive models (Green 1979; Levin 1989; Pickett *et al.* 1987; Peet 1992).

A theoretical framework can be created by specifying the direct and indirect linkages between vegetation and its causal factors in a causal diagram (Saris and Stronkhorst 1984). A first approximation of a theoretical framework for vegetation dynamics (Figure 2.1) comes from a synthesis of Pickett *et al.* (1987), Pickett and Kolasa (1989), Austin and Smith (1989) and Smith and Huston (1989). It is general enough to accommodate the various successional causes and patterns proposed in the literature (Finegan 1984; Pickett *et al.* 1987; Peet 1992; McCook 1994). The theoretical framework is probabilistic since it incorporates a combination of stochastic (e.g.

dispersal, disturbance characteristics) and deterministic variables (e.g. plant functional type, certain site type attributes such as soil depth).

Even though the theoretical framework (Figure 2.1) is not exhaustive, it still identifies an impracticably large number of causal variables for field work. Fortunately, causal theory (Cook and Campbell 1979; Saris and Stronkhorst 1984) provides the basis for designing a study to include only those causal variables which are "ultimate" in nature vis-à-vis the question at hand. Ultimate causal variables are essentially those in the sequential causal hierarchy whose causes do not have a substantial influence on the object of study. For example, although climate has substantial influences at the community level, the variables which determine climate do not, and need not be measured.

The theoretical framework (Figure 2.1) suggests that the ultimate causal factors in community level vegetation dynamics are site type (physical and chemical properties of the site), landscape configuration (arrangement of landforms, water bodies and vegetation types), disturbance type, climate, soil organisms, plant functional type (genotypic limitations on the transformation of resources into growth and reproduction; Smith and Huston 1989), herbivory and disease. Age does not appear as a causal variable but is included implicitly via the temporal dimension of the causal variables. Age summarizes the effects of autogenic processes such as plant population dynamics (Peet 1992). Disturbances at the stand and gap scale deflect and sometimes disrupt gradual autogenic change. Vegetation has feedback effects via pre-disturbance vegetation, competition, interactions with soil processes and canopy effects on understory light intensity and microclimate.

Climate and plant functional type[3] can be ignored when a community scale study occurs within an ecodistrict since these variables are relatively homogenous by definition (CCELC 1989). Of the remaining causal factors, research demonstrates that site type, age, disturbance type and pre-disturbance conditions influence the species composition of boreal communities (Jeglum 1971, 1972; Carleton 1982; Bergeron and Bouchard 1983; Carleton *et al.* 1985; Kenkel 1986,

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[3] In a community level study, plant functional type effectively refers to the pool of species available to sites in the study area.

1987; Brumelis and Carleton 1988, 1989; Bergeron and Dubuc 1989; Harvey *et al.* 1995). The influence of site type is substantial when extremes of moisture or nutrient gradients are included.

The effect of age is closely linked with stand replacing disturbance in the boreal forest. Wildfire has historically been the dominant form of disturbance (Payette 1992) but the importance of clear-cut logging is steadily increasing. A typical post-fire succession can be divided into developmental stages such as establishment, shrub, canopy closure, maturity and senescence. These stages represent conspicuous differences in physiognomy and species composition. The shrub stage occurs when tree saplings have over-topped and shaded vegetation in the ground and herb layers. It marks the end of the post-fire ephemeral invasion period (Shafi and Yarranton 1973; Ohmann and Grigal 1979). With canopy closure begins the period of asymmetric competition for light and self-thinning (Carleton and Wannamaker 1987; Kenkel *et al.* 1997). Community maturity occurs when the rate of density dependent tree mortality has declined substantially and species composition is relatively stable. Senescence is poorly understood since disturbance usually recurs prior to this stage (Bergeron and Dubuc 1989) but evidence suggests that regression to an open shrubland rather than self-replacement may occur (Rowe 1961; Dix and Swan 1971; Cogbill 1985).

Although post-fire vegetation dynamics are adequately described (cf. Dix and Swan 1971; Shafi and Yarranton 1973; Black and Bliss 1978; Carleton and Maycock 1978; Ohmann and Grigal 1979; Clayden and Bouchard 1983; Cogbill 1985; Foster 1985; Payette 1992; Rowe 1983; van Cleve *et al.* 1986; Bergeron and Dubuc 1989; De Grandpré *et al.* 1993), they are still only partially understood (Bonan and Shugart 1989). Even less is known about post-logging vegetation dynamics. Previous research generally focused on commercial tree species (Yang and Fry 1971; Jeglum 1983) or recovery periods too short to assess resilience to logging (Ellis and Mattice 1974; Noble *et al.* 1977; Abrams and Dickman 1982; Harvey and Bergeron 1989; Walsh and Krishka 1991; Harvey *et al.* 1995; Johnston and Elliott 1995). Only one study directly compares the post-fire and post-logging recovery of most components of the plant community beyond the first 15 years and this is confined to peatlands (Brumelis and Carleton 1988, 1989).

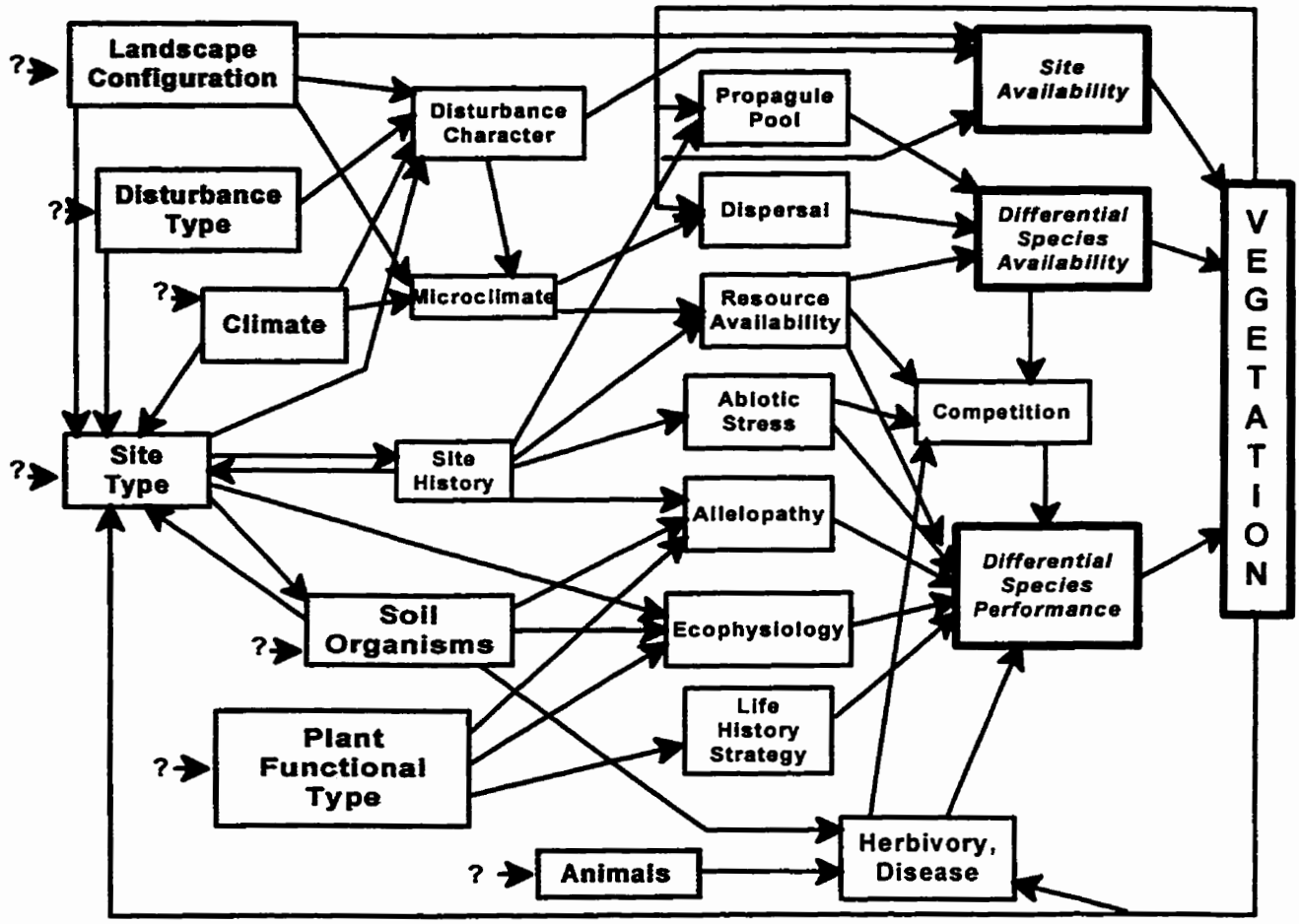


Figure 2.1. Theoretical framework for vegetation dynamics.

Shaded boxes identify causal variables which are "ultimate" at the site scale. Arrows depict the hypothesized direction of cause and effect. Some variables and linkages are not shown. A few of the feedback effects of vegetation are indicated.

This chapter compares the species composition of naturally regenerating boreal plant communities classified by site type, age and disturbance type. It also ranks the relative influence of these factors in the study area and suggests implications for forest management.

Numerous authors emphasize the importance of not confounding spatial, temporal and disturbance factors with each other (cf. Green 1979; Carleton 1982; Kenkel 1986; Bergeron and Dubuc 1989). The strength of inferences derived from a study is determined by the degree to which these and other causal factors are accounted for in study design. Causal factors were accounted for, to the extent possible, through a quasi-experimental approach (Cook and Campbell 1979) which used the theoretical framework to identify the causal factors that needed to be either measured or controlled by statistical (replication, randomization and interspersion) or experimental methods[4]. Age was represented at the shrub (13 years), canopy closure (37 years) and maturity (65 years) stages. Sixty-five year old post-logging communities were not included because of the great dissimilarities in the logging methods in use at that time and in the surficial geology of the areas cut. For each site type, the species composition of 65 year old post-fire communities was taken to represent the typical mature state (Ahlgren 1974; van Cleve and Viereck 1981; Carleton and Wannamaker 1987; Kenkel *et al.* 1997).

• It should be emphasized that references to "causal" variables are for the purpose of study design so that control is implemented for factors which could confound the results. It does not imply that any subsequent associations found between outcomes and variables is a causal one. In the context of results, these variables are viewed as explanatory.

2.2 Methods

2.2.1 Study Area

The 900,000 hectare study area is located on the Canadian Shield of eastern Manitoba, Canada between latitudes 50° 20' N and 51° 5' N and longitudes 95° 7' W and 96° 15' W (Figure 2.2). It is dominated by granitic and basaltic bedrock outcrops, glacial deposits less than 100 cm deep and poorly drained organic accumulations. Mineral deposits are predominantly sandy loam in texture. Fibrisols, mesisols, dystric brunisols and gleysols (Agriculture Canada 1987) cover most of the area (Eilers *et al.* undated).

The study area lies within the Subhumid Transitional Low Boreal Ecoclimatic Region (CCELC 1989). Winters are cold and relatively dry while summers are warm. Bissett is the most appropriate location for weather information. There, mean daily temperatures are -19.5°C in January and 18.6°C in July (Canada, Atmospheric Environment Service 1993). Average annual precipitation is 565 mm with 360 mm falling from May to September. The mean number of degree days above 5°C is 1576 (Canada, Atmospheric Environment Service 1993). Warm summers and moderate precipitation combine to produce a moisture index just above the borderline for moisture deficit (Rowe 1972).

Rowe's (1972) Lower English River and Northern Coniferous Forest Regions meet in the study area. Their boundary occurs where the Canadian Shield ceases to dominate surficial geology. Mature post-fire communities on mineral soils typically consist of a *Pinus banksiana* and/ or *Picea mariana* tree canopy, sparse shrub and herb layers and a forest floor covered with mosses, *Cladina* lichens and coniferous litter. Communities on peatlands are characterized by *Picea mariana*, a low shrub layer dominated by *Ledum groenlandicum* and a *Sphagnum* moss ground cover.

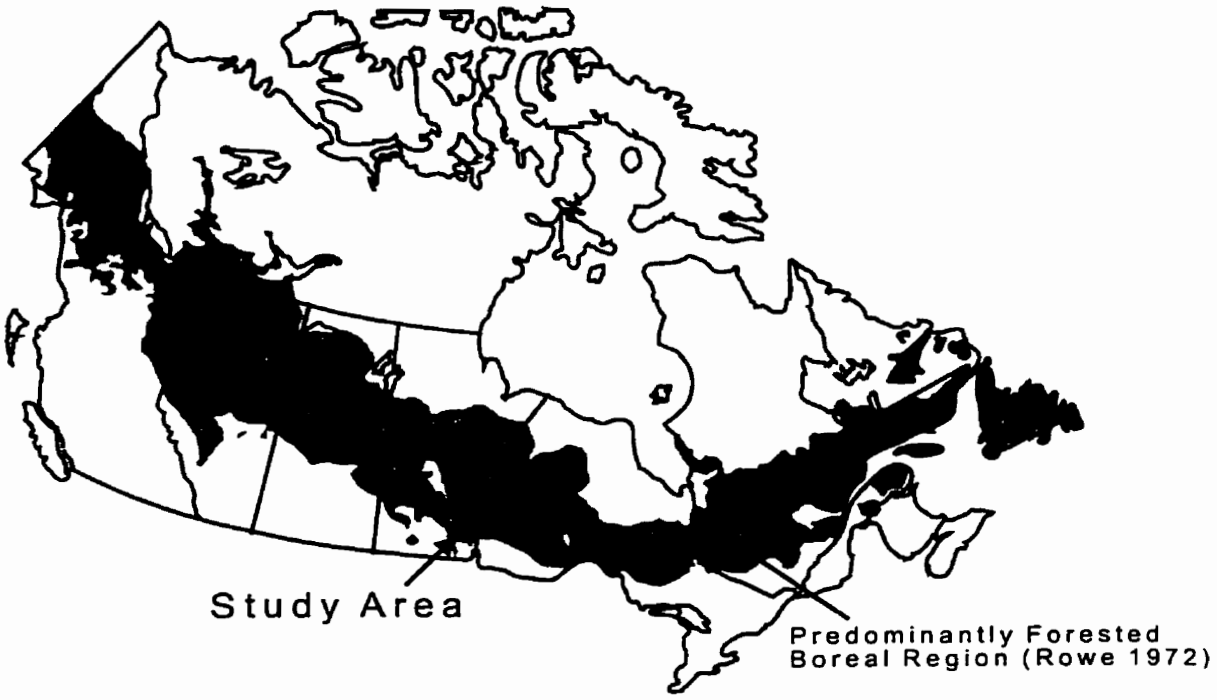


Figure 2.2. Study area location.

Wildfire has been and still is a substantial agent of disturbance in the area despite active fire suppression. Most of the area which burned in the boreal forest prior to fire suppression burned in a small proportion of years when climatic events created conditions that favored the spread of fires over large areas (Cogbill 1985; Johnson 1992; Hunter 1993). Historical maps indicate that approximately 80% of the study area burned at least once during the 104 year period between 1885 and 1989. Some of these areas have burned several times. The years with several large fires were 1885, 1895, 1929, 1936, 1955, 1979, 1980, 1983 and 1989.

Fire ignition and initial spread are a function of weather and local conditions (e.g. vegetation type and site type). However, Johnson (1992) argues that the area burned is largely determined by climatic events. Large fires (i.e. > 200 ha) generally occur on windy days after extended periods of drought because these conditions dry fine fuels and duff layer and thus favor rapid fire spread.

Due to the conditions which favor them, large fires tend to be moderate to high intensity (i.e. "hot") fires and thus kill the above-ground parts of trees and understory vegetation (Heinselman 1981; Rowe 1983; Cogbill 1985; Eberhart and Woodard 1987; Johnson 1992). The wildfires included in this study are considered comparable in terms of their background conditions since 1) the years included in this study are all years that had numerous large fires and 2) the amount of global change which occurred during the 52 year time period covered by the study was unlikely to substantially alter the wildfire disturbance regime.

Fire intensity and severity can vary greatly within a wildfire due to factors such as fuel type, slope, rainfall, wind and site type. This can be accounted for with replication and becomes part of the sampling variability.

Documentation of logging methods was accomplished through interviews with three Pine Fall's Paper Company (PFPC; formerly the Pine Falls Division of Abitibi Price) employees who had been involved in the logging operations, a brief written summary of the logging history of the Pine Falls operation (Peacock unpublished), photographs from PFPC's archives and Abitibi Price's company magazine. The company magazine contained numerous photographs and

articles from 1950 to the 1980's. Of seemingly special interest to the magazine were new developments at each of its mills and woods operations, such as the elimination of horsepower.

Between 1953 to 1981, logging took place almost exclusively between beginning of November and the end of March when the ground was frozen. Cutting occurred on all site types and all commercially usable *Picea mariana* and *Pinus banksiana* stems were cut. Throughout the period, branches were left near the stump and regeneration was natural.

Logging methods changed between 1953 to 1981. From about 1953 to 1978, cutting proceeded perpendicular to the logging road in strips 1 chain wide (20 m) and approximately 91 m deep. Trees were felled by chainsaws towards the edge of the strip and delimbed where they landed. Either a horse, farm tractor or D-6 crawler used a chain to drag the delimbed bole to the center of the strip. This was often difficult as the butt of the log dug into the snow and occasionally got hung up on stumps. In the center of the strip the bole was cut into 1.2 m (4 foot) lengths and stacked in 1 cord piles. Later, the wood was loaded by hand onto sleighs and hauled to a river or main haul road by horses or tractor. Wood hauled to a river was stacked on the ice to await the spring thaw.

By 1979, trees were cut by mechanical fellers and delimbed at the stump. Mechanical skidders hauled numerous trees at one time to the roadside. The greater power and maneuverability of skidders permitted the removal of larger trees than during the strip cutting era. Skidders dragged the entire bole to the roadside where it was bucked into 2.4 m (8 foot) lengths by chainsaw or mechanical slasher and then loaded onto a tractor trailer. The butts of these trees were lifted off the ground resulting in less damage to the ground than in strip cutting. The skidders weighed more and because they criss-crossed over larger areas they may have caused greater damage to advance regeneration than during the earlier era when skidding tended to be perpendicular to a single trail down the center of the strip.

Although there were substantial changes in the way trees were cut and skid, substantial differences in ground disturbance were not expected because the ground was frozen and snow covered. The fact that former haul roads were the only places where ground disturbance was still evident at the time of sampling provided some corroboration of this.

2.2.2 Sampling

The sampling design was three stage with random, blocked random and systematic sampling occurring at the successive stages (Figure 2.3). Sampling frames were constructed by digitizing the disturbance history maps of Pine Falls Paper Company. A replicate was a geographically distinct disturbance (i.e. the outer boundary of the disturbance polygon including skipped patches) separated from the nearest disturbance the same disturbance type/ age class combination by at least 3 km. Four replicate burns or cutovers were randomly selected for all but one (where only three were available) of the five combinations of disturbance type and age class. Each replicate was subdivided into three equal-width blocks to ensure adequate dispersion of plots within it. A transect was randomly located within each block. Plots were systematically located along each transect beginning from a random starting point after leaving a 100 m edge buffer. During the first field season, data was collected at all systematic locations in a 2 x 5m understory plot nested within a 10 x 10m tree plot. This design supported unbiased estimation of species composition parameters by site type, age class and disturbance type (Cochran 1977, 1983).

Understory percent cover was estimated in contiguous 1 x 1 m quadrats within the 2 x 5 m understory plot. Cover was estimated for trees, saplings, tree seedlings, shrubs, forbs, graminoids, terrestrial bryophytes and lichens and non-living ground cover in the tall shrub, medium shrub, herb, and ground layers (Table 2.1). Separate estimates were made for mature tree, sapling and tree seedling cover in each of the understory layers. Species difficult to identify in the field were grouped into broader taxa such as *Carex* spp. or foliose lichen spp. (see Appendix A for a species list). Canopy closure (percent cover of the overstory) and tree density, circumference at breast height (CBH) and height were recorded in the tree plot. Increment cores were taken at breast height from at least two individuals representing the largest and intermediate sized individuals of each conifer species in the plot. This provided limited radial growth information and corroborated the expected time since disturbance. A soil pit was dug to 1m or lithic contact to describe the soil profile (Agriculture Canada 1987; Sims *et al.* 1989), hand texture the horizons, establish the site type and obtain soil samples. Information relating to topography and disturbance

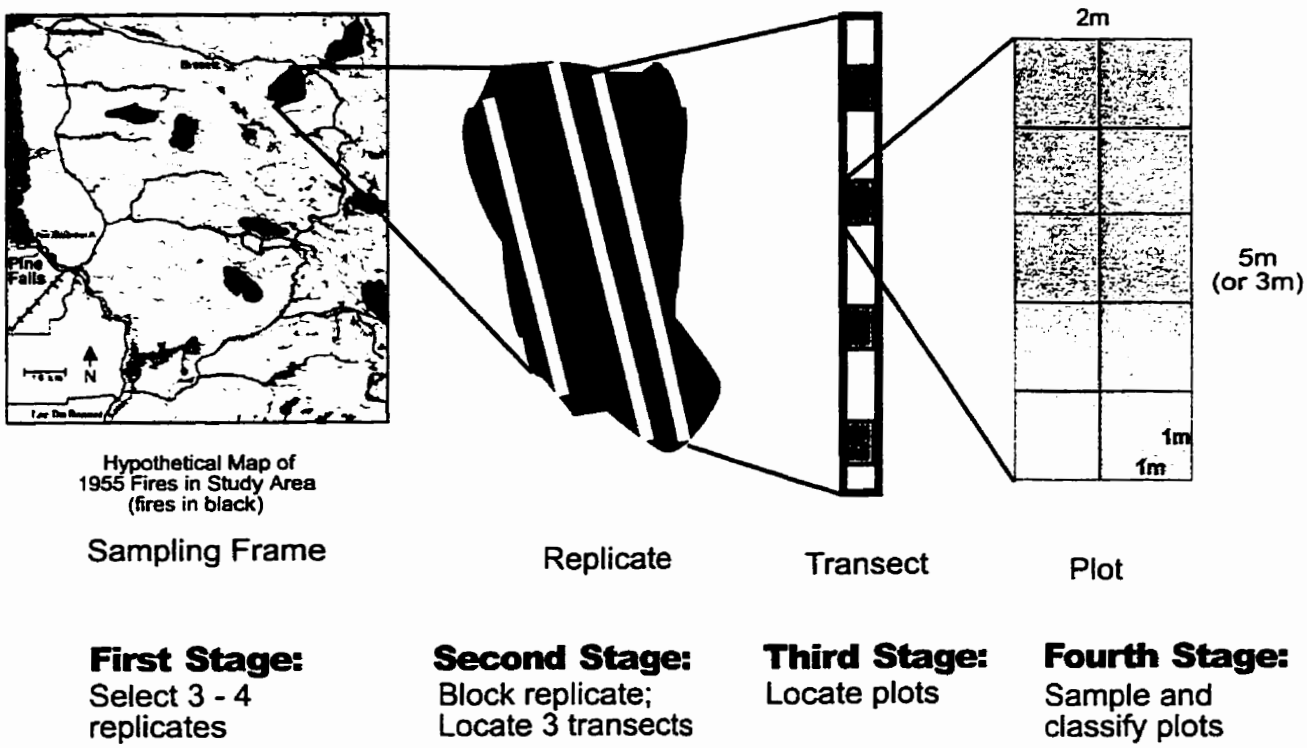


Figure 2.3. Sampling design. All reported results are based on a 2 x 3m plot size.

Table 2.1. Cover type and layer definitions.

Category	Definition
Cover type	
Tree	Individual of a tree species with CBH at least 10 cm
Sapling	Individual of a tree species with CBH < 10 cm and height ≥ 0.5 m
Seedling	Individual of a tree species with CBH < 10 cm and height < 0.5 m
Tall shrub	Woody plant other than a tree species which typically grows to a height > 2.0 m
Medium shrub	Woody plant other than a tree species which typically grows to a height between 0.5 and 2.0 m
Low shrub	Woody plant other than a tree species which typically grows to a height < 0.5 m
Forb	Non-woody vascular plant in a family other than Gramineae or Cyperaceae
Graminoid	Member of Gramineae, Cyperaceae or Juncaceae
Bryophyte*	Ground moss or hepatic and *Selaginella densa*
Lichen	Ground lichen
Conifer litter	Coniferous leaf litter
Other litter	Litter and decaying material not included in another category
Wood litter	Wood touching the ground which has not decayed to the stage where it can be crumbled by hand
Snag	Base of a standing dead tree
Stump	Rooted above-ground remains of a cut tree
Trunk	Base of a living tree
Mineral	Exposed mineral soil
Rock	Exposed rock
Water	Exposed water
Layer	
Tall shrub	> 2.0 m in height
Medium shrub	0.5 - 2.0 m in height
Herb	< 0.5 m in height
Ground	Reserved for bryophytes, lichens and non-living ground cover

* *Selaginella* is not a bryophyte but is included in this cover category due to its physiognomic similarity with bryophytes.

history was collected at each plot. Plots and their surroundings were examined for evidence of the appropriate disturbance. In the case of wildfire, the requirement was complete mortality of the overstory and understory. In cutovers, a disturbed plot was one which had stumps in or adjacent to it.

Results from the first field season were used to derive the quadrat, understory and tree plot sizes and shapes, subsample size, sample size and a site type classification for subsequent field seasons. Given the total sampling effort available, choices were made that optimized statistical precision for the most abundant species using a combination of power analysis (Sokal and Rohlf 1981) and the first two criteria of Kenkel and Podani's method (1991). Plot sizes were reduced for the final two field seasons to 2 x 3 m for understory cover and to 5 x 5 m for trees . All reported results are based on these plot sizes. A 2 x 3 m portion of the 2 x 5 m understory plots and a 5 x 5 m portion of the 10 x 10 m tree plots were used for the first field season's data. No other adjustments to the data or analyses were necessitated by the plot size changes since data were collected in contiguous incremental quadrats (Figure 2.3). The site type classification was validated with cluster analysis and multiple discriminant analysis using data from the second field season (Appendix B).

Classification of plots into one of the seven site type categories was based on the thickness of the surface organic layer (LFH plus O layer where present), depth to bedrock (depth from top of organic layer to bedrock) and moisture regime (Sims *et al.* 1989). The site types encountered often enough to include were outcrops (mean depth of mineral material < 4 cm in the plot), shallow mineral soils (mean depth of mineral soil between 4 and 20 cm), moderately deep mineral soils (mean depth of mineral soil between 20 and 100 cm) and peatlands (surface organic layer at least 20 cm thick and derived primarily from mosses). At least six plots per site type were sampled, where available. Systematic plot locations were skipped once the quota for the site type was met. If three transects did not yield an adequate number of plots, an additional transect was randomly located. Sampling took place from about June 10 to August 15 of 1992 to 1994 in 12 burns and 8 cutovers. Nineteen of these replicates and 413 plots within them met the selection criteria (Table 2.2).

Quasi-experimental control of the ultimate causal factors (Cook and Campbell 1979) was identified as a key concern of the study. Statistical control was provided for all factors with randomization, replication and interspersion. Climate and plant functional type (the pool of species available to sites) were assumed to be homogenous throughout the study area. Site type, age and disturbance type were controlled experimentally by classification for site type and in the construction of sampling frames for age and disturbance type. To be considered candidates for sampling, areas were disturbed only once either by wildfire or logging since 1900 and were presumed to have been disturbed only by wildfire during the Holocene. In addition, each plot and its surroundings were examined for evidence of other types of disturbance. If found, the plot was skipped. Control for variability in disturbance characteristics (e.g. fire severity), site history and soil organisms was statistical. To control for landscape configuration, areas with atypical surficial geology were eliminated from the sampling frame. Partial experimental control was provided for pre-disturbance vegetation to the extent that historical forest resource inventory maps were used to determine whether sampling units had a softwood overstory prior to disturbance.

2.2.3 Data Analysis

Tree and understory data were analyzed separately due to the differences in data types, the importance of the overstory in vegetation dynamics (Rowe 1956; Dix and Swan 1971; Pastor *et al.* 1987) and the small number of tree sized individuals in 13 year old communities. Taxa which occurred in less than four plots from a site type were excluded from analysis unless they had three occurrences in one replicate. Outlier understory plots were identified based on plot means of normalized species values (Hair *et al.* 1987), K-means cluster analysis, principal components analysis and correspondence analysis. There was no evidence that these plots were affected by some factor not of interest to the study but which could confound its results (e.g. spruce budworm). Therefore, they were retained.

Table 2.2. Number of plots included in data analysis by age class, disturbance type and site type.

Age Class	Disturbance Type	Site Type				Total
		Outcrop	Shallow	Mod. Deep†	Peatland	
13 year	F1*	7	7	5	6	25
	F2	5	7	6	7	25
	F3	6	6	‡	3	15
	F4	6	6	-	7	19
	L1	7	7	5	-	19
	L2	5	6	6	4	21
	L3	5	5	6	4	20
37 year	F1	7	6	7	5	25
	F2	6	4	7	6	23
	F3	9	5	7	6	27
	F4	5	6	6	-	17
	L1	7	7	6	4	24
	L2	6	5	7	8	26
	L3	4	5	6	5	20
	L4	5	5	6	5	21
65 year	F1	6	5	6	-	17
	F2	7	6	5	6	24
	F3	6	6	6	5	23
	F4	6	6	5	5	22
Total		115	110	103	85	413

* F1 = Burn 1, etc., L1 = Cutover 1, etc.. † Mod. Deep = Moderately deep ‡ Plots logged prior to fire
Note: Outcrop = mineral soil with a mean depth < 4 cm, Shallow = mineral soil with a mean depth between 4 and 20 cm, Mod. Deep = mineral soil with a mean depth between 20 and 100 cm, Peatland = surface organic layer at least 20 cm thick and derived mostly from moss.

Plots were classified into a community type based on their site type, age, and disturbance type. Summary statistics for the site variables were prepared by community type. Several of these complicated data analysis when their values exceeded the depth of the soil section. This occurred for depth to distinct mottling and depth to water table on peatland and moderately deep mineral soils and depth to bedrock and thickness of organic material on peatlands. Since there is no way of determining how much the value of the "depth to" variable exceeded 100 cm, an arbitrary value of 150 cm was used in these situations.

Correspondence analysis extracts axes in order of decreasing influence as measured by the dispersion of objects along each axis (ter Braak 1995). In an appropriately designed study, an ordinal ranking of the relative influence of causal variables can be made on the assumption that the axes extracted by CA represent underlying ecological gradients. The relative influences of age, site type and disturbance type were assessed by visual interpretation of ordination scattergrams and by the computation of Kendall tau-b rank correlations (Sokal and Rohlf 1981) of these variables with plot scores on successive ordination axes. The site type classification categories reflected increases in moisture regime while the two disturbance types reflected different disturbance intensities.

Multiple discriminant analysis (DA), applied to square root transformed understory cover data using community type as the grouping variable, was used to corroborate the results for two reasons. Discriminant analysis assumes a different underlying data structure than CA and it assists in the identification of the species which contribute most to community type differences in species composition. We expect CA and DA to produce different overall patterns if the data structure grossly violates its assumed nature for either method or if there is a substantial spurious polynomial effect in CA. Both these techniques were applied to all 413 plots so that there would be a sufficient number of variables for DA.

Principal coordinates analysis of square transformed cover data was applied to replicate means by site type. Percentage difference was used as the resemblance measure because its properties most accurately incorporated the concept of ecological distance germane to the representation of post-disturbance successional pathways in a low dimensional space. Of

particular importance was the way percentage difference preceded by a square root transformation represented abundant species relative to scarce ones, fidelity to one treatment, joint absences, equal abundances, plot abundance and different absolute abundances when relative abundances are the same (Campbell 1978; van der Maarel 1979; Hadju 1981; Greig-Smith 1983; Legendre and Legendre 1983; Faith *et al.* 1987).

Comparisons of species composition were completed separately by site type for two reasons. First, site type had the greatest influence on species composition. Second, a plot's site type is relatively permanent in this site type classification, due to the variables used, whereas age and disturbance type vary over time. Comparisons within a site type could then elucidate post-fire and post-logging vegetation dynamics without the influence of a confounding factor.

Community types were characterized using species frequency (percent of plots), presence (number of replicates) and mean cover. A species was deemed to be characteristic of a community type if it occurred in at least 66% of its replicates and 50% of its plots. A higher plot frequency is sometimes used to identify characteristic species but this is in conjunction with a larger plot size (cf. Westhoff and van der Maarel 1978).

No single method could reliably identify species which performed substantially better or worse in one or more of the community types relative to the others on the site type. Although ANOVA is the method typically used to identify "treatment" related performance differences, its results should be interpreted with caution in ecological studies because replication is typically low (Hurlbert 1984). Low replication leads to low statistical power and the possible detection of a significant treatment difference even when a species occurs in only one replicate. A further drawback of ANOVA is its insensitivity to coordinated species responses such as those identified by MANOVA. The use of MANOVA was precluded by the large number of species. Ordination is one way to reduce the number of species. It was not applied to avoid the additional assumptions it introduces into the results such as linearity.

To deal with these problems, five criteria were used in the identification of community type differences in species performance. The performance criteria involved multiple discriminant analysis, mixed model ANOVA (α = 5% and replicate treated as a random effect), cover,

frequency and presence. Multiple discriminant analysis was included to take into account multivariate relationships. It associated species with the community type where they had their highest canonical structure correlation. The veracity and substantiveness of this initial sorting was examined with the remaining performance criteria. ANOVA identified significant differences in cover. Corrections to control ANOVA's experiment-wise error rate (Harris 1985) were not made due to the large number of species and small number of replicates involved. A frequency or cover difference was considered substantial if it was three times greater than the next nearest value and the species was present in at least 66% of the replicates. Some species such as *Goodyera repens* which occur as scattered, solitary individuals may have a low frequency due to the small plot size but still be confined to a particular community type. In these situations, a frequency difference lower than the criterion was accepted if the species was present in 66% of a community type's replicates.

The performance criteria were applied in a complementary manner with greatest emphasis placed on frequency and presence results. High frequency was considered to be the best indicator of a species' ability to persist in a community while presence in most replicates ensured that the species was typical of the community type. There are similarities between these performance criteria and the manner in which TWINSPAN identifies indicator species (van Tongeren 1987).

Since a difference detected by these performance criteria is not entirely based on statistical tests, it will be referred to as a "substantial" rather than a "significant" difference in performance. In view of the high within and amongst replicate variability that is typical of ecological data, a species was identified as having a questionable difference if it almost met the criteria.

2.3 Results

Of the 619 plots sampled, 413 met the selection criteria described in the methods (Table 2.2). Most of the omitted plots represented infrequent site types or undisturbed patches. Statistical comparisons of community type differences in site variables were of limited use due to low statistical power. Instead, results were examined for consistent patterns and anomalies. Patterns across the site types indicated that moisture regime generally increased from outcrops to peatlands (Table 2.3). This was especially strong when comparisons across the site types were based on communities from the same age and disturbance type. Thickness of the LFH increased with increasing mineral soil depth (depth to bedrock minus thickness of organic material (Table 2.3)) and between 13 and 37 years. On mineral soils, canopy closure generally increased with mineral soil depth and was lower in post-logging than in post-fire communities.

