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Aspen (*Populus tremuloides*) root suckering as influenced by log storage, traffic-induced-root wounding, slash accumulation, and soil compaction

by

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Abstract

The objective of this thesis was to determine how aspen (*Populus tremuloides* Michx.) root systems and suckering are affected by decking area (the site of log processing and storage) disturbances and the seasonal timing of these disturbances. In a field study, summer-built log decks reduced regeneration by half compared to fall-built decks, and if the decks were built in the fall, 11 month and 1.5-3 month storage were similar in their impact. A growth-chamber study examined the timing of traffic-induced wounding of the root system and simulated log storage on aspen root systems and suckering. For both summer and winter treatments the combination of root wounding and log storage killed nearly the entire root system and prevented suckering. Root wounding and log storage alone caused a 35-40% reduction in living root mass, carbohydrate reserves, and sucker growth. Sucker numbers were reduced by one half for the winter but were unaffected for the summer.

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Chapter 1: General introduction

1.1 Aspen regeneration after harvesting

Trembling aspen (*Populus tremuloides* Michx.) is a deciduous tree species with slender stems, smooth white to green bark, and few branches that are clustered at the top of the tree. It grows throughout North America but is most commonly found in the aspen parkland and boreal forest. In the boreal, aspen's roles include: nutrient cycling, forest succession as a pioneering species, and providing a habitat for wildlife. Aspen is also harvested and used for the production of pulp and paper and various wood products. As a result, a large volume of aspen has been harvested over the past decades (Peterson & Peterson 1992), and the impact of harvesting on the soil system (soil, roots, organisms) has led to problems in naturally regenerating aspen (Bates et al. 1993; Berger et al. 2004; Zenner et al. 2007). Poor regeneration is a concern for maintaining aspen in the boreal forest and for forestry companies as regulations stipulate the need to regenerate the trees they harvest (e.g. Alberta Regeneration Survey Manual, Alberta Sustainable Resource Development 2008).

As aspen is a clonal species many features of its regeneration after harvesting are unique compared to other boreal forest species which are planted or seeded after harvesting (eg. pine and spruce). Although aspen trees do produce seed, seedling establishment is not common due to the need for a high level of moisture during germination and early growth (Maini 1968); consequently, aspen typically reproduces vegetatively through root suckers from the parent root system. The parent root system consists of a wide spreading lateral root system found in the top meter of soil with deeper sinker roots located throughout the root system. A single interconnected root system can cover up to 5000 m^2 and support several thousand ramets or individual stems (Peterson and Peterson 1992). Most of this root system is captured and maintained by the new crop of suckers after harvesting (DesRochers and Lieffers 2001); therefore, while the life span of the trees is typically 80 to 100 years, the root system can be much older (Peterson and Peterson 1992).

Suckering begins with the formation of adventitious buds on lateral roots that are usually 2 cm in diameter and within the top 15 cm of soil (DesRochers and Lieffers 2001). Bud formation occurs after disturbances such as harvesting or fire remove the above-ground portion of the tree and eliminate apical dominance. Apical dominance is thought to be mediated by the plant hormone auxin, which inhibits suckering (Farmer 1962; Eliasson 1971; Schier 1972; Steneker 1974). The subsequent outgrowth of these buds into suckers is mainly dependent upon soil temperature, root carbohydrates, and soil aeration (Frey et al. 2003). Soil temperatures influence growth of suckers due to its effect on root respiration (DesRochers and Lieffers 2002). Low soil temperatures can slow sucker growth, or if soil temperatures are below 8 °C, suckers can be inhibited from emerging through the soil surface (Landhäusser et al. 2006). Conversely, warmer soils increase the growth rate and emergence of suckers from the soil, and this increases growing time during their first season (Fraser et al. 2002).

Carbohydrate reserves of the parent root system are vital for the outgrowth of sucker buds (Schier and Zasada 1973; Landhäusser and Lieffers 2002).

