POST DISTURBANCE DYNAMICS OF ASPEN MIXED-WOODS:
A COMPARISON AMONG FIRE, LOGGING, AND BUDWORM OUTBREAK.

by

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ABSTRACT

Seventy-one aspen (*Populus tremuloidies* Michx.) mixedwood stands disturbed in the 1980's were sampled in southeastern Manitoba, Canada to examine the response of arboreal and understory communities to natural and management-induced disturbances. Thirty stands were disturbed by severe spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks, 21 by crown fire, and 20 by conifer-selective logging. All sampled stands were on well drained upland sites with similar pre-disturbance vegetation.

For the understory community, species diversity, richness, and presence did not differ significantly between the disturbance types. Significant differences, however, were found in species evenness with the understory of logged stands being dominated by shrubs. Coefficient of community was consistently greater than percent similarity, indicating that differences between disturbance types occur primarily in species abundance. Comparisons were made with mature aspen (≤ 25 % and conifer) and mature mixed (> 25 and < 75 % conifer) stands. Logged stands were found to be more closely associated with mature aspen stands while budworm and fire disturbed stands were intermediate between the two mature stand types. Implications for management are discussed.

Due primarily to differential canopy removal both fire and logging disturbed stands were dominated by post-disturbance aspen regeneration and contained little conifer recruitment while spruce budworm disturbed stands had abundant conifer recruitment and significantly less aspen regeneration. Seed availability and abundance was the primary factor affecting post disturbance conifer recruitment with seedbed condition and vegetative competition playing a secondary role. Timing of post-disturbance tree recruitment differed among the disturbances. Aspen was recruited more abundantly in the first five years following fire and logging and had significantly more recruitment after five years following end of budworm outbreak. White spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.) showed continual recruitment in fire and budworm disturbed stands but not in logged stands where recruitment was more abundant in the first five years. Balsam fir (*Abies balsamea* (L.) Mill.) showed continual recruitment following fire and logging, and recruited more abundantly after five years following budworm disturbance.

Key words: Disturbance, fire, logging, spruce budworm, boreal mixedwood, ecology, succession, regeneration, understory community, aspen, balsam fir, spruce.

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1. General introduction

Boreal forest ecosystems are dynamic (Shugart and West 1981, Johnson et al. 1995, Chapin et al. 1996) and subject to frequent and reoccurring natural disturbances. Within the Canadian boreal forest, upland mixedwood stands are some of the most productive forest ecosystems (Opper 1981, Peterson and Peterson 1992, Pare and Bergeron 1995). In the mixedwood stands of southeastern Manitoba, aspen (*Populus tremuloidies* Michx.) dominates the hardwood component while white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.) and, to a lesser degree, black spruce (*Picea mariana* (Mill.) B.S.P.), make up the softwood component. The dominant shrubs in these mixed stands are beaked hazel (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.). In addition to frequent wild fire (Rowe 1961, Rowe and Scotter 1973), spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks have been an important natural disturbance in boreal mixedwood stands (Ghent et al.1957, Baskerville 1975). With increasing timber harvesting logging has also become an important disturbance in southern boreal forests across Canada. Understanding the ecological impact of each disturbance and their differences is therefore fundamental to the sustainable management of boreal forest ecosystems (Rowe 1961, Rowe and Scotter 1973, Oliver and Larson 1990, Hanson et al. 1991, Attiwill 1994, Chapin et al. 1996). While numerous studies have been done on post fire and/or logging plant communities elsewhere (e.g. Dyrness 1973, Johnston and Woodard 1985, Halpern 1988, Halpern 1989, McMinn 1992, Carleton and MacLellan 1994, Qi and Scarratt 1998), no such study has been conducted in boreal mixedwood stands in southeastern Manitoba. In addition, no study has explicitly compared the ecological effect of the three common disturbances anywhere in Canada.

Different types of disturbance may affect post-disturbance plant regeneration differently due to differences in severity and the effect on existing forest floor and vegetation (Figure 1.1). Among the three common disturbances in boreal mixedwood stands, only fire can be categorized as severe while logging and spruce budworm are considered to be moderate to low severity (Frelich and Reich 1998). The severity of disturbance on the forest floor determines the development of post-disturbance plant communities, given the same pre-disturbance vegetation and site conditions, through regulating seedbed conditions and availability of buried propagules. With regard to seeds and buried propagules logging and spruce budworm outbreak have little effect on the forest floor resulting in more favorable conditions for early growth of persistent species (Nguyen-Xuan et al. 2000). On the other hand fire may result in complete consumption of the forest floor thus favoring growth of species relying on seed-dispersal. This difference may have a profound influence on the post-disturbance plant community as propagules need to be available soon after disturbance if a species is to maintain its importance on a site (Zasada et al. 1992).

In addition to the difference in post-disturbance forest floor condition, fire, logging, and budworm outbreak differ greatly in their impact on above ground vegetation. Crown fire usually kills all aboveground vegetation while logging and budworm outbreak limit their damage mainly to canopy trees. Unlike logging and fire which remove or kill the canopy in a very short period of time, mortality of infested trees following spruce budworm outbreak is much more variable (Lynch and Witter 1985) and usually occurs after a minimum of 4 to 5 years of heavy defoliation (MacLean 1980, MacLean and Ostaff 1989). Spruce budworm prefers mature balsam fir with mortality of seedlings (Bichon 1996), and of spruce being much lower (Miller 1975, Sims et al. 1990, Bergeron et al. 1995).

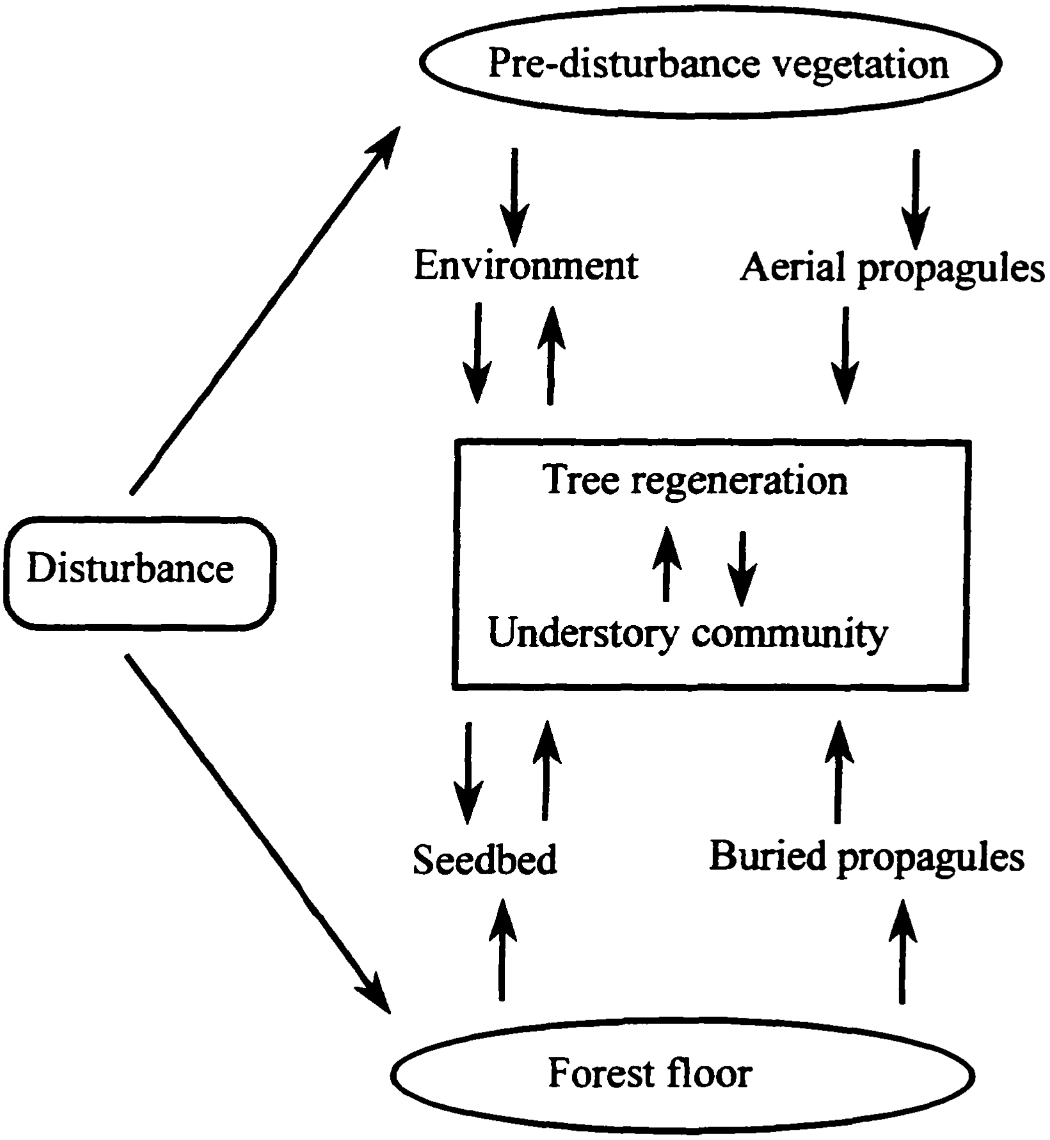

Figure 1.1. A conceptual model of post-disturbance development of plant community.

As a result, stands with high balsam fir (and to a lesser extent white spruce) content would suffer higher mortality and an open canopy condition would result, while those stands with low fir content, or with fir in the lower crown classes, would maintain a closed or partially closed canopy. With the presence of a residual canopy and relatively undisturbed understory vegetation and forest floor it is expected that budworm outbreaks. and to a lesser extent logging, would favor expansion of residual understory species and regeneration of shade tolerant species.

Following disturbance vigorous growth of trees, shrubs and herbs is characteristic in boreal forests (Ahlgren and Ahlgren 1960). Rapid vegetation growth modifies the conditions of seedbeds and micro-site environment (e.g., light), thus affecting future plant growth and survival (Figure 1.1). With time-since-disturbance tree regeneration. especially conifer establishment, becomes increasingly difficult because of poorer seedbed condition, smothering broadleaf litter, and vegetative competition (Koroleff 1954, Waldron 1966. Kneeshaw and Bergeron 1996, Liefers et al. 1996b, Cornett et al 1997, Delong et al. 1997. Galipeau et al. 1997, Beach and Halpern 2001). As exposed mineral soil is often cited as a preferred seedbed for conifer establishment (e.g. Waldron 1966, DeLong et al. 1997, Cornett et al. 1997) it is likely that fire would benefit conifer regeneration more than logging and spruce budworm disturbance given the same seed availability. However, this benefit will likely diminish with time-since-disturbance.

Fire, logging and budworm outbreak create different amounts of variation within each disturbance type, which, in turn, may affect the variation in post-disturbance development of plant communities. Although fire is generally categorized as a high impact disturbance that uniformly kills above-ground vegetation, there is great variation within a given fire disturbance (Ahlgren and Ahlgren 1960, Hely et al. 2001, Wang 2001). Patches of residual vegetation are common (Rowe and Scotter 1973, Eberhart and Woodard 1987) at the landscape level. At stand level, the depth of burn on forest floor has been shown to vary with canopy composition within aspen mixedwood stands, from light surface scorching to complete consumption of organic layers (Wang 2001). This is in contrast to budworm which creates a great amount of variation in canopy opening among disturbed stands while both understory and forest floor are uniformly preserved. Unlike natural (fire and budworm) disturbance, logging has a more uniform impact, and the least variation across disturbed stands.

Emulating the natural disturbance regime has been proposed as a viable management strategy to maintain biological diversity while allowing timber utilization in boreal forest (Denslow 1980, Halpern 1989, Attiwill 1994, Roberts and Gilliam 1995, Frelich and Reich 1998, Armstrong 1999, Wang 2001). The premise of the strategy is that boreal forest flora and fauna have adapted to the prevalent natural disturbances (Petraitis et al. 1989, Chapin et al. 1996). Emulating natural disturbance patterns in the boreal forest, however, can be difficult because frequency and severity of events change constantly over time (Frelich and Reich 1998). As stochastic and historical factors play important roles in affecting post-disturbance recovery of plant communities (Halpern 1989, Armstrong 1999) boreal forests may not follow the same regeneration and successional pathway after each disturbance. Characterizing disturbance regime and understanding how plant communities respond to different disturbance regimes therefore becomes essential in order to emulate natural disturbance through forest management. At the stand level it is critical to understand community dynamics following different types and intensities of disturbances (Attiwill 1994, Roberts and Gilliam 1995, Liefers et al. 1996b, Peltzer et al. 2000, Wang 2001). Knowledge is urgently needed on the persistence and/or regeneration of both individual species (Peltzer et al. 2000) and communities (Attiwill 1994), in short and long terms, following different types and intensities of disturbances (Roberts and Gilliam 1995, Liefers et al. 1996b). "Without a solid knowledge of the effect of disturbance on plant diversity, it will be difficult to tailor logging activities to copy primeval fire regimes and impacts" (Whittle et al. 1997).

This study was designed to provide some of the knowledge needed for the design and implementation of the 'forest management emulating natural disturbance' paradigm. The objective of this study was to compare early successional (approximately 10 years post disturbance) boreal mixedwood stands in southeastern Manitoba following stand replacing crown fire, conifer-selective logging, and severe spruce budworm outbreak. Data was collected for both the arboreal and understory community to enable comparisons of the recruitment and of trees, and the species composition and abundance of understory community among the three disturbances. To provide a reference point in community change, mature fire-origin stands sampled on boreal mixedwood sites in another study (Wang and Kemball, unpublished data) are also included. The results of this research are reported in two chapters. Chapter 2 deals with the understory community. Chapter 3 deals with the tree community.

2. Response and Recovery of Understory Plant Community Following Fire, Logging, and Spruce Budworm Outbreak on Boreal Aspen Mixedwoods.

2.1. INTRODUCTION

Plant species that make up the understory of boreal forests, including those most commonly associated with late successional stages, are well adapted to frequent disturbance (Shafi and Yarranton 1973, Rowe 1983, Halpern 1988, Whittle et al. 1997). Consequently, most understory species common in boreal forests (also referred to as persistent or resident species) are able to thrive under a variety of forest conditions or successional stages (Dix and Swan 1971, Carleton and Maycock 1981, Halpern and Spies 1995, McKenzie et al. 2000). Previous studies have shown that, after an initial increase of weedy invaders, disturbed communities vary little in species composition from pre-disturbance communities (Dyrness 1973, Johnston and Woodard 1985, Halpern 1988, Halpern 1989, McMinn 1992, Qi and Scarratt 1998), especially on mesic-hygric and rich sites (De Grandpre and Bergeron 1997). It has frequently been observed that following disturbance species richness increases as weedy invaders seize the opportunity for establishment (Dyrness 1973, Shafi and Yarranton 1973, Outcalt and White 1981, Halpern 1988, De Grandpre and Bergeron 1997, Peltzer et al. 2000). However, this increase in richness is usually short lived (Abrams and Dickmann 1982, Halpern 1988, Halpern and Spies 1995, Peltzer et al. 2000). Resident species quickly, usually within 5 to 6 years (Dyrness 1973), reestablish their dominance and persist through all stages of succession (Halpern 1989, Hanson et al. 1991, McKenzie et al. 2000, Peltzer et al. 2000).

The post-disturbance success of resident species has been largely attributed to their seed banking ability (Halpern 1988, Morgan and Neuenschwander 1988, Whittle et al. 1997, Qi and Scarratt 1998) and/or rapid vegetative reproduction and expansion (Buse and Bell 1992, Arnup et al. 1995). This dependence on *in-situ* propagules suggests the critical importance of disturbance severity. The significant effect of disturbance severity on the composition and growth of the post-disturbance community has been frequently reported (e.g., Dyrness 1973, Shafi and Yarranton 1973, Moor and Wein 1977, Johnston and Woodard 1985, Halpern 1988, Halpern and Spies 1995, Roberts and Gilliam 1995, Whittle et al. 1997, Nguyen-Xuan et al. 2000). Winter logging and spruce budworm outbreaks have little effect on understory vegetation and forest floor (i.e. buried *in-situ* propagules). Compared to logging, however, budworm disturbance retains and has more variation in residual canopy (e.g. Kneeshaw and Bergeron 1998), which could affect the development of post-disturbance understory community. Dominance by *Rubus idaeus* L., a seed banking species, has been reported in some cases (Osawa 1994, Lautenschlager 1997) following spruce budworm outbreaks. Unlike logging and budworm, fire can have a greater effect on the understory plant community (Shafi and Yarranton 1973, Moor and Wein 1977, Halpern 1988, Roberts and Gilliam 1995, Whittle et al. 1997, Nguyen-Xuan et al. 2000). Severe fire (i.e. crown fire with consumption or partial consumption of forest floor) frequently resulted in lower total coverage (Dyrness 1973, Johnston and Woodard 1985) and/or lower species richness (Halpern and Spies 1995) because *in-situ* propagules were consumed or their viability was lost due to heating. Compared to logging, fire can result in less woody vegetation recovery (Outcalt and White 1981) although the same core species are typically present indicating that a similar understory would eventually develop (Outcalt and White 1981). While fire can cause severe disturbance to the forest floor it is rarely uniform, particularly in aspen mixedwood stands where unburned and lightly burned patches are common (Wang 2001).

When patches of undisturbed soil are present within a disturbed area, residual species respond by increasing their coverage (Dyrness 1973, De Grandpre and Bergeron 1997). These undisturbed patches also act as sources for re-vegetation of the disturbed area.

The objective of the study was to compare plant communities (approximately 10 year-old) developed after crown fire, conifer-selective logging (i.e. removal of desired softwoods leaving unwanted hardwoods on site), and spruce budworm outbreak in boreal mixedwood stands in southeastern Manitoba. Two hypotheses are tested. First, given the adaptation of boreal flora to disturbance, the similarity in site and pre-disturbance stand conditions, and the age of the post-disturbance plant community, it is hypothesized that understory plant communities do not significantly differ among the three types of disturbance. Second, because of the great variation in forest floor consumption by fire, and canopy removal by budworm outbreak, it is also hypothesized that the post-disturbance plant community is more heterogeneous in both species richness and evenness in stands after fire and budworm when compared with after logging.

2.2. MATERIALS AND METHODS

2.2.1. STUDY AREA

The study area is located in the Lac Seul Upland ecoregion of the Boreal Shield ecozone (ESWG 1995) in southeast Manitoba. Climate is characterized by cold winters (mean temperature of -19.2°C in January) and relatively dry warm summers (mean temperature of 19.0°C in July). Average rainfall is about 400 mm with 270 mm falling during the growing season (May to August). Average snowfall is approximately 120 cm and the frost-free period is about 100 days. The study area lies within the Canadian shield and has a relatively flat terrain. Important soils in the study area include dystric brunisols, gray luvisols, gleysols, fibrisols, and mesisols. According to 1986 Manitoba forestry inventory, black spruce and aspen are either primary or secondary species in 88% of stands. Uplands with fine textured soils are dominated by aspen or aspen-conifer (white spruce and/or balsam fir) mixed stands while lowlands consist primarily of black spruce. Jack pine *(Pinus banksiana* Lamb.) covered granite rock outcrops are also common in this region.

2.2.2. SAMPLING DESIGN

Within the study area, boreal mixedwood stands disturbed by fire, logging and spruce budworm outbreaks were identified based on disturbance history and 1977 forest inventory database. Seventy-one mixedwood stands (21 disturbed by crown fire, 20 by conifer selection logging and 30 by spruce budworm) were sampled between 1999 and 2000. Approximate locations of the sampled stands are given in Figure 2.1. Sampled stands were selected according to the following criteria: (1) stands must be mature to over-mature

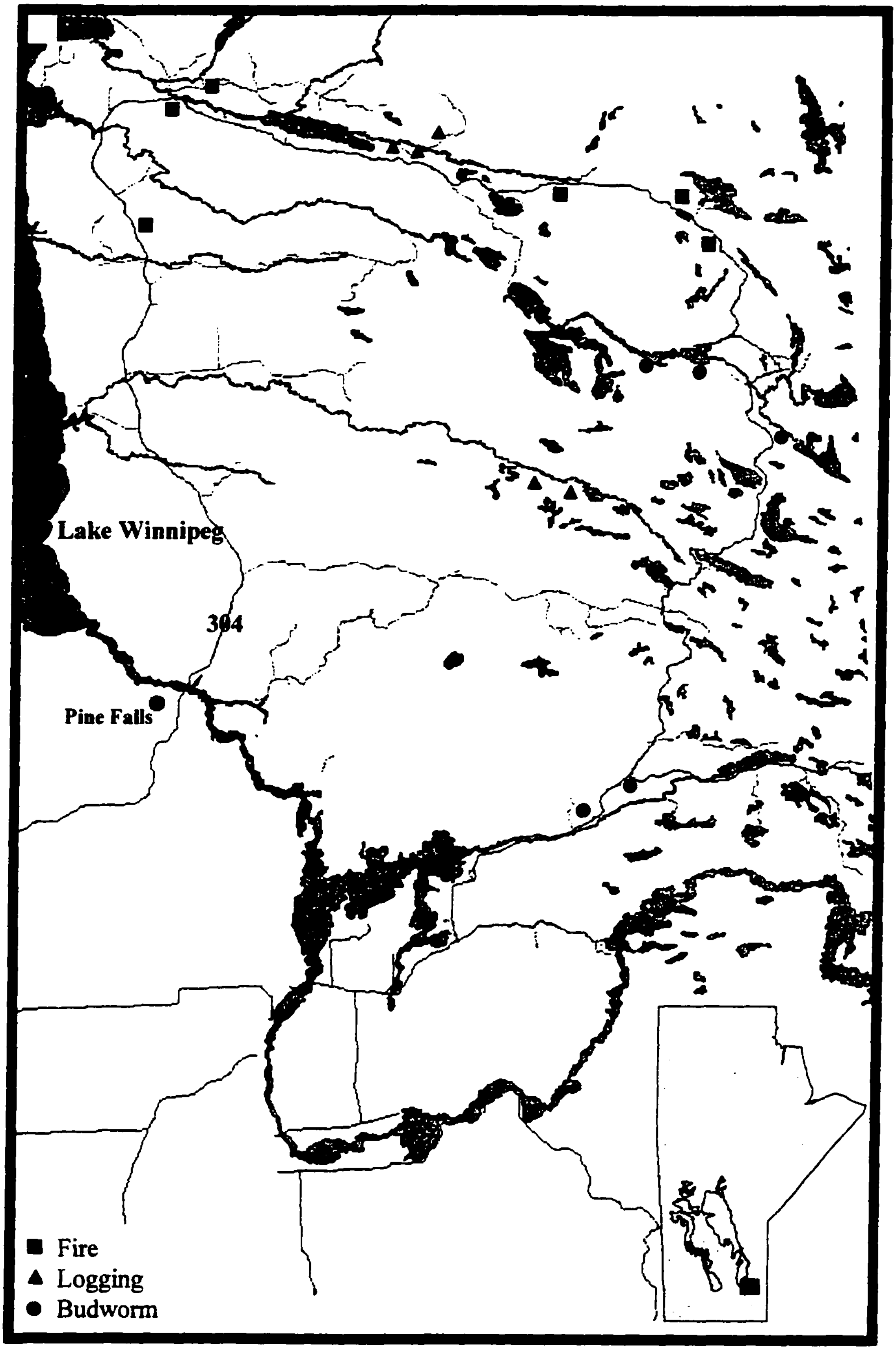

Figure 2.1. Approximate locations of sampled stands in southeastern Manitoba Canada.