Depth to water table was less in 37 year old post-fire than in post-logging communities on moderately deep soils (Table 2.3). This was not considered ecologically significant. The similar moisture regimes of post-fire and post-logging communities suggested that the difference in water availability was not substantial. Also, in moderately deep mineral soils, a mean depth to water table of 121 cm indicates that a proportion of plots had ground water in them. A water table was encountered in 6 of the 27 plots. Mean depth to water table in these plots was 46 cm. This could be important to tree species which produce a taproot (i.e. *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera*; Bell 1991) but not for other trees or low shrubs and herbs since the water table was below their rooting zone.

Many taxa were widespread. Of the 207 encountered (Appendix A), 52 (25% of the total) were found in at least 10% of the 413 plots. Forty-six (22%) taxa were found in at least 50% of the plots (i.e. were characteristic) of at least one community type. Most of these characteristic taxa were found in many of the other community types. The most frequent taxa were *Pleurozium schreberi* (frequency = 76%), *Dicranum* spp. (71%), *Cladina rangiferina* (61%), *Vaccinium myrtilloides* (59%), *Cladina mitis* (59%), *Maianthemum canadense* (59%) and *Polytrichum juniperinum* (56%). On mineral soils, mosses and lichens were the most frequent taxa: *Pleurozium schreberi* (in 77% of the 327 plots), *Dicranum* spp. (75%), *Polytrichum juniperinum* (70%), *Cladina mitis* (70%) and

Table 2.3. Site variable means (± 1 S.E.) by community type.

Site Type	Age	Disturb-ance Type	Thickness of LFH (cm)	Thickness of Organic Material* (cm)	Depth to Bedrock† (cm)	Depth to Distinct Mottling (cm)	Depth to Water Table (cm)	Drainage Regime‡	Moisture Regime‡	Slope (%)	Upslope Length (m)
Outcrop	13	Fire	0.5±0.4	0.6± 0.4	0.9± 0.4			0.9±0.1	0.3±0.2	12.1±2.1	4.8±2.3
		Log	0.9±0.4	0.9± 0.4	1.4± 0.1			1.0±0.0	0.1±0.1	12.8±2.0	6.0±1.4
	37	Fire	0.7±0.4	0.8± 0.4	1.2± 0.4			0.8±0.1	0.0±0.0	12.2±3.2	3.4±0.3
		Log	0.4±0.2	0.4± 0.2	0.4± 0.3			0.9±0.1	0.3±0.3	7.8±1.1	1.7±0.4
	65	Fire	0.5±0.2	0.5± 0.2	0.6± 0.3			0.9±0.1	0.0±0.0	13.2±1.9	6.7±2.5
Shallow	13	Fire	2.7±1.0	3.7± 1.9	12.2± 2.3			1.1±0.2	0.6±0.3	8.0±1.6	7.9±2.9
		Log	3.3±1.0	3.3± 1.0	12.3± 1.9			2.5±1.5	0.5±0.3	8.3±1.0	8.7±0.6
	37	Fire	5.6±0.5	5.7± 0.5	15.0± 2.3			1.2±0.1	0.1±0.1	8.9±2.3	4.8±0.6
		Log	3.2±1.2	5.2± 0.5	14.7± 3.3			1.3±0.2	0.3±0.2	8.8±1.6	3.7±1.4
	65	Fire	5.2±0.3	6.0± 0.8	18.0± 0.7			1.6±0.3	0.5±0.3	7.8±0.9	11.5±3.9
Mod.	13	Fire	5.9±1.7	6.0± 1.6	49.8± 8.8	124±25.8	150± 0.0	2.3±0.5	1.4±0.6	7.5±5.3	13.1±6.9
Deep		Log	7.7±1.6	7.7± 1.6	57.4± 1.9	134± 9.4	150± 0.0	2.2±0.3	1.6±0.4	8.7±2.9	8.0±2.3
	37	Fire	8.3±1.8	8.3± 1.8	62.1± 2.7	98± 7.3	121±10.2	3.3±0.4	2.6±0.4	5.7±1.8	6.6±1.9
		Log	5.6±0.9	6.4± 0.6	49.0± 4.4	122±17.8	150± 0.0	2.5±0.4	1.6±0.4	7.6±2.8	9.5±3.6
	65	Fire	7.0±0.7	7.0± 0.7	63.2± 5.1	135± 5.2	145± 4.8	3.1±0.5	2.7±0.9	7.9±3.8	19.7±7.0
Peatland	13	Fire	0.0±0.0	99.4±21.0	142.4± 4.5	144± 3.5	55±16.3	6.8±0.1	6.3±0.6	1.4±1.0	3.7±1.6
		Log	0.0±0.0	112.5±37.5	112.5±37.5	150± 0.0	50±41.0	6.9±0.1	7.4±0.4	0.0±0.0	0.0±0.0
	37	Fire	0.0±0.0	82.7±14.3	109.4±20.4	140± 9.9	25±15.2	5.7±0.2	6.9±0.2	0.0±0.0	0.0±0.0
		Log	0.0±0.0	66.0±19.3	109.6±24.3	134±10.3	90±27.0	6.5±0.6	7.0±0.1	0.2±0.2	1.0±1.0
	65	Fire	0.0±0.0	127.2± 1.2	137.5± 7.3	144± 5.6	37±13.3	6.9±0.1	7.1±0.1	0.0±0.0	0.0±0.0

* Thickness of organic material is the thickness of the LFH plus any underlying O horizon.

† Soil pits were dug to the lesser of 1m or lithic contact; a value of 150 cm was assigned where a "depth to" variable was not encountered in the soil section.

‡ Drainage regime: 1 = very rapid, 2 = rapid, 3 = well, 4 = moderately well, 5 = imperfect, 6 = poor, 7 = very poor.
Moisture regime: 0 = dry, 1 = moderately fresh, 2 = fresh, 3 = very fresh, 4 = moderately moist, 5 = moist, 6 = very moist, 7 = moderately wet, 8 = wet, 9 = very wet. (after Sims *et al.* 1989).

Note: see Table 2.2 for definitions of site types.

Cladina rangiferina (69%) followed by *Maianthemum canadense* (65%) and *Vaccinium myrtilloides* (63%). All these except *Polytrichum juniperinum* and *Cladina mitis* were also frequent on peatlands. A moss or lichen had the highest understory cover in every community type except for 13 year old communities on mineral soils.

2.3.1 Effects of Site Type, Age Class and Disturbance Type.

Site type had the strongest influence on species composition (Figure 2.4). Axis 1 of the correspondence analysis (CA) strongly separated the communities on peatlands from those found on mineral soils (percentage of total dispersion in the 413 plots accounted for by Axis 1=18%, Axis 2=10%, Axis 3=9%, Axis 4=6%, Axis 5=5%). The strongest separation was between outcrops and peatlands. Of the ultimate causal variables, site type had the highest rank correlation with plot scores on Axis 1 (Table 2.4). There was no overlap of community type centroids from one site type to the next. Thickness of surface organic layer, depth to bedrock and moisture regime were used directly and drainage regime (Sims *et al.* 1989) indirectly to classify a plot into a site type category. They were also highly correlated with Axis 1 and each other. For the site types included in the results, all the variables highly correlated with Axis 1 are indicators of increasing soil moisture. Axis 1 was interpreted as a moisture regime gradient.

The strong influence of site type continued on Axis 2 where there was no overlap of plots from each site type and outcrops were clearly separated from the other two mineral soil site types. Site type had the highest rank correlation with Axis 2. The site variables with the highest correlations were thickness of the LFH and depth to bedrock. The effect of disturbance type and age was combined on Axis 3 of the ordination scattergram. Although this axis generally represented an age gradient it also separated 13 year old post-fire communities from the remaining community types within each of the mineral and peatland community clusters. Axis 4 separated 13 year old post-fire communities on outcrops and shallow mineral soils from the remaining outcrop communities. Post-fire and post-logging communities on mineral soils were separated on axis 5.

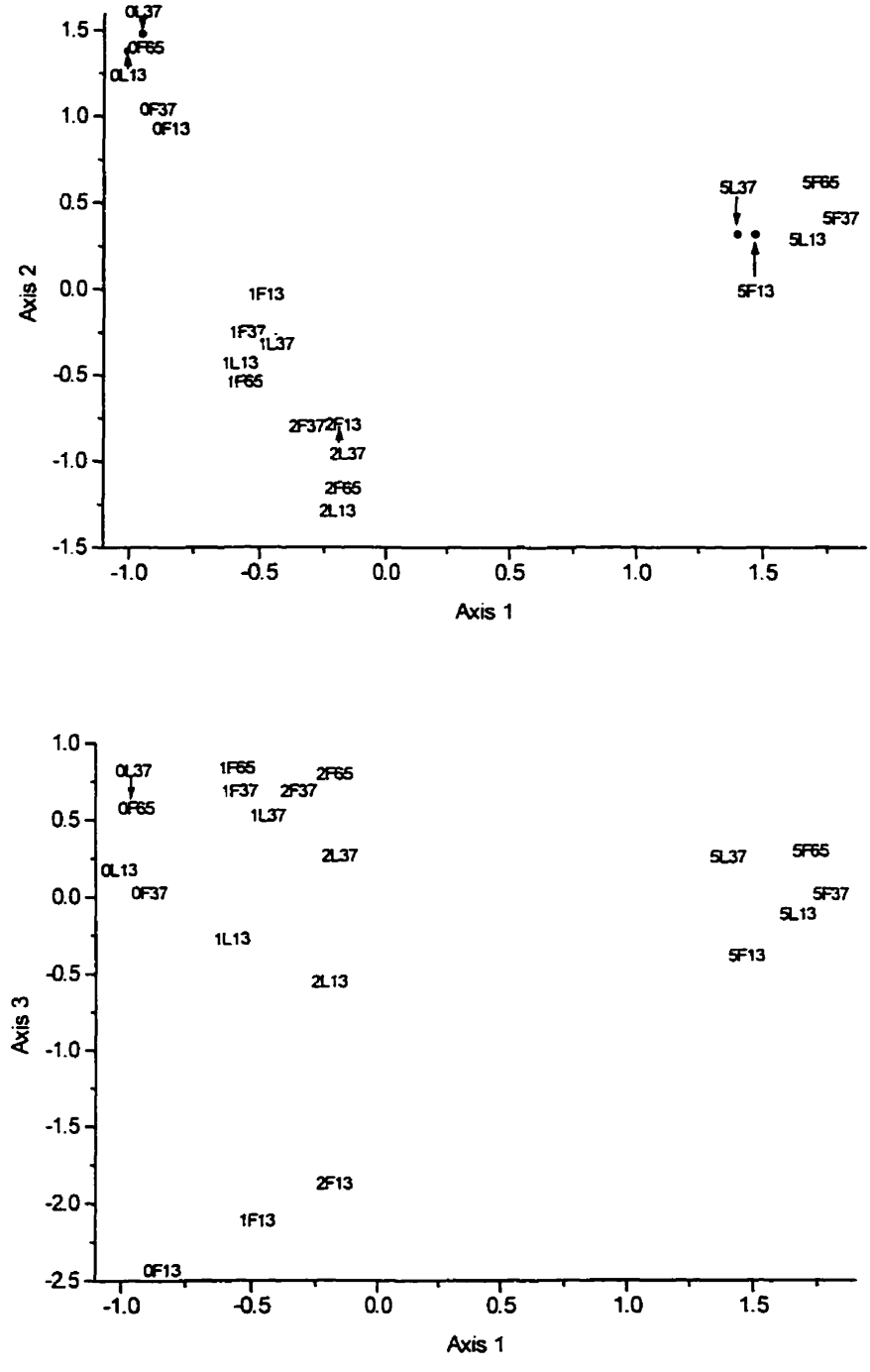
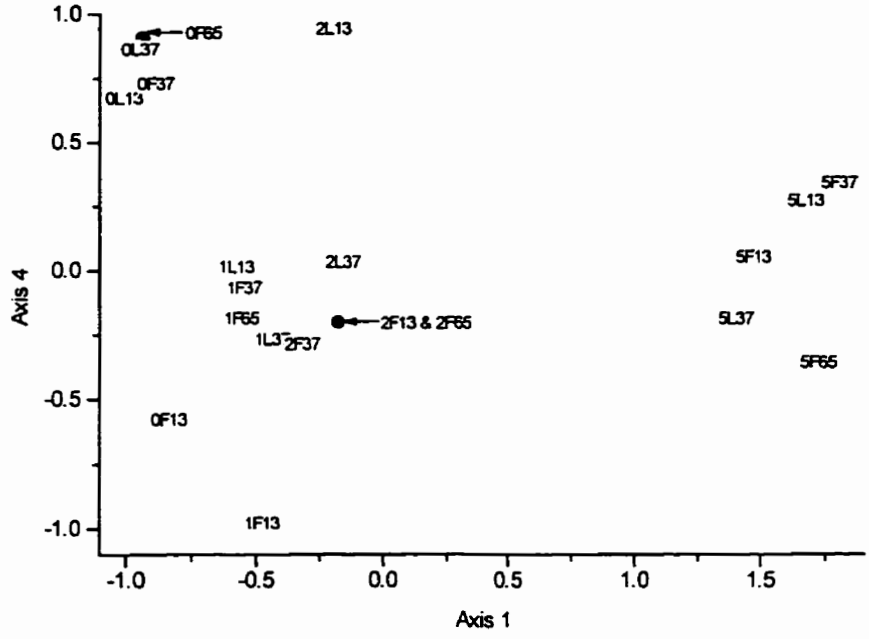


Figure 2.4. Understory correspondence analysis scattergrams for all community types.

Plotted points are community type centroids of the 413 plots (104 species). Legend: First character is site type (0=outcrop; 1=shallow mineral; 2= moderately deep mineral; 5=peatland), second character is disturbance type (F=Fire; L=Logging), third and fourth characters are age class.



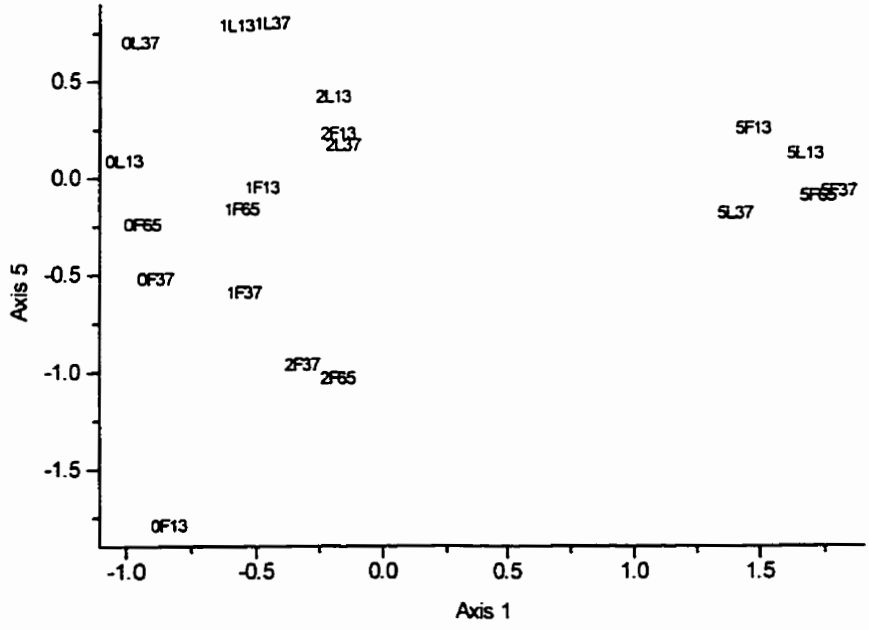


Figure 2.4 . . . continued.

Table 2.4. Kendall tau-b rank correlations of site variables with CA plot scores.

	Site Type	Age	Disturb-ance Type	Depth to Bedrock (cm)	LFH Thickness (cm)	Organic Layer Thickness (cm)	Depth to Distinct Mottling (cm)	Depth to Water Table (cm)	Drainage Regime	Moisture Regime
AXIS 1	0.74[b]	0.01	0.00	0.66[b]	0.07[a]	0.66[b]	-0.14[b]	-0.47[b]	0.58[b]	0.58[b]
AXIS 2	-0.25[b]	-0.01	-0.04	-0.27[b]	-0.48[b]	-0.18[b]	0.23[b]	-0.11[b]	-0.09[a]	-0.06
AXIS 3	-0.02	0.51[b]	0.05	0.00	0.12[b]	0.05	-0.02	0.06	-0.05	-0.07[a]
AXIS 4	-0.10[b]	0.06	0.11[b]	-0.10[b]	-0.09[b]	-0.09[b]	0.03	-0.02	-0.07	-0.10[b]
AXIS 5	0.02	-0.13[b]	0.31[b]	-0.01	-0.09[b]	-0.01	0.07	-0.01	0.05	0.06

[a] significant at $\alpha = .05$, [b] significant at $\alpha = .01$. Note: See Table 2.3 for explanations of site type variables.

Multiple discriminant analysis using community type as the grouping variable (Figure 2.5) was highly significant ($p < 0.01$) for the first 9 discriminant functions. It corroborated the results of CA by producing a similar arrangement of community type centroids. Constraining the solution to the one which most strongly separated the plots based on their community type caused influences to appear sooner and in a slightly different order than in CA. Site type appeared on the first function, disturbance by fire on the second and disturbance type on the third and fourth. On the fifth discriminant function, a separation of 13 year old post-logging communities from the others on mineral soils was paralleled by a declining age gradient on peatlands.

The DA correctly classified 78% of the 413 plots (Table 2.5). About two-thirds of the misclassifications involved confusing communities of a particular age class/ disturbance type with the same combination on another site type. For example, 12% of the 13 year old post-fire communities on outcrops were classified as 13 year old post-fire communities on shallow mineral soil. This was not surprising since the three mineral soil site types represented a continuum of site conditions. Most of the misclassifications occurred in the 13 and 65 year old age classes.

A superficial indication of why both multivariate methods strongly separated communities is provided by the distribution of cover by growth form across the site types (Figure 2.6). Peatland communities were dominated by *Sphagnum* spp. and *Ledum groenlandicum*. These taxa occurred in relatively small amounts on the other site types. Peatland was the only site type to have species that were either completely or virtually exclusive to it (*Chamaedaphne calyculata*, *Oxycoccus quadripetalus*, *Smilacina trifolia*, *Polytrichum strictum* and *Gaultheria hispidula*). Notwithstanding the distinctiveness of communities on organic soils, only 4 of the 42 taxa characteristic of at least one community type on the mineral site types were not found on peatlands. These were *Arctostaphylos uva-ursi* and the grasses *Oryzopsis pungens*, *Danthonia spicata* and *Schizachne purpurascens*.

Table 2.5. Classification accuracy (% classified to a cell) of the discriminant analysis of understory cover from all 413 plots.

Observed Group Membership			Predicted Group Membership																		
			Outcrop					Shallow					Moderately Deep					Organic				
		n	13F*	13L	37F	37L	65F	13F	13L	37F	37L	65F	13F	13L	37F	37L	65F	13F	13L	37F	37L	65F
Outcrop	13F*	24	75					25														
	13L	17		82	6		12															
	37F	27		4	74		15			7												
	37L	22				77	5				9	5		5								
	65F	25			8		72					12					8					
Shallow	13F	26	12					77	4				8									
	13L	18		6					83			6				6						
	37F	21			10					81							10					
	37L	22									82					14	5					
	65F	23					9					78					13					
Mod. Deep	13F	11						27					73									
	13L	17							6				6	82		6						
	37F	27								4		7			70	7	11					
	37L	25									4				4	80	8				4	
	65F	22		5			5										91					
Organic	13F	23																78	4	4	4	9
	13L	8																13	75	13		
	37F	17																		71	12	18
	37L	22														5	5		5	5	82	
	65F	16																	6	6	19	69

* First two characters are age class; last is disturbance type: F = Fire, L = Logging.

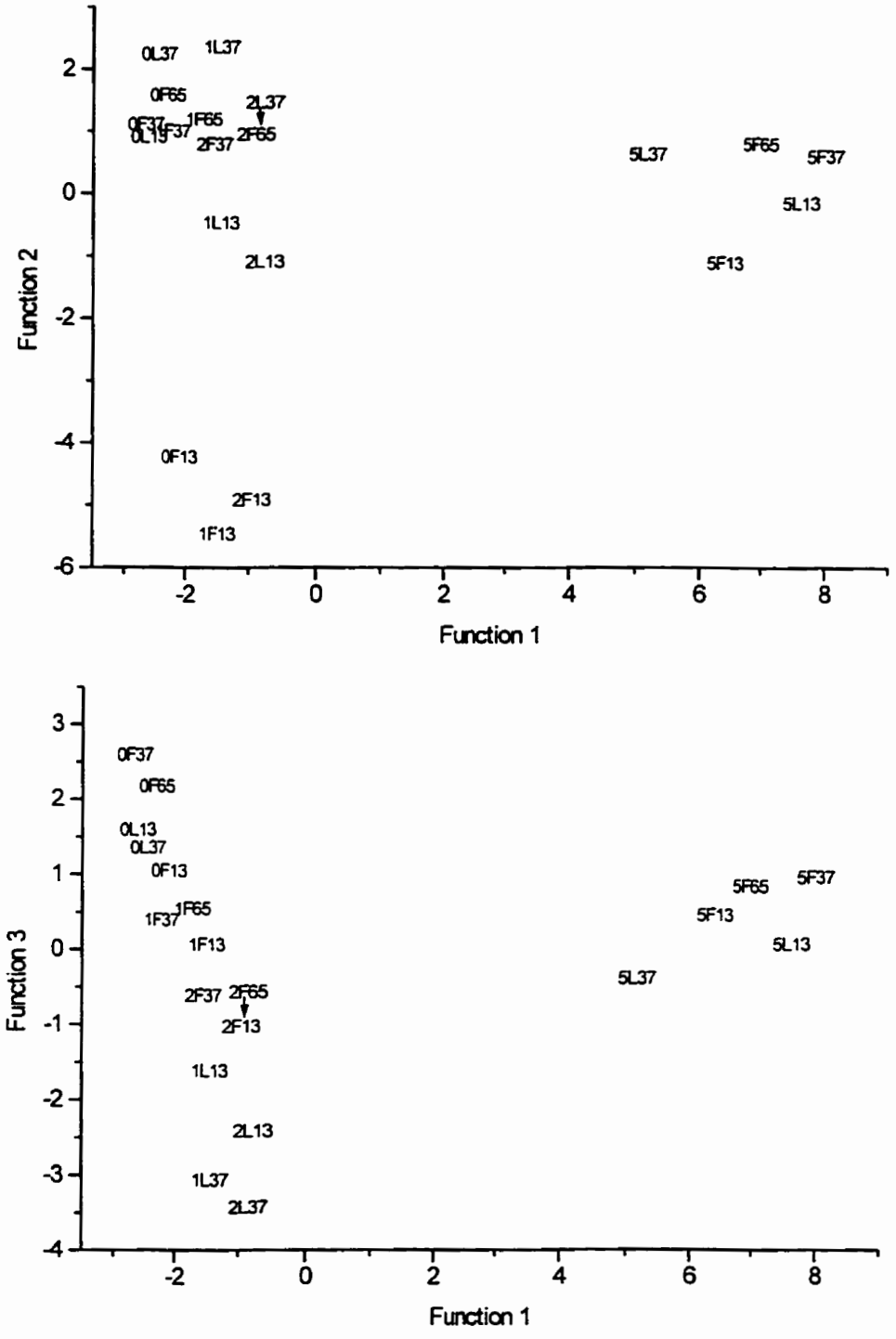


Figure 2.5. Understory multiple discriminant analysis scattergrams for all community types.

Plotted points are group centroids of the 413 plots (104 species). Legend: First character is site type (0=outcrop; 1=shallow mineral; 2=moderately deep mineral; 5=peatland), second character is disturbance type (F=Fire; L=Logging), third and fourth characters are age class.

Plant cover on outcrops was dominated by *Cladina mitis* and *C. rangiferina* followed by *Polytrichum juniperinum*, *P. piliferum* and *Dicranum* spp.. Trees, shrubs and forbs progressively increased in basal area or cover from outcrops to shallow and then moderately deep mineral soils while that of lichens declined. *Pleurozium schreberi* and *Vaccinium angustifolium* had the highest understory cover on shallow and moderately deep mineral soils.

2.3.2 Community Descriptions and Dynamics by Site Type

2.3.2.1 Outcrop Community Types

Outcrop vegetation was mostly confined to rock depressions and crevices where mineral and organic material had collected. Outcrop community types typically had exposed bedrock and patches of mineral soil which supported sparse vascular vegetation and a ground cover of mosses and lichens dominated by *Cladina* spp. (Figure 2.6A). The basal area and frequency of trees were highest in 37 year old post-fire communities but even here they occurred in less than half the plots (Table 2.6). Moss and lichen cover dominated the plant cover of all community types on outcrops (Figure 2.6A). Exposed rock had the highest percent cover (about 35%; Table 2.7) in all community types except for 37 year old post-logging communities where *Cladina spp.* had higher cover (Table 2.8)[5]. High bedrock cover, low canopy closure (Table 2.8) and xeric conditions limited the number of taxa characteristic of the outcrop community types.

Mature (65 year old) post-fire communities conformed well to the general description of outcrop communities. Only 37% of the tree plots had at least one tree in them. *Pinus banksiana* frequency was substantially higher than that of any other tree species but still only 24% (Table 2.6). None of the vascular plants reached characteristic status; *Vaccinium myrtilloides*, *Potentilla tridentata*, *Corydalis sempervirens*, *Woodsia ilvensis* and *Maianthemum canadense* were the most frequent (Table 2.8). Of the characteristic taxa, *Cladina mitis* and *C. rangiferina* had a

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[5] Species found in only one replicate in a community type were included in data analysis but not shown in tables.

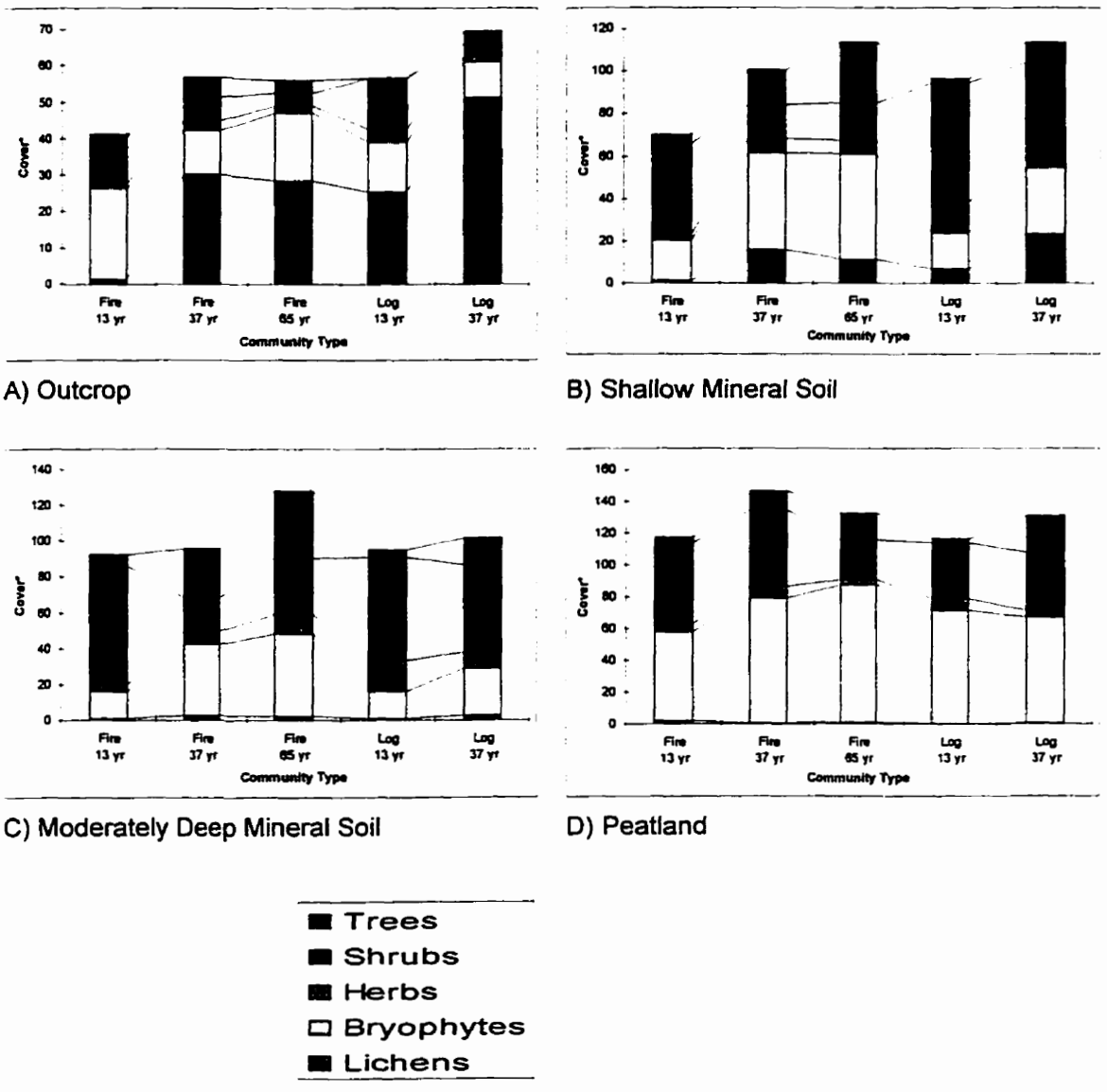


Figure 2.6. Total mean cover of trees, shrubs, herbs (includes forbs and graminoids), bryophytes and lichens by site type.
Notes: Basal area in m^2ha^{-1} rather than cover used for trees. Vertical scales differ by site type.

Table 2.6. Tree basal area, frequency and presence by community type.

	Basal Area ($m^2 ha^{-1}$) in Replicates					Frequency in Plots (%)					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age*:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Outcrop †	4	4	4	3	4	25	24	27	17	22	4	4	4	3	4
Picea mariana	1.5		0.1		0.6	8		7		9	1		2		2
Pinus banksiana	1.2	0.4	5.2	0.1	2.8	28	38	44	6	23	3	3	4	1	2
Populus tremuloides	0.8	0.0				4	4				1	1			
Shallow Mineral	4	4	4	3	4	23	26	21	18	22	4	4	4	3	4
Abies balsamea				0.3	0.2				22	5				2	1
Betula papyrifera	0.2		0.1	0.2	0.1	9		10	17	9	2		1	2	1
Picea glauca	0.3		0.1	0.2	0.1	4		5	11	5	1		1	2	1
Picea mariana	3.0		1.9	0.2	3.9	17		38	6	27	3		3	1	3
Pinus banksiana	23.4	4.0	14.4	0.8	4.6	83	65	81	33	27	4	3	4	3	3
Populus tremuloides	1.7	0.0		0.2	1.0	13	8		22	18	2	1		2	2
Mod. Deep Mineral	4	2	4	3	4	22	11	27	17	25	4	2	4	3	4
Abies balsamea	0.3		0.5		1.0	18		7		8	2		1		2
Betula papyrifera	0.2	0.1	0.3	1.2	0.3	9	18	4	24	4	2	1	1	2	1
Picea glauca	1.3		0.2		0.6	14		15		4	3		2		1
Picea mariana	10.8		7.6	0.1	5.0	59		59	6	32	4		4	1	3
Pinus banksiana	21.2	5.1	17.6	1.5	5.5	73	82	70	47	20	4	2	4	3	3
Populus tremuloides	4.0	1.3	1.4	1.6	3.1	23	55	11	65	36	4	2	2	3	4
Peatland	3	4	3	2	4	16	23	17	8	22	3	4	3	2	4
Larix laricina	1.0	0.0	0.3	0.1	1.5	25	4	12	13	27	3	1	2	1	3
Picea mariana	10.9	2.7	10.0	1.6	18.7	81	22	88	13	91	3	2	3	1	4
Pinus banksiana	4.4	1.2	2.0	0.4	2.3	44	26	24	25	18	3	3	2	1	2
Populus tremuloides	0.7					13					2				

* 65 year old post-fire communities shown in the first column because this is assumed to represent the typical pre-disturbance starting point for post-fire and post-logging pathways of recovery.

† Number of replicates or number of plots included is shown in first row of each site type.

Table 2.7. Ground cover by community type.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Outcrop †	4	4	4	3	4	25	24	27	17	22	4	4	4	3	4
Conifer litter	10.9	13.7	18.2	0.8	3.8	100	100	100	65	95	4	4	4	3	4
Other litter	6.2	10.2	4.0	17.2	7.8	100	100	85	100	95	4	4	4	3	4
Rock	36.4	43.5	35.0	34.8	21.8	88	96	93	94	91	4	4	4	3	4
Snag	0.0	0.8	0.0			8	29	4			2	3	1		
Trunk	0.0	0.0	0.0			4	8	15			1	2	2		
Wood litter	1.4	8.6	1.3	5.1	5.0	100	100	96	100	91	4	4	4	3	4
Shallow	4	4	4	3	4	23	26	21	18	22	4	4	4	3	4
Conifer litter	20.2	45.6	25.2	9.3	9.0	100	100	95	83	91	4	4	4	3	4
Other litter	13.4	18.1	8.1	57.5	28.5	100	100	100	100	100	4	4	4	3	4
Rock	2.8	10.1	2.3	3.9	2.2	65	92	67	94	45	4	4	4	3	4
Snag	0.1	0.3	0.0	0.0	0.4	43	50	33	6	18	4	4	4	1	3
Stump				0.2	0.0				28	9				3	1
Trunk	0.3	0.1	0.3	0.0	0.4	57	46	67	28	36	4	3	4	3	4
Wood litter	3.8	11.2	3.1	4.3	2.3	100	100	100	100	100	4	4	4	3	4
Mod. Deep	4	2	4	3	4	22	11	27	17	25	4	2	4	3	4
Conifer litter	21.2	23.8	32.1	6.3	12.5	100	100	100	76	88	4	2	4	3	4
Other litter	27.2	54.0	21.6	70.6	53.5	100	100	100	100	100	4	2	4	3	4
Rock	0.1	2.1	0.3	1.5	0.1	32	73	26	47	24	2	2	4	3	3
Snag	0.0	1.2	0.1	0.1	0.1	23	45	56	18	16	3	2	4	2	2
Stump	0.1			0.2	0.1	9			41	16	1			3	3
Trunk	0.6	0.1	0.4	0.1	0.3	73	64	85	59	48	4	2	4	3	4
Wood litter	4.7	8.7	4.8	5.1	5.6	100	100	100	100	100	4	2	4	3	4
Peatland	3	4	3	2	4	16	23	17	8	22	3	4	3	2	4
Conifer litter	3.5	6.4	2.1	0.4	15.2	100	96	94	88	95	3	4	3	2	4
Other litter	6.4	28.5	16.4	25.6	14.2	100	100	100	100	100	3	4	3	2	4
Snag	0.0	0.3	0.1		0.0	13	70	12		14	2	4	1		2
Stump				0.0	0.1				13	18				1	2
Trunk	0.2	0.0	0.1	0.0	0.3	81	13	59	25	59	3	1	3	2	4
Water	1.5	0.1	0.6	0.7	0.2	19	22	29	50	14	1	2	2	2	1
Wood litter	1.0	7.9	1.5	1.6	2.0	100	100	100	63	91	3	4	3	2	4

† Number of replicates or number of plots included is shown in first row of each site type.

