Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak

Kevin J. Kemball, G. Geoff Wang, and Qing-Lai Dang

Abstract: The understory plant community of 63 boreal mixedwood stands in southeastern Manitoba, Canada, that were disturbed in the 1980s (21 by crown fire, 20 by logging, and 22 by severe spruce budworm (*Choristoneura fumiferana*) outbreak) were investigated. Understory plant communities that developed after fire, logging, and spruce budworm outbreak shared a large number of species (47 out of 81 identified). However, compared with fire and spruce budworm outbreak, logging promoted the rapid expansion of tall shrubs (52.7% vs. 17.2% and 29.75% coverage, respectively), particularly *Corylus cornuta*. Significant differences were also found between disturbance types when species coverage was compared on the basis of shade tolerance and regeneration strategy. Lower shrub coverage following fire is attributed to greater disturbance severity on the forest floor, affecting in situ propagules and competition from dense trembling aspen (*Populus tremuloides* Michx.) regeneration. Lower shrub coverage following spruce budworm outbreak is attributed to slow opening of the canopy coupled with retention of a residual canopy of nonhost trees. Uniformly high shrub coverage following logging resulted in less heterogeneity and lower species diversity at both the stand and the disturbance level compared with natural disturbances. High shrub coverage may negatively impact conifer recruitment and have significant implications for future stand composition and productivity. Consideration of a natural insect outbreak model, rather than fire, for management of boreal mixedwood stands is recommended, particularly if stands are to be left to regenerate naturally.

Key words: disturbance, succession, diversity, shrubs, management, mixedwood.

Résumé : Les auteurs ont étudié les communautés végétales de sous-bois dans 63 peuplements mixtes en forêts boréale qui ont subi des perturbations au cours des années 1980; 21 perturbés par des feux de houppier, 20 par la récolte des arbres, et 22 par une sévère épidémie de tordeuse du bourgeon de l'épinette (*Choristoneura fumiferana*). Ces travaux ont été conduits dans le sud-ouest du Manitoba, au Canada. Les communautés végétales qui se développent après le feu, la récolte, et l'épidémie de tordeuse, ont en commun un grand nombre d'espèces de plantes. Cependant, comparativement au feu et à la tordeuse, la récolte favorise une rapide expansion des grands arbustes (52,7 % de la couverture contre 17,2 % et 29,75 %), surtout le *Corylus cornuta*. On observe également des différences significatives entre les perturbations, lorsqu'on compare les espèces de la couverture sur la base de la tolérance à la lumière et de la stratégie de régénération. On attribue la couverture par les arbustes plus bas, suite au feu, à une sévérité plus forte de la perturbation sur le parterre forestier, affectant les propagules in situ, et à une dense compétition par la régénération en *Populus tremuloides* Michx. Pour ce qui est de la couverture par les arbustes bas, suite aux épidémies de tordeuses, on l'attribue à l'ouverture lente de la canopée couplée avec une rétention de la canopée résiduelle par les arbres non-atteints. Une couverture uniforme par de grands arbustes, suite à la récolte, engendre une hétérogénéité réduite ainsi qu'une diversité en espèces plus faible, au niveau du peuplement aussi bien que de la perturbation, comparativement aux perturbations naturelles. Une couverture par de grands arbustes peut avoir un effet négatif sur le recrutement de conifères et avoir des implications significatives pour la composition future du peuplement et sa productivité. Pour l'aménagement des peuplements mélangés de la forêt boréale, il serait préférable de considérer comme modèle une épidémie d'insecte, plutôt que le feu, surtout si on doit permettre une régénération naturelle des peuplements.

Mots clés : perturbation, succession, diversité, arbustes, aménagement, forêt mélangée.

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Introduction

Boreal forest ecosystems are dynamic and subject to frequent and reoccurring natural disturbances such as wildfires (Rowe 1961; Rowe and Scotter 1973) and spruce budworm (*Choristoneura fumiferana*) outbreak (Baskerville 1975; Bonan and Shugart 1989). As timber harvesting increases, logging has also become an important disturbance in southern portions of boreal forests across Canada. With growing interest in developing forest-management practices that emulate natural disturbances, it becomes critical to understand the ecological impact of disturbance (Hanson et al. 1991; Attiwill 1994; Bergeron et al. 1999). However, most studies on post-disturbance vegetation recovery have focused on tree regeneration following fire and (or) logging (McRae et al. 2001). The response of the understory plant community to various types of disturbance is less well understood (Whittle et al. 1997).

The boreal mixedwood generally consists of trembling aspen (*Populus tremuloides* Michx.) and one or more conifer species including balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) BSP). The understory plant species of boreal forests, including those most commonly associated with late-successional stages, are well adapted to frequent disturbances (Shafi and Yarranton 1973; Rowe 1983; Whittle et al. 1997). Consequently, most understory species common in boreal forests are able to thrive under a variety of forest conditions or successional stages (Dix and Swan 1971; Carleton and Maycock 1981). Studies have shown that disturbed communities varied little in species composition from predisturbance communities except for an initial increase of weedy invaders (Dyrness 1973; Johnston and Woodard 1985; Halpern 1988, 1989; McMinn 1992; Qi and Scarratt 1998), especially on mesic to hygric and rich sites (De Grandpre and Bergeron 1997).

