Forest Ecology and Management 258 (2009) 256–262

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Post-fire natural regeneration of young stands on clearcut and partial-cut and uncut sites of boreal mixedwoods

Junlin Li, Qing-Lai Dang *, Titus Fondo Ambebe

Faculty of Forestry and the Forest Environment, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1, Canada

ARTICLE INFO

Article history:
Received 10 September 2008
Received in revised form 3 April 2009
Accepted 9 April 2009

Keywords:
Harvesting
Natural and anthropogenic disturbances
Trembling aspen
Jack pine
Boreal forest

ABSTRACT

Boreal mixedwoods are an important element and the most productive forest type in the Canadian boreal forests. However, they experience frequent disturbances. In order to better understand the responses of boreal mixedwoods to different combinations of anthropogenic and natural disturbances, we investigated the natural regeneration of boreal mixedwoods that were previously subjected to three different harvesting treatments (clearcut, partial-cut and uncut control) and naturally regenerated, but subsequently burnt by a severe natural fire 6 years later. The study was conducted 8 years following the fire. Significant interactions were found among harvesting method, species and block in several regeneration variables. There were a total of 12 woody species (trees and shrubs) regenerated, but not all the species were present in all the sites. In general, the species richness and species diversity of the new stands were lowest on clearcut sites while the differences between partial-cut and control varied with blocks. However, the combined total density for all species was lowest on uncut control sites. Density and regeneration index data show that trembling aspen was the predominant tree species in all stands except at one uncut control site where jack pine was the dominant species. The density of trembling aspen generally declined from clearcut to partial to the uncut control. Pincherry, beaked hazel and mountain maple were the dominant shrub species in the new stands, but no general patterns were found in terms of variations in density with harvesting methods for any of the shrub species. Jack pine and white birch were the tallest tree species in the clearcut treatment while white birch was taller than jack pine in the partial-cut and control. The results suggest that active measures are necessary to restore the complex structure of the initial mixedwoods.

1. Introduction

Mixedwoods are a major component of the boreal forest in Canada (CCFM, 2006). They often experience various natural and artificial disturbances, such as wild fires and harvesting operations (Hannam et al., 2005; Martin and Gower, 2006). Although they can be regenerated artificially following a disturbance, a successful natural regeneration is of great importance ecologically and economically (CCFM, 2006). In general, the regeneration of boreal mixedwoods has been studied extensively (Dix and Swan, 1971; MacDonald et al., 2001; Bell and Newmaster, 2002; Lieffers and Stadt, 2003; Chen and Wang, 2006). However, the previous studies have generally focused on the post-disturbance regeneration of mature stands (e.g., Greene et al., 1999; Chen and Popadiouk, 2002; Johnstone et al., 2004). Because of the long rotation of boreal forests and the frequent occurrence of natural disturbances in the eastern boreal region, such as fires (Greene et al., 1999; Chen and Popadiouk, 2002; Martin and Gower, 2006), the new forest can experience further disturbances at any stage of the stand development. The knowledge on the success rate and species composition of natural regeneration following these further disturbances is critically important for developing long term forest management plans. However, such information is currently not available.

The successful natural regeneration of a tree species following a severe disturbance depends on its means of reproduction, the availability of reproductive materials, and its interactions with other plants. The primary means of regeneration vary with species. Trembling aspen (*Populus tremuloides* Michx.), white birch (*Bettula papyrifera* Marsh.), black spruce (*Picea mariana* (Mill.) BSP.) and jack pine (*Pinus banksiana* Lamb.) are typical pioneer species in the boreal mixedwoods of northwestern Ontario (Messier et al., 1999). Although trembling aspen is capable of reproducing from stump sprouts (Schier et al., 1985) and seeds (Perala, 1990), root suckering is the primary means of natural regeneration (Frey et al., 2003). Suckers are formed from newly initiated meristems

* Corresponding author. Tel.: +1 807 343 8238; fax: +1 807 343 8116.
E-mail address: Qinglaidang@hotmail.com (Q.-L. Dang).