Table 2.8. Outcrop community types- canopy closure and understory mean cover, frequency and presence.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
N (or n for plots):	4	4	4	3	4	25	24	27	17	22	4	4	4	3	4
Canopy Closure*	1.8	0.5	7.0	0.0	0.4										
Shrub†															
Amelanchier alnifolia			0.0	0.6	0.4			7	18	18			2	2	2
Amelanchier sanguinea	0.0		0.0	0.6	0.4	4		7	29	9	1		2	2	2
Arctostaphylos uva-ursi	0.8	1.9	0.2	8.9	0.1	12	13	22	59	14	2	3	3	2	3
Betula papyrifera	0.0	0.0	0.0	0.3		8	8	11	12		2	1	3	1	
Diervilla lonicera	0.1	1.1	1.0	0.2	0.0	12	25	33	29	9	3	2	3	3	2
Juniperus communis	1.1	0.1	0.8	1.1	0.1	12	4	15	29	5	2	1	2	2	1
Linnaea borealis	0.1	0.0	1.6			12	8	22			1	2	2		
Picea mariana	0.5	0.3	0.1		0.3	20	29	11		9	1	4	2		1
Pinus banksiana	0.1	7.4	1.0	0.1	0.5	20	83	22	6	18	3	4	3	1	2
Populus tremuloides	0.0	0.2	0.3	0.3		8	33	11	12		2	3	2	2	
Prunus pensylvanica	0.2	0.1	0.1	0.2	0.2	16	33	19	18	32	3	4	3	1	3
Prunus pumila	0.0		0.0	0.5		16		7	35		2		2	3	
Prunus virginiana		0.0		0.3			13		6			2		1	
Rosa acicularis	0.0	0.0	0.4	0.0	0.0	8	8	22	6	5	2	2	3	1	1
Rubus idaeus		0.1	0.0	0.0	0.1		17	15	6	9		1	2	1	2
Salix spp.		0.3	0.0	0.0	0.2		21	7	6	5		3	2	1	1
Spiraea alba	0.0	0.1	0.1	0.4	0.4	12	17	30	59	27	2	2	3	3	3
Vaccinium angustifolium	0.0	2.6	0.0	0.5	4.1	4	33	15	41	45	1	2	2	2	3
Vaccinium myrtilloides	0.4	0.4	0.7	0.6	1.0	24	54	52	35	36	3	4	4	2	4
Vaccinium vitis-idaea			0.0		0.1			4		14			1		2
Forb															
Achillea millefolium	0.0			0.0		8			12		1			1	
Apocynum androsaemifolium	0.1	0.0	0.0	0.0	0.1	8	4	4	6	18	1	1	1	1	2
Aster ciliolatus		0.0	0.0	0.0			4	22	12			1	3	1	
Campanula rotundifolia	0.0	0.0	0.0	0.0	0.0	16	8	37	29	9	3	1	3	2	2
Comandra umbellata				0.0					12					1	
Cornus canadensis	0.7	0.4	0.8		0.0	16	21	26		5	1	2	3		1
Corydalis sempervirens	0.0	0.0	0.0	0.0	0.1	36	8	19	35	41	4	2	2	2	4
Cypripedium acaule	0.0		0.1	0.0	0.0	12		4	12	5	3		1	1	1
Epilobium angustifolium		0.1	0.1	0.0	0.0		29	22	6	9		2	2	1	1
Fragaria virginiana	0.0	0.0	0.2	0.1		8	4	30	24		2	1	3	1	
Galium boreale			0.0	0.0				15	18				2	1	
Gaultheria procumbens		0.0		0.3			8		18			1		2	
Goodyera repens	0.0		0.0			4		11			1		2		
Heuchera richardsonii		0.0	0.1	0.0			4	7	12			1	1	1	
Lathyrus venosus	0.0		0.0	0.0		4		4	12		1		1	2	
Lepidium densiflorum				0.0					12					1	

Table 2.8 . . . continued.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Maianthemum canadense	0.6	0.3	0.4	0.2	0.7	32	46	48	41	50	3	4	3	2	4
Melampyrum lineare	0.0		0.1	0.0	0.0	20		37	12	32	4		4	1	3
Polygonum cilinode	0.4	0.0		0.0	0.3	16	8		6	23	3	1		1	3
Potentilla norvegica	0.0		0.0			8		11			1		2		
Potentilla tridentata	0.1	0.4	0.7	1.3	0.4	44	50	44	71	36	3	4	4	3	3
Rubus pubescens			0.0					19					2		
Solidago hispida			0.0					11					2		
Viola adunca		0.0	0.0	0.0	0.0		17	11	18	5		3	2	2	1
Woodsia ilvensis	0.4	0.2	0.1	0.2	0.0	36	8	19	18	5	3	2	1	2	1
Graminoid															
Agropyron trachycaulum	0.0		0.0	0.4	0.0	8		19	35	5	1		2	3	1
Agrostis hyemalis	0.1	0.0	0.1	0.4	0.1	48	4	48	71	55	4	1	3	3	4
Carex spp.	0.1	0.0	0.1	0.1	0.1	44	42	52	47	59	4	3	4	3	4
Danthonia spicata	0.0	0.0	0.1	0.1	0.0	32	13	52	65	27	4	2	4	3	3
Oryzopsis asperifolia	0.0	0.0	0.1	0.2	0.0	8	4	33	29	5	2	1	4	2	1
Oryzopsis pungens	0.0	0.1	0.1	0.1	0.1	32	46	48	47	55	4	3	4	3	4
Panicum spp.	0.0	0.0	0.0	0.0		16	4	11	12		2	1	3	2	
Schizachne purpurascens	0.0	0.0	0.1	0.0	0.1	12	13	11	24	23	1	2	2	2	2
Bryophyte & Lichen															
Aulacomnium palustre	0.2		0.1	0.0		4		19	12		1		3	2	
Cladina mitis	17.0	0.6	16.5	13.2	25.8	92	83	100	100	100	4	4	4	3	4
Cladina rangiferina	4.7	0.0	7.7	9.6	20.5	88	13	96	100	100	4	2	4	3	4
Cladina stellaris	0.0			0.0	1.6	4			6	45	1			1	4
Cladonia spp.	1.1	2.4	1.7	2.4	1.6	96	88	100	94	100	4	4	4	3	4
Dicranum spp.	2.4	0.0	2.4	3.8	2.3	88	21	78	82	86	4	3	4	3	4
Pleurozium schreberi	14.6	0.1	7.5	7.3	5.3	64	21	78	53	73	4	3	4	3	4
Polytrichum commune	0.5	0.8	0.0		0.0	20	17	4		5	4	1	1		1
Polytrichum juniperinum	1.1	14.2	2.1	3.5	3.5	80	100	89	94	82	4	4	4	3	4
Polytrichum piliferum	0.4	8.9	1.5	2.6	0.1	60	83	78	71	27	4	4	4	3	4
Selaginella densa ‡	0.0	0.0	0.1	0.1	0.3	24	17	19	18	32	3	3	3	2	4

* % cover of overstory; N was 3 for all community types except for 37 year old post-fire which was 4. † Tree species cover value is the maximum of tree, sapling or tree seedling cover in the herb and shrub layers. ‡ Included here due to similarity of growth form.
Notes: Includes species found in at least three plots and more than one replicate in a community type. A blank means that the taxon did not occur in the replicate's plots, 0.0 denotes mean cover > 0 and < 0.05%. See Table 1 for definitions of cover types.

combined cover of 21.7% and combined frequency greater than 90%. *Pleurozium schreberi* had the next highest cover (14.6%). Other taxa characteristic of mature communities included *Cladonia* spp., *Dicranum* spp., *Polytrichum juniperinum* and *P. piliferum*.

A principal coordinates analysis of the replicate means indicated that the residual effects of wildfire were still strong at 13 years (cumulative percentage of total dispersion: Axis 1 = 23.3, Axis 2 = 37.5, Axis 3 = 45.1, Axis 4 = 51.2). All four 13 year old post-fire replicates were strongly separated from the rest on the first axis (Figure 2.7). The second axis weakly represented an age pattern while the third separated post-fire from post-logging communities. Although 37 year old post-logging communities appeared the most similar to 65 year old post-fire in the space represented by the first two axes, an evaluation of the distances using a more appropriate method indicated that 37 year old post-fire communities were the ones most similar (see Chapter 3). It is noteworthy that for most of the age class/ disturbance type combinations, three of the four replicates are clustered together but the remaining one appears as an outlier.

Fire's effects on species composition were still apparent after 13 years of recovery. Snags were scattered in the mineral soil patches and *Pinus banksiana* was growing from the shrub into the tree layer (Table 2.8, Table 2.6). Shrub, bryophyte and bedrock cover was higher than in mature communities while the reverse was true for herbs and lichens (Figure 2.6A). Although shrubs and bryophytes collectively appeared to benefit from fire, there were definite winners and losers within these groups. *Picea mariana*, *Pinus banksiana*, *Populus tremuloides*, *Salix* spp., *Vaccinium myrtilloides*, *Viola adunca*, *Polytrichum juniperinum* and *Polytrichum piliferum* had substantial increases in frequency and/ or cover (i.e. at least 3 times higher and in at least 66% of replicates; see Methods). *Cladina spp.* and *Pleurozium schreberi* had the largest decreases in cover. *Dicranum* spp. and several herbs had substantial decreases in frequency.

Mosses and *Cladina* spp. accounted for the largest proportion of the frequency and cover of 37 year old post-fire communities (Figure 2.6A, Table 2.8). Shrubs, forbs and graminoids were frequent but limited in their cover. *Pinus banksiana* had grown to an average height of 8m and was found in the tree layer of 44% of the plots (Table 2.6). Its understory cover was lower than in 13 year old post-fire communities but this was primarily due to height growth from the shrub to the

tree layer. Beyond this, the primary cover differences in the species composition of 13 and 37 year old post-fire communities were higher values for *Cladina spp.*, *Pleurozium schreberi* and *Dicranum* spp. and lower ones for *Polytrichum juniperinum* and *P. piliferum*. These cover changes represented progression toward levels typical of mature communities. By 37 years, shrub frequencies were not substantially different from those in mature communities. *Polygonum cilinode*, *Cypripedium acaule* and *Polytrichum commune* were the only species with substantially lower frequencies according to the performance criteria. Although the difference in plot frequencies of *Cypripedium acaule* in mature and 37 year old communities was only 8%, this was considered substantial. *Cypripedium acaule* occurs as solitary individuals and its frequency in the replicates declined from 75% to 25%. Conditions in 37 year old communities seemed to favor *Fragaria virginiana*, *Aster ciliolatus*, *Oryzopsis asperifolia* and *Aulacomnium palustre* since their frequencies were substantially higher than in shrub stage or mature communities.

Thirteen year old post-logging communities were more open than any of the others on outcrops (Table 2.8) due to the poor growth of trees and shrubs (Figure 2.6A, Table 2.6) that regenerated well after fire. Shrub cover was substantially higher than in mature communities and lichen cover was only slightly lower. *Pinus banksiana* was the only tree encountered and these were individuals left at the time of logging. Its tree and shrub frequencies were substantially lower than in mature and 13 year old post-fire communities. Frequencies were substantially higher than in mature communities for *Arctostaphylos uva-ursi*, *Spiraea alba*, *Amelanchier sanguinea*, *Vaccinium angustifolium*, *Amelanchier alnifolia*, *Gaultheria procumbens*, *Viola adunca*, *Agropyron trachycaulum*, *Oryzopsis asperifolia* and *Aulacomnium palustre*. *Pleurozium schreberi* cover was half of that in mature communities while that of *Potentilla tridentata* was substantially higher. The combined cover of *Cladina mitis* and *C. rangiferina* was similar but their combined frequency was slightly higher than at 65 years. *Viola adunca* was the only taxon that seemed to benefit from overstory removal alone since its frequency was substantially higher in these and 13 year old post-fire communities than in mature communities. *Arctostaphylos uva-ursi*, *Spiraea alba*, *Amelanchier sanguinea* and *Amelanchier alnifolia* benefited more from logging than fire as they had substantially higher cover and frequency when compared with 13 and 65 year old post-fire

communities. In contrast with 13 year old post-fire communities, substantial cover differences relative to mature communities were not observed for *Pinus banksiana*, *Polytrichum juniperinum*, *P. piliferum*, *Cladina mitis* and *C. rangiferina*.

The openness of post-logging communities and virtual absence of snags was conspicuous at 37 years. Canopy closure was only 0.4% (Table 2.8). Shrub, herb and bryophyte cover was lower in 37 year old post-logging communities than in the other community types on this site type. This was more than offset by higher lichen cover. When compared with mature communities, 37 year old post-logging communities had higher total frequency (48% versus 37%) and total density of trees (674 stems ha^{-1} versus 481 stems ha^{-1}). The combination of higher *Pinus banksiana* basal area and lower density indicated that the tree component of 37 year old post-logging communities was composed of fewer, larger individuals than in mature post-fire communities. Increment cores suggested that these were post-logging residuals rather than individuals which established after logging and grew rapidly. Cover and/ or frequency increases between 13 and 37 years suggested that *Vaccinium angustifolium*, *V. myrtilloides*, *Cladina mitis* and *C. rangiferina* continued to benefit from the effects of logging. *Vaccinium angustifolium* and *Cladina stellaris* had substantially higher frequencies than in mature communities while those of *Woodsia ilvensis* and *Polytrichum commune* were substantially lower.

The performance criteria indicated that 65 year old post-fire communities were distinguished from the other four community types by few taxa (Table 2.9). Most of the species which distinguished 13 year old post-fire communities did so by their poor performance and, in some cases, absence. Species which performed best in this community type were those typically regarded as post-fire pioneers: *Pinus banksiana*, *Polytrichum juniperinum* and *P. piliferum* (Rowe 1983). Thirty-seven year old post-fire communities had the highest number of species with substantially better performance. Most were shrubs; the rest were forbs. *Rubus pubescens* and *Solidago hispida* were exclusive to 37 year old post-fire communities. This was the only community type on outcrops to have exclusive species. Shrubs and grasses distinguished 13

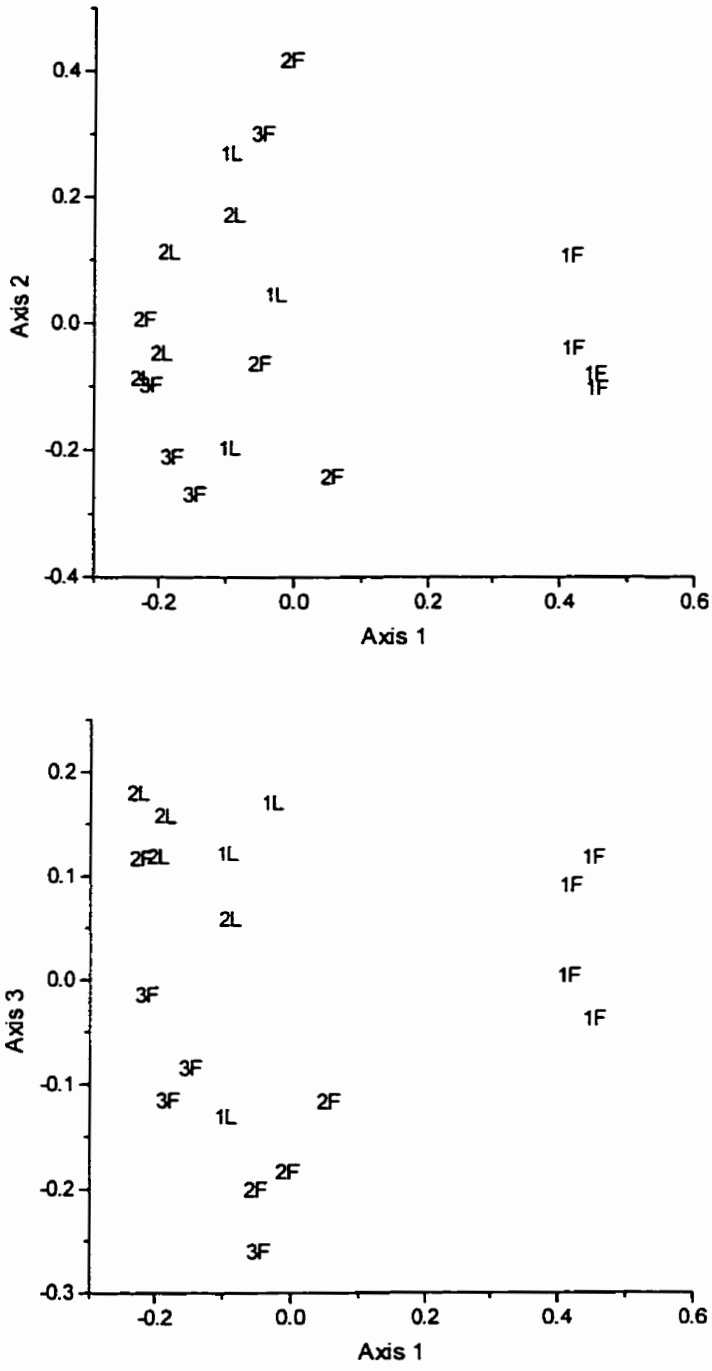


Figure 2.7. Principal coordinates analysis of outcrop replicate means.

Legend: first character is age class, 1 = 13 years, 2 = 37 years, 3 = 65 years; second character is disturbance type, F = fire, L = logging.

Table 2.9. Community types in which a species performed substantially better or poorer when compared with the remaining community types on the site type.

Site Type:	Outcrop					Shallow Mineral					Moderately Deep Mineral					Peatland				
Disturbance Type:	Fire			Log		Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Shrub																				
Alnus rugosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-
Amelanchier sanguinea	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-	-	-	-
Arctostaphylos uva-ursi	-	-	-	B	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-
Betula papyrifera	-	-	-	-	-	-	-	-	-	-	-	-	-	B	-	-	-	-	B	-
Chamaedaphne calyculata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Diervilla lonicera	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-
Kalmia polifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P
Larix laricina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-
Ledum groenlandicum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	B	-	-	-	-	-
Linnaea borealis	-	-	-	-	-	-	-	B	P?	-	-	-	B?	-	-	-	-	-	-	-
Oxycoccus quadripetalus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Picea mariana	-	-	-	P	-	-	-	-	P?	-	-	-	P	-	-	-	-	-	-	-
Pinus banksiana	-	B	-	P	-	-	B	-	-	-	-	B	-	-	-	-	B	-	-	-
Populus tremuloides	-	B?	-	-	P	-	B?	P?	-	-	-	B	-	-	-	-	B	-	B?	-
Prunus pensylvanica	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-
Prunus pumila	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ribes glandulosum	-	-	-	-	-	-	-	-	-	-	-	-	-	B	-	-	-	-	-	-
Rosa acicularis	-	-	B?		-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-
Spiraea alba	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vaccinium angustifolium	-	-	-	-	B	-	-	-	B	B	-	-	-	B	B	-	-	-	-	-
Vaccinium myrtilloides	-	-	-	-	-	-	-	-	-	-	P?	-	-	-	-	-	-	-	-	-
Vaccinium vitis-idaea	-	-	-	-	-	-	-	-	-	B	-	-	-	-	B	-	-	-	-	-
Forb																				
Aralia nudicaulis	-	-	-	-	-	-	-	-	-	-	-	-	-	B?	B?	-	-	-	-	-
Aster ciliolatus	-	-	B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Chimaphila umbellata	B?	-	-	-	-	B	-	-	-	-	B	-	-	-	-	-	-	-	-	-
Cornus canadensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-
Cypripedium acaule	-	P	-	-	-	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-
Drosera rotundifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	B?	-	B	-
Epilobium angustifolium	-	-	-	-	-	P	B?	-	-	-	-	B?	-	-	-	-	B?	-	-	-
Equisetum arvense	-	-	-	-	-	-	-	-	-	-	-	-	B	-	-	-	-	-	-	-
Equisetum sylvaticum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-
Fragaria virginiana	-	-	B?	-	P	-	P	-	-	-	-	P?	-	-	-	-	-	-	-	-
Galium boreale	-	-	-	-	-	-	-	-	B?	-	-	-	-	-	-	-	-	-	-	-
Goodyera repens	-	-	-	-	-	B	-	B	-	-	-	-	-	-	-	-	-	-	-	-
Lathyrus ochroleucus	-	-	-	-	-	-	-	-	-	P	-	-	-	-	-	-	-	-	-	-
Lycopodium obscurum	-	-	-	-	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-
Maianthemum canadensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	P	-	-
Melampyrum lineare	-	P	-	P?	-	-	P?	-	-	-	-	-	-	-	-	B	-	-	-	-
Mitella nuda	-	-	-	-	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-
Polygonum cilinode	-	-	P	-	-	-	-	-	B	B?	-	-	-	-	-	-	-	-	-	-
Potentilla tridentata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pteridium aquilinum	-	-	-	-	-	-	-	-	-	-	-	-	-	B?	-	-	-	-	-	-
Pyrola asarifolia	-	-	-	-	-	-	-	-	-	-	-	-	B?	-	-	-	-	-	-	-
Pyrola secunda	-	-	-	-	-	-	-	-	-	-	-	-	B?	-	-	-	-	-	-	-

Table 2.9 . . . continued.

Site Type:	Outcrop					Shallow Mineral					Moderately Deep Mineral					Peatland				
Disturbance Type:	Fire			Log		Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Rubus pubescens	-	-	B	-	-	-	-	B?	-	-	-	P	-	-	-	-	-	-	-	-
Smilacina trifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-
Solidago hispida	-	-	B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Trientalis borealis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	P	-	-	-	-
Vicia americana	-	-	-	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-	-
Viola adunca	P	-	-	-	-	-	-	-	-	-	-	-	-	B	-	-	-	-	-	-
Viola spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	B	-	-
Graminoid																				
Agropyron trachycaulum	-	-	-	B	-	-	-	-	B?	-	-	-	-	-	-	-	-	-	-	-
Agrostis hyemalis	-	P	-	B	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-
Calamagrostis canadensis	-	-	-	-	-	-	-	-	B	-	-	-	-	B?	-	-	-	-	-	-
Danthonia spicata	-	-	-	-	-	-	P?	-	B	P	-	-	-	B?	-	-	-	-	-	-
Eriophorum vaginatum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	B	-	-	-
Oryzopsis asperifolia	-	-	-	-	-	-	P	-	-	-	P?	P	-	-	-	-	-	-	-	-
Oryzopsis pungens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schizachne purpurascens	-	-	-	-	-	-	P	-	B?	-	-	-	-	B?	B?	-	-	-	-	-
Bryophyte & Lichen																				
Cladina mitis	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cladina rangiferina	-	P	-	-	B	-	P	-	-	B	-	P	-	-	-	-	-	-	-	-
Cladina stellaris	-	-	-	-	B	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-
Cladonia spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dicranum spp.	-	P	-	-	-	-	P	-	-	-	-	P	-	-	-	-	-	-	-	-
Pleurozium schreberi	-	P	-	-	-	-	P	-	-	-	-	P	-	-	-	-	-	-	-	-
Polytrichum commune	B	-	-	-	-	-	-	-	-	P	-	-	-	-	P?	-	-	-	-	-
Polytrichum juniperinum	-	B	-	-	-	-	B	-	-	-	-	B	-	-	-	-	-	-	-	-
Polytrichum piliferum	-	B	-	-	-	-	B	-	-	-	-	-	-	-	-	-	B	-	-	-
Ptilium crista-castrensis	-	-	-	-	-	-	-	-	-	-	B?	-	B?	-	-	-	-	-	-	-
*Selaginella densa**	-	-	-	-	B	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sphagnum spp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

* = included here due to similarity of growth form.
Notes: B = species had substantially better performance in this community type based on the performance criteria. P = species had substantially poorer performance in this community type. ? = Displayed the property of the type of performance indicated in the preceding letter but did not quite meet the performance criteria.

year old post-logging communities. *Picea mariana* and *Pinus banksiana* in the shrub layer had their poorest performance in this community type. *Vaccinium angustifolium*, *Cladina spp.* and *Selaginella densa* had their best performance in 37 year old post-logging communities. *Populus tremuloides* and *Fragaria virginiana* were conspicuously absent in this community type. There were other species found in only community type but they did not occur in enough replicates to be considered exclusive.

2.3.2.2 Shallow Mineral Soil Community Types

Compared with outcrops, the shallow soil communities had a more continuous overstory layer. Canopy closure was generally higher and this was accompanied by higher moss and lower lichen cover (Table 2.10, Figure 2.6 A, B). Shrub and herb plant cover was also higher than on outcrops. This was attributed to the higher soil depth rather than higher canopy closure. *Vaccinium myrtilloides*, *Diervilla lonicera*, *Maianthemum canadense*, *Dicranum* spp., *Pleurozium schreberi*, *Polytrichum juniperinum*, *Cladonia* spp., *Cladina mitis* and *C. rangiferina* were frequent in at least 4 of the 5 community types on shallow mineral soils. Temporal and disturbance type patterns of species composition were similar to those observed on outcrops.

Principal coordinates analysis strongly separated 13 year old post-fire communities on the first axis (Figure 2.8; cumulative percentage of dispersion: Axis 1 = 21.4, Axis 2 = 31.4, Axis 3 = 39.9, Axis 4 = 47.8). No clear interpretation could be given to the Axis 2. Axis 3 separated post-fire from post-logging communities.

Mature post-fire communities on shallow soils typically had a tree canopy at about 12 m, sparse cover in the shrub and herb layers and a ground cover dominated by mosses (Figure 2.6B). In the tree layer, *Pinus banksiana* had the highest frequency and basal area (Table 2.6). *Picea mariana* was the only other tree found in the majority of replicates. The understory taxa which characterized shallow mineral soils in general were the most conspicuous in mature communities (Table 2.10). *Potentilla tridentata* and *Oryzopsis pungens* were also characteristic. *Chimaphila umbellata* had its highest frequency in mature communities.

In 13 year old post-fire communities, a partial canopy was formed in the tall shrub layer by the post-fire cohort of *Pinus banksiana* saplings and small trees. Numerous snags protruded from the shrub canopy. Other than a few shrubs, the understory was sparse (Table 2.10). Forbs, graminoids and lichens had their poorest and bryophytes their second poorest performance on shallow soils in this community type (Figure 2.6B). *Picea mariana* and other trees had not joined *Pinus banksiana* in the tree layer because of their slower growth rates. *Pinus banksiana*, *Populus tremuloides*, *Epilobium angustifolium Polytrichum juniperinum* and *P. piliferum* appeared to benefit greatly from fire since their cover and/ or frequencies were substantially higher than in any of the other community types. The reverse was true for *Amelanchier sanguinea*, *Fragaria virginiana*, *Oryzopsis asperifolia*, *Schizachne purpurascens*, *Dicranum* spp., *Pleurozium schreberi*, *Cladina mitis* and *C. rangiferina*. Most of the taxa with substantially lower frequency than in mature communities were herbs.

After 37 years of post-fire recovery, there was a more extensive *Pinus banksiana*. Shrub, forb, graminoid, bryophyte and lichen cover had returned to levels similar to those found in mature communities. *Pleurozium schreberi* and *Cladina mitis* cover was substantially higher than that of other species. A large number of taxa were characteristic of 37 year old post-fire communities: *Vaccinium myrtilloides*, *Diervilla lonicera*, *Linnaea borealis*, *Maianthemum canadense*, *Aralia nudicaulis*, *Fragaria virginiana*, *Melampyrum lineare*, *Oryzopsis pungens*, *O. asperifolia*, *Dicranum* spp., *Pleurozium schreberi*, *Polytrichum juniperinum*, *Cladonia* spp., *Cladina mitis* and *C. rangiferina* (Table 2.10). Taxa with substantially higher frequencies than in mature communities included *Epilobium angustifolium*, *Rubus pubescens* and *Lathyrus venosus* while *Chimaphila umbellata* had substantially lower frequency.

Tree regeneration was poor and snags were absent in 13 year old post-logging communities (Figure 2.6B). Despite having high shrub cover and all six of the common boreal tree species in the tree layer, canopy closure was lower than in similar post-fire communities (Table 2.10, Table 2.6). This was thought to be a result of logging since, with the exception of *Abies balsamea*, the understory frequency of the tree species was less than in 13 year old post-fire communities.

Table 2.10. Shallow mineral soil community types- canopy closure and understory mean cover, frequency and presence.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
N (or n for plots):	4	4	4	3	4	23	26	21	18	22	4	4	4	3	4
Canopy Closure*	20.3	14.4	28.6	2.6	14.5										
Shrub†															
Abies balsamea		0.2	1.1	0.5	0.3		4	14	17	9		1	2	1	2
Amelanchier alnifolia	0.2	0.7	0.0	0.7	0.6	9	12	5	28	23	2	1	1	3	2
Amelanchier sanguinea	0.8	0.0	0.2	0.9	0.6	35	8	48	50	32	3	1	3	3	4
Arctostaphylos uva-ursi	0.9	1.6	2.0	3.8	4.1	35	19	48	44	36	3	2	3	3	3
Betula papyrifera	0.3	0.1	0.1	1.9	1.7	17	23	10	22	32	3	3	2	2	3
Cornus stolonifera	0.0		0.2			4		19			1		2		
Corylus cornuta	0.7			2.4	2.7	4			11	18	1			2	2
Diervilla lonicera	4.6	3.1	1.7	6.0	1.3	70	46	67	78	18	4	4	4	3	2
Juniperus communis	1.9	0.0	0.3	0.0	2.3	13	4	14	6	14	2	1	2	1	1
Ledum groenlandicum		1.2	0.9	0.3	1.0		8	5	6	18		2	1	1	3
Linnaea borealis	0.4	0.5	1.6	0.1	0.1	43	23	62	11	32	3	2	4	1	2
Picea glauca	0.3	0.0	0.0	0.8		4	12	5	11		1	1	1	2	
Picea mariana	1.5	1.8	2.4	2.4	3.7	26	58	43	11	45	4	4	4	2	4
Pinus banksiana	0.1	18.5	1.6	8.5	0.4	22	100	24	33	23	3	4	4	2	3
Populus tremuloides	0.0	2.4	0.0	0.2	1.5	13	50	5	44	18	2	4	1	3	3
Prunus pensylvanica	0.1	0.0	0.1	0.4	0.7	13	23	19	17	23	3	2	3	2	2
Ribes glandulosum		0.0	0.0	0.0	0.0		12	5	11	5		2	1	2	1
Rosa acicularis	0.3	0.0	0.3	0.2		30	8	43	28		3	2	4	3	
Rubus idaeus	0.0	0.0	0.1	0.1	0.0	4	12	10	17	9	1	2	1	2	2
Salix spp.	0.1	2.2	0.4	1.9	0.5	17	50	19	28	18	4	4	3	2	3
Spiraea alba	0.3	0.2	0.0	1.3	0.6	26	23	24	44	18	3	3	2	3	3
Symphoricarpos albus	0.0	0.0	0.1	0.0	0.3	4	4	10	17	5	1	1	2	2	1
Vaccinium angustifolium	2.6	5.0	0.0	18.2	17.1	39	42	19	72	77	4	4	2	3	4
Vaccinium myrtilloides	2.1	3.8	2.5	5.0	3.2	78	77	81	89	82	4	4	4	3	4
Vaccinium vitis-idaea	0.0	0.1		0.0	1.2	4	8		6	36	1	2		1	4
Forb															
Apocynum androsaemifolium	0.0		0.0	0.1	0.3	4		5	22	9	1		1	2	2
Aralia nudicaulis	1.0	0.2	0.5	0.9	0.7	30	31	52	17	32	4	2	2	1	2
Aster ciliolatus	0.1	0.0	0.1	0.6	0.0	17	8	24	33	9	2	1	2	2	2
Campanula rotundifolia	0.0		0.0	0.0	0.0	13		29	17	5	3		3	2	1
Chimaphila umbellata	0.0			0.0		22			6		4			1	
Clintonia borealis	0.3	0.0	0.0	0.1	0.1	4	4	10	28	23	1	1	1	3	3
Cornus canadensis	1.5	0.2	1.0	1.4	0.6	30	15	48	39	27	3	2	3	3	2
Cypripedium acaule	0.0		0.0		0.0	9		5		14	1		1		3
Epilobium angustifolium	0.0	0.1	0.1	0.3	0.1	9	62	29	33	27	2	4	3	3	4
Fragaria vesca			0.1	0.0				14	6				2	1	
Fragaria virginiana	0.1		1.0	0.7	0.5	30		62	33	14	3		3	3	2
Galium boreale	0.0		0.0	0.3	0.0	4		14	28	5	1		2	3	1
Gaultheria procumbens	0.2	0.9		3.7		17	12		28		1	1		2	
Goodyera repens	0.0		0.0			13		19			3		3		

Table 2.10 . . . continued.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Hieracium scabriusculum	0.0	0.0	0.0	0.0	0.0	9	8	5	11	5	2	1	1	1	1
Lathyrus ochroleucus	0.6	0.0	0.0	0.1		30	15	29	33		4	2	3	3	
Lathyrus venosus	0.1	0.0	0.1	0.1	0.0	4	4	19	11	5	1	1	3	2	1
Lycopodium obscurum	0.0		0.0	0.5	0.0	4		5	28	9	1		1	3	1
Maianthemum canadense	1.9	0.4	1.4	1.5	1.2	87	50	86	83	82	4	3	4	3	4
Melampyrum lineare	0.1	0.0	1.0	0.0	0.3	30	12	57	33	50	3	1	3	3	3
Mitella nuda				0.0					11					2	
Polygonum cilinode				0.0	0.0				17	9				2	2
Potentilla tridentata	0.5	0.4	0.5	0.9	0.0	61	35	48	39	14	4	3	3	2	2
Pyrola asarifolia	0.0		0.0	0.0	0.0	9		14	6	5	1		3	1	1
Rubus pubescens	0.0		0.2	1.3	0.0	9		38	11	9	1		3	2	1
Solidago hispida	0.0	0.1	0.1	0.0	0.0	9	19	19	6	5	2	2	3	1	1
Trientalis borealis	0.0	0.0	0.1	0.0	0.1	4	8	19	17	23	1	2	2	2	4
Vicia americana			0.0					19					2		
Viola adunca	0.0	0.0	0.0	0.0	0.0	9	12	19	39	5	1	1	2	3	1
Graminoid															
Agropyron trachycaulum	0.0		0.0	0.0	0.0	9		10	22	9	1		2	3	1
Agrostis hyemalis		0.0	0.0	0.3	0.0		8	19	28	14		1	2	3	3
Calamagrostis canadensis		0.0		0.1	0.0		12		39	9		2		3	1
Carex spp.	0.0	0.0	0.0	0.1	0.0	13	12	14	33	9	3	1	2	3	2
Danthonia spicata	0.0	0.0	0.0	0.7	0.0	35	8	19	39	5	4	2	2	3	1
Oryzopsis asperifolia	0.1		0.1	0.6	1.0	43		76	50	32	4		3	3	3
Oryzopsis pungens	0.1	0.1	0.1	0.1	0.0	61	42	67	67	27	4	4	4	3	3
Panicum spp.		0.0	0.0	0.0			12	10	11			2	2	2	
Schizachne purpurascens	0.0		0.0	0.2	0.2	22		33	50	36	3		3	3	2
Bryophyte & Lichen															
Aulacomnium palustre	0.0	0.0	0.0	0.1		4	8	10	22		1	1	2	2	
Cladina mitis	4.4	0.1	9.1	3.4	2.5	70	65	76	89	77	4	4	4	3	4
Cladina rangiferina	5.8	0.0	4.5	2.6	17.4	87	19	95	83	91	4	3	4	3	4
Cladina stellaris	0.1		0.0		2.9	9		5		41	1		1		3
Cladonia spp.	0.3	1.3	1.4	0.6	0.5	91	100	90	100	86	4	4	4	3	4
Dicranum spp.	8.5	0.0	2.9	4.7	7.2	96	35	95	94	86	4	4	4	3	4
Hylocomium splendens	0.1		0.8	0.0	0.0	13		33	6	5	3		2	1	1
Liverwort spp.	0.0			0.1	0.0	9			22	5	2			2	1
Pleurozium schreberi	40.2	0.4	39.8	8.7	21.6	96	54	100	94	95	4	4	4	3	4
Polytrichum commune	0.8	3.9	0.7	0.7	0.0	26	31	33	28	5	3	3	2	2	1
Polytrichum juniperinum	0.2	13.5	1.4	2.5	0.2	48	96	67	94	41	4	4	4	3	4
Polytrichum piliferum	0.0	0.9	0.2	0.1	0.0	17	46	19	17	5	3	4	2	2	1
Ptilium crista-castrensis	0.1		0.0			4		19			1		2		
Sphagnum spp.	0.0	0.1			2.0	4	12			5	1	2			1

* N was 3 for 13 year old post-fire communities. † Tree species cover value is the maximum of tree, sapling or tree seedling cover in the herb and shrub layers.
Notes: Includes species found in at least three plots and more than one replicate in a community type. A blank means that the taxon did not occur in the replicate's plots, 0.0 denotes mean cover > 0 and < 0.05%.

