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VEGETATION RESPONSE TO HARVESTING, HARVESTING AND PRESCRIBED-BURNING AND WILDFIRE IN NORTHWESTERN ONTARIO: PATTERNS OF REPRODUCTIVE STRATEGIES AND NUTRIENT ACCUMULATION

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fulfillment of the requirements for the degree of
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ABSTRACT

Rintoul, T. L. 1996. Vegetation response to harvesting, harvesting and Prescribed-burning, and wildfire in Northwestern Ontario: Patterns of reproductive strategies and nutrient accumulation. 150 pp. (Advisor: Dr. M. Johnston).

Key Words: initial species composition, multiple successional pathways, propagule bank, nutrient retention

Initial species composition was investigated on a group of boreal mixedwood sites that had experienced various forms of disturbance. The hypothesis explored was that environmental changes caused by different disturbances would be reflected in patterns of revegetation. The disturbance types were as follows: (1) Harvest, winter, full tree logged cutovers, delimbed at the road side; (2) Prescribed-burn, cutovers burned in early spring; (3) Reburn, cutovers which were Prescribed-burned and subsequently experienced a wildfire; (4) Wildfire, a low severity crown fire in mature forest; (5) Control, 70 year old forest with a species composition of white spruce (*Picea glauca* (Moench)Voss), black spruce (*Picea mariana* (Miller) Britton), balsam fir (*Abies balsamea* (L.) Miller) and white birch *(Betula papyrifera* Marshall).

Results indicated that species composition differed consistently among control and recently disturbed sites. Feather moss species, *A. balsamea* and *Acer spicatum* Lam. had significantly greater cover on Control sites. Prescribed-burn sites had high cover values for *Polygonum convolvulus* L., *Prunus pensylvanica* L.f. and *Epilobium angustifolium* L.. Reburn sites had greater cover of *Geranium bicknellii* Britton. Disturbance species were also present on Harvest and Wildfire sites but the species' relative abundance was not as great when considering the conditions created by these disturbances.

Greenhouse germination experiments indicated that the seed bank on the harvested and adjacent undisturbed sites were similar and consistently different from those that had experienced any of the fire treatments. Species regenerating by recently dispersed seed (*B. papyrifera*) or rhizomes (*Maianthemum canadense* Desf. and *Coptis trifolia* (L.)) found on the surface organic layer in the Control and Harvest treatments were likely consumed by the fire in burned treatments.

Plant tissue nutrient samples were taken for five species (*C. canadensis* (L.), *G. bicknellii*, *R. idaeus* L., *P. pensylvanica* and *B. papyrifera)* and were selected to represent different understory layers and reproductive strategies.

Nutrient concentrations differed according to disturbance type and most elements had higher concentrations in the Control plots, except for nitrogen. Nitrogen generally increased from Control, Harvest, Reburn, Prescribed-burn to Wildfire. *G. bicknellii* and *P. pensylvanica*, which revegetated by seed, generally had higher concentrations of nitrogen, potassium and phosphorous, especially on burned sites and seems to reflect nutrient concentrations of soil on the various treatments. This suggests that species' ability to accumulate nutrients following disturbance may be related to its regenerative strategy.

Since plant species differentially absorb various nutrients, as a disturbance influences the initial species composition it also determines the element composition of the site and the ability of vegetation to act as a nutrient sink. Species composition differed and continued to diverge over the growing season according to disturbance type. As resource managers attempt to emulate natural disturbance and predict successional pathways following harvesting and fire a better understanding of early successional species and their role in nutrient retention needs to be considered.

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CHAPTER I

BACKGROUND

1.1 INTRODUCTION

Change is an underlying quality of nature. Understanding the direction and character of ecological change requires an awareness of evolutionary trends, species adaptations and environmental conditions (Van Wagner and Methven 1980). Changes can be as subtle as plants adjusting to shifting microclimates or as momentous as fire returning a mature forest to the seedling stage. Succession describes a directional, cumulative change in the species that occupy an area through time (Barbour *et al.* 1987). Disturbance, a more abrupt change, is defined as an event which results in the removal of organisms and the creation of space for the establishment of similar or different organisms (Begon *et al.* 1990).

Historically, fire has been a main disturbance force in the boreal forest (Heinselman 1973a). Due to fire suppression and increased harvesting efforts, timber extraction has become a more prominent disturbance force in the managed forest (Ward and Tithecott 1993). Harvesting and fire physically alter canopy characteristics, and interact with propagule banks and nutrient cycles according to the degree of biomass removal or consumption and heat penetration into the soil (Mou *et al.* 1993; Heinselman 1981). Johnston and Elliott (1996) found that herbaceous species compositions were more similar between burned cutover and wildfire sites than burned cutover and cutover sites, suggesting that fire and harvesting affect the environment in different ways. Fire changes the physical and chemical soil environment which, in turn, stimulates chemical reactions, and affects plant response (Ohmann and Grigal 1979). To manage a forest in a sustainable manner these differences need to be recognized.

A recent environmental assessment of timber operations in northern Ontario concluded that "...Crown forests and their associated ecological processes and biological diversity should be conserved..." and that forest practices should "...emulate natural disturbances and landscape patterns..." (Crown Forest Sustainability Act 1994, p. 1). A clear understanding of how natural forces influence the structure and function of forest ecosystems has yet to be determined.

Prescribed-burning is a vegetation management tool that allows forest managers to more closely `emulate natural forces'. Prescribed-burns are used to meet vegetation management goals while maintaining the safety of human life, property and resources. Managers identify the desired results, degree of organic layer removal and soil heating in order to determine the type of fire needed (Haeussler *et al.* 1990). Fires are ignited under a prescription which stipulates acceptable ranges in temperature, relative humidity, fuel moisture and wind direction and speed (Fuller 1991).

1.2. PURPOSE of STUDY

Many studies have described the diversity and species composition of early successional stages after fire (Methven and VanWagner 1975: Heinselman 1973a; Scheiner and Teeri 1981), and changes in nutrient availability and productivity (Ohmann and Grigal 1979; Raison 1979; MacLean et al. 1983). However, few studies have compared differences between burned and harvested sites. This study concentrated on the processes and mechanisms of revegetation after harvesting, harvesting combined with various degrees of burning, and wildfire. Data on fire characteristics, comparisons with unburned adjacent forest and complementary soil research helped to distinguish among different types of disturbance and how they influenced plant response.

The three hypotheses of this study were that:

1) various disturbance produce different initial species compositions;

2) the propagule bank will differ according to the disturbance type; and

3) nutrient concentration and allocation will differ among disturbance types for five selected species.

1.3. PROJECT DESIGN

For ease of interpretation this project has been divided into the three main themes; Initial species composition, Reproductive strategies, and Nutrient accumulation patterns. In Chapter 2, an investigation of early plant revegetation over the first growing season is presented. Initial plant succession is determined by disturbance characteristics and species survival strategies. Understanding plant responses can help identify successional pathways of future plant communities

In Chapter 3, propagule bank dynamics as a mechanism that influences future species composition is explored. Soil disturbance brings seeds to the surface and fire severity influences the viability of propagules and the germination conditions. Studying seed/bud bank dynamics will indicate regeneration potential of the site and support predicted changes for different disturbance conditions. Important concepts that are discussed include: dispersal patterns, germination requirements and how disturbance severity interacts with seed bank characteristics to determine post-disturbance species composition and density.

In Chapter 4, an investigation of variations in nutrient concentrations among disturbance types and different species is presented. *Cornus canadensis, Geranium bicknellii*, *Rubus idaeus, Prunus pensylvanica* and *Betula papyrifera* (a complete list of species names and authorities is found in

Appendix A) were chosen to represent different strata and reproductive strategies (seed, vegetative). Revegetation is the primary biotic mechanism that prevents the loss of mineralized nutrients after disturbance (Marks and Bormann 1972).

1.4 SITE DESCRIPTION

The study site is located in northwestern Ontario, 240 km NW of Thunder Bay (Figure 1.1). The site is about 900 ha and varies from gently rolling to hummocky, and includes moderately steep slopes with mineral soil and organic lowland sites scattered through the area. Two landform types formed during the Wisconsin Glaciation period characterize the site. The northern area is an esker complex of sand, gravel and boulders (soil type SS5). To the south, aeolian deposits of fine sand and silt are found. The moisture regime is dry to fresh (soil type S2 Sims *et al.* 1989) . Lowland sites have varying depths of organic soil.

Figure 1.2 indicates the spatial relation of disturbance types (Control, Harvested, Prescribed-burn, Reburn and Wildfire) and the distribution of research plots over the site. Upland sites were classified mostly as V-type 25, White spruce-Balsam fir / feather moss (Sims *et al.* 1989) and about 50 years old. Lowland sites were generally V-type 33, Black spruce/feather moss and about 100 years old (OMNR 1995). Sites that were not cut contained

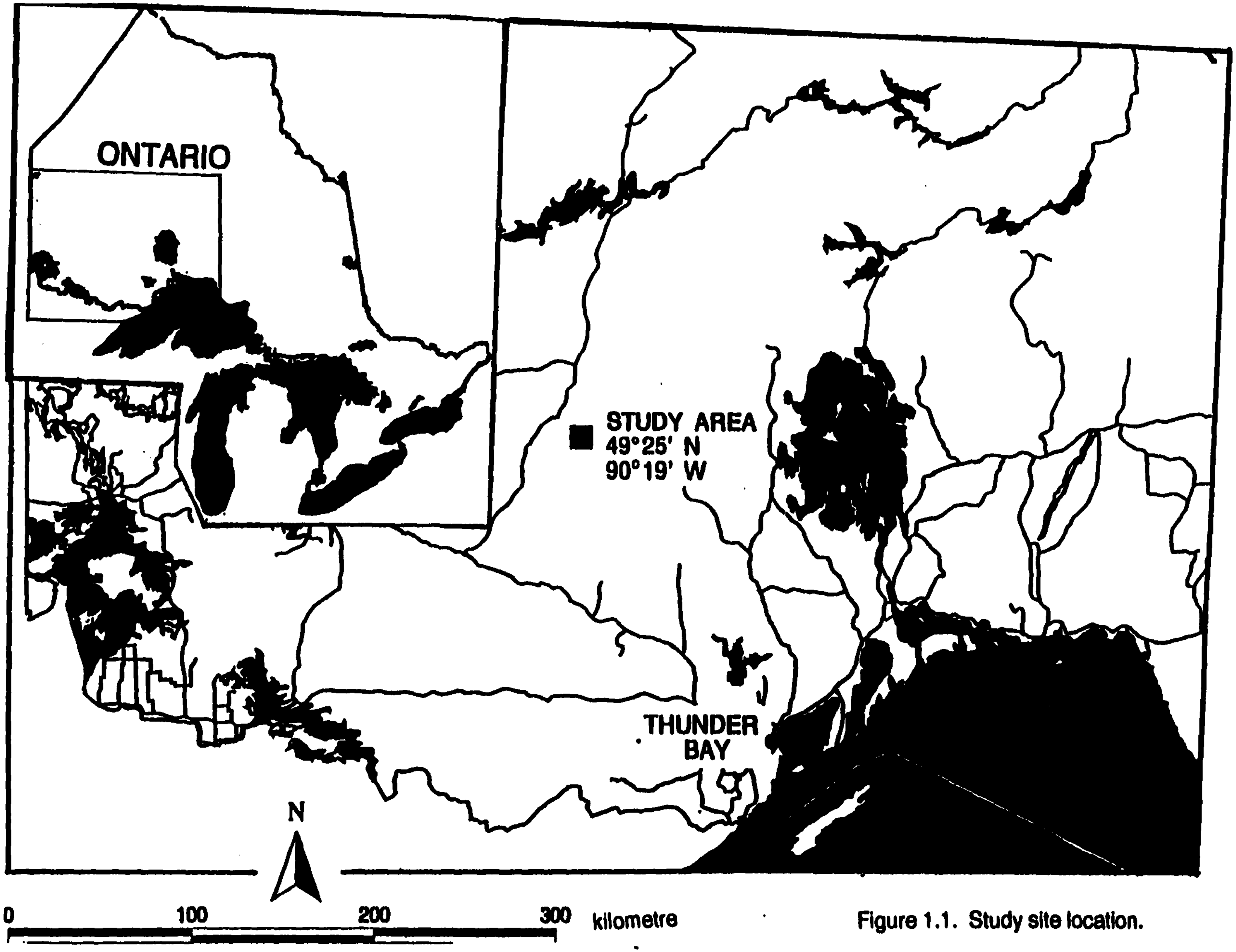


Figure 1.1. Study site location.

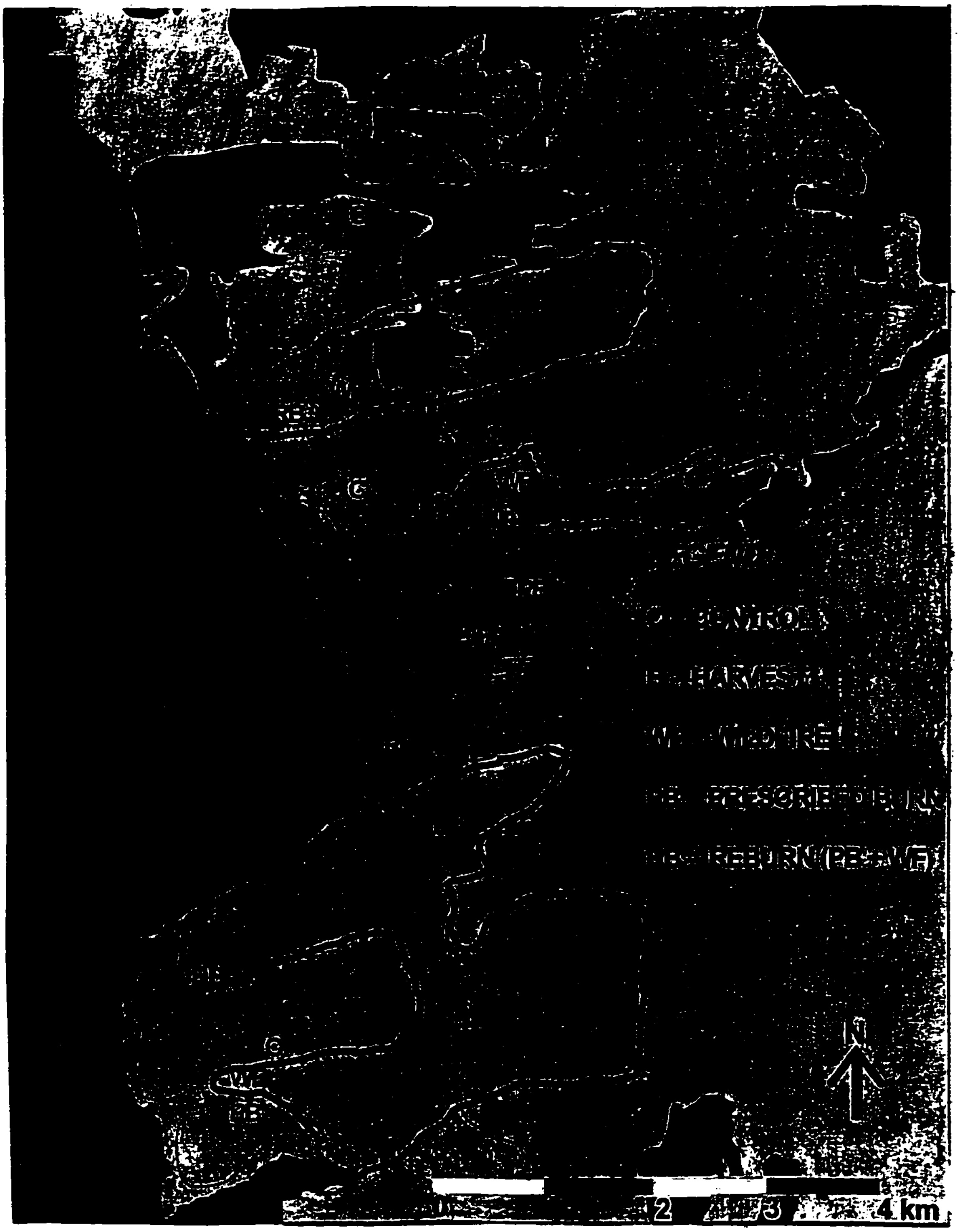


Figure 1.2. Plot layout. Harvested sites are shaded. Thin line represents harvested and Prescribed-burned sites (Prescribed-burn). Thick line oulines three wildfires, areas overlapping prescribed burn sites were designated Reburn and fire in surrounding forest are Wildfire sites. Control plots were placed in 'undisturbed' buffer zones.

budworm-killed balsam fir and blowdown. Charcoal at the organic / mineral soil interface indicated the stand is of fire origin.

The grouping of the Harvested treatments was unavoidable since the disturbances had occurred before this study was proposed. Soil textural differences were not significant between the northern and southern sites (Stronach 1996) and soil and vegetation analysis did not separate the Control block located near the harvested site from the other Control blocks. Details about the disturbance descriptions are included in Appendix B and summarized in Table 1.1. In order to quantify fire behaviour, study sites were located close (within 20 m) to of fuel sampling plots that were established before the Prescribed-burn.

The combinations of harvesting and burning disturbances on a similar site type provided an opportunity to study patterns of initial vegetation recovery. Although the Control site originated before 1934 (OMNR 1995), it would be inaccurate to call this site ‘undisturbed’ since disturbance takes many forms and occurs over different temporal and spatial scales (i.e. the site has been influenced by the spruce budworm). The Control treatment was included in the study to act as a benchmark indicating the nature of the original stand and the likely future composition of the disturbed communities.

Table 1.1. Summary of disturbance type characteristics. Details are given in Appendix B.

CONTROL	HARVESTED	PRESCRIBED BURN	REBURN	WILDFIRE
70 Years *Picea glauca*, *Abies balsamea*, Moss, Spruce Budworm Killed	Full-Tree, Delimbed at Roadside Winter 1992/93 Scalped 1994	Low intensity Prescribed Burn MAY 3, 1995	Prescribed Burn MAY 3 Wildfire MAY 30,1995	Wildfire May 30, 1995 Crown fire
DEPTH OF ORGANIC LAYER				
7.68 cm	6.1 cm	3.5 cm	2.8 cm	4.5 cm
FINE FUEL CONSUMPTION (0-6.99 cm in diameter)		16-48%	62-74%	
DUFF CONSUMPTION		4.5%-17%	23.4-43.8%	

CHAPTER II

INITIAL SPECIES COMPOSITION

2.1 INTRODUCTION

Initial plant establishment in the boreal forest after disturbance is the repair phase in a replacement cycle (Marks 1974; Halpern 1989). In the boreal forest, succession does not necessarily mean a change in species composition, but more accurately, a series of gradual shifts in a species' dominance (Ohmann and Grigal 1979; Halpern 1988; Brumelis and Carleton 1989).

Species of the boreal forest have evolved in the presence of fire (Heinselman 1973a). Many species have the ability to exist over many successional stages by sprouting from underground storage organs. Others have evolved to resist the stresses of disturbance either directly with thick bark or indirectly through abundant seed stored in the soil (Rowe 1983). Change in forest characteristics also involves structural changes as different species mature at different rates (Peet and Christensen 1980). Some sites have better growing conditions, so plants have the ability to mature more rapidly than on sites of lower productivity. As different phases of succession occur over the landscape, the area is maintained in a state of dynamic equilibrium (Wright and Heinselman 1973).

Harvesting and fire directly and indirectly affect the physical, chemical and biological environment. Changes at microhabitats influence the pattern of initial species establishment. Therefore, several potential successional pathways can occur, a concept known as multiple pathways of succession (Cattelino *et al.* 1979).

In this chapter different revegetation patterns and trends in species composition and diversity among disturbance types are explored. Divergence in recovery patterns among sites suggests that species are responding to ecological conditions created by the disturbance types. In this study, vegetation was classified by regeneration strategy and shade tolerance using the vital attributes system (Noble and Slatyer 1980). The concepts of regeneration niche (Grubb 1977) and multi-path succession (Cattelino *et al.* 1979) are explored in relation to the results. Understanding establishment patterns of the initial species composition may give some indication of the productivity of the site and the successional pathway that the plant community will follow.

2.2 LITERATURE REVIEW

2.2.1 Characteristics of fire-adapted species

Many survival strategies of boreal forest species are found in plants living in environments where other forms of stress, such as drought and herbivory, exist (Rowe 1983). Most boreal species are capable of more than one means of reproduction, sprouting vegetatively in mature communities and germinating from abundant seed when resources are liberated (Rowe 1983). Some plants also have a relatively large degree of phenotypic plasticity that allows them to adjust physiologically to a range of environmental conditions (Sultan 1987), from the harsh post-fire setting to nutrient poor mature forest. To ensure continued existence at a site, species must strike a balance between tolerating the present conditions while ensuring the ability to respond to a changing future environment (Pickett 1976).

Noble and Slatyer (1980) developed a method of classifying species according to: 1) their method of arrival or persistence; 2) their ability to establish and grow to maturity; and 3) the time it takes to reach reproductive maturity (Table 2.1). Since many boreal species have more than one reproductive method, they can fall into more than one category.

Rowe (1983) has further classified boreal species using their vital attributes to describe how species react to fire using the following terms: Invaders, Evaders, Resisters, Endurers and Avoiders. Invaders (DI species, Table 2.1) produce abundant wind-dispersed seed and are short-lived. *Epilobium angustifolium* and *Betula papyifera* are examples; once established they flower profusely and/or spread vegetatively (Dyrness 1973; Oswald and Brown 1993).

Table 2.1 Classification of Vital Attributes (modified from Noble and Slatyer 1980)

1. *Mode of regeneration and reproduction - first vital process.*

Vegetative-based:
V - able to resprout if burned in the juvenile stage
W - able to resist fire in the adult stage and to continue extension growth after it (fire kills juveniles)

Disseminule-based:
D - species with highly dispersed propagules
S - species store long-lived propagules in the soil
C - species store propagules in the canopy

2. *Communal relationships-second vital process*

T - tolerant species that can establish immediately after a fire and can persist indefinitely thereafter without further perturbations
R - tolerant species that cannot establish immediately after fire but must wait until some requirement has been met (e.g. for shade)
I - intolerant species that can only establish immediately after a fire. Rapid growth pioneers, they tend to die out without recurrent disturbance.

3. *Time scale of critical life history events - third vital process*
Measured from time zero (most recent fire) and plotted using the following symbols on a linear time axis:

p - time at which propagules arrive on burned site
m- time at which reproductive maturity reached, production of propagules
l - time at which species is lost from community by senescence
e - time at which propagules are lost from stored sources; species is locally extinct

Evaders (SI, CI, and ST species) use long-lived seed stored in the soil or the canopy to regenerate. Short-lived species deposit a 'one-shot' seed source on the charred surface that will remain dormant until the next disturbance (Rowe 1983). *Geranium bicknellii* (Schimmel and Granstrom 1993) and *Aralia hispida* are short-lived Evader species. *Prunus pensylvanica* is a species that is semi-tolerant to shade and will live for a longer period of time (Marks 1974). *Pinus banksiana* is an example of a CI species.

Resisters (WI species) have thick, protective bark that allows the species, usually a tree, to survive a fire. *Pinus strobus* is a species that uses this strategy.

Endurers (VI and VT species) have reproductive organs below the soil surface which are protected from above-ground disturbance (e.g. fire or harvesting). Although above-ground tissue may be removed by disturbance, underground buds will sprout depending on the depth of disturbance. Two-thirds to three-quarters of species found in northern forests and tundra use vegetative means of reproduction, so they make an important contribution to the plant community (Rowe 1983). Examples include *Populus tremuloides*, (shade intolerant), *Cornus canadensis* and *Pteridium aquilinum* (semi-tolerant to shade-tolerant).

Avoiders (DT and DR species) are late successional species that occupy unburned areas. They require a moist or shady environment and are susceptible to fire damage but can reestablish from unburned islands (Rowe 1983). *Abies balsamea* and *Linnaea borealis* are Avoiders.

2.2.2 Diversity

Diversity is an attribute of a community that describes both the number of species (richness) and their relative abundance (evenness) (Shafi and Yarranton 1973). A community that has a larger number of species but is dominated by one or two species is not as diverse as a community that has fewer species but all at a similar level of abundance. Alone, diversity indices are rather ambiguous but they are useful when comparing plant communities in different areas or over time.

Maintenance of higher diversity is usually associated with periodic disturbance (Connell 1978; Denslow 1980). Species likely co-exist because of resources liberated by disturbance, rather than because they have evolved together (Bratton 1976). In a black spruce site in northern Quebec, Morneau and Payette (1989) found that species diversity increased to a maximum at 23 years and declined to its lowest value at 250 years. After fire in black spruce sites in northeastern Ontario, Shafi and Yarranton (1973) found high diversity values for 4-11 years followed by a long decline. Diversity in northern ecosystems depends on scale and pattern of disturbance. Within-stand diversity may be low, but fire patterns over the landscape create between-site diversity and a spatial mosaic of community types and ages (Shafi and Yarranton 1973).

Disturbance characteristics such as size, frequency (Miller 1982) and intensity (or severity when describing fire) (Malanson 1987) influence the level of diversity found in post-disturbance communities. The intermediate disturbance hypothesis suggests that species of different regeneration strategies should be able to coexist if a disturbance occurs in the middle range of size, frequency and severity gradients (Malanson 1987).

2.2.3 Regeneration Niche and Multiple Successional Pathways

The regeneration niche encompasses all biotic and abiotic factors influencing the emergent seedling or sprout and its immediate environment. Such factors can include light, moisture, physical and chemical soil properties, type of surrounding vegetation and litter, exposure, competition and probability of predation (Grubb 1977; Collins and Good 1987; Farmer 1996). Since, unlike animals, plants require the same essential resources, Grubb (1977) suggests that it is the heterogenous character of the environment that maintains species richness and that species diversity is more related to a species' regeneration requirements than the habitat niche of adults.

After a disturbance, a community has the potential to follow a variety of successional paths depending on pre-disturbance species composition, disturbance characteristics, different responses of the vegetation and the heterogeneity of the post-disturbance environment (Halpern 1988).

Generally, annual and early successional species have similar responses to a broad range of environmental conditions and this tolerance narrows with later successional species (Bazzaz 1991). *E. angustifolium, Calamagrostis canadensis* (Landhausser and Leiffers 1994) and *Polygonium convolvulus* can germinate and become dominant over a range of soil, moisture and nutrient conditions if the site is competition free. Early successional species are often able to respond to changing conditions by adjusting morphologically (Sultan 1987; Bazzaz 1991).

2.3 METHODS

2.3.1 Data Collection

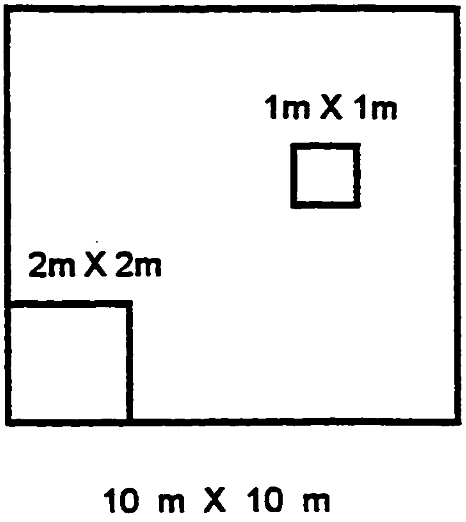
Within three weeks of the wildfire (site and disturbance description are given in section 1.2 and Appendix B), plots were chosen subjectively to represent average conditions for each of the disturbance types. Fuel sample plots had been established before the fire to characterize the fuel complex (amount, size, distribution, depth of duff). Fuels data were recollected after the fire on the same plots and calculations of fuel consumption and duff reduction were made using the Canadian Forest Fire Behaviour Prediction System (Fire Danger Group 1991) . Results are summarized in Appendix B, Table B.4. All

Prescribed-burn and Reburn vegetation blocks were established in association with fuel sample plots so pre-/ post-fire fuel and duff conditions could be quantified and related to vegetation response.

A 10 x 10 m plot was established on which diameter at breast height (DBH) and condition of trees greater than 50 cm in height were recorded. Within the 10 x 10 m plot, four 2 x 2 m shrub plots and five 1 x 1 m herb plots were randomly located (Figure 2.1). Percent cover of shrubs and trees less than 50 cm in height and herbs was recorded. Percent cover observations were recorded during the third week of June, July and August 1995.

2.3.2 Data Analysis

Ordination analysis describes species assemblages as a continuous arrangement over a gradient. Direct ordination uses both species and environmental data to arrange samples along the ordination axis (ter Braak 1994). In this study, disturbance type was the environmental variable and herb or shrub abundance data were the species variable. Canonical correspondence analysis (CCA; ter Braak 1987) was used for ordination analysis. CCA arranges points in ordination space so as to maximize the dispersion of species scores along the first axis, while constraining species scores to be maximally correlated with the supplied environmental variables. The second and succeeding axes provide other linear combinations which



TREES : ONE 10 m X 10 m PLOT

SHRUBS : FOUR 2 m X 2 m PLOTS

HERBS : FIVE 1 m X 1 m PLOTS

Figure 2.1. Vegetation plot layout. Herb and Shrub plots were randomly placed within the Tree plot.

maximally disperse species scores but are also uncorrelated with previous axes (ter Braak 1987). An eigenvalue is associated with each axis that identifies the percent variance explained by the axis. In the ordination diagram, similarities or difference among sample plots can be interpreted by the distance among the points or direction across the diagram (ter Braak 1994). All ordination analyses were carried out with the program CANOCO (CANOnical Community Ordination) (ter Braak 1990).

Shrub data were analyzed for the third collection period, which was taken to represent the sum of vegetation recovery after the growing season. Species data were transformed to 1+(log abundance) to reduce the influence of the most abundant species. Species with a "Fit" > 15% were identified and included in the ordination diagram. "Fit" expresses the proportion of variance in species abundance accounted for in the ordination.

Herb data were analyzed using the three sampling periods. Connecting temporally related vegetation blocks in the ordination diagram indicated how species composition changed over the growing season. Halpern (1988) used a similar method to display successional trends over a 21 year period. Distance and direction of the trajectories in the ordination field creates a visual representation and quantifies the divergence of plant communities.

