POST-FIRE NATURAL REGENERATION OF YOUNG STANDS ON CLEARCUT, PARTIAL-CUT AND UNCUT SITES OF BOREAL MIXEDWOODS:

Fire NIP 10 Burned Stands Regeneration Analysis

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It is made available for loan by the faculty for the purpose of advancing the practice of professional and scientific forestry.

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ABSTRACT

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Boreal mixedwoods are an important element and the most productive forest type in the Canadian boreal forests. This research focused on the regeneration of stands burned by an intense wild fire in Black Sturgeon Boreal Mixedwoods on former clearcut, partial-cut and uncut compartment. Species diversity, density, regeneration index and height of regenerations were examined. A total of 12 species regenerated across the three different harvesting operations. In general, the regeneration species richness in clearcut compartment was the lowest among the three harvesting operations, but the differences between partial-cut and uncut compartment varied. Regeneration was dominated by trembling aspen and jack pine. The total density of all regeneration species was higher in harvested compartment than uncut control compartment. The density and regeneration index of trembling aspen had a regeneration trend of decreasing from clearcut to partial-cut to uncut, while the opposite was true to jack pine. Trembling aspen, jack pine and white birch formed the main canopy of the new stands while pin cherry, beaked hazel and mountain maple dominated the understory layer. White spruce, black spruce and balsam fir failed to regenerate in the burned clearcut, partial-cut and uncut compartment of this boreal mixedwoods.

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INTRODUCTION

Boreal mixedwoods are a major component of the boreal forest in Canada (CCFM 2006). The successful natural regeneration of boreal mixedwoods is important both ecologically and economically. Effects of disturbances (e.g. fires, harvesting, and the outbreak of insects and diseases) on the natural regeneration of boreal mixedwoods has been studied extensively over three decades (Dix and Swan 1971; MacDonald et al. 2001; Bell and Newmaster 2002; Lieffers and Stadt 2003). However, most of the studies have focused on the post-disturbance regeneration of mature stands (Greene et al. 1999; Chen and Popadiouk 2002; Johnstone et al. 2004). The effects of stand age and species composition at the time of disturbance on regeneration are not well understood.

The primary means of regeneration are different among species. Trembling aspen (*Populus tremuloides* Michx.), white birch (*Bettula papyrifera* Marsh.) and jack pine (*Pinus banksiana* Lamb.) are typical pioneer species in the boreal mixedwoods of northwestern Ontario (Messier et al. 1999). After a fire, trembling aspen generally regenerates quickly from root suckers, although it can also regenerate from stump sprouts (Schier et al. 1985) and seeds (Perala 1990). Suckers can originate from newly initiated meristems, pre-existing primordia, or suppressed short shoots (Schier 1973) on roots of trees from one-year-old seedlings to mature trees (Perala 1990). Root suckers are formed when the transportation of auxin from leaves to roots is interrupted, such as following harvesting operations or severe fires (Eliasson 1971a; Eliasson 1971b; Schier et al. 1985). Fire severity significantly affects the density and growth of trembling aspen suckers in the first year, but not in the second or third year following a fire (Wang 2003). Jack pine and black spruce (*Picea mariana* (Mill.) BSP.), on the other hand, mainly reproduce from seeds released from serotinous or semi-serotinous cones that open in response to high temperatures, such as that caused by fires (Dix and Swan 1971; Rudolph and Laidly 1990; Viereck and Johnston 1990). White birch regenerates from seeds and stump sprouts (Safford et al. 1990). In contrast to those pioneer species, balsam fir (*Abies balsamea* [L.] Mill) and white spruce (*Picea glauca* [Moench] Voss) generally regenerate from seeds under a forest canopy (MacDonald 1995). Balsam fir seeds are disseminated up to 60 meters from the mother tree by wind (Frank 1990; Galipeau et al. 1997; Chen and Popadiouk 2002). White spruce seeds can travel as far as 70 meters (Frank 1990; Galipeau et al. 1997; Greene and Johnson 2000; Chen and Popadiouk 2002). Understory species have different strategies to regenerate after a disturbance. For example, pin cherry (*Prunus pensylvanica* L.fil) can recruit from the soil seed bank (Marks 1974), and its seeds in the soil can remain viable for 50 to 150 years (Wendel 1990). Pin cherry as an understory avoider species (Lieffers 1994) regenerates well from its soil seed bank following the removal of the forest canopy. Beaked hazel (*Corylus cornuta* Marsh.)

regenerates from its root suckers, and mountain maple (*Acer spicatum* Lam.) revitalizes by underground stem sprouting or layering (Haeussler and Coates 1986).

Fire is the most common natural disturbance in the boreal forests (Greene et al. 1999; Chen and Popadiouk 2002; Martin and Gower 2006). Regeneration rate of dominant tree species is the highest in first 5 years after a fire, and no additional recruitment is observed after 10 years (Johnstone *et al.* 2004). The population of white and black spruce is relatively stable during the first decade following a fire while the density of trembling aspen declines (Johnstone *et al.* 2004).

The Black Sturgeon Boreal Mixedwoods Research Program was established in 1993 to examine the effects of clearcut and partial-cut harvesting operations on regeneration and other ecological aspects of boreal mixedwoods. The harvesting operations were conducted from October to December of 1993. The clearcut and partial-cut compartment were regenerated naturally. However, most of the experimental compartment including uncut control compartment were burned by a severe wildfire in May 1999 (Scarratt 2001), which created an opportunity for investigating the natural regeneration of forests with different ages and densities caused by different harvesting operations.

The objective of this study was to examine the species diversity, density and growth of regenerations that established after the fire on clearcut, partial-cut and uncut compartment. I hypothesize that the density of jack pine regeneration would increase from clearcut to partial-cut and to uncut compartment as the density of seed bearing trees increases, the density of trembling aspen regeneration would decline from clearcut to partial-cut to uncut compartment as root density decreases, and the species diversity would increase from clearcut to partial-cut and to uncut compartment as the density of overstory species declines.

LITERATURE REVIEW

Natural regeneration of the boreal mixedwoods is a consequence of interaction of the boreal mixedwood species, environmental factors and disturbances. It is the act of replacing old trees (and damaged trees) naturally. In almost all forest regions, natural regeneration and development of new stands proceeds either from already established survivors, or from the germination of seeds (Smith et al. 1997). In other words, natural regeneration is regrowth that occurs naturally after stress or disturbance. It may be developed from seeds of both pioneer and permanent species, and from lignotuber or rootstock (Temple and Bungey 1980). In order to better understand the regeneration of boreal mixedwoods following disturbances, it is essential to understand definition of boreal mixedwood, regeneration sources, the environment influence on regeneration and effects of disturbances on regeneration. To prepare experiment design, background information of the Black Sturgeon Boreal Mixedwood Research Project is needed. This review focuses on: (1) Definitions of boreal mixedwood, disturbance and natural regeneration, (2) sources of the natural regeneration of boreal mixedwoods after fire, (3) environmental effects on natural regeneration, (4) effects of disturbances on the natural regeneration of boreal mixedwoods, (5) Black Sturgeon Boreal Mixedwood research compartment.

Definitions of boreal mixedwoods, disturbance and natural regeneration

Boreal mixedwoods are a complex system due to their disturbance histories, site types, stand structures and successional dynamics. The definition of boreal mixedwoods is important for communicating between scientists and practitioners (Chen and Popadiouk 2002). I will use the definition of a boreal mixedwoods proposed by MacDonald (1995) that considers boreal mixedwoods to occur at "site", "stand" and "forest" scales. A boreal mixedwood site is an area with climatic, topographic and edaphic conditions that favour the production of closed canopies dominated by trembling aspen, or white birch in early successional stages, black spruce or white spruce in mid-successional stage, and balsam fir in late successional stages. It is often difficult, expensive (and sometimes impossible) to maintain a pure stand composed of a single species because mixedwood sites tend to have favorable conditions for a variety of species (Smith et al. 1997). A boreal mixedwood stand is a tree community on a boreal mixedwood site in which no single species comprises more than 80% of the total basal area. A boreal mixedwood forest is the aggregation of all boreal mixedwood sites in any distinct area (MacDonald 1995). Boreal mixedwoods are more productive and resistant to damage than pure stands, and they are attractive and support a wider diversity of wildlife (Man and Lieffers 1999).

Disturbances are temporary changes in environmental conditions that cause pronounced changes of forests. Disturbance forces often act quickly and with great effect, sometimes resulting in the removal of large amounts of biomass (Dale et al. 2001). Fires, windstorm , ice storms, snow breakages, insects and diseases outbreaks are major natural disturbances (Chen and Popadiouk 2002). Harvesting operations and introduction of exotic species are major anthropogenic disturbances in forest. such as clearcut harvesting operation of stands and the introduction of new species (Dale et al. 2001).

Natural regeneration is the process of naturally replacing trees are old (Smith et al. 1997) or damaged or destroyed by disturbances . The regeneration period begins when preparatory measures start, and it ends when young trees are dependable established in acceptable numbers. Regeneration can arise from any source—that is, from new seedlings, advance regeneration, sprouts, planted stock, or combinations of all of these. Natural regeneration sources include seeds or spores spread by wind, water, or animals. In almost all forest regions, natural regeneration and development of new stands proceeds either from already established survivors, or from the germination of seeds (Smith et al. 1997). Natural regeneration is reproduction from self-sown seeds or by vegetative recovery (sprouting from stumps, lignotubers, rhizomes or roots) after disturbances, since the tops of the plants have been damaged (by fire, cutting, browsing, etc) (Cremer 1990). In other words, natural regeneration is re-growth that occurs naturally after stress or disturbance. It may be developed from seeds of both pioneer and permanent species, and from lignotuber (e.g. Eucalyptus spp.), rootstock (e.g. Melaleuca spp.), etc; remaining under the ground. (Temple and Bungey 1980). In comparison, artificial regeneration involves planting seedlings and/or direct seeding to re-establish vegetation following disturbance. Regenerating trees artificially is usually a human activity by hands or machines, which assists and speeds up the natural process of forest creation.

Sources of the natural regeneration in boreal mixedwoods after fire

Both seeds and vegetative materials are regeneration sources of the boreal mixedwoods after fire. The regeneration sources used in boreal mixedwoods are different by various boreal mixedwood species. The most common tree species in boreal mixedwoods (MacDonald 1995; Scarratt 2001) are: white spruce (*Picea glauca* [Moench] Voss), black spruce (*Picea mariana* [Mill.], BSP), balsam fir (*Abies balsamea* [L.] Mill.), trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera* Marsh.). Secondary species common in boreal mixedwoods include: jack pine (*Pinus banksiana* Lamb.), white pine (*Pinus strobes* L.), red pine (*Pinus resinosa* Ait.), eastern hemlock (*Tsuga Canadensis* [L.] Carriere), eastern white cedar (*Thuja occidentalis* L.), tamarack (*Larix laricina* (Du Roi) K. Koch), largetooth aspen (*Populus grandidentata* Michx.), balsam poplar (*Populus balsamifera* L.), black ash (*Fraxinus nigra* Marsh.), and white elm (*Ulmus Americana* L.) (MacDonald 1995; Scarratt 2001). Trembling aspen, white birch and jack pine are pioneer overstory species that regenerate quickly after disturbances (Dix and Swan 1971; Rudolph and Laidly 1990; Messier et al. 1999). Pin cherry, beaked hazel and mountain maple are the main understory shrub species that typically occur in association with these overstory species in the Great Lakes regions (Kurmis and Sucoff 1989; Wendel 1990). The main shrub species in boreal mixedwoods are: Beaked hazel (*Corylus cornuta* Marsh), Mountain maple (*Acer spicatum* Lam.), Prickly wild rose,(*Rosa acicularis* Lindl.), Bush honeysuckle (*Diervilla Lonicera* Mill.), Dwarf raspberry (*Rubus pubescens* Raf.), Wild red current (*Rubus idaeus* L.), Red osier dogwood (*Cornus stolonifera* Michx.), Saskatoon serviceberry (*Amelanchier alnifolia* Nutt.), Twinflower (*Linnaea borealis* L.), High bush cranberry (*Viburnum trilobum* Marsh.), Choke cherry (*Prunus virginiana* L.), Downy arrow-wood (*Viburnum rafinesquianum* Schultes), willow (*Salix* sp.), Wild gooseberry (*Ribes hirtellum* Michx.), Skunk currant (*Ribes glandulosum* Grauer), Hudson Bay currant (*Ribes hudsonianum* Richards.), Bristly black currant (*Ribes lacustre* (Pers.) Poir.) (Baldwin and Sims 1997; Kemball et al. 2005)

Different tree species of boreal mixedwoods have different strategies to reoccupy burned compartment; vegetative suckers (aspen), seeds (jack pine, black spruce), or sprouts (white birch) can support abundant regeneration after fire (Eberhart and Woodard

1987; Hill and Morris 1992; Weir and Johnson 1998). After disturbances, early regeneration tree species include both hardwoods and conifers. These pioneer species that establish following a fire are typically shade intolerant species (Kimmins 2004).

Trembling aspen

Trembling aspen suckers are most productive source in the early stage of natural regeneration of boreal mixedwoods, though trembling aspen seeds can be regeneration source. Suckers are the main source of trembling aspen regeneration after fire disturbance (Horton and Maini 1964), because roots below the surface 4-12 cm are usually undamaged, which supply suckers with sufficient nutrients at least the first year after fire (Perala 1990; Peterson and Peterson 1992). The plant hormone regulates sucker formation. The main components acting as regulator for sucker initiation are cytokinnin and auxin, which are produced by roots and shoots. It is the higher ratio of cytokinnin to auxin that stimulates suckering. Disturbances, such as fire or harvesting operations, damage or remove shoots, which cut off the way of transportation of auxin to roots, so the ratio of cytokinnin to auxin goes up, therefore, suckering is promoted (Schier 1973; Schier et al. 1985; Perala 1990; Peterson and Peterson 1992). After sucker initiation, trembling aspen regeneration density and growth depend on root carbohydrate reserves, soil temperature, root damage, and vegetation competition (Graham et al. 1963; Horton and Maini 1964; Perala 1990; Greene et al. 1999). One year trembling aspen seedling is already capable of suckering. These root suckers are major source of trembling aspen regeneration after disturbances (Perala 1990; Groot et al. 1997; Greene et al. 1999). Root suckers originate from newly initiated meristems, preexisting primordia , or suppressed short shoots (Schier 1973). In the first year after disturbance, aspen sucker density can reach 250,000 stem/ha in the north-central U.S. (Frey et al. 2003a). Trembling aspen produces seeds annually beginning at age 2 or 3, but the optimum age is 50 to 70, and a 23-year-old trembling aspen tree may produce 1.6 million seeds (Perala 1990). The viability of trembling aspen seeds is high, however, it only lasts a short duration. If favorable conditions are reached, trembling aspen seeds can germinate one or two days after dispersal. however, trembling aspen is mainly regenerated by means of vegetative reproduction (Perala 1990).