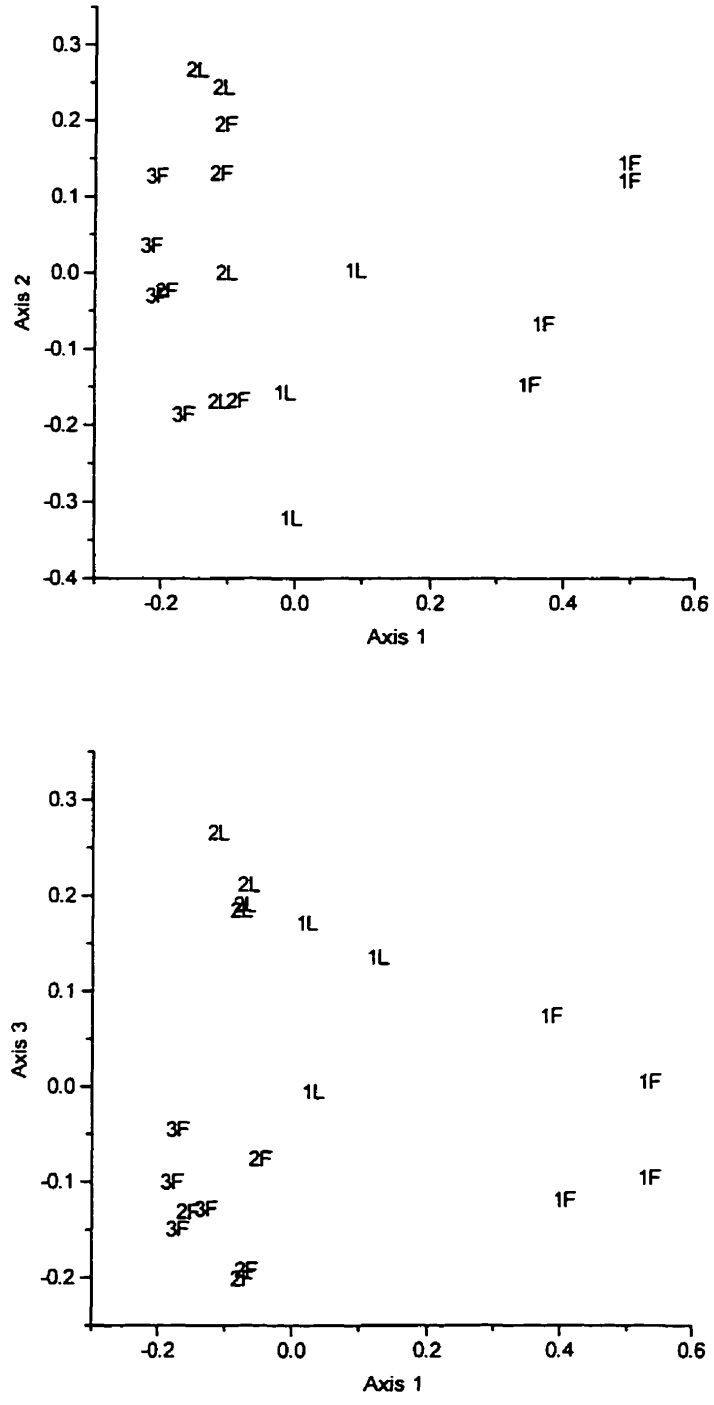


Figure 2.8. Principal coordinates analysis of shallow mineral soil replicate means.

Legend: first character is age class, 1 = 13 years, 2 = 37 years, 3 = 65 years; second character is disturbance type, F = fire, L = logging.

Shrubs, forbs and graminoids responded well to a more open canopy. Cover in the shrub layer was dominated by low and medium shrubs such as *Vaccinium angustifolium*, *V. myrtilloides*, *Diervilla lonicera* and *Arctostaphylos uva-ursi* rather than *Pinus banksiana*. Shrubs had their highest cover in this community type. Most of the understory vascular plants (20 of 28 taxa) present in at least 3 of the 4 mature replicates appeared to benefit from overstory removal as evidenced by their higher frequency in 13 year old post-logging communities. The majority of these higher frequencies were accompanied by higher cover. Colonization by *Calamagrostis canadensis*, *Agrostis hyemalis* and *Panicum* spp. was apparently facilitated by overstory removal since they were not found in mature communities. Mosses characteristic of mature communities were adversely affected by overstory removal. Higher light intensity and reduced competition presumably accounted for the substantial increase in *Polytrichum juniperinum* cover.

Thirty-seven year old post-logging communities typically had a relatively open canopy, a low shrub layer dominated by *Vaccinium angustifolium* and a ground cover dominated by mosses and lichens (Figure 2.6B, Table 2.10). Tree density was 957 stems ha^{-1} compared with 2637 stems ha^{-1} in mature and 3200 stems ha^{-1} in 37 year old post-fire communities. *Pinus banksiana* and *Picea mariana* accounted for the majority of the basal area. The higher basal area per individual indicated that these were primarily trees not felled at the time of logging. The understories of 37 year old post-logging communities differed from mature communities in a number of ways. Post-logging communities were more open than mature ones. Despite this, species with substantially higher cover were generally those found most frequently on nutrient poor soils (Bakuzis and Kurmis 1978; Klinka *et al.* 1989). These included *Arctostaphylos uva-ursi*, *Ledum groenlandicum*, *Vaccinium angustifolium*, *V. vitis-idaea Cladina rangiferina* and *C. stellaris*. Of these, *Ledum groenlandicum* was the only one with cover as high as that in 37 year old post-fire communities. *Betula papyrifera* and *Populus tremuloides* also had substantially higher cover than in mature communities. This may be the result of more suckering in these relatively open conditions and a more extensive root system. Most of these taxa, as well as *Epilobium angustifolium*, *Clintonia borealis*, *Trientalis borealis* and *Calamagrostis canadensis* had substantially higher frequencies than in mature communities. Those with substantially lower frequencies included *Diervilla*

Ionicera, *Rosa acicularis*, *Potentilla tridentata*, *Lathyrus ochroleucus*, *Chimaphila umbellata*, *Goodyera repens*, *Danthonia spicata*, *Polytrichum commune* and *P. piliferum*.

Chimaphila umbellata and *Lycopodium obscurum* had their peak performance in 65 year old post-fire communities (Table 2.9). More taxa distinguished 13 year old post-fire communities than any of the other community types. Most of these did so by their poor performance- *Vicia americana* and *Schizachne purpurascens* were absent. *Pinus banksiana*, *Polytrichum juniperinum* and *P. piliferum* had their best performance in this community type. *Vicia americana*, *Linnaea borealis* and *Melampyrum lineare* had their best performance in 37 year old post-fire communities and *Vicia americana* was only found here. *Goodyera repens* was confined to this and the 65 year old post-fire community type. All but one of the species which distinguished 13 year old post-logging communities were herbs. *Mitella nuda* was unique to this community type. *Vaccinium angustifolium*, *Corylus cornuta* and *Polygonum cilinode* distinguished both 13 and 37 year old post-logging communities and *Polygonum cilinode* was found only in post-logging communities. The only community type that was distinguished by strong lichen performance was the 37 year old post- logging type. *Cladina rangiferina* and *C. stellaris* performed substantially better in this type as did *Vaccinium vitis-idaea* and *Cypripedium acaule*. *Rosa acicularis* was not encountered and *Diervilla lonicera* and *Polytrichum commune* had their poorest performance in 37 year old post-logging communities.

2.3.2.3 Moderately Deep Mineral Soil Community Types

Pair-wise comparisons of the moderately deep mineral soil community types with the same community types on shallow soils indicated that the increase in mean soil depth was associated with higher basal area, canopy closure, shrub cover and herb cover and lower moss and lichen cover (Figure 2.6 B, C). Many of the same species characterized communities on both site types, albeit with site type related differences in mean cover. *Picea mariana*, *Populus tremuloides*, *Rosa acicularis* and *Cornus canadensis* were more frequent than on shallow soils while *Oryzopsis pungens*, *Polytrichum juniperinum*, *Cladina mitis* and *C. rangiferina* were less frequent (Table 2.11).

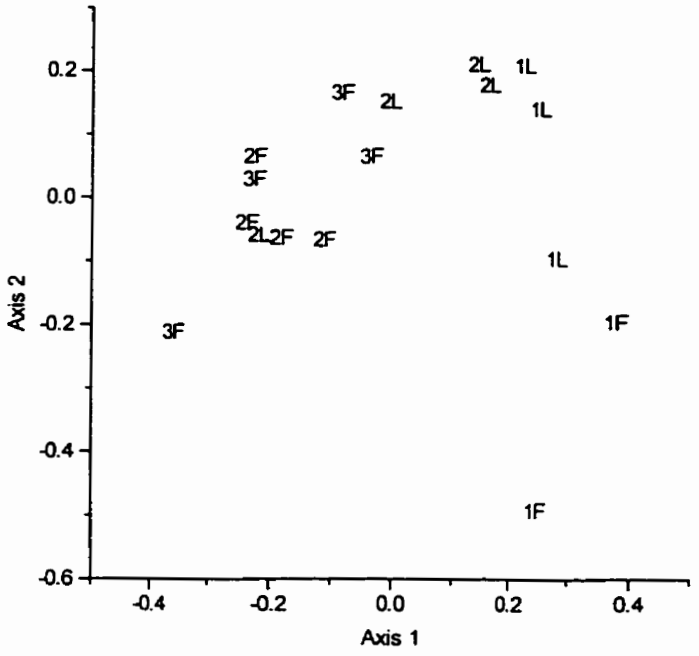
Table 2.11. Moderately deep mineral soil community types- canopy closure and understory mean cover, frequency and presence.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
N (or n for plots):	4	2	4	3	4	22	11	27	17	25	4	2	4	3	4
Canopy Closure	46.8	38.3	40.4	17.4	26.8										
Shrub†															
Abies balsamea	2.8	0.4	0.2	0.8	2.4	23	9	19	12	28	2	1	2	1	3
Acer spicatum	0.1		0.2	5.6	0.0	5		4	18	4	1		1	2	1
Alnus crispa	3.1	2.7		0.8	0.8	23	18		18	8	2	1		2	1
Alnus rugosa	3.9		0.1		0.9	9		4		12	1		1		2
Amelanchier alnifolia			0.0	0.4	0.4			11	18	12			3	2	2
Amelanchier sanguinea	0.2	0.8	0.1	1.0	0.6	23	9	15	47	24	2	1	3	2	4
Arctostaphylos uva-ursi	1.5		1.0	0.3	1.2	9		15	18	8	2		2	2	2
Betula papyrifera	0.7	0.6	0.2	3.4	0.3	14	18	22	59	16	3	1	4	3	3
Cornus stolonifera	0.9	0.0	0.0	0.4		9	9	7	24		1	1	1	2	
Corylus cornuta	4.5		0.3	6.4	3.1	5		15	47	40	1		2	2	3
Diervilla lonicera	3.1	9.2	1.1	7.6	5.0	36	45	44	71	40	3	1	4	3	3
Ledum groenlandicum		1.4	0.0	2.7	5.3		9	4	18	44		1	1	2	4
Linnaea borealis	0.6	0.0	1.9	0.1	0.5	59	18	67	18	44	4	2	4	3	3
Picea glauca	0.1	0.2	1.0	0.1	0.1	18	9	15	18	8	3	1	2	3	2
Picea mariana	5.7	4.9	5.4	0.6	3.3	50	64	63	12	56	4	2	4	2	4
Pinus banksiana	0.1	14.7	0.3	4.5	0.5	14	91	11	59	20	3	2	2	3	3
Populus tremuloides	0.3	12.2	0.1	2.5	0.6	36	82	19	65	32	4	2	3	3	3
Prunus pensylvanica		0.2	0.0	0.6	0.1		36	4	24	12		2	1	2	1
Ribes glandulosum			0.0	0.2	0.0			4	29	8			1	3	2
Ribes triste			0.2	0.0	0.2			11	6	12			2	1	2
Rosa acicularis	0.3	0.4	0.5	0.4	0.4	27	27	48	29	24	4	2	4	3	4
Rubus idaeus	0.1	0.3	0.0	0.3	0.1	14	45	7	29	20	2	2	1	2	4
Salix spp.	0.8	6.6	1.0	1.7	1.6	18	82	41	29	24	3	2	4	3	4
Spiraea alba		0.0	0.1	0.3	0.0		9	11	24	4		1	2	2	1
Vaccinium angustifolium	0.1	6.9	1.2	11.5	11.1	27	45	26	71	84	4	2	3	3	4
Vaccinium myrtilloides	0.9	3.8	3.4	5.2	8.4	59	55	70	71	80	4	2	4	3	4
Vaccinium vitis-idaea	0.6		0.1		0.9	9		7		48	2		1		4
Viburnum rafinesquianum	0.7				0.2	5				16	1				2
Forb															
Anemone quinquefolia	0.0		0.0		0.0	14		7		8	1		2		2
Apocynum androsaemifolium	0.0	0.0	0.0	0.1	0.7	5	9	4	18	24	1	1	1	2	3
Aralia nudicaulis	1.6	0.5	0.6	2.7	2.2	41	18	37	65	60	3	1	4	3	4
Aster ciliolatus	0.0	0.0	0.2	0.3	0.0	5	9	52	35	16	1	1	4	3	2
Chimaphila umbellata	0.0		0.0			18		4			3		1		
Clintonia borealis	1.5	0.6	0.2	0.8	1.1	27	36	26	53	56	3	1	4	3	4
Coptis trifolia	0.1		0.0	0.0	0.0	5		11	6	4	1		2	1	1
Cornus canadensis	3.4	0.9	2.1	3.6	1.9	73	45	63	76	64	4	2	4	3	4
Epilobium angustifolium	0.1	0.6	0.1	0.3	0.1	14	100	30	59	28	2	2	3	3	3
Equisetum arvense			0.0					15					3		
Equisetum sylvaticum	0.0	0.0	0.0	0.1	0.2	5	18	7	12	16	1	2	2	2	3
Fragaria virginiana	0.2	0.0	0.5	0.5	0.3	23	9	67	41	40	3	1	4	3	4
Galium boreale			0.0	0.1	0.0			11	24	12			2	2	3
Galium triflorum	0.0		0.0	0.0	0.0	5		7	12	8	1		2	2	2
Gaultheria procumbens		0.1		1.2			18		18			1		2	
Goodyera repens	0.0		0.0			23		19			3		2		

Table 2.11 . . . continued.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Hieracium scabriusculum		0.0	0.0	0.0	0.0		9	7	12	12		1	1	1	2
Lathyrus ochroleucus	0.2	0.2	0.1	0.3	0.0	14	18	7	35	4	2	1	1	2	1
Lathyrus venosus	0.1		0.0	0.1		5		7	24		1		1	2	
Lycopodium annotinum	0.3		0.1		0.2	9		4		12	2		1		2
Lycopodium clavatum	0.1		0.0	0.0		18		4	6		2		1	1	
Lycopodium complanatum				0.0	0.1				6	12				1	2
Lycopodium obscurum	0.4	0.0	0.0	0.0	0.0	18	9	4	18	8	3	1	1	3	2
Maianthemum canadense	0.8	0.3	1.3	1.7	0.9	82	45	78	94	68	4	1	4	3	4
Melampyrum lineare	0.0		0.3	0.0	0.2	5		41	18	48	1		4	2	3
Mitella nuda	0.1		0.2	0.0	0.0	5		22	12	4	1		2	2	1
Petasites palmatus	0.1		0.1	0.9	0.1	9		30	18	16	1		4	2	4
Potentilla tridentata	0.0	0.0	0.3	0.3	0.1	9	9	15	12	12	2	1	2	2	3
Pteridium aquilinum			0.1	0.7	0.0			4	18	4			1	2	1
Pyrola asarifolia			0.1	0.0	0.0			15	6	4			3	1	1
Pyrola secunda	0.0	0.1	0.0	0.0		5	9	19	6		1	1	4	1	
Rubus pubescens	1.7		0.8	1.6	0.2	23		44	41	32	3		4	3	4
Solidago hispida			0.0	0.2	0.0			4	18	8			1	2	2
Streptopus roseus			0.1	0.1	0.2			7	24	20			2	2	3
Trientalis borealis	0.0	0.1	0.1	0.3	0.1	27	18	30	53	40	3	1	4	3	4
Viola adunca	0.0		0.0	0.0	0.0	9		4	24	8	1		1	3	2
Viola spp.	0.1		0.1	0.3	0.0	9		33	12	12	1		3	2	2
Graminoid															
Agrostis hyemalis	0.0		0.0			5		11			1		2		
Calamagrostis canadensis	0.0	0.3	0.1	0.3	0.0	14	27	11	47	20	1	1	2	3	3
Carex spp.	0.0	0.1	0.1	0.1	0.0	14	36	26	53	20	1	2	4	3	3
Danthonia spicata			0.0	0.0	0.0			7	24	8			2	2	2
Oryzopsis asperifolia	0.0	0.0	0.1	0.2	0.3	23	9	56	65	52	2	1	4	3	4
Oryzopsis pungens	0.0		0.0	0.1	0.0	9		19	29	28	1		2	3	4
Schizachne purpurascens	0.0	0.0	0.0	0.3	0.3	5	18	22	41	48	1	1	2	3	4
Bryophyte & Lichen															
Aulacomnium palustre	0.1	0.7	0.6	0.1	0.0	14	27	22	12	12	3	2	3	2	2
Cladina mitis	0.8	0.0	1.0	0.1	0.4	32	18	48	35	36	3	1	4	3	4
Cladina rangiferina	0.9	0.0	0.9	0.4	1.3	32	9	81	41	76	3	1	4	3	4
Cladonia spp.	0.2	1.2	0.8	0.6	0.7	91	91	96	94	92	4	2	4	3	4
Dicranum spp.	5.6	0.0	3.8	1.4	5.0	86	27	96	65	76	4	2	4	3	4
Hylocomium splendens	2.3		0.7		0.5	45		26		12	4		3		2
Pleurozium schreberi	33.7	0.1	29.7	6.3	17.6	91	36	100	88	96	4	2	4	3	4
Polytrichum commune	1.4	2.1	3.1	0.1	0.0	41	36	41	18	4	4	2	3	2	1
Polytrichum juniperinum	0.1	8.6	0.4	2.2	0.1	14	91	67	76	28	2	2	4	3	4
Polytrichum piliferum		0.1	0.1	0.0	0.0		18	15	18	4		2	2	2	1
Ptilium crista-castrensis	0.2		0.1		0.1	14		26		8	3		4		1
Sphagnum spp.	1.0	0.0		4.1	0.3	18	9		18	4	2	1		2	1

† Tree species cover value is the maximum of tree, sapling or tree seedling cover in the herb and shrub layers.
Notes: A blank means that the taxon did not occur in the replicate's plots, 0.0 denotes mean cover > 0 and < 0.05%. Includes species found in at least three plots and more than one replicate in a community type.



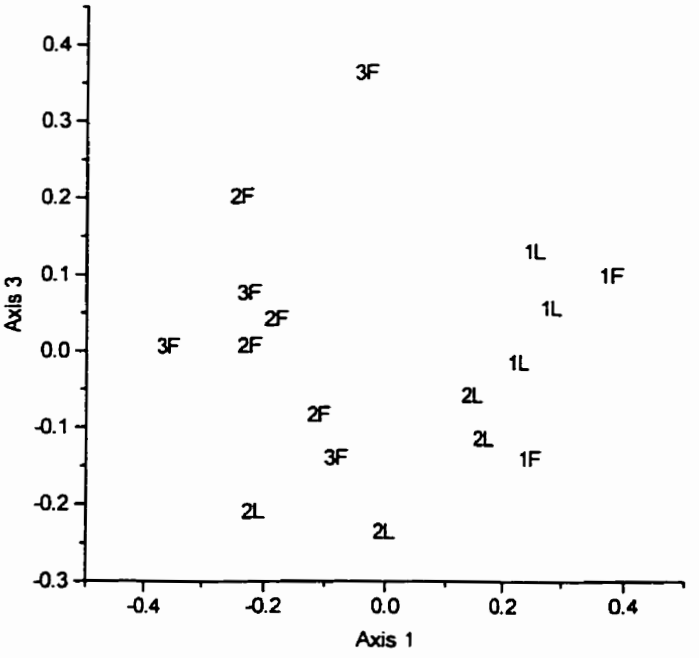


Figure 2.9. Principal coordinates analysis of moderately deep mineral soil replicate means. Legend: first character is age class, 1 = 13 years, 2 = 37 years, 3 = 65 years; second character is disturbance type, F = fire, L = logging.

The principal coordinates analysis of moderately deep mineral soil replicates (Figure 2.9; cumulative percentage of dispersion: Axis 1 = 19.8, Axis 2 = 32.9, Axis 3 = 41.9, Axis 4 = 48.7) yielded less clear patterns than those for the other two mineral soil site types. Axis 1 weakly paralleled an age gradient. Thirteen year old post-fire communities were separated on a combination of the first two axes. Axis 3 separated 37 year old post-logging communities from 37 and 65 year old post-fire communities.

Mature communities on moderately deep soils typically had a *Pinus banksiana* canopy at about 13m which shaded *Picea mariana* trees, a sparse vascular understory and a bryophyte ground cover dominated by *Pleurozium schreberi* (Figure 2.6B, Table 2.11). *Pinus banksiana* was dominant in terms of basal area as well as height (Table 2.6). Of the shrubs which met the characteristic criteria, *Linnaea borealis* and *Vaccinium myrtilloides* were the most frequent while *Picea mariana* had the highest cover. Other characteristic understory taxa included *Diervilla lonicera*, *Maianthemum canadense*, *Cornus canadensis*, *Pleurozium schreberi*, *Dicranum* spp. and *Cladonia* spp..

Thirteen year old post-fire communities had numerous standing snags protruding through a shrub canopy (Figure 2.6C, Table 2.11). Shrubs dominated the cover of this community type largely due to tree seedlings and saplings. The balance of the understory was sparse. *Pinus banksiana*, *Populus tremuloides* and *Salix* spp. formed the shrub canopy and were frequently joined in the lower layers by *Vaccinium myrtilloides*, *Picea mariana*, *Epilobium angustifolium*, *Polytrichum juniperinum* and *Cladonia* spp.. *Pinus banksiana*, *Salix* spp., *Prunus pensylvanica*, *Epilobium angustifolium*, *Polytrichum juniperinum* and *P. piliferum* appeared to benefit from fire because their frequencies and cover were substantially higher than in mature communities. Fire had the opposite effect on *Linnaea borealis*, *Goodyera repens*, *Rubus pubescens*, *Chimaphila umbellata*, *Pleurozium schreberi*, *Dicranum* spp., *Hylocomium splendens*, *Polytrichum commune* and *Cladina rangiferina*.

In 37 year old post-fire communities, *Pinus banksiana* generally formed a continuous canopy at a mean height of 10m over *Picea mariana*. Occasionally, the overstory was either pure *Pinus banksiana* or *Picea mariana*. A well developed tree canopy limited the cover of all other growth

forms except shade tolerant bryophytes. Although the cover of understory plants was generally low, many were found in at least half the plots. By 37 years, the cover of most species was similar to that in mature communities. Exceptions included *Amelanchier alnifolia*, *Linnaea borealis*, *V. angustifolium*, *Vaccinium myrtilloides*, *Pyrola asarifolia* and *Hylocomium splendens*. In addition to these taxa, *Aster ciliolatus*, *Equisetum arvense*, *Melampyrum lineare*, *Petasites palmatus*, *Viola* spp., *Pyrola asarifolia*, *Polytrichum juniperinum* and *Cladina rangiferina* had substantially higher frequencies than in mature communities while *Chimaphila umbellata* and *Lycopodium obscurum* had substantially lower frequencies.

The physiognomy of 13 year old post-logging communities was more varied than post-fire communities of the same age. A tall shrub canopy and numerous snags were replaced by a mixture of low, medium and tall shrubs with low shrubs having the highest frequency and cover (Figure 2.6C). The more open nature of the shrub canopy facilitated relatively high forb and graminoid cover. Total bryophyte and lichen cover was similar to that in 13 year old post-fire communities but different species were the most abundant. This was accompanied by substantially higher "other litter" (primarily deciduous leaf litter) and lower conifer litter (Table 2.7). *Populus tremuloides* was the only tree to characterize 13 year old post-logging communities. Many taxa had higher frequencies and cover than in mature communities. Exceptions were *Picea mariana*, *Linnaea borealis*, *Chimaphila umbellata*, *Goodyera repens* and *Hylocomium splendens*. With the exception of *Picea mariana*, all of these also had lower frequencies in post-fire communities suggesting that the adverse effects were related to canopy removal. *Picea mariana* exhibited limited ability to regenerate naturally after logging. In the ground layer, *Pleurozium schreberi* and *Dicranum* spp. had substantially lower cover than in mature communities.

In general, the recovery pattern established at 13 years in post-logging communities continued to 37 years. Thirty seven year old post-logging communities were more open than post-fire communities of the same age. A mixture of low and medium shrubs formed the most conspicuous understory layer although their cover was not as high as in 13 year old communities. Herbs were scattered amongst a ground cover dominated by "other litter" and *Pleurozium schreberi*. *Populus tremuloides* was the most frequent tree in 37 year old post-logging

communities but it was not characteristic. The more open nature of post-logging compared with post-fire communities was also evidenced by lower total basal area (Figure 2.6C), total frequency (72% vs. 100%), total density (1074 vs. 3587 stems ha^{-1}) and canopy closure (Table 2.11). The cover of *Ledum groenlandicum*, *Vaccinium angustifolium*, *V. myrtilloides*, and *Oryzopsis asperifolia* was substantially higher than in mature communities while the reverse was true for *Pleurozium schreberi*. One-third of the taxa with a frequency difference relative to mature communities had lower frequencies in 37 year old post-logging communities. Many of these demonstrated sensitivity to canopy removal in the other site types.

As expected, the basal areas of *Pinus banksiana*, *Picea mariana* and *Populus tremuloides* were highest in mature communities (Table 2.11). *Chimaphila umbellata* performed substantially better in the understory of mature communities while *Goodyera repens* and *Ptilium crista-castrensis* almost met the performance criteria (Table 2.9). *Prunus pensylvanica*, *Vaccinium myrtilloides* and *Oryzopsis asperifolia* were on the borderline of substantially poorer performance. At 13 years of age, post-fire communities were distinguished by taxa representing a variety of growth forms. *Pinus banksiana* and *Populus tremuloides* had the largest differences in terms of cover while *Polytrichum juniperinum* had the largest frequency difference. *Equisetum arvense* was the only taxon to be confined to one community type, namely 37 year old post-fire communities. Most species were found in all the community types but *Vaccinium angustifolium*, *Schizachne purpurascens* and *Aralia nudicaulis* had their best performance in 13 and 37 year old post-logging community types. *Gaultheria procumbens* was not found in mature communities. *Fragaria virginiana* and *Oryzopsis asperifolia* performed substantially poorer in 13 year old post-logging communities.

2.3.2.4 Peatland Community Types

The species composition of peatland communities differed greatly from that of communities on mineral soils. *Picea mariana* was the major tree species (Table 2.6). The low shrub layer was more significant than on the other site types and had the second highest cover after mosses (Figure 2.6D). Although *Ledum groenlandicum* dominated vascular understory cover, it was generally accompanied by *Picea mariana*, *Chamaedaphne calyculata*, *Oxycoccus quadripetalus*, *Vaccinium vitis-idaea*, *Smilacina trifolia* and *Carex* spp. (Table 2.12). *Sphagnum* was the most abundant taxon on peatlands with a frequency ranging from 91% to 100% in the five community types and cover ranging from 51% to 70%. *Sphagnum* spp. were generally accompanied in the ground layer by *Pleurozium schreberi*, *Dicranum* spp., unidentified mosses and *Cladonia* spp..

Principal coordinates analysis separated 13 year old post-fire communities on the first axis (Figure 2.10; cumulative proportion of dispersion: Axis 1 = 14.4, Axis 2 = 27.6, Axis 3 = 38.3, Axis 4 = 47.7). This axis also reflected an age gradient for both disturbance types. Axis 2 separated 37 year old post-logging from 37 and 65 year old post-fire communities. No clear pattern could be associated with Axis 3.

Mature communities differed from the general situation on peatlands because *Kalmia polifolia*, *Smilacina trifolia*, *Polytrichum strictum* and *Aulacomnium palustre* were also characteristic, shrub cover was lowest and moss cover was highest (Figure 2.6D, Table 2.12).

Standing and fallen snags were a conspicuous feature of 13 year old post-fire communities. Unlike similar communities on mineral soils, they had no tall shrub canopy. *Picea mariana* saplings were scattered within a low shrub layer and a *Sphagnum* moss ground cover (Figure 2.6D). In contrast with the general situation on peatlands, *Oxycoccus quadripetalus* and *Dicranum* spp. did not characterize this community type but *Salix* spp., *Pinus banksiana*, *Vaccinium myrtilloides*, *Epilobium angustifolium*, *Equisetum sylvaticum*, *Polytrichum strictum* and unidentified mosses did. *Picea mariana* regenerated well (understory frequency = 100%; Table 2.12) as did *Pinus banksiana*, *Populus tremuloides*, *Alnus rugosa*, *Linnaea borealis*, *Spiraea alba*, *Vaccinium angustifolium*, *Epilobium angustifolium* and *Polytrichum piliferum*. Substantially higher frequencies in post-fire and post-logging communities at 13 years suggested that *Betula papyrifera*, *Vaccinium*

Table 2.12. Peatland community types- canopy closure and understory mean cover, frequency and presence.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
N (or n for plots):	3	4	3	2	4	16	23	17	8	22	3	4	3	2	4
Canopy Closure (%)	13.7	6.9	17.9	0.8	26.2										
Shrubs†															
Abies balsamea			0.0		1.0			6		14			1		2
Alnus rugosa	0.7	4.2	6.8	1.4	1.8	13	30	59	63	36	2	4	3	2	4
Betula glandulosa	0.1	0.1	0.5	0.7		19	4	18	38		1	1	3	1	
Betula papyrifera		0.5	0.1	1.0	0.1		22	6	63	18		3	1	2	2
Chamaedaphne calyculata	3.5	1.8	6.4	2.2	1.8	81	48	53	50	36	3	4	3	2	3
Corylus cornuta			0.1					12					2		
Gaultheria hispidula	0.1	0.1	0.2	0.4	0.4	13	26	35	38	50	1	2	3	1	3
Kalmia polifolia	0.2	0.1	0.2	0.1	0.1	63	39	35	50	18	3	4	2	2	2
Larix laricina	0.2		0.2	0.8	0.1	19		29	38	14	2		3	1	2
Ledum groenlandicum	13.6	24.6	20.6	17.3	22.6	94	96	100	100	91	3	4	3	2	4
Linnaea borealis		0.0	0.1		0.0		22	18		5		3	1		1
Oxycoccus quadripetalus	0.2	0.6	0.8	0.7	0.2	75	70	71	63	41	3	4	3	2	3
Picea mariana	4.9	4.2	9.1	3.4	6.0	94	100	82	88	86	3	4	3	2	4
Pinus banksiana	0.1	4.1	0.2	0.7	0.0	13	83	18	13	5	2	4	3	1	1
Populus tremuloides	0.0	0.6		0.6	0.0	6	48		38	9	1	4		1	1
Ribes glandulosum		0.0	0.0		0.0		9	12		5		2	2		1
Rubus idaeus			0.0	0.2				12	38				2	1	
Salix spp.	0.5	1.8	2.0	1.5	0.9	31	70	76	88	27	3	4	3	2	4
Spiraea alba		1.0		0.0	0.0		13		13	9		3		1	2
Vaccinium angustifolium	0.0	0.8	0.0	0.4	0.4	6	35	18	13	41	1	4	2	1	4
Vaccinium myrtilloides	0.1	1.4	0.1	0.6	0.4	38	57	29	50	41	3	4	3	1	4
Vaccinium vitis-idaea	0.5	3.9	0.4	3.8	0.9	69	65	41	50	86	3	4	3	1	4
Forbs															
Cornus canadensis		0.6	0.3	0.5	0.4		39	41	38	41		3	3	1	4
Drosera rotundifolia		0.0		0.0			13		25			2		2	
Epilobium angustifolium		0.1	0.0	0.1	0.0		52	6	25	5		4	1	1	1
Equisetum arvense		0.1	0.0	0.0	0.1		17	12	13	14		3	2	1	2
Equisetum fluviatile			0.0	0.1	0.0			6	25	5			1	1	1
Equisetum pratense			0.1					12					1		
Equisetum sylvaticum	0.1	0.3	2.0	0.5	0.8	19	52	65	25	41	3	4	3	2	4
Lycopodium annotinum	0.8	0.2	0.5	1.0	1.3	19	4	12	25	9	2	1	1	1	1
Maianthemum canadense	0.0	0.4	0.0	0.9	0.3	6	48	6	100	45	1	4	1	2	3
Melampyrum lineare	0.0					13					2				
Rubus chamaemorus	0.3	0.1			0.5	25	17			18	2	1			1
Rubus pubescens	0.1	0.0	0.9		0.1	6	4	24		9	1	1	2		2
Smilacina trifolia	1.9	0.4	0.9		0.0	69	48	53		23	3	3	3		3
Trientalis borealis	0.1	0.1	0.1	0.1	0.0	6	26	29	38	18	1	3	3	1	2
Viola spp.	0.0	0.0	0.1		0.0	6	4	18		5	1	1	3		1

Table 2.12 . . . continued.