(cutting class 4 or 5) mixedwoods (containing aspen and from 26 % to 74% white spruce and/or balsam fir) prior to disturbance, (2) disturbance must have occurred in 1980's, (3) stands must have similar site conditions, and (4) no secondary disturbance (e.g., salvage logging, site preparation, or planting) occurred after the primary disturbance. Forest inventory data only provide a very coarse estimation of stand composition. It typically underestimates balsam fir and overestimates spruces. Consequently, sampled stands varied greatly in species coverage.

The 21 fire stands were disturbed in either 1987 (9 stands) or 1989 (12 stands). The 1987 fire began on May 5 and burned 24,268 hectares. The 1989 fire began May 11 and burned 37,008 hectares. The 20 logged stands were disturbed in 1986 (6 stands), 1987 (1 stand), 1988 (7 stands), and 1989 (6 stands). During the conifer-selective logging all softwood was removed while the unwanted hardwoods were either left standing or felled to facilitate softwood harvest. Therefore few mature stems remained following logging resulting in a near total clear-cut. Also, harvesting occurred after winter freeze-up and no special effort was made to preserve advance regeneration. For spruce budworm attacked stands, the end of the last outbreak was used as the disturbance date. According to this criteria, the 30 spruce budworm attacked stands were disturbed in 1984 (8 stands), 1985 (12 stands), 1986 (3 stands), and 1988 (7 stands). Annual provincial spruce budworm density reports were used to identify stands and ensure that subsequent outbreaks had not occurred (Knowles 1991, Knowles and Matwee 1996, 1997, 1999, 2000). Outbreak dates were confirmed by annual ring width measurements of cores taken from survived white and black spruce (Swetnam et al. 1988).

2.2.3. DATA COLLECTION

A 20 x 20 m plot was established in each stand, within which five 2 x 2 m quadrats were randomly located. In each plot, all trees greater than 2 m tall were counted by species and their diameter at breast height (DBH) was measured using a caliper. Trees were placed into diameter classes (Appendix 1) and three randomly selected trees were cored from each diameter class for each species to determine age and regeneration status (i.e., residual tree or post-disturbance regeneration).

In each quadrat, percent cover of shrubs, herbs, graminoids, and mosses were visually estimated in the field, and their averages were calculated for each plot (Appendix 2). Herbs and shrubs within each quadrat were identified to species, and the percent cover of each species was visually estimated in the field. Coverage of shrubs > 2 m tall was also recorded. Graminoids were not identified to species as sampling occurred over a period of two months and accurate identification was not always possible due to lack of flowering. Mosses were largely confined to growing on decaying wood; they were not identified to species. To ensure that randomly located quadrats accurately reflected the total coverage of shrubs, herbs and grasses visual estimation was also made for entire 20 X 20 m plot.

In each plot, soil and topography was described following procedures of the Canadian Soil Survey Committee (CSSC 1978). A soil pit was dug at a representative location within each plot. Relative soil moisture, and soil nutrient regimes were classified in the field according to the procedure of Wang et al. (1994). Soil drainage was classified according to Zoladeski et al. (1995). Forest floor and mineral soil (top 30 cm only) samples were analyzed for pH, soil texture, and % organic matter content using 0.01 m $CaCl_2$ solution, pipette analysis, and loss on ignition method respectively. Procedures for soil analyses followed those described by Scott (1995). Most sampled stands were classified as subhygric (5) in relative soil moisture regime, except two fire stands classified as hygric (6). Similarly, most sampled stands were classified as medium in soil nutrient regime, except 2 fire and 6 budworm stands classified as poor to medium. All sampled stands were well to moderately well drained with the exception of 2 fire plots classified as imperfectly drained. Only one fire plot was classified as both hygric in SMR and poor to medium in SNR. Soil description and analysis confirmed that there was no significant difference in any soil variable among the three disturbances. A brief summary of site attributes is given in Table 2.1.

Table 2.1. A brief summary of site attributes (mean with standard deviations in parenthesis) according to disturbance type. Relative soil moisture regime and soil nutrient regime classified according to Wang et al. (1994). Soil drainage classified according to Zoladeski et al. (1995).

Variable	Fire (n = 21)	Logging (n = 20)	Budworm (n = 30)
pH (forest floor)	5.6(0.6)	5.5(0.7)	5.1(0.4)
pH (mineral soil)	5.5(0.5)	5.2(0.8)	5.0(0.8)
Organic matter (%)	4.9(2.5)	5.0(1.9)	4.7(2.0)
Forest floor (cm)	9.1(3.9)	9.7(2.4)	8.2(2.5)
L	2.9(1.4)	3.1(0.8)	2.1(0.8)
F	3.6(2.3)	4.6(1.5)	4.0(1.6)
H	2.6(1.2)	2.0(1.0)	2.0(1.5)
Depth of A horizon (cm)	2.4(1.4)	2.4(0.9)	3.7(1.7)
Texture, Sand (%)	24.9(25.1)	12.4(15.8)	22.7(22.4)
Silt (%)	37.5(14.5)	50.1(16.1)	54.6(15.8)
Clay (%)	37.4(21.4)	37.4(14.9)	22.7(13.3)
Soil moisture regime*	5	5	5
Soil nutrient regime†	medium	medium	medium
Drainage‡	well-modwell	well-modwell	well-modwell

* two fire plots were moisture regime 6.

† two fire and six budworm plots were poor to medium, all others were medium.

‡ two fire plots were classified as imperfectly drained.

2.2.4. DATA ANALYSIS

Based on DBH data, basal area was calculated to quantify canopy composition for each sampled stand. Differences in tree species composition and in the covers of shrubs, herbs, grasses and mosses among disturbance types were analyzed by analysis of variance (ANOVA) followed by Tukey HSD multiple comparisons using SYSTAT (Wilkinson 1990). Individual shrub species were compared using Kruskal-Wallis nonparametric tests (Wilkinson 1990). Each species was also ranked according to its shade tolerance from 1 (most tolerant) to 5 (most intolerant) after Bakuzis and Kurmis (1978) (Appendix 3). ANOVA followed by Tukey HSD multiple comparisons was then used to compare the portion of shade tolerant (1 and 2), intermediate (3), and intolerant (4 and 5) species across the disturbance types.

Mean species abundance data was used to calculate the percent similarity between disturbance types, mature aspen ($\leq$ 25 percent conifer), and mature mixed (> 25 and < 75 percent conifer) stands. The six mature aspen and seven mature mixed stands are of fire origin (1929) and were sampled in the same area in 1998-99 (Wang and Kemball submitted). Percent similarity (PS) was calculated as:

$$PS = 200 \sum min\ (P_{ix}, P_{iy})$$

where P_{ix} *and* P_{iy} are the minimum quantity (percent cover) of the *i*th species in disturbance type x and y expressed as proportions of the quantity of all species in samples x and y (Pielou 1975). PS is 0 if no species are in common and 100 if all species are in common and in the same proportion. Coefficient of community (CC) was calculated as:

$$CC = 200\ S_{xy} / (S_x + S_y)$$

where S_{xy} is the number of species common to disturbance types x and y, and S_x and S_y are the species richness of x and y respectively. CC is 0 if no species are in common and 100 if species lists are identical (Pielou 1975).

Detrended Correspondence Analysis (DCA) with downweighting of rare species was used to compare the herb and shrub understories of the three disturbance types using CANOCO 4 software (Ter Braak and Smilauer 1998). The mean species coverage of each disturbance type, the mature mixed stands, and the mature aspen stands were added to ordination for comparison. Means were added supplementary to diagrams so as not to affect ordination (Ter Braak and Smilauer 1998).

Species coverage data was used to determine alpha (α) richness, evenness and diversity of the herb and shrub communities within each plot. Richness (S) was the total number of species found in a plot. Diversity (H) was calculated as:

$$H = -\sum_{i=1}^{s} p_i \ln p_i$$

where H is the Shannon diversity index, and p_i is the proportion of the ith species. Evenness (J) was calculated as:

$$J = H / \ln S$$

where J is the index of species equitability (Pielou 1975), H is the Shannon index of diversity, and S is the species richness. Gamma (γ) diversity and evenness were also calculated in the same manner using the mean species coverage for each disturbance type. Gamma (γ) richness was the total number of species found within a disturbance type. To provide a simple measure of change from plot to plot within a disturbance type, beta (β) richness, evenness and diversity was calculated as:

$$\beta = \gamma / \alpha$$

To determine the effect of unequal sample size (i.e. 30 budworm vs. 21 fire and 20 logging) 5 sub-sets of 20 budworm plots were randomly selected for comparison.

Multivariate analysis of variance (MANOVA) was used to simultaneously compare α richness, evenness and diversity between the disturbance types. ANOVA followed by Tukey HSD multiple comparisons were used to compare richness, evenness and diversity between the three disturbances (Wilkinson 1990).

2.3. RESULTS

Among the four vegetation layers (shrubs, herbs, grasses and mosses) compared in the study, significant differences were found in shrubs and mosses among the three disturbances (Table 2.2). Significantly higher shrub cover and tall shrub cover was found in logged stands when compared to burnt and budworm attacked stands. Significantly higher cover of mosses was found in budworm attacked stands when compared to burnt and logged stands (Table 2.2). No significant differences were found for herb and grass coverage.

Table 2.2. A summary of mean understory stand attributes (standard deviation in parentheses) for major life forms according to disturbance type. Entries in rows with different superscript are significantly different (p = 0.05).

Variable	Fire (n = 21)	Logging (n = 20)	Budworm (n = 30)
Shrubs (%)	39.4(33.1)^{b}	84.5(29.5)^{a}	49.1(32.7)^{b}
Shrubs > 2m (%)	17.2(19.0)^{b}	52.7(28.6)^{a}	29.7(29.2)^{b}
Herbs (%)	38.9(20.6)^{a}	32.6(18.9)^{a}	30.3(14.4)^{a}
Grass (%)	9.6(15.7)^{a}	6.3(6.1)^{a}	8.7(7.4)^{a}
Moss (%)	3.9(4.4)^{b}	3.7(3.5)^{b}	31.8(24.3)^{a}

A list of shared and exclusive herb and shrub species shows that the three disturbances are very similar in species composition (Table 2.3). There were 49 species shared between the three disturbances while less than 6 species were exclusive to any single disturbance (Table 2.3). Of the exclusive species only *Asarum canadense* (L.) is considered rare. The remaining exclusive species are introduced weedy species (e.g. *Taraxacum officinale* Weber, *Chenopodium album* (L.)), or are typically found on wetter (e.g. *Viola palustris* (L.), *Impatiens capensis* Meerb) or dryer (e.g. *Lonicera dioca* (L.), *Juniperus communis* (L.)) sites than those studied. All exclusive species, regardless of disturbance type, were present only infrequently (Table 2.3) and are most likely incidental or chance species.

Table 2.3. Shared and exclusive species for herb and shrub communities. Numbers in parentheses indicate the number of sampled stands in which species was present.

	Fire (n = 21)	Logging (n = 20)	Budworm (n = 30)
Shared	49	49	49
Exclusive:			
	1. *Lonicera dioca* (2)	1. *Alnus rugosa* (1)	1. *Juniperus communis* (1)
	2. *Asarum canadense* (1)	2. *Rhamnus alnifolia* (1)	2. *Agrimonia striata* (2)
	3. *Chenopodium album* (1)	3. *Anemone canadense* (1)	3. *Chimpaphila umbellata* (1)
	4. *Heracleum lanatum* (1)	4. *Geum aleppicum* (1)	4. *Impatiens capensis* (1)
	5. *Taraxacum officinale* (4)	5. *Gymnocarpum dryopteris* (1)	
	6. *Viola palustris* (1)	6. *Osmorhiza despauperta* (1)	

	Fire & Logging	Fire & Budworm	Logging & Budworm
Shared	56	54	51
Exclusive:			
	1. *Alnus crispa* (1,2)	1. *Vaccinum angustifolium* (2.1)	1. *Viburnum edule* (1,1)
	2. *Ribies hiritellum* (1,2)	2. *Vaccinium myrtiloidies* (3,2)	2. *Gerainium bicknellii* (1,1)
	3. *Ribies triste* (5,5)	3. *Lathrus venosus* (4,6)	3. *Viola nephraphylla* (1,2)
	4. *Symphoricarpus albus* (5,2)	4. *Ledum palutre* (4,3)	
	5. *Viburnum opulus* (9,7)	5. *Petridium aquilinum* (4,4)	
	6. *Actae rubra* (2,3)	6. *Pyrola secunda* (1,5)	
	7. *Anemone quinquefolia* (3,2)	7. *Vicia americana* (5,1)	
	8. *Aquilegia brevistyla* (1,3)		
	9. *Solidago canadense* (2,1)		
	10. *Sonchus arvensis* (2,3)		

When ranked according to shade tolerance, species coverage differed among the disturbance types. Budworm had a significantly higher proportion of shade tolerant species than logging ($p = 0.002$) but not fire ($p = 0.277$), and fire had slightly higher proportion than logging ($p = 0.125$) (Figure 2.2A). Logging had higher proportion of intermediate shade tolerant species than fire ($p = 0.021$) or budworm ($p = 0.036$) while fire and budworm were not significantly different ($p = 0.898$) (Figure 2.2B). Fire had significantly higher proportion of shade intolerant species coverage than budworm ($p = 0.021$) but not logging ($p = 0.273$) while logging and budworm did not differ significantly ($p = 0.252$) (Figure 2.2C).

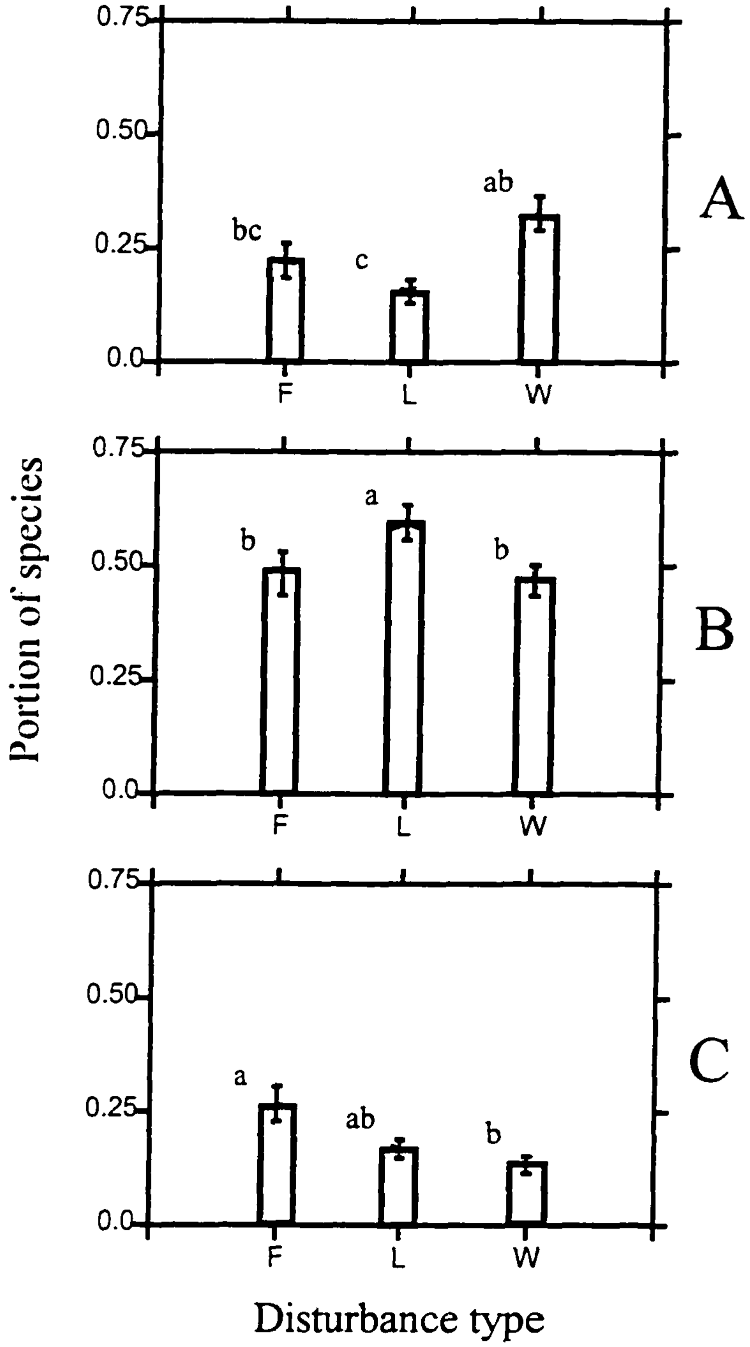

Figure 2.2. Mean and standard errors for proportions of shade tolerant (A), intermediate (B), and shade intolerant (C), herb and shrub species for fire (F), logging (L), and budworm (W) disturbance types. Different letter indicates significant difference.

The shrub community was dominated by three species: mountain maple (*Acer spicatum* Lam), beaked hazel (*Corylus cornuta* Marsh), and wild raspberry (*Rubus idaeus* L.). Beaked hazel was the most abundant shrub for all three disturbance types, with mean percent coverage of 48.5, 12.3, and 12.4 for logged, burnt and budworm attacked stands respectively. Logged stands had significantly higher coverage of beaked hazel compared to burnt and budworm attacked stands (Kruskal-Wallis $p < 0.000$). There was no significant difference in percent coverage for mountain maple (Kruskal-Wallis $p = 0.224$) or wild raspberry (Kruskal-Wallis $p = 0.345$) between the disturbance types. However, coverage of mountain maple and wild raspberry never exceeded 47% for maple or 16% for raspberry, on logged and burnt stands, while some budworm attacked stands had coverage exceeding 80% (Appendix 2).

List-wise pair-comparison of the three disturbance types and the two mature stand types revealed a wide range in percent similarity (32.8 to 72.4) but a narrow range in coefficient of community (63.5 to 85.1). For each paired comparison, CC was higher than PS (Table 2.4) indicating that major differences among those paired comparisons were due more to differences in abundance and less to differences in presence. Between disturbances, the greatest difference in PS was found between logging and fire, and the most similar were budworm and fire. When the three disturbance types were compared to the two mature stand types it was found that PS was highest between the logging disturbance and the mature aspen (PS = 72.4) and lowest between logging disturbance and the mature mixed (PS = 32.8). For CC logging is most similar to mature stands regardless of aspen or mixed stands, and budworm is least similar to mature stands. Among the three disturbance types, logging and budworm were most similar in CC (Table 2.4).

Table 2.4. Comparison of percentage similarity (PS) and coefficient of community (CC) based on herb and shrub species between fire (F), logging (L), spruce budworm (W) disturbances, and also mature aspen (AM) and mature mixed (MM) stands.

		PS				
		F	W	L	AM	MM
CC	F	—	**63.9**	**60.3**	**52.6**	**42.4**
	W	*65.1*	—	**49.1**	**44.9**	**33.9**
	L	*65.2*	*67.2*	—	**72.4**	**32.8**
	AM	*75.6*	*66.1*	*78.3*	—	**34.7**
	MM	*75.2*	*63.5*	*79.7*	*85.1*	—

DCA ordination based on the herb community showed no distinct grouping corresponding to either burnt or logged stands while budworm attacked stands grouped toward the top and right of the ordination due to the greater abundance of shade tolerant species such as *Cornus canadense* L., *Clintonia borealis* (Ait.) Raf., *Viola renifolia* Gray, *Pyrola asarifolia* Michx.(Figure 2.3). DCA based on the shrub community did not show a clear separation among the three disturbances. Burnt stands were spread over the entire ordination. Although intermingled with budworm attacked stands, logged stands were generally positioned at lower and middle part of the ordination (Figure 2.4). Three distinct groupings existed among budworm stands, with *Rubus ideaus* associated with the grouping on the left, and *Acer spicatum* associated with the grouping on the right (Figure 2.4). The stands grouped in the middle of the diagram were not dominated by either *Rubus ideaus* or *Acer spicatum.*

DCA based on the entire understory community was used to display both the ordination of individual stands and the means for each disturbance, mature aspen and mature mixed stands (Figure 2.5). Although not well separated from fire and budworm stands, the logged stands again appeared as a group occupying the low and middle portion of the ordination. Their mean appeared much closer to the mean of mature aspen stands than to the mean of mature mixed stands. Fire and budworm disturbances were intermingled together, with their means very close and between those of mature mixed and mature aspen stands (Figure 2.5).