Differences in relative abundance of species among disturbance types were tested for significance using a Kruskal-Wallis test, which is a nonparametric alternative to a one-way ANOVA. This test assumes the populations have equal means and variance but are not necessarily from a normal population (Norusis 1994b). The Mann-Whitney U test was also used as a pair-wise test to determine whether population means for the two groups are the same. Combined data values are ranked for two groups from which the average rank is derived (Norusis 1994b). A Bonferroni correction was used which adjusts the observed significance level by dividing it by the number of comparisons being made. In this case, a comparison of 5 disturbance types yields a total of 10 comparisons. Therefore $p= 0.05/10 =0.005$ for a species abundance to be significant at 0.05 level (Narusis 1994b). Herb and shrub species were also classified by vital attributes used by Noble and Slatyer (1980) (Table 2.1) and related to disturbance type.

Plant species diversity was calculated for herb and shrub strata using Shannon's index, H' (Ludwig and Reynolds 1988). This index combines information on the number of species and their relative abundance. H' will equal zero if there is a single species in the sample; H' is greatest when all species have equal abundance. H' is defined as:

$$H' = -\sum p_i \log_e p_i,$$

where p_i corresponds to the cover of species i as a proportion of the total cover among the n species.

The use of Shannon Index assumes that diversity of a natural system can be measured in a similar manner as information in a code or message (Magurran 1988). The index measures the average degree of 'uncertainty' in predicting to which species an individual will belong when chosen randomly from a collection of individuals. As the number of species increases and their distribution becomes even the average uncertainty will increase (Ludwig and Reynolds 1988).

Hill's E5 index (Ludwig and Reynolds 1988) was used to test species evenness among disturbance types. This index is relatively unaffected by species richness. Evenness approaches zero as a species becomes more independent, and is defined as:

$$E = \frac{(1/\lambda)-1}{e^{H'}-1} = \frac{N2-1}{N1-1}$$

where N2 ($1/\lambda$) is the number of very abundant species and N1 ($e^{H'}$) is the number of abundant. Shannon's index was calculated using Biological Tools 0.11 for Microsoft Excel (Hanks 1995).

Difference in species diversity among disturbance type was tested for significance using a Mann-Whitney U test with a Bonferroni correction. Species richness and evenness values are also included and tested using ANOVA.

2.4 RESULTS AND DISCUSSION

2.4.1 Initial Species Composition and their Vital attributes

An adequate number of samples were taken for the herb and shrub data as indicated by species/sample curves (Appendix C Table C.1. and C.2.). Curves leveled between 9 (Wildfire) and 19 (Reburn) samples for herbs and 6 (Harvested) and 13 (Control) samples for shrubs.

A complete summary of species composition and their vital attributes by disturbance type is shown in Table 2.2 (herbs) and 2.3 (shrubs). Due to the distribution pattern of the vegetations early recovery and the modest sampling size, abundance of species is not significantly different among disturbance types but trends are evident. Species with significantly greater cover on Control sites were feather moss (*Pleurozium schreberi, Ptilium crista-castrensis* and *Hylocomium splendens*), *Dicranum spp.*, *Abies balsamea, Acer spicatum* and *Alnus crispa*. These species can further be classified as Avoiders (VT) and Endurers (DT/DR) (Rowe 1983) and were common on mature sites studied by Dyrness (1973), Ohmann and Grigal (1979) and Johnston and Elliott (1996).

Harvested and Wildfire sites hosted a combination of shade-tolerant, vegetative, residual species (Endurers) and disturbance, seed species (Evaders and Invaders) without a strong dominance by any one species, resulting in higher diversity. Although species in these two disturbance types

Table 2.2. Relative abundance and Vital attributes (Table 2.1.) of herbs among disturbance types. Cover values with dissimilar letters represent significantly different species cover among disturbance types (p<0.05). Some vital attributes were assigned with reference to Heinselman (1981).

SPECIES	CONTROL	HARVEST	PRESCRIBED - BURN	REBURN	WILDFIRE	VITAL ATTRIBUTE
Aralia hispida	0	0	<1	<1	<1	SI
Aralia nudicaulis	3	<1	<1	0	<1	VT
Aster macrophyllus	0	3	<1	0	0	VT
Carex spp.	0	3	<1	3	3	DI
Clintonia borealis	1	<1	<1	<1	3	VT
Cornus canadensis	10	3	3	3	3	VT
Coptis trifolia	3	<1	<1	<1	0	VT
Corydalis sempervirens	0	<1	0	3	1	SI
Dicranum spp.	1 (a)	<1 (a)	0 (b)	0 (b)	0 (b)	DR
Epilobium angustifolium	0	0	6	<1	0	VI/DI
Epilobium leptophyllum	0	<1	0	<1	0	DI
Gaultheria hispidula	<1	0	0	0	0	VT
Geranium bicknellii	0 (a)	<1 (ab)	<1 (ab)	3 (b)	<1 (ab)	SI

Table 2.2. (Continued) Relative abundance and Vital attributes of herb species among disturbance types.

SPECIES	CONTROL	HARVEST	PRESCRIBED - BURN	REBURN	WILDFIRE	VITAL ATTRIBUTE
Goodyeara repens	<1	0	0	0	0	VR
Hylocomium spendens, Pleurozium schreberi & Ptila crista-castrensis	61 (a)	1 (ab)	0 (b)	0 (b)	0 (b)	DR
Linnaea borealis	5	3	0	<1	<1	VT
Lycopodium annotinum	0	0	0	0	<1	VT
Maianthemum canadense	4	1	<1	1	<1	VT
Polygonum convolvulus	0 (a)	8 (b)	21 (b)	8 (b)	1 (b)	SI
Rubus pubescens	0	0	0	<1	4	SI
Streptopus roseus	<1	<1	<1	<1	0	VT
Trientalis borealis	1	3	<1	<1	<1	VT
Viola spp.	0	<1	0	0	<1	ST

Table 2.3. Relative abundance and Vital attributes of shrubs among disturbance types. Cover values with dissimilar letters are significantly different among disturbance types (p<0.05). Some vital attributes were assigned with reference to Heinselman (1981).

SPECIES	CONTROL	HARVEST	PRESCRIBED -BURN	REBURN	WILDFIRE	VITAL ATTRIBUTE
Abies balsamea	4 (a)	0 (b)	0 (b)	0 (b)	0 (b)	VT
Acer spicatum	11 (a)	4 (a)	0 (b)	0 (b)	<1 (ab)	DT
Alnus crispa	2	0	2	0	0	VT
Betula papyrifera	<1 (a)	3 (b)	1 (b)	1 (a)	3 (b)	DI / VI
Diervilla lonicera	0	2	0	1	0	SI
Ledum groenlandicum	<1	0	0	0	0	VI
Prunus pensylvanica	0 (a)	2 (b)	3 (b)	4 (b)	3 (b)	SI
Populus tremuloides	0 (a)	0 (a)	<1 (a)	16 (b)	0 (a)	VI
Ribes spp.	0	<1	0	0	0	ST
Rosa acicularis	<1	0	<1	0	<1	VI
Rubus idaeus	1	10	5	15	5	VI / SI
Sorbus americanus	2	2	<1	0	0	ST
Salix spp.	0	<1	1	<1	0	VI / SI
Vaccinium angustifolium	0	<1	0	<1	0	VI
Vaccinium myrtilloides	1	3	1	1	<1	VI

show similar regeneration characteristics, the composition may have resulted from different causes. The wildfire occurred early in the burning season and the duff moisture code (DMC) was greater than that in areas that had been both harvested and burned (see Appendix B Table B.2.). A moist organic layer would have reduced the severity of the fire and protected rhizomes. Higher variability and larger areas of low duff consumption would have decreased the dominance by seed species. Species reproducing by seed would have to compete against vegetatively reproducing species and those stimulated by a heat pulse, like *G. bicknellii*, may not have been able to germinate as successfully under these wildfire conditions. In addition, Wildfire sites were not recently disturbed before the fire so *E. angustifolium* and *R. idaeus* would not have been present to reproduce vegetatively. Harvested sites have exposed mineral soil and disturbance species such as *P. pensylvanica* and *P. convolvulus,* but these species did not dominate the site. Harvested sites did, however, have significantly higher number of *B. papyrifera* seedlings.

Prescribed-burn and Reburn sites were dominated by species that are shade-intolerant and reproduce by seed (Endurers and Invaders). Typical post-fire species were well represented on burn plots. Abundance of *E. angustifolium* was higher on Prescribed-burn and Reburn plots and cover of *G. bicknellii* was higher on Reburn. These species are known for their dispersal or seed banking abilities (Archibold 1980; Heinselman 1980; Schimmel and

Granstrom 1993), and are able to dominate sites that are severely burned. In this case, it is likely that *E. angustifolium* became established after harvesting and rapidly reproduced vegetatively on Prescribed-burn sites. Observations during the seed banking portion of this study (Chapter 3) confirmed that *E. angustifolium* rhizomes were present in the soil collected in June but seed was not present. Halpern (1988) also found that post-logging establishment of *E. angustifolium* influenced post-fire abundance. *Rubus idaeus* was abundant on all disturbed sites. *R. idaeus* is a seed-banker but it also likely established after harvesting and sprouted vegetatively after the fire.

Some Endurers (VT) were also present but at a lower relative abundance, and the heat and drought of post-fire conditions caused their cover to decline. The fuel consumption data (Appendix B Table B.4.), showed that a larger percent of duff was consumed in Reburn plots. Greater fire severity on these sites may have volatilized a larger portion of nutrients and created drier, hotter growing conditions. Schimmel and Granstrom (1993) found that post-fire mortality was likely to be less severe if the canopy or dead trees persisted (e.g. wildfire sites in this study). Thus, although a variety of species occurred on Reburned plots, none was able to dominate. Sites that experienced a combination of harvesting and fire experienced the greatest degree of soil disturbance, which in turn, caused the greatest change in species composition.

Individuals of most species were found on sites of all disturbance types, including the Control. Shafi and Yarranton (1973), Brumelis and Carleton (1989), Hughes and Fahey (1991) and Mou *et al.* (1993) all noted that species composition was related to the heterogeneity of pre-disturbance vegetation and that the presence of vegetative reproduction allowed for *in situ* plant regeneration.

2.4.3 Diversity

In the herb stratum, diversity was highest on Harvested, Wildfire and Reburn plots (Table 2.4); only Harvested and Prescribed-burn plots differed significantly ($p<0.05$). Species were more evenly distributed on the Reburned and Wildfire plots than on Control and Prescribed-burn plots where moss or *E. angustifolium* and *P. convovulus* dominated. Richness was significantly less ($p<0.05$) on Prescribed-burn and Reburn sites.

In the shrub stratum, Harvested plots again displayed the greatest diversity and had significantly higher species richness. Evenness values were not significantly different among the various treatments.

Johnston and Elliott (1996) also found that diversity was greatest on harvested sites compared to burned and control areas. Five years after disturbance, mean Shannon's H' was 2.7 on the harvested site, 1.9 on wildfire sites, 1.7 on the burned cutover sites and 1.2 on the undisturbed . They

Table 2.4. Species diversity (Shannon's H'), evenness, and richness compared among disturbance types. Values in a row followed by dissimilar letters are significantly different (pair-wise Mann-Whitney U test with Bonferonni correction; $p< 0.05$).

HERBS	CONTROL	HARVEST	PRESCRIBED-BURN	REBURN	WILDFIRE
Species Diversity	0.9 (±0.5) (ab)	1.3 (±0.5) (a)	0.8 (±0.4) (b)	1.1 (±0.4) (ab)	1.1 (±0.6) (ab)
Evenness	0.5 (±0.3)	0.7 (±0.2)	0.6 (±0.3)	0.8 (±0.2)	0.8 (±0.2)
Richness	5.7 (±2.2) (a)	6.4 (±2.7) (a)	3.9 (±1.5) (b)	4.2 (±1.6) (b)	5.0 (±2.7) (b)
SHRUBS					
Species Diversity	0.5 (±0.4) (a)	1.3 (±0.2) (b)	0.5 (±0.5) (a)	0.4 (±0.4) (a)	0.5 (±0.4) (a)
Evenness	0.8 (±0.2)	0.8 (±0.1)	0.9 (±0.1)	0.8 (±0.3)	0.8 (±0.2)
Richness	1.9 (±1.1) (a)	4.9 (±0.9) (b)	2.5 (±1.5) (a)	2.3 (±1.3) (a)	2.1 (±1.0) (a)

hypothesized that harvesting created environmental conditions to which species were not adapted, and therefore, no single species could dominate the plant community. In contrast, on burned sites, *E. angustifolium* and *Polytrichum juniperinum* rapidly sequestered resources not found on harvested sites and dominated the vegetation (Johnston and Elliott 1996).

2.4.4 Successional Pathways

Knowledge of vital attributes helps identify how species are able to survive a disturbance and suggests the conditions under which the plant is more likely to regenerate. This information can be used to predict potential successional pathways that a community will follow. For example, *E. angustifolium* likely became established from seed after harvesting and reproduced vegetatively on Prescribed-burn sites. After flowering and dispersing its seed during the 1995 growing season, *E. angustifolium* will likely dominate many burned communities in the 1996 growing season.

Changes in species composition over time could be a reflection of how species are adjusting in response to their regeneration niche. Figure 2.2 shows changes in herb species composition for the four vegetation blocks from each disturbance type over the growing season. Axis 1 accounts for 60% of the variance in overall species-environment relationship and Axis 2 expresses an additional 12%. Axis 1 represents a soil disturbance gradient from Control

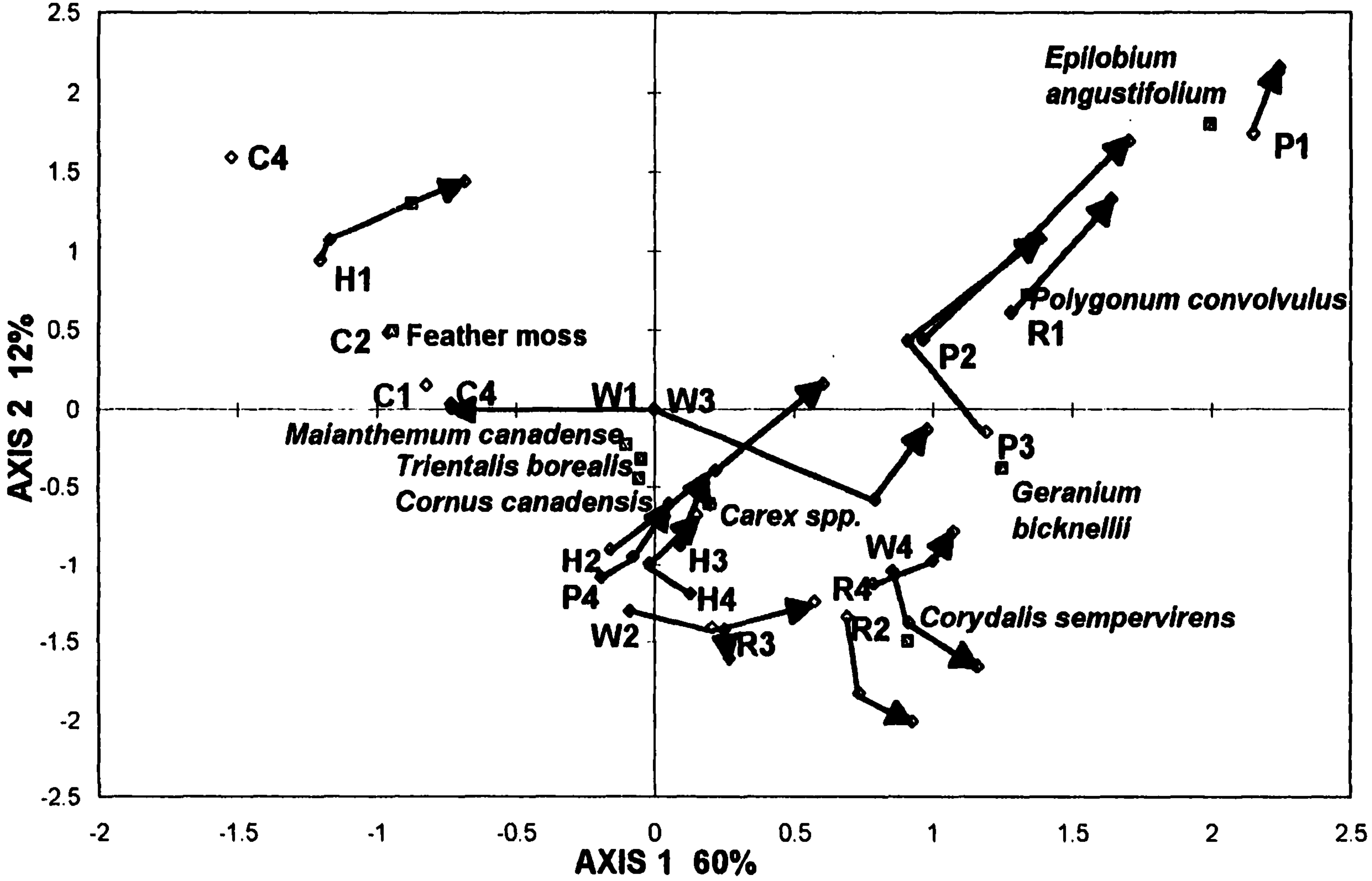


Figure 2.2. CCA ordination of herbaceous data showing the relationships between species composition and disturbance types over the growing season. Four vegetation plots represent the disturbance types which are abbreviated as: C, Control; H, Harvested; P, Prescribed-burn; R, Reburn and W, Wildfire. Species with a Fit >15 and relationships between species abundance and site are also included.

on the left to Harvested and Wildfire blocks in the centre and Prescribed-burn and Reburned blocks on the right. The Inter-set correlation of environmental variables with species axis is shown in Table 2.5. The correlation also identifies which disturbance type is best explained by each axis (ter Braak, 1987). Control blocks have a strong negative correlation with axis 1 that represents the separation of undisturbed and disturbed vegetation from the disturbance blocks. The second axis represents the primary dimension of variability between the three burned disturbance types.

Within each disturbance treatment there is one vegetation plot with a slightly dissimilar species composition. For example, a Harvested block (H1) happened to have some residual moss so it is found with the Control blocks. Over the growing season the moss dried and declined and *E. angustifolium* expanded its cover, moving this block's trajectory toward the right.

Flinn and Wein (1988) found that most species show some regrowth in the first month. In the first three weeks, many Harvested and some Wildfire blocks are situated near the origin and are associated with vegetative species like *C. canadensis, T. borealis* and *C. borealis*. Prescribed-burn blocks were associated with *E. angustifolium* and *P. convolvulus* and Reburn blocks by *G. bicknellii* and *C. sempervirens*.

As the growing season progressed, movement of blocks to the right seems to be influenced by the increasing cover of *E. angustifolium* and *P.*

Table 2.5. Inter set correlations of environmental variables with species axes among the four vegetation blocks within each disturbance type. C, control, H, Harvest, P, Prescribed-burn, R, Reburn and W, Wildfire. Plots where no vegetation was present during the first sampling period are identified by 'no veg'.

PLOT	JUNE		JULY		AUGUST	
	AXIS 1	AXIS 2	AXIS 1	AXIS 2	AXIS 1	AXIS 2
C1	-.16	.26				
C2	-.18	.82				
C3	-.19	.18				
C4	-.14	.06				
H1	-.10	.71	-.97	.78	-.63	.12
H2	-.20	-.98	.31	-.50	.10	.23
H3	.15	-.13	.30	-.83	.36	-.10
H4	.12	-.93	-.02	-.93	.18	-.73
P1	.20	.14	.36	.30	.37	.31
P2	.58	.23	.10	.72	.16	.11
P3	.41	-.05	.55	.23	.11	.74
P4	-.10	-.51	-.07	-.74	.06	-.60
R1	no veg	no veg	.86	.36	.18	.16
R2	.30	-.51	.84	-.18	.19	-.23
R3	no veg	no veg	.14	-.71	.20	-.10
R4	.47	-.60	.88	-.19	.14	-.90
W1	-.04	-.23	-.04	-.23	-.43	.00
W2	-.06	-.78	.22	-.13	.88	-.17
W3	.03	-.34	.56	-.36	.95	-.11
W4	.30	-.32	.87	-.12	.13	-.24

convolvulus to the upper right, or *G. bicknellii* and *C. sempervirens* to the lower right. Sites that were both harvested and burned had initial species compositions that were the most different and trajectories that moved the farthest away from their original composition (Control). The exception, a Wildfire block (W1) produced very little vegetation but species that did appear were vegetatively regenerated, e.g. *L. borealis* which was strongly associated with Control blocks.

In a similar analysis involving harvesting, burning and both disturbances over a 21 year period, Halpern (1988) found that the direction and magnitude of the original trajectory was related to soil disturbance. Trajectories reflected changes in dominance by annuals and perennials to transient and persistent woody vegetation. Convergence of trajectories occurred with a gradual decline in invading species and recovery of initial understory composition. Rapid change relative to undisturbed sites lasted one to two years after fire, after which herb dominance declined (Halpern 1988).

Figure 2.3 and 2.4 show the spatial relation of individual herb and shrub sample plots based on their species composition at the end of the growing season. Due to the variability in fire behaviour and the short recovery period, sample plots were not restricted to the area around the disturbance centroid. However, the spatial relationship of disturbance centroids along Axis 1 does suggest a disturbance gradient moving from control plots right to left. The

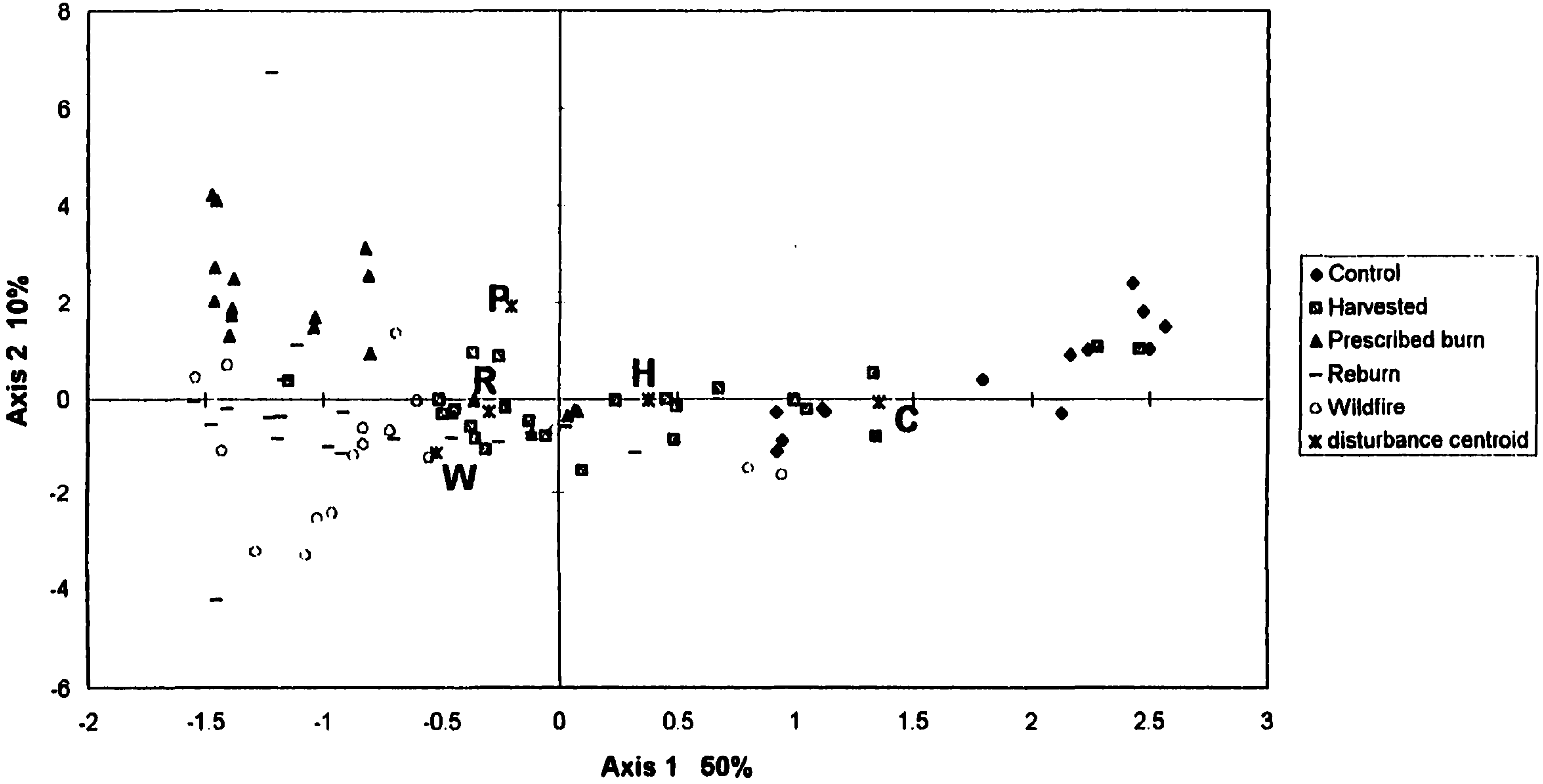


Figure 2.3. CCA ordination of herbaceous data showing the relationship between sample plot species composition and sites. Site abbreviations: C, Control; H, Harvested; P, Prescribed-burn; R, Reburn and W, Wildfire.

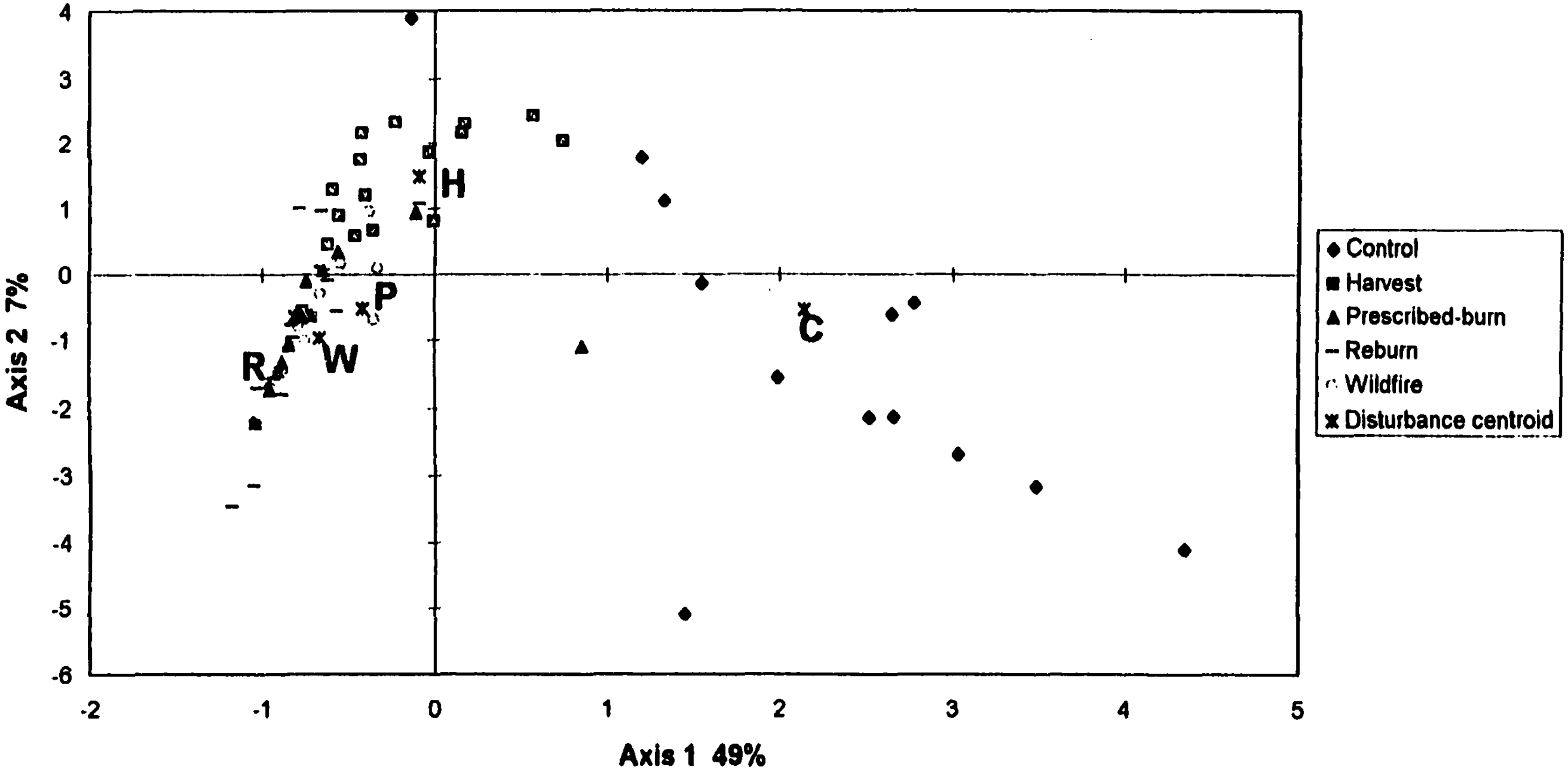


Figure 2.4. CCA ordination of shrub data showing the relationship between sample plot species composition and sites. Site abbreviations as in Figure 2.3.

general ordination pattern for herb composition is very similar to that found by Johnston and Elliott (1996) five years after plots had experienced harvesting, harvesting and fire, and wildfire. Again, Axis 1 had a strong relationship with Control plots and expressed 50% (herb) or 42% (shrub) of the variance in species-environment relationship (Table 2.6). The linear pattern found in the shrub strata in the Control plots (Figure 2.4) correlates with the abundance of *Abies balsamea* that occurred on the plot and with the degree of species richness.

Species placement along the axes may also indicate other environmental gradients such as moisture, exposure and nutrient availability. Figure 2.5 identifies shrub species associated with the various disturbance types (a Fit > 15%). Species such as *E. angustifolium* (Figure 2.2), *R. idaeus* and *P. pensylvanica* were associated with areas that experienced fire and are known for their ability to rapidly sequester resources (Marks 1974; Landhausser and Lieffers 1994). This topic is explored further in Chapter 4.