	Mean Cover (%) in Replicates					Frequency (%) in Plots					Presence in Replicates				
Disturbance type:	Fire			Log		Fire			Log		Fire			Log	
Age:	65	13	37	13	37	65	13	37	13	37	65	13	37	13	37
Graminoids															
Calamagrostis canadensis	0.1	0.1	0.2	0.3	0.0	19	39	65	50	9	2	3	3	2	2
Carex spp.	0.2	2.1	0.7	2.4	0.4	75	91	94	100	77	3	4	3	2	4
Eriophorum vaginatum	0.0	0.2	0.0	0.2	0.0	13	17	6	13	5	1	3	1	1	1
Bryophytes & Lichens															
Aulacomnium palustre	0.2	1.1	0.1	0.1	0.1	50	39	59	38	55	3	4	3	2	4
Cladina mitis	0.0	0.1	0.2	0.0	0.0	19	26	6	13	14	1	3	1	1	2
Cladina rangiferina	0.8	0.0	0.0		0.2	38	13	18		59	3	2	2		4
Cladonia spp.	0.3	1.5	0.1	0.1	0.3	56	83	59	63	91	3	4	3	2	4
Dicranum spp.	2.3	0.2	0.3	0.0	2.4	69	43	35	50	77	3	3	3	2	4
Hylocomium splendens	0.5	0.1	0.2		0.3	19	4	18		5	3	1	2		1
Liverwort spp.	0.1	0.0	0.0		0.0	19	13	18		14	1	2	2		3
Moss spp.	0.0	1.0	1.6	0.4	2.0	38	74	71	88	91	3	4	3	2	4
Pleurozium schreberi	12.6	0.1	4.4	1.7	10.5	81	65	65	63	86	3	4	3	2	4
Polytrichum commune	1.6	1.4	0.6	0.0	0.0	31	35	18	13	14	3	3	2	1	3
Polytrichum piliferum		0.1			0.3		22			5		3			1
Polytrichum strictum	0.8	1.1	0.4	0.4	0.1	56	52	35	50	18	3	4	3	1	3
Ptilium crista-castrensis	0.3		1.4	0.0	0.1	19		6	25	14	3		1	1	3
Sphagnum spp.	68.0	51.4	70.1	69.0	51.2	100	96	100	100	91	3	4	3	2	4

† Tree species cover value is the maximum of tree, sapling or tree seedling cover in the herb and shrub layers.
Notes: Includes species found in at least three plots and more than one replicate in a community type. A blank means that the taxon did not occur in the replicate's plots, 0.0 denotes mean cover > 0 and < 0.05%.

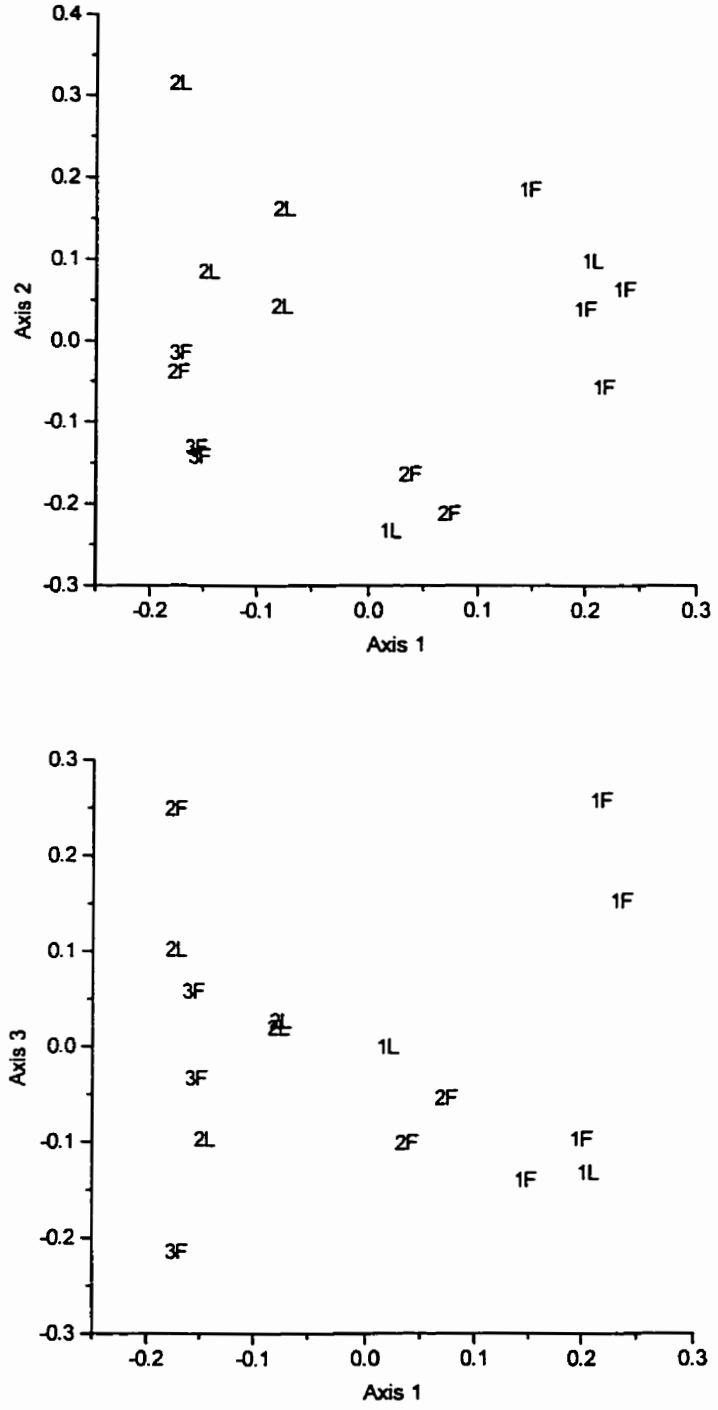


Figure 2.10. Principal coordinates analysis of organic soil replicate means.

Legend: first character is age class, 1 = 13 years, 2 = 37 years, 3 = 65 years; second character is disturbance type, F = fire, L = logging.

vitis-idaea and *Maianthemum canadense* were capable of rapid recovery after both fire and logging. In addition to these taxa, *Trientalis borealis*, *Cornus canadensis*, *Equisetum arvense* had substantially higher frequencies in 13 year old post-logging communities when compared with mature ones. Taxa slow to recover from fire included *Hylocomium splendens* and *Ptilium crista-castrensis*.

Contrary to the self-thinning pattern found on the three mineral soil site types, total density was lower at 37 than at 65 year in post-fire communities. Total frequency was the same in both community types. Other than this difference, 37 year old post-fire communities were similar to mature communities, although some vascular plants performed better than in mature communities. These were *Alnus rugosa*, *Betula glandulosa*, *Equisetum sylvaticum*, *Cornus canadensis*, *Gaultheria hispidula*, *Trientalis borealis*, *Rubus pubescens* and *Calamagrostis canadensis*. Bryophytes and lichens such as *Pleurozium schreberi*, *Dicranum* spp., *Polytrichum commune* and *Cladina rangiferina* performed more poorly.

Interpretation of results was more difficult for 13 year old post-logging communities than the other community types because only two of the cutovers had enough peatland plots to form replicates. These communities were virtually devoid of standing snags. Total tree density and basal area were about half of their levels in similar post-fire communities (400 stems ha^{-1} vs. 888 stems ha^{-1}; Table 2.6). Other than the differences in the tree layer, these communities were similar in appearance to mature ones. When compared with the taxa typically found in all community types on peatlands, 13 year old post-logging communities were also characterized by *Equisetum sylvaticum*, *Aulacomnium palustre* and unidentified mosses but not by *Dicranum* spp.. Substantially higher frequency in this community type when compared with mature communities indicated that overstory removal benefited *Alnus rugosa*, *Vaccinium angustifolium*, *Corylus cornuta*, *Ribes glandulosum*, *Rubus idaeus*, *Equisetum sylvaticum*, *Rubus pubescens*, *Trientalis borealis*, *Viola* spp., *Cornus canadensis*, *Equisetum arvense* and *Calamagrostis canadensis*. The reverse was true for *Smilacina trifolia* and *Hylocomium splendens*.

Recovery in 37 year old post-logging peatland communities was better than similar communities on the other site types. Canopy closure was higher than in mature communities

(Table 2.12) but there was more variability in the height of trees. The response of the understory to greater shading was mixed. Shrub cover was higher than in mature or 13 year old post-logging communities; herb and bryophyte cover was lower (Figure 2.6D). Although total tree frequency was similar in 37 year old post-logging and mature post-fire communities (Table 2.6), total density was slightly lower (3328 stems ha^{-1} vs. 3796 stems ha^{-1}). Higher total basal area combined with total density indicated that basal area per stem was higher in post-logging communities. This suggested that a high proportion of the trees originated from seedlings, saplings and layered branches which survived logging. *Picea mariana*, *Ledum groenlandicum*, *Vaccinium vitis-idaea* and *Carex* spp. characterized the shrub and herb layers. The taxa generally characteristic of the ground layer of peatlands were accompanied by *Aulacomnium palustre* and *Cladina rangiferina* in this community type. When compared with mature communities, *Gaultheria hispidula*, *Vaccinium angustifolium*, *Maianthemum canadense* and *Cornus canadensis* had substantially higher frequency while that of *Kalmia polifolia*, *Smilacina trifolia*, *Polytrichum strictum* and *Hylocomium splendens* was substantially lower.

Melampyrum lineare was the only species to distinguish mature peatland communities by substantially better performance (Table 2.9). Two frequent taxa on peatlands, *Alnus rugosa* and *Salix* spp., had substantially poorer performance in this community type. The post-fire pioneers *Pinus banksiana*, *Populus tremuloides* and *Epilobium angustifolium* performed substantially better in 13 year old post-fire communities. Further support for the sensitivity of *Larix laricina* to fire (Burns and Honkala 1990) was provided by its absence in this community type. *Smilacina trifolia* was not found in 13 year old post-logging communities. *Drosera rotundifolia* almost satisfied the better performance criteria in both of the 13 year old community types. The understories of both post-logging community types were distinguished by a tree species not characteristic of typical mature communities: *Betula papyrifera* at 13 years of age and *Abies balsamea* at 37 years. *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Oxycoccus quadripetalus*, *Picea mariana*, *Pleurozium schreberi*, *Sphagnum* spp. and *Cladonia* spp. were widespread on peatlands.

2.3.3 Overall Patterns of Species Composition

The performance criteria identified species which had a substantial performance difference in one community type compared with the others (Table 2.9). Performance was examined across the site types to determine which species responded in a similar fashion to age and disturbance type. Species which had questionable performance differences were included in this analysis.

Pleurozium schreberi and *Cladonia* spp. were widespread on all site types. On mineral soils, most of the widespread taxa were bryophytes and lichens. *Dicranum* was widespread on all three mineral site types, *Polytrichum juniperinum*, *Cladina mitis* and *C. rangiferina* on outcrops and shallow mineral soils. *Vaccinium myrtilloides* and *Maianthemum canadense* were widespread on shallow and moderately deep mineral soils. Several taxa were widespread only on peatlands (e.g. *Kalmia polifolia*, *Smilacina trifolia*, *Drosera rotundifolia*).

Chimaphila umbellata performed better in mature communities than in the other community types on more than one site type. Better performance at 13 years in post-fire but not post-logging communities indicated that strong *Pinus banksiana*, *Populus tremuloides*, *Epilobium angustifolium*, *Polytrichum juniperinum* and *Polytrichum piliferum* regeneration was stimulated by fire. *Epilobium angustifolium* appeared to require at least moderate levels of moisture and nutrients judging from its increasing frequency in the sequence of 13 year old post-fire communities found on outcrops, shallow and moderately deep mineral soils. *Fragaria virginiana*, *Melampyrum lineare*, *Oryzopsis asperifolia*, *Dicranum* spp., *Pleurozium schreberi* and *Cladina rangiferina* were slow to recover from fire on mineral soils based on their poor performance in 13 year old post-fire communities. The latter three taxa performed poorly despite having high frequencies in all community types and relatively high cover in 37 and 65 year old communities. Their poor performance after 13 years of post-fire recovery was not attributed to the desiccating effects of direct sunlight since similar post-logging communities were more open. Perhaps this was the result of slower growth rates and/ or a competitive disadvantage arising from early post-fire environmental conditions.

Although many species had their best performance in 37 year old post-fire communities, none did so across most of the site types. It was noteworthy that most of the species which distinguished this community type did so by better performance.

Five grasses distinguished 13 year old post-logging communities on mineral soils. All had substantially better performance on shallow soils. *Agropyron trachycaulum* and *Agrostis hyemalis* also did so on outcrops while *Calamagrostis canadensis*, *Danthonia spicata* and *Schizachne purpurascens* also did so on moderately deep soils. *Betula papyrifera* responded well to logging during the early stage of recovery on moderately deep mineral soils and peatlands. An early strong positive response to the effects of logging was carried forward to 37 years for *Vaccinium angustifolium* on the mineral soil site types. Substantially poorer performance by *Picea mariana* on outcrops and shallow mineral soils suggested that it had difficulty regenerating in 13 year old post-logging communities.

Thirty-seven year old post-logging communities were distinguished from the other community types based on the better performance of *Cladina mitis* and *C. rangiferina* on outcrops and shallow mineral soils and by *Vaccinium angustifolium* and *V. vitis-idaea* on shallow and moderately deep mineral soils. *Polytrichum commune* had substantially poorer performance in 37 year old post-logging communities on shallow and moderately deep mineral soils.

The numerous performance differences in 13 and 37 year old post-logging communities (Table 2.9) indicated that logging had short and medium-term effects on species composition. Most species which distinguished 13 year old post-logging communities from the other four community types did so by better performance (29 better compared with 5 poorer performances). Forbs and graminoids benefited most from logging. Post-logging communities had lower canopy closure than post-fire at 13 years. This was the result of poorer tree regeneration and a greater proportion of treeless plots in post-logging communities. In the understory strata, *Pinus banksiana* had substantially lower cover in post- logging than in post-fire communities on all four site types while *Picea mariana* performed more poorly in post-logging communities on outcrops and moderately deep soils. *Betula papyrifera* was the only tree species to perform better in a post-logging community type and it did so on moderately deep soils. Species which performed poorest

in 13 year old post-logging communities were generally species which regenerate well after fire (e.g. *Pinus banksiana*; Rowe 1983).

By 37 years of age, 16 of the 26 performance differences in post-logging relative to post-fire communities were better performances. However, direct comparisons of 37 year old post-fire and post-logging communities portrayed a different picture. This pairwise comparison is more relevant in a detailed comparison of disturbance type effects than when identifying distinguishing or "indicator" species. When direct comparisons of 37 year old post-fire and post-logging communities were made, the number of performance differences increased and the majority were poorer (32 of 54; see Chapter 3). *Vaccinium* species and *Cladina* spp. were the main exceptions to poorer performance in post-logging communities.

These overall species composition patterns were generally evident in the DA of all the plots (Figure 2.5). Discriminant Function 1 distinguished peatland communities from the others based on the performance (in order of declining canonical structure correlation) of *Sphagnum* spp., *Ledum groenlandicum*, *Oxycoccus quadripetalus*, *Chamaedaphne calyculata* and *Kalmia polifolia*. Function 2 separated 13 year old post-fire communities from the rest. *Pinus banksiana* and *Polytrichum juniperinum* had their highest positive structure correlations with this community type while *Dicranum* spp. had its highest negative correlation with it. Post-logging communities were separated from post-fire on the third and fourth discriminant functions. *Rosa acicularis*, *Linnaea borealis*, *Fragaria virginiana* and *Goodyera repens* had high canonical structure correlations with post-fire communities and *Corylus cornuta*, *Vaccinium angustifolium*, *V. vitis-idaea*, *Petasites palmatus*, *Schizachne purpurascens* and *Cladina stellaris* had high structure correlations with post-logging communities on these two discriminant functions.

2.4 Discussion

Communities were classified into types based on selected causal factors (Figure 2.1) rather than on vegetation. By presenting results in this manner, the focus is implicitly on factors influencing spatial patterns at the landscape level and the vegetation dynamics typical for a site type. The results provide community level generalizations and cannot predict what will happen on a particular site. A finer scale examination which relates the individual components of the causal variables to each other would be required to account for between site variability.

2.4.1 Influence of Site Type

Site type had the strongest influence on species composition followed by disturbance by wildfire. Age and disturbance either by wildfire or logging followed these but their rank order was ambiguous since it differed in the correspondence analysis (CA) and discriminant analysis (DA). Although the sampling design supported inferences about the region, a broad generalization about the relative importance of site type must be qualified for several reasons. First, the contrasts expected to produce the greatest age and disturbance type differences in species composition were missing (i.e. one month to one year old post-fire communities vs. either mature or 13 year old post-logging communities; Carleton *et al.* 1985). Second, logging can have large impacts on species composition when it occurs on more eutrophic sites or uses methods which create more ground disturbance than found in this study (Abrams *et al.* 1985; Brumelis and Carleton 1988, 1989). The relative influence of site type, age and disturbance on species composition might have changed had these situations been included. Third, disturbance type can interact with site type. For example, harvesting machinery generally impacts more on humid, fine textured soils than on drier or coarser deposits when the ground is not frozen.

Even though a broad generalization about the relative influence of these factors was not possible, the substantial effect of site type was clear. Research elsewhere indicates that site type has an overriding influence on species composition at the landscape scale albeit with regional differences in the species involved (Mueller-Dombois 1964; Carleton and Maycock 1978; Jeglum 1973; Kenkel 1986; Bergeron and Dubuc 1989; Harvey and Bergeron 1989; Jeglum 1992; La Roi

1992; Harvey *et al.* 1995). This emphasizes the importance of control for site type in community level vegetation studies so that its effects are not confounded with other factors of interest.

Of the variables used in the site type classification, moisture regime was most highly correlated with site type and species composition. Moisture regime appears to be an effective way to distinguish vegetation types at the landscape scale (Bergeron and Bouchard 1983; Kenkel 1986). Nutrient and light intensity gradients become influential when the focus narrows to variability among sites with a similar moisture regime (Kenkel 1987; Brumelis and Carleton 1989; Jeglum and He 1995) or to temporal changes on particular sites (Carroll and Bliss 1982).

The strongest differences in species composition occurred at the extremes of the moisture regime gradient as represented by peatlands and outcrops. Peatland communities were the most distinct having species that were either exclusive to them or with much higher cover than on the other site types. A wet moisture regime creates an anaerobic environment which retards decomposition and leads to the accumulation of organic material (Laiho 1997). Concomitant invasion and spread of *Sphagnum* spp. increases soil moisture further and lowers pH (Jeglum 1973). As these conditions become more extreme, growth and species richness decline (Jeglum and He 1995). Brumelis and Carleton (1989) list numerous adaptations which enable species to grow in oligotrophic peatlands. Examples include efficient translocation, evergreen leaves and insectivory. All are strategies to cope with low nutrient uptake but do not specify the source of limitation. Low pH and aeration seem to be the ultimate controlling factors (Lieffers and Rothwell 1987) because they either inhibit plant nutrient uptake (Heinselman 1963; Jeglum and He 1995) or they reduce nutrient availability directly or indirectly through reduced soil temperature, microbial activity and rooting zone volume. Nutrient uptake may be more limiting than availability since the latter is generally adequate for plant growth in aerated peatland soils due to their high cation exchange capacity (Brady 1974). The high frequency and peak abundance of *Picea mariana*, *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Oxycoccus quadripetalus*, *Smilacina trifolia*, *Polytrichum strictum* and *Sphagnum* spp. on peatlands indicated that they are well adapted to these conditions.

The xeric end of the moisture gradient was typically represented by outcrops, coarse-textured mineral soils or soils with a high proportion of coarse fragments. Exceptions occurred when these sites had a high water table or were in a toe-slope position. Species which characterized xeric sites included *Pinus banksiana*, *Polytrichum juniperinum*, *P. piliferum*, *Cladina mitis* and *Woodsia ilvensis*. *Pinus banksiana* usually avoids soil water stress by producing a taproot to access the water table and by completing most of its growth and carbon storage during the first six weeks after the spring thaw (Sims *et al.* 1990) when soil moisture is usually adequate. Bryophytes and lichens are generally subject to greater water stress than vascular plants because they derive most or all of their water from precipitation and few have effective mechanisms to minimize water loss during photosynthesis (Crites and Dale 1995). Some do well in xeric conditions (e.g. *Cladina mitis* and *Polytrichum juniperinum*) because they become dormant when water stressed (Hale 1983; Vitt *et al.* 1988).

A mesic moisture regime reduces the need for adaptations to cope with water stress and thereby accommodates species which have higher maximum growth rates or tolerate low light intensity (Smith and Huston 1989). Thus, it increases the number of species which can occur on a site. This is expected to lead to higher species density and greater heterogeneity in species composition within and between sites (Jeglum 1972; Smith and Huston 1989; Harvey *et al.* 1995). In this study, a superficial indication of this was provided by the number of characteristic vascular plants and by *Abies balsamea*, *Picea mariana* and *Populus tremuloides* tree frequencies. All these measures increased on the moisture gradient represented by outcrops, shallow and moderately deep mineral soils.

Smith and Huston (1989) provide a potential explanation for the strong influence of site conditions on species composition. They argue that physiological mechanisms prevent most vascular plants from being simultaneously adapted to grow rapidly at 1) both high and low levels of light intensity or water or 2) when water and light intensity are both at low levels. Adaptations which permit a plant to cope with water or light stress generally reduce its maximum growth rate, maximum size and maximum age. These adaptations stem from tradeoffs between water loss and CO_2 uptake through stomata and between resource allocation to above and below-ground

growth. Their model can include nutrients but Smith and Huston (1989) confine themselves to the influence of water and light intensity because water and light intensity encompass a fundamental physiological tradeoff and their range of variability in space and time is greater than that of nutrients. The theoretical implications of these tradeoffs are consistent with observations. For example, species often have similar physiological but different ecological optima on resource gradients. Differences in maximum growth rates can lead to competitive advantages and differentiation along resource gradients. In addition, simulations based on these physiological tradeoffs generate plausible spatial and temporal patterns of species composition (Smith and Huston 1989). Spatial patterns of species dominance result primarily from allogenic differences in water availability while temporal changes are influenced by autogenic changes in light intensity.

Water availability (i.e. moisture regime) is expected to have a greater influence than light intensity on the spatial pattern of species composition in regions dominated by frequent disturbance that kills aboveground vegetation. In the boreal forest, fire usually kills aboveground foliage (Heinselman 1981; Cayford and McRae 1983) so that high light intensity levels are found on all sites within a burn. The range of moisture regimes found on the post-fire landscape will be much greater than that of light. A longer moisture regime gradient can incorporate the ecological optima of more species and thereby have a greater initial influence on the spatial pattern of vegetation. This initial influence can become a long-term one because trees are long-lived and overstory composition influences understory composition (Rowe 1956). As vegetation develops and creates shade, some understory species are inhibited while others are facilitated. Thus, the influence of light intensity on species composition is primarily temporal within a site (Smith and Huston 1989; Peet 1992).

Consistent with this theory, moisture regime was highly correlated with the strong separation of community types into site types by CA and DA. We cannot say that soil moisture was the sole or major cause of this for two reasons. First, a measure of nutrient regime was not included. Second, moisture and nutrient availability are correlated with increasing soil depth in mineral soils.

The influence of site type was manifested primarily in terms of frequency and cover/ basal area rather than the limitation of species to particular site types. Other than the small group of

species confined to peatlands, most species characteristic of at least one community type within a site type also occurred on the other site types. Two factors may account for the limited effect of site type on floristics. First, boreal plants can tolerate a wide range of site conditions, light intensities and disturbance characteristics (Carleton and Maycock 1981). This could be a consequence of adaptation to frequent, catastrophic disturbance by fire and the need to tolerate large changes in light intensity and other conditions between fire events (Shafi and Yarranton 1973; Johnson 1979; Rowe 1983). Second, within a community, habitat heterogeneity provides favorable microsites for the persistence of some species (De Grandpré *et al.* 1993). For example, *Cladina rangiferina* was found on exposed *Sphagnum* hummocks in peatlands.

2.4.2 Influence of Age and Disturbance Type

Age and disturbance are fundamentally different influences in that age is a continuous process and primarily autogenic while disturbance is allogenic, discrete and periodic (Peet 1992). Despite this, ordination results indicated that the effects of age and disturbance cannot be easily separated. Disturbances disrupt or reinitiate succession and this is often revealed indirectly over time. The difficulties involved in untangling the indirect effects of disturbance from temporal change in this study will become apparent below. To a large degree they stem from the absence of a one year old age class which could indicate differences in the direct effects of wildfire and logging.

On each site type, mature post-fire communities were assumed to represent the typical pre-disturbance state and the state to which post-fire communities were recovering. The climate change which occurred in the 52 year time span between the initiation of the youngest and oldest age classes was not expected to be long enough to produce a substantial change in what was typical of a site type and age class combination. Frelich and Reich (1995) provide some support for this assumption based on results from the Boundary Waters Canoe Area, Minnesota. Aerial photos covering a 57 year time span were compared with a chronosequence of stands ranging in age from 15 to 190 years. Successional pathways derived from historical stand information and chronosequences were the same.

Temporal differences in species composition were manifested primarily as changes in the cover/ basal area and frequency of species which persist throughout most of the successional cycle. Shrub stage (13 year old) post-fire communities differed dramatically from mature communities and reflected the residual effects of fire. A tree canopy was absent. The understory cover of post-fire thrivers such as *Pinus banksiana*, *Populus tremuloides*, *Epilobium angustifolium*, *Polytrichum juniperinum* and *P. piliferum* was substantially higher in shrub stage than mature post-fire communities; the reverse was true for *Dicranum* spp., *Pleurozium schreberi*, *Cladina mitis* and *C. rangiferina*. Rowe (1983) lists a number of species which are typically absent in young communities because they are fire intolerant. The low frequencies of *Abies balsamea*, *Picea glauca* and *Linnaea borealis* at the shrub stage corroborated Rowe's view that they are fire intolerant but do not depend on the conditions created by a mature forest. Species which depend on the conditions created by a mature forest were not encountered in the 13 year old replicates (i.e. *Chimaphila umbellata*, *Goodyera repens*, *Hylocomium splendens* and *Ptilium crista-castrensis*).

Post-fire recovery between 13 and 37 years was relatively rapid. By 37 years, the frequencies and/ or cover of most post-fire thrivers, and species slow to recover from fire, were approaching mature levels. A number of species had their best performance in 37 year old post-fire communities but only *Rubus pubescens* did so on more than one site type. This demonstrates that species performance is affected by the interaction between life history strategies and site conditions. On mineral soils, recovery was slowest for *Chimaphila umbellata*, *Lycopodium obscurum*, *Goodyera repens* and *Ptilium crista-castrensis*.

These results support the consensus in the literature that post-fire vegetation dynamics generally involve immediate *in situ* regeneration of most pre-disturbance vascular plants, the rapid growth and demise of colonizing herbaceous species and gradual change in bryophyte and lichen floristics (Noble et. al 1977; Black and Bliss 1978; Ohmann and Grigal 1979; Outcalt and White 1981; Rowe 1983; Viereck 1983; Cogbill 1985; Foster 1985; Brumelis and Carleton 1989; Halpern 1989; Stelfox 1995). Deviations occur due to variability in fire intensity and severity. Although most pre-disturbance species regenerate quickly *in situ*, differences between pre- and post-fire species

composition are conspicuous due to the growth of herbs which thrive shortly after fire (Cogbill 1985) and the slow recovery of species removed by fire. Some post-fire thrivers such as *Epilobium angustifolium* are present prior to fire but shade suppressed while others colonize the community. Many colonizers are shade intolerant and either reproduce entirely from the seed bank or invade rapidly from outside the burn. The cover of herbaceous post-fire thrivers gradually declines as the slower growing *in situ* regenerators become taller and expand their cover. The shrub stage is reached about 10 years after a fire. Most herbaceous post-fire thrivers have disappeared leaving a community that is floristically similar to the one there prior to fire (Shafi and Yarranton 1973; Ohmann and Grigal 1979). As evidence of this, some species which are found in the study area and characteristic of the establishment stage (Black and Bliss 1978; Rowe 1983) were not encountered in at least three plots. They were *Geranium bicknellii* and *Marchantia polymorpha*. The effects on many other bryophytes or lichens could not be assessed because identification beyond growth form was undertaken only for those species easily identified in the field.

Some evidence was found for the post-fire moss and lichen succession reported by others (Black and Bliss 1978; Clayden and Bouchard 1983; Foster 1985). *Marchantia polymorpha* is typically confined to the establishment stage. It was not encountered in any age class presumably because shading and/ or competition had eliminated them by the shrub stage. Mid to late successional species (i.e. *Ptilium crista-castrensis*, *Hylocomium splendens* and *Cladina stellaris*) were rarely encountered at the shrub stage. Most other identified mosses and lichens were frequent in all age classes but had large changes in cover.

If succession is viewed in terms of changes in peak cover rather than floristics (Clayden and Bouchard 1983), then a clear post-fire succession of mosses and lichens was observed between 13 and 65 years The peak cover sequence began with *Polytrichum juniperinum*, *P. piliferum* and *Cladonia* spp. at 13 years and then proceeded to *Pleurozium schreberi*, *Cladina mitis* and *C. rangiferina* at 37 years and ended with *Dicranum* spp., *Ptilium crista-castrensis*, *Hylocomium splendens* and *Cladina stellaris* at maturity.

Rowe (1983) describes attributes that promote species survival in a region subject to frequent disturbance by fire. Shade intolerant trees such as *Pinus banksiana* and *Populus tremuloides* are capable of rapid growth, early and prolific seed production and have a long life span relative to the fire cycle (Burns and Honkala 1990; Bell 1991). *Populus tremuloides* clone ramets have the ability to sucker in the gap created by the death of a parent. *Pinus banksiana* and some other shade intolerant species persist through serotinous cones or in the seedbank where they are protected from the heat of the fire. Many boreal plants regenerate quickly after fire from underground organs and remain part of the community in a shade-suppressed state until the next fire (e.g. *Vaccinium angustifolium*, *Epilobium angustifolium*). Still others invade rapidly from unburned patches or other favorable areas. Unburned outcrops often provide refugia for post-fire invaders since many are xerophytes (Rowe 1983).

Post-fire invaders often are present only in the propagule bank of (Rydgren and Hestmark 1997) or absent in a mature, closed community. Thus, they are the species most likely to depend on fire's effects to maintain their distribution on the landscape. These species are weak competitors and/ or shade intolerant. *Marchantia polymorpha*, *Ceratodon purpureus* and *Polytrichum piliferum* are among this group (Rowe 1983). *Marchantia polymorpha* could be particularly sensitive to fire suppression. It was not encountered in any of our communities and its high moisture requirement (Klinka *et al.* 1989) excludes outcrops as potential refugia. There may be other species dependent on fire in the study area but the absence of an establishment stage age class precludes listing them here.

Post-fire thrivers are expected to have their abundance affected by unmitigated fire suppression or logging. This will affect ecosystem diversity if it causes communities to be classified into a different vegetation type. Ordination scattergrams (Figure 2.7 to Figure 2.10) suggested that differences in the species composition of comparable post-fire and post-logging communities were large enough for them to be classified differently. *Pinus banksiana*, *Populus tremuloides*, *Epilobium angustifolium*, *Polytrichum juniperinum* and *P. piliferum* were among the post-fire invaders that contributed to the separation of post-fire and post-logging communities. *Pinus banksiana* regeneration is poor beyond the first few years after fire as dispersal becomes

limited and favorable seedbeds disappear (Cayford and McRae 1983; Bell 1991). Seedlings which establish under a closed canopy rarely survive due to shade intolerance (Bell 1991). Notwithstanding its inability to regenerate under a closed canopy, *Pinus banksiana* has generally maintained a presence in the community due to a life span longer than the mean fire return interval. Fire suppression will have the same effect as lengthening the fire return interval and thereby reduce the distribution of *P. banksiana* and other post-fire thrivers (Bergeron and Dubuc 1989; Frelich and Reich 1995).

Post-logging vegetation dynamics can be quite variable depending on factors such as logging method, proportion of biomass removed and season of cut. In general, winter logging of softwood stands on non-eutrophic sites results in minimal ground disturbance, limited mortality of understory vegetation and little change in site availability (Rowe 1983; Zasada 1986; Brumelis and Carleton 1989). Species that can be eliminated from a site by winter logging include commercially valuable trees and certain bryophytes and lichens. Some bryophytes and lichens depend on an old forest for the microclimatic conditions or the range of woody material decay stages found in it (Crites and Dale 1995). Logging may eliminate such species. With the possible exception of the sensitive species, the initial effect of winter logging on understory floristics is relatively small (Noble *et al.* 1977; Outcalt and White 1981; Abrams et. al 1985; Brumelis and Carleton 1988, 1989; Walsh and Krishka 1991; Johnston and Elliott 1995). The outcome can be quite different either on eutrophic sites where one or more residual species respond strongly to overstory removal and quickly dominate the community (Abrams *et al.* 1985; Brumelis and Carleton 1989) or where the establishment of aggressive invaders is facilitated by disturbance of the ground layer (Brumelis and Carleton 1988, 1989; Harvey *et al.* 1995).

Further evidence that winter logging has limited short-term effects on vascular understory floristics was found in this study. *Smilacina trifolia* was the only species found in mature and 13 year old post-fire communities but not in 13 year old post-logging communities. This occurred on peatlands. A small proportion of the species that characterize mature communities demonstrated sensitivity to overstory removal by substantial reductions or increases in their frequency in 13 year old post-logging communities. Several herbs and *Polytrichum juniperinum* had strong positive

frequency responses while *Linnaea borealis* generally responded negatively. On moderately deep mineral soils, several shrubs also had strong frequency responses to overstory removal ostensibly due to better moisture and nutrient availability than on more shallow soils.

Although logging had little effect on floristics over the short-term, differences in cover were substantial. Poor tree regeneration in post-logging communities resulted in higher understory light. Species tolerant of high light intensity and not requiring fire for establishment had their best performance in 13 year old post-logging communities. Most of these were forbs and graminoids. Shrub cover also increased substantially in response to overstory removal on all the site types but this increase did not persist to 37 years for most species. The cover increase relative to 65 year old post-fire communities was maintained for *Vaccinium angustifolium* and *V. myrtilloides* on mineral soils and *Ledum groenlandicum* and *Alnus rugosa* on peatlands.

Logging had substantial medium-term effects on species composition as evidenced by differences in comparable 37 year old post-fire and post-logging communities. The most conspicuous differences occurred on mineral soils. Post-fire pioneers such as *Pinus banksiana*, *Picea mariana* and *Polytrichum* spp. performed more poorly in post-logging communities while *Vaccinium* spp. and *Cladina* spp. performed better than in post-fire communities. Disturbance type comparisons of species composition and their implications for community resilience are analyzed in more detail in Chapter 3.

2.4.3 Implications for the Study of Vegetation Dynamics and Forest Management

Stochastic factors such as fire severity (Bonan and Shugart 1989) or post-disturbance weather (Cayford and McRae 1983) can have a substantial influence on vegetation (Figure 2.1). Walker and Chapin (1987) suggest that the relative importance of stochastic factors can be assessed by examination of between replicate variability of communities established on similar substrate. Such variability was apparent in the ordination scattergrams (Figure 2.7 - Figure 2.10). Most of the age class, site type and disturbance type groupings had one of its replicates separated from the others. This emphasizes the importance of adequate replication to provide statistical control for stochastic factors.

The strong association of species composition with site type (Mueller-Dombois 1964; Carleton and Maycock 1978; Kenkel 1986; Bergeron and Dubuc 1989; Harvey and Bergeron 1989; Jeglum 1992; Harvey *et al.* 1995) tempts one to generalize that site conditions have the greatest influence on species composition in the boreal forest. A determination of the relative importance of causal factors can only be accomplished by sampling the range of levels of all the causal factors in a region (Bergeron and Bouchard 1983; Jeglum and He 1995). Even if this could be accomplished, broad generalizations would be complicated because 1) vegetation dynamics are a function of geographic location (many of the ultimate causal factors identified in the theoretical framework are a function of it); 2) the relative influence of factors changes with the scale of analysis; 3) stochastic factors limit the predictability of successional pathways (Walker and Chapin 1987).