Post-disturbance success of many understory species has been largely attributed to vegetative regeneration (Buse and Bell 1992; Arnup et al. 1995) and (or) seed banking (Halpern 1988; Morgan and Neuenschwander 1988; Whittle et al. 1997; Qi and Scarratt 1998). The relative importance of sexual versus asexual reproduction is poorly understood. Though asexual reproduction likely plays a greater role (Halpern et al. 1999; Strong 2004), many species are capable of both. Dependence on in situ propagules suggests the critical importance of disturbance severity. A significant effect of disturbance severity on the composition and growth of post-disturbance plant communities has been frequently reported (e.g., Dyrness 1973; Shafi and Yarranton 1973; Moore and Wein 1977; Johnston and Woodard 1985; Halpern 1988; Halpern and Spies 1995; Roberts and Gilliam 1995; Nguyen-Xuan et al. 2000).

Compared with spruce budworm outbreak and logging, fire has by far the greatest impact on the forest floor. Deep burning or intense heat can consume or kill buried in situ propagules (Ahlgren and Ahlgren 1960; Moore and Wein 1977; Carleton and MacLellan 1994). Consequently, severe fire disturbances have frequently resulted in lower total plant coverage (Dyrness 1973; Johnston and Woodard 1985) and (or) lower species richness (Halpern and Spies 1995). However, fire severity is rarely uniform, particularly in boreal mixedwood stands. Wang (2002) found that following crown fire, forest-floor conditions within the same mixedwood stand ranged from total consumption of organic layers, exposing mineral soil, to light surface scorching that consumed only surface litter.

In contrast to fire, winter logging and spruce budworm outbreak have little impact on the forest floor (Outcalt and White 1981; Keenan and Kimmins 1993; Nguyen-Xuan et al. 2000) and the in situ propagules it contains. Logging on flat terrain results in little soil erosion (Keenan and Kimmins 1993). Though rutting and compaction can be a problem, they are minimal if harvesting is carried out in the winter, as is the case in much of the boreal forest. With regard to spruce budworm outbreaks, the spruce budworm does not consume nonhost species (Miller 1975) and has no direct impact on the forest floor. However, after a spruce budworm outbreak, unlike logging, a variable amount of residual canopy is often retained (D'Aoust et al. 2004). Differences in canopy mortality (severity) between the three disturbance types likely also play a role in understory community development.

The objective of this study was to compare understory plant communities 10–15 years after disturbance by fire, logging, or spruce budworm outbreak in boreal mixedwood stands in southeastern Manitoba, Canada. To our knowledge no study has explicitly compared how fire, logging, and spruce budworm outbreak affect the understory vegetation of boreal mixedwood stands.

Methods

Study area

The study area covered a 6900 km^2 section of the Lac Seul Upland ecoregion of the Boreal Shield ecozone (Ecological Stratification Working Group 1995) in southeastern Manitoba. The climate is characterized by cold winters (mean temperature –19.2 °C in January) and relatively dry, warm summers (mean temperature 19.0 °C in July). The average rainfall is about 400 mm, with 270 mm falling during the growing season (May to August). The average snowfall is approximately 120 cm and the frost-free period is about 100 d. Soils in the study area include dystric brunisols, gray luvisols, gleysols, fibrisols, and mesisols. According to the 1986 Manitoba Forest Resource Inventory (FRI), white spruce and trembling aspen are either primary or secondary species in 88% of the stands. Uplands with fine-textured soils are dominated by trembling aspen, while lowlands consist primarily of black spruce. Balsam fir is a minor component of many upland stands, with abundance generally increasing over time. Jack pine (*Pinus banksiana*) covering granite rock outcrops are also common in this region.

Sampling design

Within the study area, boreal mixedwood stands disturbed by crown fire, conifer-selection logging, or severe spruce budworm outbreak were identified based on the 1977 Manitoba FRI database and the disturbance history since 1977. Of all identified stands, 63 (21 disturbed by fire, 20 by logging, and 22 by spruce budworm outbreak) were sampled in 1999 and 2000 and used in the study. An additional eight stands were sampled but not included, as it was not possible

to confirm whether they met all the sampling criteria. Difficulty in accessing many of the identified burned stands for sampling ultimately limited the sample size. However, based on Manitoba FRI descriptions the sampled stands are representative of all those meeting the selection criteria, which were (*i*) stands were >5 ha in size; (*ii*) stands were mature to overmature (Manitoba FRI cutting class 4 or 5) boreal mixedwood stands with white spruce, black spruce, and (or) balsam fir constituting >25% but <76% of predisturbance basal area; (*iii*) site conditions were similar (i.e., less than 5% slope and similar soil moisture regime, soil drainage, and texture as measured in the field); (*iv*) the disturbance occurred in 1980*s*; (*v*) no secondary disturbances (e.g., salvage logging, site preparation, or planting) occurred after the primary disturbance.

Of the 21 burned stands, 9 were burned in 1987 and 12 in 1989. The 1987 fire began on May 5 and burned a total of 24 268 ha. The 1989 fire began on May 11 and burned a total of 37 008 ha. The 20 logged stands were harvested in 1986 (6 stands), 1987 (1 stand), 1988 (7 stands), and 1989 (6 stands). Although this was termed conifer-selection logging, it was practically clear-cutting, as few mature stems were left standing. Because of access constraints, and to avoid rutting, harvesting in the area is conducted primarily in the winter. During the 1980*s* the typical harvest method was full tree harvesting, with processing at roadside. Equipment used included a feller buncher and a cable or grapple skidder, along with a stroke delimber and slasher at roadside. Depending on amount, slash was either left piled or burned at roadside, and rarely redistributed over the cut block. During the selection harvest most nontarget hardwood trees were also felled and piled to facilitate the softwood harvest, as well as possible future forest-renewal activities. For spruce budworm attacked stands, the end of the last severe outbreak was used as the disturbance date. Accordingly, the 22 spruce budworm stands were disturbed in 1984 (5 stands), 1985 (11 stands), 1986 (2 stands), and 1988 (4 stands). Annual provincial spruce budworm reports were used to identify stands and ascertain that subsequent outbreaks had not occurred (Knowles 1991; Knowles and Matwee 1996, 1997, 1999, 2000). The outbreak dates were confirmed by measuring annual ring widths of surviving white spruce and black spruce according to Swetnam et al. (1988).