Mean alpha, beta and gamma richness, evenness and diversity for herb and shrub communities are given in Table 2.5. Sub-sets of budworm plots differed little in alpha richness (range of 18.9 to 21.9), evenness (range of 0.7 to 0.68), or diversity (range of 1.93 to 2.1) from those calculated based on the entire data set (Table 2.5). Beta and gamma richness were lower for the sub-sets (range of 2.1 to 3.1, and 56 to 57 for beta and gamma richness respectively). As alpha differences were slight the entire budworm data set was used for all subsequent calculations. Significant (MANOVA, Wilks'Lambda $p = 0.008$) differences were found among the three disturbances when alpha richness, evenness and diversity index were considered together. When each index was considered separately, alpha richness of logged stands was significantly ($p = 0.037$) higher than that of budworm attacked stands. Alpha evenness was higher on burnt ($p = 0.048$) and budworm attacked ($p = 0.047$) stands compared to logged stands. Alpha diversity index, however, did not differ significantly ($p = 0.184$) among the three disturbances (Table 2.3). At the level of disturbance, gamma richness, evenness and diversity index were the highest for fire disturbance. Similarly, beta richness, evenness and diversity index also were the highest for fire disturbance (Table 2.5).

Table 2.5. Alpha (α), beta (β), and gamma (γ) richness, diversity and evenness for each disturbance type. For α level only, entries in rows with different letters are significantly different ($p = 0.05$).

Disturbance		Fire	Budworm	Logging
Richness	α	22^{ab}	20^{b}	23^{a}
	β	3.36	3.2	3.0
	γ	74	64	69
Evenness	α	0.7^{a}	0.69^{a}	0.6^{b}
	β	1.08	1.0	0.97
	γ	0.76	0.69	0.58
Diversity	α	2.16^{a}	2.04^{a}	1.9^{a}
	β	1.51	1.41	1.28
	γ	3.27	2.88	2.43

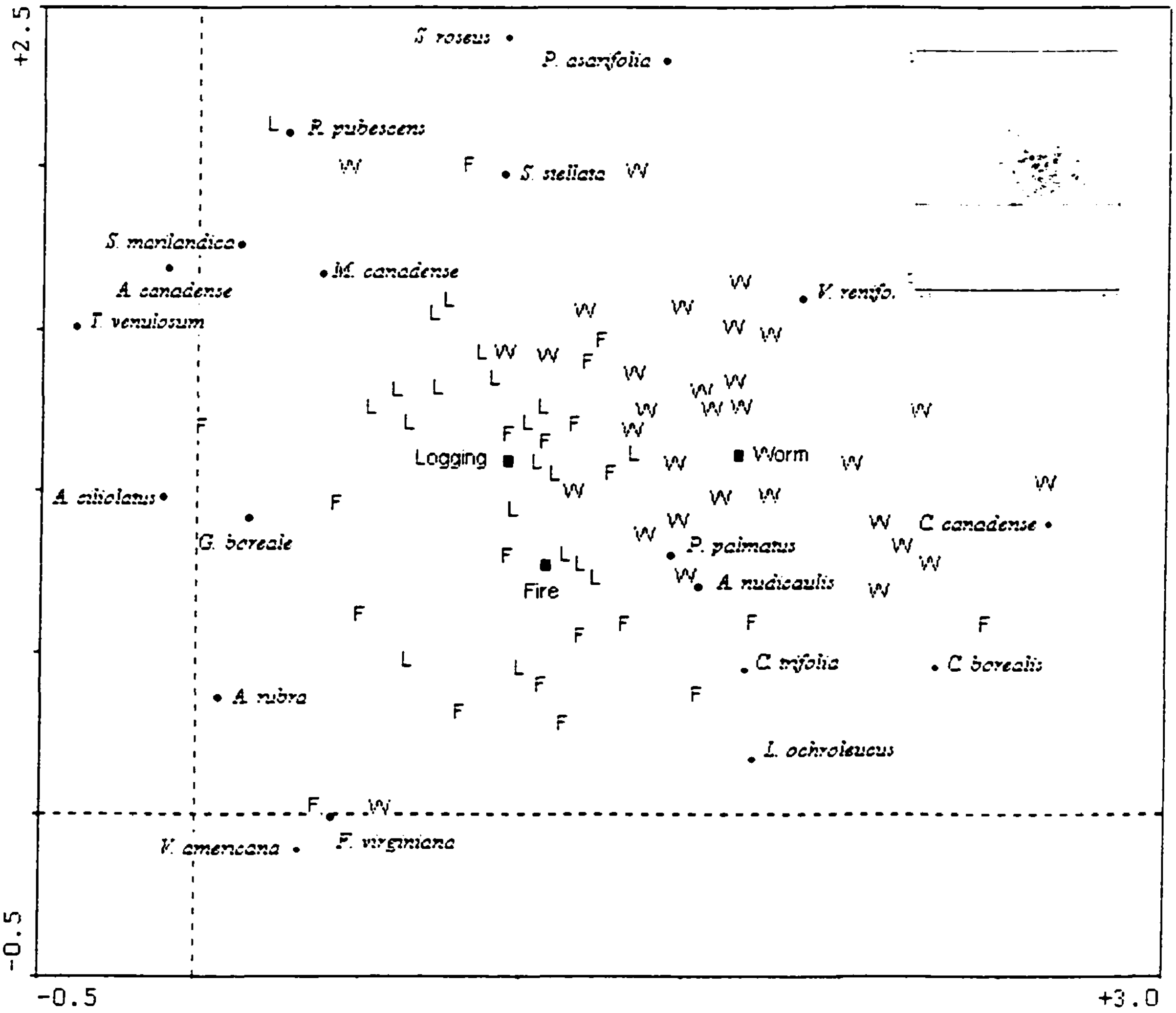

Figure 2.3. Ordination (DCA) plot of herb community for fire (F), spruce budworm (W), and logging (L) disturbances. Unexpanded plot in top right corner of diagram. Means (squares) for each disturbance type were added supplementary to ordination (Ter Braak and Smilauer 1998). First through fourth eingenvalues are 0.368, 0.206, 0.172, and 0.094.

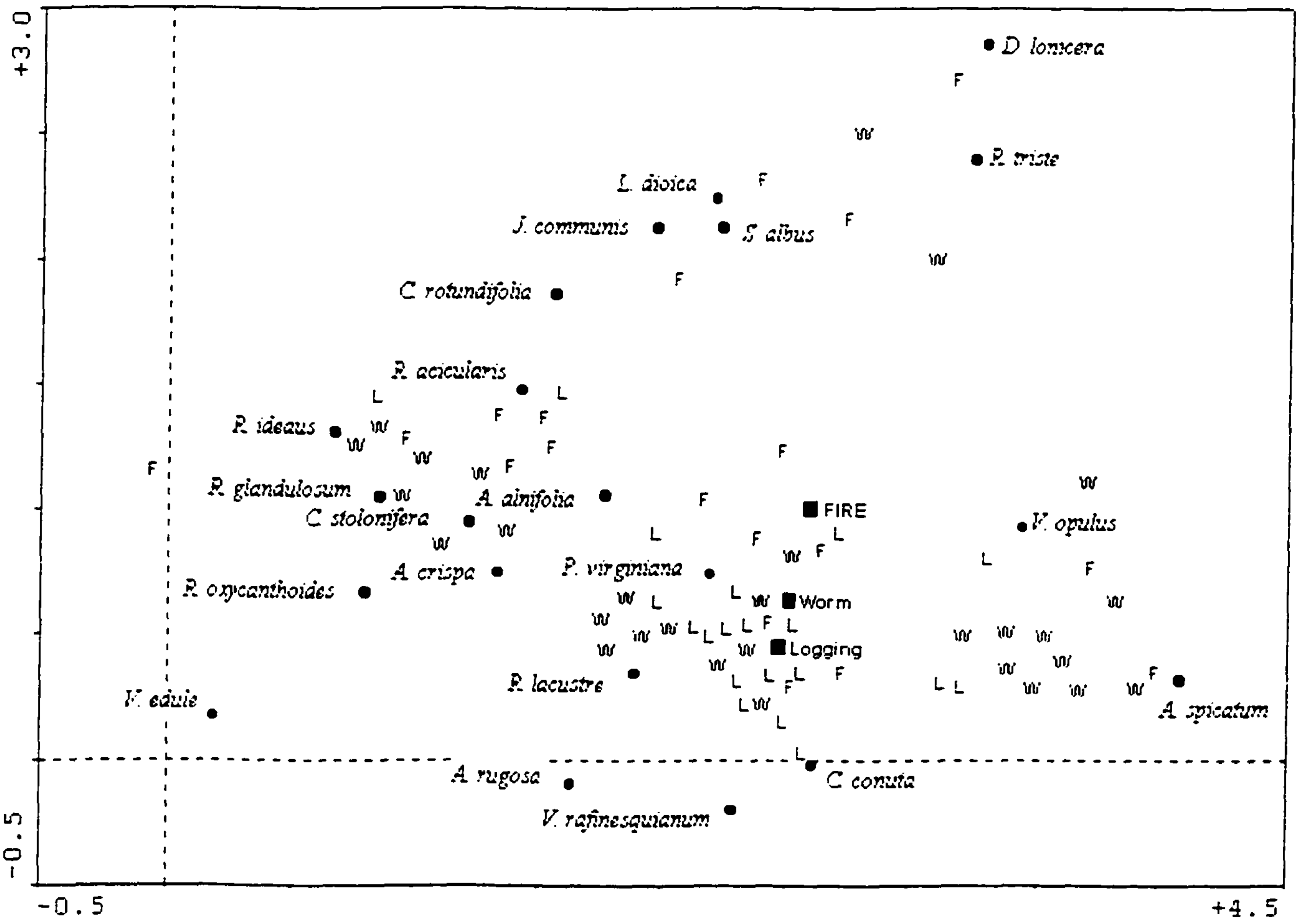

Figure 2.4. Ordination (DCA) plot of shrub community for fire (F), spruce budworm (W), and logging (L) disturbances. Means (squares) for each disturbance type were added supplementary to ordination (Ter Braak and Smilauer 1998). First through fourth eingenvalues are 0.616, 0.315, 0.153, and 0.079.

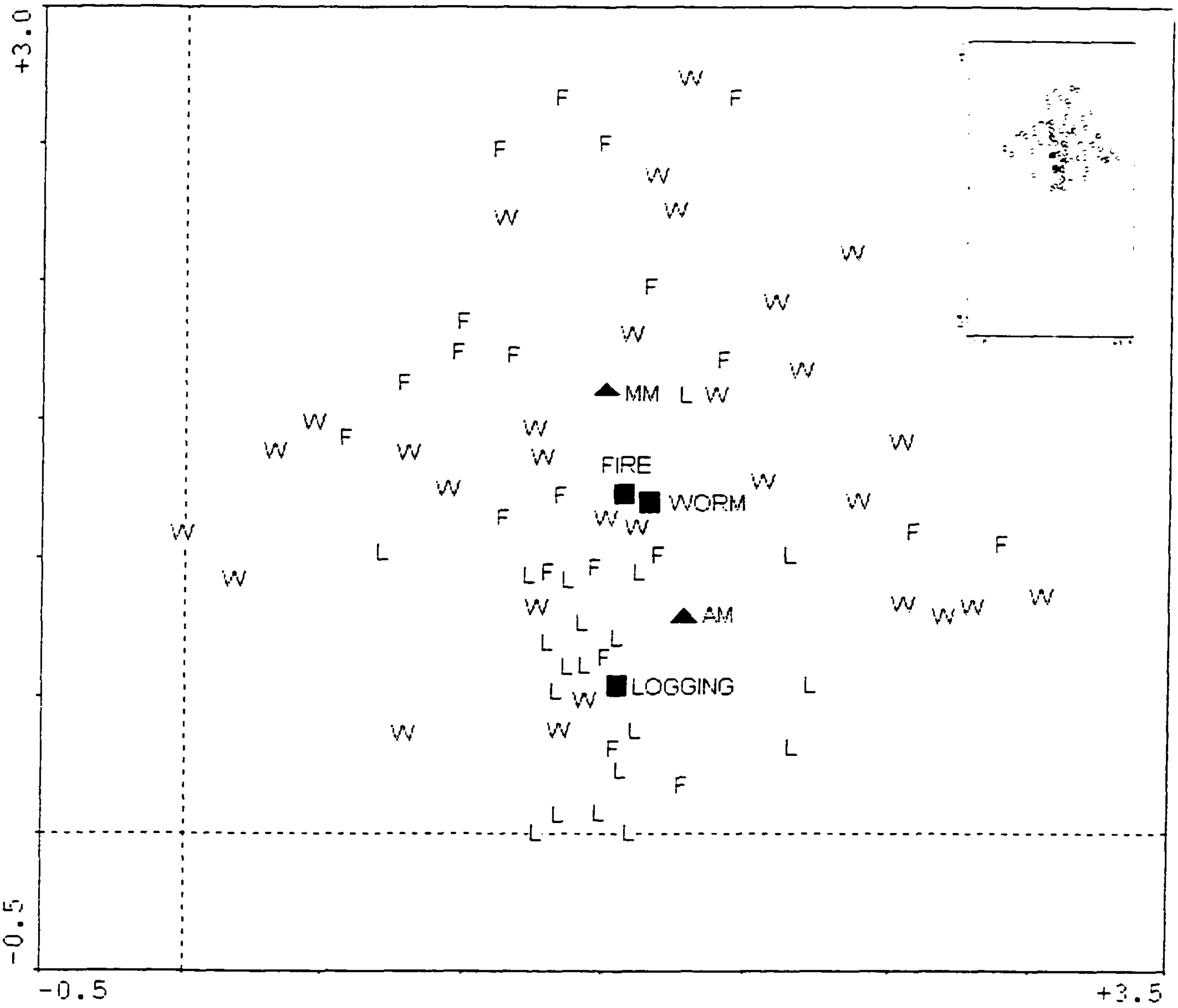

Figure 2.5. Ordination (DCA) plot of herb and shrub community for fire (F), spruce budworm (W), and logging (L) disturbances. Unexpanded plot in top right corner of diagram. Mean for each disturbance type (squares) and for mature stands (triangles), mature mixed (MM) and mature aspen (AM), were added supplementary to ordination (Ter Braak and Smilauer 1998). First through fourth eingenvalues are 0.414, 0.260, 0.155, and 0.104.

2.4. DISCUSSION

Significantly higher shrub coverage was found in logged stands. Rapid development of shrubs within such a short period of time (about 10 years) in logged stands could have significant implications to future succession. Shrubs are important competitors of conifers (Liefers et al. 1996a, Kneeshaw and Bergeron 1996,1999, Cornett et al. 1997, Beckage et al. 2000). Broadleaf litter fall was reported to smother young conifer germinants thus negatively affecting understory conifer recruitment (Korolef 1954, Waldron 1966, DeLong et al. 1997). Aggressive shrub development has been blamed for insufficient or lack of conifer recruitment (Batzer and Popp 1985, Kneeshaw and Bergeron 1996, Galipeau et al. 1997), which could result in arrested succession of some aspen stands (Rowe 1961, Dix and Swan 1971, Carlton and Maycock 1978, Wang and Kemball, submitted). Along with an increased or sustained high level of shrub coverage, basal area of aspen in stands under arrested succession decline with disturbance age (Wang and Kemball, submitted). Pare and Bergeron (1995) found that the decline in above-ground biomass 75 years after fire is positively related to the proportion of aspen in the canopy. Therefore, timber productivity may be compromised if no corrective silvicultural treatments were applied following logging.

Differences in shrub abundance among the three disturbance types may be attributed to (1) differential survival of existing plants and (2) *in-situ* propagules as well as (3) light intensity under residual and regenerating tree canopy. The effect of disturbance on buried viable propagules is critical to vegetation re-establishment (Archibold 1978, Shafi and Yarranton 1973, Moor and Wein 1977, Halpern 1988, Roberts and Gilliam 1995, Whittle et al. 1997, Nguyen-Xuan et al. 2000). On flat terrain, thus without soil erosion (Keenan and Kimmins 1993), only fire has a significant impact on the forest floor (Outcalt and White

1981, Keenan and Kimmins 1993, Nguyen-Xuan et al. 2000). Deep burning or intense heating can kill or render buried propagules unviable (Ahlgren and Ahlgren 1960, Moor and Wien 1977, Carleton and MacLellan 1994). Logging, however, has little effect on total number of species present in seed bank (Qi and Scarrat 1998). This is particularly true for winter logging. The low impact of logging on the forest floor, with respect to the propagules contained within (Qi and Scarratt 1998, Nguyen-Xuan et al 2000), coupled with lower mortality of existing vegetation at time of disturbance (Keenan and Kimmins 1993), enable shrubs to develop more abundantly than after fire. Therefore the much greater shrub coverage following logging, as compared to fire, was not an unexpected result. Abundant shrub development following logging has also been reported elsewhere (e.g. Outcalt and White 1981, Constabel and Liefers 1996).

When in-situ propagules are present, light becomes the most likely limiting factor for shrub development. Development of a stable and dense shrub community following thinning of overstory aspen has been frequently reported (Dix and Swan 1971, Brumelis and Carleton 1988, Galipeau et al. 1997, Constabel and Liefers 1996). Crown fire kills all existing above ground vegetation and creates an environment conducive for the vigorous growth of aspen suckers immediately following the disturbance. Low light intensity under dense aspen suckers likely limit the development of understory shrubs. Unlike logged and budworm attacked stands, shrubs must reestablish themselves in burnt stands. While both logging and crown fire remove or kill the overstory trees in a very short period of time, mortality following spruce budworm outbreak is much more variable (Lynch and Witter 1985) and requires a minimum of 4-5 years of heavy defoliation (MacLean 1980, MacLean and Ostaff 1989). This is further confounded by the fact that, despite its name, spruce budworm primarily kills balsam fir, with mortality of mature white spruce and black spruce being much lower (Miller 1975, Sims et al. 1990, Bergeron et al. 1995). Depending on pre-disturbance stand composition some stands had little opening of the canopy following outbreak while others had open conditions that developed slowly. As reported by others (e.g., Osawa 1994, Lautenschlager 1997) those budworm stands sampled in the study with the greatest amount of canopy opening were dominated by wild raspberry (*Rubus idaeus* L.).

Grasses, particularly *Calamagrostis canadensis* (Michx), are well known competitors of tree regeneration, especially conifers (Eis 1981, Liefers et al 1993). In this study, however, grass coverage was uniformly low across disturbance type (Table 2.2), which is likely due to all sampled stands being well drained (Table 2.1). It was noticed that sampled stands with poor drainage (not used in this study) had much higher grass coverage. Similarly, Peltzer et al. (2000) found that grass cover did not greatly increase on naturally regenerating upland sites following disturbance.

Unlike spruce-fir forests, aspen mixedwoods rarely develop a moss-covered forest floor (Dix and Swan 1971, Zoladeski et al. 1995), especially on well-drained sites. In this study moss cover was very low in burnt and logged stands. Although significantly higher in budworm attacked stands, moss coverage was not evenly distributed throughout the stands, being largely confined to decaying logs and stumps. The difference in moss coverage can be explained by the presence of residual conifer canopy and the greater amounts of decayed wood found in many of the spruce budworm attacked stands.

Similar to reports by others (e.g., Carleton and Maycock 1981, Outcalt and White 1981, Halpern 1989, DeGrandpre and Bergeron 1997), no wholesale turnover of species was found in the study. All pre-disturbance tree species were present, though in varying abundance, following each disturbance type. Similarly, the three disturbances shared a large number (49) of understory species, and only few (≤ 6) species were exclusive to any single disturbance type (Table 3). Unlike upland black spruce community which differed in herb and shrub community following logging and fire (Johnston and Elliott 1996), the low number and frequency of exclusive species in the understory community of the mixed stands in this study indicate that the three disturbances are very similar in species presence. Stands within each disturbance type were also very similar to one another. Beta richness, evenness, and diversity measures expected change from one stand to another within each disturbance type. For species richness beta values are about 3 (Table 2.5), thus one would expect a great amount of change from stand to stand within a disturbance type. In reality however, this is not the case. Stands in this study were selected to be similar in drainage, soil moisture, and soil nutrient regimes. The same understory species were typically present with only a few species (i.e., *Acer spicatum*, *Corylus cornuta*, *Rubus idaeus*) being dominant. All species including rare and infrequent (chance) species were used in calculation of beta richness, evenness, and diversity. The major effect of using all species is the increase in richness, particularly at the disturbance (gamma) level.

Despite the similarity in species presence, some differences in plant community were found among the three disturbances by DCA based on abundance. For the herb community DCA ordination suggested budworm attacked stands were different from burnt and logged stands (Figure 2.3). This difference is likely attributed to the presence and/or greater abundance of shade tolerant species (e.g. *Cornus canadensis* L., *Clintonia borealis* (Ait.) Raf., *Viola renifolia* Gray, *Pyrola asarifolia* Michx.) in budworm attacked stands. Because of the presence of a residual canopy, budworm attacked stands supported higher proportion of shade tolerant species and lower proportion of shade-intolerant species (Figure 2.2).