2.5 CONCLUSION

Characteristics of the different disturbance types initiated and supported different species compositions. Many species were found on all sites but their relative abundance varied greatly according to disturbance type. Higher diversity was found on Harvested and Wildfire sites where plants used seed

Table 2.6. Inter-set correlations of environmental variables with species axes for herb and shrub ordinations.

SITES	HERBS		SHRUBS	
	AXIS 1	AXIS 2	AXIS 1	AXIS 2
CONTROL	.81	-.34	.84	-.15
HARVEST	.22	.09	-.53	.62
PRESCRIBED-BURN	-.84	.61	-.17	-.15
REBURN	-.15	-.10	-.34	-.19
WILDFIRE	-.21	-.36	-.25	-.26
Eigenvalues	.50	.20	.42	.13

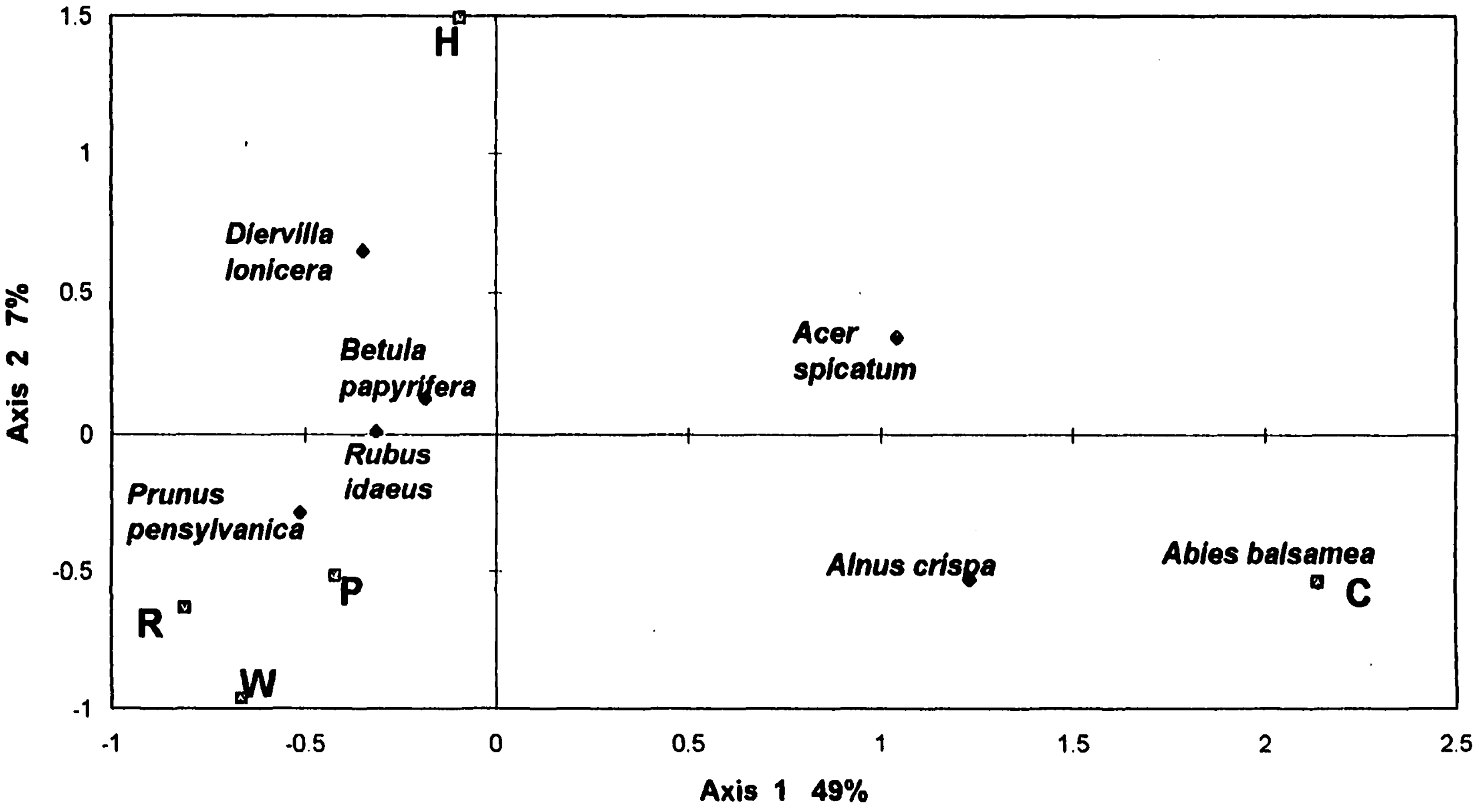


Figure 2.5. CCA ordination of shrub data showing relationships between species abundance and sites; only species with a Fit > 15% are shown. Site abbreviations as in Figure 2.3.

and vegetative means of re-establishment, but no species were able to dominate these environments.

Vital attributes of the regenerating plants indicated the degree of soil disturbance. Disturbance severity directly influenced the number of viable seed and rhizomes remaining in the soil. Patterns of reproductive strategies among different disturbance types are further explored in Chapter 3.

Although the multi-path succession exercise was exploratory in nature, it suggests that disturbance types created different regeneration niches that directed the communities on different successional pathways. The initial species composition may reflect environmental conditions created by the different disturbances. Resource availability, will influence species composition as some species are better able to dominate nutrient rich sites than others (Rodenkirchen 1995). Species establishment, early growth and survival represent critical stages in developing community structure and character (Shupp 1995). Although mature species composition may be similar, important factors such as nutrient availability may remain different over time.

CHAPTER III

DISTURBANCE AND REPRODUCTIVE STRATEGIES

3.1 INTRODUCTION

The seed and bud bank is an expression of a site's potential species composition (Harper 1977). Plants that arise from the propagule bank are influenced by both past and present selective pressures (Parker *et al.* 1989). Species that existed on the site in the past may have deposited seeds that remain dormant, and present conditions will determine if the seeds will germinate and survive.

Disturbance type and severity will have a large impact on the number of viable propagules remaining in the soil and the ability of emergents to survive in the post-disturbance environment. As a product of evolution, different species have different reproductive strategies. The purpose of this study was to compare the interaction of different disturbance types with the site's population of viable propagules. Seed banking patterns were related to quantified fire severity measurements and post-disturbance and post-growing season seed banks were compared to determine seasonal changes in propagule bank characteristics. Projections of future species composition were made by examining patterns of regeneration strategies within disturbance types.

3.2 LITERATURE REVIEW

3.2.1 Seed Banks

In the boreal forest, seed densities in the soil generally decrease with increasing latitude (Johnson 1975; Archibold 1989), although Fyles (1989) found unexpectedly high numbers at 55°N latitude.The number of viable seeds in the boreal forest differs according to species composition and age (Table 3.1). Seed numbers decrease from a deciduous to conifer dominated forest (Moore and Wein 1977; Isaac 1982; Archibold 1989). Forests dominated by deciduous species will create seed bank conditions that are more hospitable (i.e. more nutrients, less acidity). In a mature, conifer-dominated forest, seed-bed conditions are often dark, cold, acidic and low in available nutrients, leaving seeds susceptible to fungal attack, decomposition and with inappropriate conditions for germination. Average seed densities in the soil are highly variable and often bear little relation to the number of seedlings that actually emerged on a site (Morgan and Neuenschwander 1988), but seed bank composition comparisons help to identify potential dominant species.

Species of early successional plant communities produce large numbers of seed capable of wide dispersal (e.g. *Epilobium angustifolium*) or long dormancy periods (e.g. *Prunus pensylvanica*). In later successional stages, species continue to deposit seed but seeds quickly lose viability. *Picea glauca* and *P. mariana* lose viability after 5 years and 10-16 months, respectively

Table 3.1. Summary of viable seed bank size and species richness over boreal forest region. Adapted and expanded from Hills and Morris (1993).

Forest type & Location	Age (years)	Forest Origin	Viable seed. m^{-2}	Number of Species	Source
Sweden	16	-clear cut / burn	425	10	Granstrom
Pinus sylvetris	29	-control	240	7	(1982)
	50	-burned	730	10	
Picea abies	120	-selective felling	675	7	
Pinus-Picea-Populus	169	-fire origin	763	5	
New Brunswick					Moore &
Betula-Fagus	> 40	-stand replacing fire 91 years	3400 (± 910)		Wein (1977)
Acer-Fagus	> 40	ago only small fires since then.	1950 (± 620)		
Acer	5	-clear cut	1390 (± 260)		
Picea	3	-clear cut	180 (± 80)		
Acer-Abies	> 40	-stand replacing fire 91 years	1230 (± 260)		
Picea-Pinus	> 40	ago, only small fires since then.	580 (± 90)		
Picea	> 40		370 (± 140)		
Northern Alberta					Fyles
Pinus banksiana	45	-fire origin	1030 (± 175)	7	(1989)
Pinus banksiana	85		505 (± 100)	8	
Picea glauca	80		2650 (± 270)	11	
Pinus-Abies	145		1010 (± 160)	7	
Northern Saskatchewan					Archibold (1979)
Picea-Betula-Populus	0	-burned	426	15	

Table 3.1. (Continued) Summary of seed bank characteristics and species richness.

Forest type & Location	Age (years)	Forest Origin	Viable seed. m^{-2}	Number of Species	Source
Northeastern Minnesota					Ahlgren (1979a)*
Pinus banksiana	3-13	-burned	9450	11	
Pinus banksiana	30-70	-burned	4815	17	
Pinus resinosa and *P. strobus*	200+	-fire origin	2323	11	
Abies balsamea	80+	-budworm damage	7429	15	
Populus spp.	70	-fire origin	5638	11	
Pinus banksiana	12	-uncut unburn	1016	10	Ahlgren (1979b)
	12	-cut unburned	2976	10	
	12	-cut and burned	2807	7	
Pinus resinosa		-unburned	392	8	Ahlgren (1979c)
		-burned	2428	10	
Northwestern Ontario					Isaac (1982)
Mixedwood	55	-harvested	2157	44	
Populus spp	50		1880	41	
Picea mariana	60		1099		
Pinus banksiana	9	-fire origin	350	19	Vermeer (1984)
	14		358	19	
	70		151	12	
Mixedwood	85		1732	16	Collins (1985)
	85		1307	10	
	85		1273	13	
Populus-Pinus-Abies	50	-harvested	843	24	Qi and Scarratt (1996)
	0	-clear cut			
		surface - 2 cm	2430	14	
		>2 cm	4110	16	
		org. 0-3 cm	2160	11	
		min. 4-6 cm	990	8	
	0	-partial cut			
		surface-2 cm	1730	13	
		>2 cm	4210	15	
		org. 0-3 cm	2110	10	
		min. 4-6 cm	1120	7	

* Study involved counting seeds and did not use the germination method.

(Archibold 1989). Unless a site has recently experienced a good seed year, very little conifer seed is found in seed banks (Granstrom 1982; Fyles 1989; McGee and Feller 1993; Qi and Scarratt 1996). In later stages, seed input decreases and many species reproduce vegetatively (Ahlgren 1979a, b, c ; Chambers and MacMahon 1994). As a result, seed bank species composition rarely reflects the surrounding mature forest (Archibold 1979; Abrams and Dickmann1982; Granstrom 1982;Valbuena and Trabaud 1995; Qi and Scarratt 1996) and is largely determined by seed longevity (Parker *et al.* 1989).

3.2.2 Seed Dispersal

Seed dispersal allows a species to colonize new areas, escape inhospitable environments often created by parent plants, and reduces sibling competition and inbreeding (Harper 1977; Farmer 1996). Several factors influence dispersal, including: seed morphology, soil surface characteristics, abiotic (e.g. weather) and biotic factors (e.g. animal and bird dispersal). Dispersal methods include gravity, wind, water and animals as sources of movement. Seeds are generally equipped with wings, plumes, buoyancy devices, burrs or nutritional rewards to enhance the success of one of the above dispersal methods (Chambers and MacMahon 1994).

Seeds are not uniformly distributed but form clumped patterns related to when and where the mother plant occurred in the forest community or to the distribution of animal caches. Thus, seed distribution patterns in the soil vary horizontally, as one moves further from the mother plant, and vertically as the organic matter thickens with litter accumulation (Morgan and Neuenschwander 1988).

Most boreal tree species release seeds during late fall / winter. *Betula papyrifera* releases most of its seed between September and late November (Marquis 1969),*P. glauca* disperses between September and January (Ahlgren 1979a, b), while *P. mariana* stores mature seed in its canopy until a February to June dispersal period (Haavisto 1978). During favourable conditions, some trees can release seeds stored in the canopy. *Pinus banksiana* is an example, in which seed release is stimulated by the heat of fire which also creates appropriate germination conditions for the seed (Rowe 1983).

Conifer seeds fall within 60 m of the parent tree in open areas and within 30 m in a closed stand, distributed in a J-shaped pattern, skewed to the prevailing windward side (Dobbs 1976). For *Betula*, dispersal is usually limited to two times the height of the tree (Marquis 1969). In contrast, *E. angustifolium*, *Populus spp.* and *Salix spp.* produce light fluffy seed that can travel on the wind up to 300 km (Haeussler *et al.* 1990).

Once a seed has landed on a surface, seed and surface characteristics determine the extent of horizontal and vertical movement (secondary seed dispersal). Smaller seeds are able to reach greater distances either by wind, moving along the snow crust or percolating through the soil. Seed movement within the soil by water is influenced by intensity and amount of precipitation, slope, pore size, texture and organic matter content (Moore and Wein 1977; Chambers and MacMahon 1994). Soil with more varied microtopography and litter will capture more seed but these environments do not necessarily provide the best germination conditions (Lamont *et al.* 1993; Chambers 1995).

The first two centimetres of organic matter above the mineral soil contains the highest concentration of seed (Moore and Wein 1977; Granstrom 1982; Valbuena and Trabaud 1995; Qi and Scarratt 1996). Fewer seeds are found on the surface since later successional species have low seed input with short viability and seeds are susceptible to predation and pathogens or may germination.

3.2.3 Dormancy

A seed is considered dormant if it will not germinate when subjected to appropriate moisture, oxygen and temperature conditions (Murdoch and Ellis 1992). Dormancy characteristics likely developed to ensure that seeds germinate under appropriate conditions. Temperature, moisture, light and nutrient conditions indicating that spring has arrived or that a disturbance has occurred are important germination cues (Murdoch and Ellis 1992).

Since the seeds of most boreal species are dispersed in the fall / winter, they experience a conditional dormancy to ensure they will not germinate before winter. Conditional dormancy for conifers and *B. papyrifera* can be broken by longer photoperiods and / or higher temperatures (25-30°C) (Bevington 1984 in Farmer 1996). If the seeds of *P. mariana* (Farmer *et al.* 1983) and *Alnus crispa* (Farmer *et al.* 1985) experience a chilling period, they are capable of germinating in the dark at lower temperatures (10-20°C).

Impermeable seed coats inhibit the imbibition of water and thus germination. Marks (1974) found that removing the endocarp, which is impermeable to water and oxygen, increased the germination of *P. pensylvanica*. Endocarps can deteriorate naturally with age, and physical and biological weathering. Similar observations have been made for *Rubus. idaeus* (Oleskevich *et al.* 1996). Both species are sensitive to temperature fluctuations and fertilization.

Some species disperse seed with an immature embryo and require an incubation period. Dormancy of *R. stigosus* (a subspecies of *R. idaeus*) seed is caused by an acidic, ether-soluble, growth-inhibiting substance. A warm, moist stratification and prechilling were found to stimulate germination (Jennings 1988).

Seed longevity is greatest under cool, dry conditions. Cool, moist conditions allow natural stratification and increase germination whereas warm, humid conditions increase loss though decomposition and pathogens (Baskin and Baskin 1989).

3.2.4. Bud Banks

Rhizomes are an important mechanism of recolonization as they revegetate rapidly, retain nutrients on the site and prevent erosion by binding soil in root systems (Flinn and Wein 1977; Flinn and Pringle 1983). Species can coexist by rooting at different soil depths and by having various rooting morphology (e.g. fibrous roots, stolons, rhizomes and tap roots) (McLean 1969). Species have different tolerances for temperature and moisture according to conditions found at different soil depths (Bazzaz 1991).

3.2.5. Direct effects of Fire

Seed bank size is determined by fire type, severity and frequency (Archibold 1989). A crown fire will not directly affect the seed bank. Although the canopy may be consumed, it is the surface and sub-surface fires which will have a direct effect on the seed bed. Since sub-surface fuels are usually moist, most ground cover will be consumed by smoldering combustion rather than the initial flaming combustion (Schimmel and Granstrom 1993). Therefore, fire severity, or the depth of burn, is a more accurate measure of how fire affects the seed bed than fire intensity (energy released).

Heat acts as a selective agent, causing seed scarification or death (Morgan and Neuenschwander 1988). Although the size of the seed bank will decrease as seeds are consumed by fire (Abrams and Dickmann 1982; Ingersoll and Wilson 1990), often more seeds are released following fire than on unburned areas (Ahlgren 1979a; Archibold 1989). Fire adapted species release seed or break dormancy in response to heat, temperature fluctuations and greater nutrient availability.

Generally, rhizomes can tolerate heat up to 55-59°C and seeds up to 60-75°C for 10 minute exposures without being killed (Granstrom and Schimmel 1993). At 60°C, protein coagulates and causes lethal damage to plant tissue (Precht *et al.* 1973). Moisture content of plant tissue will determine a plant's heat tolerance with drier tissue able to withstand higher temperatures for longer durations (Schimmel and Granstrom 1993).

The temperature gradient through the organic layer and into the mineral soil is very steep. For example, lethal temperatures were not reached 20-30 mm under the burned surface and did not rise above 50°C below 40 mm (Schimmel and Granstrom 1993). Although there is variation in heat tolerance among species, the relationship between depth of propagule and fire severity is a more decisive factor in determining post-fire species composition (Granstrom and Schimmel 1993). Species well represented in early successional communities have rooting systems that are protected in the lower organic or upper mineral soil (Flinn and Wein 1977). The location of regenerative mechanisms for some boreal species is summarized in Table 3.2.

Sprouting and suckering in response to heat is determined by temperature, duration of exposure, physiological condition, season and degree of stored nutrient reserves (Flinn and Pringle 1983). In their study, Flinn and Pringle found that many species, such as V*accinium angustifolia* and *Cornus canadensis*, produced significantly more shoots when exposed to heat at the beginning or end of the growing season. Heat causes stress on the cytoplasm, protein coagulation and creates toxic substances (Flinn and Pringle 1983).

Geranium spp. is an example of one of the few species that requires heat to trigger germination; virtually no germination will occur with unheated seed (Abrams and Dickmann 1982; Granstrom and Schimmel 1993). Its seed coat is impermeable to water and seeds have exceptionally low moisture content, allowing it to tolerate high temperatures. Germination will progressively increase above 40-45°C (10 min. exposures), and will occur early and completely when exposed to temperatures between 50-80°C. *Geranium* germination was delayed by several days after being exposed to 90 to 95°C but was nevertheless almost complete (Granstrom and Schimmel 1993).

Table 3.2. Location of propagules for boreal species (s; seed; v, vegetative). Summarized from Flinn and Wein (1977), Flinn and Pringle (1983) and Qi and Scarratt (1996).

LITTER LAYER	F-H LAYER	MINERAL SOIL
Gaultheria hispidula (v,s)	*Aralia hispida* (s)	*Aralia nudicaulis* (s)
Trientalis borealis (v,s)	*Diervilla lonicera* (s)	*Lycopodium obscurum* (v)
Epilobium angustifolium (s)	*Rubus idaeus* (s)	*Vaccinium angustifolium* (v,s)
Maianthemum canadense (v,s)	*Rubus pubesces* (s)	*Vaccinium myrtilloides* (v,s)
Coptis trifolia (v,s)		*Cornus canadensis* (v)
Betula papyrifera (s)		*Pteridium aquilinum* (v)
Mitella nuda (v,s)		*Carex spp.* (s)
Fragaria virginiana (v,s)		*Geranium bicknellii* (s)
Linnaea borealis (v,s)		*Epilobium angustifolium* (v)

3.2.6. Indirect effects of Fire

The type of vegetation and the degree of duff consumption will determine the depth and chemical content of the ash.Thomas and Wein (1990) found that wood ash, especially aspen, reduced and prevented germination, early survival and growth of *Pinus banksiana* seedlings. Wood ash pH ranged from 10.6 to 12.5 because of the potassium carbonate content (Thomas and Wein 1990). Although species' responses varied, Henig-Sever *et al.* (1996) found percent germination declined significantly with increasing pH. *Pinus halepensis* experienced 100% germination at a pH between 6-7 but germination was reduced by 88% at a pH of 10. Toxins and heavy metal concentrations, which hinder germination and growth, will eventually leach into the soil or off the site. The greatest leaching will occur in the first 3 to 6 months and the leaching pattern may last for 1 to 3 years (Thomas and Wein 1994).

In a germination trial involving *Pinus halepensis* in various levels of ash, Ne'eman *et al.* (1993) and Henig-Sever *et al.* (1996) found ash levels had a negative effect on the germination of all species. Henig-Sever *et al.* (1996) found a negative effect because of the high osmotic potential of ash preventing water uptake by the embryo. Unleached ash is more granular and has a lower bulk density than soil. Surface crusting and poor water penetration due to hydrophobic layers will cause water stress for seedlings (Thomas and Wein 1990).

Relative `safeness' of burned sites depends on the ability to protect seedlings from exposure and provide adequate water availability (Lamont *et al.* 1993). The blackened surface has an albedo near zero and low thermal conductivity (Kimmins 1987). When air temperatures are at 38°C, surface temperatures can reach 73°C (Isaac 1938). Many seedlings will be lost due to germination and subsequent death caused by heat and drought conditions (Schimmel and Granstrom 1993).Species heat and moisture tolerance, post-fire precipitation and leaching, and ash characteristics will determine germination response. Ne'eman *et al.* (1993) suggest that ash accumulation results in different seed germination responses and may cause spatial patterns of recruitment after fire. As vegetation reestablishes on post-fire sites, it will ameliorate some of the extreme conditions. Eventually shading and competition for space become more important inhibitory factors (Trabaud 1988).

3.2.7. Harvesting and Propagule banks

Most harvesting tends to redistribute the forest floor causing vertical and horizontal changes in seed location. This, in turn, influences the conditions and rate of germination (Mou *et al.* 1993). Since the organic layer is not removed it can hinder seedling establishment. Local heterogeneity is created by the variability of soil disturbance caused by harvesting methods.

The use of heavy machinery and intensive harvesting can cause soil crusting and compaction which will preclude seed entrapment and inhibit emergence (Chambers and MacMahon 1994).

The removal and redistribution of the organic (litter and humus) layer tends to enhance germination and create a high variability in seed distribution (Qi and Scarratt 1993). Scarification tends to liberate buried seeds and rhizomes in such species as *Rubus spp.* and *P. pensylvanica* (Morgan and Neuenschwander 1988; Fyles 1989).

Species composition did not vary significantly between harvested and control sites in a boreal mixwood stand (Qi and Scarratt 1996). Several species appeared in the seed banks of both sites that did not appear in the pre-harvest vegetation (*E. angustifolium, Fragaria virginiana, Galium triflorum* and *G. bicknellii*).

3.2.8. Methodological Considerations

Two methods are widely used to estimate species composition and seed density of the soil seed bank: seeds are separated from the soil, and counted and identified (Marquis 1969; Johnson 1975; Ahlgren 1979a; Morgan and Neuenschwander 1988); or soil samples are placed in a greenhouse and species numbers and identity are estimated by germination. Separating the seed from the soil is a good method for documenting variation in seed densities and distributions; however, it is labor intensive and requires a large seed library and viability tests (Gross 1990). This method also increased variability between sites and the detection of rare species that are not useful in comparative studies (Brown 1992).

The second method will likely underestimate the seed population as not all seed will germinate under greenhouse conditions. In addition, errors associated with seed dormancy and germination requirements will be made and seedlings may die before identification. This method is recommended for community level studies when species numbers are high (Simpson *et al.* 1989) and provides an estimate of the viable fraction of the seed bank (Brown 1992).

3.3. METHODS

3.3.1. Data Collection

Four 10 X 10 cm propagule bank samples were taken, one from each side of the four vegetation blocks found in the five disturbance types described in Chapter 2. For each sample, the organic layer was measured for depth and removed and 10 cm of mineral soil was then removed. Each soil layer was placed in a separate plastic bag. Samples were immediately transported and placed in the greenhouse.

During the first week of October, another set of samples was collected adjacent to the June sampling site using the same procedure. These samples were put in cold storage at 5°C for four months and then placed in the greenhouse.

3.3.2. Germination Procedure

Moss and green vegetation were carefully removed from Control samples. Samples were placed on a layer of peat vermiculite in 6 X 4 cm peat pots; some samples required more than one pot. Greenhouse temperatures were set at 23°C during the day and 18°C at night. Daylight was enhanced by florescent light and lasted 16 hours; samples were watered as needed.

Once germinants were identified according to Morton and Venn (1990), they were removed from the soil, taking note whether they originated by seed or vegetatively. This study did not include moss, liverworts, lichens or fern thallus. Graminoids were mainly sedges but did not produce any flowers so were not identified. Other unknowns died before secondary leaves could develop. Soil samples were stirred when germinants no longer appeared. When no germinants had appeared two weeks after stirring all samples, the experiment was terminated. The June seed bank experiment lasted 15 weeks and the October experiment concluded after 14 weeks.

3.3.3 Data Analysis

Sample size directly affects the reliability of the study's results (Benoit 1989). A species-area curve was constructed to determine if the study had an adequate sample size (Hutchings 1986). Species composition data were summarized by disturbance type, according to organic / mineral soil and reproductive strategy.

Species' relative abundance was compared among disturbance types using the Kruskal-Wallis (K-W) test, a non-parametric equivalent of analysis of variance. Pair-wise comparisons using the Mann-Whitney U test with a Bonferroni correction indicated which treatments differed from one another. This was the same method as used for the vegetation data (Chapter 2).

The K-W test was also used to detect differences in total number of germinants among disturbance type, and to determine whether the incidence of seed *versus* vegetative reproduction differed among disturbance type. Differences in mean species richness among disturbance type were tested using one-way ANOVA and LSD post-hoc test. For all tests, results were considered significant at the $p<0.05$ and all tests described above were carried out using SPSS, V.6.1 (Norusis 1993a).

Species composition of the June propagule bank was compared to that of the vegetation present in June using the program CANOCO (CANOnical Community Ordination) (ter Braak 1990) to examine differences between potential and actual regeneration. June seed / bud bank data were compared with the October data to detect seasonal changes and project species composition changes into the next growing season.

3.4 RESULTS AND DISCUSSION

Species-sample curves (Appendix E) indicated that enough samples were taken within each treatment. In June, curves level off at 5 samples for Reburn sites, 10 samples for Harvested and Prescribed-burn sites and 14 samples for Wildfire and Control sites. Recently disturbed soil seemed to produce a higher variability in seed distribution. Zasada *et al.* (1983) found that within a square metre, burn variability created an organic layer that ranged between 0 and 20 cm, thus creating large micro-scale differences in seed bank characteristics. A greater sampling size may have reduced the variability of seed numbers from sample to sample but not necessarily increase species numbers.

3.4.1 Post-disturbance (June) Propagule Bank Species Composition

In Table 3.3., species composition of propagules found in the soil in June (immediately after the fires), is summarized according to disturbance type, soil horizon (mineral or organic) and species' reproductive strategy (seed or vegetative). Table 3.4 summarizes the different life forms represented in the

Table 3.3. Summary of species composition by disturbance type, soil horizon, and reproductive strategy (Sd- seed, Vg- vegetative) in the June propagule bank. Different letters indicate species with significantly different ($p<0.05$) number of emergents in the propagule bank among disturbance types.

SPECIES	CONTROL				HARVEST				PRESCRIBED-BURN				REBURN				WILDFIRE			
	Mineral		Organic		Mineral		Organic		Mineral		Organic		Mineral		Organic		Mineral		Organic	
	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg
Aralia hispida			4				1			1		2								
Aralia nudicaulis		1																		
Betula papyrifera	10		104	3 a	4	2	59	2 b			4	c				c	1		3	1 c
Clintonia borealis								1												
Coptis trifolia				14				8				5								9
Cornus canadensis		1					4	2						1						1
Corydalis sempervirens					1															
Diervilla lonicera	9		17	1 a	1	3	12	1 a	18	3	50	b	22	1	50	b	46	2	74	1 b
Epilobium angustifolium										1							4	2	3	
Gerainium bicknellii	2				3				3		2				1		1			
Gaultheria hispidula							2	1												
Linnaea borealis				1																
Maianthemum canadense		1	4	16				1												8
Picea spp.			2																	1
Polygonum convolvulus	2		1														1		1	
Prunus pensylvanica											1								2	
Rubus idaeus	6		10	6	1	2	2	7		2		1	1		2		2	1		
Rubus pubescens			3	3			2						5	2	2					
Trientalis borealis				2																
Viola renifolia																	3		1	
Salix spp.											2									
Graminoids	31		16	a	11		17	a	2		3	c			15	b	12		15	ab
Unknowns	3	1	1	3	3		1	2	1	1	2	1		1	1				2	

Table 3.4 Percentage of lifeforms represented in the June seed / bud bank among disturbance type.

LIFEFORM	CONTROL	HARVEST	PRESCRIBED - BURN	REBURN	WILDFIRE
Trees	43%	43%	6%	0%	3%
Shrub	19%	19%	71%	73%	65%
Herb	18%	16%	12%	11%	8%
Graminoid	17%	18%	5%	14%	14%

various seed and bud banks. Control and Harvested sites produced a large number of tree seedlings, dominated by *B. papyrifera* (99%), while on the burned sites *B. papyrifera* seed, which was dispersed the previous autumn, would have been consumed by the fires. Shrubs dominated burned seed banks with over 60% being *D. lonicera*.