Data collection

A 20 m × 20 m plot was established at a location representative of the Manitoba FRI canopy composition description for each selected stand. Owing to removal of canopy trees by fire or logging it was not always possible to determine a representative location. In such cases the plot was established randomly at least 100 m from the stand boundary. Within the entire 400 m^2 plot all trees >2 m were measured and cored at breast height to determine basal area and age. Based on age and type of disturbance, trees were classified as residual or regeneration. Within each plot five 2 m × 2 m quadrats were randomly located. On each quadrat, percent coverage of shrubs, herbs, grasses, and mosses was visually estimated and values were averaged for each plot. Herbs and shrubs were identified to species. Coverage of shrubs >2 m tall was also recorded. Grasses were not identi-

fied because accurate identification was not always possible, owing to lack of flowering during the 2-month sampling period. Abundance of mosses was determined as total coverage of all species.

On each plot, soil and topography were described according to the Canadian Soil Survey Committee (1978) and a soil pit was dug at a representative location. Soil moisture regimes and drainage classes were classified in the field based on topoedaphic features (e.g., slope, texture, depth, presence of mottles or gleying) according to the procedure of Zoladeski et al. (1995). Samples of forest floor and mineral soil (top 30 cm only) were analyzed for pH, soil texture, and percent organic matter content using 0.01 mole CaCl$_2$ solution, pipette analysis, and loss on ignition method, respectively. Stands were classified as fresh to very fresh in moisture regime, except two burned stands that were classified as moist. All sampled stands were well to moderately well drained with the exception of two burned stands that were classified as imperfectly drained.

Data analysis

Site and stand variables as well as coverage of shrubs, herbs, grasses, and mosses were compared among disturbance types by analyses of variance (ANOVA) followed by Tukey's HSD multiple comparisons (Wilkinson 1990). Following the 1–5 scale ranking of Bakuzis and Kurmis (1978), each herb and shrub species was classified as shade intolerant (1 and 2), moderately shade tolerant (3), or shade tolerant (4 and 5). Also, according to its regeneration strategy, each species was classified as either invader (regenerating from dispersed seeds), seed-banking (regenerating from stored seed), or vegetative (asexual regeneration), based on the literature (Ahlgren 1960; Rowe 1983; Haeussler et al. 1990; Buse and Bell 1992; Arnup et al. 1995; Fire Effects Information System 2003). Seed banking and vegetative regeneration occur together in many species because limited seed-banking ability (i.e., seeds remain viable for one or two growing seasons) is common. Consequently, species relying on in situ propagules (seed bank or vegetative reproduction) were combined into one group, called persistent species, for analysis. Finally, for each stand the proportion of total species richness contributed by each shade-tolerance class or regeneration group was determined by dividing the number of species in each class or group by the total number of species. ANOVA followed by Tukey's HSD multiple comparisons was again used to test for differences between the disturbance types in terms of percent coverage and proportion of species richness for each shade-tolerance class and regeneration group. Prior to analysis, stem count was square root transformed because of unequal group variance. Basal-area and percent-coverage data were log-transformed because of unequal group variance and to improve normality. Proportion data were not transformed.

Indicator-species analysis (Dufrene and Legendre 1997) was performed using PC-ORD (Version 4) software (McCune and Mefford 1999) on herb and shrub species data. Indicator-species analysis yields a value between 0 (no indication) and 100 (perfect indication). Perfect indication means that a species unerringly indicates a particular group. The indicator value (IV) for each species in each group is based on both frequency and abundance and is calculated as

$$\mathrm{IV}_{kj} = 100\,(\mathrm{RA}_{kj} \times \mathrm{RF}_{kj})$$

where RA_{kj} is the relative abundance of species j in group k and RF_{kj} is the relative frequency of species j in group k. A Monte Carlo test with 1000 randomizations was used to test the significance of each IV.

Species-coverage data were also examined using correspondence analysis (CA) and canonical correspondence analysis (CCA). First CA and then CCA were used to investigate possible influence of environmental variables on species ordination. Finally, CA with covariable(s) was used to compare understory species composition between the three disturbance types. Only species that occurred on three (5%) or more stands were used in analysis. To examine environment–species relationships using CCA, forward selection of variables was used (Monte Carlo tests with 999 randomizations) and only significant ($p \leq 0.05$) variables were retained. Thirteen variables were tested: forest-floor pH, mineral-soil pH, percent organic matter in solum, depth of forest floor (L, F, and H horizons together and separately), depth of A horizon, total solum depth, percent sand, percent clay, age (from disturbance date to sample year), and predisturbance trembling aspen concentration. If required, significant environmental variables were then used as covariable(s) in CA ordination. Analyses were conducted using CANOCO 4.5 software (Ter Braak and Smilauer 1998). Spearman's rank correlation (Zar 1996) was used to investigate relationships of environmental variables to ordination axes.

Species richness, species diversity, and evenness of the herb and shrub communities combined were calculated for each plot. Species diversity (H) was calculated as

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

where H is Shannon's 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 Shannon's index of diversity and S is species richness (i.e., the total number of species found in a plot). Disturbance level or gamma (γ) diversity and evenness were also calculated in the same manner using mean coverage of each species in each disturbance type. Gamma richness is the total number of species found within a disturbance type. Multivariate analysis of variance was used to simultaneously compare species richness, diversity, and evenness among the three disturbance types. If significant, ANOVA followed by Tukey's HSD multiple comparisons were used to individually compare species richness, evenness, and diversity between the three disturbances (Wilkinson 1990).

