

University of Alberta

Influences of season of harvest, machine traffic and competition on root suckering of
trembling aspen

by

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Abstract

Two field studies were conducted in Manitoba. The first examined the effects of season of harvest and machine traffic on aspen (*Populus tremuloides*) suckering following the harvest of mature aspen stands. Aspen sucker density, height and leaf dry mass were not influenced by season of cut. Sucker height and leaf dry mass were reduced in plots with traffic, although sucker density was not affected. The second study examined the influence of beaked hazel (*Corylus cornuta*) on aspen suckering and rooting depth. Aspen sucker density was reduced by high hazel density, while sucker height was not impacted. Although the total amount of aspen roots in the top 20 cm of the soil was similar whether hazel density was high or low, the amount of aspen roots in shallow soil positions (0-10 cm) was reduced where hazel density was high, which likely reduced sucker density as most suckers originate from surface roots.

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Chapter 1. General Introduction

1.1 Aspen regeneration

Trembling aspen (*Populus tremuloides* Michx.) is a common deciduous tree species in the boreal forest and aspen parkland regions of Canada. Aspen prefers upland sites and growth is impeded at extreme high and low levels of soil moisture (Doucet 1989). It is a clonal, species, with individual clones of different sexes. Reproduction can be both sexual, by seed, and vegetative by root suckering. Small seeds allow long-distance wind dispersal; however, because seeds are short-lived, are constrained by strict moisture and thermal requirements in order to germinate (Doucet 1989), and establishment depends on the availability of exposed mineral soil (Barnes 1966, Doucet 1989), regeneration by seed is less common than by root suckering. Dense aspen stands originate following disturbances such as fire or clearcut harvesting that remove or kill the entire aspen overstory, stimulating root suckering (Frey et al. 2003). Root suckers develop from adventitious buds that form on the parent root system (Schier 1973) in response to the removal of apical dominance and the disruption of auxin to the root system (Farmer 1962, Eliasson 1971b, Schier 1972, Steneker 1974). Auxin is produced in aboveground tissues and transported to the roots where it inhibits suckering (Eliasson 1971a, 1971b). When the flow of auxin is interrupted it is believed that the increased proportion of cytokinins, produced in growing root tips, relative to auxin stimulates sucker initiation (Frey et al. 2003). Once initiated, suckers rely on non-structural carbohydrates (sugars and starch) stored in the roots to sustain their growth until they reach the soil surface and commence photosynthesis (Schier 1981). The concentration of root non-structural carbohydrates has not been shown to influence the number of suckers

initiated, but suckers grow taller and produce more leaf area when root carbohydrates are high at the time of suckering (Schier and Zasada 1973, Landhäusser and Lieffers 2002).

The lateral root system of aspen is shallow, with the majority of root biomass occurring in the top 20 cm of the soil (Ruark and Bockheim 1987) and aspen suckers generally originate on roots within 8 cm of the soil surface (Schier and Campbell 1978, Brown and DeByle 1987, Navratil 1991). Sucker density can commonly reach 100,000 stems per hectare (sph) in the first growing season following harvest, and there are reports of densities in excess of 200,000 sph (Bella 1986). In some circumstances, however, density and growth of aspen suckers is low. Low soil temperatures delay sucker emergence and reduce growth (Landhäusser and Lieffers 1998, King et al. 1999, Fraser et al. 2002, Landhäusser et al. 2001, 2003, 2006), and as aspen is very shade intolerant, once suckers emerge from the soil, growth is reduced or inhibited when ambient light levels are low (Farmer 1963, Landhäusser and Lieffers 2001). Additional factors such as severe soil compaction (Bates et al. 1990, 1993, Kabzems 1995, Stone and Elioff 2000), high slash volume (Bella 1986), competition (Landhäusser and Lieffers 1998, Powell and Bork 2004, Mulak 2006) and the presence of residual stems (Stoeckeler and Macon 1956, Mulak et al. 2006) can also suppress sucker initiation and development.

1.2 Season of harvest and harvest traffic disturbance

Season of harvest has been shown to play a large role in aspen regeneration success. Aspen root carbohydrate reserves are known to vary seasonally, being lowest in the spring at the time of leaf flush and accumulating over the growing season to reach maximum levels in the late summer and early fall by the time of leaf abscission (Tew

1970, Schier and Zasada 1973, Landhäusser and Lieffers 2003). The amount of carbohydrates in the parent roots does not influence the number of suckers that develop (Tew 1970, Schier and Zasada 1973); however, higher concentrations of root carbohydrates found in the fall have been shown to increase shoot growth, root growth, and leaf area of newly initiated suckers compared to lower levels of root carbohydrate reserves found in the spring (Landhäusser and Lieffers 2002). Correspondingly, Mulak et al. (2006) observed reduced sucker height following spring cutting of juvenile aspen stands although the total number of suckers was similar to either winter or summer cuts. Unfortunately, past field studies have not maintained consistent soil disturbance over different harvesting seasons, making it impossible to separately discover the effects of root carbohydrates and soil disturbance.

Both the soil and the shallow aspen lateral root system are more susceptible to traffic disturbance during the spring and summer months when the ground is thawed, compared to the winter months when soils are generally frozen and snow-covered (Navratil 1991). Soil disturbance from harvesting traffic has often been implicated with inferior aspen suckering following harvesting during the growing season (Bates et al. 1990, 1993, Smidt and Blinn 2002). Soil compaction from machine traffic occurs when the heavy equipment exerts a force exceeding the strength of the soil, and is influenced by soil moisture. Compaction results in greater soil bulk density, lower porosity, and therefore lower infiltration rate of water and air (Alban et al. 1994, Kabzems 1995) and these effects have been shown to persist up to 16 years after harvesting and skidding (Froehlich 1979, Brais 2001). Soil compaction is also related to an increase in penetration resistance of the soil (Bezkorowajnyj et al. 1993) making it more difficult for

roots and emerging shoots to penetrate the soil. Tree growth can be stunted when soils are compacted (Froehlich 1979, Bates et al. 1993, Alban et al. 1994, Stone and Kabzems 2002) with higher soil bulk density and heightened resistance to root and shoot penetration decreasing growth, as well as make it more difficult for the trees to obtain necessary water and nutrient resources from the soil. Many studies have observed reduced aspen regeneration following spring and summer harvesting, a result that is likely closely related to the amount of root and soil disturbance (Stoekeler and Macon 1956, Bates et al. 1993). On the other hand, significantly higher, yet more variable, aspen regeneration has been observed following summer harvesting (Bella 1986). The denser patches of suckers are likely due to higher temperatures and lower competition on localized areas where disturbance exposed the soil, removed vegetation (Navratil 1991), and wounded roots, thereby stimulating aspen suckering (Fraser et al. 2004). Obviously a key determinant of aspen regeneration success following different seasons of harvest has been the level of soil and root system disturbance resulting from harvesting traffic. It is not known, however, whether one season produces better aspen regeneration than another, if soil disturbance is kept consistent in different seasons.

1.3 Competition and *Corylus cornuta* Marsh.

Aspen is a fast-growing, highly competitive tree species and aspen suckers usually overtop all competing vegetation during their first growing season. The negative effects of *Calamagrostis canadensis* (Michx.) Beauv. competition and litter on aspen growth and suckering have been documented (Landhäusser and Lieffers 1998, Powell and Bork 2004, Mulak 2006). As the emergence and growth of aspen suckers is reduced

and delayed by soil temperatures below 8°C (Landhäusser et al. 2006), thick grass litter that reduces soil temperatures (Hogg and Lieffers 1991) will negatively impact suckering. Likewise, as aspen is very shade intolerant, shading of emerging aspen suckers will also reduce their growth (Farmer 1963, Landhäusser and Lieffers 2001, Mulak 2006).

The understory shrub beaked hazel (*Corylus cornuta* Marsh.) has many characteristics that may allow it to compete effectively with aspen. Hazel is a common shrub species in the understory of boreal aspen forests, reaching densities of 50,000 sph beneath aspen-birch canopies (Kurmis and Sucoff 1989). Hazel achieves maximum growth at light intensities between 30 and 40% of full sunlight (Hsiung 1951), but can successfully proliferate following overstory removal and release into full sun conditions (Mallik et al. 1997, 2002, Kemball et al. 2005). Therefore, following the harvest of a stand with a dense hazel understory, the established hazel will compete with naturally regenerating or planted trees.

At high densities, the aboveground hazel stems will significantly reduce the amount of light available to emerging aspen suckers. With leaf area indices reaching 5.8 (Stadt and Lieffers 2005), the light intensity beneath a dense hazel thicket may be as low as 2 % of full sun (Hsiung 1951). Farmer (1963) observed diminished aspen height growth under low light intensities and Landhäusser and Lieffers (2001) found that aspen seedlings grown at 21.5 % of full sunlight exhibited significantly reduced height growth, shoot and root mass, and leaf area and death after two years. In addition, soils may be cooler beneath the shade of a dense hazel understory. Cool soil temperatures have been shown to delay the emergence time of suckers (Maini and Horton 1966, Fraser et al. 2002, Landhäusser et al. 2006) and retard aspen seedling growth (Landhäusser and

Lieffers 1998, King et al. 1999, Landhäusser et al. 2001, 2003, 2006) when compared with warmer soil temperatures. Furthermore, suckers growing beneath hazel cover may be physically impeded by the density of roots and stems they must grow through.

Hazel root and underground shoot systems are shallow and extensive (Hsiung 1951). Over ninety percent of hazel roots and underground shoots are located within 15 cm of the soil surface (Hsiung 1951), often directly above the mineral soil (Buckman 1964). Aspen also exhibits a shallow lateral root system with the majority of aspen suckers originating on roots located within 8 cm of the soil surface (Schier and Campbell 1978, Brown and DeByle 1987, Navratil 1991) and root biomass declining with depth, especially below 20 cm (Ruark and Bockheim 1987). This similarity in rooting depths suggests potential for intermixing of roots or root competition leading to exclusion of one species by the other. There is evidence that hazel clones exclude roots of competing species, especially from an area near the centre of a clonal hazel thicket (Hsiung 1951). The density and biomass of hazel roots has been shown to decline with increasing distance from the centre of a clone, while over the same distance root numbers and biomass of other species rises (Hsiung 1951).