Other species that differed significantly by disturbance type included *R. idaeus,* and *Carex spp.* Moore and Wein (1977), Archibold (1979), Fyles (1989) and Qi and Scarratt (1996) also found *B. papyrifera, Carex spp* and *R. idaeus* to be a large component of the seed bank. *R. idaeus* seed was in greater numbers in Control samples than in burn samples, and has been found in sites that have not experienced disturbance for 80 or 100 years indicating long dormancy capabilities (Whitney 1986). There was a lack of *R. idaeus* seed in Harvested and burned soils. *R. idaeus* is known to respond rapidly to disturbance (Oleskevich *et al.* 1996), establishing in the first year when conditions are favourable (Whitney 1986). Seed on disturbed sites were likely lost to germination. Significantly fewer ($p<0.05$) graminoids were found on Prescribed-burn sites and *M. canadense* was more frequent in Control samples than in burned samples, as was the case for most sprouting species.

Organic soil had over twice as many propagules as mineral soil. The mineral soil, composed of very fine sand, probably did not hold seed very well. On Reburn sites where the average depth of the organic layer was 3.6 cm, 68% of the emergents rose from the organic layer. In central Alberta, Fyles (1989) estimated that the removal of the organic layer destroyed 47-78 % of seed banks.

3.4.2 Comparison of Propagule bank with Vegetation Data

Species composition (based on species occurrence) was compared to what actually grew after the disturbances (Figure 3.1). Species composition of the seed and bud banks was more similar among disturbance types than between the samples and the vegetation found on the sites, especially between Control vegetation and its propagule bank. In the inter-set correlation table (Table 3.5), the vegetation of the disturbance types (environmental variables) is positively correlated with the first axis, especially the Control. This indicates that the first axis represents the separation of the vegetation and propagule species composition. Eigenvalues indicate that 56% of the variance in species composition is represented by the first axis and 8% by the second axis.

Species with extended seed longevity, but not a wide dispersal, such as *R. idaeus*, *Carex spp.* and *G. bicknellii* (Schopmeyer 1974), were found in larger numbers in Control soil samples, although they were not found among the vegetation. Seeds of these species have been found in undisturbed propagule banks in other studies (Fyles 1989; Qi and Scarratt 1996). Tree and shrub species characteristic of the mature forest were not represented in the

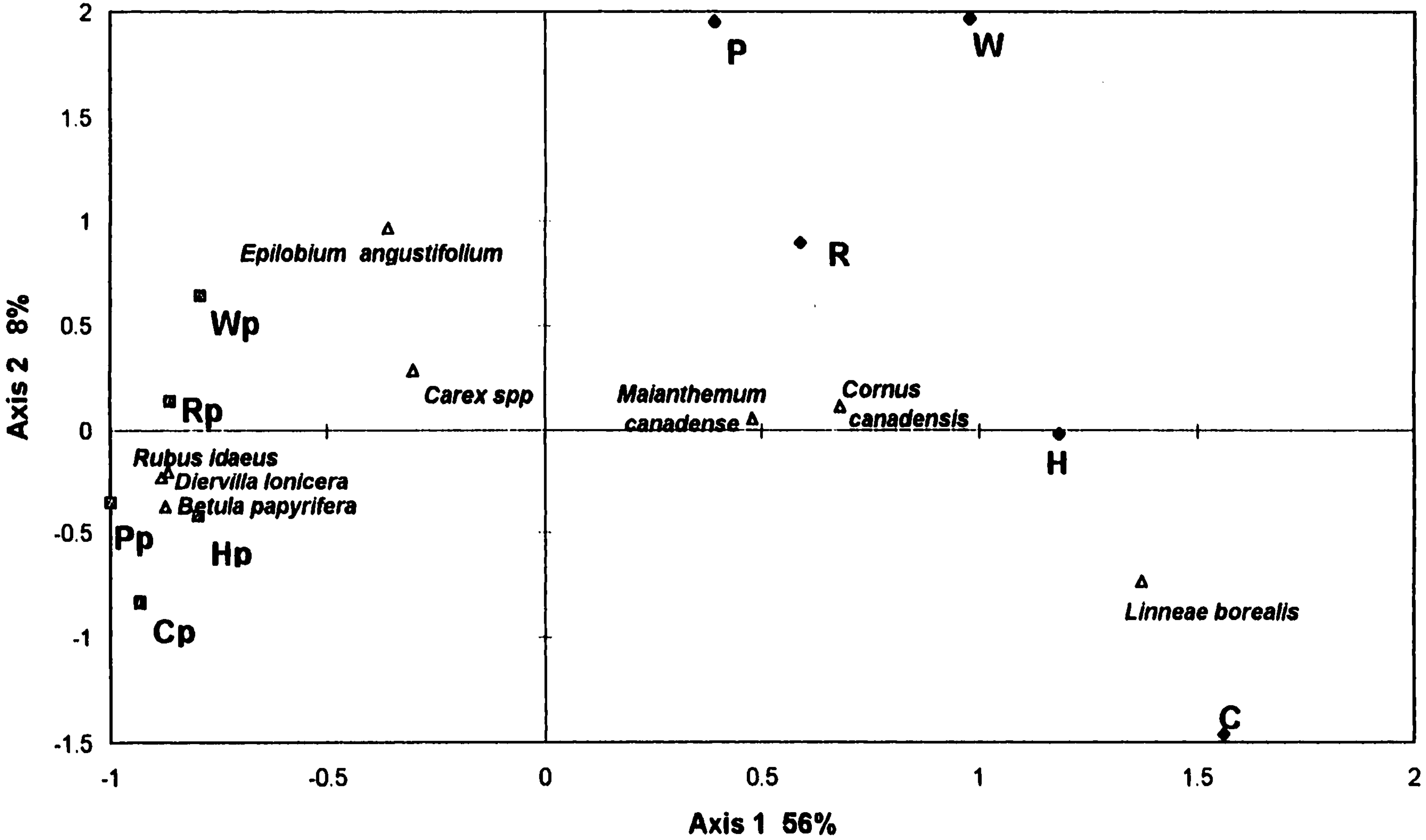


Figure 3.1. Comparison of species composition (based on species presence) between vegetation on site and propagule bank. Abbreviations are as follows; C, Control; H, Harvested; P, Prescribed-burn; R, Reburn; W, Wildfire. A 'p' indicates the propagule bank for each disturbance types.

Table 3.5. Inter-set correlations of environmental variables (disturbance types) with species axes for propagule and vegetation species composition ordinations.

DISTURBANCE TYPE	VEGETATION		PROPAGULE	
	AXIS 1	AXIS 2	AXIS 1	AXIS 2
CONTROL	.56	-.44	-.32	-.14
HARVEST	.44	-.01	-.32	-.24
PRESCRIBED-BURN	.11	.48	-.30	-.09
REBURN	.13	.16	-.20	.03
WILDFIRE	.20	.34	-.27	.19
Eigenvalues	.56	.18		

seed bank, especially *A. balsamea, Vaccinium spp., Alnus crispa* and *Acer spicatum.* In many studies, seed banks represent only about half the taxa found on the site (Frank and Safford 1970; Fyles 1989; McGee and Feller 1993).

Overall, propagule banks more closely resembled vegetation found on disturbed sites than that on the Control sites. Although Archibold (1980) found that *E. angustifolium* was less abundant on lightly burned sites, areas of the Prescribed-burn plots were dominated by this species. Post-fire soil samples produced little *E. angustifolium* but those that did emerge were vegetative in origin. Rhizomes of *E. angustifolium* are generally found between 2-8 cm and respond well to heat (Moss 1936; McLean 1969; Myerscough 1980).

P. pensylvanica and *P. convolvulus* characterized the vegetation on the disturbance sites but were not well represented in the seed bank, suggesting that most viable seed had already germinated on the site.

Conditions were hot and dry during the summer of 1995 (Appendix B, Table B.1), and could have killed emergents during the first growing season (Schimmel and Granstrom 1993). Cover values for *T. borealis, M. canadense* and *C. canadensis* declined over the summer, especially on Harvested and Reburn sites.

3.4.3 Seasonal Changes in Propagule Bank Characteristics and Species Composition

A summary of species composition by disturbance type, soil and reproductive strategy is shown in Table 3.6. Species composition did not change significantly over the season but both seed and rhizome numbers were greater in the October propagule bank.

A comparison of seed bank characteristics between the June and October samples is shown in Table 3.7. In June, total seedling emergence and species richness decreased with the degree of soil disturbance. Number of seedlings decreased significantly ($p<0.01$) from Control sites to Harvested, Prescribed-burn and Reburned sites. In Wildfire sites much of the fuel was in the form of standing dead trees. The fire seemed to consume less organic soil, which was characterized by moss cover, than harvested and burned sites, allowing for a greater propagule survival. Species richness was also significantly greater ($p<0.01$) for Control and Harvest samples than for Prescribed-burn and Reburn. Wildfire had significantly greater species richness than Reburn samples ($p<0.01$).

Referring to the literature summary of mixed-wood and *Picea* forests (Table 3.1), undisturbed sites and those that were just harvested were found to contain between 2428 seeds m^{-2} with 10 species (Ahlgren 1979c) and 350 seeds m^{-2} with 19 species (Vermeer 1984). Cut and burned sites ranged from

Table 3.6. Species composition by disturbance types, soil horizon and reproductive strategy (Sd- seed or Vg- vegetative) in the October propagule bank. Different letters indicate species with significantly different ($p<0.05$) number of emergents frequencies within the propagule bank among disturbance types.

SPECIES	CONTROL				HARVEST				PRESCRIBED BURN				REBURN				WILDFIRE			
	Mineral		Organic		Mineral		Organic		Mineral		Organic		Mineral		Organic		Mineral		Organic	
	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg	Sd	Vg
Aralia hispida							1								1	2			1	2
Aralia nudicaulis				2				1				1								2
Betula papyrifera	2		68	a	2		36	2ab	3	1	36	ab			13	b			14	1 b
Clintonia borealis				2																2
Coptis trifolia		1		10				3												2
Cornus canadensis	2	5	3	8	4	4	3	4	1	2	2	6	1	3			3	9	2	3
Corydalis sempervirens															2		1		2	
Diervilla lonicera	7		21		2		3	7	5	2	40	1	23		27	a	23	1	89	3 b
Epilobium angustifolium			6	a	1		160	9 b	6	10	497	24c	5		36	2 b	4	2	44	9 b
Epilobium leptophyllum			8				13	3	4		65	3				a			28	2ab
Gerainium bicknellii									1											
Gaultheria hispidula							4				1	1								
Maianthemum canadense			3	27		3	1	9				3							3	11b
Polygonum convolvulus											4									
Prunus pensylvanica						1		2					2	3		1				86
Rubus idaeus	5	6	13	4	5	13	37	32	12	3	1	3	29	12	16	10	14	6	10	7
Rubus pubescens							1	2	1								2	8		
Trientalis borealis												5							1	5
Vaccinium angustifolium															1					1
Viola renifolia							1													
Graminoids	36		5	a	13		16	a	9		13	a	2			b	21		23	a
Unknown				1	2	1	1	1							2				1	

Table 3.7. Seed bank characteristics for June and October samples: seed densities, species richness, ratio of seed to vegetative reproduction and ratio of seed in organic to mineral soil. Values with dissimilar letters within a column are significantly different ($p<0.05$).

DISTURBANCE	JUNE				OCTOBER			
	Seeds m^{-2}	# Species	Seed : Veg	Org : Min	Seeds m^{-2}	# Species	Seed : Veg	Org : Min
CONTROL	1 350 (± 1105) (a)	15 (a)	80:20	76:24	1 075 (± 857) (a)	11 (ab)	73:27	74:26
HARVEST	769 (± 470) (b)	14 (a)	80:20	80:20	1 906 (±3 720) (ab)	15 (a)	76:24	88:12
PRESCRIBED-BURN	556 (± 480) (b)	11 (b)	84:16	69:31	4 338 (±5 481) (b)	14 (a)	91:9	92:8
REBURN	569 (± 729) (b)	6 (c)	95:5	68:32	944 (± 978) (a)	10 (b)	83:17	58:32
WILDFIRE	1 100 (± 1 605) (ab)	11 (b)	87:13	62:38	1 831 (± 680) (ab)	17 (a)	78:22	75:25

425 seeds m^{-2} with 10 species (Granstorm 1982) to 2807 seeds m^{-2} with 7 species (Ahlgren 1979b), but these sites were over 12 years old. The variability of seed numbers within the treatments is higher than in other studies reported (Table 3.1), indicating that the early age and the affect of soil disturbance may increases the clumped and uneven distribution of the seed.

In October, Prescribed-burn sites produced 4337 seeds m^{-2} (± 5481), this was significantly greater ($p<0.05$) than Control (1075 seeds m^{-2} ± 859) and Reburn (944 m^{-2} ± 978). The large increase and associated variability can be attributed to the wind dispersal of *E. angustifolium* seed. Species richness also increased so that the only significant difference ($p<0.05$) was between Harvested and Reburn sites.

In June, the importance of seed as a reproductive strategy increased slightly with increased soil disturbance, ranging from 80% for the Control and Harvested samples to 95% for Reburned samples. Schimmel and Granstrom (1993) noted that severely burned sites were dominated by seed species, originating from the seed bank or dispersal to the site. The Control had significantly more vegetative growth than Reburned soil ($p<0.05$).

In October, the greater importance of *E. angustifolium* is reflected in the greater percent of the herb lifeform shown in Table 3.8. It is possible to find small numbers of *E. angustifolium* seed in the spring (Myerscough 1980) or directly after a fire (Archibold 1980) but generally viable seed is only found

Table 3.8 Percentage of lifeforms represented in the October seed / bud bank among disturbance types.

LIFEFORM	CONTROL	HARVEST	PRESCRIBED -BURN	REBURN	WILDFIRE
Trees	29%	10%	5%	9%	4%
Shrub	14%	26%	9%	66%	36%
Herb	31%	57%	83%	26%	38%
Graminoid	17%	7%	3%	1%	12%

between July and March. Since *E. angustifolium* is capable of producing 76 000 seeds / plant (Myerscough 1980), and the species was well represented on the site, it is most likely that the seed was deposited on the site and indicates seasonal input. Granstom (1986) identified *E. angustifolium* and *Betula spp.* as the only species that were quantitatively important in seed rain during the first season. Archibold (1980) also found that seed from the herb stratum was high (63.4% of the vegetation) and was dominated by *E. angustifolium* (63%), and that *B. papyrifera* represented 80% of the tree life form during the first growing season after fire. Graminoid and shrub numbers did not change greatly over the season but *R. idaeus* emergents demonstrated more vegetative growth than seed.

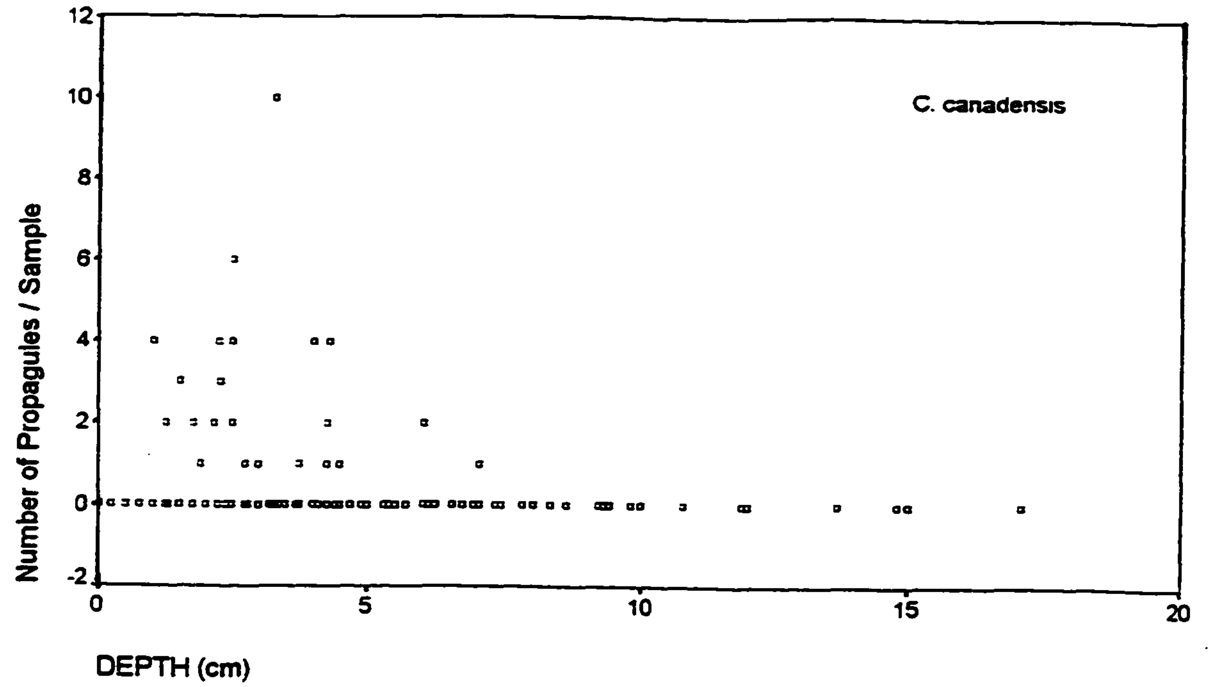
Vegetative emergence was significantly higher ($p<0.05$) in Control, Harvested and Prescribed-burn soils than Reburn soils and increased significantly ($p< 0.01$) from June to October samples. Flinn and Pringle (1983) and Zasada *et al.* (1994) found that species tolerance to heat and disturbance varied over different seasons, being lowest during the growing season and highest when reserves are stored underground. Therefore, it is likely that rhizomes included in the October sample have higher viability than those that were collected in June after the fire.

3.4.4 Species' response to Fire Severity

Species composition between mineral and organic soils differed significantly ($p<0.05$), with a higher frequency of *D. lonicera, Coptis trifolia, B. papyrifera* and *A. hispida* in the organic horizon. Therefore the consumption of the organic layer by fire will influence the initial species composition and species' densities.

The germination of some species seems to be greater on burned sites than on unburned sites and correlates with the depth of the organic layer (Table 1.2). This could indicate a heat interaction or the location of the propagules in the soil. Both rhizome and seed species, such as *C. canadensis*, *D. lonicera* and *R. idaeus*, seem to correlate with greater fire severeties (Figures 3.2 and 3.3). Although little has been written about *D. lonicera*, the large numbers of germinants found in burned samples suggest that the seed may break dormancy after exposure to heat. In comparison, *M. canadense* did not show as clear a trend with organic depth.

Seasonal changes were evident in the correlation of seed occurrence and soil depth for *E. angustifolium* and *B. papyrifera* (Figure 3.4. and 3.5.). In June, *E. angustifolium* reproduced vegetatively and its rhizomes were found at depths between 5 and 10 cm. After seed dispersal in October, seeds were concentrated at depths between 0.5 and 5 cm. *B. papyrifera*, which was dispersed on the forest floor, was not correlated with soil depth in June samples.



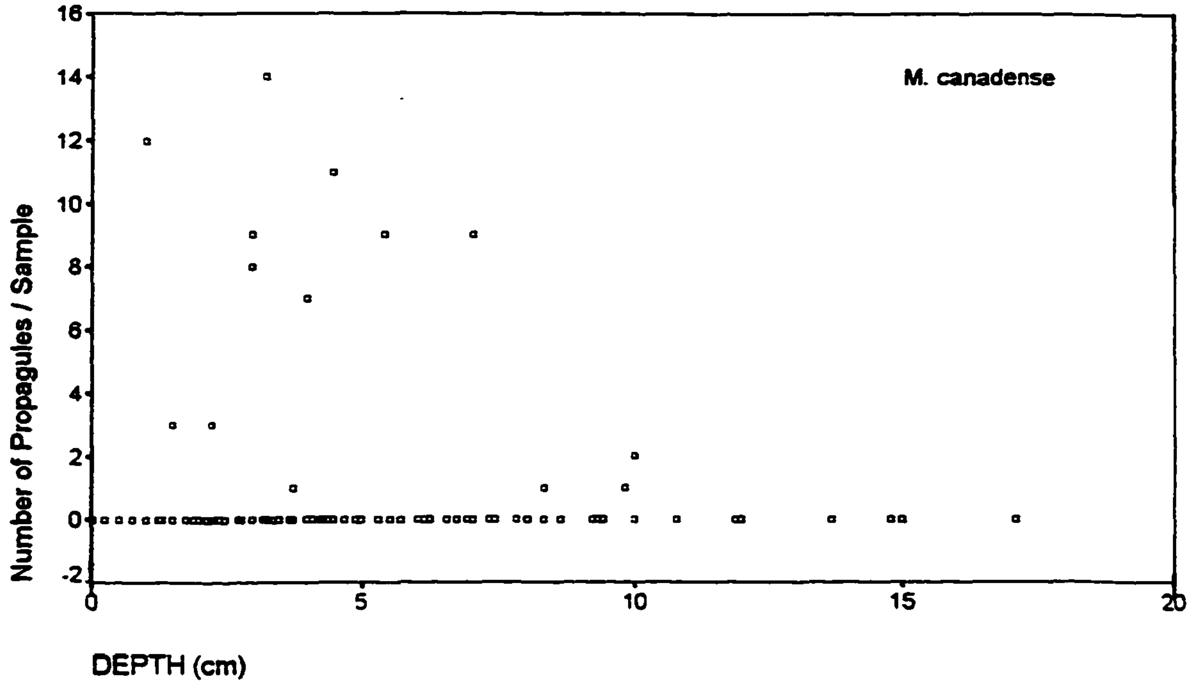
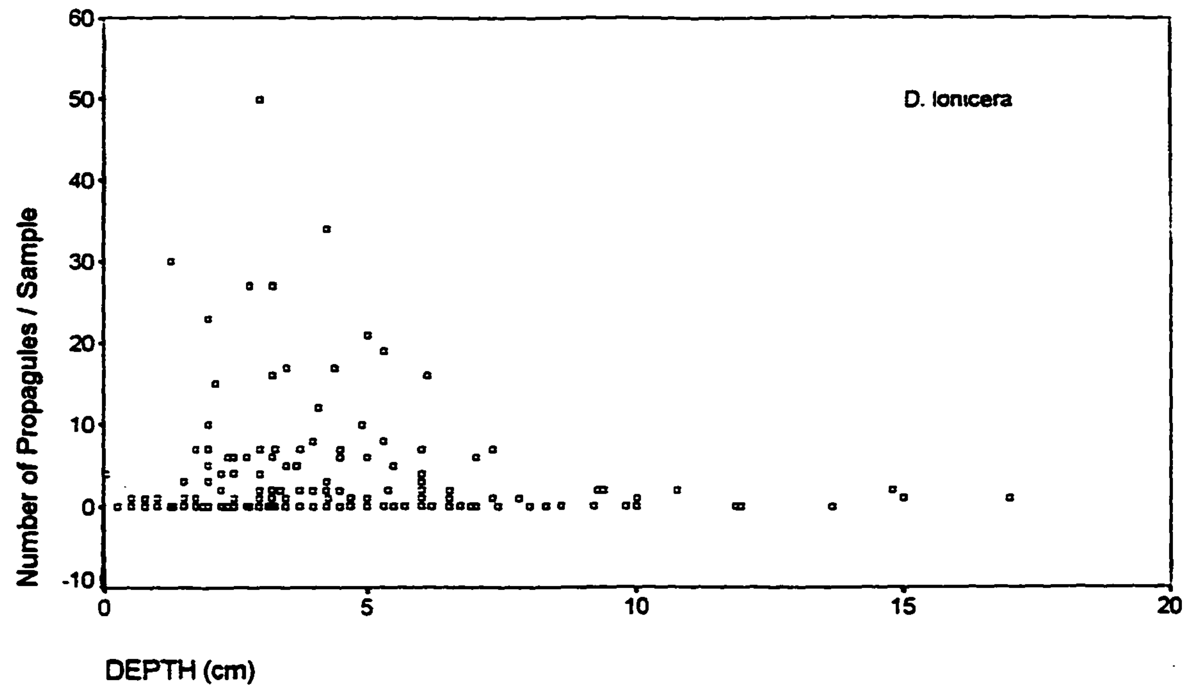


Figure 3.2. Number of propagules by depth of organic layer for *Cornus canadensis* and *Maianthemum canadensis*. June and October sampling periods are combined.



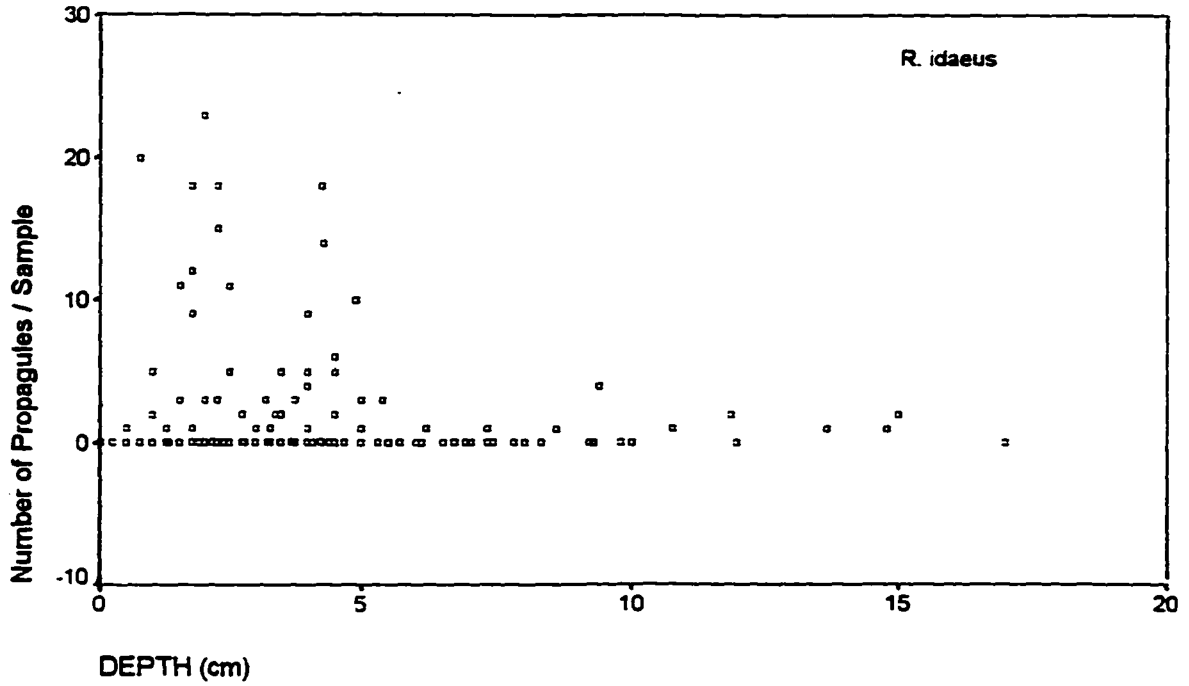
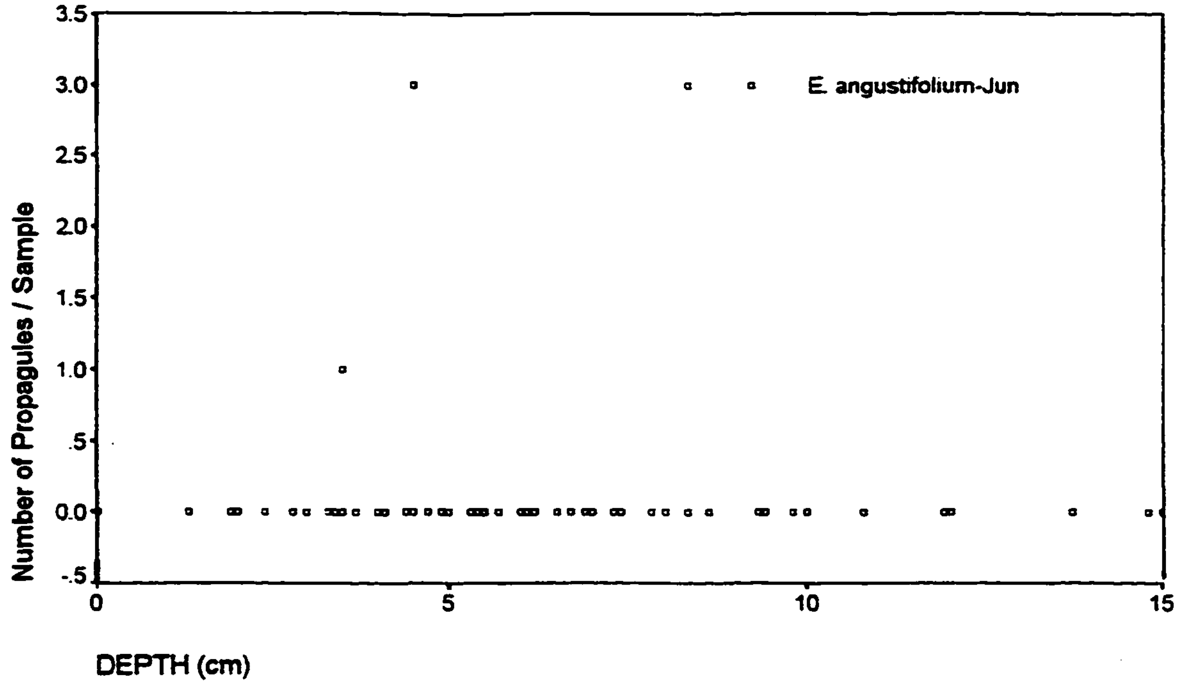


Figure 3.3. Number of propagules by depth of organic layer for *Diervilla lonicera* and *Rubus idaeus*. June and October sampling periods are combined.