Recent literature reviews have concluded that the study of vegetation dynamics requires a general theory or framework that focuses on mechanisms rather than describing patterns (Peet 1992; McCook 1994). None of the models currently in use can serve as a general model that can apply to all stages of succession or for all species within a succession (Finegan 1984; McCook 1994; Miles 1987; Pickett *et al.* 1987; Walker and Chapin 1987). The theoretical framework for vegetation dynamics used in this study is a crude approximation of a framework. It was constructed in the context of Levin's (1989, p. 244) statement that "Theory without data is sterile, while data without theory is uninterpretable." The theoretical framework was useful in this study's design, execution and analysis.

As the scale of human disturbance manifested through global change and direct activities such as logging increases, so does the need for improved understanding of vegetation dynamics. A general model of vegetation dynamics is a means to enhance this through the synthesis of descriptive and theoretical work into testable hypotheses. Once validated for a particular region, the model can help us predict the effects of human activities such as fire suppression and logging and how they might be modified to mimic nature's effects on ecosystems.

The importance of disturbance type is a case in point. Some of the species that characterize the boreal forest apparently require some of fire's effects to maintain their natural distribution on the landscape (Bergeron and Dubuc 1989; Frelich and Reich 1995). This is because they are

shade intolerant, they require a mineral seedbed, their germination/ dispersal is stimulated by high temperatures and/ or they are weak competitors (Cayford and McRae 1983; Rowe 1983). *Pinus banksiana* is a good example of a species affected by all these conditions (Cayford and McRae 1983). Understanding the implications of this for landscape patterns is becoming increasingly germane as the extent of fire suppression and logging expands. Effects on species distribution or abundance will affect the goals of sustainable forest management related to the conservation of ecosystem and species diversity (CCFM 1995). These results suggest that unmitigated fire suppression or logging could limit the distribution of some species and reduce the abundance of others.

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Chapter
3
Resilience of Naturally Regenerating Plant Communities to Wildfire and Logging

3.1 Introduction

Although some agricultural systems demonstrate that intensive management can sustain an ecosystem in a state far outside its natural range of variability (Allen and Hoekstra 1994), forest managers have not attempted to do this on a widespread basis in the Canadian boreal forest. In fact, recent policy documents from the Canadian Council of Forest Ministers ({CCFM} 1995) use natural conditions to provide targets for sustainable forest management. Two of the criteria set out by the CCFM (1995) are the conservation of biological diversity and the maintenance of ecosystem condition and productivity; both of which are the outcomes of ecological patterns and processes (Urban 1994). An indication that processes have not been impaired by human disturbance is that relevant indicators are restored to levels similar to those that eventually occur after natural disturbance. Because plants are synthetic indicators of environmental conditions (Gauch 1982; Klinka *et al.* 1989), plant community resilience can be used as one indicator that biodiversity is conserved at the community level and that site scale ecological processes have not been adversely affected by disturbance (Westman 1978).

The terminology applied to resilience and its components is not consistent (Westman 1978). Halpern (1988) defines resilience as the rate, manner or degree to which initial community characteristics are restored following displacement and resistance as the extent to which a community resists change by disturbance. Resilience has typically been assessed in terms of the recovery of communities on particular sites or within particular disturbance events over time (cf. Westman and O'Leary 1986; Halpern 1988). Westman (1978) notes that complete recovery to the pre-disturbance species composition is unrealistic due to natural and sampling variability. Stochastic events and the interaction of many factors lead to the potential for multiple

successional pathways on a given site (Abrams *et al.* 1985; Bergeron and Dubuc 1989; Fastie 1995; Harvey *et al.* 1995). Case studies have dealt with the variability of particular sites in three ways. In the first, it is concluded that a community has recovered sufficiently when its mature stage and pre-disturbance species composition have a dissimilarity of less than 15% (Westman 1978). Second, by using the variability of pre-disturbance sample plots to define a 95% confidence recovery cube in three-dimensional ordination space (Bloom 1980). Halpern (1988) extracts the stochastic component of a disturbance event by conducting separate analyses of two watersheds and then comparing patterns.

The case study approach can satisfactorily elucidate the resilience of a community to disturbance at a particular site or by a particular event but the lack of replication precludes generalizations about resilience to particular types of disturbance such as wildfire or logging. An alternative, complementary approach would incorporate natural variability by defining typical community conditions at the landscape level. In a region with homogenous climate, it is thought that a statistically stable mixture of vegetation types occurs on the natural landscape. This is the result of the interaction between stochastic events (e.g. fire severity, post-disturbance weather) and deterministic influences (Urban 1994; Frelich and Reich 1995). Life history strategy, interspecific interactions, distance from propagule sources and site conditions are among the deterministic influences which limit the number of potential successional pathways (Steinhorst *et al.* 1985; Halpern 1988, 1989; Bergeron and Dubuc 1989; Smith and Huston 1989; Fulton 1993; Fastie 1995). The natural range of community variability produced is relatively stable; it shifts at the pace of global change.

Natural variability can be used to establish a regional benchmark for community resilience. When applied to forest ecosystems where temporal change is largely influenced by the dynamics of long-lived species (Peet 1992), it is suggested that a community is resilient to a particular type of disturbance when its species composition regenerates to a mature state typical for the site type within an appropriate length of time. A community has reached a mature state when it has a physiognomy typical for the dominant long-lived pioneer species, site type and region and when changes in species composition primarily involve small changes in abundance rather than in the

species present. An appropriate length of time is determined by the natural vegetation dynamics of the region. Post-fire dynamics can provide a model for natural recovery in the boreal forest because boreal plant species are adapted to frequent, catastrophic disturbance by fire (Rowe 1983). On sites with a mean fire return interval of about 100 years, post-fire recovery to a typical mature state is generally reached between 50 and 100 years (Ahlgren 1974; van Cleve and Viereck 1981; Abrams *et al.* 1985; Carleton and Wannamaker 1987; Kenkel *et al.* 1997).

This approach eliminates the need to assume that pre-disturbance vegetation, site conditions and post-disturbance influences are uniform among sites. However, like long-term permanent plot studies, it does not eliminate the assumption that climate and other factors which influence vegetation dynamics have not undergone ecologically significant changes during the period. Nor does it eliminate the potential bias introduced by the non-random location of treatments.

Post-logging recovery is likely to occur at rates and along pathways that differ from those after fire since these types of disturbance differ in their direct effects (Zasada 1986). Research indicates that logging without substantial ground disturbance initially alters understory species composition less than a fire that kills all above-ground parts (Ellis and Mattice 1974; Noble *et al.* 1977; Brumelis and Carleton 1988, 1989; Walsh and Krishka 1991; Harvey *et al.* 1995; Johnston and Elliott 1996). Apparently, this is due to the less severe direct effects of logging on vegetation and to its failure to create conditions suitable for the establishment of post-fire pioneers.

Although communities may exhibit higher resistance to logging than to fire, this does not ensure higher resilience. The complexity of ecosystem interactions coupled with the differences in the direct effects of fire and logging can lead to medium and long-term disturbance type differences in ecosystem functions and the rates of processes (Fastie 1995). Community resilience may then be delayed or even precluded. Little is known about community resilience to logging in the boreal forest. Only one study (Brumelis and Carleton 1988, 1989) directly compared post-fire and post-logging communities over a recovery period longer than 15 years and it was confined to peatland sites.

Concerns about the resilience of communities to certain types of logging are raised by a number of studies. They indicate that post-logging conversion to a different forest cover type is

common (Jeglum 1983; Brumelis and Carleton 1988, 1989; Carleton and MacLellan 1994) and that conversion to a shrubland or grassland is possible (Abrams *et al.* 1985). The relative contributions to these conversions by immediate, direct effects and medium-term, indirect effects such as reduced nutrient availability has not been determined for boreal post-logging communities. Such a distinction should be made since medium and long-term impacts on ecological processes are not likely to be mitigated by post- logging regeneration treatments such as planting or vegetation management.

This chapter compares the resilience of naturally regenerating plant communities to wildfire and winter logging in the southern part of the central Canadian boreal forest. Resilience was assessed in terms of the degree to which the species composition of communities at the shrub and canopy closure stages (13 and 37 years old) had recovered to the typical mature state represented by 65 year old post-fire communities. Sixty-five year old post-logging communities were not included because of the great dissimilarities in the logging methods in use at that time and in the surficial geology of the areas cut. Disturbance type and age class differences in species composition were used to suggest mechanisms responsible for the differences.

3.2 Methods

3.2.1 Sampling

Sampling methods were described in Chapter 2.

3.2.2 Data Analysis

The comparability of site conditions in burns and cutovers from the same age class was assessed by applying mixed model ANOVA (replicate as a random effect, α = 5%) to site variables. The variables examined were slope, position, slope length, upslope length, aspect (degrees from north), depth of mineral soil, moisture regime, percent stoniness, depth to bedrock and depth to gleying. Several of these complicated data analysis when their values exceeded the depth of the soil section. This occurred for depth to distinct mottling and depth to water table on peatland and moderately deep mineral soils and depth to bedrock and thickness of organic material on peatlands. Since there is no way of determining how much the value of the "depth to" variable exceeded 100 cm, an arbitrary value of 150 was used in these situations.

Overstory and understory resilience were assessed by comparing the species composition (species present and their cover or basal area) of 13 and 37 year old post-fire and post-logging communities with that of 65 year old post-fire communities. Others have measured community resilience either as the Euclidean distance between points in two or three-dimensional ordination space (Halpern 1988) or by direct application of a resemblance measure to species composition data (Westman and O'Leary 1986; Malanson and Trabaud 1987). The latter approach was taken so as to incorporate all the available species information. Percentage difference where k is species number and i and j are treatment numbers), preceded by a square root transformation, was applied to disturbance type means for percent cover of understory species. A review of the relevant literature (cf. Campbell 1978; van der Maarel 1979; Hadju 1981; Greig-Smith 1983; Legendre and Legendre 1983; Faith *et al.* 1987) suggested that this combination was appropriate for a comparison of treatment effects. Of particular importance was the way percentage difference preceded by a square root transformation represented abundant species relative to scarce ones,

fidelity to one treatment, joint absences, equal abundances, plot abundance and different absolute abundances when relative abundances are the same.

Successional pathways were thus represented as successive changes in "ecological distance" from the typical mature state (i.e. 65 year old post-fire communities). Post-fire successional pathways were extended to 65 years since the dissimilarity of these communities to the typical mature state becomes equal to 0 in a typical successional cycle.

The significance of disturbance type differences in the overstory and understory of 13 and 37 year old communities was tested by randomization (Manly 1991; Good 1994). Randomization testing reduced the number of assumptions implicit in significance tests and avoided the variable reduction problem imposed by MANOVA. The test statistic used was an equivalent of the F-statistic (Good 1994) calculated following 1,000 randomizations.

$$\text{Randomization test statistic} = \sum_{j=1}^{k}\sum_{i=1}^{T} \text{var}(A_{jN_1}, A_{jN_2} \ldots A_{jN_i}) * (N_i - 1)$$

where A = abundance of species i, k = number of species, T = number of treatments, N_i = number of replicates in treatment i.

Tests of disturbance type differences in species composition were based on replicate means of square root transformed basal area for trees and percent cover for understory species. Results were corroborated with scattergrams from principal coordinates analyses using percentage difference which was applied to replicate means of square root transformed cover data.

Interpretation of disturbance type differences in species composition was assisted by the performance criteria outlined in Chapter 2 methods. The criteria were applied to pairwise comparisons of post-fire and post-logging communities by site type and age class.

3.3 Results

3.3.1 Comparison of Site Conditions in Burns and Cutovers

In the 13 year old age class, significant differences were not detected for any of the site variables which might indicate that a causal factor other than disturbance type might be responsible for observed differences. In fact, most comparisons had high probabilities (> 0.50) that a significant difference did not exist. Caution must be exercised when interpreting these results since, in a number of cases, they were derived from only two replicates[6] and statisticai power was low.

In the 37 year old age class, the only outcrop site variable which had a significant disturbance type difference was upslope length. It had a mean of 3.4 m in post-fire communities compared with 1.7 m in post-logging communities. The main influence of upslope length is on the amount of water which flows through the plot during and after a rainfall. On outcrops, soils are so thin and patchy that the amount of water percolating through a plot was expected to have a limited effect unless it was in a toe position. This small difference in length was not considered to be ecologically significant especially when no difference was observed in any other site variable.

Shallow soils showed significant differences for aspect and depth of mineral and organic layers in the soil section. Mean aspect in post-fire communities was east whereas it was south-southeast in post-logging communities. It is questionable whether this difference was ecologically significant, especially when there was no difference in slope and mean percent slope was only 7%.

Differences in the depth of soil can be ecologically important, especially when it occurs together with differences in water availability because one of the main effects of shallow soil is a limitation on moisture availability. However, the difference in mean depth of mineral and organic soil was only 4 cm. This small difference in depth, when coupled with no significant difference in

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[6] There are a number of site variables for which the number of replicates used in the analysis is less than that used in the corresponding vegetation analysis. This occurred because data were not collected for these variables during the first field season. The variables include percent canopy closure, slope length, upslope length, drainage regime and percent stoniness in soil profile.

moisture regime or any other edaphic variable, was not considered to be ecologically significant.

3.3.2 Trees

Species that occurred as trees (CBH > 10 cm) in at least 4 plots included *Pinus banksiana* and *Picea mariana* on all site types, *Populus tremuloides* on the upland site types and *Larix laricina* on peatlands (Table 3.1).

Overstories were more resilient to fire than to logging at 13 and 37 years (Figure 3.1). Significance tests were not performed on 13 year old overstory composition since there were substantial disturbance type differences in the nature of the overstory. Most saplings in post-fire communities were entering the tree layer at this age while basal area in post-logging communities was dominated by residual trees.

The disturbance type difference in overstory composition in 37 year old communities (Table 3.1) was significant for communities on shallow ($P = 0.04$) and moderately deep mineral soils ($P = 0.03$). *Pinus banksiana* basal area, density and frequency were substantially lower in post-logging communities on these site types. For the four conifer species, densities were generally lower and basal area per tree higher in post-logging than in post-fire communities. Conifer basal area in post-logging communities was dominated by residuals suggesting that conifer regeneration after logging was poor on all site types. On logged peatlands, the *Picea mariana* stems and layers which survived logging led to higher basal areas, densities and frequencies in 37 year old post-logging than in 37 and 65 year old post-fire communities. On shallow and moderately deep mineral soils, poorer conifer regeneration was accompanied by higher *Populus tremuloides* basal area, density and frequency. Post-logging communities were more open than post-fire on the upland site types and less open on peatlands (Chapter 2).

Table 3.1. Tree basal area, density and frequency for 65 and 37 year old communities.

Site Type:	Outcrop			Shallow**			Moderately Deep**			Peatland		
Age:	65	37	37	65	37	37	65	37	37	65	37	37
Disturbance type:	Fire	Fire	Log	Fire	Fire	Log	Fire	Fire	Log	Fire	Fire	Log
Basal Area (m^2/ ha)												
N:	4	4	4	4	4	4	4	4	4	3	3	4
Abies balsamea	0.0	0.0	0.0	0.0	0.0	0.2	0.3	0.5	1.0	0.0	0.0	0.2
Betula papyrifera	0.0	0.0	0.0	0.2	0.1	0.1	0.2	0.3	0.3	0.0	0.0	0.5
Larix laricina	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.3	1.5
Picea glauca	0.0	0.0	0.0	0.3	0.1	0.1	1.3	0.2	0.6	0.0	0.0	0.0
Picea mariana	1.5	0.1	0.6	3.0	1.9	3.9	10.8	7.6	5.0	10.9	10.0	18.7
Pinus banksiana	1.2	5.2	2.8	23.4	14.4	4.6	21.2	17.6	5.5	4.4	2.0	2.3
Populus tremuloides	0.8	0.0	0.0	1.7	0.0	1.0	4.0	1.4	3.1	0.7	0.0	0.0
All Trees	3.5	5.3	3.5	28.7	16.5	9.9	37.7	27.6	15.4	17.0	12.3	23.3
Mean/ Tree (cm^2/ tree)	72.5	78.9	166.3	108.7	51.6	103.3	105.1	54.7	143.9	44.8	46.1	70.0
Density (stems/ ha)												
N:	4	4	4	4	4	4	4	4	4	3	3	4
Abies balsamea	0	0	0	0	0	120	120	43	74	0	0	25
Betula papyrifera	0	0	0	33	33	29	53	29	33	0	0	133
Larix laricina	0	0	0	0	0	0	0	0	0	196	116	180
Picea glauca	0	0	0	17	17	14	97	60	17	0	0	0
Picea mariana	267	53	74	627	687	394	1810	1612	555	3102	2004	2550
Pinus banksiana	181	621	136	1867	2463	194	1317	3205	131	427	551	440
Populus tremuloides	33	0	0	93	0	206	190	100	264	71	0	0
All Trees	481	674	210	2637	3200	957	3587	5048	1074	3796	2671	3328
Frequency (% of plots)												
n:	25	27	22	23	21	22	27	22	25	16	17	22
Abies balsamea	0	0	0	0	0	5	20	7	8	0	0	6
Betula papyrifera	0	0	0	8	8	7	9	4	4	0	0	8
Larix laricina	0	0	0	0	0	0	0	0	0	24	12	33
Picea glauca	0	0	0	4	4	4	14	15	4	0	0	0
Picea mariana	8	8	8	18	34	27	58	59	30	83	89	92
Pinus banksiana	29	48	19	82	82	26	73	71	20	43	23	23
Populus tremuloides	4	0	0	14	0	17	23	11	37	12	0	0
All Trees	37	48	27	96	90	63	96	100	72	94	94	95

** = Disturbance type difference in tree species composition (using basal area) of 37 year old communities was significant at α = 5%.

3.3.3 Understory

Understories were more resilient to logging than to fire at 13 years (Figure 3.2A - D). However, recovery between 13 and 37 years was slower in post-logging than post-fire communities on all site types (Figure 3.2A - D). By 37 years relative resilience had reversed. The similarity of post-fire communities to mature ones was greater than that of post- logging communities on the upland sites. On peatlands it was similar.

Disturbance type differences in understory species composition were significant for 13 year old communities on outcrops and shallow mineral soils ($P = 0.03$ for both) and for 37 year old communities on outcrops ($P = 0.08$), shallow mineral soils ($P = 0.03$) and moderately deep mineral soils ($P = 0.06$). Low statistical power was a concern for all comparisons (Hurlbert 1984). This was especially true for 13 year old communities on moderately deep mineral soils since the disturbance type difference in resilience was relatively large and post-fire communities had only two replicates. A disturbance type effect was apparent in the ordination scattergram where the first two axes separated the two post- fire from the three post-logging replicates (Figure 3.3A). This was corroborated by the performance criteria (Table 3.2). Thirteen year old communities on moderately deep mineral soils had the highest number and proportion of species with a disturbance type differences in performance (Table 3.3). In combination, these results suggest that there was a disturbance type difference in species composition in 13 year old communities on moderately deep mineral soils (Figure 3.3A) but it could not be detected due to low statistical power.

Species which performed more poorly in post-logging than post-fire communities at 13 years (Table 3.2) were generally those which regenerate well in the conditions created by fire. Understory *Pinus banksiana* performed more poorly in post-logging communities on all site types as did *Picea mariana* on outcrops and moderately deep mineral soils. Logging apparently failed to eliminate *Pleurozium schreberi* and *Cladina* spp. ground cover. This was associated with poorer *Polytrichum juniperinum* and *P. piliferum* performance in post-logging communities.

Species which performed better in 13 year old post-logging communities were those thought to be present at the time of logging and which tolerated or even benefited from overstory removal.

Examples included *Vaccinium angustifolium*, *V. myrtilloides*, *Cornus canadensis*, *Maianthemum canadense*, *Agrostis hyemalis*, *Calamagrostis canadensis*, *Danthonia spicata*, *Oryzopsis asperifolia*, *Schizachne purpurascens*, *Pleurozium schreberi*, *Cladina mitis* and *C. rangiferina*.

Overall patterns across all four site types were examined. At 13 years of age there were 47 situations where a species performed better in post-logging communities relative to post-fire communities and 15 situations where a species performed more poorly (Table 3.3). By 37 years of age, the pattern had reversed; there were 22 situations where a species performed better in post-logging communities and 32 situations where a species performed more poorly. Of the 31 species which performed better in post-logging communities on at least one site type at 13 years, only *Vaccinium angustifolium*, *V. myrtilloides*, *Schizachne purpurascens*, *Cladina mitis* and *C. rangiferina* maintained this status to 37 years. Understory *Picea mariana*, *Smilacina trifolia*, *Polytrichum juniperinum*, *P. piliferum* and *P. commune*, were the only species which performed more poorly in 13 and 37 year old post-logging communities. Many of the better performers in 13 year old post-logging communities had declines in performance between 13 and 37 years to the extent that there was no difference when compared with their conspecifics in post-fire communities. Species whose performance switched from better in post-logging communities at 13 years to poorer by 37 years included *Rosa acicularis*, *Rubus pubescens*, *Danthonia spicata*, *Pleurozium schreberi* and *Sphagnum* species.

If a community type is resilient to logging then the proportion of species with disturbance type differences in performance should approach zero over time. Although the dissimilarity of post-fire communities with mature ones generally decreased by about one-half between 13 and 37 years (Figure 3.2), the proportion of performances differences declined by only 20% (Table 3.3).

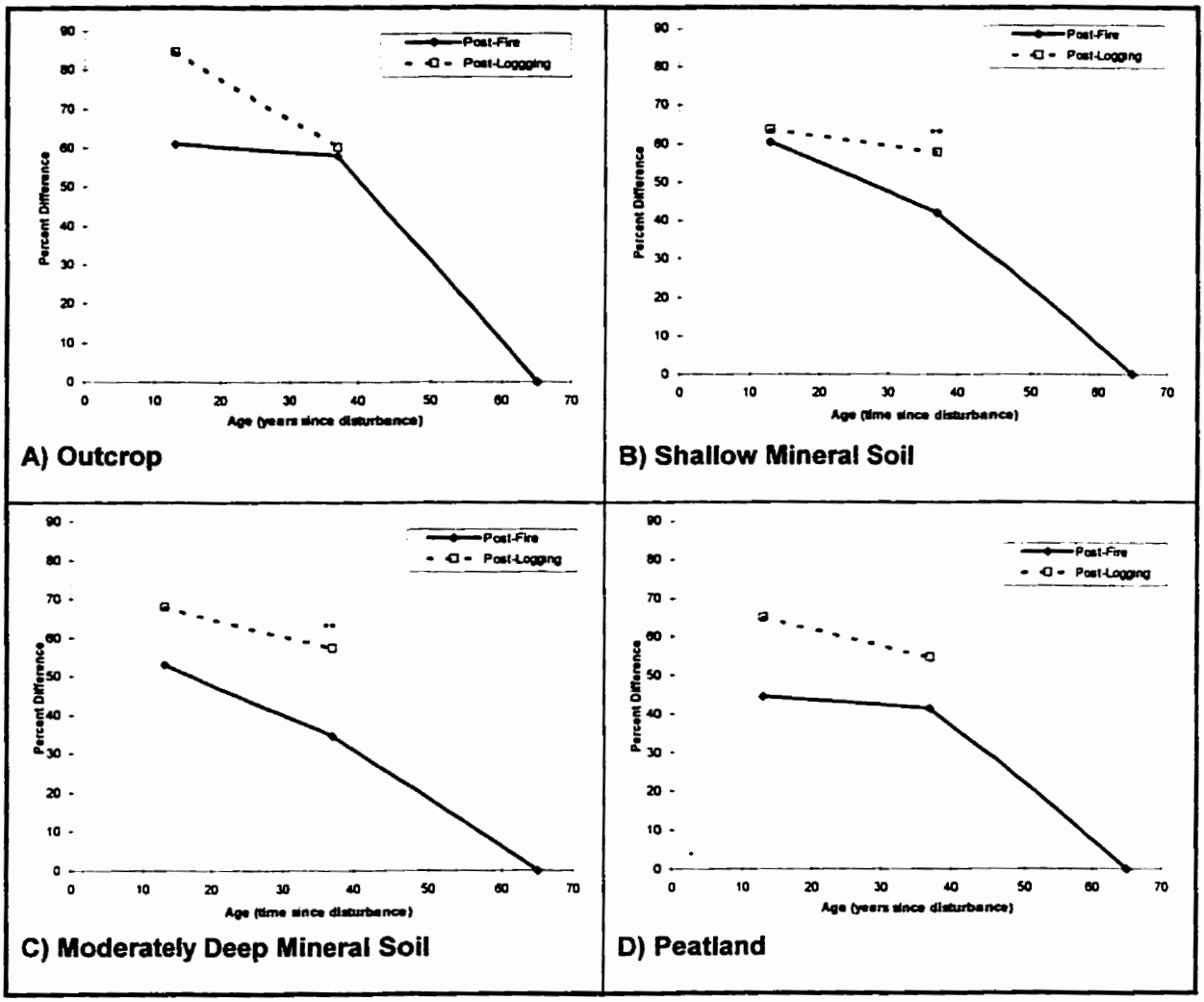

Figure 3.1. Overstory resilience based on dissimilarity of the communities with the typical mature state.

* = disturbance type difference in species composition significant at α = 10%, ** α = 5%.

Notes: Basal area used in the percentage difference calculations. Statistical comparisons not performed at 13 years due to high proportion of post-fire individuals still at the sapling stage.

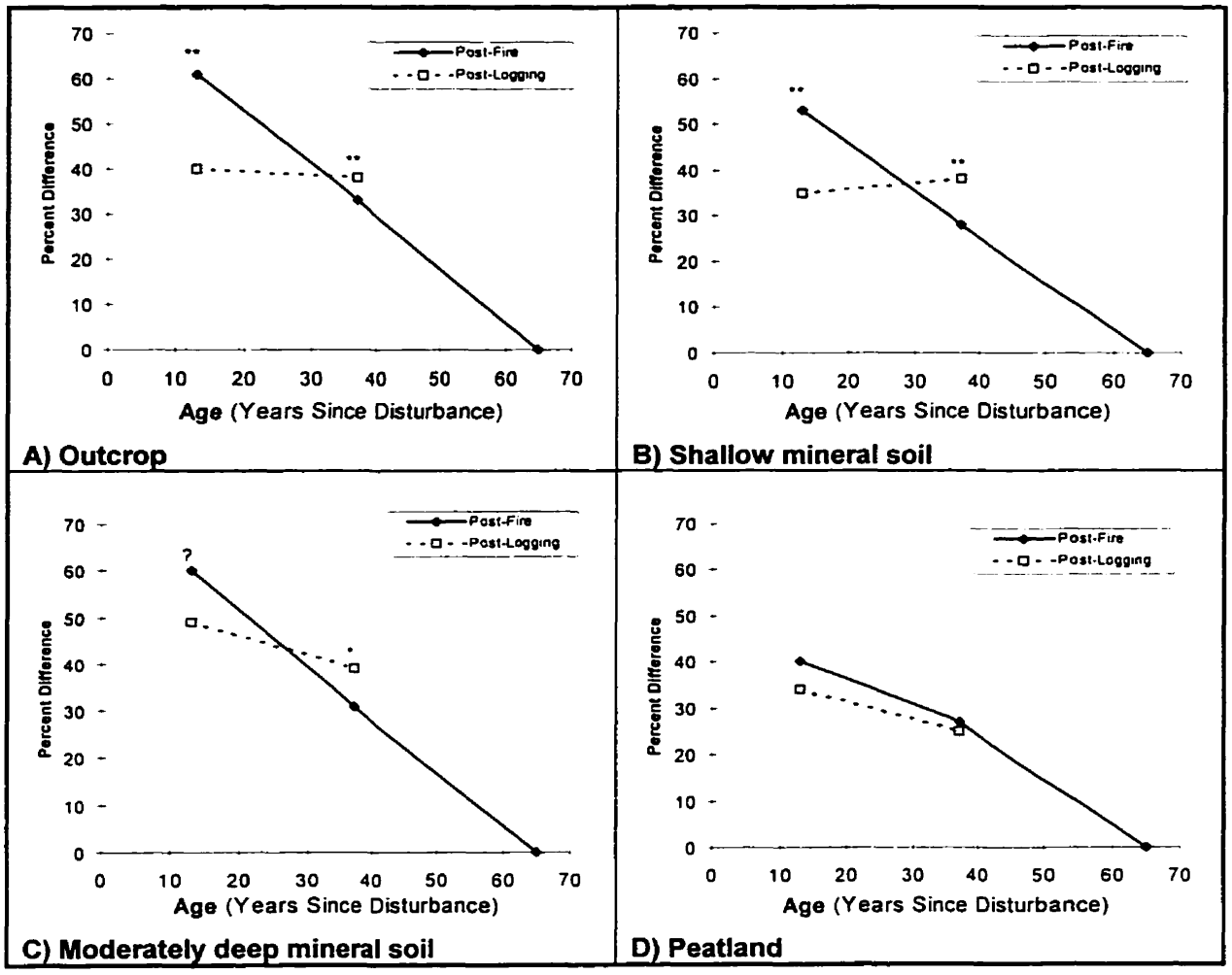

Figure 3.2. Understory resilience based on dissimilarity of the communities with the typical mature state.

* = disturbance type difference in species composition for this age class is significant at α = 10%,
**= significant at α = 5%, ? = Low statistical power was a concern.
Note: Percent cover used in the percent dissimilarity calculations.

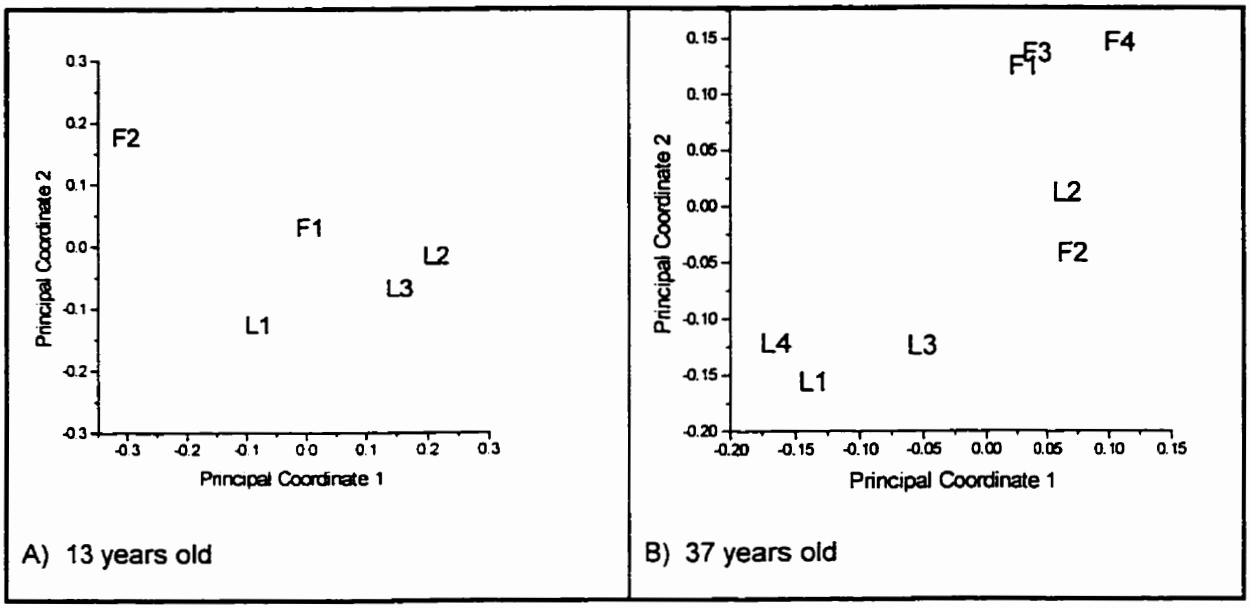

Figure 3.3. Principal coordinates analysis scattergrams of centroids for 13 and 37 year old communities on moderately deep mineral soils.

Legend: F1 = Fire replicate 1, F2 = Fire replicate 2 . . . ; L1= Logging replicate 1 . . . .

Table 3.2. Species which performed more poorly (P) or better (B) in post-logging than post-fire communities by age class and site type based on the performance criteria.

To deal with the weaknesses presented by each method on its own, a set of complementary performance criteria were used: 1) multiple discriminant analysis associated species with the community type where they had their highest canonical structure correlation; 2) ANOVA identified significant differences in cover; 3) a substantial frequency or cover difference was one that was 3 times greater in one disturbance type than in the other and the species was present in at least 66% of the replicates where it had the higher cover or frequency. See Methods of Chapter 2 for a detailed explanation.

Age Class:	13 years				37 years			
Site Type:	Outcrop	Shallow	Mod. Deep	Peatland	Outcrop	Shallow	Mod. Deep	Peatland
Trees								
Abies balsamea		B*						
Betula papyrifera		B*	B?				P?	
Picea glauca		B*						
Picea mariana							P?	
Pinus banksiana	P	P	P	P	P?	P	P	
Populus tremuloides		B*?					B?	
Tree species in understory								
Betula papyrifera			B					
Picea mariana	P*		P				P?	
Pinus banksiana	P	P	P	P				
Populus tremuloides							B?	
Shrubs								
Alnus rugosa								P
Amelanchier sanguinea	B*	B*					B	
Arctostaphylos uva-ursi	B							
Chamaedaphne calyculata								P
Corylus cornuta			B*					
Ledum groenlandicum							B	
Linnaea borealis				P*		P	P	
Prunus pumila	B*							
Ribes glandulosum			B*					
Rosa acicularis		B				P*		
Spiraea alba	B							
Vaccinium angustifolium		B	B?			B	B	B
Vaccinium myrtilloides			B?				B	
Vaccinium vitis-idaea						B*	B	B
Forbs								
Apocynum androsaemifolium		B*					B	
Aralia nudicaulis			B					
Aster ciliolatus					P*		P	
Clintonia borealis		B					B	
Cornus canadensis			B					
Epilobium angustifolium			P					
Equisetum arvense							P*	
Fragaria virginiana		B*	B		P*			
Galium boreale		B*						
Goodyera repens							P*	

Table 3.2 . . . continued.

Age Class:	13 years				37 years			
Site Type:	Outcrop	Shallow	Mod. Deep	Peatland	Outcrop	Shallow	Mod. Deep	Peatland
Lathyrus ochroleucus						P*		
Lycopodium obscurum		B*						
Maianthemum canadense		B	B	B				B
Melampyrum lineare					P			
Polygonum cilinode					B*			
Potentilla tridentata						P		
Pyrola secunda							P*	
Rubus pubescens			B*				P	
Smilacina trifolia				P*				P
Viola adunca		B	B*					
Viola spp.							P	
Graminoids								
Agropyron trachycaulum		B*						
Agrostis hyemalis	B	B						
Calamagrostis canadensis		B						P
Danthonia spicata	B		B*		P			
Oryzopsis asperifolia		B*	B		P			
Oryzopsis pungens			B*			P		
Schizachne purpurascens		B*	B				B	
Bryophytes & Lichens								
Aulacomnium palustre					P*			
Cladina mitis	B	B			B			
Cladina rangiferina	B	B	B		B	B		B
Cladina stellaris					B*	B		
Pleurozium schreberi	B	B	B	B		P?	P	B
Polytrichum commune			P				P	
Polytrichum juniperinum	P	P	P			P	P	
Polytrichum piliferum	P			P*	P	P		
Ptilium crista-castrensis							P	
Sphagnum spp.				B				P
Other Ground Cover								
Coniferous litter		P	P	P	P		P	B?
Non-coniferous litter		B	B?				B	
Wood litter					B		B	
Exposed rock		P			P?			
Standing dead tree		P		P				

Notes: * = species was exclusive to the disturbance type where it performed better; ? = questionable performance differences.