There has been little research into the potential competitive effects of hazel on regenerating aspen. Under ideal conditions aspen regeneration density may reach upwards of 200,000 sph (Bella 1986). A high density of aspen regeneration is important for maintaining the parental root system (DesRochers and Lieffers 2001). Anecdotal and some published evidence suggests that a dense hazel understory can drastically impact aspen regeneration following harvest (Stoekeler and Macon 1956). If the presence of hazel lowers the density of aspen regeneration the emerging aspen suckers may not be

able to sustain the parent root system, leading to root death and the possibility that the site will not be successfully recaptured (DesRochers and Lieffers 2001).

The primary objective of this thesis was to examine how several factors affect aspen regeneration. Specifically, the research objectives were first, to investigate the role of season of harvest on aspen suckering; second, to examine the impact of machine traffic on aspen suckering; and third, to study the competitive influences of beaked hazel (*Corylus cornuta* Marsh.) on aspen suckering.

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Chapter 2. Effects of season of harvest and machine traffic on aspen regeneration

2.1 Introduction

Aspen (*Populus tremuloides* Michx.) is a clonal species that regenerates naturally by suckering from the parent root system following a stand-replacing disturbance such as fire or clearcut harvesting (Frey et al. 2003). Season of harvest has often been cited as a major influence on aspen regeneration success partially in response to seasonality of root carbohydrate status. Root carbohydrate reserves are highest in the late summer and early fall, when shoot elongation has ceased but leaves are still green (Landhäusser and Lieffers 2003). There is a steep decline after leaf abscission in late fall which coincides with an increase in the production of new fine roots (Landhäusser and Lieffers 2003) and minimum levels are reached in the spring immediately during leaf flush (Schier and Zasada 1973, Landhäusser and Lieffers 2003). Root carbohydrates accumulate over the growing season and the rate of accumulation increases after the cessation of shoot elongation in mid summer (Landhäusser and Lieffers 2003). Although root carbohydrate reserves do not influence the number of suckers initiated (Tew 1970, Schier and Zasada 1973), they will sustain suckers through their growth out of the soil and prior to the development of photosynthetic tissue (Schier 1981). Correspondingly, Landhäusser and Lieffers (2002) found that suckers were taller, had more biomass, and higher leaf area when sprouts from root systems were cut in the fall, coinciding with peak levels of root carbohydrate reserves.

Seasonal differences in soil susceptibility to trafficking disturbance have also been shown to influence aspen regeneration (Stoekeler and Macon 1956, Bella 1986, Bates et al. 1993), although there has not been consensus in the literature regarding which

harvesting season produces optimal regeneration. Winter logging has commonly resulted in higher aspen regeneration densities and growth compared to summer logging (Stoekeler and Macon 1956, Bates et al. 1993), which is believed to be partly the result of reduced soil compaction and root destruction when harvesting on snow covered ground and frozen soils (Bates et al. 1989, 1993). On the other hand, much higher aspen regeneration has been observed following mid summer harvest (Bella 1986), with the increased ground disturbance and destruction of understory vegetation caused by summer logging. While severe soil compaction and damage to roots has been shown to be detrimental to sucker regeneration density and growth (Bates et al. 1990, 1993, Kabzems 1995, Stone and Eliooff 2000), minor damage due to cutting or scuffing of roots will stimulate suckering (Fraser et al. 2004) and the removal of duff layers will allow soil temperatures to rise (Navratil 1991), which can lead to faster sucker emergence (Maini and Horton 1966, Fraser et al. 2002, Landhäusser et al. 2006) and enhanced growth (King et al. 1999, Landhäusser and Lieffers 1998, Landhäusser et al. 2001, 2003, 2006). Therefore, one of the major difficulties with past work examining the effects of season of harvest on suckering is that soil disturbance has not been consistent among different seasons of cut.

It appears that mature aspen clones invest a large portion of the carbohydrate reserves accumulated in the roots over the summer in the production of new fine roots (Landhäusser and Lieffers 2003). It is not clear, however, if comparable root growth still occurs if the mature stand is harvested during the summer months, or if the carbohydrate reserves are conserved for production of suckers in the following growing season.

The objectives were 1) to determine if number or growth of suckers is affected by the season of harvest (mid summer, late summer, or winter), without the confounding influence of soil disturbance; 2) to test if areas that experience machine traffic have reduced aspen suckering densities and growth; and 3) to test if new root growth is lower in summer-harvested than unharvested stands.

2.2 Methods

2.2.1 Study area and experimental design

Two mature aspen-dominated sites with uniform density were selected from the aspen parkland ecoregion near Roblin, Manitoba (51°13'N, 101°20'W). Stands had minor components of balsam poplar (*P. balsamifera* L.) and white spruce (*Picea glauca* Moench.). The understory was dominated by beaked hazel (*Corylus cornuta* Marsh.) with minor components of pin cherry (*Prunus pensilvanica* Auth.), rose (*Rosa acicularis* Lindl.) and raspberry (*Rubus idaeus* L.). The aspen in the sites was 95 years old on average with an average height of 19 m. Preharvest density and basal area measurements were taken at 12 locations in each site that had previously been designated as the study plots. The average study plot density was 1000 ± 275 stems per hectare (\pm standard deviation (SD)) and the average diameter at breast height (DBH) was 18.5 ± 2.2 cm (\pm SD) resulting in an average basal area of 27.1 ± 6.6 m² per hectare (\pm SD). Soils were well-drained silty clay loams with some sand.

The experiment was set up as a complete randomized block design. Three blocks were located at each of the two sites for a total of six blocks. Each block was 120 m by 120 m and contained four 50 m by 50 m corner plots separated by 20 m shared buffer

strips to be used as skid trails during the plot harvests. The blocks represented areas of uniform aspen density and basal area. All areas immediately surrounding the blocks including the 20 m buffers separating the individual 50 m by 50 m study plots were cut conventionally, using a fellerbuncher and grapple skidder prior to the harvest of the study plots (see below).

Three of the four treatment plots within each block were randomly assigned to one each of mid-summer, late-summer or winter harvest, while the fourth treatment plot remained as an unharvested control. Prior to harvest all understory shrubs were manually cut with brush saws. Harvesting was done by hand-felling trees using a chain saw. All trees in the plots were line-skidded with a cable skidder with no machine traffic in the 50 m by 50 m plots; traffic was constrained to the surrounding 20 m skid trails. The 6 blocks were harvested in the same sequence at each season of harvest treatment. The mid-summer harvest started on July 27, 2005 and finished August 16, 2005. The late summer harvest went from August 24, 2005 to September 7, 2005 and the winter harvest went from November 21 to November 30, 2005. For the winter harvest air temperatures were well below freezing and soil temperature was approaching freezing. The first harvest (mid-summer) took the longest amount of time because the cable skidding followed the harvesting at each plot and subsequent plots were not harvested until the skidding from the previous plot was complete. During the two subsequent harvesting seasons trees from all treatment plots were felled first and skidding only occurred after all felling was completed in order to reduce the time spanned by the harvest. Furthermore, in the mid-summer harvest the trees were all felled by hand with a chain saw whereas in the two subsequent harvest times the outer 8 m rim of trees from each plot was cut and

taken from the plot by a fellerbuncher, thereby decreasing the time required to harvest each plot. A visual assessment following each of the harvests indicated that soil disturbance from the hand-felling and cable-skidding was negligible. The forest floor remained intact with limited disturbance to the herbaceous layer.

In the spring of 2006 an additional six plots were established adjacent to each of the six experimental blocks, in areas impacted by conventional harvesting traffic (fellerbunchers and grapple skidders). Plots were selected prior to suckering and were chosen from areas expected to receive average skidder traffic: midway between block edge and landing and well away from block features that would concentrate skidder traffic. These six conventionally harvested plots were cut between July 13 and September 8, 2005.

2.2.2 Regeneration survey

Regeneration was measured in 16, 10 m² circular subplots in the centre of each 50 m by 50 m plot. The centres of the subplots were arranged in a 4 m by 4 m grid pattern centered on plot centre so that an area of 16 m by 16 m in the centre of each plot contained all subplots. The number of individual suckers was measured within each subplot. In each plot the heights from the 10 tallest suckers were measured and the leaves of those 10 suckers were collected from four subplots located at each corner of the 16 m by 16 m sampling area. The leaves were kept cool until they could be dried at 70°C. Dry leaf mass was computed on a per sucker basis.

2.2.3 *Root carbohydrates and root growth*

In order to determine seasonal variation in root carbohydrate reserves before, during and after suckering, roots were collected in mid July 2005, late July 2005, late August 2005, mid October 2005, mid April 2006, late May 2006, mid August 2006, and mid October 2006. In the control plots, roots were collected adjacent to aspen trees. Following the cutting, root samples were collected next to stumps while following suckering, roots were collected adjacent to suckers. Three root samples 5 to 10 cm long and between 0.5 cm and 1.5 cm in diameter were collected from each plot. All root samples were placed on ice in the field and frozen as soon as possible afterward. Roots were washed and dried at 68°C until constant weight and then ground in a Wiley Mill to pass a 40 mesh screen. Sugars were extracted three times with hot 80% ethanol, followed by a reaction between the extract and phenol-sulfuric acid which allowed sugars to be measured colourimetrically. To measure starch concentrations the tissue remaining after the ethanol extraction was digested with the enzymes α -amylase and amyloglucosidase followed by a colourimetrically measurable reaction with peroxidase-glucose oxidase-*o*-dianisidine (Chow and Landhäusser 2004).