0378-1127/$ – see front matter
doi:10.1016/j.foreco.2009.04.012

and pre-existing primordia (Schier, 1973) when the aboveground part of the tree is destroyed or severely damaged (Eliasson, 1971a, 1971b; Schier et al., 1985). The suckering capacity generally does not vary with tree age (Perala, 1990; Smith et al., 1997). Jack pine and black spruce mainly reproduce from seeds contained serotinous or semi-serotinous cones in northwestern Ontario although black spruce layering is common in other regions (Dix and Swan, 1971; Rudolph and Laidly, 1990; Viereck and Johnston, 1990). White birch, in contrast, can regenerate readily from seeds and sprouts (Safford et al., 1990). Balsam fir (*Abies balsamea* (L.) Mill) and white spruce (*Picea glauca* (Moench) Voss) can regenerate following the establishment of other species (Frank, 1990; MacDonald, 1995; Galipeau et al., 1997). The regeneration of trees is also influenced by the presence and abundance of other plants, such as shrubs. Pincherry (*Prunus pensylvanica* L.fil), Beaked hazel (*Corylus cornuta* Marsh.) and Mountain maple (*Acer spicatum* Lam.) are the common shrub species in the region. Pincherry can recruit swiftly from the soil seed bank and start fast growth following a disturbance (Marks, 1974; Lieffers, 1994). Beaked hazel can regenerate from root suckering, layering or seeds. Mountain maple (*Acer spicatum* Lam.) revitalizes by underground stem sprouting or layering (Haeussler and Coates, 1986).

Harvesting methods affect the diversity and abundance of reproductive materials. Clearcutting stimulates vigorous suckering and sprouting as well as the regeneration from seeds of pioneer species (Perala, 1990; MacDonald and Thompson, 2003). Although partial-cutting also stimulates suckering and sprouting, the species composition of the new stand can be controlled by selecting residual trees to keep and to reproduce and by varying harvest intensity (Frey et al., 2003). Fires, on the other hand, can destroy all the seed sources other than those in serotinous (jack pine) or semi-serotinous (black spruce) cones while having little effect on the suckering capacity. Serotinous and semi-serotinous cones open and release seeds when exposed to fires, often resulting in dense regenerations. However, the degree of effects varies with the severity of the fire (Wang, 2003). Since the seed-bearing capacity varies with tree age, the success rate and species composition of regenerations following a fire are also influenced by the developmental stage of the stand as well as its original species composition.

The Black Sturgeon boreal mixedwoods research program was initiated in 1993 to examine the effects of clear- and partial-cutting on the natural regeneration and ecology of boreal mixedwoods in comparison with uncut stands (Scarratt, 2001). However, some of the sites were burnt by a severe wildfire in May 1999 (Scarratt, 2001). This has created a unique opportunity for investigating the regeneration of forests that have experienced different combinations of anthropogenic and natural disturbances. The objective of this study was to examine the post-fire natural regeneration of stands that were previously clearcut, partial-cut, or uncut. We have focused on the species composition, diversity, density and growth of the new stands. Since young trees with limited or no seed-bearing capacity can produce vigorous root suckers and stump sprouts, we hypothesize that the density of seed-originated trees/species would increase while the proportion of vegetatively regenerated trees or species would decrease from clearcut, partial-cut, to uncut controls. Because the diversity of regeneration sources increases from clearcut to partial-cut to uncut sites, we hypothesize that there would be a corresponding increase in the species diversity in the new stands.

2. Materials and methods

2.1. Study sites

The study was carried out in the Black Sturgeon Boreal mixedwood research sites. The sites are located in the Black Sturgeon River valley (49°11.4′N, 88°42.5′W) approximately 120 km northeast of Thunder Bay, Ontario (Scarratt, 2001). The area lies on a large recessional moraine of glaciofluvial origin, underlain by sedimentary rocks of the Sibley Group and comprises mostly coarse red sand, gravel and shale with variable amounts of silt and small cobbles. The annual mean daily maximum and minimum temperatures are 7.6 and −4.1 °C, respectively, with a daily mean temperature of 1.8 °C. The total annual degree-days above 5 °C and above 0 °C are 1377 and 1678, respectively. On average, there are 101 frost-free days. The length of growing season is between 150 and 160 days. The average annual total precipitation is 831.4 mm, of which 232.2 mm falls as snow (Scarratt, 2001).

The forests in the area resulted primarily from understory saplings, seedlings and suppressed trees of the original stands that were harvested in the 1940s. However, the density of trembling aspen in the new forests was generally greater than in the original stands as a result of vigorous suckering from harvested trees or damaged residual trees (Scarratt, 2001). There were also some regenerations of white birch, white spruce, black spruce, balsam fir and jack pine. Based on the method (%basal area) of Allison et al. (2003), the stands were composed of 30–60% balsam fir, 20–50% trembling aspen, 10–20% black spruce, 10% white spruce, 10% white birch and less than 10% jack pine (Scarratt, 2001). Mountain maple and beaked hazel were the major shrub species.

The Black Sturgeon boreal mixedwoods research project was designed to examine the effects of alternative management practices on the natural regeneration and ecology of boreal mixedwoods (Scarratt, 2001).