Table 3.3. Number and percentage of species which performed more poorly or better in post-logging than post-fire communities based on the performance criteria.

Age:	13 Year Old Communities					37 Year Old Communities				
Site type:	Outcrop	Shallow	Mod. Deep	Peatland	All	Outcrop	Shallow	Mod. Deep	Peatland	All
Trees										
More poorly	1	1	1	1		1	1	3	0	
Better	0	4	1	0		0	0	1	0	
Understory										
Trees										
More poorly	2	1	2	1		0	0	1	0	
Better	0	0	1	0		0	0	1	0	
Shrubs										
More poorly	0	0	0	1		0	2	1	2	
Better	4	3	4	0		0	2	5	2	
Forbs										
More poorly	0	0	1	1		3	2	6	1	
Better	0	7	6	1		1	0	2	1	
Graminoids										
More poorly	0	0	0	0		2	1	0	1	
Better	2	5	4	0		0	0	1	0	
Bryophytes										
More poorly	2	1	2	1		2	3	4	1	
Better	1	1	1	2		0	0	0	1	
Lichens										
More poorly	0	0	0	0		0	0	0	0	
Better	2	2	1	0		3	2	0	1	
Understory Total										
More poorly	4	2	5	4	**15**	7	8	12	5	**32**
Better	9	18	17	3	**47**	4	4	9	5	**22**
Percentage*	34	38	41	26	**35**	25	20	31	32	**27**

* Percentage of understory species present in more than three plots that had a disturbance type difference in performance.

Seven exotic species were encountered (Crescent Botanical Services 1994), but none in more than three plots within a site type. The species were *Agropyron repens, Bromus inermis, Cirsium arvense, Poa compressa, Sonchus arvensis, Taraxacum officinale* and *Vicia cracca*. These species were found in post-fire communities more often than in post- logging communities. The surprisingly low number of exotic species probably reflects the distance of sites from roads.

Most of the age class/ site type combinations had one replicate which was atypical when compared with the remaining two or three. For example, in 37 year old communities on moderately deep soils, three of the four replicates from each disturbance type were tightly clustered and the between cluster separation was large relative to the within cluster separation (Figure 3.3B). Each disturbance type had one outlying replicate. This likely reflects the broad range of factors subjected to statistical control in the study design and emphasizes the need for replication within an age class and disturbance type when comparisons of species composition are required.

3.4 Discussion

The overstory of post-logging communities recovered less than those of post-fire communities over the short (i.e. at 13 years) and medium-terms (i.e. at 37 years) on all site types. In contrast, understory recovery was greater in post-logging communities in the short-term but less over the medium-term on the three mineral soil site types. To the extent that the space-for-time substitution (Pickett 1989) was valid and the background conditions of post-fire and post-logging communities conditions were comparable, these recovery patterns implied that short-term resilience was a good predictor of medium-term resilience for the overstory but not the understory.

The overstory resilience pattern was somewhat misleading since resilience was based on basal area. At 13 years, post-logging basal area was dominated by advance tree regeneration whereas, in post-fire communities, most individuals were not included because they were still at the sapling stage.

Understory recovery between 13 and 37 years was slower in post-logging than in post-fire communities on all site types. The difference in recovery rates was large enough to cause a crossover of the successional pathways of post-logging and post-fire communities on mineral soils. The recovery patterns on all site types suggested that resilience should occur within an appropriate length of time in post-fire communities but not in post-logging communities. Recovery in post-logging communities on outcrops and shallow soils was of special concern as understory species composition on outcrops changed little between 13 and 37 years of age; on shallow soils the difference increased.

Degree of short-term resilience is a function of degree of resistance and the subsequent speed of recovery. Evidence suggests that the understory of boreal plant communities is more resistant to logging than to fire on non-eutrophic sites when ground disturbance is minimal (Noble *et al.* 1977; Johnston and Elliott 1996). Nevertheless, in vegetation types similar to those in the study area, short-term recovery is more rapid after fire than after logging albeit not fast enough to lead to higher short-term resilience to fire (Noble *et al.* 1977; Brumelis and Carleton 1989). Our results supported the finding that short-term recovery is faster after fire than after logging. At 13

years, post-fire communities were more dissimilar to mature communities than post-logging communities and short-term post-fire resilience was lower than post-logging resilience.

Differences in degrees of resistance to logging and fire are due to disturbance type differences in immediate, direct effects on the vegetation and site conditions. Fire's direct effects on species composition and site conditions are generally more severe than those of winter logging. Fire kills most of the living ground cover and destroys more small branches and foliage than logging (Zasada 1986; Brumelis and Carleton 1989). This creates differences in site availability, competitive relations and standing residual material. Site availability increases more after fire than after logging, both in terms of its variability and its extent, and thereby provides more opportunities for colonization (Zasada 1986). Understory light intensity also differs greatly and this is expected to lead to disturbance type differences in species performance since light intensity has a major influence on the understory of boreal communities (Rowe 1956; Dix and Swan 1971). Standing dead trees are the predominant source of shade in recently burned *Pinus banksiana* communities (Cayford and McRae 1983). Residual trees, saplings and shrubs provide a variety of light intensity niches in post-logging communities.

Life history strategies determine how species respond to the effects of fire and logging (Rowe 1983; Zasada 1986). Two responses to fire have important implications for resilience. Some species are typically only present or perform best in the conditions which exist immediately after fire (post-fire thrivers) while others are intolerant of fire (fire intolerants). Unless the fire is severe, post-fire thrivers such as *Pinus banksiana*, *Epilobium angustifolium* and *Polytrichum juniperinum* regenerate rapidly and grow well in full sunlight (Rowe 1983). Such species are either present prior to fire in a shade suppressed state or they invade the community from the seedbank and unburned areas adjacent to or within the burn (e.g. "fire skips"). Fire promotes these species because it creates available sites, stimulates seed release or germination, eliminates competitors and mobilizes nutrients. Logging generally affects these factors to a lesser degree (Zasada 1986; Sims *et al.* 1990) so that establishment of post-fire thrivers is limited in post-logging communities.

Fire intolerants are species that generally do not survive fire and either require several years or more to disperse into a burn or may disperse more quickly but regenerate slowly. Examples

include *Abies balsamea*, *Picea glauca*, *Goodyera repens*, *Pyrola secunda* and *Cladina rangiferina* (Rowe 1983). They, along with most other vascular understory species, are shade suppressed in mature communities. This typically maintains total vascular understory cover well below 100%. In our mature communities, the vascular component of understory cover ranged from 2.6% to 43.3% across the site types. Many vascular plants respond to logging by replacing shade leaves with sun leaves and then increase their cover above pre-disturbance levels (Brumelis and Carleton 1989; Bell 1991). The combined effects of release from shade suppression in post-logging communities and elimination of foliage in post-fire communities should permit some pre-disturbance species to perform better in post-logging than post-fire communities. Fire intolerants should be especially favored by logging with the largest disturbance type differences occurring for slow growing taxa such as *Cladina* spp. (Kershaw 1977; Foster 1985).

Post-logging communities initially exhibit greater resilience than post-fire communities because they retain many fire intolerants and some post-fire thrivers are absent or perform poorly. This creates floristic differences in species composition shortly after disturbance which are soon exacerbated by the strong performance of post-fire thrivers in post- fire communities. These differences decline as 1) woody post-fire thrivers suppress herbaceous and non-vascular post-fire thrivers, 2) the cover of *in situ* post-fire regenerators approaches that of post-logging residuals and 3) fire intolerants re-establish in post-fire communities (Cogbill 1985).

In many upland post-fire communities, *Pinus banksiana* saplings form a canopy after 5 - 10 years (Ohmann and Grigal 1979). This reduces understory light intensity and increases below-ground competition for resources which then leads to reduced performance of herbaceous species. Short-term recovery in post-logging communities is somewhat different. Release from shade suppression, limited competition and poorer natural tree regeneration permit many residual species in post-logging communities to expand their cover and perform better than their conspecifics in post-fire communities for the first 10-15 years (Noble *et al.* 1977; Brumelis and Carleton 1988, 1989). This can lead to higher short-term understory resilience to logging than fire.

These results are consistent with generalizations about short-term patterns of post-disturbance recovery. By 13 years of age, the main disturbance type differences in species

composition were not in the species present but in the abundance of some post-fire thrivers and post-logging residuals including fire intolerants (Chapter 2). In the understory, *Picea mariana*, *Pinus banksiana*, *Polytrichum juniperinum* and *P. piliferum* were the only post-fire thrivers to perform better in post-fire communities on more than one site type. The cover of these two mosses was thought to have expanded more slowly and peaked later than that of other post-fire thrivers.

The difficulties that post-fire thrivers such as *Pinus banksiana* and *Picea mariana* have regenerating naturally in upland post-logging communities are well documented (Yang and Fry 1981; Cayford and McRae 1983; Jeglum 1983; Zasada 1986; Brumelis and Carleton 1988, 1989; Harvey and Bergeron 1989; Carleton and MacLellan 1994). Seedling germination and survival for these species is best on exposed moist, mineral soils or mineral soils with a thin, compacted surface organic layer (Bell 1991; Burns and Honkala 1990). Logging without a regeneration treatment generally does not create these conditions. Understory post-fire thrivers expected to experience similar establishment difficulties in post-logging communities (Rowe 1983) include *Geranium bicknellii*, *Marchantia polymorpha*, *Ceratodon purpureus*, *Polytrichum juniperinum* and *P. piliferum*.

Most of the species which performed better in 13 year old post-logging communities on mineral soils were not post-fire thrivers and occurred in at least 25% of the plots in similar mature communities. This suggested that logging provided an advantage for certain pre-disturbance species. Depending on the site type, some of the species included were *Vaccinium angustifolium*, *Maianthemum canadense*, *Agrostis hyemalis*, *Danthonia spicata*, *Oryzopsis asperifolia*, *Schizachne purpurascens* and *Pleurozium schreberi*. *Cladina mitis* and *C. rangiferina* were the only fire intolerants that had a disturbance type difference in performance at 13 years.

Some post-fire thrivers and fire intolerants were expected to have disturbance type differences in performance at 13 years. They accounted for 15 (involving 6 species) of the 62 (39 species) performance differences found when post-fire and post-logging communities were compared (some species had a performance difference on more than one site type). Of the remaining 33 species whose performance differed on at least one site type at 13 years, 31

performed better in post-logging communities. Disturbance type differences in direct and indirect effects probably contributed to the large number of better post-logging performances at 13 years. Many post-logging residuals apparently benefited from limited competition immediately after logging, continued poor establishment of new species and higher light. In contrast, species in post-fire communities had to either germinate from the seed bank or grow from surviving underground parts before they could begin to compete with rapidly growing herbaceous post-fire thrivers. Once trees became well established in post-fire communities, rapid regeneration reduced understory light intensity and that prevented most species from performing as well as their conspecifics in post-logging communities at 13 years.

Many of the disturbance type differences in environmental conditions and species composition persisted or developed further between 13 years and 37 years. Post-logging communities on mineral soils remained more open than their post-fire counterparts at 37 years of age. Post-fire thrivers continued to perform more poorly and fire intolerants better in post-logging than in post-fire communities. The number of disturbance type differences in performance declined from 55 to 44 between 13 and 37 years.

If communities are resilient to fire and logging then the species composition of post-fire and post-logging communities should converge and become similar to mature communities. Concomitantly, the number of performance differences should decline over time. Continued lower light intensity in post-fire communities should limit the ability of species present at 13 years to recover to the degree that they outperform their conspecifics in post-logging communities at 37 years (Rowe 1956; Dix and Swan 1971).

Surprisingly, most of the poorer performances at 37 years were in post-logging and not post-fire communities. The main exceptions were *Vaccinium angustifolium*, *V. vitis-idaea*, *Cladina rangiferina* and *C. stellaris*. The persistence of poorer *Picea mariana* and *Pinus banksiana* performance was linked with the continued inability to establish on an undisturbed forest floor. Poorer bryophyte performance was attributed to higher deciduous litterfall and light intensity. Understory post-fire thrivers normally decline in cover once *P. banksiana* forms a canopy in the

tall shrub layer. As expected, *P. banksiana* was the only post-fire thriver that continued to perform more poorly in post-logging communities.

Most of the poorer performers in post-logging communities were forbs and graminoids. The number of poorer forb and graminoid performances increased from 1 to 14 between 13 and 37 years while the number of better performances declined from 24 to 4. Even species which typically benefit from overstory removal performed more poorly in the more open post-logging communities (i.e. *Aster ciliolatus*, *Fragaria virginiana*, *Potentilla tridentata*, *Oryzopsis asperifolia* and *O. pungens*).

A number of potential explanations for poorer forb and graminoid performance are suggested by the medium-term consequences of differences in the immediate, direct effects of fire and logging on vegetation and site conditions. Poor tree regeneration in post-logging communities led to lower canopy closure than in post-fire communities (Chapter 2). This was thought to have led to higher light intensity levels and more light intensity niches in post-logging than in post-fire communities. Some residual species in post-logging communities respond vigorously to overstory removal (Marks and Bormann 1972; Bell 1991) in much the same way that *Pinus banksiana* often responds vigorously to fire. They may then have suppressed other species in post-logging communities to the extent that their conspecifics in post-fire communities were able to overtake them. This explanation was not supported by our results. Cover in the tree, shrub and herb layers was too low at 13 and 37 years for shade suppression to occur. Vascular plant cover in 13 year old post-logging communities ranged from a low of 7.5% on outcrops to a high of 58.0% on shallow mineral soils. By 37 years, the combined cover of vascular plants was less than 46% on all site types and the only species to have cover greater than 10% were *Vaccinium angustifolium* on shallow and moderately deep soils and *Ledum groenlandicum* on peatlands. When bryophyte and lichen cover were also included, only peatlands had total cover greater than 100%. If competition occurred then it probably was not related to light. Over the medium-term, disturbance type differences in light intensity apparently led to better performance for only a few species such as *Cladina rangiferina*. For a number of species typically favored by overstory removal, other factors seemed to counteract the benefits of higher light.

Disturbance type differences in overstory characteristics was another of the factors that may account for some of the poor medium-term forb and graminoid performances in post-logging communities (Rowe 1956). Herbs such as *Equisetum arvense*, *Goodyera repens* and *Pyrola secunda* were expected to perform more poorly in post-logging communities because they are typically associated with a closed coniferous canopy. These species were exclusive to post-fire communities. However, there were many other herbs which should have benefited from the combination of a more deciduous and open overstory. In boreal communities, species richness and vascular understory cover generally increase as the canopy becomes more open and the proportion of deciduous trees increases (Rowe 1956). On this basis, a high proportion of understory species should perform better in post-logging than post-fire communities at 37 years, all other things being equal. This was not observed so alternative explanations were explored.

Another potential factor counter-acting higher light intensity and contributing to poorer forb and graminoid performance in post-logging communities was better *Cladina* spp. performance there. *Cladina* spp. provide a less hospitable seed bed and nurse site for seedlings than organic material or mosses (Foster 1985). They may also inhibit the growth of other plants by exuding allelopathic chemicals (Kershaw 1985). *Cladina* cover was high enough on outcrops (48.8%) to inhibit the performance of other species compared with their conspecifics in post-fire communities. Their cover on shallow mineral soils was 24.6% compared with 14.4% in post-fire communities. These cover differences were thought to be high enough to lead to disturbance type differences in the performance of a number of bryophytes. If *Cladina* spp. had an effect on species composition then it probably occurred through below-ground processes (Auclair 1985) and applied only to outcrops and shallow mineral soils.

Disturbance type differences in understory light, overstory composition and *Cladina* spp. cover could not adequately explain the large number of poorer forb and graminoid performances in 37 year old post-logging communities on mineral soils. These explanations were especially unsatisfactory when the large reversal in herb performance between 13 and 37 years was considered. This suggests that logging may have had indirect impacts on below-ground processes which were not revealed until after 13 years.

Research which has compared nutrient removal by logging with assumptions about long-term replacement rates predicts that nutrient removal is expected to be a problem for shallow mineral soils such as those included in this study (Weetman and Webber 1972; Gordon 1983; Timmer *et al.* 1983; Weetman and Algar 1983). The nature of disturbance type differences in species composition supports the possibility that there were impacts on site fertility. The species which benefited most from logging, *Cladina mitis*, *C. rangiferina, C. stellaris*, *Vaccinium angustifolium* and *V. myrtilloides*, are found most frequently on nutrient poor sites (Bakuzis and Kurmis 1978; Bell 1991). Concomitantly, shade intolerant species which should have benefited from the more open conditions in post-logging communities performed more poorly than in post-fire communities. Examples include *Apocynum androsaemifolium*, *Fragaria virginiana*, *Potentilla tridentata*, *Amelanchier sanguinea*, *Rosa acicularis*, *Rubus idaeus* and *Spiraea alba.* All are typically associated with moderate to rich nutrient regimes (Bakuzis and Kurmis 1978; Klinka *et al.* 1989; Bell 1991).

Both fire and logging remove nutrients. Volatilization losses from fire are substantial only for nitrogen unless temperatures are unusually high (MacLean *et al.* 1983; Aber and Melillo 1991). Viro (1974) notes that the ecological significance of volatilization losses of N is much less than the positive effect of an increase in mineralized N. In addition, increased N fixation during the initial stage of post-fire succession partially compensates for volatilization losses. Leaching losses from a site immediately after fire are generally small due to a combination of absorption on cation exchange sites in the organic and mineral horizons and immobilization by rapidly regenerating post-fire pioneers (Viro 1974; MacLean *et al.* 1983). Exceptions occur in medium to coarse textured mineral soils when the organic layer is consumed by fire.

In comparing the short-term effects of fire and logging on ecological processes, Bormann and Likens (1979) hypothesized that logging creates a greater potential for nutrient loss than fire. Today there seems to be a consensus that logging lowers soil pH, increases nitrification and increases the potential for nutrient losses through leaching (Huttl and Schaaf 1995). Leaching loss is governed by soil pH, anion availability and the ability of soil organisms and residual vegetation to utilize available ammonium during the initial post-logging period (Vitousek and Matson 1984;

Zak *et al.* 1990; Aber and Melillo 1991; Cole 1995). The pathways involved are complex and vary with a number of factors including disturbance characteristics, soil type, pre-disturbance vegetation and post-disturbance vegetation.

Two disturbance type differences in direct effects on soils are key to subsequent indirect effects on ecosystem dynamics. They relate to differential effects on soil pH and energy sources for microbial populations. Microbial populations in boreal soils are typically energy limited (Flanagan 1986). Fire maintains this state because it oxidizes readily decomposable carbon and lowers the C:N ratio. In contrast, logging slash left on site is energy rich (Bormann and Likens 1979).

Fire increases soil pH by rapidly mobilizing nutrients and thereby adding bases (MacLean *et al.* 1983). High nutrient concentrations in the soil solution facilitate the displacement of protons from cation exchange sites (Aber and Melillo 1991). This restores the percent base saturation and buffering capacity of the soil.

Soil pH does not increase after logging because the release of nutrients is delayed and less concentrated (Dahlgren and Driscoll 1994). Even in the relatively acidic soils of post-logging communities, ammonium is readily nitrified (Dahlgren and Driscoll 1994; Munson and Timmer 1995). Each ammonium ion yields one highly mobile nitrate anion and two protons which further acidify the soil solution (Cole 1995). This exacerbates the soil acidification effect of logging and maintains cations in solution. That is, the solubility of cations generally increases with decreasing soil pH (Eilers *et al.* undated). Highly mobile nitrate anions attract cations to maintain charge balance and thereby further increase the potential for leaching (Dahlgren and Driscoll 1994; Cole 1995).

Concomitantly, energy and ammonium limited decomposer populations in post-logging communities are stimulated by the energy rich logging residues and the increase in soil moisture which results from reduced transpiration and an intact forest floor (Bormann and Likens 1979; Flanagan 1986; Dahlgren and Driscoll 1994). Microbial populations respond by undergoing rapid growth (Dahlgren and Driscoll 1994). In the process they immobilize a large proportion of mineralized nutrients before they are leached away (Vitousek and Matson 1984). As the energy

rich logging residues and the forest floor are decomposed, the C:N ratio declines. In hardwood and softwood ecosystems in the Hubbard Brook Experimental Forest, microbial populations crashed within one year of logging (Dahlgren and Driscoll 1994). Decomposing microbial biomass releases nutrients into the soil solution where a high proportion may be permanently leached away due to low pH and limited vegetative recovery.

There are two apparent upshots for ecosystem dynamics. First, the concentration of mobile nutrients in the soil solution during the establishment stage is higher after logging than after fire. Second, when microbial populations crash, nutrients are released below the surface organic layer where most herbs root. Through this, and other effects, logging creates nutrient fluxes which differ from those after fire and this leads to the potential for higher nutrient losses (MacLean and Wein 1977; Adams and Boyle 1982; Zak *et al.* 1990; Dahlgren and Driscoll 1994; Cole 1995; Paré *et al.* 1993).

Vegetation performs a critical function in determining the degree of nutrient loss through leaching (Dahlgren and Driscoll 1994). Pioneers such as *Prunus pensylvanica*, *Vaccinium* spp. and *Ledum groenlandicum* can intercept nutrients after logging and thereby retain them in the biogeochemical cycle through rapid biomass accumulation (Marks and Bormann 1972; Auclair 1985). Potential for nutrient losses is greatest during the spring melt or after disturbance when mineralization is rapid and plant uptake is limited (Likens *et al.* 1977; Zak *et al.* 1990; Dahlgren and Driscoll 1994; Munson and Timmer 1995). The extent to which *Pinus banksiana* and/ or *Picea mariana* ecosystems can immobilize a post- logging nutrient flush may be limited by the sparse pre-disturbance vascular understory, bryophyte mortality resulting from overstory removal and low *Cladina* spp. productivity. Perhaps these limitations are exacerbated by winter logging which leaves evergreen understory vascular plants unprepared for the spring nutrient flush. Such species must replace shade leaves with sun leaves to cope with overstory removal (Brumelis and Carleton 1989). In addition, although post-logging residual plants have a cover head-start when compared with conspecifics in post-fire communities, they may accumulate biomass at a lower rate. The maximum growth rates of most post-logging residuals are lower than those of herbaceous post-fire thrivers. Meanwhile, woody post-fire regenerators are rapidly replacing stem

tissue. Low soil pH may also contribute to lower growth rates in post-logging communities by limiting nutrient availability to plants. If establishment stage nutrient leaching is higher in post-logging communities and plant biomass accumulates at a rate equal to or less than that in post-fire communities, then indirect nutrient losses during the establishment stage may be higher in post-logging communities.

Halpern and Spies (1995) provide a framework for evaluating the impacts of logging based on how disturbance characteristics interact with species life history strategies to influence population dynamics and thereby alter the rate or pathway of succession. They recommend that the effects of forest management activities be grouped into those which arise from the initial disturbance (e.g. fire type, logging method or site preparation) and those which arise from follow-up activities such as planting or thinning. The initial disturbance largely determines which species can establish whereas subsequent activities affect the relative performance of established species.

Life history strategies and disturbance characteristics are only two of the factors which can have a large influence on the rate or pathway of succession (Pickett *et al.* 1987). Post-disturbance vegetation dynamics can only be understood by incorporating all the mechanisms and interactions which have a substantial influence on ecological patterns, abiotic states and ecological processes such as population dynamics (Waring and Schlesinger 1985; van Cleve *et al.* 1986; Pickett *et al.* 1987; Aber and Melillo 1991; Peet 1992). Incorporation of ecological processes points to the importance of examining longer-term, indirect as well as immediate, direct effects since some effects may be delayed for a considerable time (Adams and Boyle 1982; Burgess *et al.* 1995). On this basis, it is suggested that Halpern and Spies' (1995) approach to evaluating the effects of management practices be generalized to apply to different types of disturbance. At the same time, their approach can be elaborated beyond distinguishing between the effects of initial and follow-up activities. As the first elaboration, the direct effects on the vegetation and the site are distinguished from effects on ecological processes (e.g. nutrient cycling). Effects on ecological states (e.g. species availability, site availability, soil pH) provide important initial conditions for processes which generate subsequent ecosystem dynamics. Many effects on ecological processes are indirect and may reduce site productivity. A second elaboration separates effects

into those which occur immediately and those which do not appear for several years or more (MacLean *et al.* 1983). Immediate effects are those which develop during the first year following disturbance when most establishment occurs and when nutrients can be lost from the biogeochemical cycle because the rate of biomass accumulation is low. Longer-term effects influence conditions at maturity such as site fertility which, in turn, influence relative dominance, species diversity, and whether conditions favorable for late successional species will be present. Thus, disturbance impacts can be grouped hierarchically into: 1) those which arise from initial or follow-up activities; 2) effects on ecological states versus effects on ecological processes; 3) immediate versus longer-term/ delayed effects. Separation of effects into categories does not imply that the mechanisms they represent act independently. Rather, the classification incorporates the chronology of causality and thereby helps partially to expose the mechanisms of ecosystem dynamics.

This framework is used to summarize the previous discussion and to suggest how the patterns of resilience and species performance on mineral soils developed. There were no follow-up activities in this study (e.g. planting, scarification) so that portion of the classification hierarchy is ignored. Immediate (year 1) differences in disturbance type effects probably varied by site type. Those which related to ecological states in post-logging relative to post-fire communities were thought to include 1) higher levels of nutrient export, nutrient retention in the living ground cover, soil moisture; 2) lower levels of pre-disturbance vegetation mortality, *in situ* propagule stimulation, soil pH and site availability in terms of variability and extent and 3) a failure to neutralize allelopathic lichen compounds (Auclair 1985) or break down compounds highly resistant to decay (Aber and Melillo 1991). The effect of logging on soil temperature is difficult to predict and probably varied by site type. Differential effects on processes in post-logging relative to post-fire communities probably included 1) higher nutrient mineralization and immobilization by microbial populations and 2) lower nutrient immobilization by accumulating plant biomass (Adams and Boyle 1982; Dahlgren and Driscoll 1994),

These immediate differences in effects on states and processes developed into short-term (1-15 year) effects on species composition. Expanding microbial biomass in post-logging

communities immobilized available nutrients. Once their rich energy source was depleted, microbial populations crashed and produced a nutrient flush. While this enhanced plant performance, it also resulted in leaching losses. Higher retention of cations in solution due to low pH and the deposition of nutrients below the surface organic layer limited retention by cation exchange capacity and made nutrients highly susceptible to leaching. Higher nutrient losses occurred because the root systems of vascular plants could not intercept the high concentration of nutrients leaching downward. The root system was too sparse and low pH limited nutrient uptake.

Higher nutrient losses depleted the small nutrient reserves contained in the thin LFH and siliceous soils which characterize the soils of the study area (Weetman and Webber 1972). More than 13 years were required for the effects of nutrient removals to become evident in understory cover because losses were initially offset by reduced tree uptake. Since the effects of nutrient and organic matter depletion were delayed, short-term post-logging population dynamics were predominantly affected by higher light intensity and nutrient availability that was adequate for the species that survived logging. Consequently, most residual vascular plants and lichens in post-logging communities performed better than they did in post-fire communities for the first 13 years.

Between 13 and 37 years, sufficient quantities of nutrients were immobilized in tree biomass and the forest floor to reduce availability to herbs to a critical level (Foster and Morrison 1976; Huttl and Schaaf 1995). This situation may have been exacerbated by negative impacts on other factors such as poorer litter quality to further reduce nutrient availability (Pastor *et al.* 1987). Consequently, the short and medium-term effects of logging on ecological processes were not manifested until after 13 years. They combined with logging's immediate effects on the population dynamics of the most abundant pre-disturbance species to affect herb performance in 37 year old communities on mineral soils.

This pathway of ecosystem dynamics is one of many which are consistent with our results. Detailed information on the life histories of the species affected could reveal causes unrelated to site fertility or other below-ground processes. Unfortunately, the information required to assess this is unavailable for many species (Halpern 1989). In depth research across a range of climatic conditions and types of surficial geology is also needed to elucidate the mechanisms which

control nutrient losses, the population dynamics of the most abundant species, ecosystem states and ecological processes (McCook 1994). This understanding is required if forest management practices are to be modified to sustain ecosystem functions.

Westman and O'Leary (1986) suggest that higher relative resistance may be a good predictor of higher relative resilience. Halpern (1988) found that this was the case up to 22 years for different degrees of logging disturbance in *Pseudotsuga* forests. The relationship between high resistance and high resilience was interpreted to be the result of the interaction of disturbance intensity with species life history strategies. Higher disturbance intensity simultaneously kills more above-ground plant structure and facilitates better establishment of invaders.

Adaptation to frequent fire enables many boreal plant species to survive disturbance or regenerate *in situ* regardless of whether the community is burned or logged provided that the fire is not severe or that logging has not resulted in substantial ground disturbance (Noble *et al.* 1977; Archibold 1979; Ohmann and Grigal 1979; Outcalt and White 1981; Rowe 1983; Viereck 1983; Abrams *et al.* 1985; Foster 1985; Brumelis and Carleton 1989; Walsh and Krishka 1991; Johnston and Elliott 1996). This provides boreal plant communities with some inherent resistance to disturbance (see Halpern 1988 for similar results from *Pseudotsuga* forests).

Boreal or near-boreal research which has compared early post-fire and post-logging recovery found that communities are less resistant to fire than to logging (Noble *et al.* 1977; Johnston and Elliott 1996). If it is assumed that our communities were less resistant to fire than logging, then our results supported the resistance/ resilience relationship to 13 years for all site types but not to 37 years for the three upland site types. Superficially, the relationship failed because slower post-logging recovery caused post-logging and post-fire successional pathways to cross some time between 13 and 37 years (Figure 3.2A to Figure 3.2D).

Halpern (1988) notes that the relationships between relative resistance, relative resilience and disturbance intensity are modified by site history, stochastic factors and initial site conditions. Our results suggest that they may also be modified by a disturbance's short and medium-term indirect effects on below-ground ecological states and processes. When this occurs, resistance and short-term relative resilience can be misleading indicators of medium-term relative resilience.

Communities should be monitored to maturity to establish resilience. Unfortunately, even when this is possible, the application of results to forest management will be constrained by continual change in logging methods and climate unless the results contribute to our understanding of the controls on site level ecosystem dynamics. An understanding of mechanisms will enhance our ability to predict how forest ecosystems will respond to new logging methods or different climatic conditions. Such predictions are critical to an assessment of the potential long-term effects of human activities.

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Chapter 4

Conclusion

This study examined the short (13 year) and medium-term (37 year) effects of fire and logging on the species composition of boreal plant communities using 65 year old post-fire communities to represent the typical mature state. A chronosequence approach was employed. This approach assumes that background conditions were similar in each age class. The two major factors subject to change over the time elapsed between age classes were climate and logging methods. Climate affects vegetation dynamics in two ways. First, it is the major influence on the fire regime. Changes in the fire regime could lead to differences in the mean and/ or variance of fire intensity and/ or severity across the age classes. Any change in climate normals which occurred during the time period was not considered to be large enough to lead to substantial changes in the fire regime. Second, year to year changes in climate lead to differences in moisture and irradiance over the growing season. This can have important consequences for seedling establishment. Numerous large fires usually occur after long periods of drought. Control for climatic variability was implicitly provided by selecting years in which there were numerous large fires.

Logging methods changed over the time period included in the post-logging chronosequences. It is not known to what extent these changes influenced the interpretation of the results. The differences in methods may have caused different degrees of ground disturbance and/ or above-ground mortality. Substantial differences in either of these effects was not expected because logging occurred when the ground was frozen and, in many cases, when the understory vegetation was snow covered. If these differences were ecologically significant, the implication for the results is that the pathways exhibited by connecting the two age classes may change. However, this does not affect the validity of the comparisons of post-fire and post-logging communities at 13 or 37 years.

These results are applicable only to winter logging. Different results are expected to occur for summer logging since it has a greater impact on ground disturbance and compaction, especially on fine textured soils and peatlands.

Differences in disturbance intensity and severity were not examined due to the time elapsed since the disturbances. Their influences on vegetation dynamics were controlled experimentally to the extent possible by including only those years which hosted numerous large fires. On this basis, all wildfires were assumed to be of moderate to high intensity. In the case of wildfires, trees were aged to ensure overstory mortality in the plot was complete. In the case of cutovers, haul roads were not sampled and understory plots were required to have at least one stump inside or adjacent to it. Replication, randomization and interspersion provided statistical control for these factors.

The principal conclusion of this study is that the short and medium-term effects of wildfire and winter logging on species composition are substantially different and this has negative implications for medium-term resilience to logging. Communities were expected to exhibit short-term differences in species composition because fire alters the state of vegetation and soil more than logging. Despite this, long-term conversion to an atypical community type usually does not occur. Boreal plant species are well adapted to regenerate *in situ* after fire and this imparts inherent resistance and resilience to fire at the community level. Fire also provides opportunities for some species to establish and grow vigorously and performs key functions. It rejuvenates the site by not only arresting the successional decline in nutrient availability, pH and, in some cases, soil temperature but also elevates these factors to levels more favorable for plant growth.

The life history traits associated with adaptations to fire also enable many species to survive and even benefit from the conditions that generally accompany winter logging. Because many species suffer little damage and post-fire invaders are inhibited after logging, communities exhibit higher resistance and short-term resilience to logging than to fire. By 13 years, species which typically thrive after fire performed more poorly in post-logging than in post-fire communities while fire intolerants and species commonly found in mature communities performed better.

Notwithstanding higher short-term resilience, recovery was slower in post-logging communities and this led to lower medium-term resilience. Winter logging's frequent failure to stimulate dispersal and germination or rejuvenate site conditions was thought to have contributed to the medium-term differences in species composition. The density and basal area of *Pinus banksiana* and *Picea mariana* were lower on mineral soils and species which are typically abundant in the mature community performed more poorly. In contrast, several species tolerant of moderate to high light intensity and low nutrients (*Vaccinium* spp. and *Cladina* spp.) maintained or expanded their cover in post-logging communities by 37 years. In a complete reversal of the situation at 13 years, by 37 years most of the species which performed more poorly in one disturbance type did so in post-logging communities. Most of the poorer performers were herbs; some were shade intolerants which typically require a moderate to rich nutrient regime.

The number of poorer herb performances in 37 year old post-logging communities was not expected given their better performance at 13 years and the continued openness of post-logging communities. Based on the species which had disturbance type differences in performance at 37 years, it appears that logging may also have had medium-term impacts on ecological processes which led to lower soil fertility. The extent to which there were reductions in soil fertility cannot be determined from these data. Medium-term disturbance type differences in species composition could be the result of differences in immediate direct effects on vegetation and the site or the indirect effects on soil processes or both. Mitigation of impacts is critically affected by this distinction. For example, if logging has altered below-ground processes then post-logging activities such as planting or vegetation management may do little to prevent this. It is important to examine both the immediate, direct effects as well as longer-term, indirect effects of disturbance on population dynamics and other ecological processes. Comprehensive, site level studies of ecosystem dynamics are needed to deepen our understanding of processes (McCook 1994).

Many factors in addition to disturbance have a substantial influence on vegetation dynamics and, thereby, landscape patterns. This study found site type to be the most influential explanatory factor on community level species composition followed by fire, age, and disturbance by fire or logging. This ranking is a function of a number of variables which include the scale of observation

(e.g. stand vs. landscape) and the proportion of the potential range of a factor that is sampled. Site type is most influential when a broad range of moisture regime is incorporated. Whether it is the most influential depends on the type of disturbances with which it interacts. Fire has a substantial influence on vegetation dynamics when it kills above-ground vegetation. Although fire had the second largest influence on species composition in this study, it may have proven to be the largest had a younger age class been included.