Jack pine and black spruce

Regeneration of black spruce and jack pine following a fire is typically from seeds released from serotinous or semi-serotinous cones (Dix and Swan 1971; Rudolph and Laidly 1990). Jack pine's serotinous cones have physiologically adapted the post fire regeneration, but jack pine seedlings cannot survive from fire (Rudolph and Laidly 1990). Viable seeds in jack pine cones can be released many years after fire (Dix and Swan

1971). Jack pine begins to flower at 5 to 10 years old. Jack pine seed viability reduces significantly after 5 to 10 years (Rudolph and Laidly 1990). Seed viability of jack pine and black spruce is only affected when cones are heated to their ignition temperature (Greene and Johnson 1999). Jack pine rarely reproduces by vegetative means under natural conditions, and regenerating from seeds in jack pine's serotinous cones is the major means to reproduce (Rudolph and Laidly 1990). Jack pine begins to flower at very young age. Female flowering takes place at 12 months under near optimum growing conditions in the greenhouse or nursery, but male flowering begins until the fourth year (Rudolph 1979a; Rudolph 1979b). Black spruce cones remain partially closed and disperse seed for several years (Viereck and Johnston 1990); these semiserotinous cones provide seeds that may remain viable for as long as 25 years. Black spruce seedlings may be reproduced by layering, whereby mosses cover the lower branches of black spruce tree, and the covered branch takes roots and becomes a new seedlings or saplings (Stanek 1975). Germination rates of black spruce and jack pine were very low the initial summer of the fire.There was a peak in recruitment in the first post-fire summer, and then by the fourth year, the recruitment declined to nearly zero (Charron and Greene 2002).

White birch

White birch regenerated from both seeds and sprouts (Safford et al. 1990).

Though white birch regenerates from its sprouts, the amount of reproduced sprouts often hardly bears enough seedlings to reproduce mature stands (Marquis et al. 1969). Newly germinated white birch seedlings are very fragile because of its small seed size, and the seedlings are very sensitive to moisture, temperature, sunlight and seedbed conditions. For example, in full sun light site, only 50% white birch germinates as it in shaded compartment (Safford et al. 1990).

White spruce and balsam fir

White spruce and balsam fir mainly regenerate from their seeds. White spruce can be reproduced by layering and it is a way of maintaining the stand when sexual reproduction is limited; however, naturally, sexual reproduction is white spruce's major means of reproduction (Nienstatedt and Zasada 1990). Balsam fir, like white spruce, also can be reproduced by layering, but it is not an important means of regeneration, the major regeneration source is from seeds (Bakuzis and Hansen 1965; Frank 1990)

White spruce initial regeneration affects its delayed regeneration. Peters, et al. (2006) studied initial patterns versus delayed regeneration of white spruce in boreal mixedwoods. They found that seven out of 20 stands were dominated by initial regeneration, six were dominated by delayed regeneration, and seven were even-aged mixtures of trembling aspen and white spruce. Dominance of a site by initial or delayed regeneration could not be simply explained by burn timing relative to mast years or distance to seed source; they suggested that fire severity and the competitive influence of initial regeneration on delayed regeneration were important at fine scales (Peters et al. 2006).

Pin cherry

Pin cherry is regenerated from its seeds and root suckers (Wendel 1990). Pin cherry seeds usually remain their viability quite a long time buried in the soil, where pin cherry once grew (Wendel 1990). Pin cherry seeds viable number is from 345,000/ha to 494,000/ha, and they may keep their viability as long as 150 years buried in forest floor (Marks 1974; Graber and Thompson 1978; Wendel 1990).

Beaked hazel and mountain maple

Shrub species regenerate from both seeds and vegetative materials. Beaked hazel sprouts from its root crown and also layer, and its sprouting promoted by disturbances, such as fire, heavy browsing and mechanical damage (Yerkes 1960). Mountain maple regenerates from its seeds and underground stems, however, suckering is not a major means to regeneration (Krefting et al. 1956) .

Environmental effects on natural regeneration

Natural regeneration of boreal mixedwoods is influenced by environmental factors. These factors include soil types, forest floor, microclimate, nutrient availability and microsite. Soil types can influence height growth significantly, for example, trembling aspen, black spruce, and jack pine grew taller on clay soils than sandy soils (Martin and Gower 2006) .Diameter growth decreased as competition increase for black spruce and jack pine in the burned stands as usual (Martin and Gower 2006). Forest floor differences may cause regeneration differences. Hannam et al. (2005) examined a trembling aspen / white spruce forest floor using cross-polarization magic-angle spinning ^{13}C nuclear magnetic resonance spectroscopy (CPMAS^{13}C NMR), and found that clearcut compartment became more humified. Nevertheless, there was no differences in the chemical properties of the forest floors between clearcut and uncut compartment of trembling aspen and white spruce in northern Alberta (Hannam et al. 2005). Nutrient availability in boreal mixedwoods and vegetation establishment were more strongly controlled by forest floor disturbance than by partial canopy retention (Frey et al. 2003b). Optimum growth of spruce and pine seedlings can be achieved by clearcut and frequent weeding (MacDonald et al. 2004), but scalping prior to planting has been shown to provided no benefit (MacDonald and Thompson 2003). Frequent weeding may not be an acceptable option for producing integrated species mixtures because of associated declines in stocking, growth, and quality of hardwood crop trees (MacDonald and Thompson 2003).

Seedbed types are another reason for regeneration differences. Charron and Greene (2002) examined jack pine, black spruce and white spruce establishment on different seedbeds. They found that seedbeds of mineral soil, thin *Polytrichum* Hedw. moss, and humus are more favorable than the organic fermentation and/or litter. They noticed that the first year of a cohort has the highest rate of mortality, about 85% on mineral and humus seedbeds and 98% on organic fermentation seedbeds, differences in age-specific survivorship between seedbeds become muted by the end of the second year, and survivorship rates approach 1 by the end of the third summer (Charron and Greene 2002).

Seed germination and seedling survival are related to the depth of organic layer and distance from seed source. Purdy et al. (2002) examined white spruce regeneration in aspen dominated mixedwoods 1 year, 2 years, 4 years, 6 years and 14 years after fire. At the tree plot scale, presence of white spruce seedlings 1-year post-fire could be reliably predicted by organic layer depth and distance to seed source. None of the biotic or abiotic factors measured were strongly correlated with occurrence or density of white spruce seedlings 6- and 14- years post-fire. At the microsite scale, seedling recruitment immediately post-fire was limited to a distinct subset of available microsites. Seedling occurrence in older burns was associated with distinct microsite conditions. Less than 3% of seed sown 1 year post-fire survived to become 1-year-old germinants, survival was 41% over the next three years. Availability of suitable regeneration microsites declines rapidly with time-since-fire, less than 0.3% of seed sown 4 years post-fire survived one year (Purdy et al. 2002).

The different quality of seedbeds is the results of the diversity of soils on boreal mixedwood sites. Spruce germination is up to five times higher on till than on clay deposits. Balsam fir shows a similar trend, but even more important for this species is the distance to the unburned forest edge (Galipeau et al. 1997). Paper birch never produces as many seedlings on fine textured soils as on coarser substrates (Weir and Johnson 1998). Soil condition affects regeneration for a longer time than the duration of the stage of stand development (DeLong et al. 1997). Exposure can also be an important factor during the regeneration process. Young tender trees may suffer from late spring frost damage because open areas experience larger amplitudes in daily temperature. Among boreal mixedwood species, white spruce has been frequently reported as susceptible to frost damage (Cole et al. 1999). Although white birch tolerates even the coldest north and east aspects (Safford et al. 1990), repeated frosts cause seedlings to grow as shrubs on these sites because dormant root collar buds are forced to form new shoots in addition to the parent stem (Perala and Alm 1990).

Effects of disturbances on the natural regeneration of boreal mixedwoods

Disturbance is an important factor of natural regeneration in boreal mixedwoods. Forest ecosystems have evolved to cope with, and recover from, most natural disturbances including outbreaks of insects and diseases, or wildfires (CCFM 2006). Some of these disturbances, such as wildfires in the boreal forest, even play a key role in forest renewal. This relationship between forests and disturbances has been ongoing for ages, allowing forests to renew themselves and maintain their productivity (CCFM 2006).

Disturbances not only influence the overstory of boreal mixedwoods, but also greatly influence many understory species of boreal mixedwoods, which has been largely attributed to vegetative regeneration. 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 regeneration, and 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 (Kemball et al. 2005).

Fire is not the only stand-replacing disturbance in the boreal forest; other disturbances such as windstorms, snow breakages, ice storms, insects and diseases outbreaks may also initiate new stands, but these different disturbances may lead to different regeneration processes (Frelich and Reich 1999). Spruce budworm and tent caterpillar (*Malacosoma disstria*) are the most aggressive and widespread defoliators in boreal mixedwood forests(Ghent 1958; MacLean 1985; Morin et al. 1993; Archambault et al. 1998; Cameron et al. 1999). Nealis and Ortiz (1996) found that significant mortality of balsam fir appeared only after 10 years of heavy defoliation by spruce budworm. Insect outbreaks usually lead to stand replacement only when followed by a severe fire (Stocks and Walker 1973).

The regeneration process is determined by the type and severity of disturbance. An intensive stand-replacing fire often eliminates most of the existing vegetation. Increased light availability from light fires favors late successional species by providing a favorable light environment and seedbed conditions. Light fires may reshape understory composition by eliminating nontree vegetation (Day and Harvey 1981). Stand-replacing fire, severe fire, is the most important factor of rejuvenating mixedwood stands (Ritchie 1976; Tolonen 1983; Wein and MacLean 1983; Bergeron and Harvey 1997; Larsen and MacDonald 1998)

Regeneration rates are different as the time passing after disturbances. Johnstone et al. (2004) reported recruitment rates of dominant tree species were highest in the first 5 years after fire, and additional net establishment was not observed after 10 years (Johnstone et al. 2004). The postfire population of spruce (*Picea mariana* [Mill.] BSP and *Picea glauca* [Moench] Voss.) remained constant after the first decade in their study areas.

Populations of aspen (*Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) both declined after 10 years in mixed-species stands. Mortality rates of aspen and pine were positively correlated with their initial densities, indicating that thinning occurred as a density-dependent process (Johnstone et al. 2004).

The timing of a disturbance in relation to the seed crops and the growing season is also important in affecting regeneration. The timing of a fire during the growing season can also affect regeneration. Substantial variations exist in site conditions because of the wide variation in climate, topography, slope, aspect, exposure, parent material, soil texture, depth and type of organic matter, and associated soil physical, chemical, and microbial properties. These variations determine the availability of essential resources for the plant community, which are solar radiation, temperature, soil moisture, nutrients, aeration, and microbial communities. They not only affect productivity and diversity of boreal mixedwoods (Chen et al. 1998), but also the process of stand development (Oliver and Larson 1996; Galipeau et al. 1997) During regeneration, niche separation gives a competitive advantage for one plant species over another, corresponding to different levels of resources availability (Oliver and Larson 1996).

Predisturbance stand composition determines the regeneration composition. Birch becomes dominant after a fire if birch was a major component of the old stand, and aspen will more likely dominate the new stand if it dominated the old stand. Shade-intolerant tree species such as aspen, birch, jack pine, and lodgepole pine will comprise the new stand in the same proportion as their basal area in the old stand (Greene and Johnson 1999; Greene et al. 1999; Greene and Johnson 2000).

Harvesting operations are artificial disturbances to forests. Harvesting operations inevitably impacts advance regeneration directly by physically disturbing seedlings that are already established in the understory, and indirectly by altering the microenvironment. Harvesting operations may cause stress to the small trees that have developed under lower light conditions because removal of the overstory dramatically alters their light environment. Clearcutting often has a dramatic effect on the survival and thus the abundance of advanced regeneration following the disturbance (Greene et al. 1999). Based on their researches, MacDonald et al. (2004) did not recommend that partial cutting to promote conifer advance regeneration on boreal mixedwood sites by post-harvest height comparisons among conifers, hardwoods, and shrubs. Meanwhile, maintaining a viable understory of shade-tolerant conifers for the next rotation may be more feasible than promoting conifer–hardwood overstories (MacDonald et al. 2004). They suggest that if the objective is to favour growth of hardwood regeneration, then the harvesting operation should remove the entire overstory.