To determine seasonal root growth, ingrowth cores (15 cm in diameter and 15 cm deep) were established in the control and late-summer harvest treatment plots in late July 2005 one month prior to harvest (following Conlin and Lieffers 1993). There were twelve cores in each plot to allow for the extraction of subsamples of three cores at each of 4 sampling times. Following the removal of the native soil from the core, the holes were filled with approximately 2.7 dm³ lightly packed growing medium formulated with peat, vermiculite, perlite, and limestone. Cores were extracted in late August 2005, mid-

October 2005, mid-August 2006 and mid-October 2006. Unfortunately, fallen litter tended to camouflage cores leaving only two subsamples in some instances. After extraction cores were chilled and subsequently frozen to avoid any decomposition of the fine roots. In the lab aspen roots were separated from the soil, dried at 68°C and weighed.

At the same time the ingrowth cores were established, HOBO temperature sensors (Onset Computer Corporation, Bourne, MA) were also inserted into the soil at a depth of 10 cm. Like the ingrowth cores, these sensors were only put in the plots harvested in late summer and the control plots. Soil temperature was monitored from August 2005 until October 2006. Soil degree-days were calculated by summing the average daily temperature above 5°C on a per plot basis and then averaging the sums by treatment.

2.2.4 Data analysis

All data were analyzed with mixed models in SAS (SAS Institute, Cary, NC). Regeneration data for the different seasons of harvest were compared with season of harvest as the main factor and site, site*season of harvest and block(site) as random factors. Regeneration data for the different harvesting methods were compared with harvesting method as the main factor and site and site*harvesting method as random factors. Data from mid- and late-summer untrafficked plots were pooled for comparisons with trafficked plots because the conventional harvesting spanned both of these time periods. Root total non-structural carbohydrate concentrations and root ingrowth data were compared using repeated measures procedures with collection date as the repeated factor. All 2005 preharvest carbohydrate concentrations were pooled as unharvested

controls and analyzed as a linear regression using general linear models in SAS. There were no significant site*treatment interactions for any response variables. Root ingrowth data were *ln*-transformed to meet the assumption of normality. All other data met the assumptions of analysis of variance. Multiple comparisons were performed using the Tukey test.

2.3 Results

2.3.1 Effect of season of harvest

Density of aspen regeneration was not influenced by season of harvest in the first growing season following harvest ($P=0.7006$). After mid-summer harvest, aspen regeneration density was 69 900 stems per hectare (sph), compared to 61 100 sph after late summer harvest, and 63 400 sph following winter harvest (Fig. 2.1A). Similarly, sucker height and leaf dry mass per sucker were not affected by season of harvest. Aspen sucker height was 107 cm following mid-summer harvest, 112 cm for late-summer and 115 cm for winter harvest ($P=0.4320$) (Fig. 2.1B). Leaf dry mass per sucker was 12.4 g per sucker following mid-summer, 12.7 g for late-summer, and 14.2 g for winter harvest ($P=0.6486$) (Fig. 2.1C).

In 2005, total non-structural carbohydrate (TNC) (sum of soluble sugars and starch) concentration increased in aspen roots in the control treatment from mid summer to mid October. Concentrations increased linearly from 18.0% in mid July, to 19.5% in late July, 22.3% in late August and 22.6% in mid October ($R^2 = 0.15$, $P=0.0631$). By the end of winter, in early April 2006 before leaf flush, TNC concentrations in roots had dropped to 17.1% and decreased further to 12.6% by mid May at time of leaf flush. By

August and October 2006, TNC concentrations in roots had recovered to levels similar to the fall of 2005 (24.1% and 25.2%, respectively) (see control Fig. 2.2C).

In early April, root TNC concentrations were higher in roots from plots harvested in the winter compared to both the mid- and late-summer harvests ($P=0.0076$). At this stage root TNC concentrations in the winter-harvested plots were not different from the controls ($P=0.6678$). However by May 2006, all treatment including the controls had their lowest root reserves and no treatment differences could be detected ($P=0.5672$). After May root TNC increased in all four treatments peaking in October 2006 (Fig. 2.2C). In August 2006 TNC concentrations in roots collected from the unharvested control plots were significantly higher than those following the three seasons of harvest ($P<0.0001$), but this trend had weakened by October 2006 ($P>0.05$). In both August and October 2006 there were no differences among the three seasons ($P>0.05$) (Fig. 2.2C).

When TNC concentrations were separated into soluble sugars and starch concentrations, there was no observed difference in sugar concentration among the treatments at any of the four collection times ($P>0.05$) (Fig. 2.2A), while differences observed in TNC were reflected in the root starch concentrations (Fig. 2.2B).

2.3.2 *Effect of harvest traffic*

Although density of aspen regeneration in the first growing season following harvest was similar between machine harvest (63 900 sph) and no-impact harvest (65 500 sph) ($P=0.8906$) (Fig. 2.3A), both average height and leaf dry mass per sucker were different between the treatments. The average height of suckers following conventional harvesting was 88 cm, compared with 109 cm following no-impact harvest ($P=0.0109$)

(Fig. 2.3B) and leaf dry mass per sucker was 8.9 g following conventional harvest and 12.5 g after no-impact harvest ($P=0.0020$) (Fig. 2.3C).

During the first growing season following harvest, root TNC concentrations did not differ between machine harvest and no-traffic harvest at either the August 2006 ($P=0.4163$) or the October 2006 ($P=0.5341$) collection times (Fig. 2.4C). Similarly there were no differences in sugars in August ($P=0.1020$) or October ($P=0.7681$) (Fig. 2.2A) or starch in August ($P=0.7280$) or October ($P=0.1447$) (Fig. 2.2B).

2.3.3 *Root growth*

There was negligible root ingrowth into the cores from both the harvested and unharvested plots collected in August 2005 and October 2005. However, toward the end of the first growing season following harvest (August 2006), aspen root ingrowth was higher in the unharvested control plots (0.30 g dry mass) than those plots harvested in late summer 2005 (0.10 g) ($P=0.0062$) (Fig. 2.5). This same trend in root dry mass per soil core was still apparent in October 2006 but not significant ($P=0.1933$) (Fig. 5).

Soil temperature from August 27, 2005 to October 10, 2006 did not differ whether the stand was harvested (6.4°C) or left unharvested (6.1°C) ($P=0.1222$). Nor did the total number of degree days greater than 5°C differ between the late-summer harvested plots (1349 degree-days) and the unharvested control plots (1328 degree-days) ($P=0.7858$).

2.4 Discussion

Density of aspen suckers was similar whether stands were harvested in mid-summer, late-summer or winter. This corresponds with findings of Bates et al. (1993), who harvested mature stands in summer and winter and also minimized harvesting traffic, and with Mulak et al. (2006) who cut juvenile aspen stands at different seasons. In addition, sucker height and leaf dry mass did not differ following the three seasons of harvest. This is similar to Bates et al. (1993); however, reduced height growth (Mulak et al. 2006), biomass and leaf area (Landhäusser and Lieffers 2002) have been observed after spring cutting of immature aspen. Although total non-structural carbohydrate (TNC) concentrations (soluble sugars and starch combined) for the unharvested control plots in 2005 tended to increase from mid-summer to late fall, they were similar among all cut plots by May 2006, just prior to suckering. Therefore, in terms of root carbohydrates, the often-held hypothesis that there will be increased TNC reserves available to support growth of suckers following winter cutting (Bates et al. 1989, 1993) was not supported by this experiment. The elevated TNC concentrations found in the dormant roots of the winter-cut plots in April 2006, driven by higher concentrations of starch, suggests that there were indeed more root carbohydrates available than in the plots cut in summer. This was likely due to carbohydrate accumulation during the longer growing season into the late summer and fall, prior to the winter harvest. However, the depletion of these reserves prior to suckering indicated that most of the TNC reserves built up by late fall were lost over winter because of root growth (Landhäusser and Lieffers 2003) or other undescribed processes.

It is apparent that differences in aspen regeneration found by previous season of harvest studies that included harvesting traffic in their experimental designs (Stoekeler and Macon 1956, Bella 1986, Bates et al. 1993) were highly influenced by the trafficking disturbance. It has long been known that aspen regeneration can be negatively affected by severe soil and root disturbance inflicted by machine traffic (Bates et al. 1990, 1993, Kabzems 1995, Stone and Elioff 2000), while lower levels of compaction (Corns and Maynard 1998) and root disturbance (Fraser et al. 2004) can stimulate suckering. In this study aspen regeneration density was similar whether stands were harvested with or without machine traffic; however, both sucker height growth and leaf dry mass were significantly reduced under conventional harvesting methods. Similarly, Alban et al. (1994) and Stone and Kabzems (2002) did not observe significantly different densities of aspen suckers between compacted and non-compacted plots, while they both observed reductions in sucker height growth. A reduction in leaf dry mass following harvesting may limit the ability of the stand to maintain its parent root dry mass in the early years of sucker development (DesRochers and Lieffers 2001, Landhäusser and Lieffers 2002). We did not observe a difference in root carbohydrate reserves (sugars, starch or TNC) between trafficked and untrafficked plots; however, the lower leaf dry mass in trafficked plots will likely reduce the suckers' ability to accumulate carbohydrate reserves for future growth.

Root growth was negligible in both harvested and unharvested stands in the fall immediately after the ingrowth cores were established, and it is likely that roots had not recovered from being severed. By August 2006, however, total root growth in unharvested plots was three times greater than in plots that had been harvested in late

summer 2005, suggesting that unharvested stands invested significantly more carbohydrate reserves into root growth. Indeed, total non-structural carbohydrate concentrations were higher in unharvested plots by August 2006. Between August and October 2006 the rate of root growth was similar between the harvested and unharvested plots and just slightly lower than that observed by Landhäusser and Lieffers (2003), which suggests that the harvested plots were starting to recover their root growth to levels of the uncut forest. Landhäusser and Lieffers (2002) found that sucker root mass was correlated with leaf mass. In our study, as sucker leaf area reached its peak towards the end of the growing season it is likely that root growth also increased.