The results suggest that unmitigated fire suppression or logging could limit the distribution of some species and reduce the abundance of others. Species with life history strategies that take advantage of niches created by fire have difficulty regenerating when some of fire's key effects are absent. This has important implications for forest management where the conservation of ecosystem and species diversity is a management goal. In addition to the need for further research which compares the effects of fire and logging on ecological processes, research on the interaction between life history strategies, site type and disturbance type is required. Increased understanding of natural and human initiated ecosystem dynamics is essential if management is to be successful in maintaining ecological functions for future generations.

4.1 Conclusions

1) Site type had the strongest influence on plant species composition at the landscape scale. Wildfire had the second strongest influence.
2) The effects of logging on overstory and understory species composition did not mimic those of fire during the first 37 years of recovery.
3) The understories of plant communities were more resilient to logging than to fire at 13 years. That is, 13 year old post-logging communities were more similar to 65 year old post-fire communities than 13 year old post-fire communities. However, at 37 years, the reverse was true with post-fire communities more closely resembling the typical mature state as represented by 65 year old post-fire communities.
4) Greater resilience to logging than to fire at 13 years was a poor predictor of whether communities would have greater resilience to logging at 37 years.
5) Differences in the understory composition of 37 year old post-logging and post-fire communities suggested that logging may have had negative impacts on the fertility of mineral soils.
6) At 37 years, *Pinus banksiana* and *Picea mariana* density on the three mineral soil site types was lower in post-logging than post-fire communities. Basal area was also generally lower. This could be of concern to the forest industry since it implies lower timber volumes at maturity.
7) Species such as *Goodyera repens* appear to require some of the effects of fire to maintain their abundance and distribution on the landscape. Also, this study supports the well known fact that *Pinus banksiana* is a fire dependent species. This has important implications for the conservation of ecosystem diversity.

4.2 Suggested Directions for Future Research

The findings of this study indicate that further work is required in a number of areas:

1) Research on soil processes (e.g. decomposition, nutrient uptake, weathering) and their interactions with plant community recovery after fire and logging. This is required if we are to understand how to better approximate the effects of wildfire on ecosystem dynamics. Such research should include microbes and invertebrates.
2) Research on the ecology of species which seem to require some of the effects of fire. Examples include *Linnaea borealis*, *Goodyera repens* and *Chimaphila umbellata*.
3) Develop indicators of soil fertility and plant community composition so that ecosystem rather than just tree recovery can be monitored.
4) Direct comparisons of the species composition of one or two year old post-fire and post-logging communities. This will add the establishment stage to post-fire and post-logging successional pathways.
5) Describe post-fire communities older than 100 years so as to complete the post-fire successional pathways.
6) Research on the effects of tree planting on plant community resilience to logging.

5

Appendix A - Species List

Species difficult to identify in the field were grouped into a taxon. Nomenclature follows Scoggan (1979) except for ferns and fern allies, Cody and Britton (1989) for ferns and fern allies, Hale (1979) for lichens and Ireland (1982) for bryophytes.

Vascular plants

Abies balsamea (L.) Mill.

Acer spicatum Lam.

Achillea millefolium L.

Actaea rubra (Ait.) Willd.

Agropyron repens (L.) Beauv.

Agropyron trachycaulum (Link) Malte

Agrostis hyemalis (Walt.) BSP.

Allium cernuum Roth

Alnus crispa (Ait.) Pursh

Alnus rugosa (Du Roi) Spreng.

Amelanchier alnifolia Nutt.

Amelanchier sanguinea (Pursh) DC.

Anaphalis margaritacea (L.) Clarke

Andromeda polifolia L.

Anemone canadensis L.

Anemone quinquefolia L.

Antennaria dioica (L.) Gaertn.

Apocynum androsaemifolium L.

Aquilegia canadensis L.

Aralia hispida L.

Aralia nudicaulis L.

Arctostaphylos uva-ursi (L.) Spreng.

Asarum canadense L.

Aster ciliolatus Lindl.

Aster laevis L.

Aster puniceus L.

Aster simplex Willd.

Aster umbellatus Mill.

Athyrium filix-femina (L.) Roth

Epilobium palustre L.

Equisetum arvense L.

Betula glandulosa Michx.

Betula papyrifera Marsh.

Botrychium virginianum (L.) Sw.

Bromus ciliatus L.

Bromus inermis Leyss.

Calamagrostis canadensis (Michx.) Nutt. (includes *C. inexpansa, C. lapponica, C. neglecta*)

Campanula rotundifolia L.

Carex species

Chamaedaphne calyculata (L.) Moench

Chimaphila umbellata (L.) Barton

Chrysopsis villosa Ell.

Cinna latifolia (Trev.) Griseb.

Circaea alpina L.

Cirsium arvense (L.) Scop.

Cirsium muticum Michx.

Clintonia borealis (Ait.) Raf.

Comandra umbellata (L.) Nutt.

Coptis trifolia Salisb.

Corallorhiza trifida Chat.

Cornus canadensis L.

Cornus stolonifera Michx.

Corydalis sempervirens (L.) Pers.

Corylus cornuta Marsh.

Cypripedium acaule Ait.

Danthonia spicata (L.) Beauv.

Diervilla lonicera Mill.

Drosera rotundifolia L.

Dryopteris austriaca var. *spinulosa* (Muell.) Fiori

Epilobium angustifolium L.

Equisetum fluviatile L.

Equisetum hyemale L.

Equisetum pratense Ehrh.

Equisetum scirpoides Michx.

Equisetum sylvaticum L.

Eriophorum species

Eriophorum vaginatum ssp. *spissum* (Fern.) Hult.

Fragaria vesca L.

Fragaria virginiana Dcne.

Fraxinus nigra Marsh.

Galium boreale L.

Galium triflorum Michx.

Gaultheria hispidula (L.) Muhl.

Gaultheria procumbens L.

Geocaulon lividum (Richards.) Fern.

Geranium bicknellii Britt.

Goodyera repens (L.) R. Br.

Gymnocarpium dryopteris (L.) Newm.

Habenaria obtusata (Pursh) Richards.

Habenaria orbiculata (Pursh) Torr.

Halenia deflexa (Sm.) Griseb.

Heuchera richardsonii R. Br.

Hieracium scabriusculum Schwein.

Houstonia longifolia Gaertn.

Iris versicolor L.

Juniperus communis L.

Kalmia polifolia Wang.

Lactuca canadensis L.

Larix laricina (Du Roi) Koch

Lathyrus ochroleucus Hook.

Lathyrus palustris L.

Lathyrus venosus Muhl.

Ledum groenlandicum Oeder

Lepidium densiflorum Schrad.

Lilium philadelphicum L.

Linnaea borealis L.

Listera cordata (L.) R. Br.

Lonicera dioica L.

Lonicera oblongifolia (Goldie) Hook.

Lonicera species not included in another taxon

Lonicera villosa (Michx.) R. & S.

Lycopus americanus Muhl.

Lycopus uniflorus Michx.

Lycopodium annotinum L.

Lycopodium clavatum L.

Lycopodium complanatum L.

Lycopodium obscurum L.

Maianthemum canadense Desf.

Melampyrum lineare Desr.

Mentha arvensis L.

Mitella nuda L.

Monotropa uniflora L.

Oryzopsis asperifolia Michx.

Oryzopsis pungens (Torr.) Hitchc.

Oxycoccus quadripetalus Gilib.

Panicum depauperatum Muhl.

Panicum leibergii (Vasey) Scribn.

Panicum species not not included in another taxon

Petasites palmatus (Ait.) Gray

Petasites sagittatus (Banks) Gray

Petasites vitifolius Greene

Picea glauca (Moench) Voss

Picea mariana (Mill.) BSP.

Pinus banksiana Lamb.

Poa compressa L.

Poa palustris L.

Poa pratensis L.

Polygonum cilinode Michx.

Polypodium virginianum (L.) Hulten

Populus tremuloides Michx.

Potentilla norvegica L.

Potentilla palustris (L.) Scop.

Potentilla tridentata Ait.

Prunus pensylvanica L. f.

Prunus pumila L.

Prunus virginiana L.

Pteridium aquilinum var. latiusculum (L.) Kuhn var. (Desv.) Underw.

Pyrola asarifolia Michx.

Pyrola elliptica Nutt.

Pyrola secunda L.

Pyrola virens Schweigger

Quercus macrocarpa

Rhamnus alnifolia L'Her.

Rhus glabra L.

Ribes americanum Mill.

Ribes glandulosum Grauer

Ribes lacustre (Pers.) Poir.

Ribes oxyacanthoides L.
Includes (*Ribes oxyacanthoides var. hirtellum*)

Ribes triste Pallas

Rosa acicularis Lindl.

Rubus chamaemorus L.

Rubus idaeus L.

Rubus pubescens Raf.

Salix species

Sanicula marilandica L.

Saxifraga virginiensis Michx.

Schizachne purpurascens (Torr.) Swallen

Selaginella densa Rydb.
Includes *Selaginella rupestris*

Shepherdia canadensis (L.) Nutt.

Smilacina trifolia (L.) Desf.

Solidago canadensis L.

Solidago gigantea Ait.

Solidago hispida Muhl.

Solidago species not included in another taxon

Sonchus arvensis L.

Sorbus decora

Spiraea alba var. *latifolia* (Ait.) Ahles

Spiranthes romanzoffiana Cham.

Stellaria longipes Goldie

Streptopus amplexifolius (L.) DC.

Streptopus roseus Michx.

Symphoricarpos albus (L.) Blake

Taraxacum officianale Weber

Taxus canadensis Marsh.

Thalictrum venulosum Trel.

Tofieldia glutinosa (Michx.) Pers.

Trientalis borealis Raf.

Vaccinium angustifolium Ait.

Vaccinium caespitosum Michx.

Vaccinium myrtilloides Michx.

Vaccinium vitis-idaea L.

Viburnum edule (Michx.) Raf.

Viburnum opulus var. americanum L.

Viburnum rafinesquianum Schultes

Vicia americana Muhl.

Vicia cracca L.

Viola adunca Sm.
Includes *V. conspersa*

Viola species not included in *V. adunca*

Woodsia ilvensis (L.) R. Br.

Mosses

Aulacomnium palustre (Hedw.) Schwaegr

Dicranum species

Hylocomium splendens (Hedw.) BSG.

Pleurozium schreberi (Brid.) Mitt.

Polytrichum commune Hedw.

Polytrichum juniperinum Hedw.

Polytrichum piliferum Hedw.

Polytrichum strictum Brid.

Ptilium crista-castrensis (Hedw.) De Not.

Sphagnum species

Lichens

Cladina mitis (Sandst.) Hale & Culb.
(includes *C. arbuscula*)

Cladina rangiferina (L.) Harm.

Cladina stellaris (Opiz) Brodo

Cladonia species

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6

Appendix B – Validation of Site Type Classification

6.1 Introduction

Data analysis following the second field season determined whether the site type categories produced an ecologically meaningful grouping of the plots, were statistically efficient (i.e. maximized the precision of estimates) and were operationally useful. The efficiency of the site type classification was of concern because it was derived from univariate criteria using the most frequent and abundant species in a pilot study which lacked replication. Also, site type categories were constructed as part of a simultaneous decision which also determined the plot, subsample and sample size and were corroborated by the NWO FEC (Sims *et al.* 1989).

Cluster analysis was used to validate the classification since it has several attractive features. It automatically forms groups or clusters of plots and outputs its results in two dimensions so there is no need to make a judgment as to how many "axes" to retain (as in ordination methods). Cluster analysis makes no explicit assumptions about data structure. It is also put forward as a non-linear technique but this can be misleading since the method operates on a resemblance measure which itself may be sensitive to certain properties of the data such as non-linearity.

Cluster analysis has weaknesses such as sensitivity to outliers, the cluster algorithm and, where applicable, the number of clusters the algorithm is directed to retain in the final solution. Punj and Stewart (1983) provide an assessment of a number of different clustering algorithms. K-means clustering is the algorithm least sensitive to outliers, to the resemblance measure chosen and to sampling errors (Hair *et al.* 1987). Its drawbacks are that it requires a starting cluster configuration and a specification of the number of clusters to be produced. If the starting clustering is chosen randomly or using some other criterion such as the plots having maximum distance, it can produce a final solution which is nonsensical in ecological terms. The use of a hierarchical method such as Ward's as a first step is designed to minimize this shortcoming. Punj and Stewart (1983) suggest a three step approach to cluster analysis to avoid pitfalls:

1. Obtain an initial clustering using Ward's method or average linkage;
2. Use these results to determine the desired number of clusters in the final solution;
3. Perform a K-means cluster analysis using the clusters obtained from Ward's method as a starting configuration.

6.2 Methods

The approach recommended by Punj and Stewart (1983) was adopted. Percentage difference was selected as the resemblance measure preceded by a logarithmic transformation[7] of cover values on the basis that this combination most accurately reflects the concept of ecological distance implicit in the objectives of this study (Austin and Greig-Smith 1968; Jensen 1970; Noy-Meir 1973; Noy-Meir *et al.* 1975; Campbell 1978; Lamont and Grant 1979; Van Der Maarel 1979; Clymo 1980; Hadju 1981; Greig-Smith 1983; Faith *et al.* 1987). Outliers were removed prior to cluster analysis[8]. Ward's method was the algorithm used in the first step of cluster analysis. Determination of the number of groups to be carried forward to K-means clustering was based on changes in inter-group distances.

Only 37 year old post-fire communities were included in cluster analysis since these were the 'natural' state with which logging was compared. Amalgamation of post-fire and post-logging communities could lead to a confounding of disturbance type with site type effects in the cluster solution. Data from the outcrop, shallow mineral, moderately deep mineral, deep dry mineral, deep wet mineral and organic site type categories were included in the analysis. Clustering was performed on the vegetation and not the site (i.e. soils and topographic variables) data. Given the manner in which the replicates were selected, site variables were expected to be the main influence on the vegetation within a burn. Thus, the vegetation should generally reflect underlying differences in site type characteristics. The objective of the site type classification is to minimize within group variability so that the statistical power of treatment comparisons could be maximized. A site type classification derived from a cluster solution using the methods proposed, by definition minimizes within group variation and maximizes between group variation and will be the most

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[7] Note that data analysis after the final field season determined that a square root transformation performed better than a logarithmic on the complete dataset.

[8] An outlier is defined as a plot in which the mean of normalized species cover values is greater than 2. In the two field season dataset, this occurred for five plots in post-fire communities and no plots in post-logging communities.

efficient for use in hypothesis testing[9] provided that the cluster solution has an ecological interpretation both in terms of the vegetation and site variables.

The site variables were used to examine the ecological interpretation of the clusterings. ANOVA (α=5%) was performed on the site variables with plots grouped based on the various cluster solutions. Tests were not conducted to determine which group's mean was different or whether the mean was different in more than one group (a Scheffe's contrast, for example, would be required for that). This is the approach to the interpretation of cluster results advocated by Hair *et al.* (1987).

Selection of the number of groups to be used in the site type classification was based on the cluster solution minimized within group variance. Within group variance was calculated as the sum of species variances within a group, for each level of clustering. The cluster solution with the lowest overall variance was selected. This was a crude means of comparison. Canonical variates analysis of the vegetation using the clusterings as group membership variables was one alternative method of evaluating the efficiency of cluster solutions. However, a canonical variates analysis of the vegetation would be circular since the clustering was based on the vegetation. Therefore, variance summation was used as a mathematically independent method to evaluate the cluster solutions. Its results were corroborated by canonical variates analysis. A canonical variates analysis was appropriate for the site type variables. It was applied using the group membership variables provided by the selected cluster solution to corroborate the results from the vegetation analysis.

A six group K-means clustering of site variables was completed for comparison purposes. The procedure followed was the same as for the vegetation data except that all site variables were standardized by their range. The variables included were percent canopy closure, aspect, percent slope, plot shape, slope length, upslope length, depth of organic material, depth of solum, depth to bedrock, depth to distinct mottling, depth to prominent mottling, depth to gleying, depth to water table, drainage regime, moisture regime and percent stoniness.

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[9] An incidental benefit is that, by focusing on the vegetation, methodological problems which would arise in an analysis of site variables are also avoided. Those problems relate to variable selection and standardization to remove scale differences.

6.3 Results and Discussion

The Ward's clustering indicated that relatively large inter-group distances were maintained as the number of groups retained increased up to five groups. Changes in intergroup distance then became small until a nine group cluster solution was reached[10]. A nine group classification was not feasible given the total sampling effort available. Four, five and six level clusterings were examined further.

Any clustering which has ecological meaning should recognize the vegetation types which the research of others has shown to be distinct. In this study, these were the vegetation of peatland soils (wet, very to moderately nutrient poor) and outcrops (dry, nutrient poor). Examination of dendrograms from the four, five and six level groupings produced by Ward's method clustering revealed an ecological interpretation for each level of clustering. In all three, the peatland and outcrop site types were the most distant from each other. The major difference in the clusterings was the manner in which the vegetation on intermediate site conditions was grouped. Because the resolution of the four group solution was too low, only the five and six group solutions were carried forward to the next step. One note of interest was that each replicate was represented in each group of each clustering (except where no plots were available for a replicate in the site type category). This suggested that differences in site type variables had more influence on the vegetation than differences in location within the study area.

K-means clustering, using the groups produced by Ward's method as starting configurations, was the next step in analysis. K-means clustering reclassified 5 out of the 97 plots from the five group solution and 4 from the six group solution. All reclassifications were of plots from intermediate moisture regimes. Ward's method and K-means clustering created similar groupings for this dataset.

Cluster solutions obtained from K-means clustering were reviewed for their ecological interpretation using Baldwin and Sims (1989), Bell (1991), Klinka *et al.* (1989), Sims *et al.* (1989) and Vitt *et al.* (1988). The five and six level groupings both had a defensible ecological

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[10] As a word of caution, Sneath and Sokal (1973) indicate that cluster analysis is better at representing between plot distances within groups than between group distances.

interpretation in terms of the vegetation. That is, the groups contained species which commonly occur together and give similar indications about site conditions. Based on the indications of species, both clusterings appeared to group vegetation most strongly on moisture regime. Mineral soil depth appeared to be next in importance. The six group solution provided better resolution of the vegetation on soils with intermediate moisture regimes.

The site data were used to examine the ecological interpretation of the clusterings further. Means for those site variables which ANOVA indicated had a significantly different mean for at least one group within a cluster solution are given in Table 6.1. In the tables that follow, the group numbers used for each cluster solution are intended to correspond to similar vegetation types across the two clusterings.

As expected, the variables depth to water table, drainage regime, moisture regime and existing site type category all reflected the trends in the moisture gradient detected in the vegetation clusterings. Each clustering also exhibited patterns in depth of solum and depth to bedrock consistent with the ecological interpretation of the clusterings. Patterns were the strongest for the first, second and last groups in the five and six level solution whereas there were no strong trends for the middle groups. Analysis of the site variables indicated that the creation of group 3 in the six cluster solution separated out drier sites from group 2 of the five cluster solution. This was consistent with the vegetation interpretation given to group 3.

An ecological interpretation for the five and six group cluster solutions was possible. A six group clustering provided the lowest overall variance in vegetation (Table 6.2). Increasing the number of groups from five to six resulted in a small decrease in Group 1 variance, a large decrease in Group 2 (interpreted as closed, fresh coniferous stands) variance along with a concomitant variance in newly created Group 3 (interpreted as closed, dry coniferous stands) which was lower than the mean group variance of the five group clustering. Vegetation in groups 2 and 3 are commonly logged.

Table 6.1. Mean values for site variables which had a statistically different mean in at least one group within a cluster solution based on ANOVA (α = 5%).

Site Variable	Five Group					Six Group					
	0	1	2	4	5	0	1	2	3	4	5
Percent canopy closure						24	26	34	33	14	36
Plot aspect (degrees North, 0 = no aspect)	166	155	78	144	0	166	156	75	97	144	0
Plot slope (%)	10	7	4	3	0	10	8	3	6	3	0
Site slope length (m)	15	20	21	42	0	15	21	29	8	42	0
Site upslope length (m)	4	6	7	15	0	4	6	9	4	15	0
Depth of organic layer (cm)	1	6	6	6	24	1	6	6	7	6	24
Depth of solum (cm)	4	26	59	55	27	4	23	60	57	55	27
Depth to bedrock (cm)	4	29	81	85	81	4	26	87	66	85	81
Depth to distinct mottling (cm)	n/a	87	69	67	97	n/a	89	69	70	67	97
Depth to water table (cm)	n/a	94	77	78	18	n/a	96	83	67	78	18
Drainage regime *	0.4 (rapid)	0.9	3.5	3.3	5.6 (poor)	0.4 (rapid)	0.9	4.3	1.6	3.3	5.6 (poor)
Moisture regime *	0.0 (dry)	0.6	2.9	2.6	6.3 (wet)	0.0 (dry)	0.6	4.0	0.9	2.6	6.3 (wet)
Stoniness in soil profile (%)	3	25	13	25	1	3	26	6	25	25	1
Existing site type category **	0.2 Outcrop	1.7	2.9	3.0	5.0 Peatland	0.2 Outcrop	1.6	3.2	2.4	3.0	5.0 Peatland

* Drainage regime runs from 0 for very rapid to 7 for very poor. Moisture regime runs from 0 for dry to 9 for very wet. Moisture regime is a composite variable derived from drainage regime, depth to bedrock and soil texture. It is intended to reflect moisture availability throughout the growing season. ** Existing site type categories range from 0 for outcrops (dry) to 5 for peatland (wet).

Table 6.2. Variance of species means summed for each group for 5 and 6 group K-means clusterings, existing site type categories and 6 group K-means clustering of site variables.

Classification	Group						Mean
	0 Outcrop	1	2	3	4	5 Peatland	
Five Group K-Means Clustering	2.96	3.30	3.31		4.67	3.84	3.62
Six Group K-Means Clustering	2.96	3.25	2.39	3.56	4.67	3.84	3.44
Site Type Classification	2.76	3.88	4.32	4.17	5.09	3.84	4.01
Site Variables Clustering	4.75	4.93	5.12	4.98	5.89	4.05	4.95

Table 6.3. Variance of site variable means summed for each group for 5 and 6 group K-means clusterings, existing site type categories and 6 group K-means clustering of site variables.

Classification	Group						Mean
	0	1	2	3	4	5	
	Outcrop					Peatland	
Five Group K-Means Clustering	2.85	6.20	9.59		7.74	4.85	6.25
Six Group K-Means Clustering	2.85	6.11	9.13	7.74	7.82	4.85	5.42
Site Type Classification	2.55	3.69	7.23	6.78	5.83	4.85	5.16
Site Variables Clustering*	3.54	7.25	5.71	6.08	5.37	2.47	5.07

* Variables included were percent canopy closure, aspect, percent slope, plot shape, slope length, upslope length, depth of organic material, depth of solum, depth to bedrock, depth to distinct mottling, depth to prominent mottling, depth to gleying, depth to water table, drainage regime, moisture regime and percent stoniness. Each site variable standardized to its maximum across all groups.

Table 6.4. Summary statistics from canonical variates analysis of site variables using various classifications as the group variables.

Classification	R^2	Chi-Square	Wilk's Lambda
Five Group K-Means Clustering	0.91	319	0.239
Six Group K-Means Clustering	0.91	348	0.017
Site Type Classification	0.93	500	0.003

The outcrop grouping is the only one for which the existing site type classification was superior in terms of variance minimization of the vegetation data (Table 6.2). It performed as well for the peatland group but for the other mineral soil groups it performed more poorly than any of the vegetation clusterings. Vegetation variance values resulting from a clustering based on site variables indicated that it performed more poorly at minimization of vegetation variance than any of the other approaches (Table 6.2).

The variance in site type variables was also examined (Table 6.3). Based on variance alone, it would appear that the six group solution performs better than the five. In contrast with the vegetation results (Table 6.2), the site type classification and the site variables clustering produced lower within group variances than the K-means vegetation clusterings. Although the site variables clustering had the lowest overall variance, it did more poorly than the 6 group K-means classification for 2 of 6 groups. Examination of the data indicated why the site variable clustering was inferior to the others at minimizing vegetation variance despite its better performance on the site variables. The site variable clustering moved a number of plots from the peatland group, a vegetation type that is known to be distinctive, into other very different vegetation types. This may be a reflection of the methodological problems involved with site type variables and may be altered by changing the variables included in the analysis or the standardization applied. However, the variables sampled were included based on prior ecological knowledge. Changes in variable selection were not justified at this stage especially when the existing site type categories already minimized the variance of site variables more than either of the K-means classifications (Table 6.3). The site variables classification was disqualified from further consideration based on its poor performance at minimizing vegetation variance, minimizing site variable total variance for groups 0 and 1, and its misclassification of some peatland plots.

A series of canonical variates analyses performed on the site variables using the same four classifications produced a trend of variance similar to that of the variance summation method (Table 6.4). A considerable improvement in Wilk's Lambda was obtained by increasing the number of groups from five to six. The existing site type categories were substantially superior to both of the K-means vegetation classifications based on R^2, Chi-Square and Wilk's lambda. The

vegetation approach to clustering appeared to separate two vegetation types which both occurred on a more broadly defined intermediate site category- one mixedwood or deciduous and the other coniferous. In other words, two major vegetation types were encountered in that cluster group. What caused one to be present and not the other was just as likely to be a function of historical factors, dispersal, stochastic events, etc. as of the most recent fire. Therefore, while cluster analysis of vegetation data accomplished its variance minimization objective for the vegetation data, it did so in a manner which went beyond grouping plots based on site conditions to further resolution based on other explanatory factors. When variance minimization of the vegetation and soils was considered in conjunction with ecological interpretation and operational usefulness, the existing site type categories performed best.

The ecological resolution of the vegetation found on deep mineral soils (Groups 3 and 4) is still poor. Earlier results indicated that at least three more site type categories would be required to improve resolution for these two groups. This was not feasible given the implications for sampling effort. Moreover, the categories which would gain higher resolution are infrequent in the study area.

A review of the existing site type categories using cluster analysis indicated that they minimized within-group variance for site related variables. Cluster analysis could create a classification which would result in lower vegetation variance for some groups. However, this seemed to be accomplished by recognizing different vegetation types across a broad range of site conditions. Treatment effects were thereby confounded with other ecological factors. Consequently, the existing site type classification was retained.

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7

Appendix C – Application of Performance Criteria to Shallow Mineral Soils

Shallow mineral soils are used to illustrate how discriminant analysis was used to gain an initial indication of the age class or disturbance type in which a species had either its best or worst performance. Community types were associated with a particular discriminant function through visual interpretation of discriminant analysis (DA) scattergrams. Species were assigned to the discriminant function with which they had their highest absolute canonical structure correlation. On shallow mineral soils, DA separated 13 year old post-fire communities from the rest at the negative end of the first discriminant function (Figure 7.1). Therefore, species which had their highest absolute canonical structure correlation with this function and whose correlation was negative, were identified as those which had their best performance in 13 year old post-fire communities. These species are listed in Table 7.1. This initial allocation was examined further with ANOVA, frequency and presence. The remaining community types were clumped together at the positive end of the first discriminant function. Therefore, species which had their highest absolute canonical structure correlation with this function and whose correlation was positive, were identified as those which had their poorest performance in 13 year old post-fire communities.

Discriminant function 2 separated out 37 year old post-fire communities at its positive end so that species which had their highest absolute canonical structure correlation with function 2 and whose correlation was positive, were identified as those which had their best performance in 37 year old post-fire communities. Thirteen year old post-logging communities were separated from the rest at the negative end of function 2. Species which had their highest absolute canonical structure correlation with function 2 and whose correlation was negative, were identified as those which had their best performance in 13 year old post-logging communities. Results for function 3 are also shown.

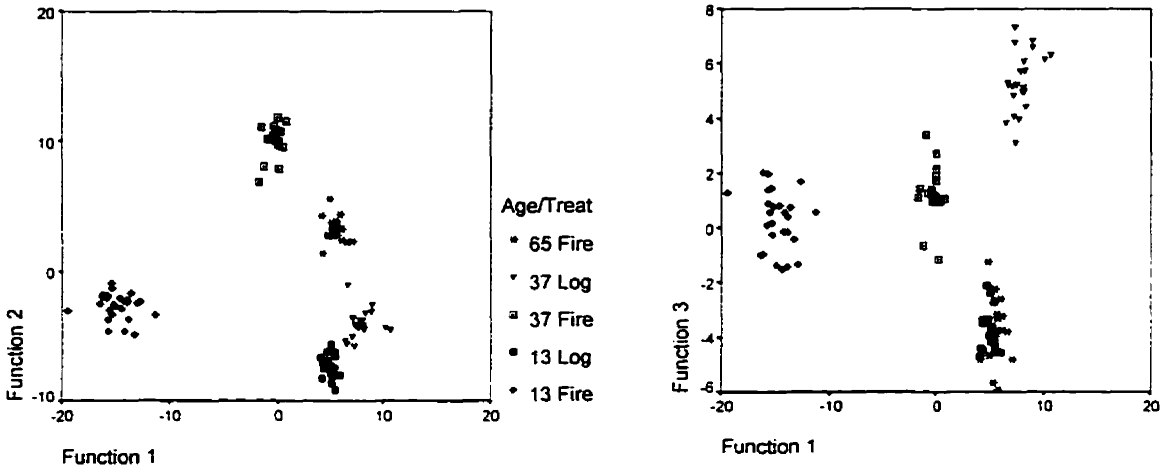


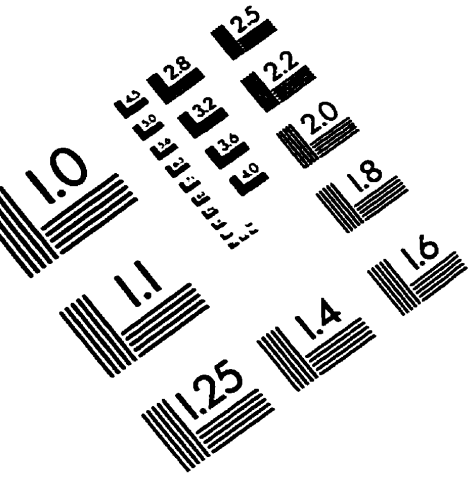
Figure 7.1 Discriminant analysis of shallow mineral soils and species associated with community types on the first three discriminant functions.

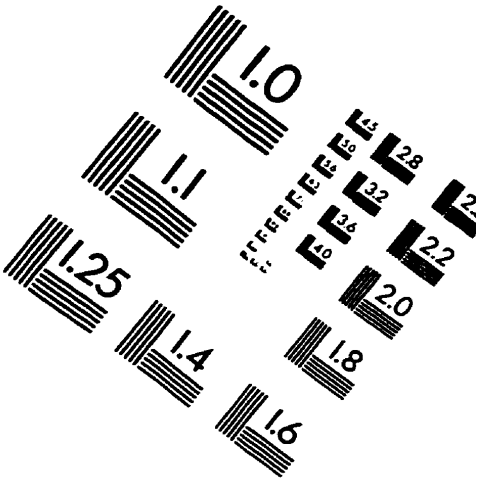
Notes: Proportion of variance included in the functions were: function 1 = 59%, function 2 = 28%, function 3 = 9%, function 4 = 5%. Of the 100 plots from this site type, 100% were correctly classified by the discriminant analysis.

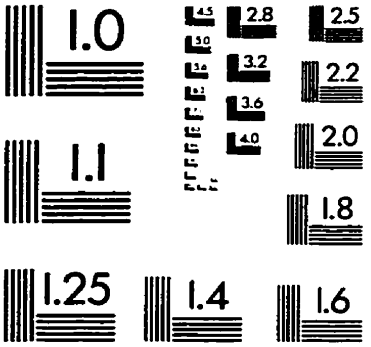
Table 7.1. Community types in which species had their best or worst performance based on interpretation of discriminant analysis.

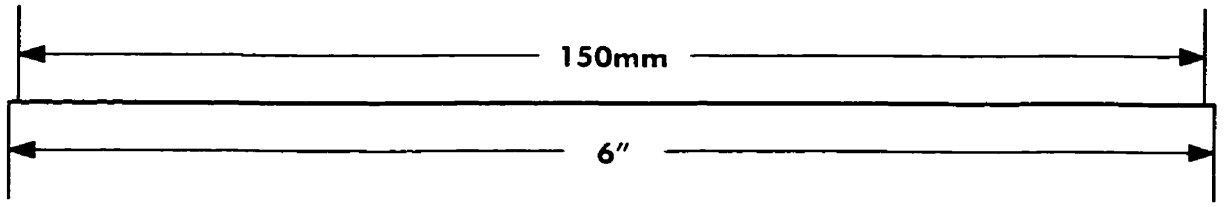
Function 1		Function 2		Function 3	
Best in 13 Fire	**Worst in 13 Fire**	**Best in 37 Fire**	**Best in 13 Log**	**Best in 37 Log**	**Worst in 37 Log**
Pinus banksiana	*Clintonia borealis*	*Ptilium crista-castrensis*	*Vaccinium angustifolium*	*Cladina stellaris*	*Diervilla lonicera*
Polytrichum juniperinum	*Dicranum* spp.	*Goodyera repens*	*Spiraea alba*	*Vaccinium vitis-idaea*	*Lathyrus ochroleucus*
P. piliferum		*Cladina mitis*	*Salix* spp.	*Cladina rangiferina*	*Potentilla tridentata*
Prunus virginiana		*Linnaea borealis*	*Amelanchier alnifolia*	*Picea mariana*	*Oryzopsis pungens*
Woodsia ilvensis		*Pleurozium schreberi*	*Betula papyrifera*	*Prunus pensylvanica*	*Gaultheria procumbens*
			Corylus cornuta	*Sphagnum* spp.	*Rosa acicularis*
				Ledum groenlandicum	
				Populus tremuloides	
				Symphoricarpos albus	

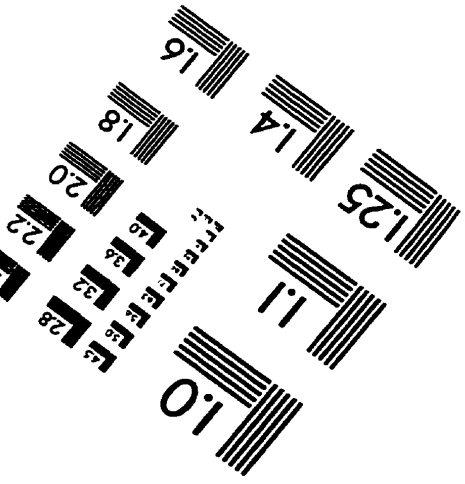
IMAGE EVALUATION
TEST TARGET (QA-3)

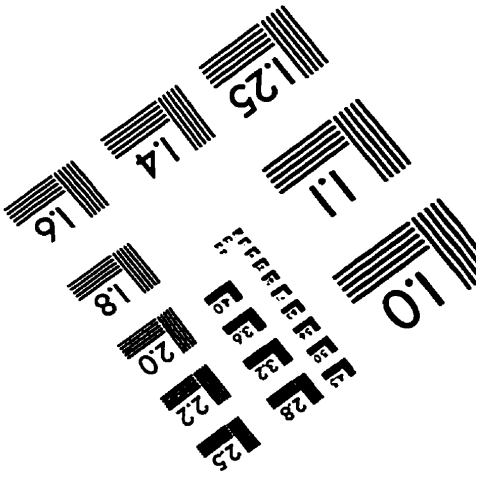












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