Results

A summary of site characteristics is given in Table 1. No significant difference in any site variable was detected among the three disturbances. A summary of stand characteristics is given in Table 2. At the current stage of development, trembling aspen regeneration dominates burned and logged stands, while spruce budworm attacked stands consist of a mixture of regeneration and residuals of both trembling aspen and conifers. Logged stands had significantly ($p \leq 0.003$) lower total basal area than spruce budworm attacked or burned stands, which in turn have a lower basal area ($p = 0.055$) than spruce budworm attacked stands.

Among the four life-form groups (shrubs, herbs, grasses, and mosses), significant differences were found only for shrubs and mosses ($p \leq 0.001$). Total and tall shrub coverage were higher on logged stands than on burned or spruce budworm attacked stands (Table 3). In addition, shrub coverage was uniformly high following logging, only two stands (10%) having coverage <50%. Shrub coverage was much more variable following fire and spruce budworm attack, 13 stands in each type of disturbance (62% and 54% of stands, respectively) having less than 50% shrub coverage. Significantly higher coverage of mosses was found on spruce budworm attacked stands than on burned or logged stands (Table 3).

Among the three disturbance types, significant differences in both coverage and proportion of species richness were found for the moderately shade tolerant ($p \leq 0.018$) and shade-intolerant ($p \leq 0.001$) classes, while only proportion of species richness was found to differ significantly for the shade-tolerant class ($p = 0.033$). Spruce budworm attacked stands had significantly less coverage of shade-intolerant species, while logged stands had significantly greater coverage of moderately shade tolerant species (Table 4). Spruce budworm attacked stands had a significantly higher proportion of shade tolerant species richness, while burned stands had a significantly higher proportion of shade intolerant species richness. Among regeneration-strategy groups, significant differences were found in both coverage ($p = 0.032$) and proportion of species richness ($p = 0.042$) for the invader species group, and in proportion of species richness for the persistent species group. Burned stands had higher coverage of invader species, while logged stands had higher coverage of persistent species. Burned stands also had a higher proportion of invader species, and thus a lower proportion of persistent species (Table 4).

Of the 81 herb and shrub species identified, 47 were found to be common to all three types of disturbance (Table 5): 14 of these were shrub species, of which *Corylus cornuta* was the most abundant. With the exception of *Acer spicatum*, logged stands had the highest coverage of tall shrub species, including *Amelanchier alnifolia*, *Cornus stolonifera*, *C. cornuta*, *Prunus virginiana*, and *Viburnum rafinesquianum*. Indicator-species analysis showed that among the 20 species found to be significant indicators (values in boldface type in Table 5), tall shrubs were all associated with logging except for *A. spicatum*, which was associated with spruce budworm disturbance, and *Viburnum trilobum*, which was associated with fire. Of the four significant invader species, two, *Epilobium angustifolium* and *Taraxacum officinale*, were associated with fire.

Initial CA ordination (Fig. 1) showed burned, spruce budworm attacked, and logged stands intermingled, though logged stands tended to occupy the bottom left of the ordination. Together, the first and second axes explained 42% of the variation in species data. Only *A. spicatum* was strongly correlated with the first axis ($r = 0.89$), while total shrub

Table 1. Site attributes of burned, logged, and spruce budworm disturbed stands.

Variable	Fire (n = 21)	Logging (n = 20)	Spruce budworm outbreak (n = 22)
pH			
Forest floor	5.6 (0.6)	5.5 (0.7)	5.2 (0.4)
Mineral soil	5.5 (0.5)	5.2 (0.8)	4.9 (0.8)
Percent organic matter	4.9 (2.5)	5.0 (1.9)	4.8 (2.0)
Forest-floor depth (cm)	9.1 (3.9)	9.7 (2.4)	8.2 (1.8)
A-horizon depth (cm)	2.4 (1.4)	2.4 (0.9)	3.3 (1.6)
Solum depth (cm)	21.7 (13.6)	25.6 (7.9)	27.6 (10.5)
Texture			
Percent sand	24.9 (25.1)	12.4 (15.8)	19.4 (21.8)
Percent clay	37.4 (21.4)	37.4 (14.9)	26.0 (12.0)
Soil-moisture regime*	Fresh to very fresh	Fresh to very fresh	Fresh to very fresh
Drainage[†]	Well to modwell	Well to modwell	Well to modwell
Humus form[‡]	Mor	Mor	Mor

Note: Values are given as the mean with the standard deviation in parentheses. Soil-moisture regimes and drainage classes were classified according to Zoladeski et al. (1995).
*Two burned stands were classified as moist.
[†]Two burned stands were classified as imperfectly drained.
[‡]One burned stand was moder.

Table 2. Stand characteristics of burned, logged, and spruce budworm attacked stands.

Variable	Fire (n = 21)	Logging (n = 20)	Spruce budworm outbreak (n = 22)
Stand density	20301 (7746.1)a	7423 (3711.5)b	2210 (1864.5)c
Basal area ($m^2 \cdot ha^{-1}$)			
Aspen regeneration	27.6 (15.4)a	12.9 (6.6)b	10.8 (6.2)b
Conifer regeneration	0.25 (0.5)b	0.15 (0.2)b	6.8 (5.1)a
Residual aspen	0	3.09 (3.1)b	11.1 (5.8)a
Residual conifer	0	0.14 (0.2)b	6.6 (5.2)a
Total	27.9 (15.4)a	16.3 (7.6)b	35.2 (13.3)a

Note: Stand density is the total number of trees >2 m in height (stems·ha^{-1}). "Regeneration" denotes trees younger than the disturbance date. "Residual" denotes trees older than the disturbance date. Values in a row followed by a different letter are significantly different ($p \leq 0.05$).

coverage (r = –0.80), tall shrub coverage (r = –0.74), *C. cornuta* (r = –0.69), and *E. angustifolium* (r = 0.49) were correlated with the second axis. None of the site variables measured showed any strong trend along either axis. Subsequent CCA analysis with forward selection of variables showed that forest-floor depth (L, F, and H horizons together, p = 0.019) and percent sand (p = 0.002) were significant. Together forest-floor depth and percent sand account for 9.9% of the variance (cumulative percent variance for axes 1 and 2) in the weighted averages for the species.