Patterns displayed by DCA ordination based on the shrub community (Figure 2.4) largely reflect the abundance of a few common shrub species. Logged stands were overwhelmingly dominated by beaked hazel, and appeared together as a group in the ordination (mean coverage of beaked hazel was 48.5% on logged stands). For budworm attacked stands those with shrub communities dominated by wild raspberry were grouped on the left of the ordination, representing stands subjected to the greatest mortality thus canopy opening. Pre-outbreak composition of these stands likely had the highest balsam fir component with the least amount of understory shrubs as wild raspberry is known to be a poor competitor with previously established shrubs (Buse and Bell 1992). Shrub communities dominated by mountain maple were grouped on the right of the ordination, representing stands subjected to least mortality and canopy opening. Stands grouped in the middle were primarily beaked hazel with intermediate mortality and canopy opening. Both wild raspberry and beaked hazel are classified as intermediate in shade tolerance and mountain maple is classified as tolerant (Bakuzis and Kermis 1978). Unlike logged or budworm attacked stands, burnt stands appear scattered throughout the ordination diagram reflecting the great heterogeneous effect of fire on the forest floor (e.g. Nguyen-Xuan et al. 2000, Wang 2001).

The primary difference in the understory between mature aspen and mature mixed stands is the presence of a well-developed shrub layer in mature aspen stands (Wang and Kemball submitted). As a result PS was the highest between the logged stands and the mature aspen stands and the lowest between logged stands and the mature mixed stands. Between disturbances the greatest difference in PS was found between logging and fire and the most similar were budworm and fire (Table 2.4). These results were consistant with DCA ordination (Figure 2.5). When compared to mature stands, logged stands were more similar to the mature aspen stands while fire and budworm attacked stands were between mature mixed and mature aspen stands (Figure 2.5). Their relation to the two mature stand types has some interesting implications for succession. Succession of aspen, to mixedwood, to conifer, hinges on the early recruitment of conifers which will promote further recruitment (Greene et al 1999, Wang and Kemball submitted). In the absence of early conifer recruitment a stable shrub understory develops following aspen self-thinning which limits further conifer recruitment (Korolef 1954, Liefers et al. 1996b, Galipeau et al. 1997). With an already established shrub understory it is more likely that logged stands will progress toward an aspen-shrub community (Rowe 1955), the succession of which is arrested.

Compared to other disturbances, logging has higher species richness but lower evenness (Table 2.5). There was no difference in the Shannon diversity index, which measures both richness and evenness (Pielou 1975), among the three disturbances. The higher richness found in logged stands may be attributed to greater canopy removal compared to budworm attacked stands, which favors invasion of new species, and its lower impact on understory and forest floor compared to fire stands, which favors survival of existing species. The lower evenness is likely caused by the clear dominance of beaked hazel in logged stands. The total diversity (γ) of each disturbance type, and changes in diversity (β) between stands within each disturbance type, were highest in fire stands and lowest in logged stands. The greater within-disturbance heterogeneity caused by fire and budworm outbreak when compared to logging is the most likely explanation for the observed differences.

2.5. CONCLUSION

Post-disturbance plant communities developed after fire, logging and spruce budworm outbreaks were similar in species but differed in species abundance. Therefore, analysis did not support the hypothesis that understory plant communities do not significantly differ among the three types of disturbance. Compared to logged stands, burnt and budworm stands displayed higher within-disturbance variation in composition of the understory community. Therefore, the analyses support the hypothesis that the post-disturbance understory community, due to the greater variation in severity, is more heterogeneous in fire and budworm attacked stands. Logging promoted the rapid expansion of shrubs, dominated by beaked hazel, when compared to fire and budworm disturbances in which shrub composition and abundance were variable. Budworm outbreak facilitated the growth of more shade tolerant species in the herb community, which separated budworm from fire and logging. At the current stage of development, logged stands were more similar to mature aspen stands. Burnt and budworm attacked stands were equally similar to both mature aspen and mature mixed stands.

The adaptation to disturbance of many understory species (e.g., seed dispersal, seedbanking, vegetative propagation and expansion) enables rapid recovery and expansion following disturbance. Aspen is also well adapted to disturbance and capable of rapid recovery. This is not the case for the conifer component (white spruce and balsam fir) of mixed stands which are limited by seed supply and dispersal, as well as difficulties in establishment and slow growth. The removal of seed trees coupled with poor seedbed conditions (i.e. no exposed mineral soil) and rapid development of competing vegetation, particularly shrubs, makes abundant natural conifer regeneration following conifer-selection logging of aspen mixedwood stands unlikely. Without silvicultural treatment logged mixedwood stands are likely to remain aspen dominated with little, if any, future conifer recruitment. Dominance by wild raspberry in some budworm attacked stands is also likely to limit future conifer recruitment. The similarity in the composition of the understory community between mature and post disturbance aspen mixedwood stands indicate that natural recovery to pre-disturbance community condition is likely. However, the dominance of beaked hazel on logged stands and of wild raspberry in some open canopy budworm attacked stands may greatly limit the abundance of other species.

3. Natural Tree Regeneration of Boreal Mixedwoods in Response to Fire, Logging, and Spruce Budworm Disturbance.

3.1. INTRODUCTION

In boreal forests, nearly all species involved in succession are found at the early stage of post-disturbance community. Particularly in the western boreal the Clementsian view of continual recruitment leading to an all-aged stand has not been evident (Rowe 1961, Dix and Swan 1971, Carleton and Maycock 1978, Bergeron and Dubuc 1989, Oliver and Larson 1990, Peltzer et al. 2000). Zasada et al. (1992) argue that a species would not likely become an important component on a particular site if its propagules were not available soon after a disturbance. The initially recruited species often persist on a site until the arrival of the next disturbance (Methven et al. 1975, Nobel and Slaytor 1980. McCune and Allen 1985, Attiwill 1994) and inter-disturbance compositional changes are mainly expressions of different growth rates of these initially established species (McCune and Allen 1985). As a result of frequent disturbance, the boreal forest appears as a mosaic of patches of even-aged stands, each patch dating from the last disturbance but varying in species composition with site factors, propagule sources, and disturbance regimes (Carleton and Maycock 1978, Cattelino et al. 1979, Nobel and Slaytor 1980, Heinselman 1981). An understanding of both temporal and spatial dynamics of boreal forests is critical to the prediction of pathways of early forest succession following different disturbances.

Most studies on forest dynamics are focused on explaining species replacement along a chronosequence as well as composition and structure of 'climax' community. Given the new realities of forest management more information is needed on the initial development of the post-disturbance community (Attiwill 1994), which has been commonly perceived as more complex and difficult to study due to the influence of many factors. Existing evidence indicates that site (e.g., resource availability), historical (e.g., the type and intensity of disturbances, pre-disturbance vegetation status), and spatial (e.g., extent of disturbance, tree survival within a disturbance, surrounding landscape elements) factors all affect early forest recovery following disturbance (McCune and Allen 1985, Halpern 1988, Diotte and Bergeron 1989, Peterson and Carson 1996). Although site factors have been frequently studied, historical and spatial factors are rarely subject to rigorous studies despite considerable importance having been given to them (e.g., Whittaker 1953, Egler 1954, Auclair and Cottam 1971, Heinselman 1981, McCune and Allen 1985, Halpern 1988, Peterson and Carson 1996).

The significant role of pre-disturbance vegetation in affecting post-disturbance succession has been supported by the strong resemblance between pre- and post-disturbance composition of tree (Dix and Swan 1971, Carleton and Maycock 1978, Heinselman 1981, Johnson and Fryer 1987, Lyon and Stickney 1976, Methven et al 1975, Van Wagner 1983) and understory species (Martin 1955, Abrams and Dickman 1984, Foster 1985, Methven et al.1975). Disturbance types such as crown fire, spruce budworm outbreak, and timber harvesting differ greatly in their impact on the forest floor and pre-disturbance vegetation, and thus may lead to different pathways of post-disturbance forest recovery (Abrams et al 1985).

Depending on the severity and type of disturbance, survivors (advance regeneration and residual canopy trees) may comprise an important component of the post disturbance community (Ghent et al. 1957, Baskerville 1975, MacLean 1984, Brumelis and Carleton 1988, Halpern 1988, Morin 1993, Osawa 1994, Greene et al. 1999). Species with *in-situ* propagules surviving disturbance have an advantage over other species in early recruitment (Ahlgren and Ahlgren 1960, Dix and Swan 1971, Rowe and Scotter 1973, Attiwill 1994, Greene and Johnson 1999, Greene and Johnson 2000). Although the effectiveness of canopy-stored seeds and vegetative reproduction (Dix and Swan 1971, Methven et al. 1975, Lyon and Stickney 1976, Carleton and Maycock 1978, Johnson and Fryer 1987) and the limitation of soil seedbanks (Vierech 1973, Johnson 1975, Elliott 1979, Foster 1983) in post-disturbance regeneration has been acknowledged, the importance of dispersed seeds is not clear (Cattelino et al. 1979). Seed input depends on the extent of a disturbance, tree survival within a disturbance, and surrounding forest communities (Rowe 1983, Diotte and Bergeron 1989, Bergeron and Brisson 1990, Liefers et al 1996a). The arrival, proportion, and abundance of seed input may profoundly influence post-disturbance forest recovery (Carleton and Maycock 1978, Rowe 1983, Peterson and Carson 1996). Most boreal tree species have a very short distance (< 200 m) of primary dispersal (Burns and Honkala 1990a,b). Even though trembling aspen can transport its seeds over long distances vegetative regeneration is the dominant strategy, with possible exceptions on the rocky terrain of the Precambrian Shield (Rowe 1983). Given the dominant role of *in situ* propagules (i.e., canopy-stored seeds and survived vegetative parts) in early forest recovery following disturbances, it is not clear whether a significant improvement can be made in predicting post-disturbance tree regeneration by quantifying spatial variables that affect seed dispersal.

The most abundantly recruited species following disturbance of boreal mixedwoods, particularly after fire, is aspen. Aspen's ability to produce numerous and rapidly growing suckers following disturbance is well documented (e.g. Ahlgren and Ahlgren 1960, Dix and Swan 1971, Brown and DeByle 1987, Bergeron and Dubuc 1989, Bonan and Shugart 1989, Harvey and Bergeron 1989, Peterson and Peterson 1992, Greene and Johnson 1999). Established aspen stands usually start to self-thin around 20 years old, and by 55 to 90 years most stands are experiencing rapid decay (Haeussler et al. 1990, Sims et al. 1990). In the absence of disturbance aspen abundance would decrease in favor of longer lived and more shade tolerant (i.e., white spruce and balsam fir) species (Ahlgren and Ahlgren 1960, Bergeron and Dubuc 1989, Sims et al. 1990, Arnup et al. 1995), or in some cases may lead to parkland (Rowe 1961). Potential successors to aspen, including white spruce, black spruce and balsam fir, are not seed banking species (Fyles 1989, Burns and Honkala 1990a, Sims et al. 1990, Houle and Payette 1991, Qi and Scarratt 1998). Post-disturbance recruitment of these conifer species depends on both initial dispersal of seeds and subsequent establishment of seedlings (Ahlgren and Ahlgren 1960, Moor and Wein 1977, Archibold 1980, Eberhart and Woodard 1987, Brumelis and Carleton 1988, Halpern 1988, Sirios and Payette 1989, Zasada et al. 1992, Carleton and MacLellan 1994, Whittle et al. 1997, Greene et al. 1999, Greene and Johnson 1999, Greene and Johnson 2000, Beach and Halpern 2001). Therefore, the timing of conifer recruitment following disturbance can be highly variable. Recruitment has been reported immediately following disturbance (Dix and Swan 1971, Day 1972, Kabzems et al. 1986, Liefers et al. 1996a, Galipeau et al. 1997), and after a short or long delay (Rowe 1955, Liefers et al. 1996a, Bergeron 2000). Without adequate conifer recruitment succession can become arrested, and stands remain aspen dominated, or eventually develop into aspen parklands (Rowe 1961, Dix and Swan 1971, Carlton and Maycock 1978, Kabzems et al. 1986).

The objective of this study was to compare early (approximately 10 years post disturbance) tree regeneration and growth of boreal mixedwood stands in southeastern

Manitoba following stand replacing crown fire, conifer selective logging, and severe spruce budworm (*Choristoneura fumiferana* Clem.) outbreak. To avoid confounding effects of site factors and pre-disturbance vegetation, all sampled stands were limited to the same site type that supported similar pre-disturbance tree composition. Based on the interaction between disturbance type and species' life history traits, it is hypothesized that tree regeneration follows these priority orders in terms of post-disturbance density: At (trembling aspen) > Pj (jack pine) > Sb (black spruce) > Sw (white spruce) > Fb (balsam fir) for fire; At > Fb > Sw > Sb > Pj for logging; and Fb > At > Sw > Sb for severe spruce budworm outbreak. If more than one species are present in pre-disturbance stands, species with higher priority are favored to establish after disturbance. Because of their reliance on seed dispersal, it is also hypothesized that post-disturbance establishment of white spruce and balsam fir is limited by spatial segregation (distance) from seed sources and competition from vegetation originating from *in-situ* propagules.

3.2. MATERIALS AND METHODS

Description of the study area and sample design are given in section 2.2.

3.2.1. DATA COLLECTION

A 20 x 20 m plot was established within each sampled stand, within which five 2 x 2 m quadrats were randomly located. In each plot, all live trees (including residual trees and trees regenerated after the disturbance) greater than 2 m tall were counted by species and their diameter at breast height (DBH) was measured using a caliper. For trees greater than 9 cm DBH age was determined by taking cores. Aspen trees were cored at breast height (130 cm) while conifer trees were cored at 30 cm above ground. All cores were brought to the lab, sanded, and rings counted under a binocular microscope. For budworm plots annual ring width was measured for black spruce, white spruce, and balsam fir cores using WinDENDRO V6.5 software (Regent Instruments Inc. 1999). Heights of three trees in each DBH class greater than 9 cm were measured with a clinometer. For each species trees less than 9 cm DBH were destructively sampled (3 for each DBH class 2, 4, 6 and 8), height was measured and stem sections were taken at the root collar, 30, 60, 90, 130, 230 cm, and every subsequent 100 cm for conifers; and at the root collar, 60, 130, 230 cm and every subsequent 100 cm for aspen. Stem sections were brought to the lab, sanded, and rings counted in two directions under a binocular microscope.

All residual trees and regeneration less than 2 m in height were destructively sampled. Individuals in which the root collar could not readily be identified (i.e. layers) or that showed signs of adventitious root development were counted but not aged. Those stems for which the root collar was readily identifiable were dug up and the substrate was recorded as either decayed wood or other. Samples were brought to the lab and age was determined by counting growth whorls/bud scars, and from section taken at the root collar. Annual height growth was also measured (from current year down as far as possible) using growth whorls/bud scars. On those plots that contained abundant small seedlings sampling was done within the five 2 x 2 m quadrats using the same procedures as above.

In each plot snags and downed woody material (DWM) were measured. Snags were defined as dead trees standing at ≥ 45° angle and were measured at breast height. Dead trees on the forest floor or standing at < 45° angle were considered DWM. To measure DWM two perpendicular 40 m transects were run through each sample plot. The diameter and decomposition type was recorded for each downed log where it intercepted the transect. Only surface DWM readily identifiable was recorded. DWM was placed into one of three categories (modified from Lee et al. 1997); type 1 DWM was recently downed undeformed log with fine twigs and > 50% bark remaining, type 2 DWM was a log in which only large branches were remaining, much of bark was missing, the wood was soft in places, and the log may be partially deformed, type 3 DWM was all bark missing, log was deformed, wood was soft and covered by moss or fungi with colonization by some vascular plants in places. Volume of DWM was calculated as:

$$V=(\pi^2/8L)\Sigma(d_i)$$

where V is the volume per unit area, L is the length of the sample line, d_i is the diameter of downed log (Van Wagner 1969).

The presence/strength of potential seed sources for each plot was assessed as follows. Each plot was categorized as: (1) Abundant, if there were greater than 10 source trees within 100 m of plot edge, (2) Few, if source trees were 100 m to 300 m distant, or there were less than 10 source trees within 100 m, (3) None, if there were no source trees within 300 metres.

Only mature trees with evidence of cone production were considered as source trees.

3.2.2 DATA ANALYSIS

Analysis of variance (ANOVA), followed by Tukey HSD multiple comparisons, was used to test the differences in site and stand characteristics between the disturbances. All density data were log transformed prior to analysis due to unequal group variance. A Pearson Chi-square analysis was used to test the association between the disturbances in presence/strength of seed source. A simple correlation (Pearson) analysis was also used.

3.3. RESULTS

3.3.1 STAND CHARACTERISTICS

Significant differences in total live basal area, residual basal area, regeneration basal area, snag basal area and type 1 and 2 DWM were found among the three disturbance types (Table 3.1). Burnt stands had significantly higher total basal area while budworm attacked stands had significantly higher conifer basal area. Aspen basal area was significantly different between disturbance types, with fire > logging > budworm. No trees survived the fire disturbance therefore the basal area was comprised exclusively of regenerating aspen. Total basal area of budworm attacked stands was largely comprised of residual trees while the basal area of logged stands was largely comprised of regenerating aspen. Compared to fire and budworm, logging had significantly lower snag basal area. Snag basal area of burnt stands was largely comprised of aspen while snag basal area of budworm attacked stands was largely comprised of conifers. No significant difference in total, deciduous, or type 3 DWM was found among the three disturbance types. However, fire and budworm had significantly more conifer DWM, and fire had significantly less type 1 and more type 2 DWM (Table 3.1).

3.3.2 REGENERATION

Budworm attacked stands had significantly higher total conifer density than burnt and logged stands ($p < 0.000$ in all cases) while burnt and logged stands were not significantly ($p = 0.388$) different (Table 3.2). Advance regeneration and layers were only found in logged and budworm attacked stands. When present there was significantly more advance regeneration in budworm attacked stands ($p = 0.005$) compared to logged stands. There were no significant differences between these two disturbances in the number of layers (Table 3.2). Post-disturbance conifer regeneration showed great variation in both frequency and density

(Table 3.2). Budworm attacked stands had significantly ($p < 0.000$) more conifer regeneration than burnt or logged stands. Although conifer regeneration was more frequent in occurrence and generally higher in density following fire as compared to logging, no significant ($p = 0.563$) differences were detected. Post-disturbance conifer regeneration was mainly jack pine and black spruce in burnt stands and mainly balsam fir in logged and budworm attacked stands (Table 3.2). For the logged stands, advance conifer regeneration exceeded new post disturbance conifer regeneration (Table 3.2). Of all the sampled conifer trees and seedlings, 16.1 % for budworm, 25.1 % for fire, and 17.9 % for logged stands were found rooted in decayed wood. Total aspen stem density and post disturbance aspen regeneration density were significantly ($p < 0.000$) different among all three disturbance types with fire > logging > budworm. There were no residual aspen in any burnt stands. There were significantly more ($p = 0.027$) residual aspen in budworm attacked stands compared to logged stands.

Table 3.1. A brief summary of stand attributes (mean with standard deviation in parenthesis) according to each disturbance type. Basal areas were calculated for all trees > 1cm DBH. Residual basal area = Total live basal area - regeneration basal area. Entries in rows with different letters are significantly different ($p \le 0.05$ or $p \le 0.1$*).

Disturbance	Fire (n=21)	Logging (n=20)	Budworm (n=30)
Total Live Basal Area (m^{2} • ha^{-1})	27.9(15.3)^{a}	13.3(6.5)^{b}	17.1(6.8)^{b}
Aspen	27.6(15.4)^{a}	12.9(6.5)^{c}	9.3(6.1)^{b}
Conifer	0.3(0.53)^{b}	0.2(0.22)^{b}	7.5(5.21)^{a}
Residual Basal Area	0	3.3(3.0)^{b}	16.5(6.9)^{a}
Aspen	0	3.1(3.1)^{b}	9.0(6.5)^{a}
Conifer	0	0.2(0.2)^{b}	7.5(5.3)^{a}
Snag Basal Area	10.0(7.8)^{a}	3.0(3.4)^{b}	12.9(7.7)^{a}
Aspen	6.4(6.6)^{a}	2.8(3.5)^{b*}	2.2(3.3)^{b}
Conifer	3.6(6.9)^{b}	0.2(0.8)^{b}	10.7(5.8)^{a}
Total DWM (m^{3} • ha^{-1})	162.3(102.5)^{a}	117.2(56.5)^{a}	162.8(97.0)^{a}
Type 1	0	4.1(8.2)^{a}	3.5(8.7)^{a}
Type 2	112.3(102.9)^{a}	36.2(32.7)^{b}	64.5(61.7)^{b*}
Type 3	50.1(50.9)^{a}	76.9(43.2)^{a}	94.8(99.4)^{a}
Deciduous	109.6(74.2)^{a}	117.2(56.5)^{a}	88.2(99.6)^{a}
Conifer	52.8(57.2)^{a}	0^{b}	74.6(74.5)^{a}

Table 3.2. Tree densities (stems • ha^{-1}) for conifer (A) and aspen (B) for the three disturbance types. Mean (bold), with standard deviation and frequency below in parentheses. Total conifer or aspen = sum of all stems regardless of origin or age. Advance regen. = sum of all stems < 2 m in height and > disturbance age. Layer = sum of all stems < 2 m in height and not originating from seed. Post regen. = number of seed origin post disturbance regeneration. Entries in rows with different letters are significantly different ($p \leq 0.05$). Fb = balsam fir, Sw = white spruce, Sb = black spruce, Pj = jack pine, At = aspen.