Carbohydrates in the form of sugar and starch provide energy required for shoots to grow; thus there has been strong relationship with sucker height and root carbohydrates (Schier and Zasada 1973; Landhäusser and Lieffers 2002). Furthermore, depletion of root carbohydrates can mean that there is not enough energy in the root system for suckers to grow out of the soil surface (Buckman and Blakenship 1965; Fraser et al. 2006). Lastly, for successful sucker growth, soil aeration is needed. The root system requires oxygen for respiration and the production of suckers (Frey et al. 2003); therefore in compacted soils sucker growth can be reduced. While soil temperature, root carbohydrates, and soil aeration do not directly affect the initiation of sucker buds, they do impact the number of suckers that emerge from the soil surface as a result of their influence on sucker growth and are important drivers of suckering density as well as growth.

Densities of first-year suckers can range from 200,000 stems ha^{-1} (Bella 1986) to as low as 10,000 stems ha^{-1} (Krasny and Johnson 1992) depending on parent root and soil conditions. Low initial densities of suckers correspond to a lower leaf area resulting in less carbohydrates being produced which can lead to the death of large portions of the root system (DesRochers and Lieffers 2001; Landhäusser and Lieffers 2002). The loss of root mass can be detrimental to sucker growth in following years (Zahner and Debyle 1965) as root connections allow for the transport of water and nutrients (Debyle 1964; Shepperd et al. 2006) needed for growth and survival of suckers. Higher suckering densities are also important because of the large amount of thinning that occurs during stand development due to competition for sunlight (aspen is shade intolerant), and the susceptibility of aspen to various diseases (Peterson and Peterson 1992). A minimum of 30,000 stems ha^{-1} one year after harvesting has been suggested in order to ensure that the root system survives intact and that the stand has 500-700 stems ha^{-1} at maturity (David et al. 2001).

Disturbances caused by harvest can affect the parent root system and the surrounding soil thereby limiting suckering densities and growth. Decking areas along with skidder trails and haul roads are of particular concern for aspen regeneration (Shepperd 1993; MacIsaac et al. 2006; Zenner et al. 2007). Decking areas, also known as landings, where log processing and storage occurs often have poor or no regeneration as they are impacted by several different disturbances (Zenner et al. 2007): (i) Concentrated machine traffic as all trees are skidded to the decking area; (ii) Slash accumulation because in a full tree harvesting system, as is typical of forestry in Canada, decking areas serve as a processing site for logs. The delimbing and cutting to length of logs results in an accumulation of a thick layer of woody debris; (iii) Log storage which can occur until there are favorable hauling conditions, or storage can reduce haul weights by allowing logs to dry. These decking area disturbances can result in poor regeneration which can affect 10 to 20% of a harvested area (Kabzems and Haeusler 2005; MacIsaac et al. 2006) and is a serious concern, especially when added to the 20% of the harvested area that can be covered with naturally-occurring gaps in regeneration (MacIssac et al. 2006). Understanding the effects and mechanisms of harvest-caused disturbances on aspen regeneration and their remediation is a priority so that site productivity can be maintained.

Machine traffic has been implicated as the main driver of poor regeneration on decking areas as well as on skid trails and haul roads, and its impacts have been well documented (Bates et al. 1993; Berger et al. 2004; Zenner et al. 2007). There are two main effects of traffic: those that change the soil structure and those that directly damage the root system. Changes to the soil structure affect soil aeration, and soil with insufficient oxygen supply for the parent roots means a loss of energy from ATP necessary for initiation and growth of suckers (Stone and Elioff 1998; Corns and Maynard 1998; Stone and Elioff 2000; Berger et al. 2004; Hausseler and Kabzems 2005). Additionally, the loss of air space results in limited fine root growth as the roots are not able to obtain the resources needed from the soil (Ruark et al. 1982). Remediation of poor soil aeration involves tillage (McNabb 1994) as well as reducing soil compaction by limiting harvest to frozen soil conditions when the soil is less susceptible to compaction (Bates et al. 1993).

Damage to the parent root system caused by machine traffic has been studied less (Shepperd 1993; Fraser et al. 2004) than changes to the soil structure. Root damage is typically observed as stripping of fine roots (Shepperd 1993) as well as scuffing, crushing, and fragmenting the root system (Navratil 1991). Mild artificial wounding can increase suckering density and growth of aspen suckers (Fraser et al. 2004). In contrast, extensive wounding and fragmenting of the root system which is more typical of skid trails and landings, is detrimental to regeneration (Shepperd 1993) as the damaged root system is no longer able to supply the resources needed for sucker growth (Zahner and Debyle 1965). Root wounding also provides entry points for decay causing fungi, which in severe cases, can kill the entire root system and any suckers present (Basham 1988). To avoid the impacts of root wounding, harvesting on frozen soils can reduce the chains and lugs on skidder tires from penetrating the soil and damaging root systems (Bates et al. 1993).