There was no observed difference in soil temperature at a depth of 10 cm, so although soil temperature is known to influence aspen root growth (Landhäusser and Lieffers 1998, King et al. 1999, Landhäusser et al. 2001, 2003), it cannot be considered a factor in this study. Because our harvested plots were hand-felled, there was little disturbance to the soil surface or the herbaceous layer and the lack of soil disturbance and ground exposure likely helped to keep soil temperatures in harvested plots similar to unharvested plots, especially during the summer following aspen suckering and leaf area development.

In summary, we found that season of harvest does not affect aspen sucker density or vigour when there is no impact from machine traffic used during harvesting and skidding. However, we did not test spring or early summer harvest and the low root carbohydrate reserves at this time might reduce sucker vigour as previously observed by Landhäusser and Lieffers (2002) and Mulak et al. (2006). Machine traffic during summer harvest reduced sucker height and leaf dry mass, although density was not

affected. A reduction in vigour could lead to a decreased ability to accumulate root carbohydrate reserves and the loss of portions of the parent root system (DesRochers and Lieffers 2001, Landhäusser and Lieffers 2002). As there is little possibility of aspen being harvested economically without machines, it will likely still be best to reduce the impacts of traffic on the root system. This can be achieved by predominantly harvesting aspen stands during frozen ground conditions or by concentrating traffic in specific areas while minimizing traffic on significant portions of the harvested areas.

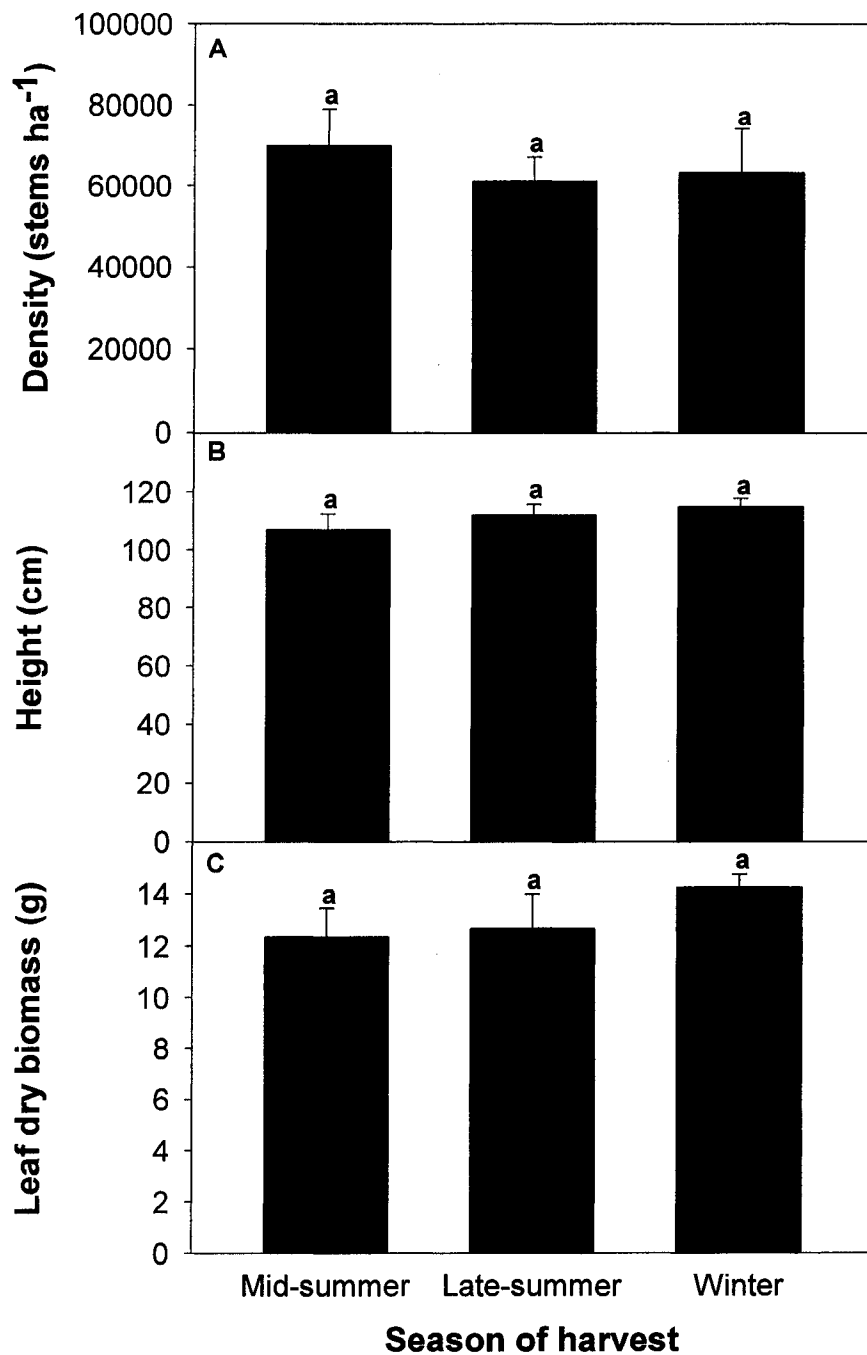


Fig. 2.1. Density (A), height (B), and leaf dry mass per sucker (C) of first-year aspen regeneration following mid-summer, late-summer, and winter harvest. Bars with different letters are significantly different at $\alpha = 0.05$. $n = 6$ for all seasons of harvest. Error bars represent standard error of the mean.

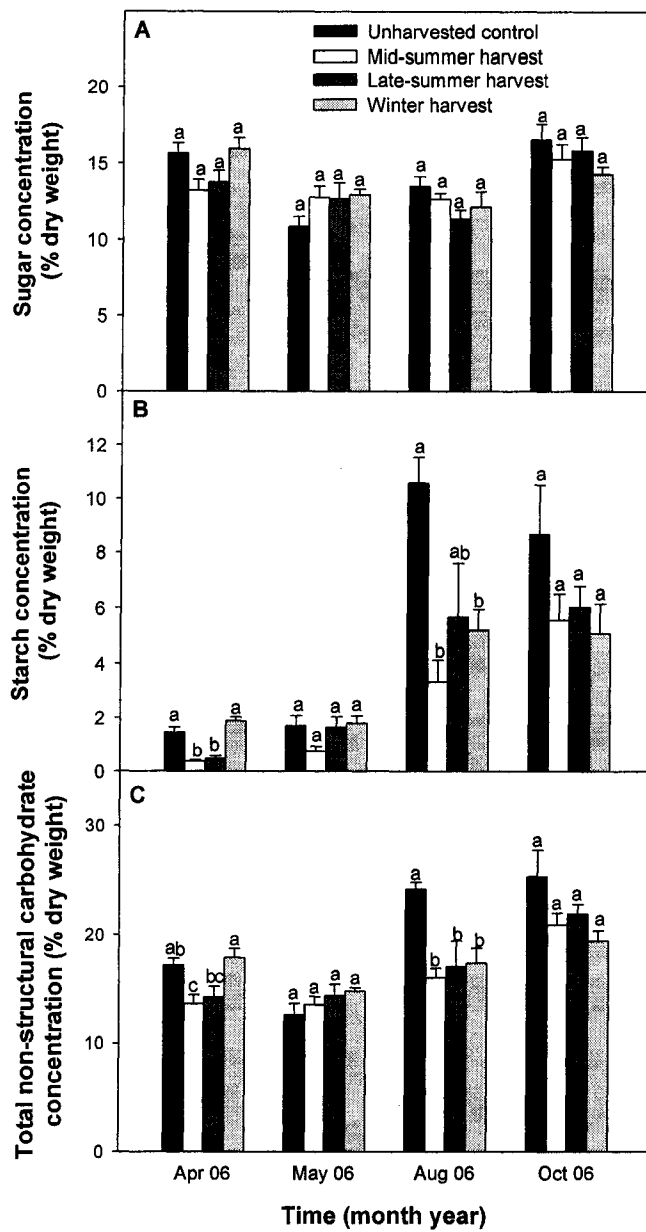


Fig. 2.2. Concentration of sugar (A), starch (B) and total non-structural carbohydrates (C) in aspen roots in relation to season of harvest. Prior to suckering, root samples (0.5 to 1.5 cm in diameter) were collected near the stumps of harvested aspen (July 05 to May 06) and following sucker initiation, root were collected near suckers (Aug 06 and Oct 06). $n = 6$ for all collection times. Error bars represent standard error of the mean. Bars with different letters are significantly different at $\alpha = 0.05$ for each collection time.