DISTURBANCE	Fire (n=21)	Logging (n=20)	Budworm (n=30)
A. TOTAL CONIFER	**2135.7**^{b}	**1098.6**^{b}	**8804.2**^{a}
	(2879.1, 16)	(1371.5, 15)	(6614.2, 30)
Fb	**404.8**	**856.1**	**7024.2**
	(1280.8, 2)	(959.3, 14)	(4672.9, 30)
Sw	**209.5**	**185.0**	**589.2**
	(660.3, 5)	(371.8, 8)	(908.9, 16)
Sb	**634.5**	**27.5**	**1188.3**
	(1122.9, 8)	(122.9, 2)	(3506.9, 12)
Pj	**886.9**	**30.0**	**2.5**
	(1735.3, 10)	(112.9, 2)	(7.6, 3)
ADVANCE REGEN.	**0**	**348.7**^{b}	**1123.3**^{a}
	--	(572.4, 12)	(966.2, 8)
Fb	**0**	**195**	**549.5**
	--	(353.5, 7)	(1428.6, 7)
Sw	**0**	**153.7**	**50.2**
	--	(364.8, 7)	(274.8, 1)
Sb	**0**	**0**	**522.2**
	--	--	(2436.3, 2)
LAYERS (Fb only)	**0**	**330**^{a}	**350**^{a}
	--	(710.2, 5)	(966.2, 5)
POST REGEN.	**2135.7**^{b}	**413.8**^{b}	**6996.5**^{a}
	(2879.1, 15)	(732.3, 8)	(4511.9, 30)
Fb	**404.8**	**337.5**	**6017.2**
	(1280.8, 2)	(643.8, 7)	(4268.8, 30)
Sw	**209.5**	**26.3**	**449.8**
	(660.3, 5)	(111.6, 2)	(734.8, 11)
Sb	**634.5**	**25.0**	**527.8**
	(1122.9, 8)	(111.8, 1)	(1262.2, 9)
Pj	**886.9**	**25.0**	**1.7**
	(1735.3, 10)	(111.8, 1)	(9.1, 1)
B. TOTAL ASPEN	**20504.8**^{a}	**7107.5**^{b}	**1354.2**^{c}
	(8194.9, 21)	(4165.1, 20)	(1452.8, 27)
POST REGEN.	**20504.8**^{a}	**7046.3**^{b}	**1130.0**^{c}
	(8194.9, 21)	(4184.7, 20)	(1455.0, 22)
RESIDUAL	**0**	**61.2**^{b}	**224.2**^{a}
	--	(71.4, 13)	(206.9, 29)

Chi-square analysis showed that the three disturbances were significantly ($p < 0.000$) different in seed source abundance/strength. Twenty-eight of 30 budworm attacked stands were classified as Abundant compared to only 3 fire and 6 logged stands. The majority of logged stands were classified as Few (12 stands) with 2 stands classified as None. Fire had 8 stands classified as Few and 10 as None. When compared across disturbances, post-disturbance regeneration was found to be significantly different among the three classes describing seed source presence/strength, with Abundant > Few ($p = 0.001$) and None ($p = 0.001$). There was no significant difference ($p = 0.707$) between classes Few and None. Mean conifer regeneration was 5838, 1392, and 952 (stems • ha^{-1}) for Abundant, Few and None classes, respectively. Among all measured stands post-disturbance regeneration was also significantly correlated with residual conifer basal area ($r = 0.439$, $p = 0.001$), total shrub cover (all measured stands $r = -0.214$, $p = 0.073$; fire stands only $r = -0.508$, $p = 0.053$), aspen density ($r = -0.347$, $p = 0.011$) and % clay content ($r = -0.514$, $p = 0.002$).

Within burnt stands, the number of black spruce, white spruce, and balsam fir recruited in the first five years following disturbance was not significantly ($p = 0.125$, 0.296, and 0.893 respectively) different from those recruited after the initial five years (Table 3.3). However, there was more jack pine ($p = 0.005$) and aspen ($p < 0.000$) recruited in the first five years following disturbance (Table 3.3). Within budworm attacked stands the number of black spruce or white spruce recruited in the first five years was not significantly ($p = 0.903$ and 0.124 respectively) different from those recruited after the initial five years. The few jack pines present were all recruited in the first five years. Balsam fir and aspen had significantly more ($p = 0.005$ and $p < 0.000$) recruitment after the first five years (Table 3.3). Within logged stands, black spruce and white spruce were all recruited in the first five years,

Table 3.3. Regeneration densities (stems • ha^{-1}) for three disturbance types (mean with standard deviation in parenthesis) in the first five years following disturbance and after five years. Fb = balsam fir, Sw = white spruce, Sb = black spruce, Pj = jack pine, At = aspen.

DISTURBANCE	Fire (n=21)	Logging (n=20)	Budworm (n=30)
Regeneration in the first five years			
Fb	**256.0**	**200.0**	**2668.3**
	(861.0)	(359.45)	(3474.6)
Sw	**158.3**	**25.0**	**133.3**
	(470.3)	(111.8)	(382.5)
Sb	**536.8**	**25.0**	**275.8**
	(993.0)	(111.8)	(683.7)
Pj	**853.6**	**5.0**	**1.7**
	(1510)	(22.35)	(9.1)
At	**18794.1**	**5895.0**	**240.9**
	(8138.9)	(4134.3)	(626.8)
Regeneration after five years			
Fb	**148.8**	**137.5**	**3348.8**
	(517.8)	(467.1)	(2252.5)
Sw	**51.19**	**1.25**	**316.5**
	(198.19)	(5.59)	(586.7)
Sb	**97.6**	**0**	**252.0**
	(232.1)	--	(634.7)
Pj	**33.3**	**0**	**0**
	(115.5)	--	--
At	**1710.7**	**1151.3**	**889.1**
	(2243.3)	(1414.2)	(1243.4)

with the exception of one white spruce. Jack pine was found on only one logged stand with recruitment in the 3rd year after disturbance. Balsam fir showed continual recruitment with no significant ($p = 0.184$) difference between the first five years and afterwards. Aspen had significantly ($p < 0.000$) more recruitment in the first five years (Table 3.3).

Among the 71 stands, 20 contained conifer seedlings regenerated within the last four years (7-12 years after disturbance). Compared to the remaining 51 stands, these stands had significantly lower shrub coverage ($p = 0.006$, 45.1% versus 60.5%) and higher residual conifer basal area ($p < 0.000$). Results were similar when balsam fir and spruce were examined separately. Residual conifer basal area was not correlated with shrub cover ($p = 0.175$).

3.4. DISCUSSION

One of the difficulties with studies of this nature is accurate age determination for conifer regeneration. This has been demonstrated for black spruce (DesRocher and Gagnon 1997) and balsam fir (Parent et al. 2001). Age determination becomes increasingly difficult with time-since-disturbance especially when the forest floor is deep and/or covered by moss (Bergeron 2000). On well-drained mixedwood stands, however, neither condition is typical (Dix and Swan 1971, Zoladeski et al 1995). In this study, no stand had extensive moss cover and forest floor depth averaged about 5 cm (Table 2.1). Furthermore any individual in which the root collar (i.e. hypocotyl region) was not readily apparent was considered a 'layer' (for ease of counting) and measured for DBH only. Therefore misidentification of root collar, thus incorrect age determination, is unlikely.

Differences in snag basal area, and DWM volume are likely caused by the differential canopy removal of the three disturbances. By completely killing the original canopy, fire left abundant snags and DWM. By killing only host species (mainly balsam fir), budworm outbreak left a residual canopy. Burnt stands had similar amount of snags and DWM as budworm stands due to only partial consumption during burning. Although timber harvesting in the study area has targeted conifers, the deciduous component (primarily aspen) of harvested stands was rarely left totally intact. In some cases the aspen was removed in order to facilitate harvesting of the desired conifers resulting in a clear-cut condition with few if any residual trees. In other cases residual aspen were subject to mechanical damage at the time of harvesting and blow-down after harvesting. As a result, few residual aspen trees were still standing ten years after logging. The mean number of aspen residuals per sample plot (400 m^2) was 2.4 with a range of 0 to 10. As expected, the extraction of conifer resulted in significantly lower abundance in snags and conifer DWM (Table 3.1). Reduction of snags and DWM may have implications for future conifer recruitment in logged stands. As other suitable seedbeds (e.g., exposed mineral soil and humus) become increasingly rare with time-since-disturbance (Dix and Swan 1971, McLaren and Janke 1996, Waldron 1966, DeLong et al. 1997, Cornett et al. 1997, Galipeau et al. 1997, Greene et al. 1999), future conifer recruitment may depend on rotten logs as suitable seedbeds (Liefers et al 1996a, McLaren and Janke 1996, Cornett et al. 1997, Beach and Halpern 2001).

Differences in the arboreal community among the three disturbance types also reflect the differential canopy survival and post-disturbance regeneration. Fire killed all existing vegetation and stimulated vigorous aspen suckering. As a result, burnt stands supported a significantly higher basal area than did logged or budworm attacked stands. Whether the current difference in stand basal area would persist over time is, however, difficult to judge, thus further study is warranted. McRae et al. (2001) report that compared to wildfire logging favors angiosperms over conifers, and that the effect of logging lasts longer than the typical rotation periods used in the boreal forest. Dominance by aspen following clear-cut logging compared to fire is also reported by Carleton and MacLellan (1994). The selective feeding habit of the spruce budworm resulted in incomplete canopy removal after outbreak. As a result, the canopy of budworm stands consists mainly of unaffected trees, and those that survived infestation, at the current stage of stand development. Though, like fire, logged stands were comprised mainly of post-disturbance aspen suckers, they had the lowest basal area. Incomplete aspen removal and shrub competition may be responsible for the less vigorous suckering of aspen.

As reported by others (e.g., Brown and DeByle 1987, Harvey and Bergeron 1989, Coats et al. 1990) a great deal of variation was found in aspen regeneration following disturbance. By killing canopy and understory vegetation and burning the forest floor, thus increasing soil temperature, fire promoted the most vigorous aspen regeneration among the three disturbances. The intermediate aspen regeneration after logging may be attributed to incomplete canopy removal, slow mortality of residual trees, and because logging occurred after winter freeze-up, less disturbance of the forest floor and understory vegetation. Peltzer et al. (2000) found there was no significant difference in aspen density following fire and clear-cut logging. As expected, budworm attacked stands had significantly less aspen regeneration than both burnt and logged stands. Spruce budworm outbreak always left intact the residual canopy of non host species, thus no direct mortality of aspen occurred. Kneeshaw and Bergeron (1999) report low numbers of shade intolerant aspen establishment in the slowly developed canopy gaps created by spruce budworm outbreak. In addition, a lack of disturbance on forest floor and in understory vegetation, did not encourage aspen suckering in budworm attacked stands.

Because of the above differences in residual canopy and aspen regeneration, pre-disturbance mixedwood stands remained mixedwood stands10 years after budworm outbreak, while fire and logging resulted in aspen dominated stands. The significantly higher conifer regeneration in budworm attacked stands suggested that succession would continue toward a conifer-dominated mixedwood. Succession pathways of fire and logged stands however, hinges on future conifer recruitment which is known to be determined by the availability of seed, receptivity of seedbeds, and vegetative competition (e.g., Koroleff 1954, Ahlgren and Ahlgren 1960, Dix and Swan 1971, Rowe and Scotter 1973, Attiwill 1994, Waldron 1966, Kneeshaw and Bergeron 1996, 1999, Liefers et al. 1996b, Cornett et al 1997, Delong et al. 1997, Galipeau et al. 1997, Beach and Halpern 2001).

Seed supply has been frequently cited as the most limiting factor to post-disturbance conifer (especially balsam fir and white spruce) recruitment (e.g., Ahlgren and Ahlgren 1960, Moor and Wein 1977, Archibold 1980, Eberhart and Woodard 1987, Brumelis and Carleton 1988, Halpern 1988, Sirois and Payette 1989, Zasada et al. 1992, Whittle et al. 1997, Greene et al. 1999, Greene and Johnson 1999, 2000, Beach and Halpern 2001). In this study, significantly higher post-disturbance conifer regeneration density was found on sites with Abundant seed source class when compared to those classified as Few and None. Given the lack of disturbance on forest floor and in understory vegetation, and the presence of a residual canopy, significantly higher post-disturbance conifer recruitment in budworm attacked stands must then be attributed to a more abundant seed supply. In this study twenty eight (93%) budworm attacked stands were classified as Abundant while only three (15%) burnt and six (30%) logged stands were classified as having Abundant seed source. Presence of scattered survivors was typical in budworm damaged stands in the study area, and seeds may only rarely be totally absent. Since this study deals only with severe budworm outbreaks (i.e. high conifer mortality) it is likely that light budworm infestations would have even less impact on post-disturbance conifer recruitment. This is particularly true for balsam fir which recruits readily under closed canopy and low light conditions (Sims et al. 1990, Galipeau et al. 1997, Greene et al. 1999). Batzer and Popp (1985) in northeastern Minnesota also found that survived host trees acted as important sources of seed. Despite less abundant seed supply, burnt stands (3 Abundant, 7 Few and 10 None) had slightly, but not significantly, more post-disturbance conifer regeneration compared to logged stands (6 Abundant, 12 Few and 2 None). This slight difference is likely attributed to better seedbed and less competition from shrubs on fire stands.

The negative correlation of total post-disturbance conifer regeneration density with aspen density and shrub cover suggested the importance of vegetative competition to conifer recruitment (Koreleff 1954, Liefers et al. 1996a, Cornett et al. 1997, Delong et al. 1997, Beckage et al 2000). While it is not possible to know the condition of the stands over the entire post-disturbance period, the present condition of understory shrubs is unlikely to have changed significantly during past few years. This may be particularly true for tall (> 2 m) shrubs. Significantly lower shrub coverage in those stands with recent (last four years) conifer recruitment compared to stands without recent conifer recruitment suggested a possible inhibitive effect of shrubs on conifer recruitment. As there were no significant differences in other measured stand or site variables, including seed source class, between the two groups of stands, late conifer recruitment, thus continuous recruitment pattern, is likely encouraged by less shrub development. As reported in previous studies (e.g. Dix and Swan 1971, Galipeau et al. 1997) the clay content of soil was also found to be negatively correlated with conifer recruitment.

On boreal mixedwood sites, early conifer recruitment is considered critical to future succession and timber productivity (Wang and Kemball, submitted). It has been proposed that there is only a narrow window of opportunity (5 years) for post-disturbance conifer recruitment, with perhaps the exception of balsam fir (Greene et al. 1999). Results from this study indicated, however, that the post-disturbance recruitment patterns depended on species and disturbance type. While the recruitment of aspen and jack pine was concentrated in the first five years in burnt stands, the recruitment of white spruce, black spruce and balsam fir continued over the entire post-disturbance period. Since white spruce and balsam fir are not seed banking species (Fyles 1989, Sims et al. 1990, Houle and Payette 1991), and aerial seed banks of black spruce are likely depleted within a few years after fire (Burns and Honkala 1990a, Attiwill 1994), there must be seeds dispersed from unburned patches to support the continuous recruitment (e.g., Archibold 1980, Greene and Johnson 2000). Residual unburned patches are not uncommon in boreal forest fires (Rowe and Scotter 1973, Eberhart and Woodard 1987), and a complete lack of live seed source within the dispersal distance was observed on only half of the burned stands. Given the relatively short (about 10 years) post-disturbance period, seed source is not likely to have changed very much on each sampled stand. Therefore, the finding that spruce and balsam fir, when present, did not have more recruitment in the first five years suggested a continuous recruitment beyond the initial five years after disturbance on boreal mixedwood stands (e.g., Day 1972, Youngblood 1995, Liefers et al. 1996a, Bergeron 2000).

In logged stands, all spruce seedlings, with exception of one white spruce, were recruited in the first five years. Despite white spruce being present in eight of the 20 stands as advance regeneration, post-logging white spruce regeneration was found in only two stands while post-logging black spruce regeneration was found in only one stand. Along with greater frequency, advance white spruce regeneration was also present in greater density. Only one stand had jack pine recruitment and that was in the third and ninth year. The seed source for the jack pine was from nearby rock outcrops. Balsam fir, however, was recruited continuously over the entire post-logging period. Low frequency and density of conifer recruitment following logging is likely the result of minimal disturbance of the forest floor (i.e. poor seedbed) and rapid expansion of other vegetation, especially shrubs (i.e., competition and smothering (Liefers et al. 1996, Beckage et al. 2000). To ensure mixedwood succession, preservation of advance regeneration with careful logging appears to be critical if harvested stands are to be left to regenerate naturally.

In budworm attacked stands, conifer regeneration was continuous during the entire post-outbreak period. However, there was more recruitment of black and white spruce and less recruitment of balsam fir during the initial five years compared to the second five year period. The difference found between spruces and fir is likely a reflection of the impact of the budworm on seed trees. As reported by others (e.g., Batzer and Popp 1985, MacLean 1980) mature white spruce and black spruce trees tended to survive while mature balsam fir trees died during the budworm outbreak. Also unique to budworm disturbance was that significantly more aspen was recruited after the first five years post disturbance. Because aspen are very shade intolerant, the late recruitment reflects the slowly opening canopy found after the budworm outbreak. It takes a minimum of 4 to 5 years of heavy defoliation to cause mortality of host trees (MacLean 1980, MacLean and Ostaff 1989), and once dead the trees remain standing as snags for many more years. As a result more aspen is recruited after the initial five years. Other factors that contribute to aspen regeneration, such as increased soil temperature and death of mature aspen trees (Mueggler 1984, Peterson and Peterson 1992), and size of canopy gaps (Kneeshaw and Bergeron 1999), would also be slow to develop with spruce budworm infestation.

3.5. CONCLUSION

The results supported the two hypotheses proposed in section 3.1. Given the similar pre-disturbance stand and site condition post-disturbance tree regeneration depends on disturbance type. Fire disturbance overwhelmingly favored aspen regeneration. It also promoted jack pine and black spruce regeneration despite their insignificant presence in pre-disturbance stands. However, it only supported sporadic regeneration of white spruce and balsam fir. Logging disturbance also favored aspen regeneration, followed by balsam fir regeneration. Other species were insignificant. Budworm disturbance promoted balsam fir regeneration, followed by aspen and the spruces. Differences in aspen regeneration reflected the severity of disturbance to the existing vegetation and the forest floor.

Although the amount of advance conifer regeneration remaining on the site depended on disturbance severity, post-disturbance conifer regeneration appears to be mainly limited by the abundance of seed supply despite the potential importance of seedbed condition and vegetative competition. Compared to the spruce budworm outbreak, conifer recruitment was significantly lower and highly variable following fire and logging. In terms of future succession, budworm attacked stands maintained a mixedwood composition with a stable or increasing conifer (balsam fir) component while fire and logging led to a transformation to aspen dominated stands. Although a significant difference was not detected in conifer regeneration between burnt and logged stands, the higher conifer densities and decreased shrub competition suggest that a greater number of burnt stands would progress into mixedwoods while more logged stands would remain aspen dominated (i.e. experience arrested succession).

Results of this study have significant management implications. The lack of new conifer regeneration in logged stands is problematic and emphasizes the importance of protecting advance regeneration during harvesting operations. As seed supply is the major factor limiting future conifer recruitment, maintaining seed trees during timber harvesting is essential. Rotten logs are both a suitable place for germination and, by being raised above the forest floor, help newly germinated seedlings avoid smothering by broadleaf litter. Significantly higher shrub cover suggests the increasing importance of rotten logs as a preferred seedbed for conifer regeneration. Therefore, sufficient structure (i.e. snags and DWM) should also be maintained during timber harvesting. As vigorous growth of aspen suckers may negatively affect shrub development clear-cutting, with removal of hardwoods as well as the desired softwoods, which promotes greater suckering may be more favorable compared to logging practices that mainly cut conifers.

4. General Conclusion

Important differences were found among the three disturbances in their impact on the forest floor, and pre-disturbance vegetation, which significantly affected post-disturbance tree regeneration and the understory plant community. The composition of the overstory community varied depending on the amount of residual canopy. Burnt and logged stands with none or few residual trees were dominated by post-disturbance aspen regeneration, while the overstory of spruce budworm attacked stands varied depending on pre-outbreak stand composition and structure. The spatial segregation and abundance of the seed source was the primary factor affecting conifer recruitment with seedbed condition and vegetative competition playing a secondary but important role. The understory herb community differed little among the disturbances in composition. However, species abundance changed with the amount of residual canopy depending on their shade tolerance. The greater heterogeneity in forest floor conditions following fire resulted in greater species richness. The increase in richness was not due to an increase on weedy invaders. At the current stage of development species composition for each disturbance type was dominated by persistent resident species and weedy invaders were virtually absent. The composition and abundance of the shrub communities were found to be quite different among the disturbances. Logged stands were dominated by beaked hazel and budworm attacked stands showed a great amount of variation that, once again, was linked to residual canopy. Beaked hazel was found abundantly in all three disturbance types, while mountain maple and raspberry, though present in all three disturbances, were only found in abundance in budworm attacked stands. Abundant raspberry cover was found only in stands with post-outbreak open canopy conditions and mountain maple was found in abundance only where pre-outbreak closed canopy conditions were maintained.

Burnt and budworm attacked stands resembled both mature aspen and mature mixed stands in species presence and abundance while the composition of logged stands was much more similar to mature aspen stands. Logged stands contained little conifer regeneration and were dominated by dense shrub growth which would likely limit future conifer recruitment. The abundant advance conifer regeneration, and post-disturbance conifer recruitment, found in most budworm attacked stands indicates that a return to the more productive post-disturbance aspen-conifer mixed stand will likely occur. For burnt stands the lower abundance of competing vegetation, particularly shrubs, and good seedbed conditions makes succession toward a mixed stand highly likely given adequate seed sources. Given an adequate seed source, conifer recruitment can continue beyond the first five years. Succession of aspen stands may be more commonly delayed than previously thought. Perhaps the future of aspen stands is not determined in the first five critical (i.e. Green et al. 1999) years but, given sufficient future seed supply, is determined in the first 10 or 20 years. This is consistent with mature mixed stands which typically show more or less continual recruitment.