The effects of slash and log storage on aspen suckering have been minimally studied (Bella 1986; Navratil 1991). Slash, consisting largely of branches, is known to result in lower soil temperatures, but its impact on soil temperature appears to be small; not great enough to impact aspen regeneration (Bella 1986). However, woody debris found on landings is denser (McNabb 1994), and it may therefore have a greater impact on soil temperatures resulting in no suckering or slow growing suckers. The effects of this dense debris may be comparable to chipping residues, which can act as a barrier to sucker growth and prevent suckers from accessing light for photosynthesis needed to maintain root carbohydrate levels, or the slash can release phenolic compounds that can be toxic to aspen (Corns and Maynard 1998; Conlin 2001; Landhäusser et al. 2007). Assessing the impact of dense slash typical of decking areas would be beneficial for the development of better slash-management plans.

There are no studies that have examined the impact of timing and duration of log storage on aspen regeneration. It has been speculated that once the logs are removed that aspen suckering will occur as it does on other harvested areas, especially if logs are decked during winter and removed prior to the upcoming growing season (Navratil 1991). However, Navratil (1991) does not address the consequences of longer storage of logs or if log storage occurs during summer. Answers to these questions as well as suggestions for the management of log decks are important as records from forestry operations indicate building and storage of log decks for up to a year after both winter and summer harvests is a common practice (eg. Personal communication, Roger Butson, Alberta Pacific Ltd.).

1.2 Research Objectives

The regeneration of aspen on decking areas, particularly in response to log storage, is poorly understood. Therefore, a field study was conducted to examine the effect of season of building log decks and duration of log storage on aspen suckering. Soil compaction, depth of slash and the root wounding associated with decking were also assessed to determine their contribution in limiting aspen regeneration. A subsequent controlled study was conducted under growth-chamber conditions to examine the mechanisms of how one-year log storage, seasonal timing of log deck building, and traffic-induced-damage to the parent root system affects aspen suckering. This was accomplished by simulating the effects of log storage and using a farm tractor to cause root wounding. These studies should provide a clearer understanding of the role that log storage, root wounding, soil compaction, and slash accumulation play in the reduced vigor of suckering on decking areas within aspen cut-blocks.

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Chapter 2: Aspen regeneration on log decking areas as influenced by season and duration of log storage*

2.1 Introduction

Numerous studies have reported insufficient aspen (*Populus tremuloides* Michx.) sucker establishment (Bates et al. 1993; Shepperd 1993; Navratil 1996; Kabzems 1996; Stone and Elioff 1998; Smidt and Blinn 2002; Berger et al. 2004; McNabb 1994; Corns and Maynard 1998; Stone 2001; MacIssac et al. 2006; Zenner et al. 2007) and growth (Bates et al. 1993; Corns and Maynard 1998; Kabzems and Haeussler 2005) on designated skid trails, haul roads, and landings after harvesting. These areas can occupy up to 20% of cutovers (Kabzems and Haeussler 2005; MacIssac et al. 2006), and poor growth of regenerating aspen on such a large area could cause a shift to a lower site index than it was originally (Kabzems and Haeussler 2005). Landings or decking areas are of particular concern as they are the most heavily impacted (Berger et al. 2004).

Typically, poor regeneration on landings has been attributed to disturbances caused by concentrated-skidder traffic on these areas (Shepperd 1993; Berger et al. 2004); however decking and storage of logs may also have an impact (Navratil 1996). After trees have been delimbed the logs are often stored in a pile (log deck) next to the road. In some instances the log deck is hauled immediately and the impact is thought to be negligible (Navratil 1996). More often, hauling is delayed which allows the logs to dry so that haul weights are

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reduced, or it allows for drier or frozen haul road conditions (Personal communication, R. Butson, Alberta Pacific Ltd.).