Harvesting operations may cause regeneration in boreal mixedwoods shift to hardwoods. Ball and Walker (1997) reported the effects of partial cutting after 37-39 years of white spruce regeneration in mixedwood stands. Their results confirm that current cutting practices in boreal mixedwoods are causing a shift to hardwoods. All of the cutting treatments illustrate the ease of renewing hardwoods compared to the difficulty renewing white spruce, with the exception of poor results arising from no disturbance. None of the cutting treatments came close to producing adequate white spruce regeneration on unscarified seedbeds(Ball and Walker 1997). MacDonald (2000) compared four harvesting methods to find the effects on regeneration of boreal mixedwood stands. The harvesting methods are: 1) 50% partial-cut without removal of residuals; 2) 50% partial-cut with residuals removed after 3 years; 3) clearcut; and 4) uncut. Careful logging practices minimized damage to the site and residual trees, that is trees were moved vertically in the cutting head from the stump to the skid trail, machine movement and turning on the cut blocks were controlled, and some trees were left along the skid trails as rub posts. All trees were cut as close to the ground as possible, except where cutting high would prevent damage to adjacent uncut trees. Therefore, partial cutting using careful logging to protect residual trees and advance regeneration is recommended as an option for increasing the conifer component. The important tool to control understory species composition and regeneration performance is canopy manipulation, which affects the performance of understory species by altering microclimatic factors such as light intensity and soil temperature (MacDonald 2000). Navratil *et al.* (1994) reported damage of stand conditions. Clear-cut harvesting resulted in 2-16 % of the immature spruce stems being left undamaged after harvesting on the control block with no attention was giving to the protection of immature spruce. In dense stands that restricted equipment entry, a relatively high level of 16% immature spruce was protected. 40 - 61% of the immature spruce stems were protected when conventional feller-bunchers and grapple skidders were used. 21-30 % of the immature spruce stems were left undamaged with the cut-to-length harvesting equipment (Navratil et al. 1994).

Harvesting operations cause some loss of seedlings that may be a source of regeneration. Youngblood (1990) reported a loss of up to 80% of the seedlings during harvesting operation. After harvest, stocking is more important than density in assuring an effectively regenerated stand. Youngblood (1990) also reported less damage to white spruce seedlings in areas where a uniform shelterwood was removed by a cable yarding system than where a ground-based system was used. His work showed that damage to advance regeneration during the process of harvesting could be reduced by properly designing the harvesting system and choosing the proper season for harvesting operations (Youngblood 1990). Hardwood stems also decreased following cutting, but their abundance relative to the conifer species was found to increase. Hardwoods have the advantage of being able to sprout from the basal bud bank after a disturbance and, unless the bud bank is destroyed, will maintain themselves in spite of fairly severe disturbance(Greene et al. 1999)

Regeneration of black spruce responds to different harvest methods relating to harvesting operation means and sizes. Regeneration seedlings were more evenly distributed in first strip-clearcut sites than large clearcut sites. About 10000 more black spruce seedlings per hectare and 20% more of stocking were observed in strip- clearcut strips sites compared to large clearcut sites (Pothier 2000). Natural regeneration of lowland black spruce forests after three harvest methods: careful logging around advanced growth (CLAAG), group seed tree (GST), and group seed tree followed by shearblading site preparation (SHE), had been studied by Chen and Wang (2006). Total density of black spruce regeneration does not differ among harvest methods (but height structure of black spruce regeneration does. The CLAAG method results in highest total regeneration density of other conifers. Decreasing density of other conifers from the CLAAG to GST to SHE sites indicates that the CLAAG method protects advance regeneration as expected and the SHE method removes advance regeneration in the path of the shearing blade. Black spruce and other conifer regeneration densities increase with increasing time since harvest. Stocking of black spruce, all conifers, or all tree species neither does not differ significantly among harvest methods, nor change with time since harvest. Stocking is nonlinearly relating to regeneration density (Chen and Wang 2006).

Black spruce regeneration responds differently to harvesting operations relating to harvest intensity.

White spruce regeneration is affected by harvesting operations. Wurtz and Zasada (2001) reported abundant white spruce natural regeneration after both clear cutting and shelterwood cutting that takes place with a large seed crop, though natural regeneration is often rarely adequate to produce well-stocked white spruce dominated stands after a stand-replacing disturbance (Wurtz and Zasada 2001).

Partial-cut may not achieve its goal of balance between biodiversity maintenance and continued timber production because of its high post-harvesting mortality, so regeneration benefits of partial-cut may not be dependable. Residual trees after partial-cut are physically damaged inevitably (Thorpe and Thomas 2007). Windthrow damaged rates reached up to 17% of residual basal area in partial-cut sites of an Ontario mixedwood stand (MacDonald and Thompson 2003). Because of the lost of residual trees, partial harvest treatment (partial-cut) should be considered a failure if the residual tree mortality rate progresses beyond 10% (Coates 1997).

After disturbances of clearcuts and wildfires, differences caused by these two different disturbances are evident. Clearcut sites had deeper organic matter accumulations and more woody debris; wildfire sites had more variability in vegetation and soil disturbance severity. Clearcut sites had more residual conifers (balsam fir, white spruce and black spruce) and tall shrubs (mountain maple and beaked hazel); wildfire sites had higher density of aspen suckers, seedling (Haeussler and Bergeron 2004).

Black Sturgeon Boreal Mixedwood Research Project

The Black Sturgeon Boreal Mixedwood Research Project was established in 1993. It concerns issues of forest ecosystem management and the impacts of forestry practice. One of three main components is evaluate the ecological impacts and responses to harvesting operations. The project aim is to gain a better understanding of the complex ecological relationships that exist within boreal mixedwood ecosystem.

Black Sturgeon Boreal Mixedwood research site is a second-growth forest, which originated from the forest that had been harvested in the 1940s (Scarratt 2001). This second-growth forest is composed of trees that used to be the understory saplings and suppressed seedling when harvest operations had been performed. Harvesting operations were conducted on 14 compartments following the project experiment design (Scarratt 2001). After those harvesting operations, trembling aspen were able to increase its density through suckering from the harvested or damaged mother trees. Meanwhile, some white birch, white spruce, black spruce, balsam fir and jack pine regenerated forming the second growth mixedwood, which was composed of 30-60% balsam fir, 20-50% trembling, 10-20% black spruce, 10% white spruce, 10% white birch and less than 10%

jack pine (Scarratt 2001).

Fire and spruce budworm were two major disturbances that devastated Black Sturgeon Boreal Mixedwood forest periodically. There was a spruce budworm outbreak in 1993-1994, which created ideal conditions for wildfire (Scarratt 2001). It was at this time that the Black Sturgeon Boreal Mixedwood Research Project (BSBMRP) was established. Three harvesting operations were conducted to examine the effects of different harvesting operations; clearcut, partial-cut and patch cut. These harvesting operations were carried out from October to December 1993 (Scarratt 2001)

Following the harvesting operations, trembling aspen, jack pine and balsam fir and white birch regenerated naturally. However, most of the Black sturgeon Boreal Mixedwood research sites were burned (Scarratt 2001) in May 1999 by a severe wildfire, which named Nipigon fire 10 (NIP 10). The fire was lasted 4 days and burned 50,000 ha of forest. Since then, new regeneration established naturally on the previously treated areas.

MATERIALS AND METHODS

Study sites

The study was carried out in the Black Sturgeon Boreal Mixedwood Research sites. These sites are situated in the Black Sturgeon River valley approximately 120 km northeast of Thunder Bay, Ontario (Figure 1). They are located within the Central Block of the Black Sturgeon Limits licensed to Bowater Inc. of Thunder Bay. Centered on latitude 49°11.4'N and longitude 88° 42.5'W, the site is bisected by the western boundary of Adamson Township, running northwards from its intersection with the main Black Sturgeon logging road (Scarratt 2001).

Harvested in the 1940s, Black Sturgeon Boreal Mixedwood forest was a second-growth forest, which was composed by trees that used to be the understory saplings/seedlings and suppressed trees at the time of harvesting. Trembling aspen was subsequently able to increase its density through suckering from the harvested or damaged residuals. Some regeneration of white birch, white spruce, black spruce, balsam fir and jack pine also occurred. Relative abundance was calculated as the percent density of all stems in the sample plots (Allison et al. 2003). The species composition of the second growth forest was 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 two abundant shrub species before harvesting. The coverage of mountain maple was 36%, 22.7% and 56.8%, respectively for the clearcut, partial-cut and uncut compartment and the coverage of beaked hazel was 11.45%, 19.15% and 15.25%, respectively (Scarratt 2001).

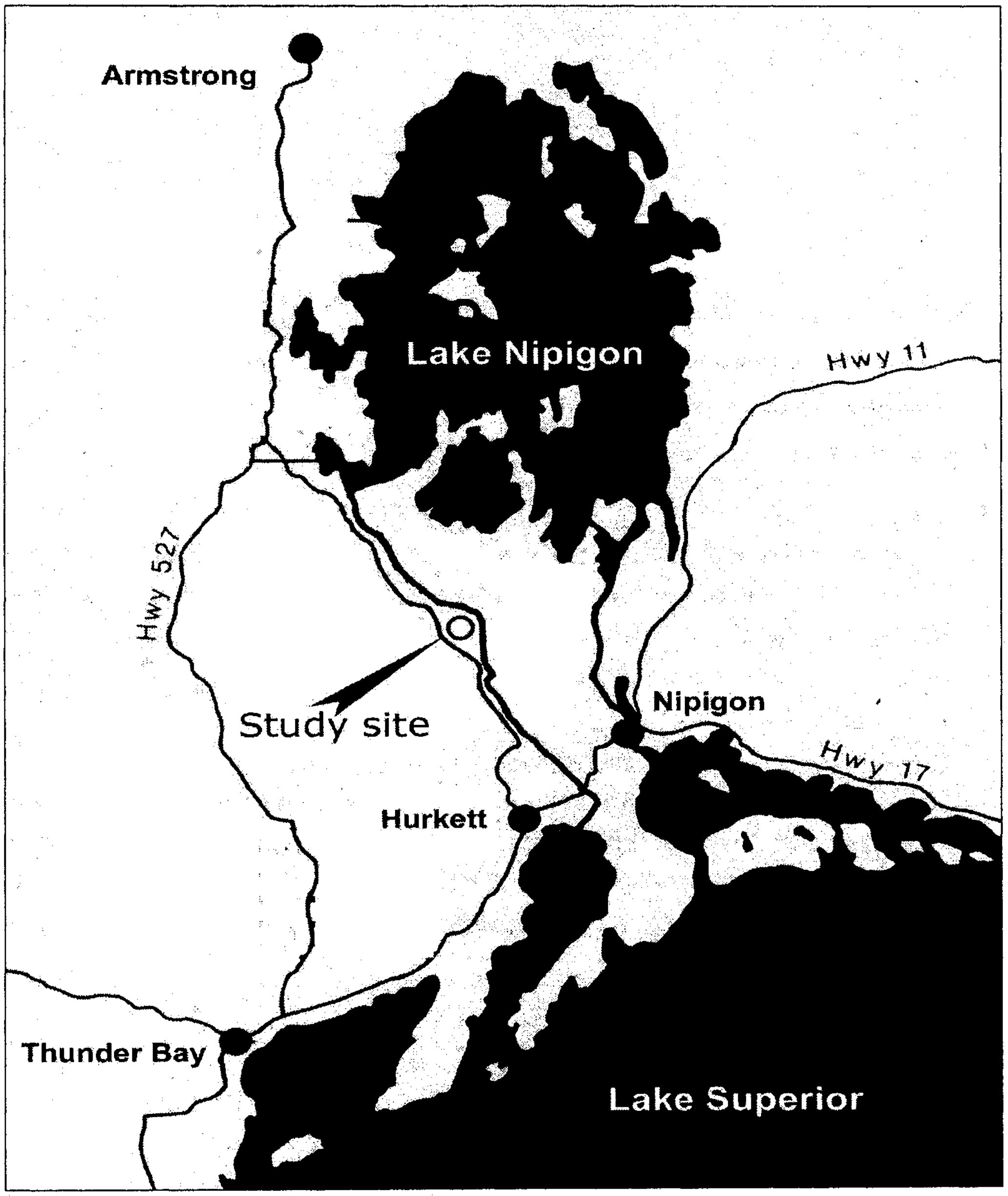

Figure 1. Location of the study site.

Compartment # 5, 6, 7, 9, 12 and 13 of the Black Sturgeon Boreal Mixedwood Research Project were chosen for this study. These were two replicates for each of the harvesting treatments: clearcut, partial-cut and uncut control. The two replicates were separated by a road (Figure 2). Each harvest operation compartment measures 315 x 320 m (10 ha). These compartments were part of the compartments established by Black Sturgeon Boreal Mixedwood Research Project in 1993 to examine long-term ecosystem responses to disturbances and silvicultural manipulations in second-growth mixedwood stands (Scarratt 2001). These compartments were the experiment units of this study. The harvest operations were conducted from October to December 1993. Clearcut removed all merchantable timber and partial-cut removed about two-thirds merchantable timber, retaining a uniform canopy of good quality trembling aspen with a scattered white spruce trees (Scarratt 2001). These six compartments contained two replicates for each harvesting treatment (Figure 2). All these compartments were burned by a severe fire in May 1999, called Nipigon fire 10. The fire severity in all compartments was within the same class, "severely burned" class (Wang 2003).

The study area lies on a large recessional moraine of glaciofluvial origin, underlain by sedimentary rocks of the Sibley Group and comprises mostly coarse red sands, gravels and shales with variable amounts of silt and small cobbles. The area has the annual mean daily maximum and minimum temperature at 7.6 and -4.1 °C, with a daily mean temperature of 1.8°C. The total annual degree-days above 5 °C is 1377 with 1678 degree-days below 0 °C. On average, there are 101 frost-free days. The average annual total precipitation is 831.4 mm, of which 232.2 mm falls as snow. The length of growing season is between 150 and 160 days (Scarratt 2001).