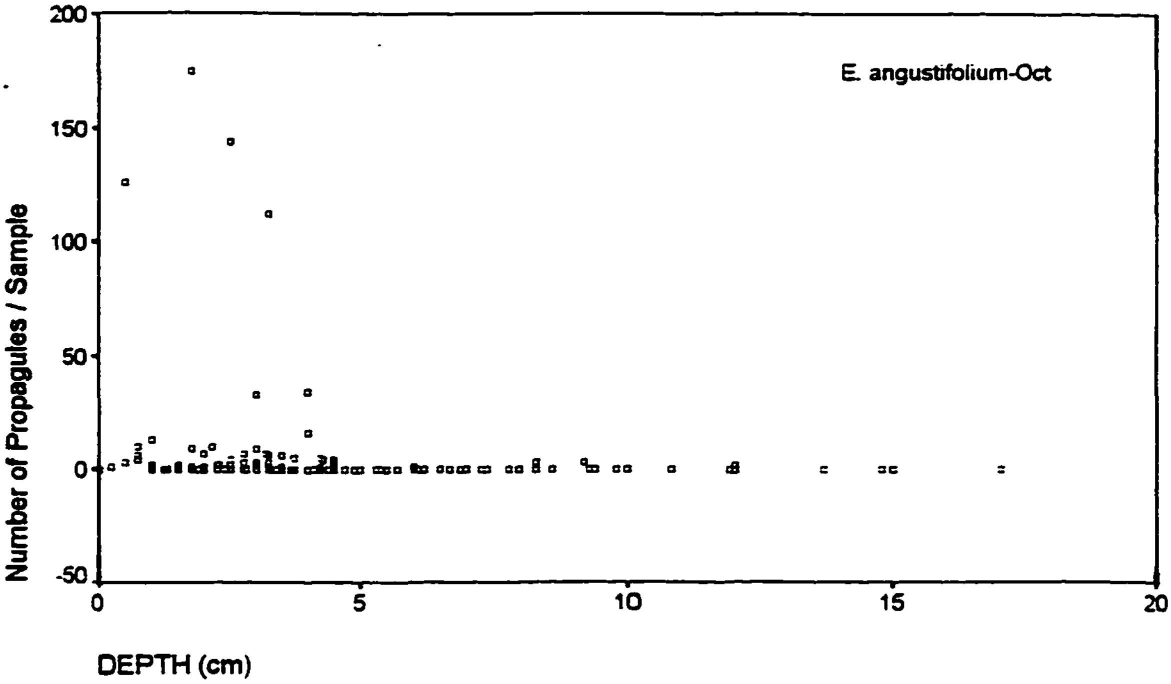
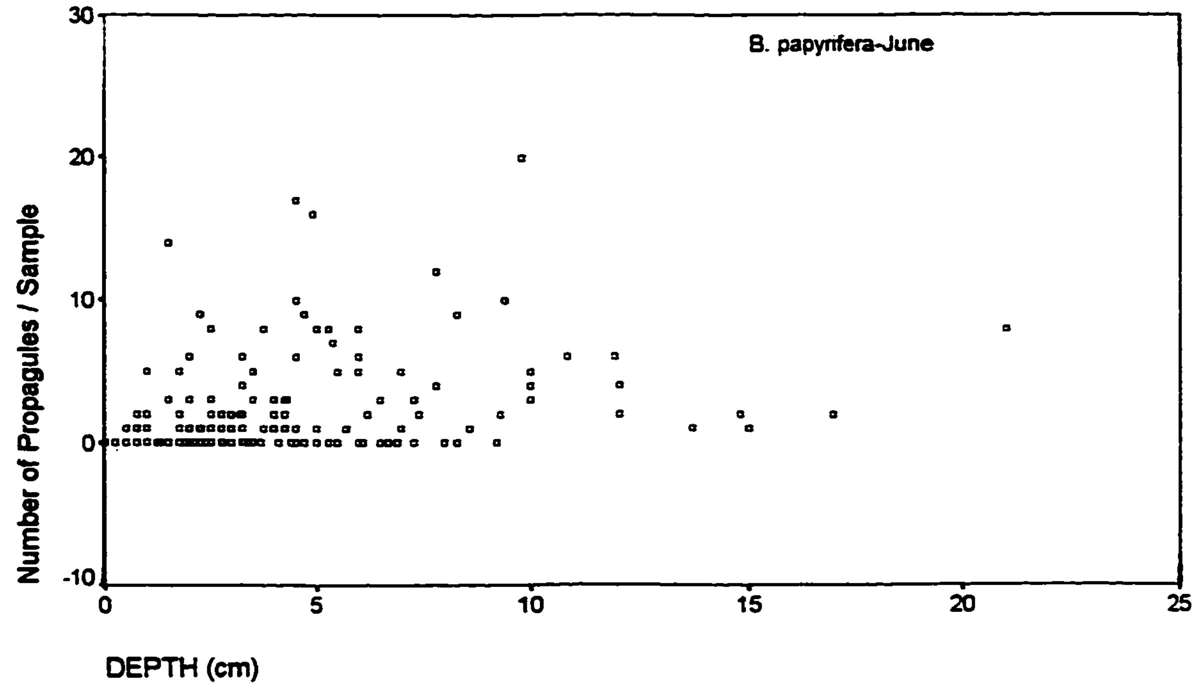


Figure 3.4. Number of propagules by depth of organic layer for *Epilobium angustifolium* for June and October sampling periods.



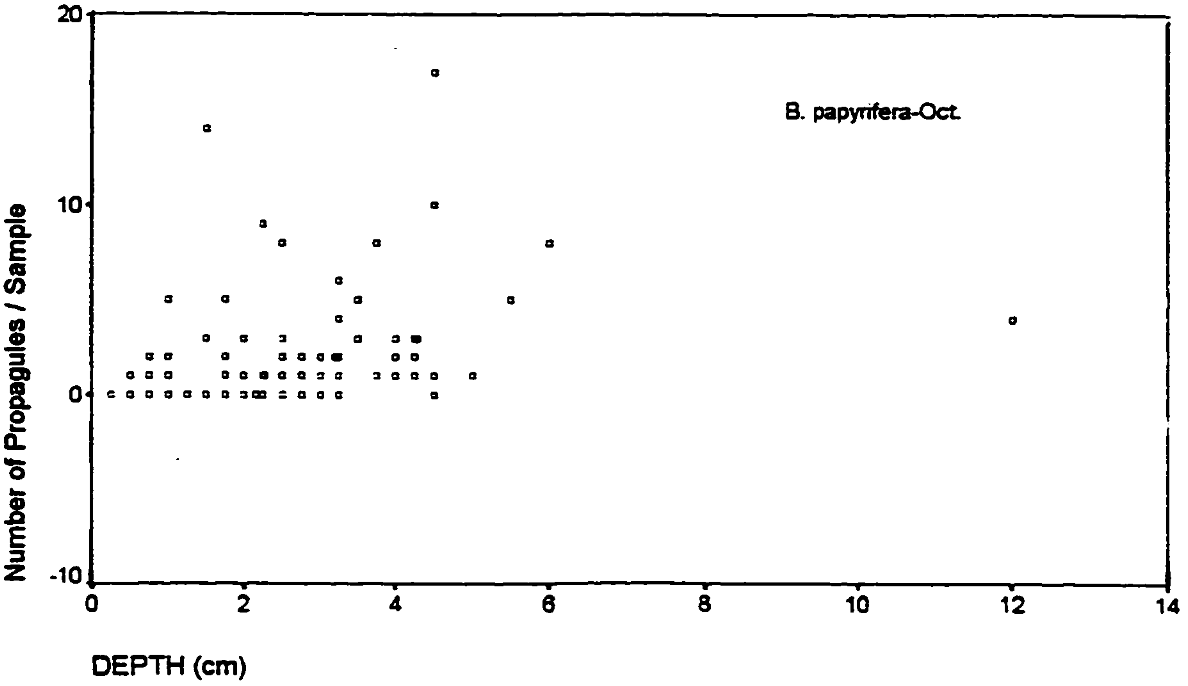


Figure 3.5. Number of propagules by depth of organic layer for *Betula papyrifera* for June and October sampling periods.

By October, which is early in the *B. papyrifera* seed dispersal period, seed distribution was concentrated on sites with soil between 0.5 and 6 cm. This seed could have been released early from stressed *Betula* trees remaining on harvested and burned areas.

3.4.5 Projection of Future Species Compositions

Although Control samples contained propagules of many species that do not appear in the vegetation (*E. angustifolium, E. leptophyllum, D. lonicera* and *Carex spp.*), it is unlikely that these species will contribute to this community until a disturbance releases them and creates appropriate germination conditions.

Soil from disturbed sites seemed to contain little or no seed of *P. convolvulus* and *G. bicknellii* which were represented in the vegetation. Abrams and Dickmann (1984) found *G. bicknellii* represented 22% of the vegetation cover but was reduced to a few individuals the following year. *G. bicknellii* is classified as an annual or a biennial (Fernald 1950). On the study site *Geranium* did not produce flowers so it should be considered a biennial strain that will produce seed in the following year. Both *Polygonum* and *Geranium* are known for their "one-shot" contribution to the seed bank, and they require disturbance and areas of low competition to germinate and survive. In Minnesota, Ahlgren (1979a) found *G. bicknellii* on three- and four-year old burns. Either the species expresses an ecotypic difference in germination requirements and did not require heat to germinate (Abrams and Dickmann 1984), or perhaps surface temperatures were warm enough to stimulate the seed. In any case, the populations of *G. bicknellii* and *P. convolvulus* are unlikely to expand beyond what has already been established.

P. pensylvanica increased slightly between June and October, although not significantly. Auchmoody (1979) found that *P. pensylvanica* did not germinate until the second season after a nitrate fertilization treatment because it likely required a second chilling period. A second chilling period was also noted by Laidlaw (1987) after treating *P. pensylvanica* with drastic temperature fluctuations. So it is possible that *P. pensylvanica* will continue to germinate in the next growing season. Auchmoody (1979) found no germination in three-year-old plots, possibly indicating short-lived germination stimulus.

Once established, *P. pensylvanica* produces a large number of shoot structures per root mass (Marks 1974). Seed production becomes more important at four years after the disturbance when it reaches reproductive maturity. The importance of *P. pensyvanica* increases around the time that *R. idaeus* is declining, allowing these species to coexist on the same site.

E. angustifolium, D. lonicera, Carex spp. and *B. papyrifera* dominated the seed bank, but their contribution to the vegetation will be determined by how severely the site was disturbed and the level of established competition (Ahlgren 1960; Achibold 1980). *D. lonicera* was not well represented in the vegetation even though the seed bank contained large quantities of viable seed. Perhaps this species is similar to *P. pensylvanica* in that it requires a second chilling period and will contribute to the vegetation in the second growing season or perhaps it has low survival. *E. angustifolium* and *B. papyrifera* lose viability within a year (Archibold 1980; Myerscough 1980), but with wide seed dispersal abilities, these species will continue to contribute to regeneration.

Many species that established after the disturbance will continue to expand vegetatively. *E. angustifolium* will flower in its first year but vegetative reproduction will have priority over seed reproduction as has been indicated by resource allocation patterns (Myerscough 1980).

R. idaeus starts producing rhizome shoots in its second year; e.g. Whitney (1982) found 16 shoots m^{-2} after three seasons. *R. idaeus* experiences an intense phase of intraspecific competition and self-thinning during which time dominant individuals increase seed production from 700 m^{-2} in the second year to 14 000 m^{-2} in the fourth year (Whitney 1982).

3.5 CONCLUSION

Species composition and seed bank characteristics (numbers and reproductive strategies) differed according to disturbance type. Characteristics were largely influenced by disturbance severity (depth of remaining organic layer).

The species composition of Control vegetation differed the most from its associated propagule bank. Many seeds of 'disturbance seed-banking' species were present in the Control propagule bank which could indicate the dominance of certain species (e.g. *R. idaeus, P. convolvulus*) in post-disturbance environment. Seeds of these species were in low abundance in soils of harvested and / or burned sites because they had germinated. Shrub species were not well represented in samples. Sample size and numbers may not have been adequate to retrieve rhizomes.

October samples indicated that *E. angustifolium* and *B. papyrifera* had the greatest contribution to seasonal inputs. An increase in the viability of vegetative propagules suggests that many species will expand beyond their current cover in the next growing season.

CHAPTER IV

NUTRIENT ACCUMULATION PATTERNS IN VEGETATION

4.1 INTRODUCTION

Site fertility greatly determines forest diversity, productivity and stability (Nams *et al.* 1993). Soil nutrient composition is a result of atmospheric inputs, weathering of parent material, and the rate and magnitude of nutrient circulation through the vegetation (Attwill and Adams 1993). In the boreal forest, nutrients become limiting as the forest matures (MacLean *et al.* 1983). As the organic layer accumulates and soil conditions become cool and more acidic, decomposition and the release of nutrients slows (Krause 1991).

Under natural conditions, fire interrupts forest succession, redistributing nutrients and stimulating nutrient cycling processes (MacLean *et al.* 1983). Fire is a driving force of change as it rapidly alters light, moisture, nutrient and temperature conditions, influencing decomposition rates and stimulating different species compositions (Chapin and Van Cleve 1979). Harvesting directly and indirectly affects nutrient distribution and cycling, but few studies have compared harvesting with fire.

Species have adapted to different resource conditions and use different strategies to exploit nutrient rich sites or tolerate nutrient poor environments. Disturbance activates the cycling of nutrients trapped in biomass so that nutrient concentrations and allocation will change within the forest strata and within the species themselves (Ohmann and Grigal 1979). Initial regeneration plays an important role in capturing released nutrients and retaining elements on the site (Marks 1974; Vitousek and Reiner 1975; Adams and Boyle 1982). Nutrient content of plant tissue reflects the nutrient availability and/or the species' ability to accumulate and store nutrients (Garten 1978; Chapin and Tryon 1983).

This portion of the study examined patterns of nutrient concentrations of nitrogen (N), potassium (K), phosphorous (P), calcium (Ca) and magnesium (Mg) for selected herb and shrub species after harvesting and/or fire to determine vegetation response to different post-disturbance environments. Plants were also compared to determine if concentration patterns relate to the species' reproductive strategy. Nutrient concentration and biomass were related to cover data of the vegetation (Chapter 2) to enable a nutrient mass (kg/ha) comparison per treatment and discuss the importance of early vegetation and nutrient retention.

4.2 LITERATURE REVIEW

4.2.1 Successional changes in Nutrient Cycling in the Boreal Forest

Most nutrient accumulation in vegetation occurs during the first 10 years of forest development (Foster and Morrison 1976). Early successional understory species play an important role in accumulating liberated nutrients in their biomass, minimizing losses after disturbance and initiating element cycling processes (Marks and Bormann 1972; Vitousek and Reiner 1975; Hendrickson 1988; Mou *et al.* 1993). After harvesting, Outcalt and White (1981) found that 75% of the site's nutrients were found in herb and shrub species. Within the Hubbard Brook watershed, the rate of N accumulation in vegetation exceeded N losses in stream flow (Mou *et al.* 1993).

Early successional species demonstrate rapid growth and have nutrient rich tissue with a greater foliage to wood ratio (Ohmann and Grigal 1979; Parrish and Bazzez 1982; Mou *et al.* 1993). Generally herbs increase in their weight per individual and standing crop m^{-2} over the first one-two years after disturbance (Ohmann and Grigal 1979). Since most early successional species are deciduous, nutrients are rapidly returned to the forest floor to form the organic layer. Litterfall is an important link for the return of Ca, N and P to the soil (Damman 1971; VanCleave and Noonan 1975; Chapin *et al.* 1978; McClaugherty *et al.* 1985). Decomposition of litter varies according to the climate (moisture, heat), species composition and litter quality, and soil micro flora and fauna (Matson and Vitousek 1981; Attiwill and Adams 1993).

Early succesional species have rooting patterns that are composed of finely divided systems of small absorbing tips. These species are less efficient at nutrient use, requiring nutrients each year to produce new leaves and roots (Chapin 1980). As nutrients become tied up in biomass, these species are not able to compete for less available nutrients. As their population declines much of their energy is directed to the production of seeds to be stored in the seed bed.

In response to disturbance, many species exhibit plasticity or flexibility in their growth rates. Some plants can adjust their nutrient uptake rate, tissue nutrient concentration and leaf turn-over rate in response to nutrient availability (MacLean 1983; Chapin and Van Cleve 1979). Early successional species (annuals) have high phenotypic plasticity, where the environment strongly influences leaf size, shape, branching pattern and height (Sultan 1986). Certain `fire survivors' specialize in conditions of different successional stages. For example, during mid-succession at around 60 years, *Vaccinium* and *Picea* are able to absorb greater P and can experience rapid growth (Chapin and Van Cleve 1979).

Mineral soil can be influenced by nitrogen-fixing shrubs, increasing N from 200-300 g m^{-2} in the shrub stage to 500-600 g m^{-2} in the hardwood tree stage (Van Cleve and Viereck 1981). Grigal *et al.* (1976) found that the accumulation of elements in five shrub species peaked between 10 and 20 years after fire. Hardwood trees absorb nutrients at a slower rate during this shrub period (the first 15 years) and then accumulation increases rapidly for the next 10 years. During that time, 10-50% of N is found in the forest floor (Van Cleve and Viereck 1981).

Rate of nutrient accumulation, element composition and litter turnover differ according to the dominant species. For example, a grass community will contain high K and low Ca compared to a community dominated by woody species (Mou *et al.* 1993). *Populus* litter of 50-100-year old stands has a turnover period of 12-13 years, while *Betula* litter requires 16 years (VanCleave and Noonan 1975). *Populus* litter in stands of 50 years had greater N and Ca than *Betula* which had higher Mg. VanCleave and Noonan (1975) suggest the difference is a reflection of microbial activity, soil aeration and the acidic nature of *Betula* litter which lowered P mobility and increased Mg availability. Soluble substances mineralize rapidly leaving slower acid soluble and insoluble chemicals, so litter lignin concentrations are good indicators of decomposition rates (Triska and Sedell 1976; Melillo *et al.* 1982).

MacLean and Wein (1977) found that nutrient accumulation occurred much faster in hardwood stands, with 50% greater N, P and Mg and 90% greater K and Ca than *P. banksiana* forests. By 30 years, the *Pinus* ecosystem reaches a steady state of addition and decomposition of organic matter. Annual accumulation of nutrients is 15-19% of earlier ages even though there is greater litter production (Foster and Morrison 1976).

Cycling within the ecosystem also occurs when precipitation leaches nutrients from leaves (throughfall) and woody material (stemflow). Potassium is most susceptible to leaching followed by P, N and Ca (Foster and Morrison

1976). Leaf characteristics that affect the loss of soluble nutrients include surface-area to volume ratio, texture and age.

As a forest community matures, evergreen species that are slow growing and have leaves that resist nutrient leaching become more abundant. Species that grow in nutrient poor environments survive, reproduce and produce biomass with low tissue nutrient content (Krause 1991). In Alaska, *Picea* often represents the mature stage of succession in which a greater degree of N, P and K is found in above ground biomass (Van Cleve and Viereck 1981). Translocation of these nutrients from leaves to stem before leaf fall is an important method of internal nutrient cycling. Up to 40-60% of N and P are stored within the stem or roots for leaf production in the following year (Chapin and Van Cleve 1979). Conifers have high nutrient re-absorption ability and low leaf turn over (Waring and Schlesinger 1984). *Picea mariana* has the ability to retain needles for 3-7 years in its seedling stage and 30 years when it is mature (Chapin and Van Cleve 1979).

Internal cycling of nutrients and increased nutrient-use efficiency creates a positive feedback system that lowers nutrient availability. Nitrogen cycling is highly influenced by the carbon:nitrogen ratio. Nitrogen may be released to the soil solution at a C:N ratio between 12-20:1 (Vitousek 1982) but minimal C:N will vary depending on the microbial population and litter quality (McClaugherty *et al.* 1985). Increasing soil acidity and inhibiting chemicals (e.g. tannins) are associated with accumulating organic matter, high C:N ratios and lower microbial activity. Species adapted to poor nutrient availability can efficiently fix more C per unit of N, but as the C:N ratio increases N can become retained in the biomass intensifying the N stress (Vitousek 1982).

In Alaska, Chapin *et al.* (1979) found that P is also closely controlled by microbial populations. Potassium can also be a limiting factor as it is supplied entirely by the parent material in the area, but it is very soluble and prone to movement out of the vegetation and, perhaps, off the site. Chapin (1980) suggests that greater concentrations of N in the soil can increase root capacity for K 10-fold.

Even in later successional stages, understory species provide the greatest contribution of nutrients because of their high foliage to wood ratio (Waring and Schlesinger 1985). *Pteridium aquilinum* accumulates K, contributing 31.4% of the K by litter and leachant in a *Pinus banksiana* stand (Carlisle *et al.* 1967 in MacLean and Wein 1977). A *Pinus* forest with *Corylus* and herbs in the understory had 1.4-2.6 times more nutrients than stands with pure *Pinus* litter which greatly influenced the turnover rate of the organic layer (Tappeiner and Alm 1975). In Newfoundland and northern Quebec, moss can account for 33-50% of above-ground biomass. The annual uptake of N, P, K, Ca and Mg by moss is estimated to be between 23-53% of the annual tree uptake. In ecosystems where the understory is dominated by moss, moss collects nutrients from precipitation, throughfall and stemflow and makes them available to trees (Damman 1971; Weetman and Temmer 1967 in Kimmins 1987).

4.2.2 Seasonal Changes and Spatial Patterns

Nutrient concentrations within a plant change according to nutrient availability and physiological processes. A nutrient pulse occurs in the spring when water allows nutrients to be efficiently leached from the soil and decaying material. Moisture plays an important role in nutrient movement. Increasing moisture availability along a N gradient allows trees to use N at greater concentrations. In Alaska, Chapin *et al.* (1978) found 40% of the P was absorbed within 10 days of snowmelt. During these periods of high nutrient availability, some species are able to absorb an excess amount of nutrients ('luxury consumption'). These stored nutrients can then be used later to support growth when nutrient supply in the soil has been exhausted (Chapin 1980).

Within the plant, nutrient concentrations are highest in areas of growth, such as root tips and foliage. Concentrations of N, P and K increase as leaves mature. Then Ca and Mg accumulate as photosynthetic products and structural tissues are produced. Grigal *et al.* (1976) found these nutrient concentration patterns for *Alnus crispa, Amelanchier spp., Salix spp.* and *Corylus cornuta* but

N and P concentrations changed little over the growing season. Before leaf abscission, many nutrients are withdrawn into the stem and roots, except Ca which is actively exported to the leaves (Grigal *et al* 1976; Waring and Schlesinger 1985).

Species composition and nutrient concentration patterns will also vary spatially with nutrient distribution. Tilman (1987) studied patterns of species dominance along an experimental N gradient. After a three-year period of transient dominance, species distributed themselves along seven experimental N concentrations. Generally, early successional annuals and short-lived perennials that were low and spreading (e.g. *Polygonum convolvulus*), peaked at low N, while high N sites were dominated by erect, long-lived herbs and woody species that were tall at maturity (e.g. *Rubus idaeus*). Garten (1978) suggests that spatial and temporal separation of a species is related to the species adaptation to the nutrient concentration. The species' phenotypic variation may reflect the plant's niche size.

4.2.3. Fire and Nutrient Cycling

Fire affects nutrient cycling during and after the disturbance. High variability in plant communities, soils and disturbance characteristics make it difficult to generalize about the changes in post-fire soil and vegetation nutrient concentrations. The amount of biomass consumed, season, fire severity and duration of heat will influence the amount of nutrients released and post-fire availability to plants.

During a fire, unavailable minerals locked in organic matter are converted to soluble forms and become available to plants. Many nutrients form solid oxides and are deposited as ash; others (e.g. nitrogen and sulfur) become gaseous and may be lost from the site in smoke (Raison, 1979). Nitrogen is the most vulnerable to volatilization loss, occurring when temperatures reach 200°C (Knight 1966). Experimental burning of *Pinus* litter indicated that 62% of N released was volatilized and would not be returned by precipitation (DeBell and Rulston 1970). Sulfur and P losses occurred at around 300° C and K at 500° C (Kimmins 1987). Fire can also indirectly cause nutrient loss. Severe fires can cause soils to become hydrophobic if soil pores become plugged, resulting in loss of ash in runoff (Kimmins 1987).

Five years after vegetation establishment, Ohmann and Grigal (1979) found N remained constant while P, K and Ca generally increased. Other studies of low intensity fires have not found a decrease in N (James and Smith 1977; Schoch and Binkley 1986). In many cases, fire may lower the total N on the site but will increase the available N (MacLean *et al.* 1983). In a *Pinus taeda* forest, burning increased decomposition and the release of N was double that found on unburned sites (Schoch and Binkley 1986).

Rate of revegetation, post-fire weather and soil characteristics will determine relative amounts of nutrient retention or loss after the fire. Texture, porosity, organic matter and clay content of the soil and the amount of precipitation after the disturbance governs whether nutrients are leached away (Smith 1970; Grier 1975). In a fire that consumed 79-90% of the organic matter, the cation exchange capacity of the L-H horizon lowered and increased nutrient solubility causing a 48% reduction in extractable P over 15 months (Smith 1970). After snowmelt, Grier (1975) found that 35% of Ca, 78% of Mg, and 85% of K were leached from the ash layer by 67 cm of percolating water, of which 90% of the elements remained in the top 19 cm of soil.

Fire changes the soil environment, altering nutrient cycling processes. Soil temperatures rise as charred surfaces absorb solar radiation, stimulating further decomposition and micorrhizal activity (Chapin and Van Cleve 1979). After five years, Monleon and Cromack (1996) found a site that experienced a low intensity prescribed burn (300 $kW\ m^{-1}$ with 40-60% duff consumption) was still releasing significantly more N and P from current litter than unburned sites, indicating increased microbial activity. An increase in water soluble P, K, Ca, and Na can occur (MacLean *et al.* 1983; Chapin and Van Cleve 1979), and in some cases it takes 20-30 years for these processes to return to pre-fire conditions (Raison 1979).

4.2.4 Harvesting and Nutrient Cycling

Harvesting effects on nutrient cycling are dependent on the type of harvesting, equipment used, season, vegetation and soil fertility (Hendrickson 1988; Mou *et al.* 1993). Harvesting has turned away from conventional main stem-only utilization with long rotations to short rotations with whole-tree harvesting (Kimmins 1987; Mann *et al.* 1988). Harvesting that removes biomass from the site also removes nutrients (Krause 1991). Hendrickson (1988) and Mann *et al.* (1988) found that harvesting methods that left more slash on the site showed higher nutrient content in the vegetation after four years than whole-tree harvesting. Mann *et al.* (1988) found a 40% loss of N for stem-only harvested sites compared to an 80% loss for whole-tree harvested sites.

Harvesting indirectly affects nutrient cycling by changing soil conditions. Nutrients can also be lost through erosion and surface run-off (Vitousek 1985; Mann *et al.* 1988). Canopy removal increased surface temperatures, temperature fluctuations and alternating wetting and drying which enhanced decomposition (Matson and Vitousek 1981; Mou *et al.* 1993). Such microclimate changes have been found to last 3-4 years (Covington 1981; Vitousek 1982).

In a northern hardwood stand that had been clear-cut, Covington (1981) found that the forest floor and fine slash were important nutrient sources for the first 15 years. Studies of nutrient concentration of early post-harvest succession indicate an increase in N, P, K, Mg, and Ca (Outcalt and White 1981; Hendrickson 1988; Roberts and Gillian 1995). Other studies show a net loss (Adams and Boyle 1982; Mann *et al.* 1988) and continued decline over 6 years until roots had contacted nutrient rich, adjacent sites (Mou *et al.* 1993). After a wildfire on a harvested site, Adams and Boyle (1982) found Ca, P increased and K and N returned to levels similar to the undisturbed forest.

Kimmins (1987) cautions against judging the fertility of a site shortly after harvesting. The post-harvest flush of high nutrient availability over the first few years allows nutrient demanding species to initially grow well but nutrient levels may decline below pre-logging levels. Kimmins attributes the decline to the high C:N ratio in the wood slash left on the site and the inability of microbes to decompose the slash without an adequate supply of nutrients.

4.3. METHODS

4.3.1 Data Collection

Geranium bicknellii, Cornus canadensis, Rubus idaeus, Prunus pensylvanica and *Betula papyrifera* were collected from around each vegetation block (Chapter 2). These species were the most widely distributed over the different treatments. *G. bicknellii* and *P. pensylvanica* were found on all disturbance types and the other species were found in both disturbed and control areas. *G. bicknellii* and *P. pensylvanica* reproduced by seed whereas the other species sprouted, suckered or had rhizomatous growth.

Percent cover was estimated on 1 x 1 m plots for herbs and 2 x 2 m plots for shrub and *Betula* suckers. Cover values were used to develop cover-biomass prediction equations. Two to four sample sets were taken of each species from each site depending on the abundance of the species in the area. Some areas did not contain all species.

Specimens were oven dried at 70° C and separated into stem and foliage tissue before weighing for biomass calculations. Each specimen was ground using a Wiley mill and stored in plastic containers for nutrient analysis.

4.3.2. Nutrient Analysis

Plant samples were analyzed for total phosphorous, total nitrogen and total cations (Ca, K, Mg). Total N was measured using digestion with H_2SO_4 and catalyst followed by a distillation in alkaline medium and titration with dilute standardized HCl. Total Ca, Mg, K and P were analyzed using HCl/HNO_3 digest on ash sample and concentrations were determined using an Inductively Coupled Plasma Spectrometer (ICP) (ICAP 9000 Jarrel Ash).

During this process samples were pumped into a plasma, chemical bonds were broken and characteristic atomic emission lines were produced. The ICP Spectrometer measured the intensity of emitted light from the excited neutral or ionized atomic species. The intensity of light is associated with a particular spectral line that is directly proportional to the number of excited atoms in the plasma or the concentration. The methodology is outlined in detail in Kalra and Maynard (1991).

4.3.3. Data Analysis

Results are presented as mg of element per kg of dried sample. Analysis of variance was used to test for differences in nutrient concentration within a species among disturbance types and to compare species within disturbance types. Differences were considered significant at a $p<0.05$.

Regression analysis of biomass (y) and the cover (x) values presented in Chapter 2 produced the following equations;

Cornus canadensis	$y=1.035\,x^{0.849}$	$R^2= 0.69$
Geranium bicknellii	$y=0.940\,x^{0.992}$	$R^2= 0.84$
Prunus pensylvanica -leaf	$y=2.456\,x^{0.965}$	$R^2= 0.84$
-stem	$y=0.992\,x^{0.978}$	$R^2= 0.67$
Rubus idaeus -leaf	$y=5.435\,x^{0.571}$	$R^2= 0.53$
-stem	$y=2.034\,x^{0.701}$	$R^2= 0.52$

B. papyrifera was not included as individuals in the cover data originated mainly from seed and nutrient analysis was done on vegetative emergents. *R. idaeus* had lower R^2 values due to its dense, shrubby nature.