The impact that log deck building and storage has on aspen regeneration is not known, but it may have several negative effects. A log deck could act as a physical barrier to emerging suckers blocking access to light which in turn prevents photosynthesis and establishment of the suckers. As a result, the carbohydrate reserves of the root system in the newly-cut area would not be maintained and portions of the root system might die, which would cause poor regeneration once the log deck is removed (DesRochers and Lieffers 2001; Landhäusser and Lieffers 2002). The large volume of logs and bark on the decking area could also produce leachates that are high in phenols. High concentrations of phenols from aspen-debris can cause a decrease in the growth of aspen (Conlin 2001).

The impacts of log storage on aspen suckering are likely greater the longer the log deck is stored because a larger amount of carbohydrates will be lost to maintenance respiration (DesRochers et al. 2002). Seasonal timing of building a log deck could have an effect as well; a log deck built in the summer when soil temperatures are warm can result in a greater depletion of carbohydrates by respiration (DesRochers et al. 2002) compared to building a log deck in the fall when soil temperatures are lower.

Conditions such as slash load and the effects of machine traffic, soil compaction and root wounding, could further reduce aspen suckering. Slash accumulation caused by delimbing can delay thawing and warming of the soil

(Bella 1986) or act as a barrier to the emergence of suckers (Landhäusser et al. 2007). Soil compaction reduces root respiration and growth (Hatchell et al. 1970; Ruark et al. 1982). Root wounding fragments the root system (Zahner and Debyle 1965), and the wounds can serve as entry points for decay (Basham 1988; Pankuch et al. 2003). All of these disturbances to the root system could lead to a reduction in the root's ability to produce adequate regeneration (Shepperd 1993).

The objective of this study was to assess aspen regeneration on log decking areas after the trees had been cut and hauled and the coarse slash (eg. logs and large branches) removed. The treatments assessed were season of building of the decks and duration of log storage. Root wounding, soil bulk density, and slash load (eg. bark, twigs, small branches) were evaluated to determine their influence on aspen regeneration.

2.2 Methods

2.2.1 Study area

The study was conducted within one of Alberta Pacific Forest Industries' 10,000 ha forestry planning unit located in the Boreal Mixedwood Ecoregion, 50 km northeast of Lac La Biche, Alberta (between 55° 6' to 55° 10' N and 111°31' to 111°41' W). This Ecoregion receives 380 mm of precipitation annually with the wettest months being June and July. Average temperatures range from 13.8 °C in the summer to -10.5 °C in the winter (Strong and Leggat 1992). The terrain was flat with a few low and wet areas. Except for the low areas, the soils were fine-textured (silty-clay) grey luvisols and uniform throughout the study area.

Low areas were avoided during the sampling regime. The dominant cover type was aspen (*Populus tremuloides* Michx.) with minor components of white spruce (*Picea glauca* (Moench) Voss), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), and black spruce (*Picea Mariana* (Mill.) B.S.P.) in low areas. Understory species were dominated by *Rosa acicularis* and *Calamagrostis canadensis*.

From late June to late October of 2006, 1100 ha of aspen-dominated sites in the planning unit were clear-cut using full tree harvesting methods. This involved cutting with a feller-buncher harvester, skidding the entire tree to a roadside decking area with grapple skidders, delimbing, and cutting the tree to length at the decking area. Following delimbing, logs were stacked into decks 1-2 m in height and less than 2 m from the road side. Decking occurred within 2 weeks after harvesting began. Log decks were placed directly on the existing soil, and as a result there was no scraping or removal of soil during building of the decking area.

Dates when the log decks were built and when logs were hauled varied between cutovers. Cutovers selected for the study were A) early summer logged (June to early July) with logs stored during the same growing season and hauled in the fall (summer - short storage); B) late summer logged (August to September) with logs hauled the same fall (fall - short storage); and C) late summer logged (August to September) with logs hauled after the following growing season (fall - long storage) (Table 2-1). After the log decks were hauled, coarse slash was spread or piled by a bulldozer and burnt (Personal communication, R. Butson, Alberta Pacific Ltd.). In most circumstances, however, there was still a consolidated layer, 2-6 cm thick, of finer slash such as twigs, small branches, and bark covering the former decking area.