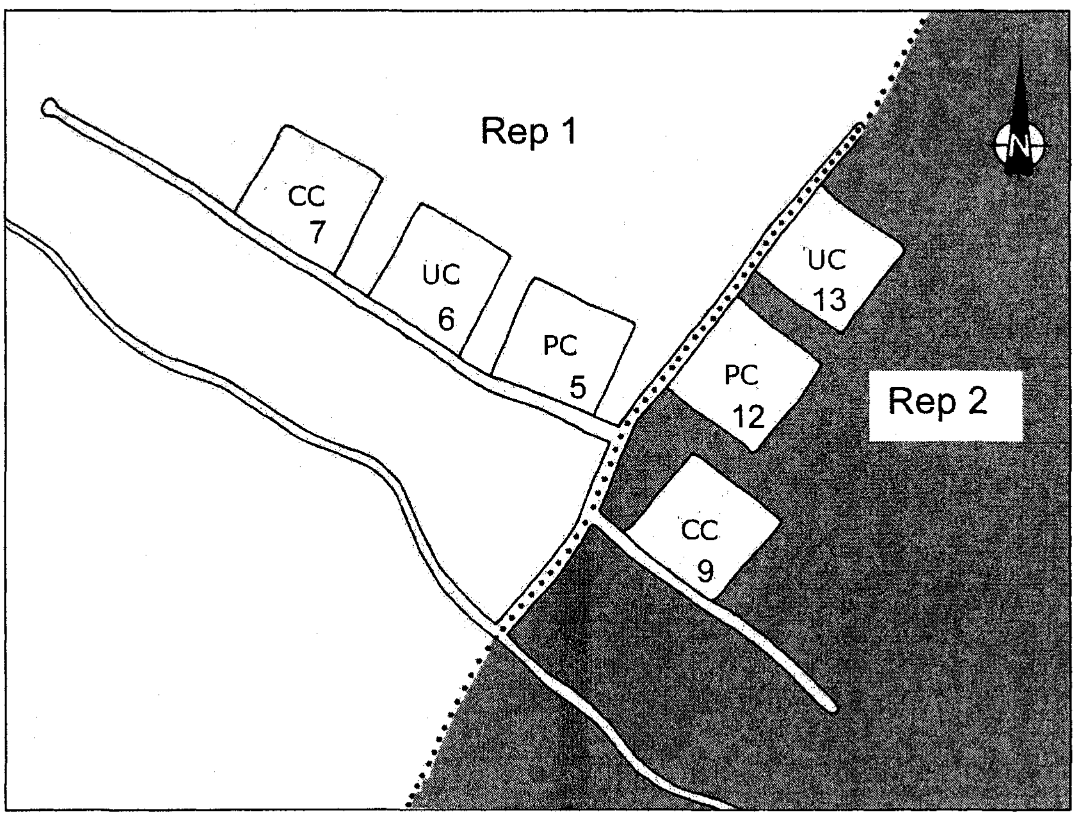

Figure 2 Location of replicate and harvesting operation of clearcut (CC), partial-cut (PC) and uncut (UC). The number 5, 6, 7, 9, 12, and 13 are compartment number of experiment design used in Black Sturgeon Boreal Mixedwood Research Project.

Data collection

Regeneration surveys were conducted on all six compartments in August, 2007. Ten 50-m^2 circular plots (radius at 3.99 m) were surveyed in each compartment. The sampling plots were distributed along three rows at 50 m apart: three plots in the first row, four plots in the second row and three plots in the third row. The sampling plots were at least 35 meters away from each other and at least 100 meters from any edge of the compartment to avoid the influence of edge effect (Figure 3). The height of all plants taller than 50 cm was measured and species identified. Species richness was calculated as the number of species presented in a sample plot. Species diversity (alpha) was calculated as the number of species presented in a sample plot divided by the logarithm of total number of individuals in the sample plot (Kimmins 1987; Kimmins 2004).

$$d = \frac{S}{LogN} \qquad (1)$$

where d is the species diversity (alpha), S is the number of species in a sample plot, N is the total number of individuals in the sample plot.

Regeneration index (RI) reflects the regeneration status of a species. This integrated indicator was calculated as the ratio of the product of density and mean height for a species to the sum of products for all species present in a sampling. Important value (IV) of the species is a product of density and mean height of a species in a certain area

(Runkle 1981; Chen et al. 2006). Regeneration index for each species was calculated as follows for each sampling plot (Grassi et al. 2004; D'Alessandro et al. 2006):

$$RI_i = \frac{IV_i}{IV_{all}} \times 100\% \qquad (2)$$

$$IV_i = H_i \times D_i \qquad (3)$$

$$IV_{all} = \sum_{i=1}^{n} (H_i \times D_i) \qquad (4)$$

where RI_i is the regeneration index for a species, IV_i is important value of the species in a plot (Runkle 1981; Chen et al. 2006); IV_{all} is the important value of all species combined, H_i is the mean height of a species; D_i is the stem density of a species in the plot, n is the number of species.

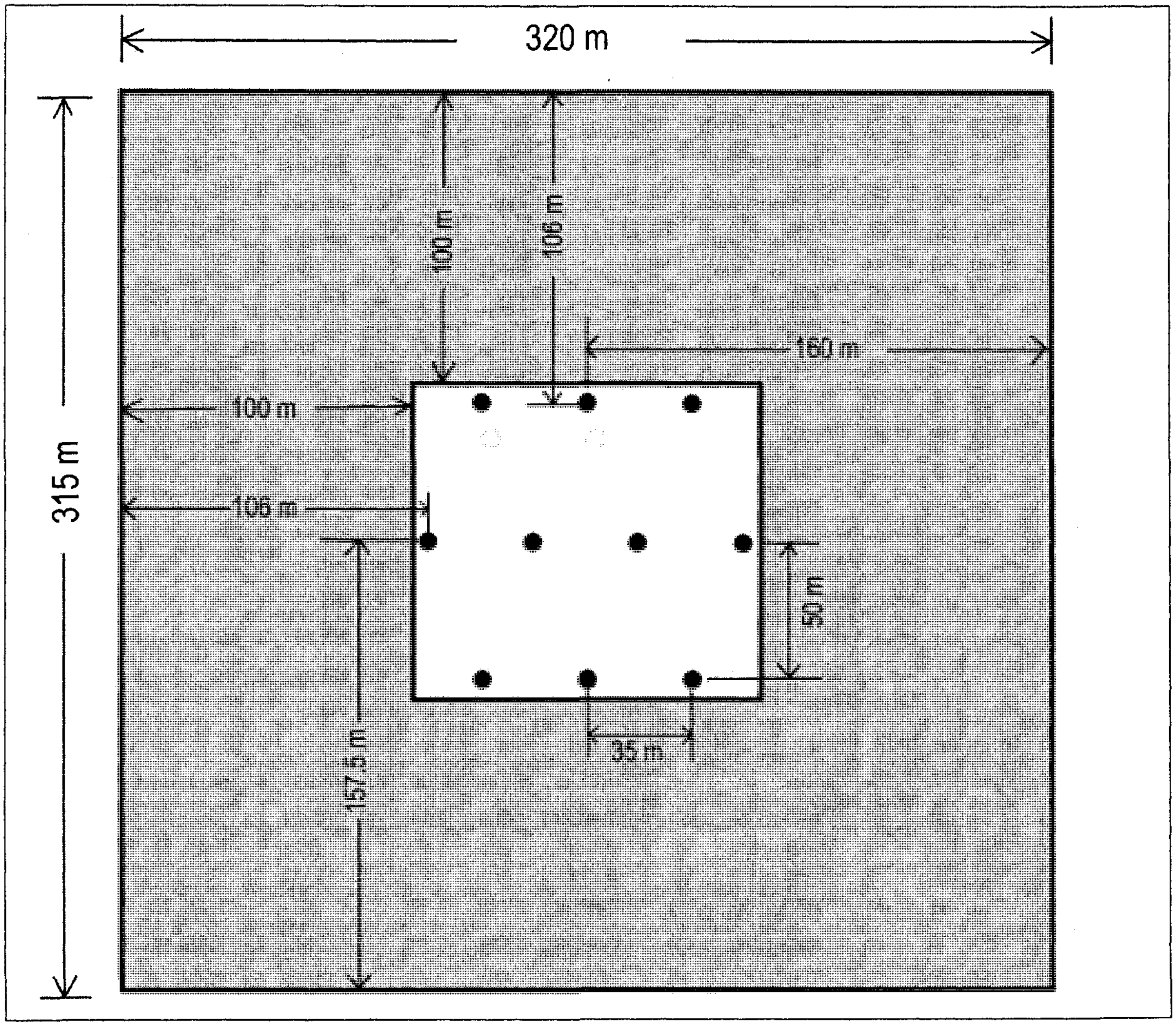

Figure 3. Distribution of sample plots in a harvesting operation site.

Data analysis

All data were examined for the normality of distribution and homogeneity of variance using Data Desk 6.0. When ANOVA showed a significant effect ($P < 0.05$), LSD multiple comparisons were conducted. This experiment was a randomized complete block design (RCBD). The following linear model was used for analyzing species richness, species diversity and total stem density of all species.

$$Y_{ijk} = \mu + H_i + R_j + HR_{ij} + \varepsilon_{(ij)k} \qquad (5)$$

. $i = 1, 2, 3; j = 1, 2; k = 1, 2, 3 \ldots 10$

Where

Y_{ijk} = species richness or diversity or total density of k^{th} plot in j^{th} replicate of i^{th} harvesting operation

μ = the grand mean

H_i =harvesting operation

R_j = replicate

HR_{ij} = interaction between harvesting operation and replicate

$\varepsilon_{(ij)k}$= random error within H and R combination

The expected mean squares for each of the term in equation 5 are given in Table 1.

Table 1. EMS for Linear Model 5

Source of variation	df	EMS	Test statistic
H_j	2	$\sigma^2+20\Phi_{(H)}$	MS(H)/MS(ε)
HR_{ij}	2	$\sigma^2+10\Phi_{(SH)}$	MS(HR)/MS(ε)
$\varepsilon_{(ij)k}$	54	σ^2	

To understand possible differences in regeneration behaviors among individual species and interactions between species and harvesting operation, the following linear model was used for analyzing density, height and RI when species was considered as a factor.

$$Y_{ijk} = \mu + H_i + R_j + HR_{ij} + S_k + HS_{ik} + RS_{jk} + HRS_{ijk} + \varepsilon_{(ijk)l} \qquad (6)$$

. i = 1, 2, 3; j = 1, 2; k = 1, 2, 3… 12; l=1, 2, 3, …, 10

Where Y_{ijkl} =density, or height or RI;

μ = the grand mean;

Hi = harvesting operation;

R_j =replicate;

HR_{ij} = H-R interaction;

S_k = species;

HS_{ik} = H-S interaction;

RS_{jk} = R-S interaction;

HRS_{ijk} = three –way interaction;

$\varepsilon_{(ijk)l}$= random error within treatment combinations.

The expected mean squares for the above model are given in Table 2.

Table 2. EMS for Linear Model 6.

Source of variation	df	EMS	Test statistic
H_j	2	$\sigma^2+240\Phi_{(H)}$	MS(H)/MS(ε)
HR_{ij}	2	$\sigma^2+120\Phi_{(SH)}$	MS(BH)/MS(ε)
S_k	11	$\sigma^2+60\Phi_{(P)}$	MS(S)/ MS(ε)
RS_{ik}	11	$\sigma^2+30\Phi_{(SP)}$	MS(BS)/ MS(ε)
HR_{jk}	22	$\sigma^2+20\Phi_{(HP)}$	MS(HS)/ MS(ε)
HRS_{ijk}	22	$\sigma^2+10\Phi_{(SHP)}$	MS(BHS)/ MS(ε)
$\varepsilon_{(ij)k}$	648	σ^2	

RESULTS

Species richness and alpha species diversity

A total of 12 species regenerated across the experimental area after the fire of May 1999, but not all the species were present in all the compartments. The regeneration species were trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), pin cherry (*Prunus pensylvanica* L. fil), beaked hazel (*Corylus cornuta* Marsh.), mountain maple (*Acer spicatum* Lam.), red-twigged serviceberry (*Amelanchier sanguinea* (Pursh) DC.), white birch (*Betula papyrifera* Marsh.), wild red raspberry (*Rubus idaeus L. Var. Strigosus* (Michx) Maxim.), prickly wild rose (*Rosa acicularis* Lindl.), upland willow (Salix *humilis* Marsh.), Canada fly honeysuckle (*Lonicera canadensis* Bartr.), and black ash (Fraxinus *nigra* Marsh.). There were significant interactions between harvesting operation and replicate on regeneration species richness (Table 3). In general, replicate 2 had greater regenerated species richness than replicate 1(Table 3, Figure 4). Replicate 2 showed a general increase in regeneration species richness from clearcut (4.70±0.32) to partial-cut to uncut compartment (6.20±0.25). In replicate 1, however, the largest regeneration species richness was in the partial-cut (6.10±0.62) compartments and lowest under clearcut compartments (2.90±0.28) (Figure 4).

Table 3. ANOVA for effects of harvesting operation (H), replicate (R) and species (S) on the number of regeneration species, stem density, height and regeneration index.

Variable	Source	df	SS	MS	F-ratio	Prob
Species richness	H	2	4.10E+01	2.05E+01	15.388	0.000
	H*R	2	2.17E+01	1.09E+01	8.138	0.001
	Error	54	7.20E+01	1.33E+00		
	Total	59	1.50E+02			
Species diversity (alpha)	H	2	9.50E+00	4.75E+00	15.714	0.000
	H*R	2	4.70E+00	2.35E+00	7.778	0.001
	Error	54	1.63E+01	3.02E-01		
	Total	59	3.16E+01			
Density of all species together	H	2	9.72E+07	4.86E+07	3.676	0.032
	H*R	2	2.23E+07	1.11E+07	0.841	0.437
	Error	54	7.14E+08	1.32E+07		
	Total	59	2.56E+09			
Density	H	2	8.10E+06	4.05E+06	2.161	0.116
	H*R	2	1.85E+06	9.27E+05	0.495	0.610
	S	11	9.59E+09	8.72E+08	465.14	0.000
	H*S	22	1.74E+09	7.92E+07	42.245	0.000
	R*S	11	9.95E+08	9.05E+07	48.259	0.000
	H*R*S	22	8.65E+08	3.93E+07	20.972	0.000
	Error	648	1.21E+09	1.87E+06		
	Total	719	1.46E+10			
Height	H	2	2.94E+03	1.47E+03	0.954	0.387
	H*R	2	2.97E+04	1.48E+04	9.626	0.000
	S	11	1.04E+06	9.48E+04	61.483	0.000
	H*S	22	8.23E+04	3.74E+03	2.426	0.001
	R*S	10	1.13E+04	1.13E+03	0.734	0.692
	H*R*S	9	2.15E+04	2.39E+03	1.548	0.132
	Error	238	3.67E+05	1.54E+03		
	Total	295	1.99E+06			
Regeneration Index	H	2	4.44E-06	2.22E-06	0	1.000
	H*R	2	3.33E-06	1.67E-06	0	1.000
	S	11	2.24E+05	2.03E+04	1644.8	0.000
	H*S	11	4.77E+04	2.17E+03	175.46	0.000
	R*S	22	1.38E+04	1.25E+03	101.13	0.000
	H*R*S	22	3.19E+04	1.45E+03	117.42	0.000
	Error	648	8.01E+03	1.24E+01		
	Total	719	3.25E+05			

Species diversity (alpha) had the same trend as species richness did. There were higher alpha species diversity in partial-cut compartment of both replicate 1 and 2 and uncut compartment of replicate 2. There were no significant difference among clearcut and partial-cut compartments in replicate 2 and uncut compartment of replicate 1. The lowest alpha species was present in clearcut compartment of replicate 1 (Table 3, Figure 4).