The treatments in the Black Sturgeon project consisted of full-tree clearcutting, tree-length clearcutting, full-tree partial-cutting, cut-to-length partial-cutting, full-tree partial-cutting with delimbing at the stump, patch partial-cutting and uncut controls. Harvesting was conducted in the fall of 1993. Clearcutting removed all the merchantable timber while partial-cutting removed about two-thirds of the merchantable timber, leaving a uniform canopy (Scarratt, 2001). Some of the sites were burnt by a severe wildfire in May 1999 (Scarratt, 2001). This provided a unique opportunity for examining the impact of mixed artificial and natural disturbances on the natural regeneration of boreal mixedwoods. However, only the tree-length clearcutting, tree-length partial-cutting with delimbing at the stump and uncut control treatments had replications (2) because other treatments were either not burnt or only one site was burnt. Therefore, our study was restricted to these three treatments. These treatment sites are located in two separate blocks with a complete replication of all three treatments in each block.

2.2. Data collection

The data collection was conducted in August 2007. Ten 50-m^2 circular sample plots (radius 3.99 m) were surveyed at each site. The plots were distributed along three rows (50 m apart): three plots in first row, four in second row and three in third row (≥35 m apart within row and staggered in adjacent rows). The plots were at least 100 m from any edge of the treatment site to minimize edge effects. The height of woody plants of 50 cm or taller was measured and species identified. Species richness was calculated as the number of species in a sample plot. Species diversity (alpha) was calculated by dividing the number of species by the logarithm of total number of individuals in the plot (Kimmins, 2004). Regeneration index reflects the regeneration status and biological importance of a woody species in a site and was calculated as the ratio of the product of density and mean height for a species to the sum of products for all woody species in the plot (Grassi et al., 2004; D'Alessandro et al., 2006).

2.3. Data analysis

All data were examined graphically for the normality of distribution (probability plots for residual analysis) and homogeneity of variance (scatter plots). Since all the data met the assumptions for analysis of variance (ANOVA), subsequent data analyses were carried out without transformation. When ANOVA showed a significant effect ($P < 0.05$), least significant difference (LSD) multiple comparisons were conducted. All the analyses were conducted using Data Desk 6.01 statistical package (Data Description Inc., 1996).

3. Results

3.1. Species richness and species diversity

A total of 12 woody species (height > 50 cm) regenerated after the fire of May 1999: trembling aspen (Po), jack pine (Pj), pincherry (Cp), beaked hazel (Hb), mountain maple (Mm), red-twigged serviceberry (Sr) (*Amelanchier sanguinea* (Pursh) DC.), white birch (Bw), wild red raspberry (Rw) (*Rubus idaeus* L. Var. *Strigosus* (Michx) Maxim.), prickly wild rose (Rp) (*Rosa acicularis* Lindl.), upland willow (Wu) (Salix *humilis* Marsh.), Canada fly honeysuckle (Hc) (*Lonicera canadensis* Bartr.), and black ash (Ab) (Fraxinus *nigra* Marsh.). However, not all the species were present in all the sites. There were significant interactions between harvesting method and block in species richness (Table 1). Block 2 had greater species richness than block 1 in clearcut and uncut control sites (Fig. 1), but the species richness was similar between the two blocks under partial-cut (Fig. 1). Within block 2, the species richness appeared to have increased from clearcut (4.70 ± 0.32) to partial-cut (5.4 ± 0.31) to uncut compartment (6.20 ± 0.25), but the trend was not statistically significant. In block 1, the partial-cut resulted in the greatest species richness in the new stand (6.10 ± 0.62) while clearcut had the lowest species richness (2.90 ± 0.28) (Fig. 1).

The trends for the alpha species diversity were generally similar to those of the species richness (Table 1 and Fig. 1). However, the uncut site in block 2 had significantly greatly species diversity than the corresponding clearcut site (Fig. 1).

Table 1
ANOVA for effects of harvesting method (H), block (B) and species (S) on species richness, species diversity (alpha), stem density, height and regeneration index.