Table 2-1: Harvest information for the log-deck sites for each log storage treatment. Cut dates indicate the start of harvest and haul dates when the logs were removed from the log decking area. Replicates indicate the number of decking areas sampled from sites with the same cut and haul dates.

Site	Treatment	Replicates/Site	Cut	Haul*
1	Fall - long	6	7-Aug-2006	20-July-2007
2		4	16-Aug-2006	23-July 2007
3		2	11-Aug-2006	27-July 2007
4		2	15-Aug-2006	27-July 2007
5		1	1-Sept-2006	20-July 2007
6		1	23-Aug-2006	25-July 2007
7	Fall - short	1	15-Aug-2006	30-Sept-2006
8		2	15-Aug-2006	17-Nov-2006
9		1	6-Sept-2006	30-Nov-2006
10		1	2-Sept-2006	30-Nov-2006
11	Summer - short	2	6-July-2006	16-Oct-2006
12		3	21-June-2006	17-Nov-2006

2.2.2 Sampling design

Twelve different sites within the 1100 ha harvested areas were sampled. Provided that decking areas greater than 250 m apart could be located, more than one decking area was sampled at each site resulting in a total of 26 decking areas being examined. Five decking areas each were examined from the summer - short storage and fall - short storage treatments. Sixteen decking areas were selected from the fall - long storage treatment areas (Table 2-1). Each of these decking areas was paired with a reference area, i.e., a logged area that was minimally disturbed by machine traffic, had little slash accumulation, and no log storage. The reference area was located approximately 15 m from the edge of the harvested area but within 100m of the log decking area.

Because log decks had been removed at the time of the study, their position was determined by the presence of bark debris near the haul road as delimbing was done on the decking areas (Personal communication, R. Butson, Alberta Pacific Ltd.). Once evidence suggested the location of a log deck, eight - 10 m^2 - subplots, on a transect running parallel to the haul road were positioned in the middle of the decking area (approximately 6 m from the road). Subplots were spaced a minimum of 5 m apart and a maximum of 15 m depending upon the length of the decking area. Subplots falling on stumps that prevented root and soil sampling, areas with visible rutting, evidence of burnt slash, or low spots were moved 2 m further along the transect. A similar transect of eight subplots was established in the control area. Subplots were averaged so that each transect represented a single replicate.

Site conditions were consistent throughout all sampled areas: decks and the paired the control. Samples were taken on well-drained upland sites with silty-clay soils that were dominated by aspen with minor components of balsam poplar (*Populus balsamifera* L.) and white spruce (*Picea glauca* (Moench) Voss).

2.2.3 Measurements

In August of 2008, two years after harvesting, measurements of sucker mean density and maximum height were made in each subplot for all treatments including the control plots. Measurements of root condition, soil bulk density, and slash coverage were taken in the odd numbered subplots (eg. 1,3,5,7). For sucker density, the number of aspen and balsam poplar suckers were counted in a circular 10 m^2 (1.6 m in diameter) regeneration subplot (as balsam poplar constituted <2% of the suckers, they were not differentiated in the results from aspen suckers). The height of the tallest aspen sucker in each quarter of the regeneration subplot was also measured. First year growth of these suckers was calculated based on a ratio that first year growth accounted for 55% of a two year old sucker's height. This ratio was determined from a random sample of 100 suckers which had their first and second year height measured separately using bud scars as to determine each year's growth.

Root condition was assessed by spading a 0.1 m^2 pit (32 x 32 cm) in the centre of every second subplot. All aspen and balsam poplar roots greater than 0.5 cm and less than 2.0 cm in diameter (considered the dominant suckering roots (DesRochers and Lieffers 2001)) were collected from each pit to a 15 cm-depth of mineral soil. Roots were stored at 5 °C and transported back to the laboratory. Total linear length of roots and lengths of root that were blackened and/or dead were measured. The proportion of dead to total length was then calculated. Number of visible wounds (scrapes, scuffs, and severed roots) that covered more than 1 cm^2 of surface area of roots (dead or alive) were counted, and expressed as the number of wounds per linear meter of root.