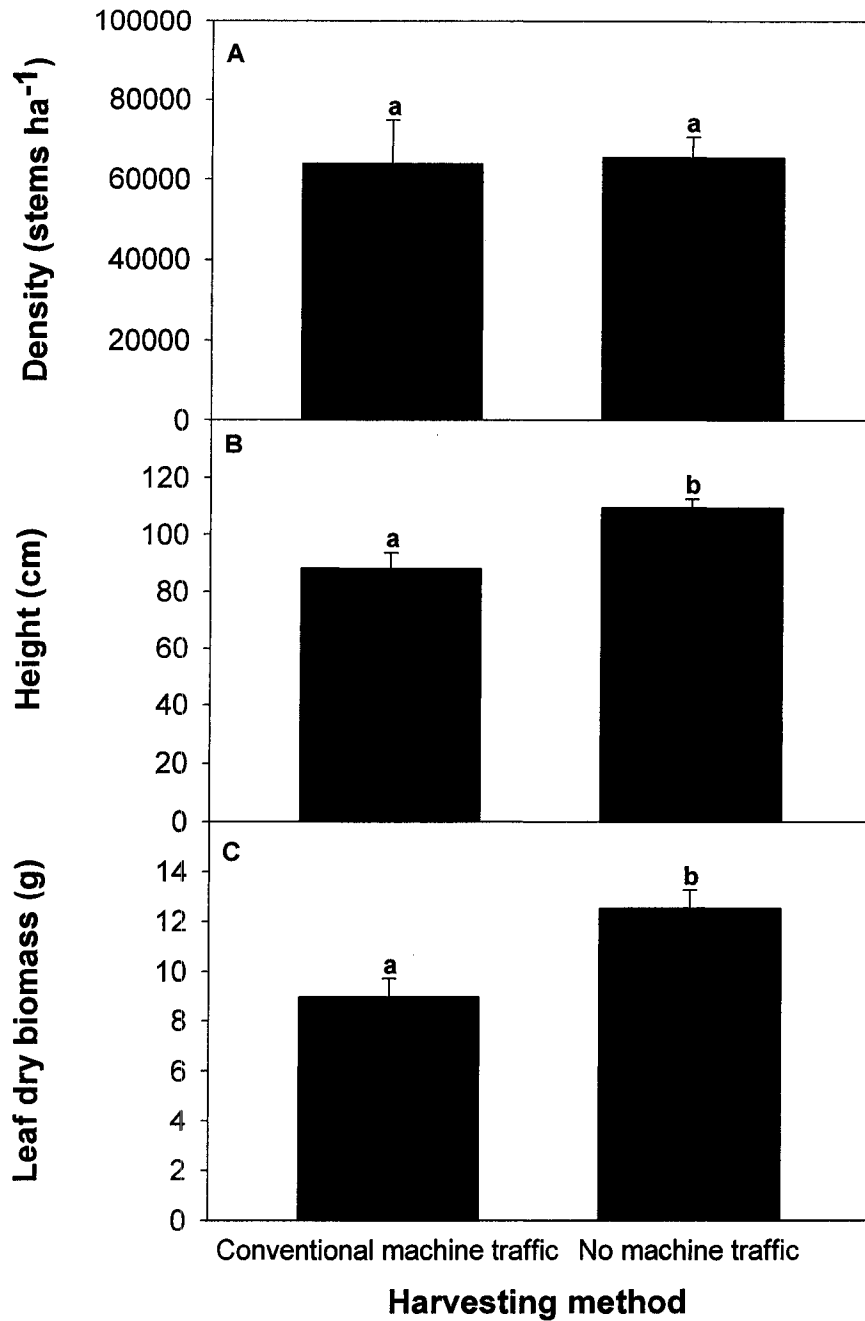


Fig. 2.3. Density (A), height (B), and leaf dry mass per sucker (C) of first-year aspen regeneration following machine and no-traffic harvesting. Bars with different letters are significantly different at $\alpha = 0.05$. $n = 6$ for both the conventional summer harvest and the no traffic summer harvest. Error bars represent standard error of the mean.

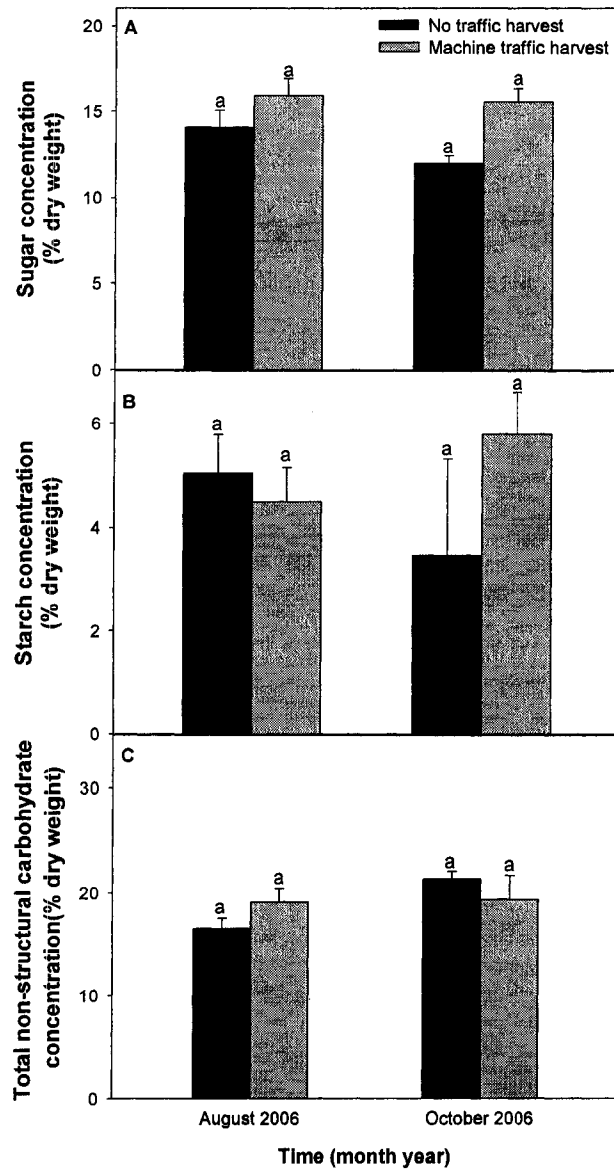


Fig. 2.4. Concentration of sugar (A), starch (B) and total non-structural carbohydrates (C) in aspen roots in relation to the presence or absence of machine traffic during harvest. Root samples (0.5 to 1.5 cm in diameter) were collected in association with aspen suckers. $n = 6$ for both levels of traffic. Error bars represent standard error of the mean. Bars with different letters are significantly different at $\alpha = 0.05$ for each collection time.

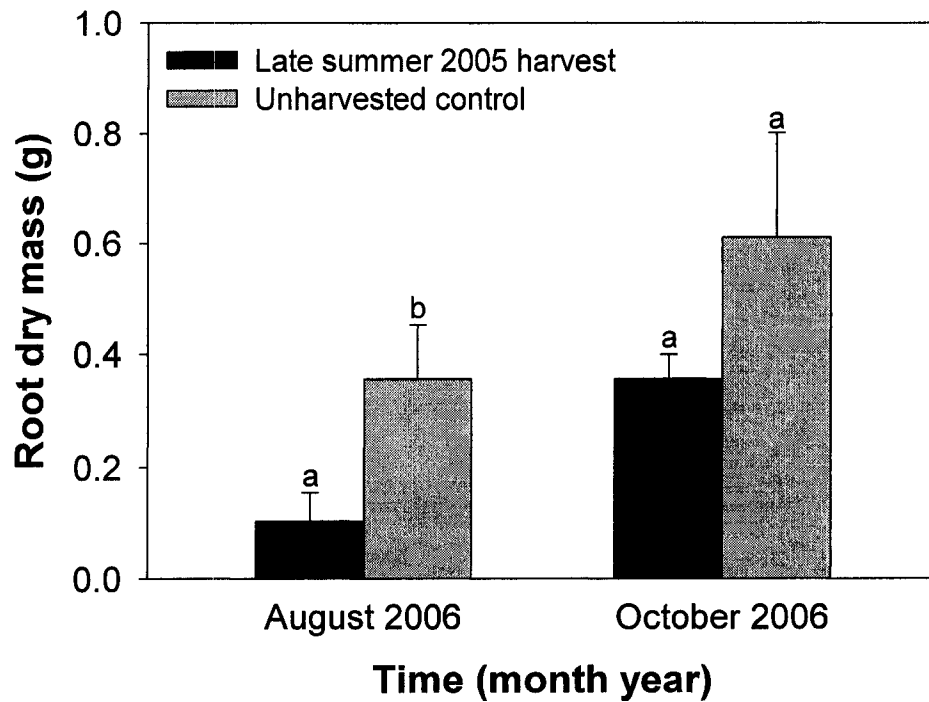


Fig. 2.5. Aspen root dry mass extracted from 2.7 dm³ root ingrowth cores as affected by late summer 2005 harvest. $n = 6$ for both treatments and collection times. Error bars represent standard error of the mean. Bars with different letters are significantly different at $\alpha = 0.05$ for each collection time.

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Chapter 3. Effects of *Corylus cornuta* on root suckering of *Populus tremuloides*

3.1 Introduction

Trembling aspen (*Populus tremuloides* Michx.) typically regenerates by sprouting from the parent root system following a disturbance that removes or kills the aboveground portion of the clone. Optimal suckering is partially dependent on preexisting clonal characteristics such as rooting depth and root carbohydrate reserves. Aspen generally has a shallow lateral root system with the majority of aspen suckers originating from roots located within 8 cm of the soil surface (Schier and Campbell 1978, Brown and DeByle 1987, Navratil 1991). Deeper roots are capable of producing suckers when the surface soil is disturbed or removed (Schier and Campbell 1978, Brown and DeByle 1987, Fraser et al. 2003); however, they usually do not sucker, likely because suckers are unable to reach the soil surface or are hormonally suppressed by the suckers that arise first from shallower roots (Eliasson 1971, Schier 1972). Root carbohydrate reserves at the time of suckering provide energy to the emerging suckers until they breach the soil surface and begin photosynthesis (Schier 1981), and have been shown to influence aspen height growth and leaf area development (Schier and Zasada 1973, Landhäusser and Lieffers 2002).

Site conditions also influence sucker development, growth, and survival. Cool soil temperatures have been shown to delay or inhibit the emergence of suckers (Maini and Horton 1966, Fraser et al. 2002, Landhäusser et al. 2006) and retard aspen seedling growth (Landhäusser and Lieffers 1998, King et al. 1999, Landhäusser et al. 2001, 2003, 2006). Furthermore, as aspen is shade intolerant, low light intensities slow sucker growth (Farmer 1963) and reduce their survival (Landhäusser and Lieffers 2001).

There is anecdotal evidence that aspen suckering is reduced in stands where beaked hazel (*Corylus cornuta* Marsh.) is abundant in the understory prior to logging, but there are relatively few published reports (Stoeckeler and Macon 1956). Hazel clones have extensive and shallow root and rhizome systems with over 90% of the underground mass occurring within 15 cm of the soil surface (Hsiung 1951). Therefore hazel occupies the same rooting zone as aspen which could lead to root competition between the two species. There is evidence that hazel clones exclude roots of other species, especially from near the centre of the hazel clone (Hsiung 1951). As hazel densities can reach 50,000 stems per hectare (sph) (Kurmis and Sucoff 1989) and leaf area indices up to 5.8 (Stadt and Lieffers 2005), the amount of light available to emerging aspen suckers can be as low as 2 % of full sun beneath high density hazel thickets (Hsiung 1951, Stadt and Lieffers 2005). Any resulting reduction in soil temperature due to shading from dense hazel may further inhibit suckers as they develop.