Variable	Source	d.f.	MS	*F*-ratio	*P*
Species richness	H	2	2.05E+01	15.388	0.000
	H × B	2	1.09E+01	8.138	0.001
Species diversity	H	2	4.75E+00	15.714	0.000
	H × B	2	2.35E+00	7.778	0.001
Total stem density	H	2	4.86E+07	3.676	0.032
	H × B	2	1.11E+07	0.841	0.437
Density of individual species	H	2	4.05E+06	2.161	0.116
	H × B	2	9.27E+05	0.495	0.610
	S	11	8.72E+08	465.14	0.000
	H × S	22	7.92E+07	42.245	0.000
	B × S	11	9.05E+07	48.259	0.000
	H × B × S	22	3.93E+07	20.972	0.000
Height of individual species	H	2	1.47E+03	0.954	0.387
	H × B	2	1.48E+04	9.626	0.000
	S	11	9.48E+04	61.483	0.000
	H × S	22	3.74E+03	2.426	0.001
	B × S	11	1.13E+03	0.734	0.692
	H × B × S	22	2.39E+03	1.548	0.132
Regeneration index	H	2	2.22E−06	0	1.000
	H × B	2	1.67E−06	0	1.000
	S	11	2.03E+04	1644.8	0.000
	H × S	22	2.17E+03	175.46	0.000
	B × S	11	1.25E+03	101.13	0.000
	H × B × S	22	1.45E+03	117.42	0.000

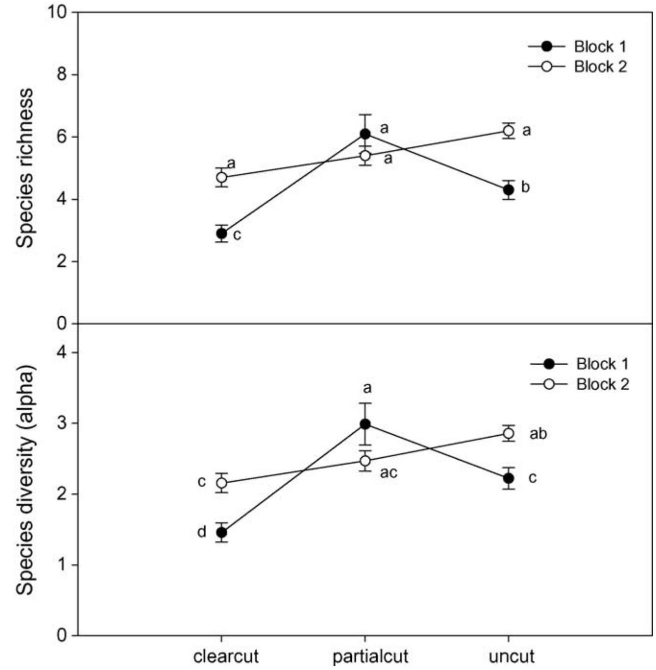

Fig. 1. Post-fire species richness (mean ± SEM, $n = 10$) and alpha species diversity (mean ± SEM, $n = 10$) in relation to harvesting method. The points with the same letter(s) are not significantly different from each other ($P > 0.05$) based on ANOVA LSD post hoc tests.

3.2. Density

The total density of all the woody species was significantly higher in the partial-cut (26670 ± 1478 stem/ha) than the uncut sites (23560 ± 1550 stem/ha), but the difference between clearcut and uncut control sites was not statistically significant (Table 1 and Fig. 2). However, there were significant variations in the density of individual species in response to interactions between harvesting method and block (Table 1). The density of trembling aspen increased from the uncut control to partial-cut and to the clearcut treatment. Additionally, the density of trembling aspen was significantly higher in block 2 than block 1 (Fig. 3). Furthermore, the density of trembling aspen was substantially higher than any other species in all

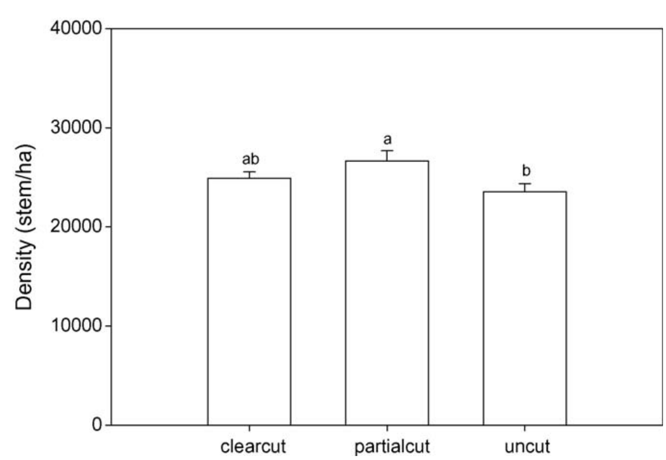

Fig. 2. Relationship between the stem density (mean ± SEM, $n = 20$) of all woody species and harvesting method. Means with same letter(s) are not significantly different from each other ($P > 0.05$) based on ANOVA LSD post hoc tests.