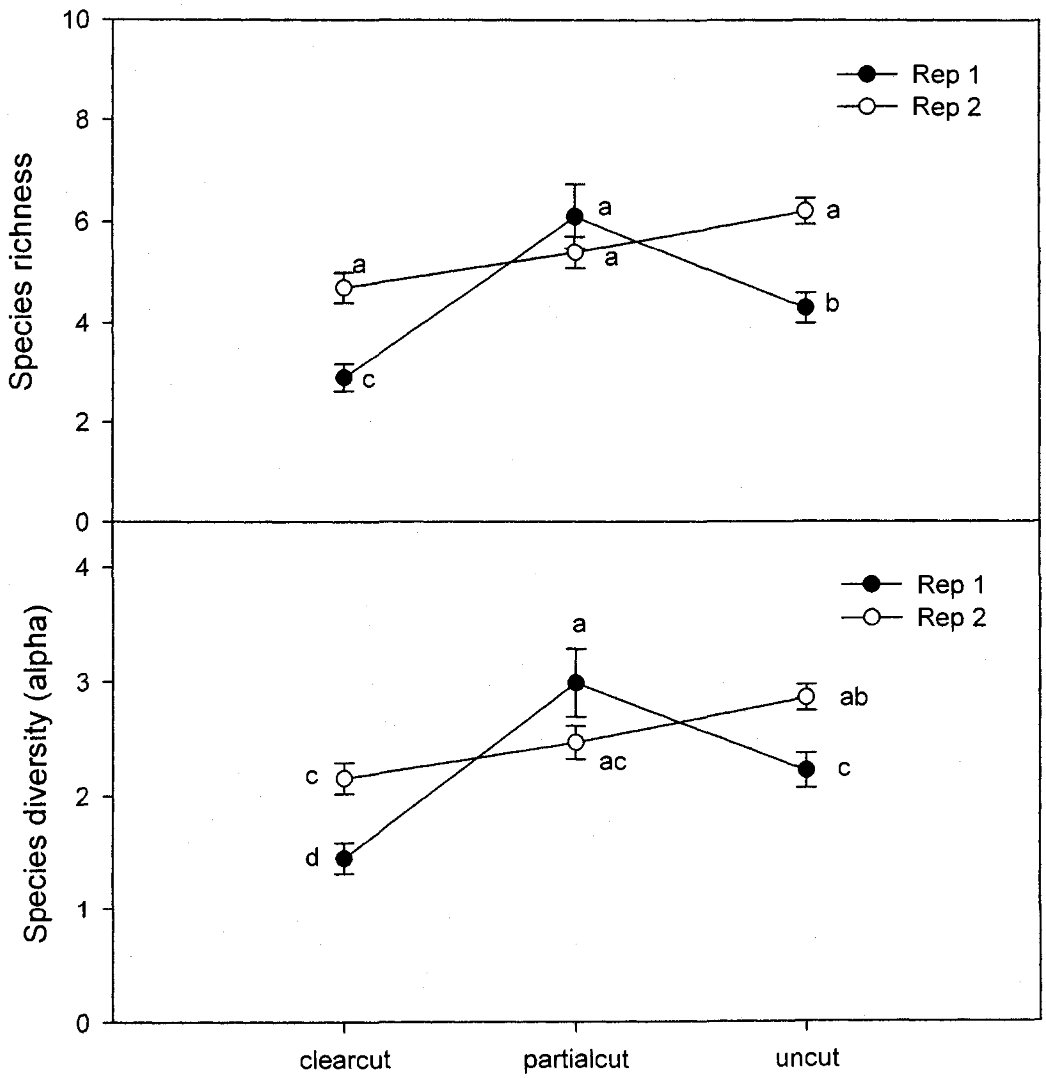

Figure 4.Relationship between regenerated species richness or alpha diversity (Mean±SEM) and harvesting operation

Density

The total density of all regeneration species together was significantly higher in that partial-cut (26670±1478 stem/ha) than the uncut compartments (23560±1550 stem/ha). However, there were no significant differences between clearcut and partial-cut or between clearcut and uncut treatment (Table 3, Figure 5). On the individual species level, there were significant 3- way interactions among replicate, harvesting operation and species (Table 3). The stem density of trembling aspen increased from uncut to partial cut to clearcut and the density was generally higher in replicate 2 than replicate 1 (Figure 6). Trembling aspen had the highest density among all the species in the clearcut and partial-cut treatments.

Jack pine regeneration was present only in replicate 1 and had highest density in the uncut control (13100±1186 stem/ha) while its densities at the harvested compartments were substantially lower (80±61 stem/ha for clearcut in and 380±150 stem/ha for partial cut, Figure 6). In fact, jack pine regeneration had the highest density among all the species in the uncut control compartment in replicate 1 (Figure 6).

Pin cherry regeneration was present in both replicates, but the density was significantly higher in replicate 2 than replicate 1 (Figure 6). While there were no significant differences among harvesting treatments in replicate 1, the density in replicate 2 generally decreased from clearcut to partial-cut to uncut compartment (5320±887 stem/ha, 4700±814 stem/ha, 3820±377 stem/ha, respectively).

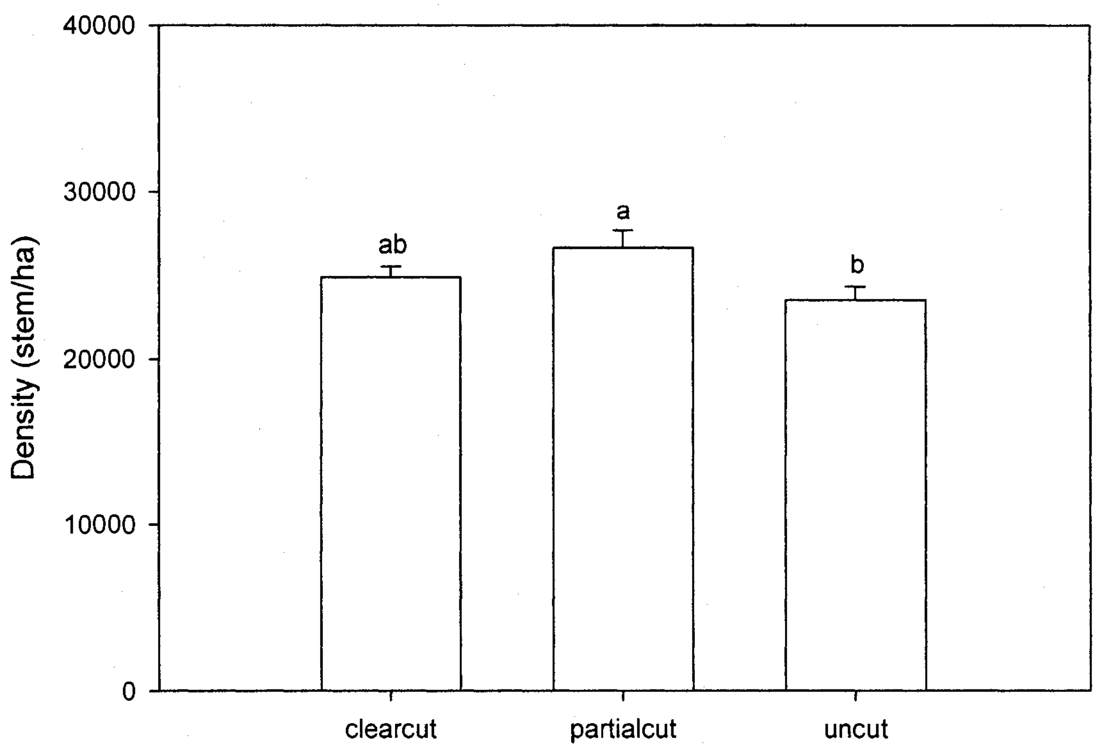

Figure 5. Relationship between the density of all species combined (Mean±SEM) and harvesting operations.

The trend for beaked hazel density was similar to that of pin cherry with significant density in replicate 2 than in replicate 1 (Figure 6). However, the highest density of beaked hazel regeneration was in the partial-cut treatment, while there were no significant differences between clearcut and uncut control in replicate 1, and there were no significant difference between partial-cut and uncut compartment in replicate 2 (Figure 6). Mountain maple regeneration also had significantly greater density in replicate 2 than in replicate 1 (Figure 6). Mountain maple was only present in the partial-cut compartment of replicate 1 with a very low density. In replicate 2, in contrast, its density increased from clearcut (2600±384 stem/ha) to partial-cut (3920±948 stem/ha) to uncut (6440±705 stem/ha) (Figure 6). There were no significant treatment effects on the density of regeneration for other species (Bw, Sr, Rw, Rp, Wu, Hc and Ab) and their densities were very low.

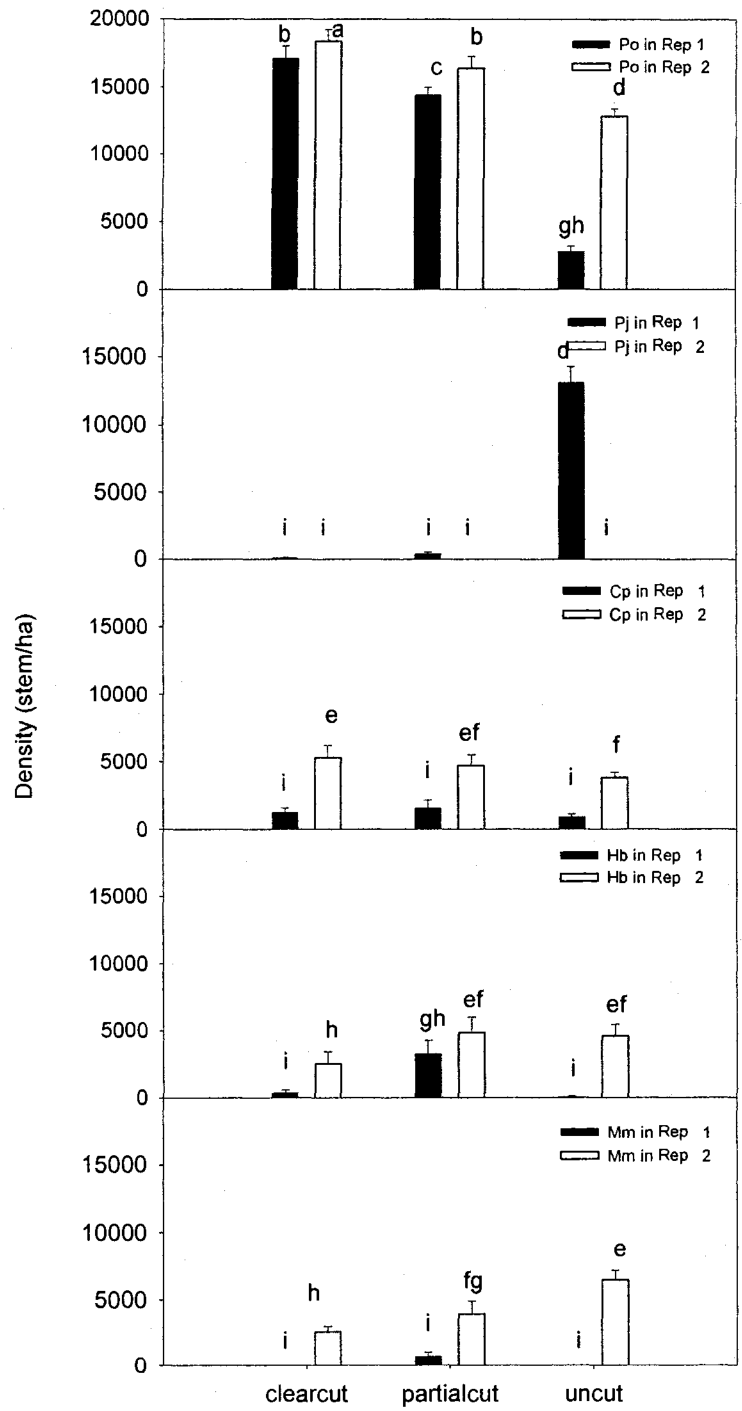

Figure 6 Relationship between regeneration density (Mean±SEM) and harvesting operations for trembling aspen (Po) jack pine (Pj), pin cherry (Cp), beaked hazel (Hb), mountain maple (Mm).

Height

There were significant interactions on the height of regenerations between replicate and harvesting operation, and between species and harvesting operation (Table 3). The highest average height was in the uncut compartment of replicate 2 (Figure 7), which was dominated by trembling aspen, pin cherry, beaked hazel and mountain maple (Figure 6). The lowest average height occurred in the uncut compartment of replicate 1 (Figure 7), which was composed mainly of jack pine, trembling aspen and pin cherry. In terms of interactions between species and harvesting operation for tree species, jack pine was tallest clearcut, trembling aspen tallest in partial-cut while there were no significant differences among harvesting methods for white birch, and there were no significant differences among the three species in the about treatment combinations (Figure 8). Trembling aspen in clearcut and partial-cut and jack pine in uncut control formed the second tallest group (Figure 8). The height of pin cherry was significantly lower in clearcut than in partial cut or uncut while there was not significant difference between the latter two treatments (Figure 8). Harvesting methods did not significantly affect the height of other species (Hb, Mm, Bw, Sr, Rw, Rp, Wu, Hc and Ab) (Figure 8).