A field study was undertaken to examine how aspen rooting depth prior to logging and subsequent sucker regeneration after harvest are affected by understory hazel density. We hypothesized that aspen rooting depth in high density hazel sites may be lower because of competition with the shallow roots and rhizomes of hazel.

3.2 Methods

3.2.1 Study area and experimental design

Study sites were selected in the aspen parkland ecoregion of western Manitoba, near the town of Roblin (51°13'N, 101°20'W). The mean January temperature at Roblin is -21.7°C and 17.5°C for July. The mean annual precipitation is 475.1 mm with 351.1

mm falling as rain. Two large aspen areas (75.8 and 86.6 ha) designated for harvest in late summer 2005 were selected for study. Sites had well-drained subxeric silty clay to clay loam soils with layered fine textured lacustrine material over medium to fine till. The forests were dominated by mature aspen with some white spruce (*Picea glauca* (Moench) Voss). The aspen was ~150 years old with an average height of 19 m. The understory was dominated by beaked hazel (*Corylus cornuta* Marsh) with some pin cherry (*Prunus pensylvanica* L.f.), Saskatoon (*Amelanchier alnifolia* Nutt.), and prickly rose (*Rosa acicularis* Lindl.).

Prior to harvest, 10, 200 m² circular study plots were chosen within each of the two cutblocks for a total of 20 plots. In each cutblock five plots were located in an area of high hazel density (47,220 sph) and five plots in adjacent areas of low hazel density (3630 sph) (Table 3.1); plots were not paired. Other woody vegetation partly compensated for the scarcity of hazel in the low density plots (19,300 sph), but total stems of all shrubs were still less than half that of the high density plots (Table 3.1). Hazel canopy height in the high density plots averaged 180 cm, while in the low density plots hazel/other shrub height was 70 cm ($P < 0.0001$) (Table 3.1) (see below for methods for hazel and other shrub measurements). Similar stand characteristics (basal area, DBH and stem density) for the aspen between the plots of the different hazel densities (Table 3.1) suggest that the main difference between the plots was the density of the hazel, presumably due to random distribution of dense hazel clones. Similarly, aspen root carbohydrate reserves prior to suckering (May 2006) were also similar between the plots (Table 3.2) (see below for methods). No differences were observed in soil characteristics between plots of different treatments. Study plots of a particular treatment were at least

50 m apart. Plots were marked and harvested between August 30 and September 27, 2005. During harvest felling equipment stayed outside the plot and reached in to remove the trees. As no machine traffic entered the plots the hazel understory was left intact and root systems were not disturbed.

3.2.2 *Regeneration survey*

In mid August 2006, after the first growing season, six 10 m² circular subplots were delineated in a circle approximately equidistant between the outer edge of each 200 m² plot and the plot centre. In each subplot all aspen suckers were counted and height was measured on the tallest ten suckers. Hazel density and canopy height, and the density of other woody shrubs were also recorded. Photosynthetically active radiation (PAR) at sucker height was measured at the time of the regeneration survey using a Sunflect ceptometer (Decagon Devices, Inc., Pullman, WA) by taking an average of readings from four opposing directions at the centre of each subplot. PAR was expressed as a percentage of above-canopy conditions using average PAR measurements taken at full light outside of the plots before and after the plot measurements. From the 20 plots, one low hazel density plot was omitted from the aspen, hazel and PAR measurements because residual aspen trees were present near the plot. Soil temperature was measured on a per-plot basis over the growing season. HOBO temperature sensors (Onset Computer Corporation, Bourne, MA) were inserted at each plot centre on May 31 at a depth of 5 cm and were removed at the time of the regeneration survey in August, 2006; thus the mean temperatures for the hazel and non-hazel plots had a sample size of 10. Soil temperature over the growing season, expressed as degree-days above 10°C, was

measured by summing the average daily temperature above 10°C on a per plot basis for 68 days from June 2 until August 8, 2006 and then averaging the sums by treatment.

3.2.3 *Root excavations*

Following the regeneration measurements, five of the six subplots within each plot were randomly chosen for root excavations. A backhoe with a bucket with a sharpened edge was used to excavate a vertical trench 1 m wide by 50 cm deep, avoiding obvious rocks and stumps and their associated large roots. The sharpened edge of the bucket cleanly cut through the roots. The face of each trench was further cleaned with a sharp square spade so that intersecting roots were clearly visible on the profile of the trench. The backhoe never entered the plots and thus did not have an impact on rooting depth. A transparent plastic sheet 50 cm across by 20 cm deep was tacked against the face of the trenches. The top of the transparencies were aligned with the top of duff layer and the positions of all visible aspen roots and hazel roots and rhizomes intersecting the trench face were marked on the sheet with a permanent marker. The cross-sections of live and dead aspen roots intersecting the soil profile were outlined on the transparencies; cross-sectional surface area of live aspen roots was calculated. There was no attempt made to discriminate among the different sizes of hazel roots. The depths of all roots were measured off of the transparencies. Equipment failure during the root excavation led to the omission of one additional plot, resulting in a sample size of 9 for each treatment.

3.2.4 *Root carbohydrate reserves*

Aspen roots were collected for carbohydrate analysis on May 31 and August 9, 2006. Root samples consisted of three to five roots 5 to 10 cm long with diameters between 0.5 and 1.5 cm. Following collection, roots were put on ice immediately and frozen as soon as possible afterward. In the lab all root samples were washed and dried at 68°C until constant weight and ground in a Wiley Mill to pass a 40 mesh screen. Sugars were extracted three times with hot 80% ethanol followed by a reaction between the extract and phenol-sulfuric acid which allowed sugars to be measured colourimetrically. To measure starch concentrations the tissue remaining after the ethanol extraction was digested with the enzymes α -amylase and amyloglucosidase followed by a colourimetrically measurable reaction with peroxidase-glucose oxidase-*o*-dianisidine (Chow and Landh usser 2004).

3.2.5 *Data analysis*

Data from aspen and hazel regeneration and root depth were analyzed with using mixed model procedures in SAS (SAS Institute, Cary, NC) with hazel density (high and low) as the main factor and site as a random factor. Root carbohydrate reserves were analyzed using repeated measures procedures with collection time as the repeated factor. All data presented conformed to the assumptions of normality and homogeneity of variances necessary to analysis of variance procedures. Aspen live root number was *ln*-transformed to meet the assumption of normality and aspen regeneration density, hazel density, and shrub density were *ln*-transformed in order to meet the assumption of homoscedasticity. Analyses showed that there were no significant site by treatment

interactions for all response variables. A significance level of $\alpha=0.05$ was used for all response variables.

3.3 Results

After logging photosynthetically active radiation (PAR) reaching the aspen sprouts was 61.5% in the high hazel density plots compared to 98% in the low density plots (Table 3.2). Soil temperature and soil degree-days above 10°C did not appear to be influenced by the hazel cover (Table 3.2), averaging 16°C over the growing season regardless of shrub density ($P=0.6859$).

Density of aspen regeneration (43 600 sph) was reduced in the high hazel density plots compared to 68 200 sph in the low hazel density plots ($P=0.0448$) (Fig. 3.1A). Sucker height of the 10 tallest suckers tended to be lower at high hazel densities (109 cm) compared to suckers at the low hazel density (120 cm), although these differences were not significant ($P=0.1281$) (Fig. 3.1B).

There were more hazel + other shrub roots within 10 cm of the soil surface in the plots with high hazel density (11.0 roots/500 cm²) than the low density treatment (6.2 roots/500 cm²) ($P=0.0022$). This was also reflected at the lower soil depth with 5.0 hazel roots/500 cm² in the high hazel density treatment and 2.9 roots/500 cm² in the low hazel density treatment ($P=0.0043$). The average rooting depth of hazel was similar at 8.1 cm for both treatments ($P=0.9303$). The total number of hazel + other shrub roots was greater in the high hazel density plots (15.9 roots /1000cm²) than in the low density plots (9.9 roots /1000cm²) ($P=0.0012$).

The number of live aspen roots did not differ between the high (11.4 roots /1000cm²) and low hazel densities (10.3 roots /1000cm²) ($P=0.5618$), nor did the average live aspen root depth (high hazel density: 11.1 cm, low hazel density: 9.75 cm, $P=0.3633$). Although total aspen root surface area was not different between the high and low densities of hazel ($P=0.3684$), it was distributed differently in the soil profile. Aspen root surface area in the top 10 cm of the soil profile was lower in the plots with high density hazel compared to low density plots ($P=0.0232$) (Fig. 3.2A), while deeper in the soil (10 – 20 cm down) surface area was not different between the treatments ($P=0.8228$) (Fig. 3.2B). Hazel density did not impact the average number of dead aspen roots ($P=0.3530$) and the average depth of these roots ($P=0.2119$). There was also no difference in the number of dead aspen roots between the two hazel densities in the 0-10 cm depth ($P=0.2532$) or 10-20 cm depth ($P=0.7459$).

Total nonstructural carbohydrates (TNC) in suckering aspen roots tended to be higher in roots collected at the end of the first growing season in August (15.5%) compared to TNC in roots collected at the beginning of the growing season in May (14%) ($P=0.0650$). However, there was no effect of hazel density on root TNC concentrations ($P=0.6488$) (Table 3.2).