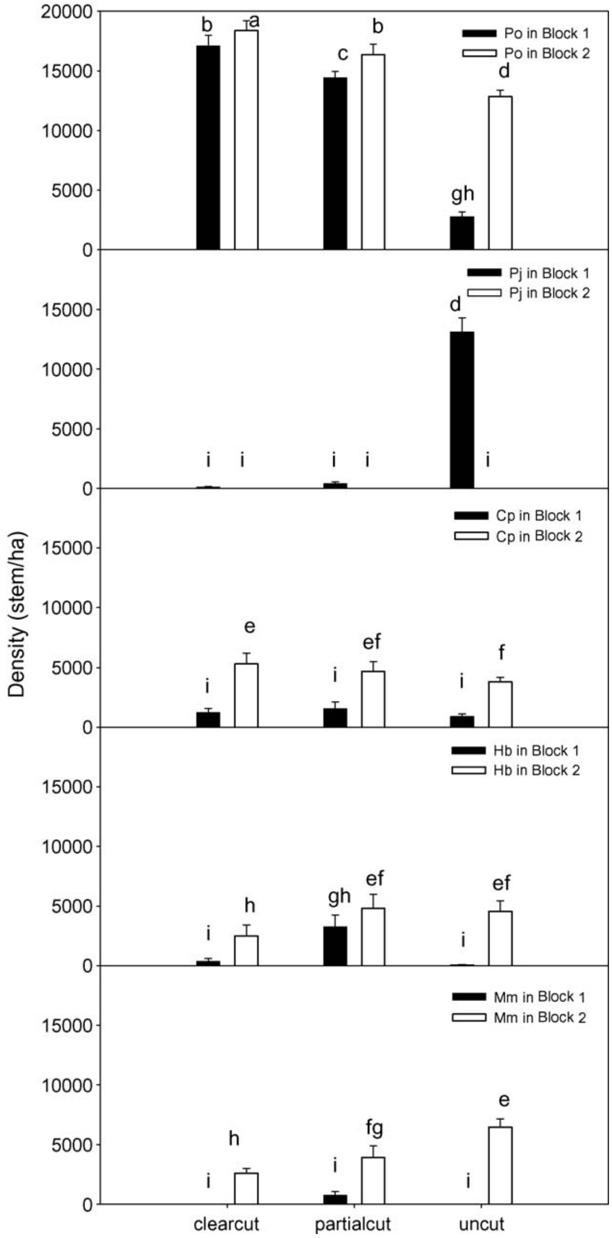

Fig. 3. Stem densities (mean ± SEM, n = 10) of trembling aspen (Po), jack pine (Pj), pincherry (Cp), beaked hazel (Hb) and mountain maple (Mm) in relation to harvesting method. Means with same letter(s) are not significantly different from each other ($P > 0.05$) based on ANOVA LSD post hoc tests.

treatments with the exception of the control site in block 1 where jack pine had the highest density (Fig. 3). Jack pine was present only in block 1. While it had highest density in the uncut control among all species (13100 ± 1186 stem/ha), its densities in the harvested treatments were substantially lower (80 ± 61 stem/ha for clearcut and 380 ± 150 stem/ha for partial-cut, Fig. 3).

Shrub species also responded to the interactions between block and harvesting method. In general, the densities of shrub species were significantly higher in block 2 than in block 1 (Fig. 3). The density of pincherry generally declined from clearcut to partial-cut and to the uncut site in block 2 (5320 ± 887 stem/ha, 4700 ± 814 stem/ha, 3820 ± 377 stem/ha, respectively) while its densities were not significantly different among harvesting treatments in block 1 (Fig. 3).

Beaked hazel had the highest density in the partial-cut site among the three harvesting treatments in block 1 (Fig. 3).

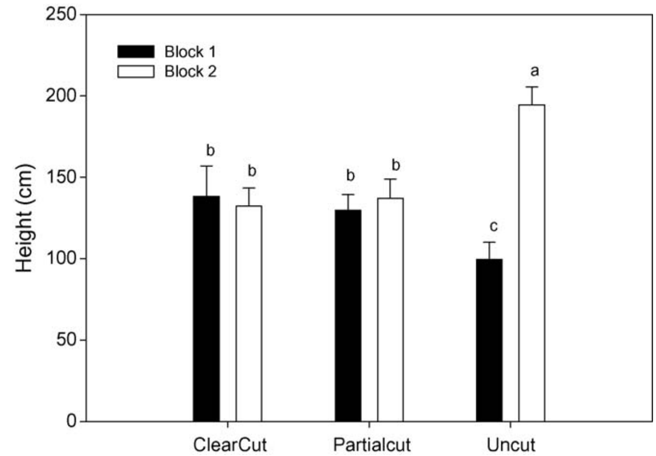

Fig. 4. Height (mean ± SEM, n = 10) of post-fire regeneration in relation to harvesting method. Means with same letter(s) are not significantly different from each other ($P > 0.05$) based on ANOVA LSD post hoc tests.