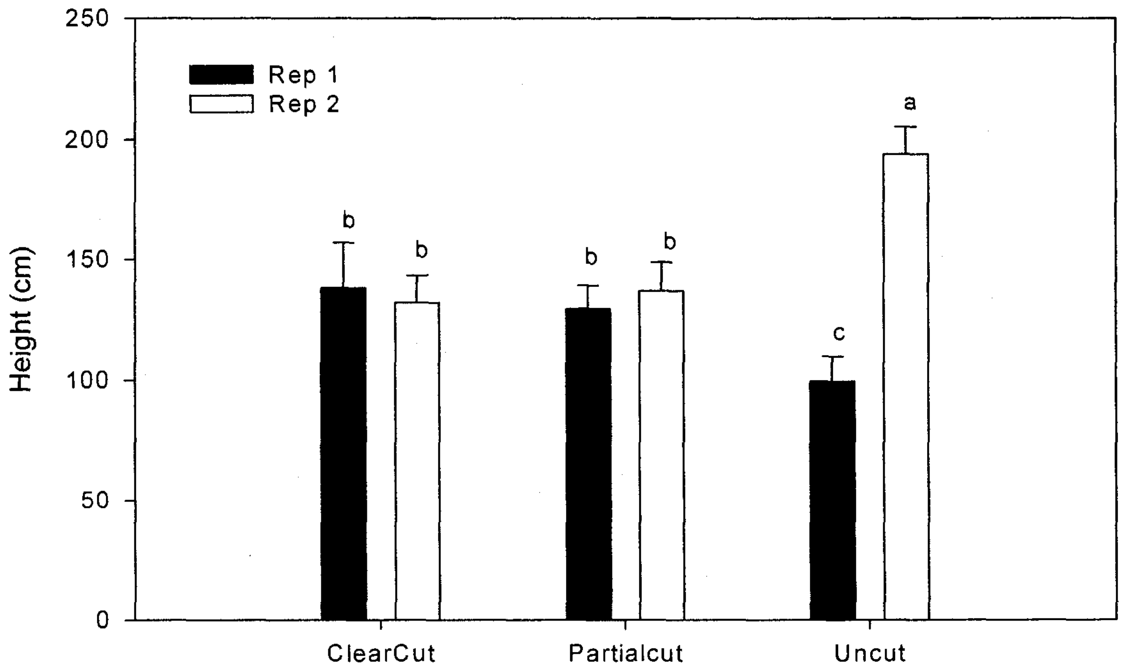

Figure 7. Effects of harvesting and replicates on the average height (Mean±SEM) of regeneration for all species.

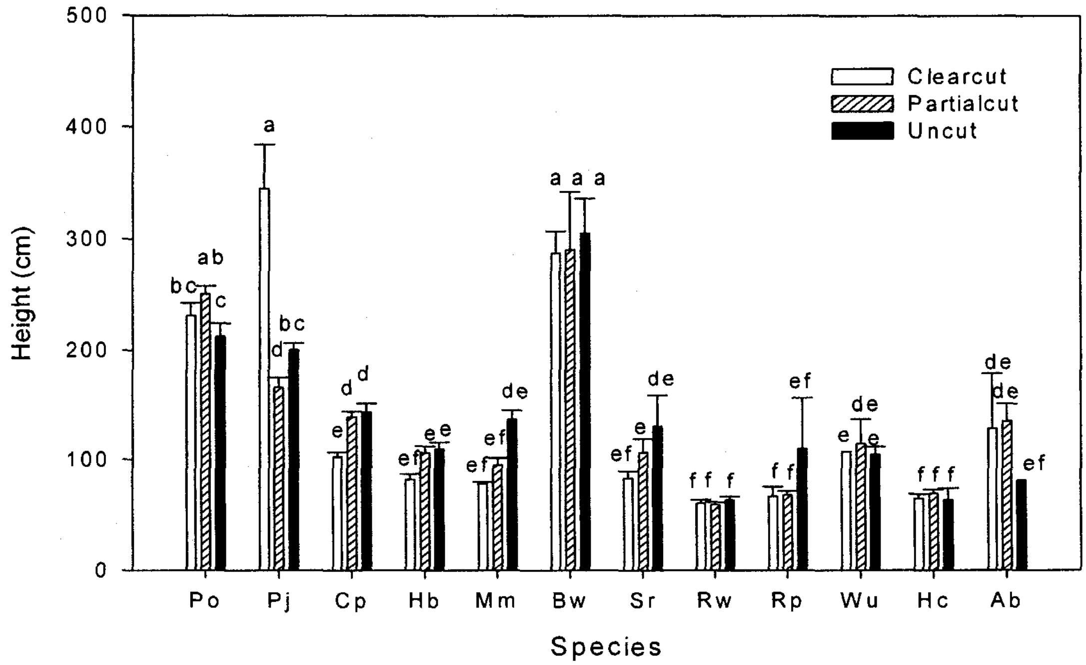

Figure 8. Interactive effects of harvesting method and species on the mean height (Mean±SEM) of regeneration. Species abbreviations are as follows: by harvesting operation for trembling aspen (Po) jack pine (Pj), pin cherry (Cp), beaked hazel (Hb), mountain maple (Mm), white birch (Bw), red-twigged serviceberry (Sr), wild red raspberry (Rw), prickly wild rose (Rp), upland willow (Wu), Canada fly honeysuckle (Hc) and Black ash (Ab).

Regeneration index (%)

There were significant 3-way interactions among harvesting method, replicate and species on regeneration index (RI) (Table 3). Trembling aspen had the highest RI among all the species in the clearcut and partial-cut, while jack pine had the highest RI in the uncut compartment of replicate 1 (Figure 9). Trembling aspen RI generally decreased from clearcut (93.58±1.47, in replicate 1; 75.82±2.64, in replicate 2) to partial-cut

(80.35±2.82, in replicate 1; 70.21±2.83, in replicate 2) to uncut (14.51±1.90, in replicate 1; 57.45±2.04, in replicate 2) and it was greater in replicate 1 than replicate 2 in the harvested, but the trend was reversed in the uncut treatment (Figure 9). Jack pine had the highest RI (79.82±2.47) in the uncut compartment of replicate 1 while there were no significant differences among other treatment combinations (Figure 9). Pin cherry had higher RI in replicate 2 than replicate 1, but harvesting methods did not significantly affect its RI (Figure 9). The RI of beaked hazel was significantly higher in replicate 2 than replicate 1, and had a trend of increasing from clearcut to partial-cut to uncut in replicate 2, while its RI was the highest in the partial-cut compartment of replicate 1 (Figure 9). The trends for mountain maple RI were similar to those of beaked hazel (Figure 9). The RI of other species (Bw, Sr, Rw, Rp, Wu, Hc and Ab) was not significantly influenced by any of the factors examined (Table 3). The RIs for those species were all below 2%.

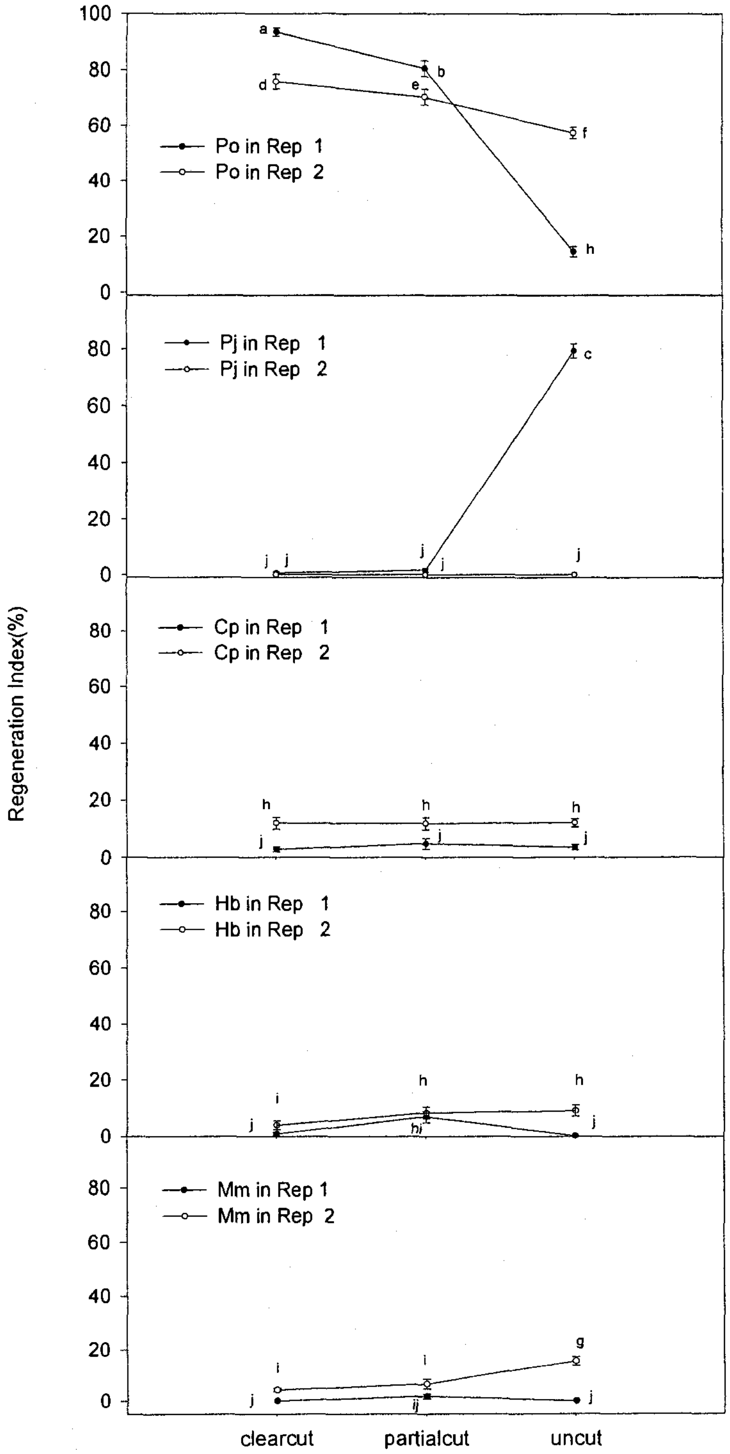

Figure 9. Regeneration index (Mean±SEM) and harvest operation for trembling aspen (Po) jack pine (Pj), pin cherry (Cp), beaked hazel (Hb), mountain maple (Mm).

DISCUSSION

Regeneration species

A total of 12 tree and shrub species regenerated after the 1999 severe fire on the previously clearcut, partial-cut and uncut control compartments in the Black Sturgeon Boreal Mixedwood Experiment(Scarratt 2001), but the species richness varied with harvesting operations. Clearcutting generally resulted in lowest species richness, suggesting that clearcutting reduced the species diversity of tree and shrub species. However, our data suggested that whether partial-cut or uncut sites would have a greater species diversity of tree and shrub regeneration following a severe fire will depend on the specific pre-fire site conditions. This variation may be due to the species diversity and density. The variation in species diversity of regeneration appears to be related to the density of the dominant overstory tree species. A higher density of trembling aspen and/or jack pine regeneration generally corresponded to lower species diversity or richness. White birch is another tree species that regenerated in all compartments following the fire. However, because its density was so low, it did not appear to have had significant impact on species diversity of post-fire regeneration. Our finding is in agreement with the observation of Messier et al. (1998) that overstory species has a direct influence on understory species. A lower density of overstory species allows more sun light reaching the understory, permitting the regeneration of more species.

Density

The total density of all regenerated species reflects the total regeneration status. In general, uncut control compartments had the lowest total density of regenerations while there were no significant differences between clearcut and partial cut. However, the density of individual species was significantly different among different harvesting operations. For example, the density of trembling aspen declined from clearcut to partial cut to uncut while jack pine had the highest density of regeneration in the uncut compartment. The results generally support the hypothesis that the density of trembling aspen regeneration would decline from clearcut to partial-cut to uncut compartment. The results suggest that harvesting operations can substantially influence the initial density of the regeneration and modify its species composition when the sites are severely disturbed following the regeneration of the harvested area. The species composition is determined by the availability and abundance of regeneration sources, such as root stocks and seeds. Since trembling aspen dominated the harvested compartments following clearcut and partial cut (Scarratt 2001), it continued the dominancy following the fire. Thus, the species composition of regeneration can be manipulated by using appropriate harvesting operations.

The results indicate that all trembling aspen suckers occurred within the first five years following the fire. This result is in agreement with the literature (Johnstone et al. 2004). Tree age is generally considered not to affect suckering capacity, though it does influence the quality and quantity of stump sprouting (Smith et al. 1997). Presumably there were no mature trees of trembling aspen in clearcut compartments at the time of the fire in 1999 while the amount of mature trembling aspen increased from partial cut to the uncut control compartment. The data suggest that the density of suckers declined from clearcut to partial-cut to the uncut control. This result is in agreement with the observation of Mulak *et al* (2006) that density of trembling aspen regeneration declined from clearcut to partial-cut (Mulak et al. 2006). The results indicate that the suckering capacity might have declined with tree age. However, this trend might also have been a result of differences in the total amount of roots present at the time of burning. Unfortunately, there were no data available on root stocking.

The density of jack pine regeneration was high in the uncut treatment compared to the other two treatments where almost no jack pine regenerated. This result partially supports the hypothesis that jack pine regeneration would increase from clearcut to partial cut to uncut control. The result probably reflects the availability of viable seeds at the time of burning. The viability of jack pine seed declines substantially after 5 years (Rudolph and Laidly 1990). Additionally, trees regenerated after the harvesting operations were likely too young to produce seeds at the time when the fire occurred. Consequently, there was probably a very low stock of viable seeds in the seed bank in the clearcut and partial cut compartment, resulting in a low regeneration. However, there were mature trees in the uncut compartment that continued seed production, resulting in a much better regeneration after the fire.