CA ordination with percent sand and forest-floor depth as covariables (Fig. 2), with cumulative percent variation explained by the first two axes at 38.5%, shows that the three disturbance types did not separate along the first axis. However, 11 stands (2 burned, 6 spruce budworm attacked, and 3 logged) did separate along the first axis. These stands all had high *A. spicatum* coverage, which is highly correlated with the first axis (r = 0.93). Along the second axis, burned and spruce budworm attacked stands appear to be intermingled, while logged stands are grouped more tightly and, with few exceptions, largely confined to the bottom of the ordination. Along the second axis, the major trends are increasing *E. angustifolium* coverage (r = 0.62) and decreasing total shrub coverage (r = –0.72) and tall shrub coverage (r = –0.76), particularly of *C. cornuta* (r = –0.80). None of the remaining species or site variables showed any strong relationship with either the first or the second axis.

Significant (multivariate analysis of variance, Wilks' λ, p = 0.008) differences were found among the three disturbance types when species richness, evenness, and Shannon's diversity index were considered together. When each index was considered separately there was no significant difference in species richness (mean S = 22, 23, and 23 for burned, logged, and spruce budworm attacked stands, respectively). Significant differences (ANOVA, $p \leq 0.05$) were found in both diversity and evenness between the disturbance types. A multiple comparison indicated that Shannon's diversity index for logged stands (H = 1.90) was significantly (p = 0.011) lower than that for spruce budworm attacked stands (H = 2.27) but not burned stands (H = 2.16). Evenness was significantly higher on burned (J = 0.71, p = 0.019) and spruce budworm attacked (J = 0.74, p < 0.001) stands than on logged stands (J = 0.60). At the level of disturbance, γ richness, evenness, and diversity were highest fol-

Table 3. Percent coverage of shrubs, herbs, grasses, and mosses by disturbance type.

Variable	Fire (n = 21)	Logging (n = 20)	Spruce budworm outbreak (n = 22)
All shrubs	41.9 (32.1)b	82.3 (28.3)a	38.2 (27.9)b
Shrubs>2 m in height	17.2 (19.0)b	52.7 (28.6)a	29.7 (26.2)b
Herbs	35.9 (20.2)a	26.5 (11.0)a	30.3 (14.7)a
Grasses	9.6 (15.7)a	6.3 (6.1)a	10.6 (7.4)a
Mosses	3.9 (4.4)b	3.7 (3.5)b	25.8 (21.5)a

Note: Values are given as the mean with the standard deviation in parentheses. Values in a row followed by a different letter are significantly different ($p \leq 0.05$).

Table 4. Percent coverage and proportion of species richness of shrubs and herbs (combined) by shade-tolerance class and regeneration-strategy group according to disturbance type.

Variable	Fire (n = 21)	Logging (n = 20)	Spruce budworm outbreak (n = 22)
Shade tolerance			
Tolerant			
Percent coverage	17.9 (15.3)a	17.3 (14.6)a	25.2 (22.6)a
Proportion	0.42 (0.12)b	0.43 (0.06)b	0.50 (0.10)a
Moderately tolerant			
Percent coverage	41.5 (28.8)b	71.4 (26.2)a	35.1 (20.2)b
Proportion	0.34 (0.08)b	0.40 (0.07)a	0.37 (0.07)ab
Intolerant			
Percent coverage	18.4 (13.1)a	20.1 (13.1)a	8.2 (5.8)b
Proportion	0.24 (0.12)a	0.16 (0.08)b	0.13 (0.07)b
Regeneration strategy			
Invader			
Percent coverage	10.3 (9.5)a	4.9 (2.8)b	5.3 (3.9)b
Proportion	0.26 (0.07)a	0.22 (0.06)b	0.22 (0.06)b
Persistent			
Percent coverage	67.5 (33.9)b	103.9 (30.2)a	63.2 (26.1)b
Proportion	0.73 (0.07)b	0.78 (0.06)a	0.78 (0.06)a

Note: Values are given as the mean with the standard deviation in parentheses. Values in a row followed by a different letter are significantly different ($p \leq 0.05$).

lowing fire (S = 70, J = 0.78, and H = 3.16). Logged stands had the lowest evenness (J = 0.58) and diversity (H = 2.43) but not richness (S = 65). Spruce budworm attacked stands had the lowest richness (S = 57) and were intermediate in evenness (J = 0.70) and diversity (H = 2.82).

Discussion

Because of their similarity in terms of site conditions and predisturbance conditions (age and canopy composition), the stands would likely have had similar understory plant communities prior to disturbance (Dix and Swan 1971; Chipman and Johnson 2002; Haeussler and Bergeron 2004). The large number of species that were shared among the three disturbance types (47), as well as the clear dominance of a small number of these common species in the understory community regardless of disturbance type, suggest that there was no wholesale turnover of species following the disturbances. This is consistent with other results (Carleton and Maycock 1981; Outcalt and White 1981; Halpern 1989; De Grandpre and Bergeron 1997; Haeussler and Bergeron

2004). Though 34 species were found in only two disturbance types or were confined to a single disturbance type, this number is likely disproportionately high, owing to the sampling methods used. To maximize the number of stands sampled, only one plot was sampled in each stand. This sampling strategy might have resulted in many more low-abundance and infrequent species than would otherwise be expected. For this reason, most of our analyses were focused on species groups, categories, or indices (e.g., shrubs, shade tolerance, diversity), not on individual species. Caution is advised when interpreting data on individual species abundance as well as indicator-species analysis.