However, its density was similar in the partial-cut and control sites in block 2 while clearcut resulted in the lowest density (Fig. 3). The density of mountain maple increased from clearcut (2600 ± 384 stem/ha) to partial-cut (3920 ± 948 stem/ha) to uncut (6440 ± 705 stem/ha) in block 2 while there were no significant differences among treatments in block 1 (Fig. 3). The densities of other species (Bw, Sr, Rw, Rp, Wu, Hc and Ab) were very low and not significantly influenced by treatments.

3.3. Height

There were significant interactions affecting the height of regenerations between block and harvesting method and between species and harvesting method (Table 1). The average height was highest in the control site of block 2 but the lowest in the control site of block 1 among all the sites while there were no significant differences among other sites or treatment combinations (Fig. 4). For the interactions between species and harvesting method (Fig. 5), jack pine was tallest in clearcut and shortest in the partial-cut. Trembling aspen was tallest in partial-cut and shortest in the control. White birch was the tallest species in the partial-cut and

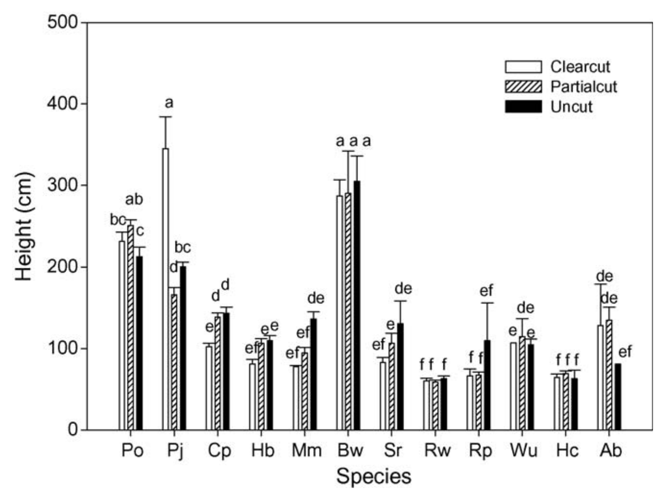

Fig. 5. Height (mean ± SEM, n = 10) of trembling aspen (Po), jack pine (Pj), pincherry (Cp), beaked hazel (Hb), mountain maple (Mm), white birch (Bw), red-twigged serviceberry (Sr), wild red raspberry (Rw), prickly wild rose (Rp), upland willow (Wu), Canada fly honeysuckle (Hc) and Black ash (Ab) in relation to harvesting method. Means with same letter(s) are not significantly different from each other ($P > 0.05$) based on ANOVA LSD post hoc tests.

control while jack pine and white birch were the tallest species in the clearcut. The height of white birch was not significantly among different harvesting methods (Fig. 5). The height of shrub species was generally not significantly different among treatments with the exception of pincherry, the height of which was significantly lower in clearcut than in partial-cut and uncut sites (Fig. 5).

3.4. Regeneration index (RI, %)

There were significant 3-way interactions among harvesting method, block and species on RI (Table 1). Trembling aspen had substantially higher RI than other species in all the sites except the control site in block 1 where the RI of jack pine was substantially higher (Fig. 6). For trembling aspen, RI generally decreased from the clearcut to partial-cut and to uncut control and the decline was particularly steep in the control site of block 1 (Fig. 6). In contrast, there was a huge increase in the RI of jack pine at the control site of block 1 while the RI of the species was very low in all other sites (Fig. 6). The RIs for shrubs were very low and there were generally little variations among harvesting methods. However, there was a small but significant decline in the RI of beaked hazel in the control site of block 1 and a corresponding increase for mountain maple on the same site (Fig. 6). The RIs for other species (Bw, Sr, Rw, Rp, Wu, Hc and Ab) were very low (<2%) and not significantly affected by treatments (data not presented).