The density of regeneration of pin cherry, beaked hazel and mountain maple was generally greater in replicate 2 than replicate 1 and the differences between the two replicates were much greater than those among different harvesting operations. These results suggest that extreme cautions should be used when attempting to generalize the effects of harvesting operations on subsequent regenerations. Results from one replicate can be totally inapplicable to another replicate. For example, the density of mountain maple regeneration showed an increasing trend from clearcut to partial-cut to the uncut control in replicate 2 whereas there were no significant differences among harvesting operations in replicate 1. This same argument holds true for all the regeneration species found in this study, such as trembling aspen and jack pine. The density of regenerated white birch was low and had no significant differences among harvesting operations. White birch produces abundant light-weight seeds and can also reproduce by stump sprouting (Weir and Johnson 1998) and thus had potential to occupy burnt areas. The low regeneration of white birch was partially attributable to its shade tolerance. White birch is less shade intolerant than trembling aspen and can easily be over-competed by more shade tolerant species (Safford et al. 1990). The quick suckering of trembling aspen probably prevented the successful establishment of white birch following the fire. In addition, the abundance of white birch was very low before the harvesting in 1993 (Scarratt 2001).

The main understory regeneration species in terms of density were pin cherry, beaked hazel and mountain maple. Other species were only a minor component of the regeneration. Pin cherry is an understory avoider which grows best in open conditions and pin cherry's seed bank is a main mechanism to maintain its population on the site after canopy closure (Lieffers 1994). Both beaked hazel and mountain maple are understory tolerant species, which grow best in the open conditions but are able to persist in the understory of many stand (Lieffers 1994). Their aggressive colonial habit made them expand rapidly after fires and compete with tree species energetically. Mountain maple sprouts from underground lateral stems (Krefting et al. 1956); beaked hazel regenerates from its root suckers (Haeussler and Coates 1986). Pin cherry grows very fast after fires (Wendel 1990). Though there were no records before the harvesting operations, pin cherry probably regenerated from its seeds stored in soil before the harvesting operations. When the canopy is opened up, pin cherry can regenerate aggressively (Wendel 1990; Lieffers 1994). Because there were no significant differences among different harvesting treatments on pin cherry's regeneration, it is reasonable to assume that before harvest operations in 1993 and after fire in 1999, the amount of pin cherry seed in the soil seed bank was similar among different treatments. The density of pin cherry regeneration agrees with the longevity of seeds in this species. Pin cherry seeds in soil seed banks can remain viable for as long as 50 to 150 years (Wendel 1990). Consequently, the overall regeneration of this species is likely controlled by the long term accumulation of seeds in the seed bank. Indeed, there was little difference in the density of pin cherry regeneration among different harvesting treatments. Since there was no pin cherry recorded in 1993 when the stands were harvested (Scarratt 2001), the seeds were liked to have been produced prior to the stand regeneration in the 1940s.

Regeneration index

Regeneration index is an integrated indicator of the regeneration status of a species. Its calculation considers both the density and average height of the regeneration. The species with the highest regeneration index generally has the best potential to form the dominant species of the stand. The data suggest that trembling aspen dominated all the compartments in this study except the uncut compartment of replicate 1. That compartment should have the highest potential to become a mixed-species stand, comprising of primarily trembling aspen and jack pine because the regeneration index of jack pine was also very high. In fact, it was higher than that of trembling aspen. The regeneration index data in this study were in a general agreement with density data, suggesting that either regeneration index or density can be used as an indicator of the future species composition of the stands.

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 meters away from nearby trees, which is further than the seed dispersal distance for all the species in the area. Some species, such as white spruce and balsam fir, were abundant prior to the harvesting operation in 1993, but failed to regenerated in the burned compartments.

CONCLUSIONS

Eight years after the severe fire in 1999, trembling aspen suckers dominated all the compartments of the clearcut, partial-cut and uncut harvesting treatments in the Black Surgeon Boreal Mixedwood Experiment site. Its stem density and regeneration index generally decreased from clearcut to partial cut to uncut. The reasons for this trend were not clear. It could have been related to the density, diameter and age of root stocks and fire severity caused by differences in fuel load among the treatments. Jack pine was a significant component of regeneration only on the uncut compartment of one of the two replicates investigated. Although a total of 12 tree and understory species were present, the majority of the compartments can be considered as pure trembling aspen stands with the exception of one uncut compartment where jack pine was the dominant tree species. Other regeneration species were white birch, pin cherry, beaked hazel, mountain maple, red-twigged serviceberry, wild red raspberry, prickly wild rose, upland willow, Canada fly honeysuckle, and black ash. The species richness was greater in partial-cut than clearcut and uncut compartment. There were a number of trees species that were present prior to the harvesting operations in 1993 but failed to regenerate following the fire. The results suggest that the regeneration of large burned areas will heavily rely on the availability of local regeneration source and can be highly variable from site to site.

However, some seeds (e.g. pin cherry) in the soil seed bank appeared to have survived the severe fire and successfully germinated.

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APPENDICES

APPENDIX I

Pre-harvest site shrub cover (%) by harvesting operation and species

(Scarratt 2001)

Harvest operations	Shrub cover (%)							
	Hb	Mm	Rp	Hc	Sb	Bf	Va	Dl
Clearcut	11.45	36.00	2.50	3.95	2.30	10.45	10.30	5.65
Partialcut	19.15	22.70	0.00	5.80	0.00	4.25	0.00	6.05
Uncut	15.25	56.80	0.00	5.30	5.80	5.90	0.00	6.40

*Note: Hb- Beaked hazel, Mm- Mountain maple, Rp-Prickly wild rose, Hc-Canada fly honeysuckle, Sb-Black spruce, Bf-Balsam fir, Va-Lowbush blueberry, Dl-Bush honeysuckle.

APPENDIX II

Regeneration relative abundance after fire by harvest operations and species

Harvest operations	Relative abundance (%)											
	Po	Pj	Cp	Hb	Mm	Sr	Bw	Rw	Rp	Wu	Hc	Ab
Clearcut	74.56	0.17	13.79	5.97	0.67	2.57	1.14	0.13	0.17	0.38	0.38	0.08
Partialcut	57.74	0.71	11.74	15.07	8.7	1.8	0.9	1.42	1.2	0.37	0.26	0.07
Uncut	33.15	27.8	10.02	9.8	13.67	0.76	1.78	1.78	0.25	0.51	0.42	0.04

Note: Po - Trembling aspen, Pj - Jack pine, Cp - Pin cherry, Hb - Beaked hazel, Mm - Mountain maple, Sr - Red-twigged serviceberry, Bw - White birch, Rw - Wild red raspberry, Rp - Prickly wild rose, Wu -Upland willow, Hc - Canada fly honeysuckle, Ab - Black ash.

APPENDIX III

Regeneration relative abundance by height class, harvesting operation and species

Height class	H.M.	Relative abundance (%)											
		Po	Pj	Cp	Hb	Mm	Sr	Bw	Rw	Rp	Wu	Hc	Ab
50-100 cm	CC	27.33	0.00	32.39	22.87	2.83	10.32	0.00	0.61	0.81	0.81	1.82	0.20
	PC	12.50	0.00	11.96	33.04	24.29	3.75	0.18	6.79	5.71	0.54	1.25	0.00
	UC	9.09	13.64	10.96	24.87	23.26	1.60	0.00	10.70	1.34	1.60	2.67	0.27
101-150 cm	CC	64.15	0.00	25.92	6.26	0.43	2.16	0.00	0.00	0.00	1.08	0.00	0.00
	PC	31.61	1.29	19.19	32.42	12.42	2.42	0.16	0.00	0.00	0.32	0.00	0.16
	UC	21.31	21.13	13.23	19.42	22.34	1.03	0.52	0.34	0.00	0.69	0.00	0.00
151-200 cm	CC	88.64	0.00	10.37	0.00	0.00	0.00	0.74	0.00	0.00	0.00	0.00	0.25
	PC	67.73	1.96	18.09	3.91	3.67	2.20	0.98	0.00	0.00	1.22	0.00	0.24
	UC	32.83	33.26	12.31	5.18	13.61	0.43	1.73	0.00	0.22	0.43	0.00	0.00
201-250 cm	CC	97.12	0.00	1.92	0.00	0.00	0.00	0.96	0.00	0.00	0.00	0.00	0.00
	PC	84.95	0.94	11.29	0.00	1.25	0.94	0.63	0.00	0.00	0.00	0.00	0.00
	UC	35.99	42.75	8.21	0.24	7.73	0.72	1.21	0.00	0.00	0.00	0.00	0.00
251-300 cm	CC	96.54	0.00	0.00	0.00	0.00	0.00	3.46	0.00	0.00	0.00	0.00	0.00
	PC	93.48	0.00	5.43	0.00	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00
	UC	49.44	38.29	6.69	0.00	2.97	0.37	2.23	0.00	0.00	0.00	0.00	0.00
>301 cm	CC	96.39	0.90	0.00	0.00	0.00	0.00	2.71	0.00	0.00	0.00	0.00	0.00
	PC	96.89	0.00	0.41	0.00	0.00	0.00	2.69	0.00	0.00	0.00	0.00	0.00
	UC	70.79	17.60	3.37	0.00	0.75	0.00	7.49	0.00	0.00	0.00	0.00	0.00

Note: H.M.-Harvesting operation. Po - Trembling aspen, Pj - Jack pine, Cp - Pin cherry, Hb - Beaked hazel, Mm - Mountain maple, Sr - Red-twigged serviceberry, Bw - White birch, Rw - Wild red raspberry, Rp - Prickly wild rose, Wu -upland willow, Hc - Canada fly honeysuckle, Ab - Black ash.
CC-Clearcut, PC-Partial-cut and UC-Uncut)

APPENDIX IV

Natural regeneration number of species ($\overline{X} \pm$ SEM) by

harvesting operation and stand

Harvesting operation	Stand 1		Stand 2	
	Mean	SE	Mean	SE
Clearcut	2.9	0.28	4.7	0.3
Partial cut	6.1	0.62	5.4	0.31
Uncut	4.3	0.30	6.2	0.25

APPENDIX V

Natural regeneration density ($\overline{X} \pm$ SEM) all species

together by harvesting operation

Harvesting operation	Mean (stem/ha)	SE
Clearcut	24920	632.95
Partial cut	26670	1021.23
Uncut	23560	809.28

APPENDIX VI

Natural regeneration density ($\overline{X} \pm$ SEM) by stand, harvesting operation and species.

Rep.	Species	Clearcut		Partialcut		Uncut	
		Density (stems/ha)	SE*	Density (stems/ha)	SE	Density (stems/ha)	SE
1	Po	17080	914	14420	545	2780	399
1	Pj	80	61	380	150	13100	1186
1	Cp	1240	345	1560	576	900	216
1	Hb	360	242	3240	996	60	43
1	Mm	0	0	720	345	0	0
1	Bw	140	103	320	161	180	121
1	Sr	420	420	500	205	0	0
1	Rw	40	40	220	105	0	0
1	Rp	0	0	600	322	0	0
1	Wu	0	0	60	43	240	115
1	Hc	120	120	40	27	200	146
1	Ab	40	27	20	20	20	20
2	Po	18380	827	16380	860	12840	548
2	Pj	0	0	0	0	0	0
2	Cp	5320	887	4700	815	3820	378
2	Hb	2480	937	4800	1182	4560	884
2	Mm	2600	384	3920	948	6440	705
2	Bw	400	314	160	88	660	227
2	Sr	800	442	460	286	360	275
2	Rw	20	20	540	295	840	268
2	Rp	80	61	40	27	120	100
2	Wu	180	180	140	119	0	0
2	Hc	60	60	100	100	0	0
2	Ab	0	0	20	20	0	0

Note: Po - Trembling aspen, Pj - Jack pine, Cp - Pin cherry, Hb - Beaked hazel, Mm - Mountain maple, Sr - Red-twigged serviceberry, Bw - White birch, Rw - Wild red raspberry, Rp - Prickly wild rose, Wu -Upland willow, Hc - Canada fly honeysuckle, Ab - Black ash.

*SE- standard error

APPENDIX VII

Height ($\overline{X} \pm$ SEM) by harvesting operation and stand

Harvesting operation	Rep. 1		Rep. 2	
	Mean (cm)	SE	Mean (cm)	SE
Clearcut	138.40	18.61	132.30	11.21
Partial cut	129.80	9.60	137.20	11.82
Uncut	99.62	10.42	194.60	10.92

APPENDIX VIII

Height ($\overline{X} \pm$ SEM) by harvesting operation and species

	Clearcut		Partial cut		Uncut	
Species	Mean (cm)	SE	Mean (cm)	SE	Mean (cm)	SE
Po	232.8	2.6	251.7	2.5	235.6	3.3
Pj	364.8	73.1	162.8	20.2	199.3	2.8
Cp	109.0	2.2	147.2	3.2	164.2	4.3
Hb	84.6	2.5	105.6	1.3	111.0	2.5
Mm	78.0	2.3	102.1	2.4	137.2	3.2
Bw	294.1	29.5	324.4	39.5	306.1	25.4
Sr	82.0	4.9	116.0	8.8	146.0	20.4
Rw	61.3	12.7	60.3	4.5	66.2	4.7
Rp	62.3	12.4	66.2	5.8	78.8	16.0
Wu	107.1	17.1	137.3	23.0	109.6	17.2
Hc	66.0	10.7	66.4	11.8	67.4	10.6
Ab	128.5	30.3	135.0	28.9	81.0	18.1

Note: Po - Trembling aspen, Pj - Jack pine, Cp - Pin cherry, Hb - Beaked hazel, Mm - Mountain maple, Sr - Red-twigged serviceberry, Bw - White birch, Rw - Wild red raspberry, Rp - Prickly wild rose, Wu -Upland willow, Hc - Canada fly honeysuckle, Ab - Black ash.

*SE- standard error

APPENDIX IX

Sample plot stems and mean height. .