4.4. RESULTS AND DISCUSSION

4.4.1. Nutrient Concentrations between Species among Disturbances

Tissue concentrations of various elements are more likely an expression of plant characteristics than a direct measurement of the element concentration available in the soil (Garten 1978), but foliar analysis can detect nutrient deficiencies if a species is compared across sites within a geographical range (Chapin and Tryon 1983). In this study, species responded differently to changes in nutrient availability caused by harvesting and/or fire. When compared, individual species also varied in their elemental composition within the same disturbance type.

4.4.1.1 *Cornus canadensis* and *Geranium bicknellii*

Among disturbance types, *C. canadensis* had significantly higher tissue concentrations of Ca, K and Mg in Control sites than other disturbance types (Figure 4.1). Nitrogen concentrations were significantly higher ($p<0.05$) in Wildfire sites than in Control, Harvested or Prescribed-burn sites.

When Ohmann and Grigal (1979) compared *C. canadensis* on burned and unburned sites, they found that plants on unburned sites had significantly greater N and K ($p<0.01$), while burned sites produced significantly greater P, Ca and Mg ($p<0.05$). The Little Sioux Fire, on which Ohmann and Grigal's

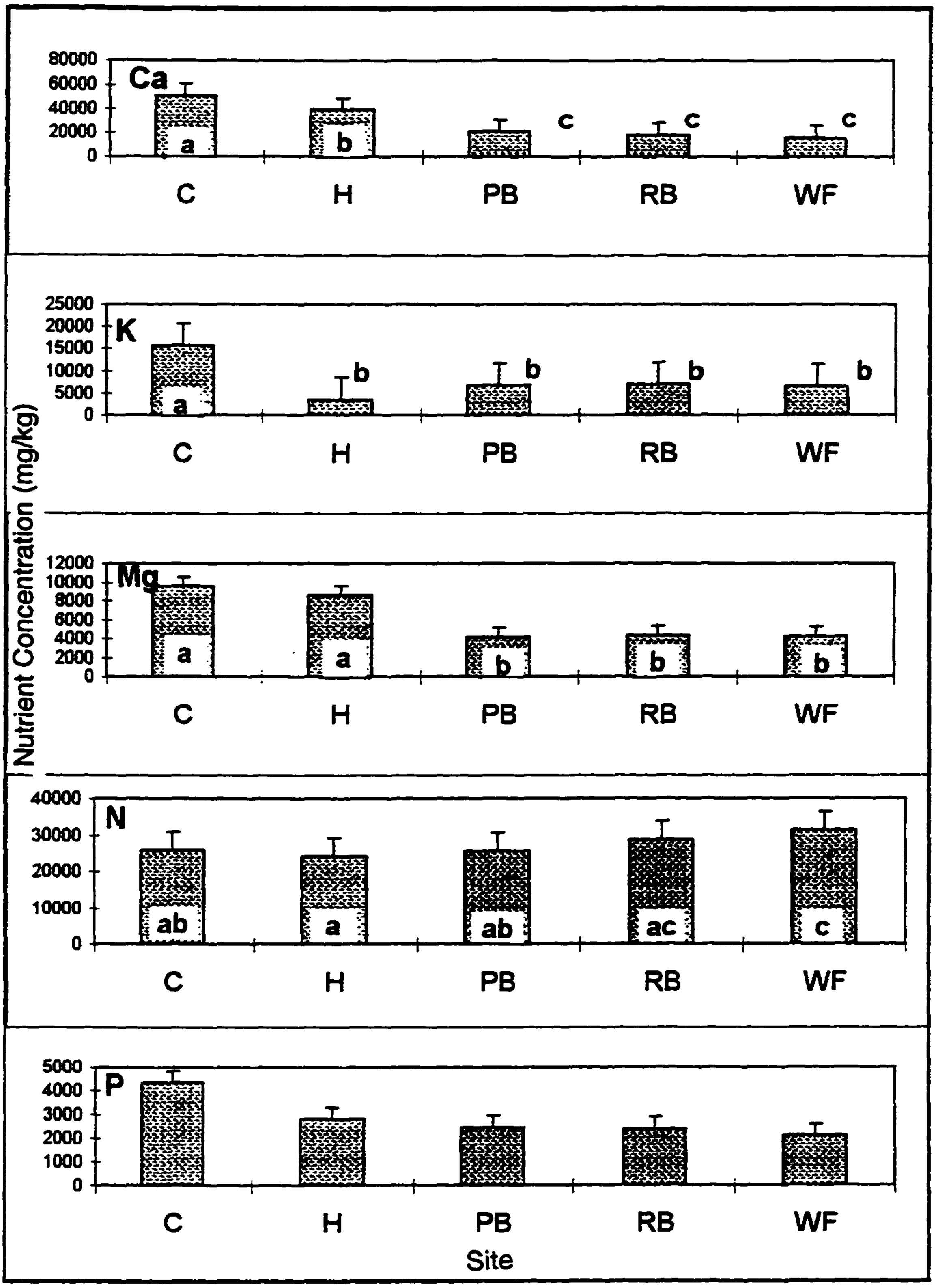


Figure 4.1. Comparison of nutrient concentrations of *C. canadensis* among different disturbance types. Site abbreviations: C, Control; H, Harvested; P, Prescribed-burn; R, Reburn; and W, Wildfire. Significant differences ($p<0.05$) among treatments are represented by different letters.

study was based, was a spring fire in which the forest floor was still moist and only 1-2 centimetres of duff were consumed. Also, their comparison between burned and unburned vegetation was made 4 years after the fire. Different fire conditions caused nutrient concentration of species on burn sites to be lower in Ohmann and Grigal's study compared to those found in this study, especially N.

G. bicknellii also had significantly higher ($p<0.05$) Ca and Mg levels in Harvested sites than most burned sites (Figure 4.2). When comparing *C. canadensis* and *G. bicknellii* (Figure 4.3), *G. bicknellii* contains significantly greater ($p<0.05$) K in Harvested, Prescribed-burned and Reburn sites than *C. canadensis.* Another trend between the herbs is the significantly greater ($p<0.05$) Ca and Mg content in *C. canadensis.* Ohmann and Grigal (1979) also found *C. canadensis* had high Ca and Mg concentrations with similar patterns over the five year study period. These elements are considered structural elements and would likely be in higher concentrations in the tougher, 'winter-green' leaves of *C. canadensis.*

Another explanation for the different concentration patterns between these species is their different reproductive strategies. *G. bicknellii* germinated from seed and thus relied totally on the nutrients found within its immediate environment. *C. canadensis* sprouted from rhizomes and relied on stored resources to establish itself. Sometimes plants that survive a disturbance experience a 'shock effect' that limits their growth rate and nutrient accumulation

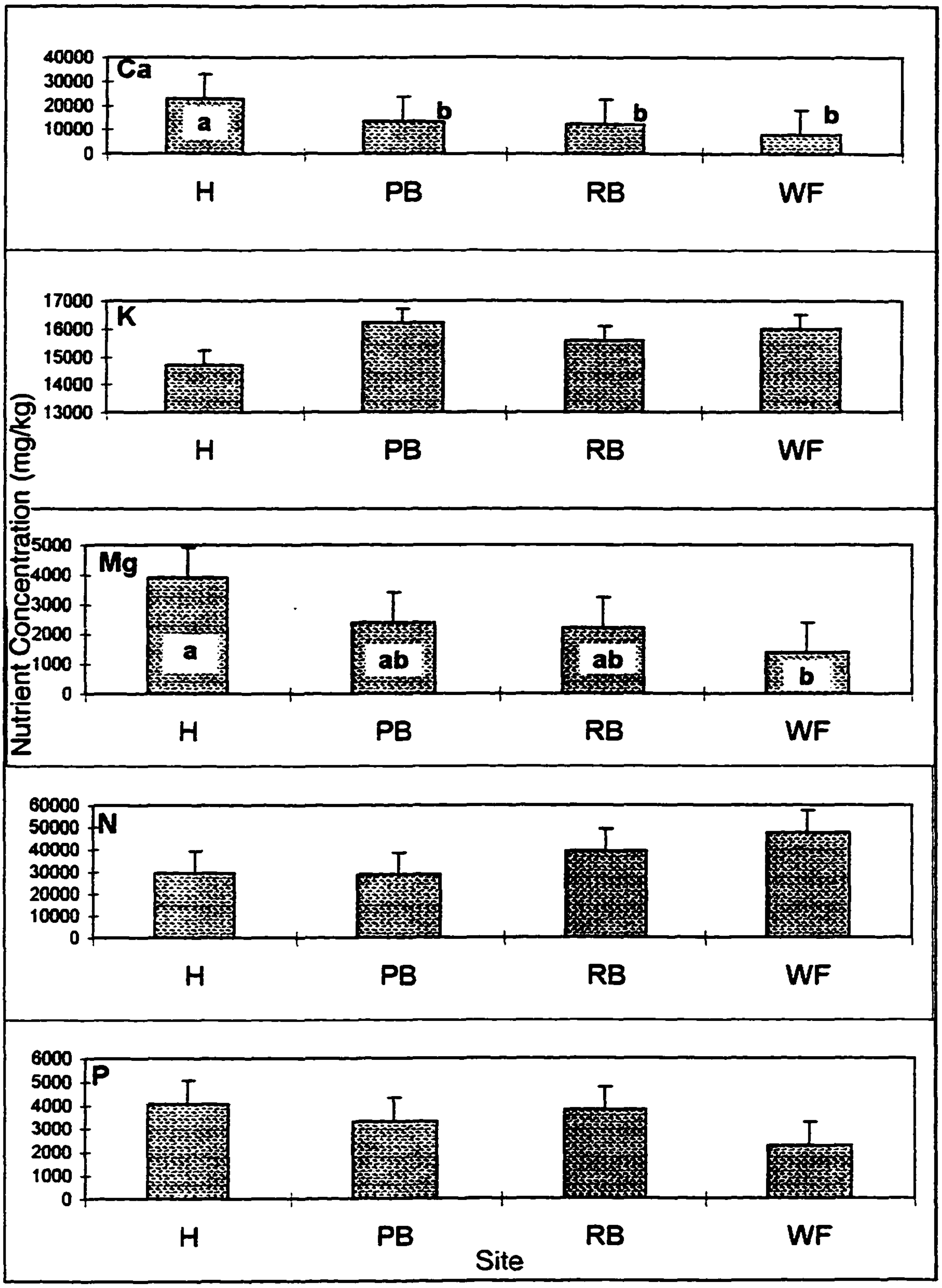


Figure 4.2. Comparison of nutrient concentrations of *G. bicknellii* among different disturbance types. Site abbreviations as in Figure 4.1.; this species not found in Control sites. Significant differences ($p<0.05$) among treatments are represented by different letters.

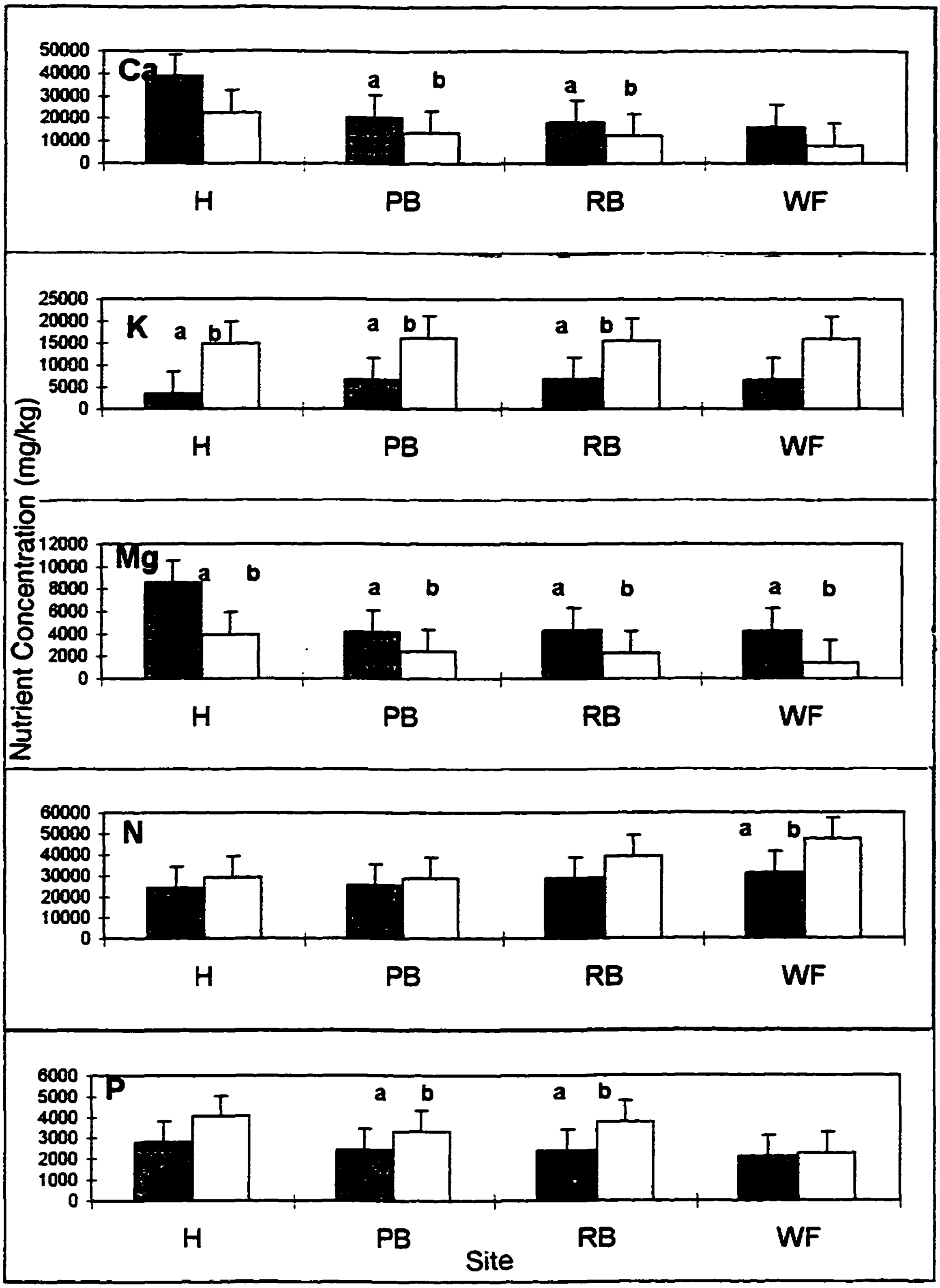


Figure 4.3. Nutrient concentrations of *C. canadensis* (shaded) and *G. bicknellii* (white). Significant differences (p<0.05) between species within treatments are represented by different letters.

during the first year. Mou *et al.* (1993) found that more severely disturbed sites usually showed greater nutrient concentrations in vegetation except for the first year after disturbance when the shock effect caused concentrations to be similar to those in undisturbed vegetation. Vegetative recovery varies with species. Calmes and Zasada (1982) exposed root cuttings to heat (25° C) and found *Rosa acicularis* emerged after seven days while *Ledum groenlandicum* sprouted after a 30 day delay. For *Rubus spectabilis*, shoot elongation does not occur until a month after bud break and continues over two months before root elongation can begin (Zasada *et al.* 1994). Mallik (1991) found that after cutting, and cutting with burning, *Kalmia spp.* produced significantly less rhizome length and dry weight. *Kalmia* allocated photosynthate to above-ground growth at the expense of below-ground growth after cutting and burning. Rodenkirchen (1995) found shade-tolerant ground vegetation had a delayed response to fertilizer treatments in a mature forest. In the N-saturated *Picea* forest, species were unable to prevent nitrate losses from upper mineral soil. Calcium, Mg and K fluxes through the ground vegetation were elevated only after three years of fertilizer treatment (Rodenkirchen 1995). The delayed response of root activity may prevent early sprouting growth from having a crucial role in nutrient retention on the site (Kramer and Kozlowski 1979; Mou *et al.* 1993). For *C. canadensis*, Messier and Kimmins (1991) found that large increases in leaf and fine root biomass occurred four to eight years after logging and burning so perhaps its role in nutrient retention is limited.

4.4.1.2. Rubus idaeus and *Prunus pensylvanica*

R. idaeus and *P. pensylvanica* are known for their favourable response to any disturbance that increases soil fertility (Marks 1974; Safford and Filip 1974; Hendrickson 1988). Although Mou *et al.* (1993) found *R. idaeus* leaf concentrations to be 2-4 times greater than that in stems and roots, these patterns were not clearly seen at this time. Areas that experienced fire produced *R. idaeus* with higher concentrations of all elements than Harvested sites, although these differences were not always significant (Figure 4.4). Nitrogen concentrations in stems were significantly higher ($p<0.05$) on Reburn and Wildfire sites than on Harvested sites but not different from Control sites.

P. pensyvanica had the greatest elemental concentrations in fire disturbed sites, especially Wildfire (Figure 4.5). In Wildfire sites, stem tissue had the highest concentrations for all elements among disturbance types, while leaf tissues had highest concentrations of K, Mg and N. Tissue nutrient concentrations in *P. pensylvanica* also seemed to correlate most closely with soils data. In June, the organic layer had significantly greater ($p<0.05$) P, Mg and K concentrations in fire treatments than in Control and Harvested sites

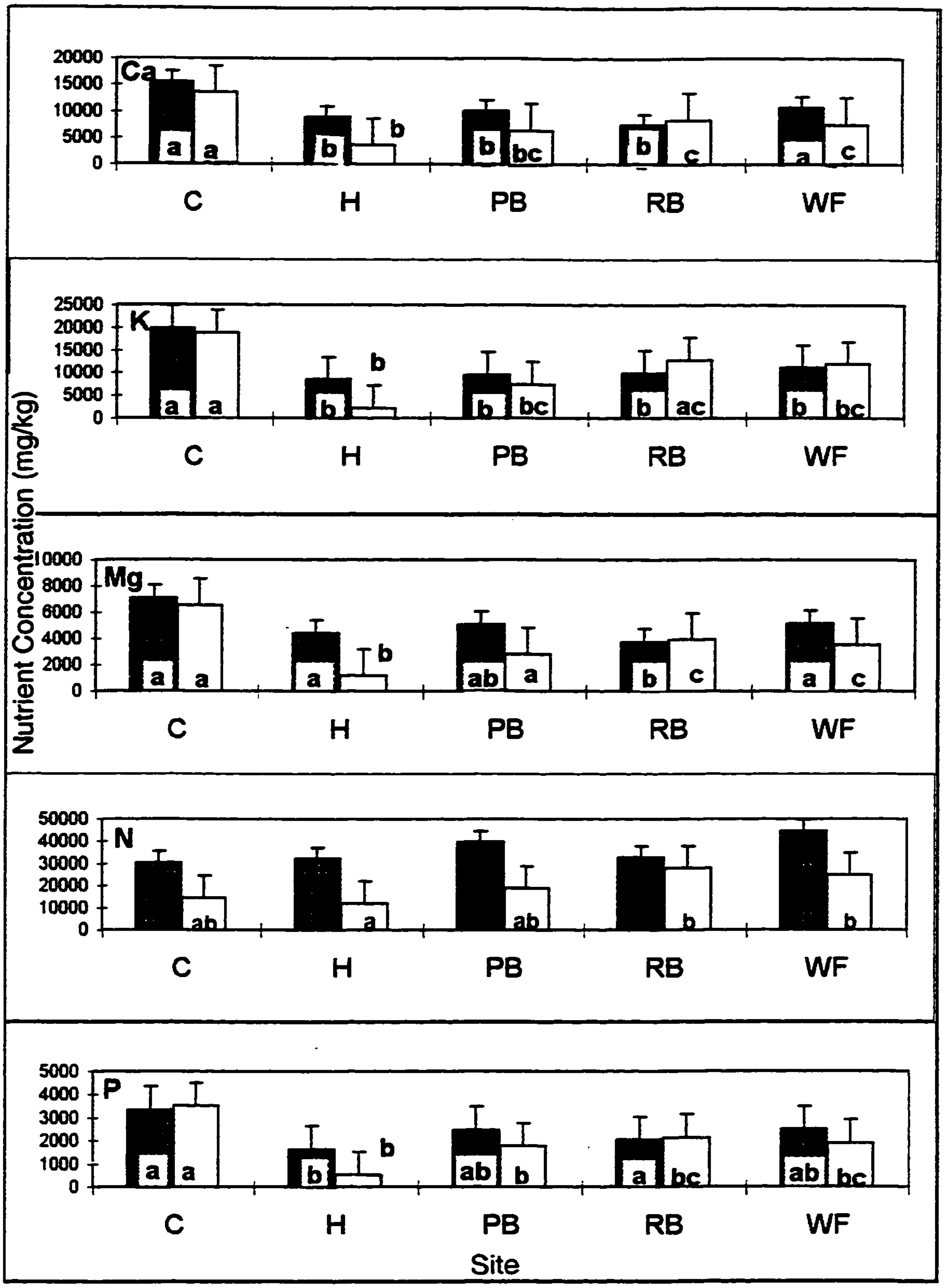


Figure 4.4. Comparison of nutrient concentrations of *R. idaeus* among different disturbance types. Leaf tissue is shaded while stem tissue is unshaded. Site abbreviations as in Figure 4.1. Significant differences ($p<0.05$) among treatments are represented by different letters.

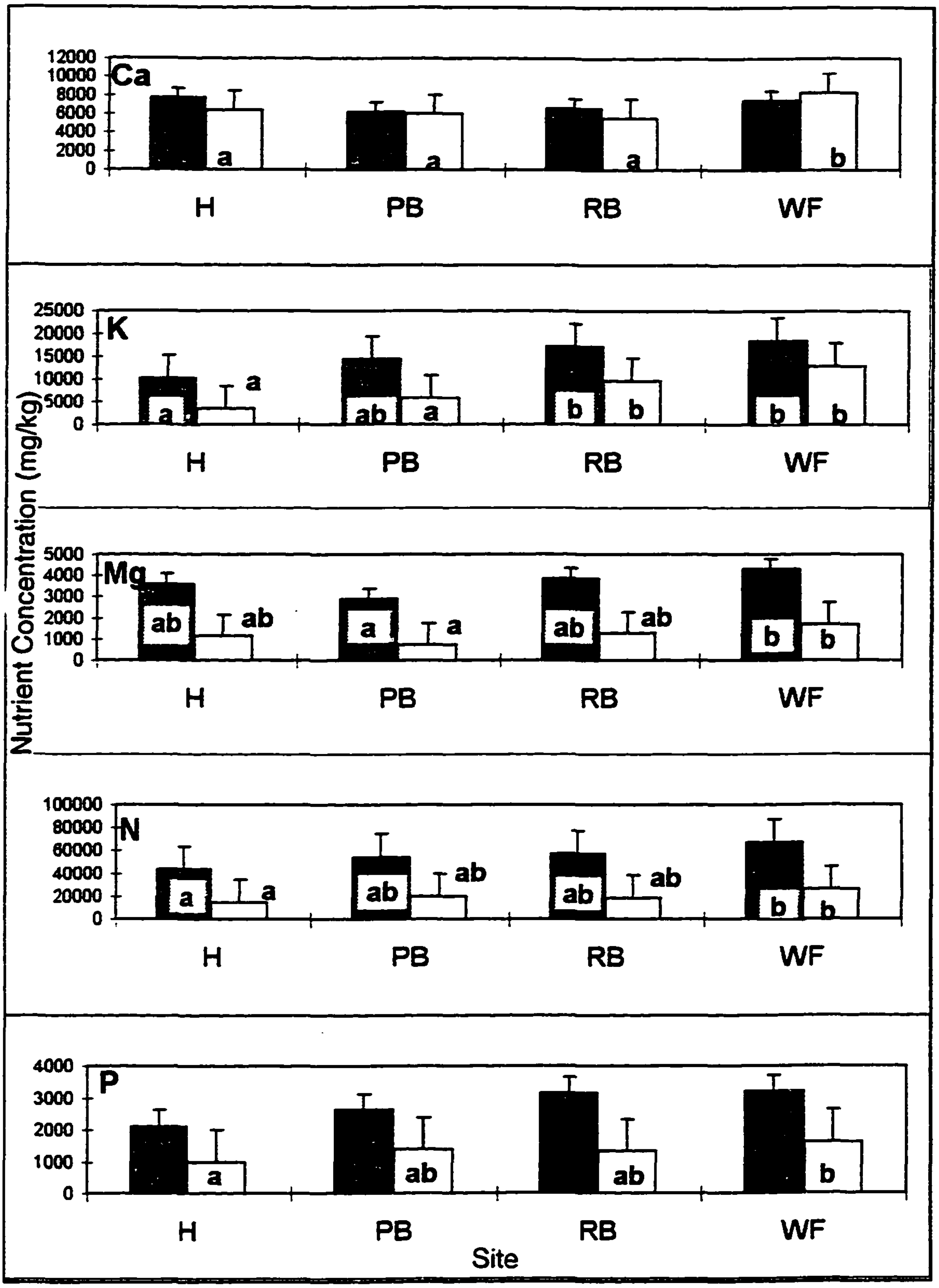


Figure 4.5. Comparison of nutrient concentrations of *P. pensylvanica* among different disturbance types. Leaf tissue shaded while stem tissue is unshaded. Site abbreviations are found in Figure 4.1. Significant differences ($p<0.05$) among treatments are represented by different letters.

(Stronach 1996). *P. pensylvanica* stem tissue generally showed lower element concentrations except for Ca due to the woody tissue's structural nature.

Although *R. idaeus* resprouted vegetatively after the fires, this species is known for is rapid growth rate and response to available nutrients, so it likely does not demonstrate the delay in nutrient uptake that shade-tolerant species do. When comparing the *R. idaeus* and *P. pensylvanica* (Figure 4.6), *R. idaeus* leaves have significantly higher Ca levels and greater Mg concentrations on Prescribed-burn and Wildfire sites. Calcium and Mg were in higher concentrations in the June organic layer after the fires than in organic soils of Harvested and Control sites (Stronach 1996), but *R. idaeus* may have had an elevated level because of root storage. Mou *et al.* (1993) found that *R. idaeus* had 0.23 % dry mass of Mg in its roots which was considerably higher than other species (e.g. *P. pensylvanica* 0.09 %, *Acer saccharinum* 0.04 %, *Aster spp.* 0.12%).

In Reburn sites, *P. pensylvanica* had significantly greater K, N and P. It has been suggested that to lower competitive pressures, these species use different forms of N or that their nitrification activity peaks at different periods in their lifecycles (Traux *et al.* 1994). Traux *et al.* found that *R. ideaus* had a growth and nutrient concentration response 10 times greater than *P. pensylvanica* following fertilizer addition and they attributed this to higher nitrate reductase activity. Nitrate reductase activity refers to the first enzyme

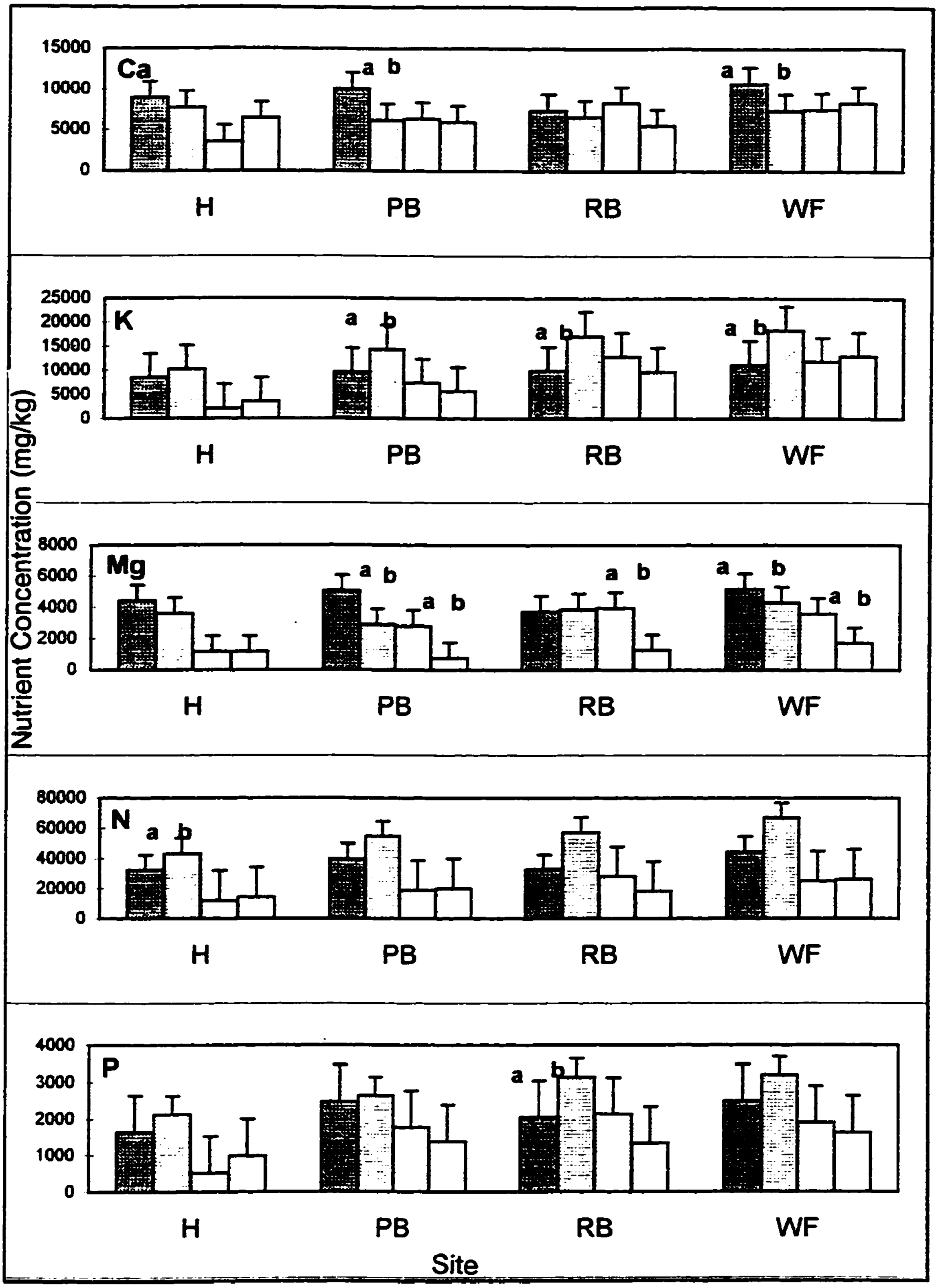


Figure 4.6. Nutrient concentrations of *R. idaeus* and *P. pensylvanica*. Leaf tissue is shaded while stem tissue is unshaded. *R. idaeus* is the first of each set of bars. Significant differences ($p<0.05$) between species within treatments is represented by different letters.

associated with NO_3^- assimilation. This high nitrification rate lasts two years while that of *P. pensylvanica* peaks at six years. Marks and Bormann (1972) identified ammonium as a potentially important N source for *P. pensylvanica* once soil conditions have become less favourable for *R. idaeus*.