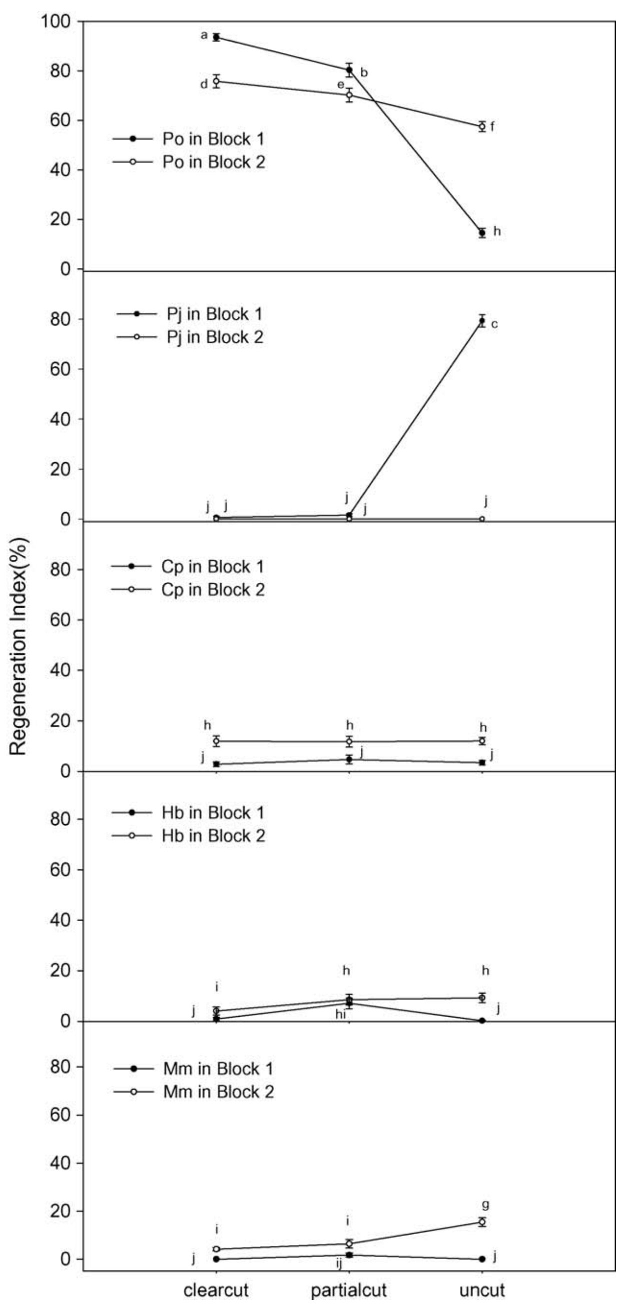

Fig. 6. Regeneration index (mean ± SEM, n = 10) of trembling aspen (Po) jack pine (Pj), pincherry (Cp), beaked hazel (Hb) and mountain maple (Mm). Means with same letter(s) are not significantly different from each other ($P > 0.05$) based on ANOVA LSD post hoc tests.

4. Discussion

Our data partially support the hypothesis that there would be an increase in the species diversity in the new stands from clearcut to partial-cut to uncut sites. Both species diversity and species richness were lowest in the clearcut among the three harvesting treatments, for example, the species diversity in the partial-cut of one block was almost 3 times as high as the corresponding clearcut. The differences in species diversity and richness between partial-cut and control, however, were much smaller and varied with blocks. The substantial decline in species diversity and richness associated with clearcutting can have enormous implications to the structure and functioning of the forest ecosystem. The decline in woody species diversity could be translated into a reduction in habitat diversity for wildlife and consequently in the diversity of ecosystem functions. Silvicultural measures may be necessary in order to restore the more complex structure of the original mixedwood, such as planting more shade tolerant trees under the canopy of the young stands.

Our data support the hypothesis that the density of seed-originated trees or species would increase while the proportion of vegetatively regenerated trees or species would decrease from clearcut, partial-cut, to uncut controls. The root suckers of trembling aspen declined in density from the clearcut to partial-cut and to the uncut control. The decline was particularly substantial at the control site in one of the blocks where there was a sharp increase in the density of jack pine which only regenerates from seeds. This trend for the density of trembling aspen suckers is consistent with the findings of Mulak et al. (2006). Although the results appear to suggest that the suckering capacity might have declined with tree age, the total root stocking within the top soil layer was probably the key controlling factor. The suckers of trembling aspen generally originate from roots of 0.8–1.8 cm diameter distributed within the top 8 cm of the soil (Davidson et al., 1989). The heavier fuel loads in the control and partial-cut sites could have also resulted in greater fire intensity, causing root damages and reducing suckering. The results of this study have important implications on the stand development trajectory and species composition of boreal mixedwood stands following multiple disturbances. While seed-origin species can regenerate following a clearcut with a resultant stand of mixed species, a subsequent major disturbance before the seed-origin species reach a seed-bearing age can eliminate the species from the stand. However, our growth data suggest that artificial seeding or tree planting will be effective in restoring the mixedwood stand structure. For example, the jack pine that regenerated from seeds following the fire was almost as tall as trembling aspen root suckers 8 years after the fire and there were no signs of being over-competed by root suckers of the same cohort.