3.4 Discussion

After harvest, aspen sucker densities were reduced by more than one third in areas dominated by hazel. Our excavations in these areas showed that the cross-sectional surface area of aspen roots (used to estimate root biomass) was lower in the upper soil profile than in areas with little hazel. The presence of less aspen root biomass in shallow

positions (0-10 cm depth) likely resulted in the reduced density of sucker regeneration. Aspen suckers typically arise from roots within 8 cm of the soil surface (Schier and Campbell 1978, Brown and DeByle 1987, Navratil 1991) and covering aspen roots with thicker layers of organic matter is known to reduce suckering (Fraser et al. 2004). Although deeper aspen roots are capable of suckering when the surface soil layer thickness is reduced by fire or site preparation (Schier and Campbell 1978, Brown and DeByle 1987, Fraser et al. 2003), sucker numbers are lower when the upper soil layers remain intact (Alban et al. 1994, Stone and Kabzems 2002, Fraser et al. 2003). This response could be owing to several factors: firstly a hormonal suppression from the first suckers to reach the soil surface, i.e., likely those originating from shallower roots (Eliasson 1971, Schier 1972); secondly, suckers originating from deeper roots need longer to reach the soil surface; and thirdly, deeper roots likely experience colder soil conditions than surface roots leading to delayed sucker growth and therefore emergence (Landhäusser and Lieffers 1998, King et al. 1999, Landhäusser et al. 2001, Fraser et al. 2002, Landhäusser et al. 2003, 2006).

The vertical stratification of roots such as seen with aspen and hazel has been attributed to interspecific root competition in other species mixtures. Bolte and Villanueva (2006) found that fine roots of *Fagus sylvatica* L. occurred deeper when it was grown intermixed with *Picea abies* (L.) Karst., and Zutter et al. (1999) found fine roots of both *Pinus taeda* L. and *Liquidambar styraciflua* L. were reduced in the top 15 cm of the soil when grown with *Andropogon virginicus* L.

The fact that sucker height growth was similar between the high and low hazel density plots was not anticipated. Similar root carbohydrate reserves were available for

sucker growth in May, just prior to suckering; however it was expected that lower light levels beneath high densities of hazel would reduce height growth. Although the hazel stems were largely undamaged by the harvesting, leaf size and leaf number of the hazel that had been protected during harvesting were much smaller than leaves on hazel growing beneath an intact aspen canopy. This allowed the aspen suckers growing beneath the high density hazel to still receive an average of 60% of full sunlight. This intensity of light is sufficient for aspen to photosynthesize close to saturation levels (Landhäusser and Lieffers 2001). It is likely that the hazel clones went into shock when released into full sun conditions. Hsiung (1951) observed that hazel stems seen thriving beneath intact canopies can die within 2 years of overstory removal but will recover through new sprouting from the root system. Indeed, hazel densities have been shown to recover quickly after overstory harvesting (Mallik et al. 1997, 2002, Kembal et al. 2005).

Although in our study, local densities of hazel patches reached 50 000 sph, the overstory of the aspen was intact and the overall vigour of hazel was probably far below that of hazel found in declining aspen stands. We anticipate that the effect of hazel competition on suckering in declining aspen stands will be much greater because of reduced root density of the aspen, especially near the surface, and because the hazel is likely less sensitive to increased exposure after harvest. In these declining stands hazel might be controlled by manual brushing, but hazel is known to quickly resprout following cutting or fire (Buckman 1964, Tappeiner 1979, Mallik et al. 2002). Herbicide application is considered to be the most effective means of hazel control (Waldron 1959, Tappeiner 1979, Mallik et al. 2002). However, the herbicides may need to be applied some years prior to harvest of the aspen to allow the aspen roots to recapture the upper

soil layers and improve the suckering response following harvest. Following harvest mechanical site preparation treatments might be also applied to remove or disturb some of the top soil layer, thereby stimulating suckering (Fraser et al. 2003).

Table 3.1. Aspen basal area, density and diameter at breast height determined prior to harvest and density and height of hazel and other shrub species determined following harvest.

		Aspen	Aspen	Hazel / other			
Hazel		BA	density	Aspen	Hazel density	Other shrub	shrub canopy
density	<i>n</i>	(m ² ha ⁻¹)	(sph)	DBH (cm)	(sph)	density (sph)	height (cm)
High	10	56.9±4.0a	1535±235a	22.4±1.3a	47220±2150a	7200±1400a	180±10a
Low	10	54.9±2.8a	1160±115a	24.0±1.2a	3630±810b ^a	19300±3700b ^a	70±8b ^a

Note: Different letters represent significant differences ($P < 0.05$).

^a*n*=10

Table 3.2. Average photosynthetically active radiation (PAR), total soil degree days (above 10°C), and aspen root total non-structural carbohydrates (% dry weight) in plots with high and low hazel densities.

Hazel density		% Full Sun PAR	Total Soil DD	Total non-structural carbohydrates May 2006 (% dry weight)	Total non-structural carbohydrates August 2006 (% dry weight)
	<i>n</i>				
High	10	61.5±0.02a	392.6±17.4a	14.3±0.5a	15.5±0.6a
Low	9	97.8±0.02b	388.9±14.5a ^a	13.7±0.8a	15.4±0.5a

Note: Different letters represent significant differences ($P < 0.05$).

^a*n*=10

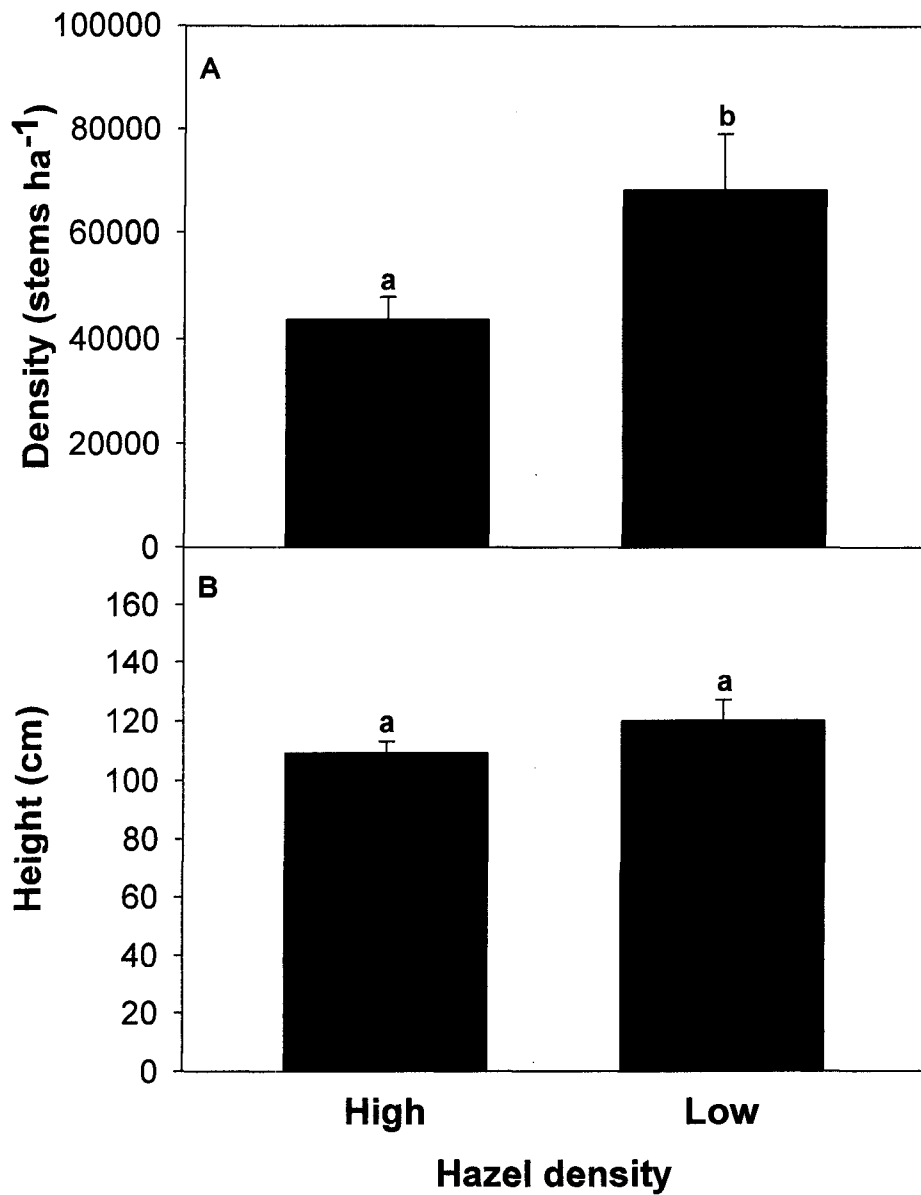


Fig. 3.1. Density of aspen suckers (A) and height of the dominant aspen suckers (B) in relation to hazel density (high or low). Bars with different letters are significantly different at $\alpha = 0.05$. Error bars represent standard error of the mean.