Results of this study indicated that *P. pensylvanica* had higher N concentration for all treatments; it was significantly higher on Harvested and Reburn sites. Since *R. idaeus'* root N concentration is lower than *P. pensylvanica* and it sprouted vegetatively, perhaps *Rubus* is expressing a delayed response to greater N availability in the soil after fire.

4.4.1.3 *Rubus idaeus* and *Betula papyrifera*

B. papyrifera had significantly lower Ca and Mg concentrations on disturbed sites (Figure 4.7). Burned areas produced stem tissue with significantly higher K and N than that found in Harvested sites and Control sites. *Betula* samples were root collar sprouts, so resources in the root system could have influenced the tissue nutrient concentrations more than soil differences.

Trends in organic soil nutrient data collected in June indicated P, N, and cations were significantly less ($p<0.05$) in Control and Harvested sites than burned sites, especially Prescribed-burn and Reburn sites that experienced severe surface fires (Stronach 1996). Nutrient availability in Control, and to some extent Harvested, sites would be lessened as elements are still locked in

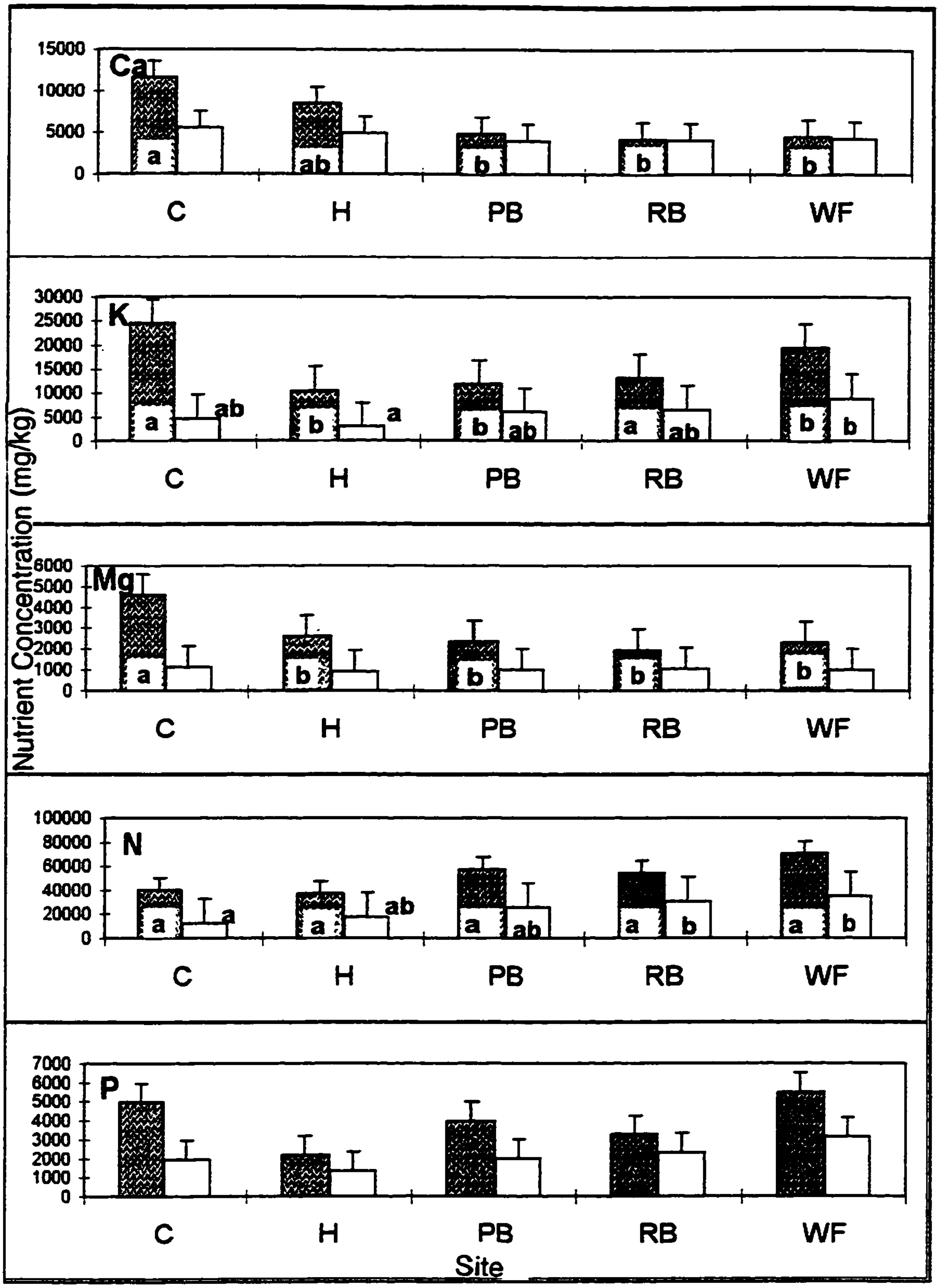


Figure 4.7. Comparison of nutrient concentrations of *B. papyrifera* among different disturbance types. Leaf tissue is shaded while stem tissue unshaded. Site abbreviations are found in Figure 4.1. Significant differences ($p<0.05$) among treatments are represented by different letters.

living or undecomposed biomass. For those species that grew in Control sites (*B. papyrifera, C. canadensis* and some *R. idaeus*), nutrient concentrations were higher on those sites than in disturbed sites for all elements except N. In other studies, nutrient concentrations were similar on undisturbed and harvested sites for *R. idaeus, P. pensylvanica* and *B. papyrifera* but these studies were conducted four years (Marks 1974; Hendrickson 1988) and six years (Mou *et al.* 1993) after harvesting.

R. idaeus leaf and stem tissue had significantly higher Ca on burned plots and Mg on Reburned and Wildfire plots than *B. papyrifera* (Figure 4.8). This is surprising since one would expect the woody stem of birch to have more of these structural elements. Stem N content for both species seemed to increase on burned sites.

4.4.1.4. *Prunus pensylvanica* and *Betula papyrifera*

A similar comparison was made for *P. pensylvanica* and *B. papyrifera* (Figure 4.9). In this case, *P. pensylvanica* had significantly higher leaf and stem Ca and Mg content on Reburn and Wildfire sites. Perhaps this is a reflection of the plant's seed origin and its ability to sequester nutrients released after the fires. Although Ohmann and Grigal (1979) did not compare these species directly, they found that *P. pensylvanica* had greater concentrations for all elements that *B. papyrifera* after fire, particularly N, P and Mg.

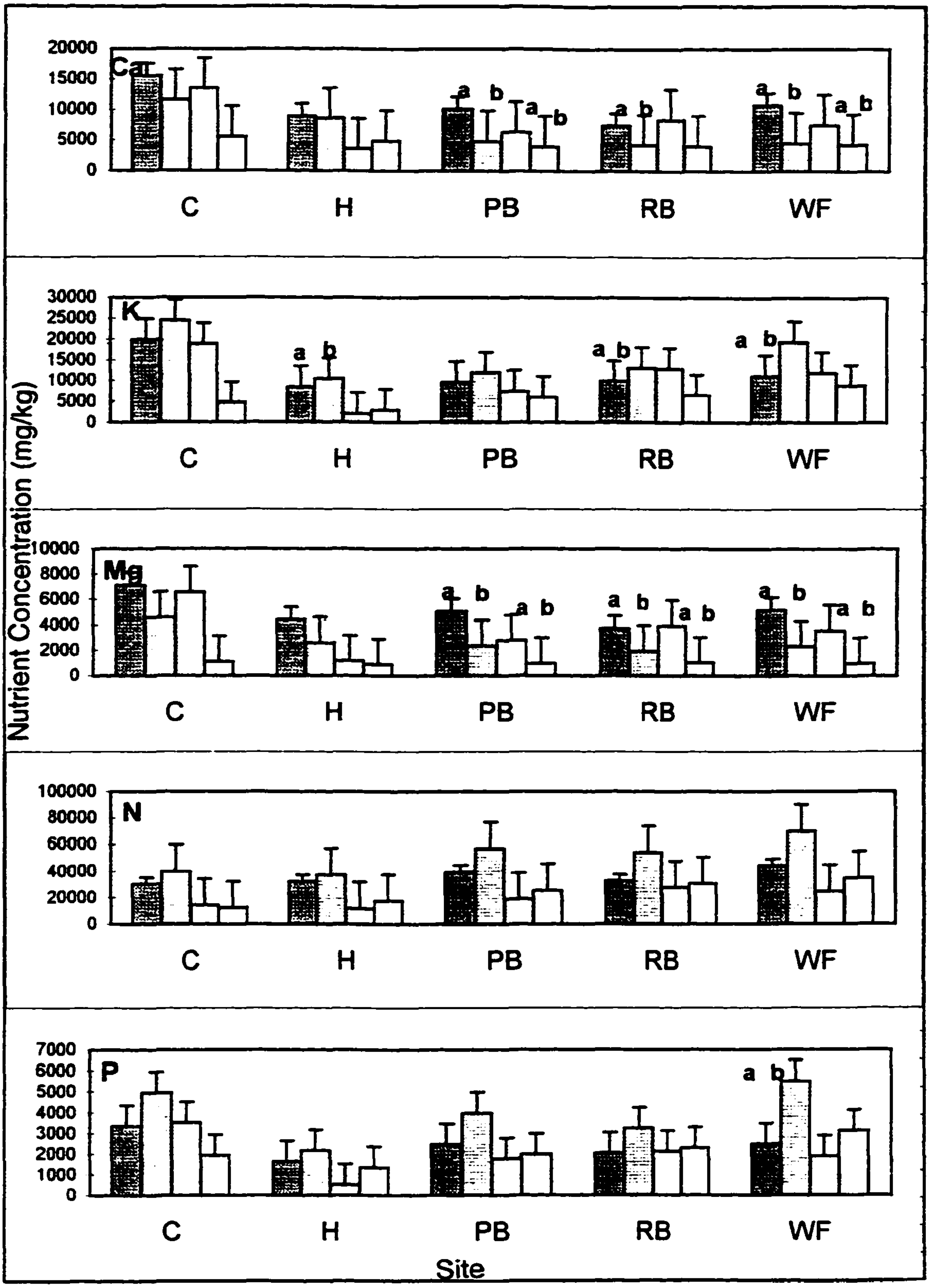


Figure 4.8. Nutrient concentrations of *R. idaeus* and *B. papyrifera*. Leaf tissue is shaded while stem tissue is unshaded. *R. idaeus* is the first of each set of bars. Significant differences ($p<0.05$) between species within treatments is represented by different letters.

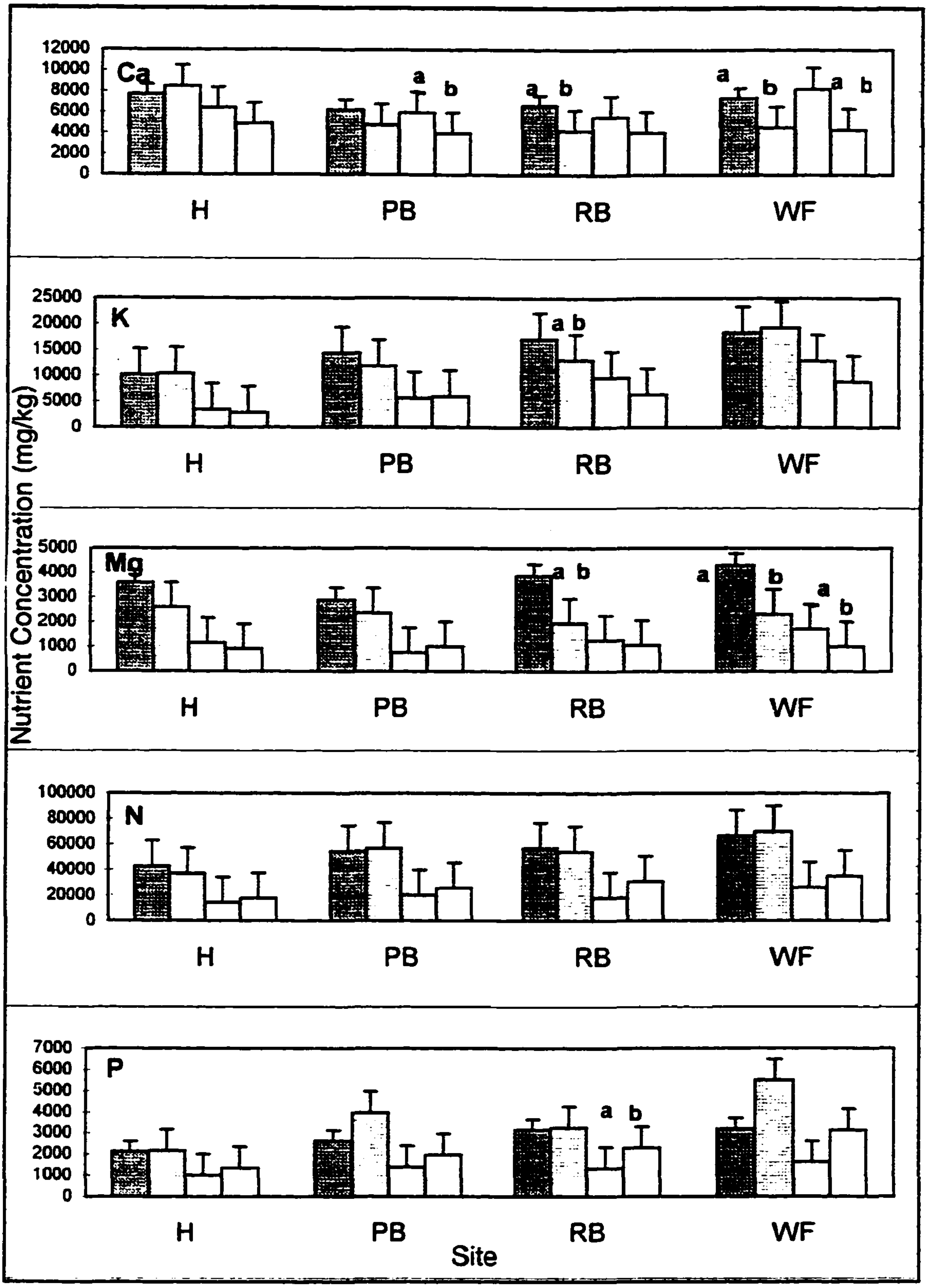


Figure 4.9. Nutrient concentrations of *P. pensylvanica* and *B. papyrifera*. Leaf tissue is shaded while stem tissue is white. *P. pensylvanica* is the first of each set of bars. Significant differences ($p<0.05$) between species within treatments is represented by different letters.

4.4.2 Biomass and Nutrients

Since the results presented in the previous section demonstrated that each species is characterized by different elemental compositions, the species composition of the site influences which elements are retained on the site and the quantity and how accessible the nutrients will be as the site matures. For example, fire severity greatly influences whether a site would be characterized by *C. canadensis* or *G. bicknellii.* Given the seed or rhizome source and appropriate regeneration niche, either species is able to revegetate a site. On a site severely burned, *G. bicknellii* may play an important role in retaining K, N and, to some extent, P on the site for a couple years afterwhich its foliage decays and the nutrients are returned to the soil.

Soils data collected in June indicate that disturbance type influenced nutrient availability (Stronach 1996), and the vegetation reflects these patterns. A summary of species nutrient concentration over the different disturbance types is summarized in Table 4.1. Due to variability in the distribution of the biomass of recovering vegetation, levels of elements were not significantly different among disturbance types but trends in elemental distribution could still be found.

C. canadensis had the greatest biomass on Control sites and contributed more Ca to the standing biomass than on Reburned sites. *G. bicknellii* and *P. pensylvanica* had greater biomass on burned than logged-only sites.

Table 4.1. Biomass and nutrient content (kg/ ha; ± standard deviation) of individual species among disturbance types. Different letters within colomns indicate significant differences ($p<0.05$) among disturbance types.

Cornus canadensis

Disturbance Type	Biomass	N	P	Ca	Mg	K
CONTROL	64.6 (±86.8)	1.65 (±2.24)	0.30 (±0.41)	3.27 (±4.37)	0.61 (±0.83)	1.00 (±1.35)
HARVEST	30.62 (±36.4)	0.75 (±0.94)	0.09 (±0.12)	1.26 (±1.50)	0.25 (±0.28)	0.11 (±0.12)
PRESCRIBED -BURN	14.9 (±32.3)	0.39 (±0.84)	0.04 (±0.09)	0.34 (±0.75)	0.06 (±0.14)	0.10 (±0.22)
REBURN	23.7) (±32.6)	0.66 (±0.87)	0.05 (±0.07)	0.44 (±0.59)	0.10 (±0.14)	0.15 (±0.21)
WILDFIRE	23.3 (±32.5)	0.71 (±1.00)	0.04 (±0.06)	0.39 (±0.57)	0.10 (±0.14)	0.15 (±0.25)

Geranium bicknellii

Disturbance Type	Biomass	N	P	Ca	Mg	K
HARVEST	0.5 (±2.3)	0.02 (±0.07)	0.00 (±0.01)	0.01 (±0.05)	0.00 (±0.01)	0.01 (±0.03)
PRESCRIBED -BURN	4.6 (±7.8)	0.11 (±0.18)	0.01 (±0.02)	0.07 (±0.11)	0.01 (±0.02)	0.07 (±0.12)
REBURN	32.9 (±66.9)	1.38 (±2.77)	0.12 (±0.24)	0.42 (±0.85)	0.07 (±0.15)	0.56 (±1.16)
WILDFIRE	4.6 (±8.5)	0.22 (±0.41)	0.01 (±0.03)	0.04 (±0.09)	0.01 (±0.02)	0.08 (±0.19)

Table 4.1. continued.

Rubus idaeus **leaf** **Disturbance Type**	**Biomass**	**N**	**P**	**Ca**	**Mg**	**K**
CONTROL	24.6 (±59.3)	0.65 (±2.22)	0.10 (±0.26)	0.48 (±1.24)	0.23 (±0.59)	0.58 (±1.46)
HARVEST	160.2 (±138.3)	5.06 (±4.29)	0.28 (±0.32)	1.43 (±1.22)	0.99 (±0.85)	1.33 (±1.11)
PRESCRIBED -BURN	98.2 (±122.5)	4.53 (±6.50)	0.25 (±0.32)	1.81 (±4.00)	0.73 (±1.07)	0.93 (±1.16)
REBURN	157.3 (±241.3)	11.44 (±26.48)	0.29 (±0.44)	1.09 (±1.64)	0.44 (±0.62)	1.71 (±2.68)
WILDFIRE	85.8 (±138.7)	3.06 (±3.91)	0.23 (±0.37)	0.86 (±1.37)	0.34 (±0.60)	1.21 (±2.12)

Rubus idaeus **stem** **Disturbance Type**	**Biomass**	**N**	**P**	**Ca**	**Mg**	**K**
CONTROL	11.6 (±29.1)	0.22 (±0.57)	0.05 (±0.13)	0.18 (±0.47)	0.10 (±0.26)	0.27 (±0.70)
HARVEST	83.5 (±87.5)	1.00 (±1.04)	0.04 (±0.06)	0.28 (±0.41)	0.09 (±0.15)	0.16 (±0.28)
PRESCRIBED -BURN	62.4 (±76.1)	1.15 (±1.54)	0.12 (±0.15)	0.41 (±0.48)	0.19 (±0.25)	0.52 (±0.74)
REBURN	95.0 (±160.3)	3.46 (±6.15)	0.26 (±0.46)	0.81 (±1.36)	0.36 (±0.61)	1.09 (±1.76)
WILDFIRE	45.3 (±83.5)	0.94 (±1.58)	0.08 (±0.13)	0.34 (±0.62)	0.14 (±0.23)	0.58 (±1.05)

Table 4.1. continued.

***Prunus pensylvanica* leaf** **Disturbance Type**	**Biomass**	**N**	**P**	**Ca**	**Mg**	**K**
HARVEST	54.1 (±62.1)	2.39 (±2.98)	0.20 (±0.42)	0.64 (±1.16)	0.29 (±0.44)	0.73 (±0.86)
PRESCRIBED-BURN	92.9 (±98.7)	5.40 (±5.74)	0.22 (±0.23)	0.54 (±0.57)	0.29 (±0.31)	1.20 (±1.27)
REBURN	91.0 (±127.4)	4.95 (±6.37)	0.28 (±0.37)	0.62 (±0.90)	0.35 (±0.49)	1.53 (±2.01)
WILDFIRE	68.4 (±67.1)	4.55 (±4.37)	0.23 (±0.23)	0.51 (±0.51)	0.29 (±0.28)	1.39 (±1.49)

***Prunus pensylvanica* stem** **Disturbance Type**	**Biomass**	**N**	**P**	**Ca**	**Mg**	**K**
HARVEST	22.2 (±25.8)	0.28 (±0.31)	0.02 (±0.02)	0.12 (±0.13)	0.02 (±0.02)	0.09 (±0.11)
PRESCRIBED-BURN	55.4 (±58.5)	0.83 (±0.81)	0.06 (±0.06)	0.33 (±0.36)	0.06 (±0.07)	0.36 (±0.43)
REBURN	46.1 (±51.6)	0.92 (±0.92)	0.06 (±0.06)	0.29 (±0.34)	0.05 (±0.05)	0.36 (±0.39)
WILDFIRE	28.2 (±27.9)	0.66 (±0.58)	0.05 (±0.05)	0.23 (±0.24)	0.05 (±0.05)	0.39 (±0.46)

Biomass trends among disturbance types for *G. bicknellii* and *P. pensylvanica* were similar to the values of Ohmann and Grigal (1979) one year after burning. *G. bicknellii* had quite low biomass on Harvested sites and plants on these sites had significantly lower ($p<0.05$) Mg. Biomass of *P. pensylvanica* and *R. idaeus* was less than that found by Marks (1974), Safford and Filip (1974) and Hendrickson (1988), whose measurements were taken four to six years after harvesting or fertilizer treatments.

Element amounts in *P. pensyvanica* and *R. idaeus* were found to be lower than in studies by Marks (1974) and Hendrickson (1988) which involved several years of recovery. Safford and Filip (1974) recorded values for unfertilized sites that were similar to Control and some Harvested sites while fertilized sites resembled burned plots. Their study showed similar stem allocation patterns for *P. pensylvanica* but leaf values were lower. Concentrations will decrease as biomass increases. Mou *et al.* (1993) found that after 2 years *P. pensylvanica* biomass had increased 14 fold but N concentrations increased only 5 fold. Very high standard deviations are found in biomass of Prescribed-burn and Reburned sites. This indicates substantial variability in regenerating vegetation likely related to either microsite variability or the distribution of propagules.

4.5 CONCLUSION

Variation in tissue concentrations of N, Ca, P, K and Mg indicated that species differentially absorb, store and cycle nutrients. Therefore, the species composition will influence a site's elemental composition. Variation in the concentrations of these nutrients was influenced by the type of disturbance experienced by the site and perhaps, by the method of regeneration.

Delayed or the prohibition of herb and shrub cover will increase the risk of nutrient loss from the site through surface runoff or leaching. Rapid regeneration after disturbance aids the recovery of nutrient cycling processes (Hendrickson 1988) through the retention of elements on the site. Patterns of biomass accumulation may dictate the degree of nutrient uptake or the effectiveness of the vegetation on the site to act as a nutrient sink. Foliage characteristics of the vegetation will influence the decomposition of litter and thus availability of the nutrients for later vegetation.

CHAPTER V

CONCLUSIONS AND RECOMMENDATIONS

5.1 SUMMARY

5.1.1. Synthesis of Study

This study has demonstrated that disturbance plays a very important role in determining the initial species composition, structure and function of plant communities. Disturbance type interacts directly with the propagule bank and nutrient cycling processes. Initial species composition is influenced indirectly by the regeneration niche created by the disturbance. The combination of direct and indirect interactions allows for the potential of many different successional paths within the same forest stand.

The high variability of seed / bud dispersal and disturbance intensity and severity over a site makes it difficult to develop detailed models of vegetation recovery. However, the importance of the pre-disturbance species composition in determining post-disturbance species composition is evident, especially on sites that were not severely disturbed. Residual populations dominated Harvested sites and were well represented on Wildfire sites. Higher disturbance severity increased the presence of seed banked and seed dispersed populations. Relative abundance of certain species was related to the disturbance type. *E. angustifolium* and *P. convolvulus* dominated areas of the Prescribed-burn plots while *G. bicknellii* was well represented on Reburn sites.

Although the divergence in species composition may only have been caused by a few species, these plants may have a more significant role than is presently understood. Studies that focus on dominant species (i.e. trees) and fail to incorporate understory vegetation, risk omitting important processes in forest recovery. Within the species studied, different ratios of the various nutrients accumulated. Thus, the initial species composition of a site will influence the element composition of the community. Litter-fall, as well as the species' decline and decomposition, will recontribute nutrients to the site and directly influence element cycling processes.

Determination of seed densities, rate of vegetative growth, natural processes that stimulate regeneration and conditions to which emergent species are adapted allow for the projection of future changes in species composition. This study showed that portions of the site will likely be characterized by *G. bicknellii* and *P. convolvulus* for two years, *E. angustifolium* and *R. idaeus* for four to six years and *P. pensylvanica* for 15 years. During this period, these early successional species will play an essential role in nutrient retention.

Soils on the site were fine sands and contained limited organic matter, leaving them susceptible to nutrient losses by leaching. Retaining nutrients on these site may be critical for future forest productivity. Vegetation from Harvested sites generally had lower nutrient concentrations which seem to be a reflection of soil nutrient content (Stronach 1996). Harvested sites were also characterized by greater vegetative regeneration. As suggested, species reproducing vegetatively may be delayed in their ability to absorb available nutrients directly after the disturbance as growth relies on stored reserves. Invader and seed-banking species were found on sites that experienced greater disturbance severity through harvesting and burning or wildfire and seemed to be composed of higher nutrient concentrations. Just as pre-disturbance species composition (including all species that deposited seed since the last disturbance) greatly influenced the post-disturbance composition, current changes in the successional direction will continue to influence communities generations from now.

5.1.2. Future Research

In this study, reproductive strategies should also have been determined in the field at the vegetation plots to confirm how the various species regenerated. Although fire severity was incorporated into the propagule bank study, the heterogeneity in organic soil depth created by fire was so diverse, even over a square metre, that it was difficult to generalize results. Further research to develop regeneration models needs to accommodate the spatial scales at which these processes are acting.

This study is limited by the lack of pre-disturbance data and the short recovery period studied. Trends that are suggested in this study will likely become more evident over time.

A better understanding of understory autecology and response to nutrient conditions would be useful for interpreting site conditions. Many species are sensitive to changes in soil fertility, and to physiographic and edaphic conditions.

5.1.3. Emulating Natural Forces

Recent forestry practices and policies concerning vegetation management are tending to incorporate the goal of emulating natural forces, although specific objectives have not been identified. Using fire as a means of slash reduction and vegetation management is recognized as a method that more closely reflects natural processes. On the site where this study occurred, hot, dry conditions allowed the fire smoldering under a slash pile to spread into the surrounding forest creating the Wildfire component of this study. Higher duff-moisture levels prevented the fire from greatly reducing the organic layer in forested areas. Some caution should be taken when interpreting this, or any other wildfire as 'natural', as the most important characteristic of 'natural' is variability. A very severe fire would have created very different results but would be just as 'natural'. This wildfire does have some very important characteristics that were absent from the other disturbance types and will be discussed accordingly.

The Wildfire seemed to share regeneration characteristics with Harvested sites but these were likely caused by different processes. Diversity levels were high on both sites because of the ability of species of seed and vegetative origin to establish. Species that relied on seed dispersal were represented on Harvested sites but had not yet reached Wildfire sites which were characterized by seed-banking species. Plant nutrient concentrations from the two sites were very different which supports Johnston and Elliott's (1995) suggestion that Harvested sites had greater diversity because 'disturbance' species were unable to dominate a site that did not have high nutrient availability.

Prescribed-burn and Reburn sites more closely resembled Wildfire sites in their species composition and nutrient concentrations, suggesting that the use of fire will more closely emulate natural processes than will harvesting alone. The most obvious difference between these disturbances is the presence of standing dead trees on Wildfire sites. These trees would moderate soil temperatures and moisture and perhaps provide a seed source. *Picea* germinants were found in Control and Wildfire soils. Harvesting before burning allowed many species to colonize the sites and revegetate rapidly after the fire. Harvesting can also make the surface of an area more homogeneous, especially when remaining slash is piled by the road. On the Wildfire site, pre-disturbance conditions would have allowed the fire to create a greater variety of burn severities.

5.4 Ecological Guidelines for Prescribed-burn Plans

While waiting for appropriate weather conditions, there was a two year fire ignition delay. The Radio Lake Prescribed burn was ignited with the intention of controlling 'competing vegetation' and enhancing the site for artificial regeneration (OMNR 1995). 'Acceptable' conditions finally occurred in early May but these conditions only allowed for a low intensity / low severity fire. This prescribed burn actually stimulated vegetative reproduction of species that had established on the site during the two year delay (e.g. *E. angustifolium, R. idaeus*). The fire that occurred on the site later in the season (Reburn) was more successful at achieving a greater duff-reduction and producing less vegetation cover.