Despite a rapid return of ubiquitous species in the initial 3–4 postfire years (Haeussler and Bergeron 2004; Wang and Kemball 2005), differences persisted between the three disturbance types with respect to shade-tolerance classes and regeneration-strategy groups. These differences may be attributed to the continued effect of differential survival of predisturbance plants and in situ propagules. In contrast to crown fires, which kill all aboveground vegetation, logging and spruce budworm outbreaks have little direct impact on

Table 5. Mean percent coverage, with frequency, number of stands containing the species (in parentheses), indicator-species value (Dufrene and Legendre 1997), regeneration strategy, and shade tolerance for species common to all three disturbance types or with a significant indicator value.

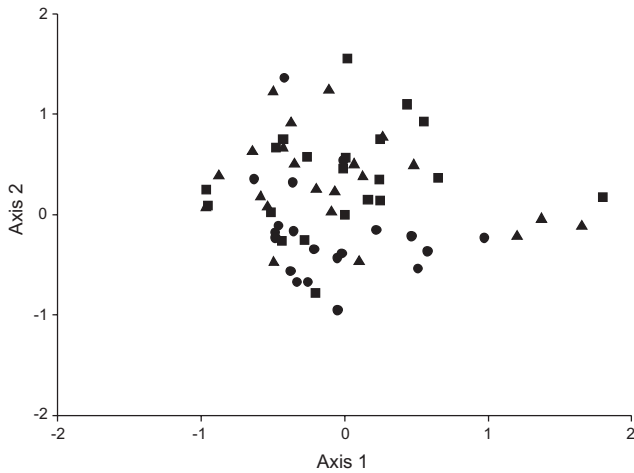|	Fire (n = 21)	Logging (n = 20)	Spruce budworm outbreak (n = 22)	Indicator-species value*	Regeneration strategy[†]	Shade tolerance[‡]
Acer spicatum	4.7 (4)	6.0 (5)	10.0 (13)	**28.5**	V	T
Amelanchier alnifolia	2.3 (7)	3.5 (13)	0.2 (1)	**38.1**	V	I
Cornus stolonifera	1.8 (8)	5.3 (10)	1.3 (5)	**31.5**	V, S	M
Corylus cornuta	12.1 (6)	48.6 (19)	14.7 (21)	**61.2**	V	M
Diervilla lonicera	7.0 (13)	3.8 (17)	2.1 (11)	33.8	V	M
Prunus virginiana	1.4 (5)	1.8 (8)	0.4 (4)	20.0	V, S	I
Ribes glandulosum	0.1 (5)	— (1)	0.3 (6)	20.6	S	T
Ribes hudsonianum	0.1 (1)	0.1 (4)	0.1 (6)	14.6	S	I
Ribes lacustre	— (2)	0.1 (2)	— (1)	5.2	S	T
Ribes hirtellum	0.2 (3)	0.2 (9)	0.1 (2)	20.3	S	M
Rosa acicularis	3.3 (19)	7.1 (19)	3.3 (17)	**49.4**	V, S	I
Rubus idaeus	2.3 (11)	1.5 (12)	5.0 (13)	33.8	V, S	M
Salix sp.	1.1 (5)	0.1 (1)	0.1 (4)	21.1	I	M
Viburnum rafinesquianum	0.2 (3)	1.1 (6)	0.4 (4)	19.3	S	M
Apocynum androsaemifolium	0.5 (4)	0.1 (7)	0.1 (2)	15.1	V	I
Aralia nudicaulis	7.9 (18)	6.5 (19)	5.0 (21)	34.9	V	M
Aster ciliolatus	1.3 (14)	1.5 (18)	0.9 (11)	36.4	I	I
Athyrium felix-femina	0.1 (3)	0.1 (1)	0.1 (3)	6.1	V	T
Circaea alpina	— (1)	— (3)	0.1 (5)	17.7	I	T
Cirsium arvense	0.2 (2)	— (1)	0.1 (1)	6.3	I	I
Clintonia borealis	2.3 (11)	1.4 (10)	2.1 (10)	20.6	V	T
Coptis trifolia	0.1 (6)	— (3)	0.1 (6)	13.7	I	T
Cornus canadense	2.9 (19)	1.1 (20)	6.3 (22)	**61.0**	V, S	T
Epilobium angustifolium	2.5 (15)	0.2 (5)	— (4)	**64.2**	I	I
Equisetum arvense	0.1 (3)	— (1)	0.3 (6)	20.2	V	T
Equisetum pratense	— (1)	— (2)	0.1 (2)	5.6	V	I
Equisetum sylvaticum	1.8 (9)	0.2 (4)	— (1)	**38.5**	V	M
Fragaria vesca	— (3)	— (2)	0.4 (11)	**46.2**	V	I
Fragaria virginiana	1.9 (17)	2.4 (20)	1.4 (17)	41.9	V	I
Galium boreale	0.5 (17)	0.4 (15)	0.3 (11)	34.2	V	I
Galium trifidum	0.2 (5)	— (3)	0.1 (5)	15.2	I	I
Galium triflorum	0.3 (8)	0.2 (11)	0.3 (10)	17.0	V	T
Lathyrus ochroleucus	0.8 (11)	0.7 (8)	— (4)	27.8	I	I
Linnaea borealis	0.7 (7)	0.2 (7)	3.7 (18)	**66.1**	V	M
Mertensia paniculata	0.9 (6)	0.3 (4)	— (1)	**20.2**	V	M
Mianthemum canadense	1.2 (20)	1.6 (20)	0.5 (15)	**48.0**	V	T
Mitella nuda	0.4 (10)	0.3 (12)	1.3 (18)	**53.4**	I	T
Petasites palmatus	2.0 (17)	1.0 (16)	2.0 (20)	36.9	I	M
Petasites sagittatus	0.1 (1)	0.1 (2)	— (1)	3.7	I	I
Pyrola asarifolia	0.2 (10)	0.4 (11)	0.4 (11)	24.0	V	T
Rubus pubescens	3.0 (20)	4.0 (20)	2.1 (21)	**43.8**	V	T
Saniculua marilandica	0.4 (7)	0.4 (11)	0.2 (3)	22.5	I	M
Smilacina stellata	— (1)	0.1 (4)	0.1 (2)	14.5	V	I
Streptopus roseus	1.2 (14)	1.3 (14)	0.9 (14)	27.8	V	T
Thalictrum venulosum	0.4 (4)	0.2 (3)	0.1 (4)	9.4	I	M
Trientalis borealis	0.3 (10)	0.2 (12)	0.5 (17)	**40.3**	V	T
Viola renifolia	0.3 (5)	0.1 (5)	0.1 (2)	15.1	I	T
Symphoricarpos albus	0.2 (2)	0.6 (5)		**18.7**	V	I
Viburnum trilobum	3.0 (9)	1.1 (7)		**31.2**	S	M
Viola nephrophylla		0.1 (5)	— (2)	**20.1**	I	M
Taraxacum officinale	0.09 (4)			**19.0**	I	I
Vicia americana	0.03 (5)			**23.8**	V, S	I