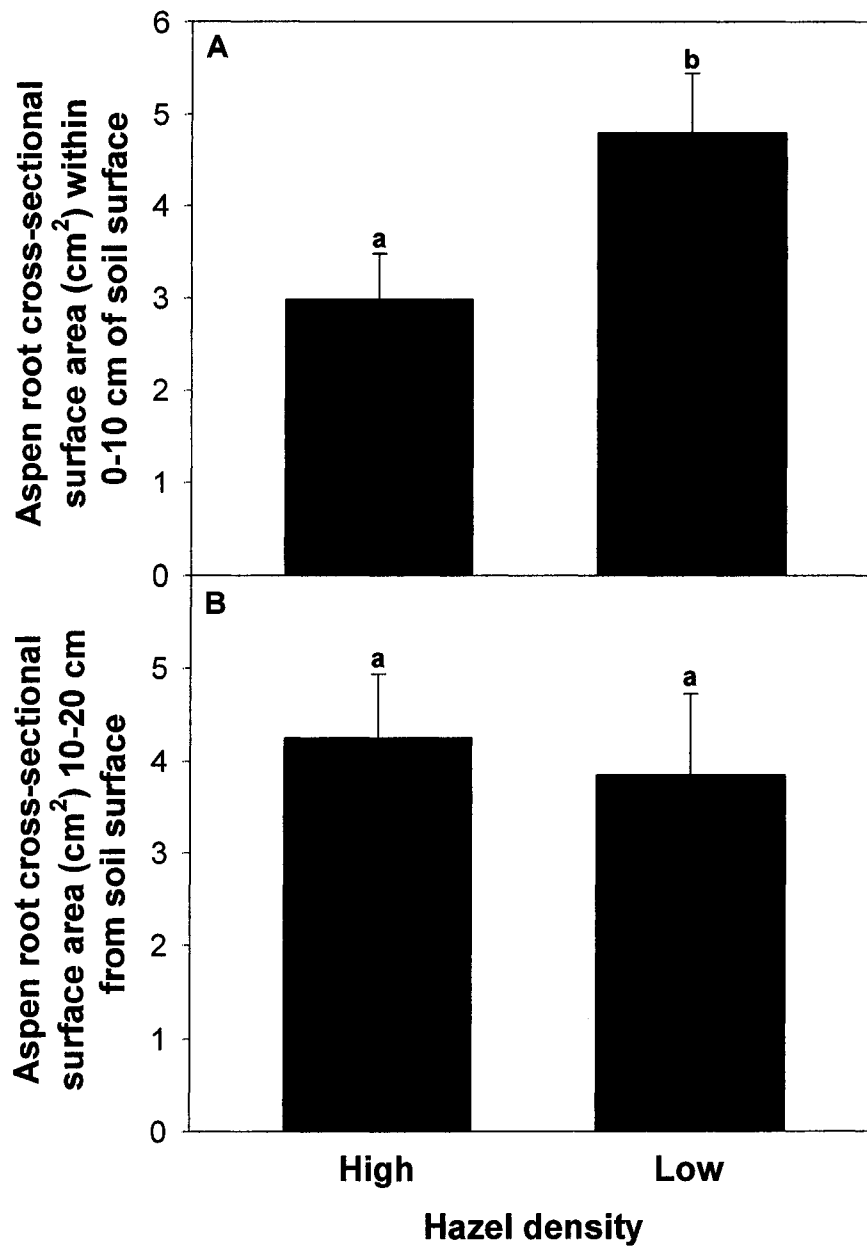


Fig. 3.2. Average cross-sectional surface area of aspen roots in (A) the top 10 cm of the soil profile and (B) between 10 and 20 cm down in the soil profile in sites with high and low hazel density. All roots were measured from a vertical profile of 500 cm² (10 cm deep by 50 cm wide). Bars with different letters are significantly different at $\alpha = 0.05$. Error bars represent standard error of the mean.

3.5. References

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Chapter 4. Research Summary, implications and future research

In this thesis I looked at how season of harvest, machine traffic disturbance, and shrub competition affect aspen regeneration densities and growth. Results from Chapter II indicated that season of harvest, when not confounded with different levels of soil and root damage from machine traffic, did not influence either aspen sucker density or vigour. There had not been a consensus in past literature regarding the best season to harvest to achieve optimal aspen regeneration. Dormant-season harvesting has often produced better regeneration, as ground disturbance is minimized and root carbohydrate levels are thought to be highest during that time (Stoekeler and Macon 1956, Bates et al. 1993); however, increased soil temperature and reduced competition (Navratil 1991) have been linked to heightened suckering following summer harvesting (Bella 1986). The similar regeneration density, height and leaf dry mass following the different seasons of harvest (mid-summer, late-summer and winter harvests) suggests that previous studies on season of harvest were likely confounded by the different levels of harvesting traffic. My study was conducted to ensure the plots harvested at different seasons received similar, but minimal soil disturbance.

By controlling soil disturbance, this study was able to effectively demonstrate the influence of aspen's physiological state on subsequent suckering and determine if this changes with season. At the time of cutting, total root carbohydrate reserves were lower during the mid-summer cut than either the late-summer or winter cuts; this is consistent with the established pattern of accumulation of carbohydrate reserves throughout the growing season (Tew 1970, Schier and Zasada 1973, Landhäusser and Lieffers 2003). It was anticipated that sucker vigour would vary based on the level of root carbohydrates

present at the time of harvest as has been previously shown in greenhouse experiments (Schier and Zasada 1973, Landhäusser and Lieffers 2002). In my field experiment, however, root carbohydrate concentrations in May, just prior to suckering, were not different among the three seasons of cut and, correspondingly, no difference in sucker density, height or leaf dry mass was observed, suggesting that differences in the physiological status of aspen roots at the time of harvest did not significantly influence aspen regeneration.

Machine traffic during summer harvests has often been implicated in reduced aspen sucker densities and vigour (Bates et al. 1990, 1993, Kabzems 1995, Stone and Elioff 2000). This is corroborated in the results of Chapter II that showed reduced aspen height and leaf dry mass when machine harvesting was employed, although aspen sucker density was not affected. A decrease in leaf dry mass can lead to heightened root death as not enough carbohydrates are synthesized to sustain the parent root system (DeRochers and Lieffers 2001, Landhäusser and Lieffers 2002).

In Chapter III I examined the effects of a dense hazel understory on aspen regeneration and rooting depth. There was anecdotal evidence from past studies that dense hazel understories impede aspen regeneration (Stoekeler and Macon 1956). In a field study I demonstrated that a dense hazel understory did in fact reduce the density of sucker regeneration compared to areas where hazel densities were low. Because aspen suckers typically originate from roots within 8 cm of the soil surface (Schier and Campbell 1978, Brown and DeByle 1987, Navratil 1991), I believe that the lower amount of roots in the upper layer of soil (0-10cm depth) under high densities of hazel was the likely cause for the observed one-third reduction in suckering. Sucker height growth was

not affected by hazel density, likely because root carbohydrate reserves were similar prior to suckering: regardless of hazel density, equivalent concentrations were available for sucker growth. Furthermore, although light levels were reduced by nearly 40% below the high densities of hazel stems, light levels were high enough to remain close to the light saturation point for open-grown aspen (Landhäusser and Lieffers 2001).

The research presented in this thesis has many implications for the successful management of aspen stands designated for harvest. Although season of harvest does not affect aspen regeneration based solely on the physiological state of the parent stand when harvested in mid-summer, late-summer or winter, site disturbance as a result of machine traffic will continue to be a factor during harvest operations. Conventional harvesting practices that employ fellerbunchers and grapple skidders will compact the soil and damage aspen root systems to varying degrees based on the condition of the soil. Damage from harvesting and skidding traffic will vary depending upon the state of the soil, whether it is frozen or thawed, and upon the soil strength as influenced by soil moisture levels and texture. As Chapter II indicated, machine traffic can reduce aspen vigour. This is likely more often the case following growing season harvests, especially when soil moisture is high. Therefore, although season does not influence suckering without machine traffic, during conventional harvesting winter harvesting will likely continue to produce higher densities and growth of suckers due to the lower impact on the soils. Therefore it is important that harvests operations during the summer months employ best practices to minimize the impact and extent of traffic on a site. During wet soil conditions, a cessation of operations should be enforced to reduce the potential to damage the soil and aspen root system.

Where competition is high, as indicated by a dense shrub understory prior to harvesting, silvicultural practices to reduce competition should be employed. Chapter III demonstrated the suppressive effect of a dense hazel understory on aspen regeneration. Since competition with hazel for rooting space appeared to be most detrimental to aspen suckering, preharvest treatments that kill the hazel and allow time for aspen roots to grow into the shallow soil layers previously dominated by hazel might improve aspen suckering. On the other hand, a post-harvest mechanical site preparation that removes or disturbs the shallow upper soil layers, which contain most of the hazel roots and rhizomes, could be an effective treatment. During conventional logging operations, hazel stems typically get smashed and broken; therefore, it is likely that overall there is little aboveground competition by the slower re-growing hazel stems with the aspen suckers.

From the research presented in this thesis, a number of further questions have arisen that can be addressed in part by the following five future research directions.

1. The effect of mature aspen harvest in the spring without machine traffic should be examined as this is the time when root carbohydrate reserves are the lowest. Aspen sucker height was reduced following spring harvest compared to summer and winter harvests of 10 year old aspen stands (Mulak et al. 2006), and spring decapitation of aspen seedlings resulted in significantly lower sucker height, biomass and leaf area (Landhäuser and Lieffers 2002). Therefore, it would be interesting see whether spring harvesting of mature aspen would also result in lower sucker vigour than was observed following summer and winter harvests. Spring harvesting is generally not conducted due spring break-up of roads and also due to the prevalence of nesting birds at this time.

2. Long-term effects of season of harvest should be studied as differences in aspen height and crown closure following early summer and winter no-impact harvesting did not arise until two years post harvest (Bates et al. 1993). Therefore, it would be prudent to measure 2nd year growth and leaf dry mass in our season of harvest study in order to test whether mid- and late-summer harvest also results in reduced 2nd year aspen growth compared to winter harvest. In addition, because aspen regeneration quickly self-thins to similar densities regardless of initial density, measurement 5 years after harvest would also be useful.
3. Further examination of the early growth of aspen suckers competing with hazel is warranted. The well-established hazel in our hazel-aspen competition study demonstrated that aspen regeneration is negatively impacted by the presence of hazel, likely perpetuated through competition for rooting space. If hazel roots could be wholly excluded from aspen roots in a more controlled common garden experiment, a more precise idea of the nature of competition between these two species could emerge.
4. Because the hazel in our study did not produce the amount of leaf area that was anticipated based on observations made prior to aspen harvest, a follow-up study that allows time for hazel leaf area to recover and measures aspen sucker density, vigour, and rooting depth would be prudent. In addition, as hazel vigour is expected to be greater in declining aspen stands due to more open canopy conditions and a reduced number of aspen roots, the effects of a dense hazel understory should be tested as it could be more negative in these stands.

5. Silvicultural applications can be investigated where hazel is dense in an attempt to increase aspen suckering. The response of aspen root growth to herbicide application a couple of years prior to harvest and subsequent suckering should be investigated. Also site preparation that removes the upper soil layers containing the bulk of hazel roots should be tested to see if suckering can be stimulated from the deeper growing aspen roots.

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