Both aspen and most understory species are quite resilient and recover rapidly following disturbance. Management of upland aspen stands hinges on the ability to predict, identify, and manipulate those factors that effect future conifer recruitment. The most critical factor for conifer recruitment is seed availability, with seedbed condition and competition as secondary considerations. Logged stands have greater competition and poorer seedbed conditions than burnt stands, and less advance regeneration than budworm stands. As conifer recruitment has been shown to extend beyond the first few years adequate amounts of snags and downed wood need to be retained as potential future seedbeds. To emulate natural disturbance, advance regeneration should be protected during harvesting and adequate amounts of seed trees should also be maintained.

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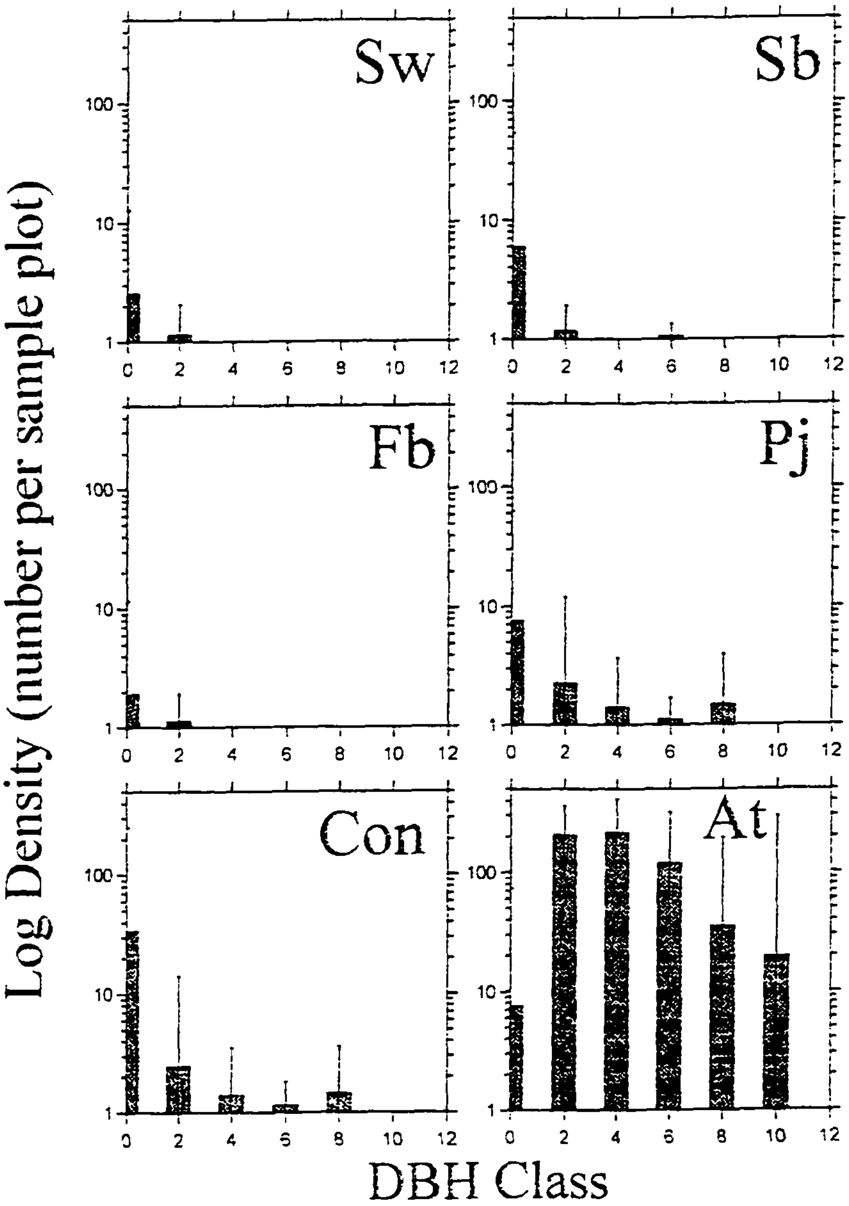
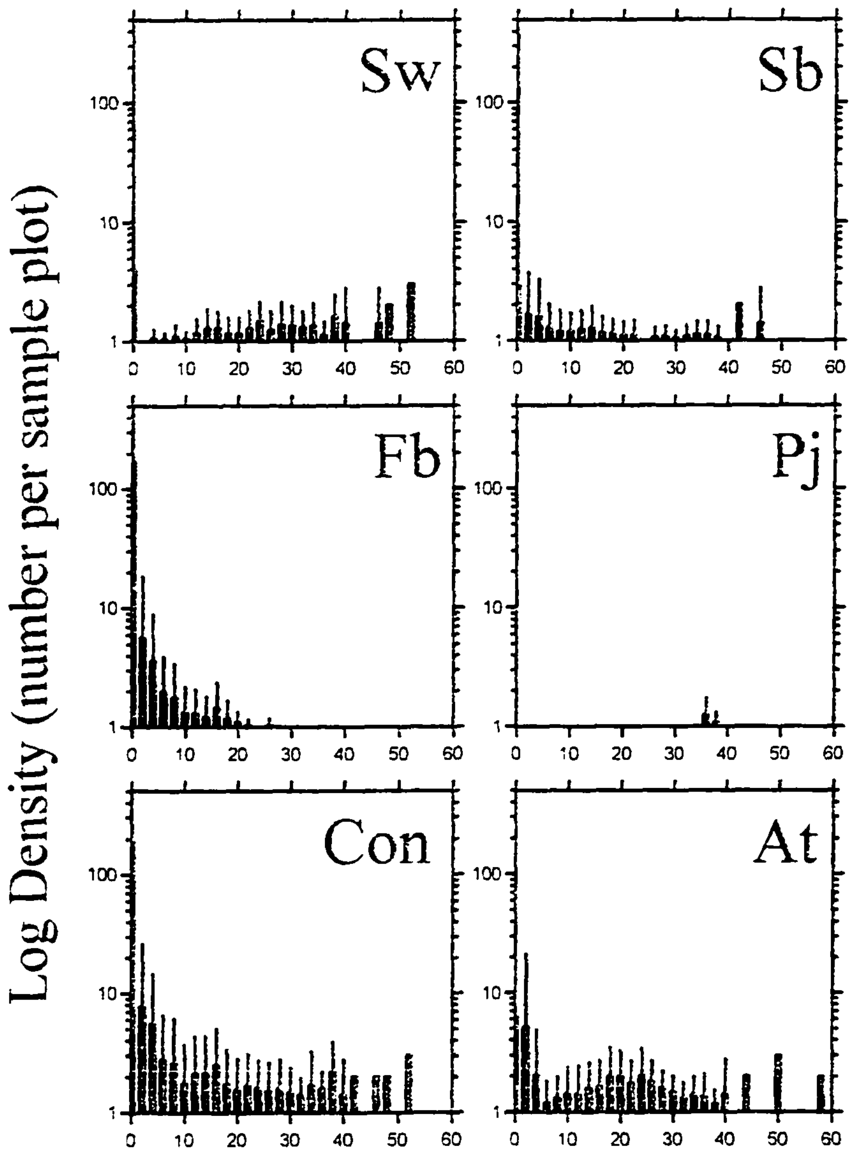
Appendix 1

DBH and density distribution.

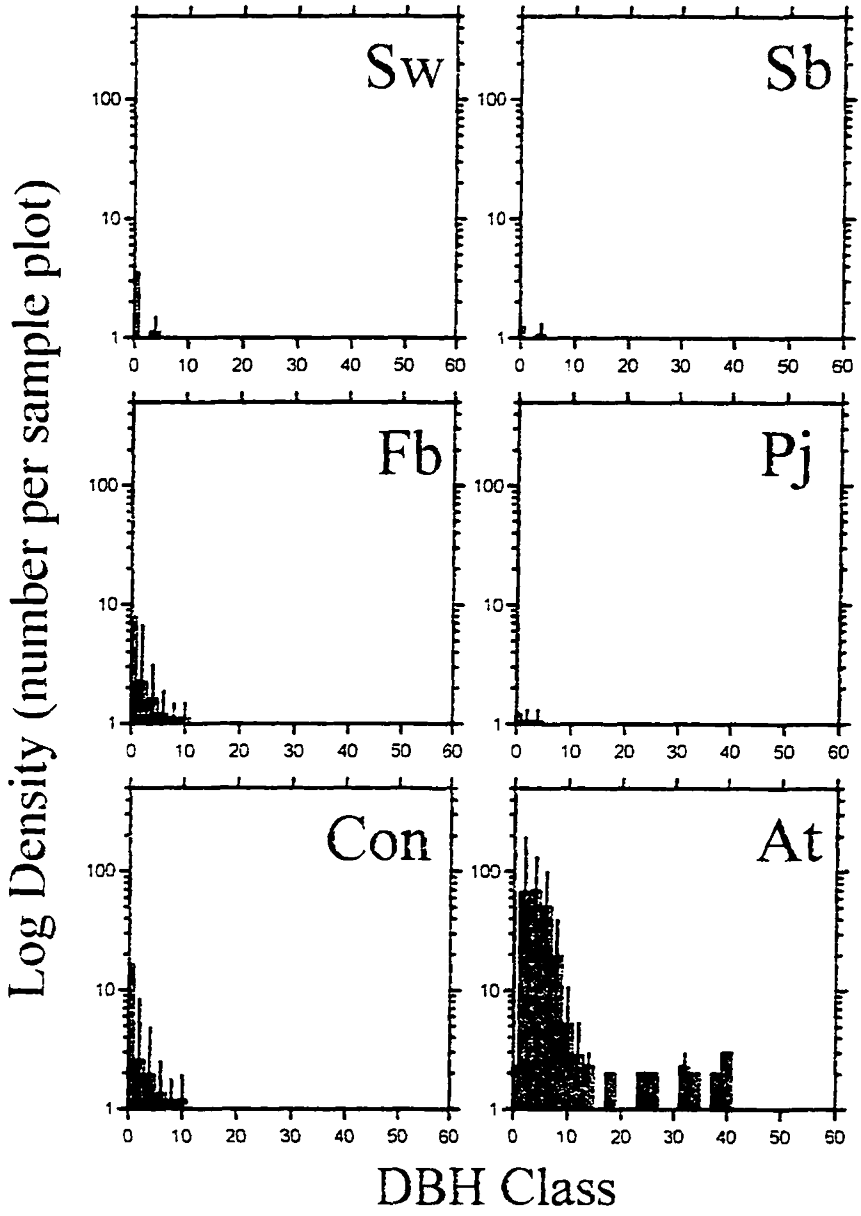
Sw = white spruce, Sb = black spruce, Fb = balsam fir, Pj = jack pine, Con = total conifer. At = trembling aspen.



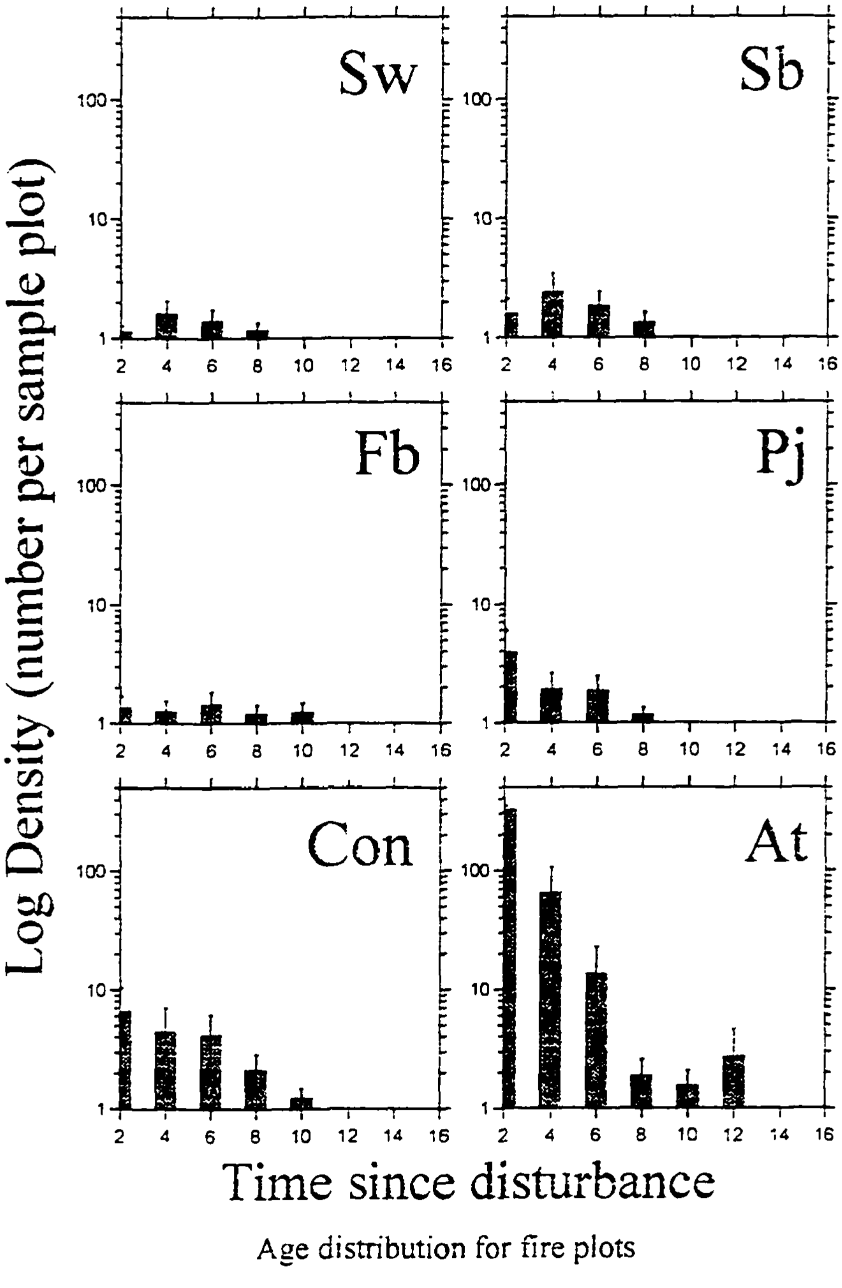
DBH distribution for fire disturbance.



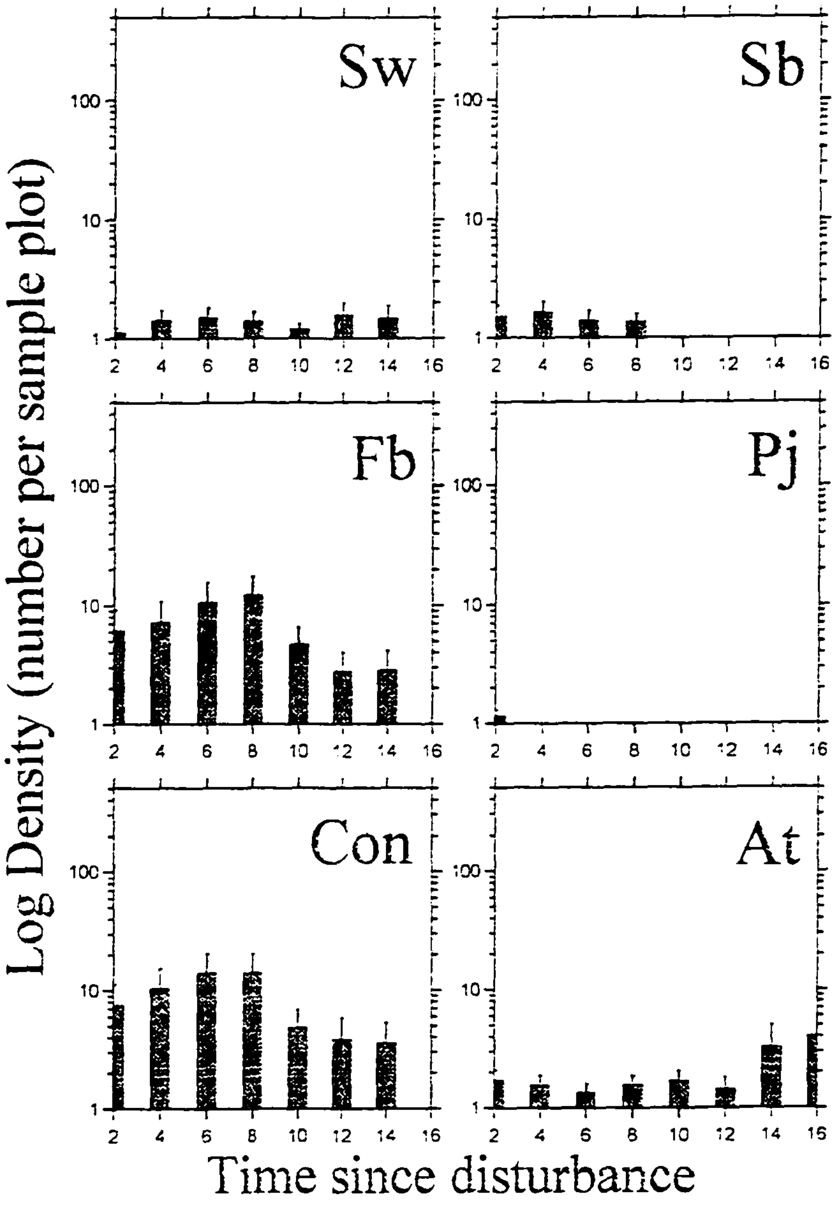
DBH distribution for budworm plots



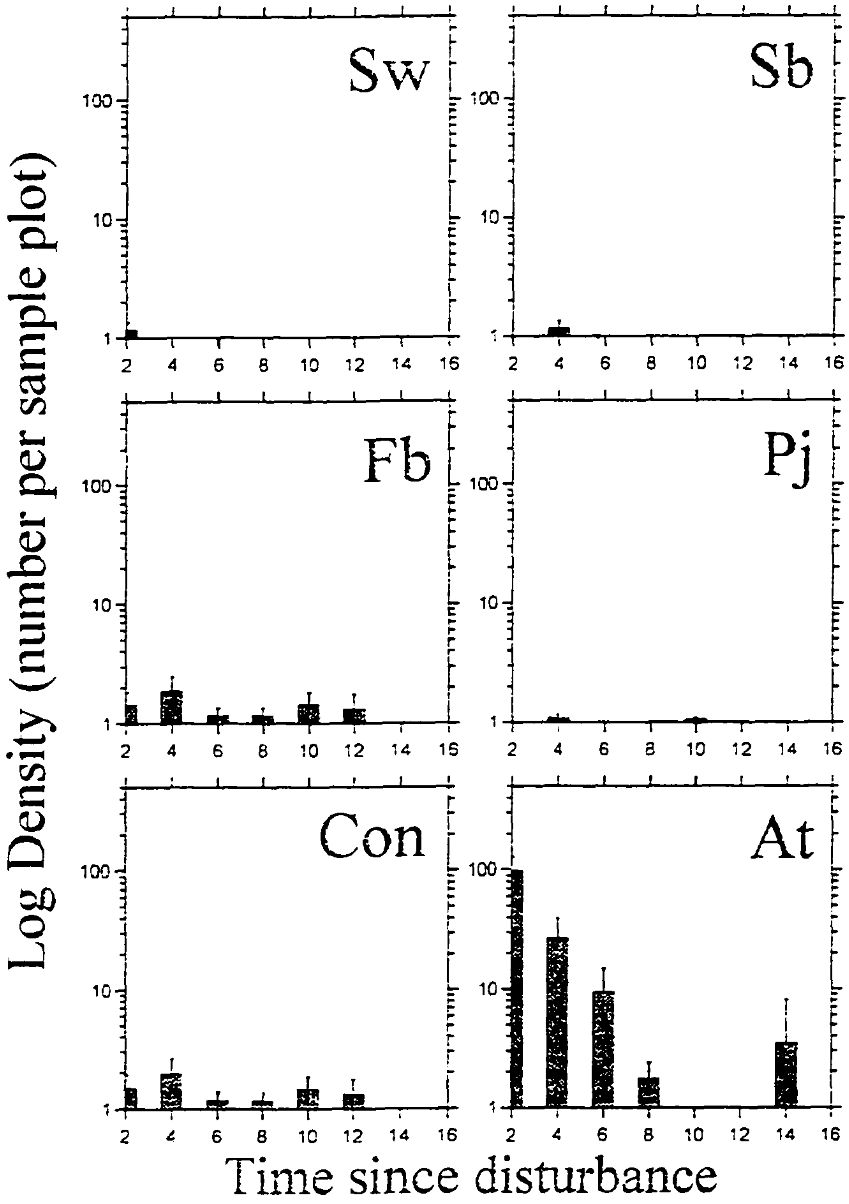
DBH distribution for logging plots



Age distribution for fire plots



Age distribution for budworm plots



Age distribution for logging plots

Appendix 2.

Mean percent coverage for logging (L, 2L), fire (F, 2F, B), spruce budworm (W, BW), mature mixedwood (MM), and mature aspen (AM) stands.