Note: Shrubs and then herbs listed are alphabetically for each group. A dash represents percent coverage <0.05.
*Values in boldface type are significant (Monte Carlo test, $p \leq 0.10$).
[†]V, vegetative regeneration; S, regeneration from seed bank; I, invading species.
[‡]I, intolerant; M, moderately tolerant; T, tolerant.

Fig. 1. Correspondence-analysis ordination plot of herb and shrub species, showing burned (■), logged (●), and spruce budworm disturbed (▲) stands. The sum of all unconstrained eigenvalues is 1.396. Cumulative percent variance of species data explained by the first four axes is 25.5, 42.0, 54.0, and 63.8.


Fig. 2. Correspondence-analysis ordination plot of herb and shrub species with percent sand and forest-floor depth used as covariables. Burned (■), logged (●), and spruce budworm disturbed (▲) stands are shown. The sum of all unconstrained eigenvalues after covariables are fitted is 1.933. Cumulative percent variance of species data explained by the first four axes is 24.0, 38.5, 50.5, and 61.0.

existing understory vegetation or the forest floor (Qi and Scarratt 1998; Nguyen-Xuan et al. 2000). Consequently, a lower abundance and proportion of persistent species and higher abundance and proportion of invading species continued 10–12 years after fire disturbance.

The post-disturbance light environment may help to explain the lower coverage, and proportion of species richness, of shade-intolerant species on spruce budworm attacked stands. Unlike fires, both logging and spruce budworm outbreaks affect only canopy trees. In the case of spruce budworm outbreaks, only host canopy trees are directly affected. Spruce budworm primarily kills balsam fir, mortality of mature white and black spruce being much lower (Miller 1975; Bergeron et al. 1995). Depending on the pre-disturbance conifer species composition, some stands may have little opening in the canopy, while others may have more open conditions following a spruce budworm outbreak. Also, in contrast to fire and logging, which remove or kill the canopy trees in a very short time, the mortality of canopy trees following a spruce budworm outbreak is much more variable (Lynch and Witter 1985) and requires 4–5 years of heavy defoliation (MacLean 1980; MacLean and Ostaff 1989). Slow opening of the canopy, and therefore a gradual increase in light, allows for species already present to expand their coverage. In contrast, rapid removal of the canopy will favor the generally faster growing shade-intolerant species.

The low impact of logging on the forest floor, coupled with the lower (compared with fire) mortality of existing shrubs at the time of disturbance, and the initially higher (compared with spruce budworm outbreak) understory light intensity, likely enabled the shrubs to expand more abundantly after logging than after either a fire or a spruce budworm outbreak. In contrast, the complete removal of aboveground vegetation by fire created an open environment, which is conducive to the vigorous growth of trembling aspen suckers and other pioneer tree species immediately following the fire. Competition from dense trembling aspen suckers likely limited the development of
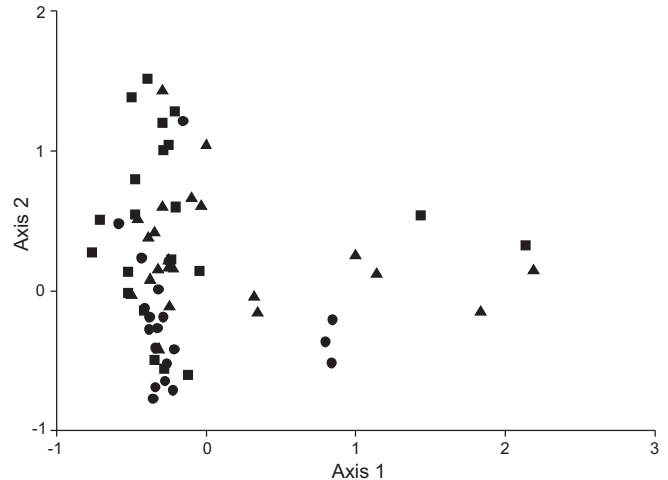
understory plants, especially shrubs, on burned stands. Abundant shrub development following logging relative to fire has been frequently reported elsewhere (Outcalt and White 1981; Carleton and MacLellan 1994; Haeussler and Bergeron 2004). The low shrub coverage on spruce budworm attacked stands likely resulted from lower light conditions due to a combination of slow opening of the canopy and retention of various amounts of residual canopy.