It is very interesting to note the relative dominance of pincherry in the understory community. Although it was only one of the three dominant understory woody species, its very different silvical characteristics make its presence somewhat surprising. Pincherry is an understory avoider and seed banking is the main mechanism to maintain its population on the site after canopy closure (Lieffers, 1994). When the canopy is opened up, it can regenerate aggressively from the soil seed bank (Wendel, 1990; Lieffers, 1994). Because we did not observe any significant differences in the density of pincherry among harvesting treatments, it is not unreasonable to assume that the amount of pincherry seeds in the soil seed bank was similar among the treatments. Since pincherry was not present in the stands in 1993 when the treatments were applied (Scarratt, 2001), it is likely that the pincherry seeds in the soil were produced prior to the stand regeneration in the 1940s. Pincherry seeds in soil seed banks can remain viable for as long as 50–150 years (Wendel, 1990). Beaked hazel and mountain maple, in contrast, are understory tolerant species, which grow best in open conditions but are able to persist in the understory of many stands (Lieffers, 1994). Their aggressive colonial habit made them expand rapidly after fires. Mountain maple sprouts from underground lateral stems (Krefting et al., 1956) while beaked hazel regenerates from its root suckers (Haeussler and Coates, 1986).

While similar general patterns of regeneration response were observed in the two blocks, there were significant interactions between block and harvesting treatment. For example, both stem density and regeneration index for trembling aspen declined from clearcut to partial-cut to control, but the magnitude of differences between treatments varied substantially with blocks. Jack pine was the dominant species only in the control treatment of one block, but not in the other block. The interactions were also reflected in the parameters for understory species. The differences in the response were largely attributed to differences in the initial stand conditions between the two blocks. For example, the initial abundance for trembling aspen and jack pine was 50% and 14%, respectively, in block 1 while the corresponding numbers were 61% and 1% in block 2 (Scarratt, 2001). Those differences were further exacerbated by the application of the harvesting treatments. For example, the abundance became 40% for trembling aspen and 8% for jack pine in block 1 while the corresponding numbers for block 2 were 50% and 0%, respectively, following the partial-cut which removed about two-thirds of the merchantable timber and retained a uniform canopy in both blocks (Scarratt, 2001). These results suggest that the operation guidelines should be modified if preserving species diversity is an objective for the partial harvesting of boreal mixedwoods. For example, a certain minimum density of species with a small initial abundance should be retained to ensure the effective regeneration of the species following the harvesting.

Stem density and regeneration index data show the same trend for the species composition of the new stands in this study. Trembling aspen will be the dominant species in all but one stand which will be dominated by jack pine. These two groups of stands will most likely follow different stand development trajectories. The two parameters show the same trend because there were only few tree species in the new stands and little differences in the height of those species. However, cautions must be exercised in parameter selections in more complex situations. For instance, density data will be misleading if the species with high density has a slower growth rate. On the other hand, regeneration index numbers can be misleading if the species with highest index is short-lived. In general, the regeneration index should be more useful for projecting the future structure of the stand, but it should be considered in conjunction with the silvical characteristics of all the species that are present.

There are some factors that are important to regeneration but could not be considered in this research because of lack of data, such as fire severity and aerial seed banks. Fire severity can significantly affect regeneration density and growth of trembling aspen suckers (Wang, 2003). Presumably there were differences in fuel load among clearcut, partial-cut and uncut treatments and consequently in fire severity, which could have influenced the amount of regeneration. Therefore, any effect that fire severity might have had cannot be differentiated from other effects associated with harvesting treatments. The factor of aerial seed source was intentionally excluded from the study by setting sample plots at least 100 m away from nearby trees. Some species, such as white spruce and balsam fir, were abundant prior to the harvest treatments in 1993. They had the potential to regenerate in areas that were within the seed dispersal range from the seed source.

Acknowledgements

The authors greatly appreciate the comments on the thesis version of the manuscript by Dr. Han Chen of Lakehead University, and Drs. D. Reid and D. Morris from the Centre for Northern Forest Ecology Research. We also thank Mr. A. Camerson for his assistance in arranging the field work of the project and Dr. C. Shahi for advice on statistical analysis. Lastly, but not the least, we want to thank two anonymous reviewers for their constructive and very useful comments on the earlier version of the manuscript. The project was funded by Graduate Student Assistantships to J.L. and NSERC grants to Q.L.D.

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