In order to accomplish the intended goals a better understanding of the characteristics of species present on the site and the ability to burn under conditions that would produce greater fire severity is needed. Some 'competing' shrub species such as *Acer spicatum* and *Alnus crispa* were visibly reduced on the burned sites to date but others such as *P. pensylvanica* and *R. idaeus* were enhanced. To reduce shrub competition, duff reduction of 50 -80% (5-8 cm) is needed; a duff reduction that characterized the Reburn site. However, for many fire-adapted species, it will be difficult to suppress them unless conditions created are unfavourable to germination and growth for any species. Also, managers are presently reluctant to light prescribed fires under such conditions.

This study demonstrated that fire and harvesting alone created different regeneration conditions and nutrient availability. Also the importance of early revegetation in retaining nutrients on the site and contributing to the nutrient composition of the community was explored. If forest management goals are to consider ecological structure and function in order to sustainably provide timber, perhaps the concept of 'competing' vegetation needs to be reexamined.

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APPENDIX A

Table A.1. Species names and authorities.

Species	**Authority**	**Common Names**	**other names**
Abies balsamea	(L.) Miller	balsam fir	
Acer saccharinum	L.	silver maple	
Acer spicatum	Lam.	mountain maple	
Alnus crispa	Dryander ex Aiton	green alder	*Alnus viridis*
Amelanchier sanguinea.	(Pursh) DC.	red-twigged serviceberry	
Aralia hispida	Vent.	bristly sarsaparilla	
Aralia nudicaulis	L.	saskatoon berry	
Aster macrophyllus	L.	large-leaf aster	
Betula papyrifera	Marshall	paper birch	
Calamagrostis canadensis	(Michx.) Beauv.	blue-joint grass	
Carex vaginata.	Tausch	sheathed sedge	
Clintonia borealis	(Aiton) Raf.	blue beaded lily	
Coptis trifolia	(L.)	goldthread	*Coptis groenlandica* (Oeder) Hulten
Cornus canadensis	(L.)	bunchberry	
Corydalis sempervirens	(L.) Pers.	pale corydalis	
Corylus cornuta	Marshall	beaked hazel	
Dicranum polysetum	Sw., D.	broom moss	
Diervilla lonicera	Miller	bush honeysuckle	
Equisetum arvense	L.	horsetail	
Epilobium angustifolium	L.	fireweed	*Chamaenerion angustifolium*
Epilobium leptophyllum	Raf.	northern willowherb	
Fagus grandifolia	Ehrh.	American beech	
Fragaria virginiana	Miller var.	strawberry	

Table A. 1. (continued) Species names and authorities

Species	**Authority**	**Common Names**	**other names**
Gaultheria hispidula	(L.) Muhlenb. ex Bigelow	creeping snowberry	
Galium triflorum	Michaux	sweet scented bedstraw	
Geranium bicknellii	Britton	Bicknel's geranium	
Goodyeara repens	(L.) R. Br.	rattlesnake plantains	
Hylocomium spendens	(Hedw.) B.S.G.	stairstep moss	
Kalmia angustifolia	L.	sheep laurel	
Ledum groenlandicum	Oeder	Labrador tea	
Linnaea borealis	L.	twinflower	
Lycopodium annotinum	L.	stiff clubmoss	
Lycopocium obscurum	L.	ground pine	*L. dendroideum* Michaux.
Maianthemum canadense	Desf.	false lily-of-the-valley	
Mitella nuda	L.	naked miterwort	
Mnium spp.		leafy moss	
Picea abies	(L.) Darsten	Norway spruce	
Picea glauca	(Moench) Voss	white spruce	
Picea mariana	(Miller) Britton, Sterns & Pogg	black spruce	
Pinus banksiana	Lambert	jack pine	
Pinus halepensis		pine	
Pinus resinosa	Ait.	red pine	
Pinus strobus	L.	white pine	
Pinus sylvetris	L.	Scots pine	
Pinus taeda	L.	Loblolly pine	
Pleurozium schreberi	(Brid.) Mitt.	Schreber's moss	
Polygonum convolvulus	L.	black bindweed	

Table A.1 (continued). Species names and authorities.

Species	**Authority**	**Common Names**	**other names**
Polytrichum juniperinum	Hedw.	hair cap moss	
Populus tremuloides	Michaux	trembling poplar	
Prunus pensylvanica	L.f.	pin cherry	
Pteridium aquilinum	(L.) Kuhn	bracken fern	
Ptilium crista-castrensis	(Hedw.) De Not.	plumb moss	
Ribes hirtellum	Michx.	gooseberry	
Rosa acicularis	Lindley	prickly rose	
Rubus idaeus	L. spp	wild red raspberry	*Rubus strigosus* Michaux.
Rubus pubescens	Raf.	dwarf raspberry	
Rubus stectabilis	Pursh	salmonberry	
Salix bebbiana	Sarg.	Bebb's willow	
Sorbus americanus	Marshall.	American mountain-ash	
Streptopus roseus	Michaux.	rose twisted stalk	
Trientalis borealis	Raf. spp.	starflower	
Vaccinium angustifolium	Aiton.	sweet and low blueberry	
Vaccinium myrtilloides	Michaux.	high bush blueberry	
Viola renifolia	A. Gray	violet	

APPENDIX B

Disturbance Characteristics

The northern portion of the area was harvested during the fall/winter of 1992/93 and the southern portion during the fall/winter of 1993/94 by Buchanan Forest Products. The horizontal arrangement and distribution of slash was characteristic of full-tree logging using feller bunchers with delimbing at the roadside where there was a heavy concentrations of slash. *Betula papyrifera* and the occasional *Picea* and *Pinus strobus* remained on site. Harvested sites located to the north were site-prepared using a bracke scarifier during the autumn of 1993/94. This method removes the organic layer to expose mineral soil and create planting or seeding microsites.

The goals of the prescribed burn were to: 1) prepare the site for artificial regeneration; 2) reduce the fine slash; 3) reduce competing vegetation; and 4) reduce residual competition and unmerchantable tree species.

Eight fuel load sampling plots were established in 1993/94, of which seven were used in this study. The prescribed burn was ignited on May 6th, 1995 and completed within that day. Ignition was a centre fire followed by strip fire beginning downwind and then strip head fires. Three weeks later, the fire resurfaced in three areas and was officially designated by Ontario Ministry of Natural Resources (MNR) as fire THU 14 on May 30th. The fires did not reach a significant size but did reburn areas of the prescribed burn and buffer zones before it was extinguished. Amount of precipitation experienced by the site during the prescribed burn and wildfire are summarized in Table B.1. Weather conditions and fire weather indices for the dates of both fire periods are found in Table B.2. Fire behaviour data for the three fire treatments are found in Table B.3.

Fuel load sampling plots were revisited and the summary of fuel and duff consumption is found in Table B.4. Prescribed burns are conducted under carefully selected `safe' weather conditions unlike most wildfire burns. Areas that were burned twice, experienced a very brief inter-fire period when vegetation started to grow followed by a greater degree of fuel reduction and duff removal.

Table B.1. Record of rainfall from the date of the initial prescribed burn until the suppression of the wildfire. Fire events abbreviations: PB, Prescribed Burn; RB, Reburn; WF, Wildfire.

Date	Event	Rainfall (mm)
6-May	PB	0
7-May	PB	0
8-May	PB	0
May 9 - 30		66.3
31-May	RB & WF	0
1-June	RB & WF	0
June 2-19		25

Table B.2. Weather data and fire indices for the dates of the Prescribed burn, and Wildfire at Radio Lake.

Weather Data						Fire Indices					
Date	**Air Temp (°C)**	**RH (%)**	**Wind Dir. (deg.)**	**Wind Speed (km/hr)**	**Rain (mm)**	**FFMC**	**DMC**	**DC**	**ISI**	**BUI**	**FWI**
Prescribed Burn											
6-May	14	31	270	4	0	80.8	12	41	1.5	14	1.4
7-May	14	35	112	7	0	86.5	15	46	3.7	17	5.4
8-May	18	37	270	13	0	88.8	18	52	6.9	19	10.2
Reburn & Wildfire											
31-May	25	45	270	7	0	90.5	20	75	6.6	24	11.1
1-June	27	49	315	4	0	90.3	24	83	5.5	28	10.4

Table B.3. Fire behaviour data for the Prescribed Burn (PB), Reburn (RB), and Wildfire (WF). Observed rates of spread taken from MNR fire report.

Treatment	Location	Forward Rate of Spread (m/min.)		Frontal Fire Intensity (kW/m)	
		7-May	8-May	7-May	8-May
PB	Plot 4	0.2	0.5	170	550
PB	Plot 10	0.2	0.7	256	827
PB	Plot 14	0.1	0.3	69	223
		31-May	1-June	31-May	1-June
RB	Plot 5	1.8	1.4	3753	2861
RB	Plot 9	0.9	0.7	1094	834
RB	Plot 12	2.4	1.8	6908	5267
RB	Plot 13	1.9	1.5	4316	3290
WF		1.4	1.1	529	434

Table B.4. Summary of fuel loading and consumption by Fire event. Fire event abbreviations: PB, Prescribed Burn; RB Reburn.

Treatment	Location	Slash Loading & Percent Consumed by Size Class				Total Slash Loading & Percent Consumed		Duff Loading & Percent Consumed		Duff Depth & Percent Reduced	
		0 - 6.99 cm		7+ cm							
		(kg/m^2)	%	(kg/m^2)	%	(kg/m^2)	%	(kg/m^2)	%	(cm)	%
PB	Plot 4	1.82	49	6.25	30	8.07	34	8.46	8	8.0	20
PB	Plot 10	1.18	16	3.46	16	4.64	16	18.88	17	13.4	32
PB	Plot 14	1.37	-10	2.71	57	4.08	35	24.88	5	16.0	14
Mean		1.46	18	4.14	34	5.60	28	17.41	10	12.7	22
RB	Plot 5	3.16	62	8.75	39	11.91	45	6.27	23	6.6	39
RB	Plot 9	2.04	58	3.13	23	5.16	37	7.81	29	7.6	45
RB	Plot 12	1.34	74	2.95	40	4.29	50	22.51	33	15.0	49
RB	Plot 13	1.83	67	3.91	45	5.73	52	10.16	44	9.0	59
Mean		2.09	65	4.69	37	6.77	46	11.69	32	9.6	84

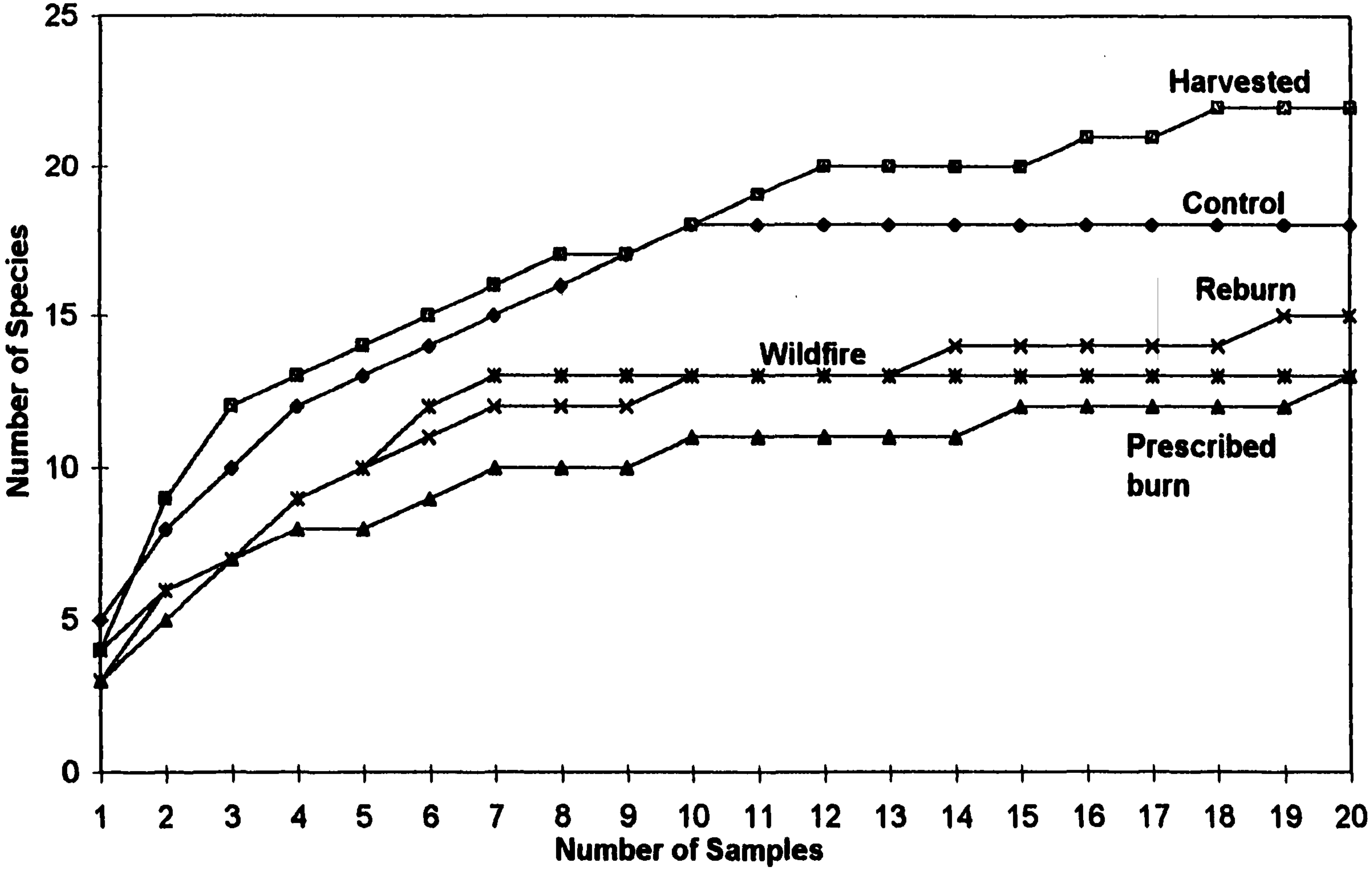


Figure C.1. Herbaceous species - vegetation sample curves for Control, Harvested, Prescribed-burn, Reburn and Wildfire sites.

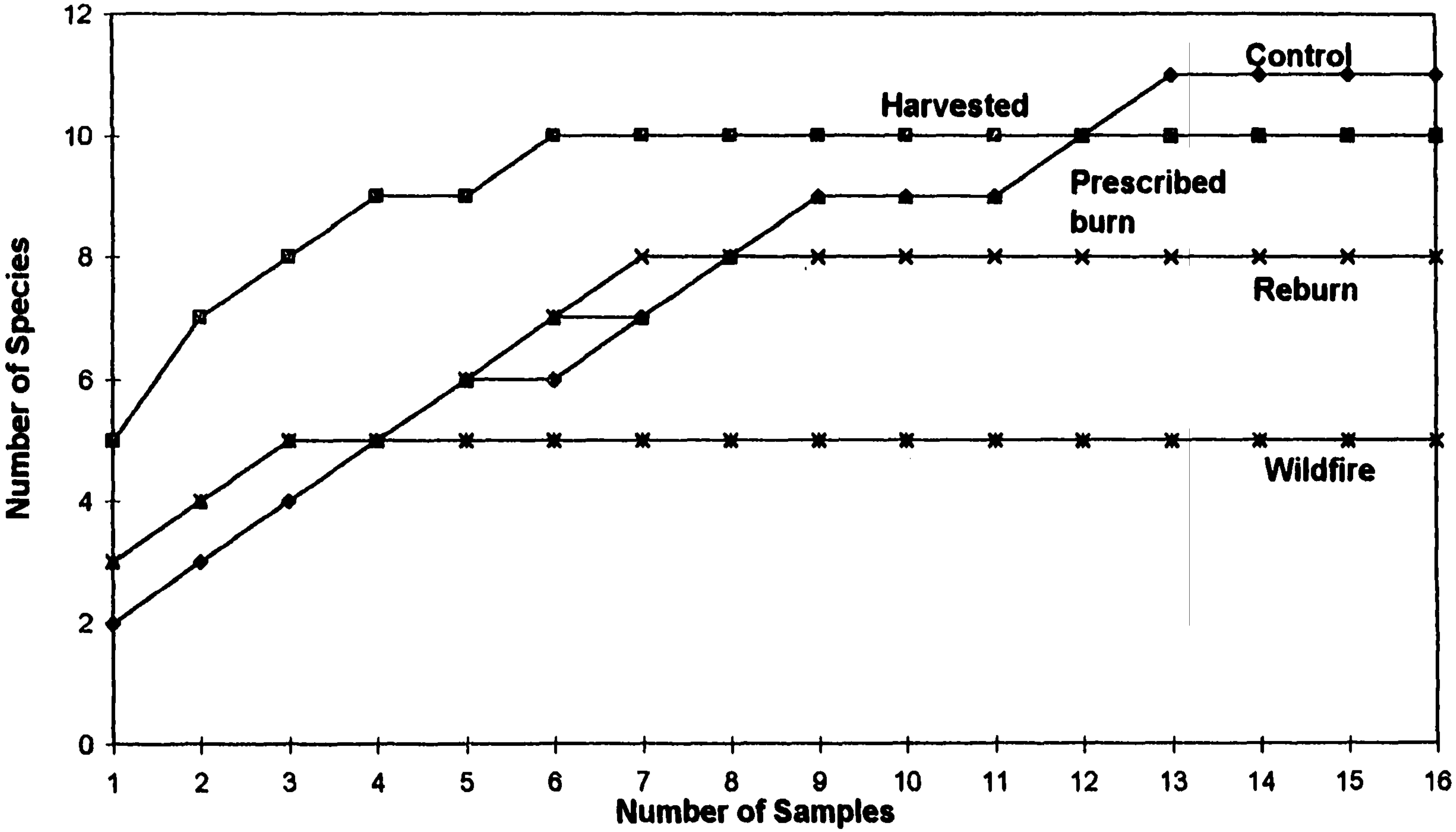


Figure C.2. Shrub species - vegetation sample curves for Control, Harvested, Prescribed-burn, Reburn and Wildfire sites

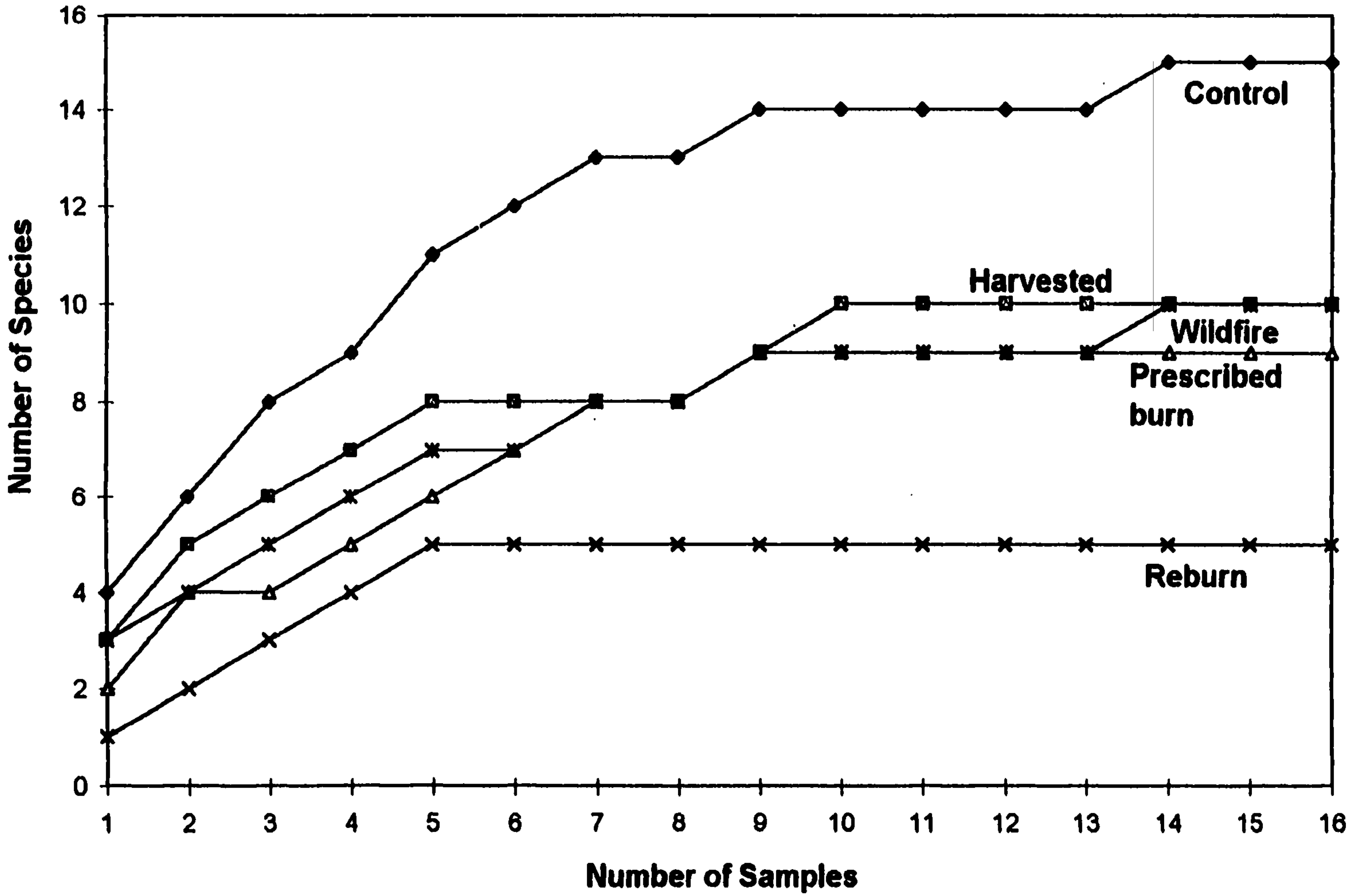


Figure D.1. June collection - propagule bank sample curves for Conrtol, Harvested, Prescribed-burn, Reburn and Wildfire sites.

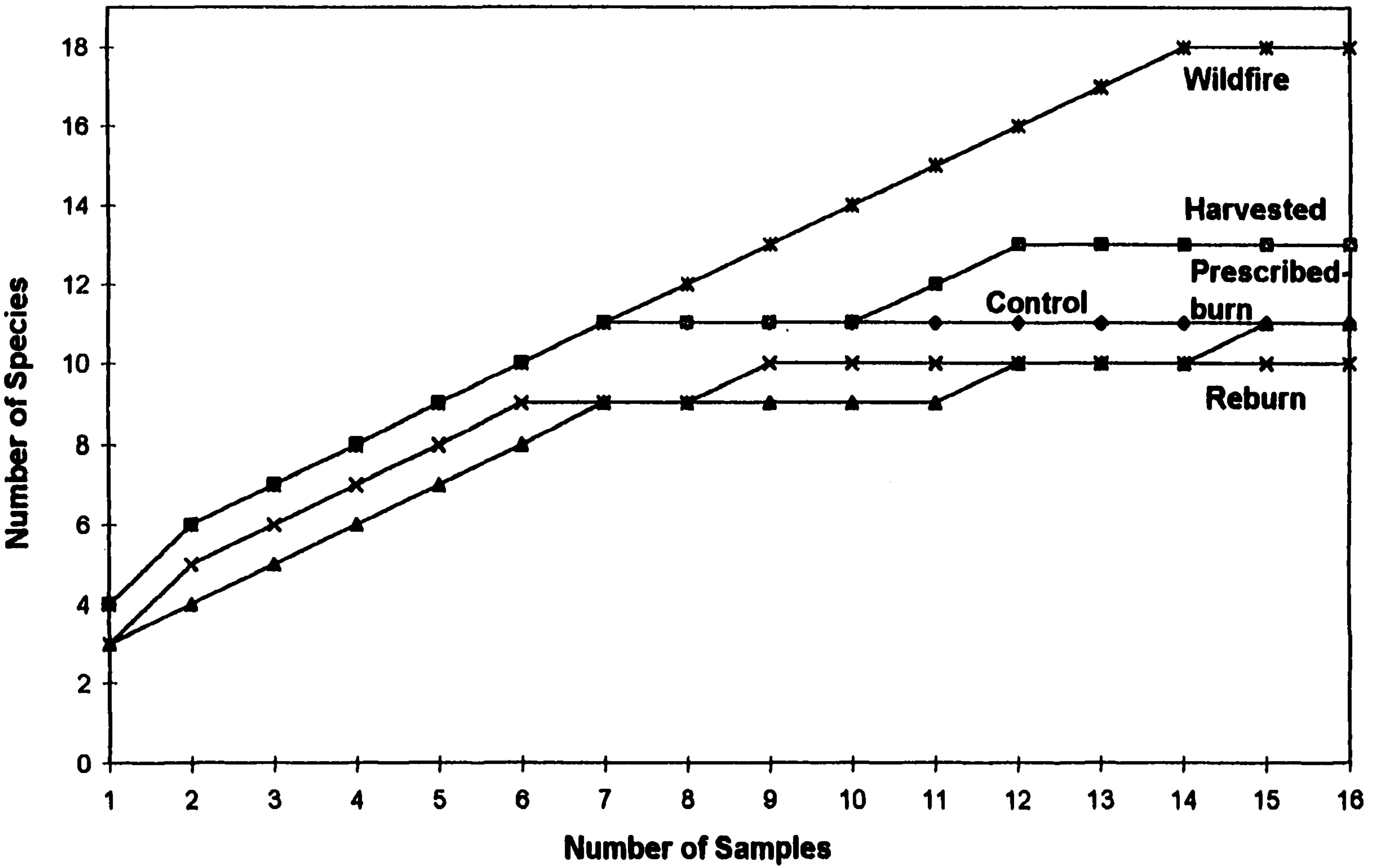
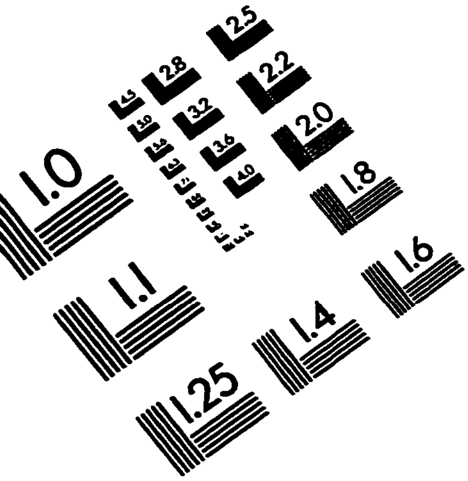
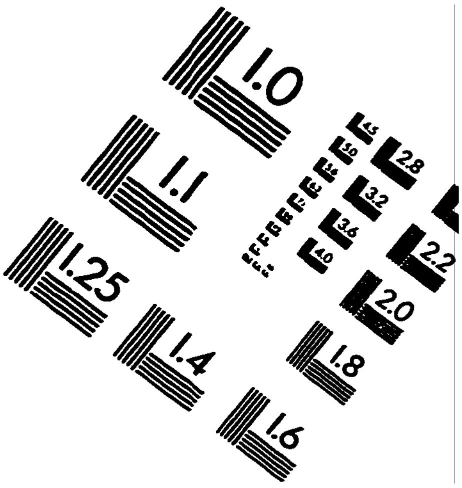
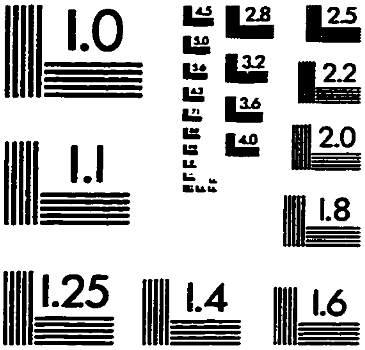


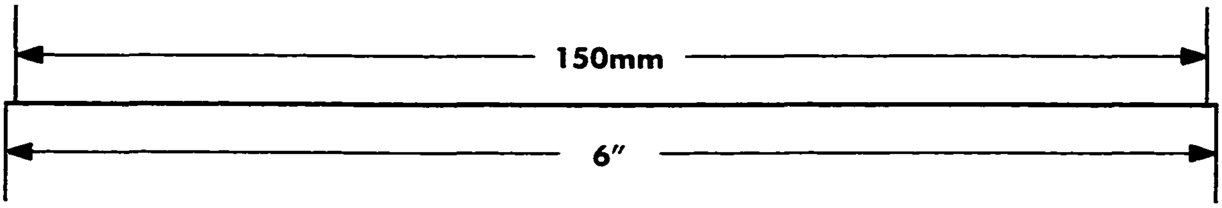
Figure D.2. October collection - propagule bank sample curves for Conrtol, Harvested, Prescribed-burn, Reburn and Wildfire sites.

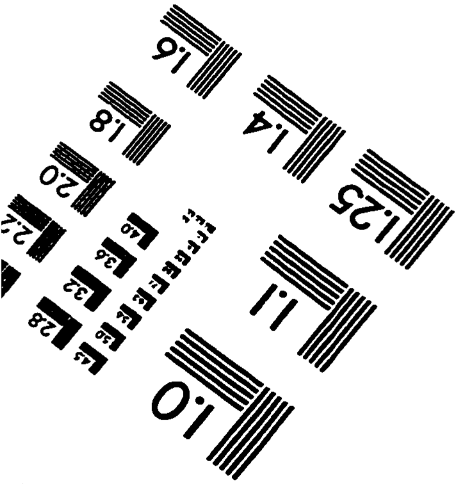
IMAGE EVALUATION TEST TARGET (QA-3)

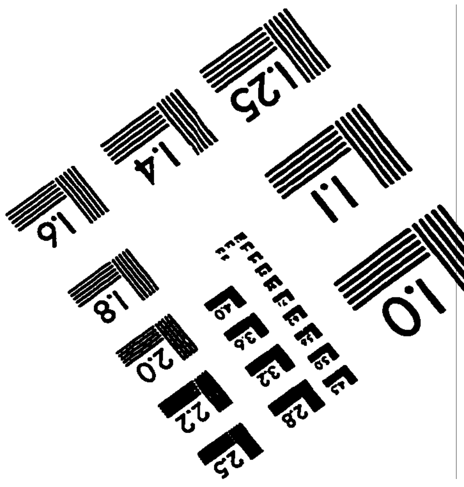












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