Species	2L4	2L6	2L7	2L9	2L10	2L5	2L8	2L3	2L2	2L1	L4	L3	L2	L1
Acer spicatum	0	3	0	0	0	0	0	0	0	37	0	0	0	0
Alnus rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0	19.4
Alnus crispa	0	0	0	0	0	0	0	2	3	0	0	0	0	0
Amelanchier alnifolia	18	0	0	0	0	0	2	7	4	0	2	2	8	1
Cornus stolonifera	2	32	0	17	1	7	14	0	5	0	1.6	0	0	0
Corylus cornuta	65	22	89.6	57	76	41	50	91	79	51	70	20.9	0.4	61
Crataegus rotundifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diervilla lonicera	5.6	0.8	0	3	3	7	2.2	1.9	8	4.8	0.7	10.4	4	2.8
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera dioica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera villosa	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0
Prunus virginiana	0	0	0	0	10.6	5	0	0	0	2	5	0	1	0
Rhamnus alnifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes glandulosum	0	0	0	0	0	0	0	0	0	0	0	0.4	0	0
Ribes hirtellum	0.4	0	0.1	0.1	0	0.2	0	0	0	0	0	0	0	0
Ribies hudsonianum	0	0	0	0	0	0	0	0	0	0	0.4	0.4	0	0.2
Ribes lacustre	0	0	0	1	0	0	0	0	0	0.1	0	0	0	0
Ribes oxycanthoides	0	0	0	0	0	0	0	0	0	0	0	0.2	0.4	2.4
Ribes triste	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa acicularis	9	2	1	3	5	13	11.2	6	11.4	1.6	12.8	0.2	32	8.6
Rubus ideaus	2	0	1	7	1	0	0.7	0	1	0	0	0.6	5.2	3.2
Symphoricapus albus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtiloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum edule	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum opulus	0	3	0	8	0	0	0	0.1	4	0	0	0	0	0
Viburnum rafinesquianum	0	0.2	0.4	2	0	0	0	0	0	0	12	0	0.4	0
Actaea rubra	1	0	0	0	0	0	0	0.8	0	0	0	0	0	0
Agrimonia striata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone quinquefolia	1	0	0	0	0	0	0	0.2	0	0	0	0	0	0
Apocynum androsaemifolium	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Aquilegia brevistyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Aralia nudicaulis	8.2	5	2.4	5	5.6	10.6	7.6	3	13.6	9	0.8	7.2	1.4	0
Asarum canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster ciliolatus	2.8	5.8	1	1.2	3.5	4.6	0.6	3.4	1.5	2.6	0.1	0	1	0.3
Athyrium felix-femina	0	0	0	0	0	0	0	0	0	0	0	1.2	0	0
Chenopodium album	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chimaphila umbellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Circaea alpina	0	0.1	0.2	0	0	0	0	0.1	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0

Species	2L4	2L6	2L7	2L9	2L10	2L5	2L8	2L3	2L2	2L1	L4	L3	L2	L1
Clintonia borealis	9.6	0	0	0	1	2	0	0	12.2	0.4	0.8	0	0.4	0.4
Coptis trifolia	0	0	0	0	0.1	0	0	0.1	0.1	0	0	0	0	0
Cornus canadense	0.6	1.6	1	0.1	0.8	2.2	2.1	0.1	3.2	1	0.2	2	0.2	0.7
Epilobium angustifolium	0	0	0	0	0	0	0	0	0	0	0	1.6	1	0.1
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum pratense	0	0	0	0.4	0	0	0	0	0	0	0	0	0	0
Equisetum sylvaticum	0	0.4	0	0	0	0	0	0	0	1.6	0	0	0	0
Fragaria vesca	0	0	0	0	0	0	0	0	0	0	0	0	0.4	0
Fragaria virginiana	2.8	1.3	1.1	4.6	3.8	1.5	0.6	1.6	0.6	1	0.8	0.6	4.4	0.6
Galium boreale	0.4	0	0	0	0.1	0	1.4	0	0.3	0.7	0.4	0.3	1.3	0.5
Galium trifidum	0	0	0	0	0	0	0	0.4	0	0	0	0	0.2	0
Galium triflorum	0.1	0.2	0	0.8	0.6	0.2	0.6	0.3	0.2	0	0	0	0	0.9
Geum aleppicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Geranium bicknellii	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0
Gymnocarpum dryopteris	0	0	0	0	0	0	0	0	0	0	0	0	0	16.6
Heracleum lanatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathyrus ochroleucus	2.7	0	0	0	0	0	0	0	1	0	0	0	1.1	0.1
Lathyrus venosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ledum palutre	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linnaea borealis	0	0	0	0	0	0.6	0	0	0	0.1	0	0	0	0
Mertensia paniculata	0	2.6	0	2.2	1.2	0.8	0	0	0	0	0	0	0	0
Mianthemum canadense	1	2.8	2.2	1.6	1.7	1.1	4.6	1.1	2.3	2.4	0.4	0.5	0.9	0.4
Mitella nuda	0	2.4	0	0	1.4	0.2	0.2	0	0.1	0.8	0	0.1	0	0
Osmorhiza depauperata	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0
Petasites palmatus	0.3	1	0	1.6	1	2.1	0.6	1	2.2	0.6	0.4	1.1	0	0.5
Petasites sagittatus	0	0	0.1	0	0	0	0.8	0	0	0	0	0	0	0
Pteridium aquilinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyrola asarifolia	0.9	0	1.4	0	0	1.4	0	1	0.5	1.2	0	0	0.4	0
Pyrola secunda	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus pubescens	2.8	6.6	6	10.4	7.6	7.4	5.4	2.5	9	2.4	0.4	2.1	0.9	1.4
Saniculua marilandica	1.8	0	0	0	0	0.5	0.2	0.6	1.2	1.6	0.2	0	0.6	0
Smilacina stellata	0	0	0	0	0	0	0	0	0	0	0	0.8	0	0
Solidago canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Streptopus roseus	0	0	0.4	1	3.4	0	2.6	0	4	3.4	1.4	0.1	0.4	1.3
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum venulosum	0	0	0	0.8	0	0	0.6	0	0	0	0	0	0	0
Trientalis borealis	0	0.1	0.4	0	0	0.6	0	0.4	0	0.4	0.1	0.3	0	0.2
Vicia americana	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola nephrophylla	0	1	0.4	0	0	0	0	0.6	0.2	0.8	0	0	0	0
Viola palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola renifolia Brainerdii	0.2	0.4	0	0.2	0	0	0	0	1.4	0.1	0	0	0	0
GRASS	11.2	1	16	3.9	3.4	4.8	7.2	6	6.4	3.1	7.9	3.6	26	0
MOSS	2.5	10	0.8	5.3	4	9	3.5	6.5	3.6	12	1.4	6.7	0.6	0.5

Species	LA	L32	L24	L20	L17	L16	2F6	2F9	2F8	2F7	2F5	2F4	2F3	2F2
Acer spicatum	0	0	3	0	41	36	0	0	0	0	0	0	42.6	0
Alnus rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus crispa	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Amelanchier alnifolia	5.4	0	17	2.2	1	0.4	23	0	0	3	0	10	0	4.4
Cornus stolonifera	9.4	0	0	16	0	0	0	3	3.6	0	1.6	1	0.4	0
Corylus cornuta	31	0	63	19	20.2	64	74	0	0	19	55	60	0	0
Crataegus rotundifolia	0	0	0	0	0	0	0	0.2	0	0	0	0	0	0
Diervilla lonicera	1.26	0	0	1	14	5	8	0	1.1	7.2	0	0.8	0	0
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera dioica	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Lonicera villosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunus virginiana	1.6	0	0	8	2	0	2	3	0	0	13	0	0	0
Rhamnus alnifolia	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
Ribes glandulosum	0	0	0	0	0	0	0	0.2	0	0	0	0	0.1	0
Ribes hirtellum	0	0	0	0	0	0	0	0	0.8	0	0	0	0	0
Ribies hudsonianum	0.4	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes lacustre	0	0	0	0	0	0	0	0.2	0	0	0	0.1	0	0
Ribes oxycanthoides	0.2	0	0	0	0	0.4	0	0	0	0	0	0	0	0
Ribes triste	0.4	0	2.2	1	2.4	1.1	0	0	0	0	0	0	0	0
Rosa acicularis	6.8	0.2	2.4	15	0	0.8	2.6	5.8	5	3.8	0.5	3	0	4.4
Rubus ideaus	0	2.2	0	1.2	5	0	0	0	6	0	0	0	0.3	3.2
Symphoricapus albus	0	0.4	3.2	6.4	1	0.9	0	0	0	0	0	0	0	0
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtiloides	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Viburnum edule	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum opulus	0	0	0	3	2.4	2	0	6	3	5	19	5	3	0
Viburnum rafinesquianum	0	0	7	0	0	0	0	0	0	3	0	0.2	0	1
Actaea rubra	0	0	0.4	0	0	0	0	0	0	0	0	2.6	0	0
Agrimonia striata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone canadense	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Anemone quinquefolia	0	0	0	0	0	0	0	0	1.4	0	0	0	0	0.7
Apocynum androsaemifolium	0	0	0.2	0.2	0	0	0	0	0	0	0	0	0	5
Aquilegia brevistyla	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Aralia nudicaulis	4.6	14	13	14	4.2	1	8	3.2	6.8	6.2	2.4	3.4	5.2	3.2
Asarum canadense	0	0	0	0	0	0	0	0	0	0	1.2	0	0	0
Aster ciliolatus	0.8	0.2	0.5	0.1	0	0.3	3.4	7.4	3	0	0.8	0	1.5	6.6
Athyrium felix-femina	0	0	0	0	0	0	0	0.8	0	0	0	0	0	0
Chenopodium album	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0
Chimaphila umbellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Circaea alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Cirsium arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	4.1
Clintonia borealis	0	1	0	0	1	0	10.1	0	0	2.6	0	0.6	0	0
Coptis trifolia	0	0	0	0	0	0	0.1	0	0	0	0.1	0.1	0.2	1.6
Cornus canadense	1.52	0.9	1.2	1	0.6	0.2	2	0	2	3.8	0.3	1	1.8	3.4

Species	LA	L32	L24	L20	L17	L16	2F6	2F9	2F8	2F7	2F5	2F4	2F3	2F2
Epilobium angustifolium	0.46	0	0	1.6	0	0	0	0	0.4	1.2	0	0.8	0	14
Equisetum arvense	0	0	0	0.2	0	0	0	0	0	0	0	0	0	0.1
Equisetum pratense	0.26	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum sylvaticum	0	1	0	0.4	0	0	0.8	20.2	13.8	0.1	0.6	0	0	0.2
Fragaria vesca	0.06	0	0	0	0	0	0	0	0	0	0	0	0	0
Fragaria virginiana	2.06	4.5	3.4	1.7	10.8	0.6	1	2.1	0.8	2.4	0	0.1	0	12.6
Galium boreale	1.06	0.9	0.8	0.2	0.1	0.1	0	0.4	1.4	1.1	0	0.6	0	0.3
Galium trifidum	0	0	0	0	0	0.1	0.1	0	0.4	0	0	0	0.2	0.2
Galium triflorum	0	0	0.1	0.6	0	0	1	1	0.9	0	0.8	0	0.6	0
Geum aleppicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium bicknellii	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnocarpum dryopteris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heracleum lanatum	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathyrus ochroleucus	0.12	0	1	1.2	6	0	0	0	0	0	0	0	0	0.8
Lathyrus venosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ledum palutre	0	0	0	0	0	0	0	0	0	0	0	0.1	0	5
Linnaea borealis	0.1	0	0.2	0.1	2.1	0.2	0	0	0	0	0	0	2.2	5.2
Mertensia paniculata	0	0	0	0	0	0	0	0	1.4	0	0	0	0	3.6
Mianthemum canadense	0.32	3.3	1.4	2	1.4	0.8	1.4	3.2	0.8	1.2	1.6	2.8	2	3.7
Mitella nuda	0.6	0.2	0.1	0.1	0	0.2	0.1	0	0	0.6	3.4	0.4	0.4	0
Osmorhiza depauperata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petasites palmatus	4.8	1.9	1.2	0.3	0	0	2.2	2.2	0.8	2.8	0	2	0	9
Petasites sagittatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteridium aquilinum	0	0	0	0	0	0	1	0	0	0	0.4	0	0	0
Pyrola asarifolia	1	0	0	0.1	0.3	0.1	0	0.8	0	1.3	0.1	0	0.1	0
Pyrola secunda	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus pubescens	1.6	2.4	1	3.4	3	2.8	1.4	7.4	1	6.1	4.2	2.6	5.2	3.7
Saniculua marilandica	0.52	0	0.6	0	0	0.1	3.4	0.1	2.1	1.4	0.4	0	0	0
Smilacina stellata	0.4	0	0.5	0	0	1	0	0	0	0	0	0	0	0
Solidago canadense	0	0.2	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0.4	0	0	0	0	0	0	1	0	0	0	0	0	2.1
Streptopus roseus	1.4	0.2	0	6	1.2	0	1.6	2	1.4	2.6	3	0.4	0	3
Taraxacum officinale	0	0	0	0	0	0	0	0.1	0.1	0	0	0	0	1.4
Thalictrum venulosum	0	3.4	0	0	0	0	1	3.8	0	0	0.6	0	0	0
Trientalis borealis	0	0.5	0.1	0	0.4	0.1	1.4	0	0.8	0.8	1.6	0.4	0.2	0.1
Vicia americana	0	0	0	0	0	0	0	0	0.1	0	0	0	0	0
Viola canadense	0	0	0.4	0	0	0	0	0	0	0	0	0	0	0
Viola nephrophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola palustris	0	0	0	0	0	0	0	0	0.4	0	0	0	0	0
Viola renifolia var. Brainerdii	0	0	0	0	0	0	0	0	0.6	0	0.6	0.2	0	0
GRASS	7.6	10	5	1	1	1	2.9	8	52	1.4	1.6	7.4	0.5	28.6
MOSS	3.26	1	0.5	1	0.5	0.5	6.2	18.2	4.3	3	3.5	6.4	10	6.1

Species	2F1	F3	F2	F1	B1	B2	B3	B18	B21	B22	B23	B25	B33	W16
Acer spicatum	0.1	0	0	0	0	8.8		0	0	47	0	0	0	0
Alnus rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus crispa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amelanchier alnifolia	0.4	0	0	0	0	0	0	0	0	0	1	7	0	0
Cornus stolonifera	5.4	0	2.4	0	0	0	0	20	0	0	0	0	0	6.4
Corylus cornuta	17	0	0	0	0	29.2		0	0	0	0	0	0	11
Crataegus rotundifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diervilla lonicera	5.4	0	0	8.26	0	27.6	0	3	25	7.2	31	22	1.25	0
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera dioica	0	0	0	0	0	0	0	0	0	0	0	0.2	0	0
Lonicera villosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunus virginiana	2	0	0	0	0	9.2	0	0	0	0	0	0	0	0
Rhamnus alnifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes glandulosum	0	0.6	0	0	0	0.2	0	0	0	0.2	0	0	0	0
Ribes hirtellum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribies hudsonianum	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ribes lacustre	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes oxycanthoides	0	0	0	0	0.7	0	0	2	0	0	0	0	0	0
Ribes triste	0	0	0	0	0	0	0	4	1	1	2	1		0
Rosa acicularis	6.4	1.66	9.4	0.8	2	6.4	0	5.5	2	1.2	1.2	4.4	2.5	5.6
Rubus ideaus	0.2	0	0.6	0	3.2	15.4	0	4.4	12.2	2	0	0.2	0	17.4
Symphoricapus albus	0	0	0	0	0	0	0	0	0.2	0	0	4	0	0
Vaccinium angustifolium	0	0	0	12.1	0	0	0	0	0	0	0	1	0	0
Vaccinium myrtiloides	0	18.8	0	0	0	0	0	0	0	0	0.2	0	0	0
Viburnum edule	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Viburnum opulus	5.1	0	0	0	0	0	0	0	0	13	0	4	0	0
Viburnum rafinesquianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actaea rubra	0	0	0	0	0	0	0	0	0	0	0	2	0	0
Agrimonia striata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone quinquefolia	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0
Apocynum androsaemifolium	1	3.2	0	0	0	0	0	0	0	0	2.2	0	0	0
Aquilegia brevistyla	2	0	0	0	0.02	0	0	0	0	0	0	0	0	0
Aralia nudicaulis	7.2	7.6	3.4	6.6	0	3.8	4.2	0	10	12	16	56	0	2.4
Asarum canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster ciliolatus	3	0	0.86	0.26	0.7	0.26	0	0	0	0.1	0.1	0.2	0	1.4
Athyrium felix-femina	0	0	0.2	0	0.7	0	0	0	0	0	0	0	0	0
Chenopodium album	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chimaphila umbellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Circaea alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	0	0	0	0	0	0	0	0.2	0	0	0	0	0	2.1
Clintonia borealis	2.5	16	0	3.6	0	1.22	4.4	0	0	2	2	3	0	2
Coptis trifolia	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0.5
Cornus canadense	5	5.2	6.4	5.6	0.5	2.2	15.5	0.2	1.9	0	1.4	0.8	2.5	4.4

Species	2F1	F3	F2	F1	B1	B2	B3	B18	B21	B22	B23	B25	B33	W16
Epilobium angustifolium	0.1	1.4	4.6	5.06	3.5	0	1	5.2	4	0.2	4	6.2	0	0
Equisetum arvense	0	0.8	0	0	0	0.84	0	0	0	0	0	0	0	0
Equisetum pratense	0	0	0	0	0.2	0	0	0	0	0	0	0	0	0.4
Equisetum sylvaticum	0.4	0.12	0	0	0	0	0	1	0	0	0	0	0	0
Fragaria vesca	0.1	0.06	0	0.06	0	0	0	0	0	0	0	0	0	0
Fragaria virginiana	4.1	1.72	1.66	0	6.6	1.8	2	0.4	1.2	0.4	0.2	1.4	0	0.6
Galium boreale	1	1.06	2.26	0.2	0.02	0.66	0	0.25	0.6	0.6	0.7	0.2	0.13	0
Galium trifidum	0	0	2.26	0	0	0	0	0	0	0	0	0	0	0.7
Galium triflorum	0	0	0	0	0	0	0	0.2	0	0.1	0	1	0	0
Geum aleppicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium bicknellii	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnocarpum dryopteris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heracleum lanatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathyrus ochroleucus	0.4	0.2	0.12	0.6	4	0	0	0	2	2.4	1.1	2.2	2.5	0
Lathyrus venosus	1.3	0	0	0.06	0.7	0	0.22	0	0	0	0	0	0	0.8
Ledum palutre	0	0	0.06	0	0	0	1	0	0	0	0	0	0	0
Linnaea borealis	0.6	0.06	0	0.8	0	0	0	0	0	1.2	0	0	5	6.2
Mertensia paniculata	6.7	1.2	0	0	5.5	0.4	0	0	0	0	0	0	0	0
Mianthemum canadense	1.3	0.06	0.06	0.06	0.82	0.64	0.06	0	0.6	1.4	1.4	2.2	0.25	0.2
Mitella nuda	0.1	0.4	0	0	0	2.2	0	0	0	0.3	0	0.2	0	1.8
Osmorhiza depauperata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petasites palmatus	7.4	5	0.26	0.32	0.72	0.8	0.22	5	1.2	0.2	0	1	0	1.4
Petasites sagittatus	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Pteridium aquilinum	0	0	0	0	1.4	2	0	0	0	0	0	0	0	0
Pyrola asarifolia	0.1	0	0	0	0.5	0	0.02	0	0	0.2	0.2	0.3	0	0.1
Pyrola secunda	0	0	0	0.06	0	0	0	0	0	0	0	0	0	0
Rubus pubescens	3.1	0.78	0.18	0.92	1.2	1.22	0.02	5	2.3	12.4	2.5	1	0	6.7
Saniculua marilandica	0.8	0	0	0	0	0	0	0.4	0	0	0	0	0	0
Smilacina stellata	0.1	0	0	0	0	0	0	0	0	0	0	0	0	0
Solidago canadense	0	0	0	0	0	0	0	0.2	1.2	0	0	0	0	0
Sonchus arvensis	0	0	0	0	0.3	0	0	0	0	0	0	0	0	0
Streptopus roseus	2.1	0	0	0	0.72	5.42	0.4	0	0	0.4	0.4	1	0	1.2
Taraxacum officinale	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0
Thalictrum venulosum	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Trientalis borealis	0.1	0.12	0	0	0	0	0.42	0	0	0	0	0	0	2
Vicia americana	0	0.06	0	0.12	0	0	0	0	0	0.2	0.1	0	0	0
Viola canadense	0	0	0	0	0	0	0	0	0.2	0	0	0	0	0
Viola nephrophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola renifolia var. Brainerdii	0	3.2	0	0	0	1.4	0	0	0	0	0	0	0	0
GRASS	8.4	11	54	3.12	7.3	7	3	10	1	0.5	0.5	1	0	8.2
MOSS	4.8	0.66	1.24	1.46	0.72	12.4	10.4	0.5	0.5	1	0.5	0.5	0.5	27

Species	W15	W14	W13	W12	W11	W10	W9	W8	W7	W6	W5	W4	W3	W2
Acer spicatum	0.8	0	0	15	1.4	1	1	62	76	0.6	0.6	0	0	0.8
Alnus rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus crispa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amelanchier alnifolia	0	0	0	0	0	0	3.4	0	0	0	0	0	0	0
Cornus stolonifera	15	3	0	0	0	0	3	0	0	0	0	1.4	0	0
Corylus cornuta	19.4	25.4	11.4	4.6	22	45.4	49.4	22	8	4	1.6	0.4	47.8	0.2
Crataegus rotundifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diervilla lonicera	0	0	0	0	0	2	1.5	1.2	0	1.2	0	0	0.4	0
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera dioica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera villosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunus virginiana	2.4	2.2	0	0.6	0	3	0	0	0	0	0	0	0	0
Rhamnus alnifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes glandulosum	1.6	0	0.8	0	0	0	0	0	0.1	0	0	0	0	0
Ribes hirtellum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribies hudsonianum	0	0	0	0.4	0	0.6	0	0	0	0.8	0.4	0.6	0.2	0
Ribes lacustre	0	0	0	0	0	0.8	0	0	0	0	0	0	0	0
Ribes oxycanthoides	0	0	0	0	0	0	0	0	0	0	1.4	0	0	0
Ribes triste	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa acicularis	0.1	9	8	1	5.6	10.6	10.2	0.2	0.6	0.6	0	1.4	0.6	0.2
Rubus ideaus	2.6	5.4	4.6	1	0	3.4	3.6	0	9	0.1	0.4	19.4	37	0
Symphoricapus albus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1
Vaccinium myrtiloides	0	0	0	0	0	0	0	0	0	0	0.6	0	0	0
Viburnum edule	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum opulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum rafinesquianum	0	0.6	1.6	0	3.8	0	3	0	0	0	0	0	0	0
Actaea rubra	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrimonia striata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone quinquefolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apocynum androsaemifolium	0	0	1	0	0	0	0	0	0	0	0	0	0	0.6
Aquilegia brevistyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aralia nudicaulis	0.8	2	8.6	7.6	6.2	6.8	5.2	3	1.2	7.2	2.3	1.4	1.5	4.5
Asarum canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster ciliolatus	5.4	2	1.8	0	0.2	0	1	0	0	0.2	0	0	0	0.6
Athyrium felix-femina	0.4	0	0	0	0	0	0	0	0	0	0.1	0	0.6	0
Chenopodium album	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chimaphila umbellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Circaea alpina	0	0	0	0	0.7	0	0.3	0.4	0.4	0	0	0	0	0.1
Cirsium arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clintonia borealis	10.6	0	0	0	2.8	0	0	0.8	1.6	0	0	0	0	0
Coptis trifolia	0.8	0	0	0	0	0	0	0	0	0.2	0.3	0.1	0	0
Cornus canadense	8	6.6	7.2	4.2	8	0.2	0.3	1	0.9	1.5	1.3	0.5	0.8	1.9