Rep.	H.M	Plot	Species	Stems	Height	Rep.	H.M	Plot	Species	Stems	Height
R1	CC	1	Po	79	280	R1	PC	7	Po	65	218
R1	CC	2	Po	103	236	R1	PC	8	Po	82	250
R1	CC	3	Po	94	260	R1	PC	9	Po	80	241
R1	CC	4	Po	114	395	R1	PC	10	Po	69	213
R1	CC	5	Po	66	245	R1	PC	1	Pj	3	158
R1	CC	6	Po	79	194	R1	PC	3	Pj	4	198
R1	CC	7	Po	78	263	R1	PC	7	Pj	1	174
R1	CC	8	Po	86	253	R1	PC	9	Pj	6	154
R1	CC	9	Po	82	199	R1	PC	10	Pj	5	146
R1	CC	10	Po	73	221	R1	PC	1	Cp	5	112
R1	CC	1	Pj	3	384	R1	PC	2	Cp	8	138
R1	CC	2	Pj	1	306	R1	PC	3	Cp	3	149
R1	CC	2	Cp	5	76	R1	PC	4	Cp	4	102
R1	CC	3	Cp	7	89	R1	PC	5	Cp	33	134
R1	CC	5	Cp	17	92	R1	PC	6	Cp	6	152
R1	CC	6	Cp	5	116	R1	PC	7	Cp	1	111
R1	CC	7	Cp	4	79	R1	PC	8	Cp	5	149
R1	CC	8	Cp	4	100	R1	PC	9	Cp	5	114
R1	CC	9	Cp	14	89	R1	PC	10	Cp	8	128
R1	CC	10	Cp	6	82	R1	PC	1	Hb	9	66
R1	CC	6	Hb	10	80	R1	PC	2	Hb	26	115
R1	CC	10	Hb	8	100	R1	PC	3	Hb	23	118
R1	CC	6	Bw	2	218	R1	PC	5	Hb	10	89
R1	CC	9	Bw	5	288	R1	PC	6	Hb	11	104
R1	CC	3	Sr	21	90	R1	PC	7	Hb	29	107
R1	CC	1	Rw	2	64	R1	PC	8	Hb	50	104
R1	CC	1	Hc	6	69	R1	PC	9	Hb	3	89
R1	CC	3	Ab	1	179	R1	PC	10	Hb	1	75
R1	CC	4	Ab	1	78	R1	PC	4	Mm	4	79
R1	PC	1	Po	62	222	R1	PC	6	Mm	15	83
R1	PC	2	Po	71	303	R1	PC	7	Mm	11	150
R1	PC	3	Po	68	279	R1	PC	10	Mm	6	75
R1	PC	4	Po	89	218	R1	PC	5	Bw	1	136
R1	PC	5	Po	67	230	R1	PC	6	Bw	5	399
R1	PC	6	Po	68	263	R1	PC	7	Bw	3	275

Rep.	H.M	Plot	Species	Stems	Height	Rep.	H.M	Plot	Species	Stems	Height
R1	PC	9	Bw	7	261	R1	UC	10	Pj	49	193
R1	PC	5	Sr	8	74	R1	UC	1	Cp	1	90
R1	PC	6	Sr	7	152	R1	UC	2	Cp	2	125
R1	PC	7	Sr	6	90	R1	UC	3	Cp	4	112
R1	PC	8	Sr	2	127	R1	UC	4	Cp	6	135
R1	PC	10	Sr	2	81	R1	UC	5	Cp	12	124
R1	PC	3	Rw	2	55	R1	UC	6	Cp	2	109
R1	PC	6	Rw	2	56	R1	UC	7	Cp	2	119
R1	PC	7	Rw	2	54	R1	UC	8	Cp	3	111
R1	PC	9	Rw	5	56	R1	UC	9	Cp	8	107
R1	PC	5	Rp	3	76	R1	UC	10	Cp	5	110
R1	PC	6	Rp	12	59	R1	UC	1	Hb	1	146
R1	PC	8	Rp	13	70	R1	UC	5	Hb	2	99
R1	PC	9	Rp	1	50	R1	UC	6	Bw	6	171
R1	PC	10	Rp	1	67	R1	UC	9	Bw	2	468
R1	PC	1	Wu	2	85	R1	UC	10	Bw	1	161
R1	PC	9	Wu	1	137	R1	UC	1	Wu	1	122
R1	PC	4	Hc	1	67	R1	UC	4	Wu	4	107
R1	PC	5	Hc	1	76	R1	UC	6	Wu	1	91
R1	PC	6	Ab	1	151	R1	UC	7	Wu	5	118
R1	UC	1	Po	14	146	R1	UC	9	Wu	1	86
R1	UC	2	Po	15	182	R1	UC	3	Hc	3	53
R1	UC	3	Po	9	181	R1	UC	9	Hc	7	74
R1	UC	4	Po	7	192	R1	UC	10	Ab	1	81
R1	UC	5	Po	9	141	R2	CC	1	Po	121	165
R1	UC	6	Po	9	262	R2	CC	2	Po	100	205
R1	UC	7	Po	10	186	R2	CC	3	Po	105	284
R1	UC	8	Po	19	170	R2	CC	4	Po	87	182
R1	UC	9	Po	26	133	R2	CC	5	Po	91	202
R1	UC	10	Po	21	142	R2	CC	6	Po	87	172
R1	UC	1	Pj	69	204	R2	CC	7	Po	84	222
R1	UC	2	Pj	86	199	R2	CC	8	Po	82	214
R1	UC	3	Pj	50	232	R2	CC	9	Po	83	210
R1	UC	4	Pj	66	193	R2	CC	10	Po	79	223
R1	UC	5	Pj	52	221	R2	CC	1	Cp	7	94
R1	UC	6	Pj	104	203	R2	CC	2	Cp	4	121
R1	UC	7	Pj	75	177	R2	CC	3	Cp	43	112

Rep.	H.M	Plot	Species	Stems	Height	Rep.	H.M	Plot	Species	Stems	Height
R2	CC	8	Cp	24	145	R2	PC	10	Po	76	264
R2	CC	9	Cp	39	117	R2	PC	1	Cp	30	164
R2	CC	10	Cp	30	125	R2	PC	2	Cp	15	144
R2	CC	2	Hb	18	62	R2	PC	3	Cp	28	128
R2	CC	4	Hb	4	62	R2	PC	4	Cp	37	177
R2	CC	7	Hb	19	80	R2	PC	5	Cp	32	153
R2	CC	8	Hb	16	78	R2	PC	6	Cp	44	136
R2	CC	9	Hb	46	92	R2	PC	7	Cp	23	182
R2	CC	10	Hb	21	96	R2	PC	8	Cp	9	163
R2	CC	1	Mm	15	75	R2	PC	9	Cp	5	125
R2	CC	2	Mm	18	76	R2	PC	10	Cp	12	117
R2	CC	3	Mm	12	77	R2	PC	1	Hb	31	112
R2	CC	4	Mm	16	78	R2	PC	2	Hb	29	130
R2	CC	5	Mm	20	77	R2	PC	3	Hb	2	153
R2	CC	6	Mm	16	78	R2	PC	4	Hb	21	105
R2	CC	7	Mm	17	84	R2	PC	5	Hb	27	102
R2	CC	8	Mm	8	84	R2	PC	6	Hb	42	97
R2	CC	10	Mm	8	72	R2	PC	7	Hb	3	161
R2	CC	3	Bw	2	357	R2	PC	9	Hb	26	81
R2	CC	7	Bw	16	299	R2	PC	10	Hb	59	107
R2	CC	9	Bw	1	249	R2	PC	1	Mm	17	86
R2	CC	10	Bw	1	312	R2	PC	2	Mm	4	70
R2	CC	1	Sr	10	76	R2	PC	3	Mm	8	83
R2	CC	5	Sr	20	70	R2	PC	4	Mm	41	94
R2	CC	8	Sr	10	96	R2	PC	5	Mm	42	89
R2	CC	10	Rw	1	57	R2	PC	6	Mm	10	94
R2	CC	4	Rp	1	75	R2	PC	7	Mm	29	118
R2	CC	7	Rp	3	58	R2	PC	8	Mm	32	144
R2	CC	5	Wu	9	107	R2	PC	9	Mm	7	70
R2	CC	2	Hc	3	61	R2	PC	10	Mm	6	90
R2	PC	1	Po	71	234	R2	PC	7	Bw	4	541
R2	PC	2	Po	94	242	R2	PC	8	Bw	2	188
R2	PC	3	Po	87	218	R2	PC	9	Bw	2	232
R2	PC	4	Po	67	269	R2	PC	6	Sr	5	65
R2	PC	6	Po	74	230	R2	PC	10	Sr	14	158
R2	PC	7	Po	93	333	R2	PC	1	Rw	5	72
R2	PC	5	Po	109	266	R2	PC	9	Sr	4	105

Rep.	H.M	Plot	Species	Stems	Height	Rep.	H.M	Plot	Species	Stems	Height
R2	PC	8	Rw	12	60	R2	UC	8	Hb	3	64
R2	PC	9	Rw	10	61	R2	UC	9	Hb	22	105
R1	UC	8	Pj	59	172	R2	CC	4	Cp	46	111
R1	UC	9	Pj	45	212	R2	CC	5	Cp	19	86
R2	CC	6	Cp	27	108	R2	PC	8	Po	68	259
R2	CC	7	Cp	27	102	R2	PC	9	Po	80	261
R2	PC	5	Rp	1	71	R2	UC	10	Hb	33	94
R2	PC	10	Rp	1	79	R2	UC	1	Mm	38	157
R2	PC	4	Wu	6	166	R2	UC	2	Mm	46	175
R2	PC	8	Wu	1	71	R2	UC	3	Mm	39	119
R2	PC	1	Hc	5	64	R2	UC	4	Mm	9	168
R2	PC	4	Ab	1	119	R2	UC	5	Mm	31	150
R2	UC	1	Po	73	288	R2	UC	6	Mm	31	104
R2	UC	2	Po	55	304	R2	UC	7	Mm	44	122
R2	UC	3	Po	56	214	R2	UC	8	Mm	36	151
R2	UC	4	Po	57	282	R2	UC	9	Mm	27	123
R2	UC	5	Po	58	243	R2	UC	10	Mm	21	96
R2	UC	6	Po	65	230	R2	UC	1	Bw	1	361
R2	UC	7	Po	77	264	R2	UC	2	Bw	9	407
R2	UC	8	Po	59	249	R2	UC	3	Bw	6	323
R2	UC	9	Po	65	218	R2	UC	4	Bw	1	286
R2	UC	10	Po	77	221	R2	UC	6	Bw	3	358
R2	UC	1	Cp	25	188	R2	UC	8	Bw	4	245
R2	UC	2	Cp	12	196	R2	UC	9	Bw	9	270
R2	UC	3	Cp	23	187	R2	UC	1	Sr	2	198
R2	UC	4	Cp	16	178	R2	UC	7	Sr	1	64
R2	UC	5	Cp	19	174	R2	UC	8	Sr	1	113
R2	UC	6	Cp	10	143	R2	UC	9	Sr	14	147
R2	UC	7	Cp	18	186	R2	UC	1	Rw	13	68
R2	UC	8	Cp	30	196	R2	UC	2	Rw	9	68
R2	UC	9	Cp	17	137	R2	UC	3	Rw	3	55
R2	UC	10	Cp	21	142	R2	UC	4	Rw	1	59
R2	UC	1	Hb	24	134	R2	UC	5	Rw	6	59
R2	UC	2	Hb	14	123	R2	UC	6	Rw	2	81
R2	UC	3	Hb	18	101	R2	UC	7	Rw	6	72
R2	UC	4	Hb	39	124	R2	UC	8	Rw	1	50
R2	UC	5	Hb	16	117	R2	UC	10	Rw	1	56
R2	UC	6	Hb	49	106	R2	UC	8	Rp	5	63
R2	UC	7	Hb	10	105	R2	UC	10	Rp	1	156

APPENDIX X

Regeneration index ($\overline{X}$ ± SEM) by Rep., harvesting operation and species.

Rep.	Species	Clearcut RI (stems/ha)	Clearcut SE*	Partialcut RI (stems/ha)	Partialcut SE	Uncut RI (stems/ha)	Uncut SE
1	Po	93.58	1.47	80.35	2.82	14.51	1.90
1	Pj	0.61	0.49	1.55	0.59	79.29	2.47
1	Cp	2.87	0.89	4.75	1.80	3.51	0.94
1	Hb	0.93	0.62	7.13	2.11	0.23	0.15
1	Mm	0.00	0.00	1.71	0.87	0.00	0.00
1	Bw	1.01	0.77	2.04	1.05	1.14	0.69
1	Sr	0.69	0.69	1.14	0.48	0.00	0.00
1	Rw	0.05	0.05	0.26	0.13	0.00	0.00
1	Rp	0.00	0.00	0.78	0.40	0.00	0.00
1	Wu	0.00	0.00	0.17	0.12	0.82	0.42
1	Hc	0.17	0.17	0.07	0.05	0.45	0.34
1	Ab	0.08	0.07	0.06	0.06	0.06	0.06
2	Po	75.82	2.64	70.21	2.83	57.45	2.04
2	Pj	0.00	0.00	0.00	0.00	0.00	0.00
2	Cp	11.96	2.07	11.77	2.14	12.02	1.47
2	Hb	4.06	1.63	8.53	2.12	9.29	1.96
2	Mm	4.20	0.68	6.45	1.79	15.44	1.79
2	Bw	2.05	1.60	0.86	0.54	3.78	1.32
2	Sr	1.33	0.70	1.00	0.72	0.94	0.76
2	Rw	0.02	0.02	0.66	0.36	0.91	0.26
2	Rp	0.09	0.06	0.04	0.03	0.18	0.12
2	Wu	0.40	0.40	0.34	0.31	0.00	0.00
2	Hc	0.08	0.08	0.12	0.12	0.00	0.00
2	Ab	0.00	0.00	0.04	0.04	0.00	0.00

Note: Po - Trembling aspen, Pj - Jack pine, Cp - Pin cherry, Hb - Beaked hazel, Mm - Mountain maple, Sr - Red-twigged serviceberry, Bw - White birch, Rw - Wild red raspberry, Rp - Prickly wild rose, Wu -Upland willow, Hc - Canada fly honeysuckle, Ab - Black ash. *RI – regeneration index. *SE- standard error