Unexpectedly, we found similar grass coverage and significant differences in moss coverage between the disturbance types. Increased post-disturbance abundance of grasses, particularly *Calamagrostis canadensis*, has frequently been cited as a management problem, especially for conifer regeneration (Eis 1981; Lieffers et al. 1993). In this study, grass coverage was uniformly low across disturbance types. Low grass coverage is likely due to all sampled stands being well drained, coupled with abundant shrub and herb competition. Similarly, Peltzer et al. (2000) found that grass coverage did not greatly increase on naturally regenerating sites that are well drained. With regard to moss coverage, trembling aspen mixedwoods, unlike spruce–fir forests, rarely develop a moss-covered forest floor (Dix and Swan 1971; Zoladeski et al. 1995), especially on well-drained sites. Despite being significantly higher on spruce budworm attacked stands, moss coverage was not evenly distributed but was largely confined to decaying logs and stumps. The difference in moss coverage is best explained by the presence of residual canopy and the greater amounts of decayed wood found on many of the spruce budworm attacked stands.

In contrast to the two natural disturbance types, logging appears to have had a more uniform impact among the sampled stands. Only two logged stands had shrub coverage <50%. Uniformly high shrub coverage is reflected in the lower evenness (*J*) and diversity (*H*) measured on logged stands. Most of the dominant shrubs, particularly *C. cornuta*, are

moderately shade tolerant and persistent species, which accounts for the considerably higher coverage of these groups on logged stands than on burned or spruce budworm attacked stands. Within burned stands, postfire vegetation response is likely affected by fire severity, and great variation in fire severity within and among burned boreal mixedwood stands has been reported (Van Wagner 1983; Nguyen-Xuan et al. 2000; Wang 2002). The heterogeneous nature of fire is reflected in the greater evenness, and thus diversity, at both the stand and the disturbance level compared with logging and spruce budworm outbreaks. For the spruce budworm attacked stands, the differences in predisturbance conifer composition (i.e., density, condition, and species of host trees) resulted in different degrees and rates of post-disturbance canopy opening. In the case of spruce budworm attacked stands, *A. spicatum* was found more abundantly on stands subjected to less canopy mortality, while *Rubus idaeus* was found more abundantly on stands subjected to greater canopy mortality. Osawa (1994) and Lautenschlager (1997) also reported high *R. ideaus* coverage following a severe spruce budworm outbreak.

To minimize the potential confounding effects of possible differences in predisturbance site and stand characteristics, only stands similar in site conditions, age, and predisturbance canopy composition were used in this study. Though no significant differences between the disturbance types were found by ANOVA (likely because of large variation), CCA indicated that forest-floor depth and percent sand did have a significant effect on species ordination. CA ordination with forest-floor depth and percent sand as covariables appears quite different from CA ordination without covariables. However, shrubs dominate the ordination and separate logged stands from burned and budworm-attacked stands in both cases. When percent sand and forest-floor depth are accounted for, spruce budworm attacked stands with high *A. spicatum* coverage are clearly differentiated from the remaining stands, as are burned or logged stands with *A. spicatum* instead of *C. cornuta* dominating the shrub component.

Because of the requirement for matching disturbance age with logging and spruce budworm outbreak, we were only able to sample stands after two fire events. Owing to their extremely large fire size (370 and 242 km^2), our sampled stands would have likely burned on different days or at different times during the day. It can be argued, therefore, that burned stands within such a large area were associated with fires with different characteristics because of differences in fire weather, fuel condition, and their interaction. For the above reason, our study treated the 21 burned stands as replicates. However, we acknowledge that only two particular fire events were sampled in the study, and caution is advised when applying the results of the study to other fire events.

Management implications and conclusion

The most significant finding of the study is that human disturbance (i.e., logging) resulted in less heterogeneity and lower species diversity at both the stand and the disturbance level, and much higher shrub coverage, than did natural disturbances. The rapid development of shrubs on the logged stands within such a short period of time could have significant implications for future forest succession and productivity. Shrubs are important competitors of conifers (Lieffers et al. 1996; Cornett et al. 1997; Beckage et al. 2000), and aggressive shrub development has been blamed for insufficient or no conifer recruitment (Kneeshaw and Bergeron 1996; Galipeau et al. 1997). Given that trembling aspen is short-lived in the region, age-related mortality starting as early as age 55 (Perala 1990), failure of conifers to regenerate under the trembling aspen canopy, or a long delay before they do, could effectively arrest succession (Rowe 1961; Dix and Swan 1971; Carleton and Maycock 1978) and significantly compromise timber productivity. Therefore, corrective silvicultural treatments are needed on these logged stands to suppress the development of shrubs and facilitate that of other species, including conifers.

Post-harvest treatment to control or limit shrub development would likely require chemical tending, as the rapid growth and asexual-regeneration capacity of the shrubs would confound most mechanical-tending alternatives. However, a viable alternative may be harvesting methods that mimic the dynamics of a severe spruce budworm attack, such as a two-pass harvesting system with sufficient canopy retention to delay shrub development. We recommend consideration of a natural insect-outbreak model, rather than fire, for managing boreal mixedwood stands, particularly if they are to be left to regenerate naturally.

Acknowledgments

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