Species	W15	W14	W13	W12	W11	W10	W9	W8	W7	W6	W5	W4	W3	W2
Epilobium angustifolium	0.2	0.2	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum arvense	0.4	0	0	0	0	1.4	1.8	0	0.1	0.1	2	0	0	0
Equisetum pratense	0	0	0	0	0	0	0	0	0	0	0	0	1.1	0
Equisetum sylvaticum	0.7	0	0	0	0	0	0	0	0	0	0	0	0	0
Fragaria vesca	0	0	0	0	0.1	0	0.1	0	0.1	0	0.2	0.2	0.1	0.3
Fragaria virginiana	2	2.9	4.4	1.8	0.8	0.7	0.8	0.4	0.1	0.3	0.2	0.5	0	1
Galium boreale	0.4	0.2	0.2	1.8	0.9	0	0.9	0.5	0	0	0	0.4	1	0.1
Galium trifidum	0	0	0	0	0	0	0	0.1	0	0.1	0.2	0	0	0
Galium triflorum	0.4	0	2.8	0	0.8	0	0	0.6	0.3	0.4	0	0.4	0	0
Geum aleppicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium bicknellii	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnocarpum dryopteris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heracleum lanatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
Lathyrus ochroleucus	0	0	0	0	0	0	0	0	0	0.1	0	0.2	0	0
Lathyrus venosus	0	0	1.8	0	0	0	0.1	0	0	0	0	0	0	0
Ledum palutre	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linnaea borealis	3	2.2	6	0	1.2	0	0	3.3	0.7	2.6	1.8	4.2	0	6.7
Mertensia paniculata	0	0	0	0	0	0	0	0	0	0	0	0	0.7	0
Mianthemum canadense	0	0.4	0	0.8	0.6	0.4	0	0.8	0.4	0.4	0.2	0.3	0	0
Mitella nuda	3.2	2.1	0	2.6	3.8	2.6	1.3	3	2.2	0.7	1.3	1.4	1.8	0.9
Osmorhiza depauperata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petasites palmatus	6.2	3	4.2	0.8	7	5.4	1.4	1.6	0.4	1.6	1.5	1.8	0.1	2.1
Petasites sagittatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteridium aquilinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pyrola asarifolia	0.1	0	0	0	2	0	0.4	0.1	0	2.7	0.3	0	0.2	0.9
Pyrola secunda	0	0	0	0	0	0	0	0	0	0	0.1	0	0	0
Rubus pubescens	6.4	3.2	2.2	1.4	3.4	4.1	2.1	1.3	0.5	1.2	0.2	0.3	0.3	0.6
Saniculua marilandica	0	2.2	0	0	0	0	0.2	1.2	0	0	0	0	0	0
Smilacina stellata	0	0	0	0	0	0	0	0	0	0	0.8	0	0	0
Solidago canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Streptopus roseus	0	0	0	1.2	0	2	1	1.8	0.2	0.4	0.6	0	0.2	0.1
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum venulosum	0	0.4	0	0	0.2	0	0	0	0	0	0	2	0	0
Trientalis borealis	0.6	0.5	0.7	0.6	1.6	1.6	0	0.4	0.9	0	0.4	0.3	0	0.4
Vicia americana	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola nephrophylla	0	0	0	0	0	0	0	0	0	0.7	0	0	0	0.1
Viola palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola renifolia var. Brainerdii	0	0	0	0	0	0	0	0	0.3	0	0	0	0	0
GRASS	8.4	7.6	16.2	6.6	13.6	12.2	31.6	20.7	4.6	4.4	2.1	8.2	7.4	17.8
MOSS	6.8	17	15.4	9.8	15.4	13.4	13.6	16.3	4.6	63	81	11	11.4	34

Species	W1	bw1	bw2	bw3	bw4	bw5	bw6	bw7	bw8	bw9	bw10	bw11	bw12	bw1
Acer spicatum	0	18.8		1.8	58	88	20.8	0	0	0	0	0	32	0
Alnus rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus crispa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Amelanchier alnifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cornus stolonifera	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Corylus cornuta	0	0.2	3	0	21	10.4	9	29	0	7	0	3	6	0.42
Crataegus rotundifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Diervilla lonicera	0	8.8	3.04	0	0.4	0	2.4	8.4	0	0	13.2	0	4.4	1.02
Juniperus communis	0	0	0	0	0	0	0	3	0	0	0	0	0	0
Lonicera dioica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera villosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Prunus virginiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rhamnus alnifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes glandulosum	1.3	0.8	0	0	0	0	0	0	0	3.4	0	2.2	0	0
Ribes hirtellum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribies hudsonianum	1.2	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes lacustre	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes oxycanthoides	2.3	0	0.2	0	0	0	0	0	0	6	0	0	0.8	0
Ribes triste	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa acicularis	2.8	0	9	2.6	3	0	1	7.4	0	2	4.4	6.8	0	0
Rubus ideaus	9.6	0	81	15.4	1.64	0	0	0	0	41	0	7	0	0
Symphoricapus albus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtiloides	0	0	0	2.4	0	0	0	0	0	0	0	0	0	0
Viburnum edule	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum opulus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum rafinesquianum	4	0	0	0	4	0	0	0	0	0	0	0	0	0
Actaea rubra	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Agrimonia striata	0.1	0	0.02	0	0	0	0	0	0	0	0	0	0	0
Anemone canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone quinquefolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Apocynum androsaemifolium	0.6	0	0	0	0	0	0	0	0	0	0	0	0	0
Aquilegia brevistyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aralia nudicaulis	0.8	15.6	0.2	0.22	13.8	3.2	18.6	10	5.2	0.04	0	7.2	7.4	4
Asarum canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aster ciliolatus	0.6	0	0	0	0.2	0	0	7	0	0	0	0	0.02	0
Athyrium felix-femina	0.8	0	0	0	0	0	0	0	0	0	0	0	0	0
Chenopodium album	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chimaphila umbellata	0	0	0	0	0	0	0	0	0.04	0	0	0	0	0
Circaea alpina	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cirsium arvense	2.9	0	0	0	0	0	0	0	0	0	0	0	0	0
Clintonia borealis	0	5	0.42	0.6	0	0.4	6	7	0	0	2.2	0	5.6	8.6
Coptis trifolia	0	1.2	0	0	2.2	0	0	0	0	0	0	0	0	0
Cornus canadense	0.4	29.2	3.04	3.84	2.82	3.4	2.02	11	0	0	17	7	9.2	15.2

Species	W1	bw1	bw2	bw3	bw4	bw5	bw6	bw7	bw8	bw9	bw10	bw11	bw12	bw13
Epilobium angustifolium	7.4	0	0.84	0.02	0	0	0	0	0.02	2	0	0.4	0	0
Equisetum arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Equisetum pratense	0	0	0	0	0	0	0	0	0	6	0	0	0	0
Equisetum sylvaticum	0	0	0	2	1.62	0	0	0	0	0	0	0	0	0
Fragaria vesca	0.1	0	0	0	0	0	0	0	0	0.6		3.22	3.22	0.46
Fragaria virginiana	1.8		0.2	0.66	5.6	0	0.62	1.84	0	0	0	0	3.4	0
Galium boreale	1.1	0	0	0	0.08	0	0.02	0.6	0	0	0	0	0	0
Galium trifidum	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium triflorum	0.1	0.2	0.94	0.66	0	0	0.42	0	0	2.82	0	0	0.6	0
Geum aleppicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Geranium bicknellii	0	0	0	0	0	0	0	0	0	0	0	0	0	0.4
Gymnocarpum dryopteris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Heracleum lanatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathyrus ochroleucus	3.6	0	4.02	0	0	0	0	0	0	0	0	0	0.02	0.22
Lathyrus venosus	0	0	0	0.4	0.2	0	0	0	0	0	0	0	0	0
Ledum palutre	0	1.4	0	0	0	0	0	0	0	0	1.8	0	0	3.22
Linnaea borealis	0.1	1.4	3.42	1.26	0	0	14	1.02	3.8	0	12.4	21.4	0.04	2.2
Mertensia paniculata	0	0	0.02	0	0	0	0	0	0	1	0	0	0	0
Mianthemum canadense	0.3	2.44	1.04	2.84	0.22	0.64	0.44	1.02	0	0	2.8	0	0.82	
Mitella nuda	0.7	0	0	1.02	1.02	5.84	0	0.02	0	5.04	0	0	0.24	0.02
Osmorhiza depauperata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petasites palmatus	2.8	0.6	0	0	1.04	0.02	2.2	0	0	0	0	3.6	0.44	1.82
Petasites sagittatus	0	0	0	0	0	0	0	0	0	0	0	0	0.62	0
Pteridium aquilinum	0	3.2	1.4	0.6	9	0	0	0	0	0	0	0	0	0
Pyrola asarifolia	0.4	0	0	0	0	2.82	0.06	0.02	3.6	0	0	0	1.2	0
Pyrola secunda	0	3.2	0	0	0.02	0.4	0	0	0	0	0	0.6	0	0
Rubus pubescens	1.4	1	1.4	1.26	2.6	2.04	0	1.42	3.62	4.02	3.4		2.22	2.02
Saniculua marilandica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smilacina stellata	0	0	0	0	0	0	0	0.22	0	0	0	0	0	0
Solidago canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Streptopus roseus	0.7	2.04	0.8	0.86	3.4	5.2	0	0	0	0.06	5.6	0	1.44	0
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum venulosum	0	0	0	0	1.42	0	0	0	0	0	0.02	0	0	0
Trientalis borealis	0.3	0	0	0.04	0.84	0.82	0	0	0.04	0	0.06	0.82	0.2	0.04
Vicia americana	0	0	0	0	0.02	0	0	0	0	0	0	0	0	0
Viola canadense	0	0	0	0	6.62	0	0.2	0	0	0	0	0	0	0
Viola nephrophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola palustris	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola renifolia var. Brainerdii	0	0	0	0.24	0	0.02	0	0	0	0	0	0.8	0	0
GRASS	4	2.3	1.04	6.04	10.4	0.1	1.66	21	0.02	3	0.88	1.62	10	14
MOSS	66	31.2	18	55.4	16.8	34	53.4	26.4	93	49	50.4	72	15.4	16.6

Species	bw14	AM1	AM2	AM3	AM4	AM5	AM6	MM1	MM2	MM3	MM4	MM5	MM6	MM7
Acer spicatum	9.02	0	29.8	9	6	43.4	0	1.88	0.5	0.88	0.38	0.75	4.38	9.63
Alnus rugosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Alnus crispa	0	0	0	2.5	0	1.25	0	0	0	0	0	0	0	0
Amelanchier alnifolia	0	10	19.4	8.88	3.88	6.63	0	9.25	0.5	0	0	0.63	0	0
Cornus stolonifera	0	0	4.38	17	0.5	5.75	0	12.3	23.8	21.4	0	1.88	0	0
Corylus cornuta	13	80	36.9	26.5	73.8	37.5	15.2	0	3.75		1.38	0.13	0.13	2.5
Crataegus rotundifolia	0	1.25	0	0	0	0	0	0	0	0	0	0	0	0
Diervilla lonicera	3.4	6.38	5	10.8	41.3	0	5	0	0	2	0	0	0	0.63
Juniperus communis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera dioica	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lonicera villosa	0	0	0	0	0.25	0	0	0	0	0	0	0	0	0
Prunus virginiana	0	1.75	8.25	8.75	4.25	3.88	2.6	0	0	0	0	0	0	0
Rhamnus alnifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes glandulosum	0.02	0	0	0	0	0	0.02	1.25	0	0	0	0	0	0
Ribes hirtellum	0	0	0.5	0	0	0.63	0	0.75	0.38	0	0	0	0	0
Ribies hudsonianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes lacustre	0	1.5	0.13	0	0	0	0	0.63	0	4.38	0	0	0	0
Ribes oxycanthoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes triste	0	1.25	1.25	6.88	6.13	1.75	0	0.63	5.88	3.25	0	0	0	0
Rosa acicularis	0	7.38	11.4	7.63	7.13	2.75	5.2	0	0	0.63	2.13	0	0	0.63
Rubus ideaus	0	0.38	0	1.38	0.88	0	0.24	3	0.25	0	0	0	0	0
Symphoricapus albus	0	2.5	1.88	0.75	2	0.13	0	1.75	1.63	1.25	0	0	0	2.5
Vaccinium angustifolium	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vaccinium myrtiloides	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum edule	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viburnum opulus	0	0	14.4	9.13	4.38	0	0	2.5	3.13	7.5	0	0	0	0
Viburnum rafinesquianum	0	6.5	5.25	3.75	1.25	0	0	0	0	0	0	0	0	0
Actaea rubra	0	0.63	0	0	0	2	0	0.25	0.25	0.13	0	0.63	0	0
Agrimonia striata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Anemone quinquefolia	0	0.13	2.63	1.13	0.63	2	0	0	2.5	0	0	0.63	1.5	0.63
Apocynum androsaemifolium	0	0	0	0	0.63	0	0	5	6.38	13.8	0	0	0	0
Aquilegia brevistyla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Aralia nudicaulis	4.4	9.38	41.9	13.1	2.63	18.1	0.2	2	0.75	0.88	2.5	0.63	1.38	1.88
Asarum canadense	0	0	0	0.63	1.25	0	0	0	0	0	0	0	0	0
Aster ciliolatus	0.02	5.63	3.88	0.5	0.75	2.75	0.62	0	0	0	0	1.25	0	0.13
Athyrium felix-femina	0	0	3.75	7.63	0	18.9	0	0	0.25	0	0	0.13	0.63	0
Chenopodium album	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Chimaphila umbellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Circaea alpina	0	0	0	0	0	0.13	0	1	0	0	1.38	0	0	0
Cirsium arvense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Clintonia borealis	0	9.38	0	2	1.88	0	0	5	8.13	10.6	0	0	0.25	0
Coptis trifolia	0	0	0	0	0	0	0	0	0	0	0	0.13	0	0
Cornus canadense	2	7.13	4.38	1.25	2.75	1	0	4.38	3.13	5.63	2.5		2	4

Species	bw14	AM1	AM2	AM3	AM4	AM5	AM6	MM1	MM2	MM3	MM4	MM5	MM6	MM7
Epilobium angustifolium	0.02	0	0.63	0.25	0	0.63	0	0	0.13	0	0	0	0	0
Equisetum arvense	0	0	0	0	0	0	0	1	0.75	4.13	0.13	2.63	0	0
Equisetum pratense	0	0	0	0	0	0.63	0	0.13	0	0	0	0	0.13	0
Equisetum sylvaticum	0	0	0	0.13	0.13	4.38	0	1.25	0	0	0	0	0	0
Fragaria vesca	0.84	0	0	0	0	0	0.86	0	0	0	0	0	0	0
Fragaria virginiana	9.6	7	1.88	1.88	2	3.38	0	0.13	0.25	0.13	0.63	0	0.13	0.63
Galium boreale	0	2	1.25	0.25	0.5	2.25	0	0.25	1.63	1.5	0.38	0.13	0	0.63
Galium trifidum	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0
Galium triflorum	0.02	2.38	0.13	0.13	0.63	0.63	0.02	0	0.75	1.75	0.75	0.13	0	0.63
Geum aleppicum	0	0	0	0	0	0	0	0	0	0	0	0.63	0	0
Geranium bicknellii	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gymnocarpum dryopteris	0	0	0	0.13	0	0	0	1.25	0	0	0	0	0	0
Heracleum lanatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Impatiens capensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lathyrus ochroleucus	0	0	1.25	0	0.5	0	0	3.75	2.13	2	0	0	0	1.38
Lathyrus venosus	0.02	0	0	0	0	0	0	0	0	0	0	0	0	0
Ledum palutre	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Linnaea borealis	5.8	0.63	0	0	0	0	0	1.25	0.13	0	0	0.63	0	0.13
Mertensia paniculata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Mianthemum canadense	0.08	6.88	11.9	3.13	2.38	5.25	0	5.13	5	7	7.13	0.75	2.5	6.25
Mitella nuda	0.26	4	2	0	1.75	3.5	0	4.5	4.38	3.13	0.75	6.25	3.25	1.38
Osmorhiza depauperata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Petasites palmatus	0.02	3.88	0	0.88	0.13	0.88	0	2	2.13	1.25	0	5	0	0
Petasites sagittatus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Pteridium aquilinum	0	1.88	0	0	0	0.63	0	0	0	0	0	0	0	0
Pyrola asarifolia	0	2.25	0.13	0.38	2.38	0	1.4	0.38	0.63	0	0	1.25	0	0
Pyrola secunda	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rubus pubescens	2.64	9.38	5.63	2.75	0	6.25	0	0	0.63	1.88	2.63	4.38	0.75	0.75
Saniculua marilandica	0	5.63	8.75	4.5	2.88	0.63	0.42	0.25	0.13	3.13	0	2.5	0	0
Smilacina stellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Solidago canadense	0	0	0	0	0	0	0	0	0	0	0	1.25	0	0
Sonchus arvensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0.13
Streptopus roseus	1.44	0	0	0	0	0	0	0	0	0	0	0	0	0
Taraxacum officinale	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thalictrum venulosum	0	0.13		0.63	1.5	0	0	1.13	0.25	1.38	0	0	0	0
Trientalis borealis	0	2.75	1.88	0.88	2	0.13	0	0		0	0	3.25	0	2.5
Vicia americana	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola canadense	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola nephrophylla	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Viola palustris	0	0	0	0	0	0	0	1.88	0	0	0	0	0.13	0
Viola renifolia var. Brainerdii	0	0	0	0	0	0.75	0	0	0.63	0	0	1.25	0.63	0
GRASS	14.6	14.1	8.13	1	2.5	8.88	1.86	0.38	1.5	1.25	0.38	7	10.9	8.63
MOSS	16.6	6	6	0	0	1	7	35	18	25	0	12	10	2

Appendix 3.

Shade tolerance rankings after Bazukis and Kurmis (1978). Ranking is from most tolerant (1) to least tolerant (5).

Species	SHADETOLERANCE
Acer spicatum	1
Actaea rubra	1
Asarum canadense	1
Athyrium felix-femina	1
Circaea alpina	1
Coptis trifolia	1
Equisetum arvense	1
Galium triflorum	1
Impatiens capensis	1
Mitella nuda	1
Rubus pubescens	1
Streptopus roseus	1
Trientalis borealis	1
Ribes glandulosum	2
Ribes lacustre	2
Ribes triste	2
Clintonia borealis	2
Cornus canadense	2
Heracleum lanatum	2
Mianthemum canadense	2
Pyrola asarifolia	2
Viola canadense	2
Viola renifolia var. Brainerdii	2
Cornus stolonifera	3
Corylus cornuta	3
Diervilla lonicera	3
Ribes hirtellum	3
Rubus ideaus	3
Viburnum edule	3
Viburnum opulus	3
Viburnum rafinesquianum	3
Agrimonia striata	3
Aralia nudicaulis	3
Chimaphila umbellata	3
Equisetum sylvaticum	3
Gymnocarpum dryopteris	3
Linnaea borealis	3
Mertensia paniculata	3
Osmorhiza depauperata	3
Petasites palmatus	3
Pyrola secunda	3
Saniculua marilandica	3
Thalictrum venulosum	3
Vicia americana	3
Viola nephrophylla	3
Viola palustris	3
Alnus rugosa	4
Alnus crispa	4
Amelanchier alnifolia	4
Crataegus rotundifolia	4
Prunus virginiana	4
Rhamnus alnifolia	4
Ribies hudsonianum	4
Ribes oxycanthoides	4
Vaccinium myrtiloides	4
Anemone canadense	4
Anemone quinquefolia	4
Aquilegia brevistyla	4
Aster ciliolatus	4
Fragaria vesca	4
Fragaria virginiana	4
Galium trifidum	4
Geum aleppicum	4
Geranium bicknellii	4
Ledum palutre	4
Petasites sagittatus	4
Pteridium aquilinum	4
Smilacina stellata	4
Juniperus communis	5
Lonicera dioica	5
Lonicera villosa	5
Rosa acicularis	5
Symphoricapus albus	5
Vaccinium angustifolium	5
Apocynum androsaemifolium	5
Chenopodium album	5
Cirsium arvense	5
Epilobium angustifolium	5
Equisetum pratense	5
Galium boreale	5
Lathyrus ochroleucus	5
Lathyrus venosus	5
Solidago canadense	5
Sonchus arvensis	5
Taraxacum officinale	5