The core method was used to determine soil bulk density (Blake and Hartage 1986). Soil cores (325 cm^3) were taken from the top 10 cm of mineral soil. Soil was taken back to the laboratory where it was dried to constant weight at 80 °C. Rocks or organic matter greater than 0.3 cm diameter were removed by sieving, and their weight and volume subtracted from the core volume. Dried soil was weighed and soil bulk densities calculated as g/cm^3.

Slash depth was quantified by taking the average depth of slash debris from three random spots within a 0.25 m^2 area at the center of each subplot. Depth was measured from the uppermost piece of slash to the top of the original LFH layer.

2.2.4 Data analysis

An initial comparison was made between decking and reference areas. This involved grouping all variables from the three log deck treatments into one. Comparison was made with a one-way ANOVA using the GLM procedure in SAS (SAS Institute, version 9.1). The statistical model was

$$Y = \mu + T + \varepsilon ,$$

where Y was the mean of the variable (sucker density, first year height of the leading sucker, percent dead root, number of wounds, soil bulk density, or slash depth); μ was the population mean for the variable; T was the effect of the treatment (decking area or reference area); ε was the random error. Significance was based on an alpha of 0.05 (for this test and all subsequent tests). Assumption of normality of the residuals was evaluated using the Shapiro-Wilk test. Homogeneity of variances was verified using Bartlett's test. These tests were used for all subsequent ANOVAs.

A separate set of one-way ANOVAs was used to compare the three log deck treatments. The statistical model and variables tested were the same as previous, but the treatments were summer - short storage, fall – short storage, or fall – long storage. Unlike the other variables, sucker density on log deck areas was found to have a significant relationship with sucker density of the paired reference area. Thus, sucker density was analyzed with ANCOVA using the sucker densities from the paired reference area as covariates. The model tested was similar to that of the ANOVA except *X* was included as the covariate;

$$Y= \mu + T + X + \varepsilon ,$$

Provided the ANOVA or ANCOVA was significant, two planned comparisons were made using LSD means comparison tests: summer - short storage vs. fall - short storage to determine the impact of season of log deck building, and fall - long storage vs. fall - short storage to assess effects of storage duration.

A final set of one-way ANOVAs were performed to evaluate any differences between growth potential of the treatment sites. Sucker density and first year height of leading suckers from the paired reference area of the three decking treatments were compared (eg. paired reference area of the summer-short was compared to the fall-short and fall-long, etc.). No means separation tests were performed as none of the ANOVAs were significant.

Multiple regressions were used to examine relationships between suckering density or height, with root wounding, soil bulk density, and slash depth. Data from all treatments and the control were used, and dummy variables were used to account for the effect of treatment. However, using stepwise selection in the regression procedure in SAS, root wounding, soil bulk density, and slash depth were not useful predictors in the model, and results of this analysis were not presented.

2.3 Results

2.3.1 General impact of decks

Density and vigour of aspen regeneration and amount of living root was significantly reduced on log decking areas compared to reference areas (Table 2-2). Sucker density on decking areas was 16,659 stems ha^{-1} (across all decking treatments) while reference areas had nearly three times the density with 47,047 stems ha^{-1} (Figure 2-1A). First year height growth of the leading suckers on decking areas was about half that of reference areas; 55 cm on the decks and 95 cm in the control (Figure 2-1B). On decking areas 58% of the roots were dead compared to 33% for the reference area (Figure 2-1C).

Root wounding, soil bulk density and slash load were significantly greater on decking areas compared to reference areas (Table 2-2; Figure 2-1D-F). Roots had 2.2 wounds per meter on decking areas compared to 1.2 for reference areas (Figure 2-1D). Soil bulk density on decking areas (1.50 g cm^{-3}) was 5% higher than reference areas (1.43 g cm^{-3}; Figure 2-1E). Difference in slash depth between decking and reference areas was large with an average of 5.9 cm on decking areas and 2.3 cm in reference areas (Figure 2-1F).

Table 2-2: One-way ANOVA results for the comparison between log deck and reference areas.

Response variable	d.f.	F-ratio	p-value
1)Sucker density	1	73.53	<0.0001
2)First year height	1	95.56	<0.0001
3)Dead root	1	20.86	<0.0001
4)Root wounding	1	13.93	0.0005
5)Soil bulk density	1	8.62	0.0050
6)Slash depth	1	54.68	<0.0001

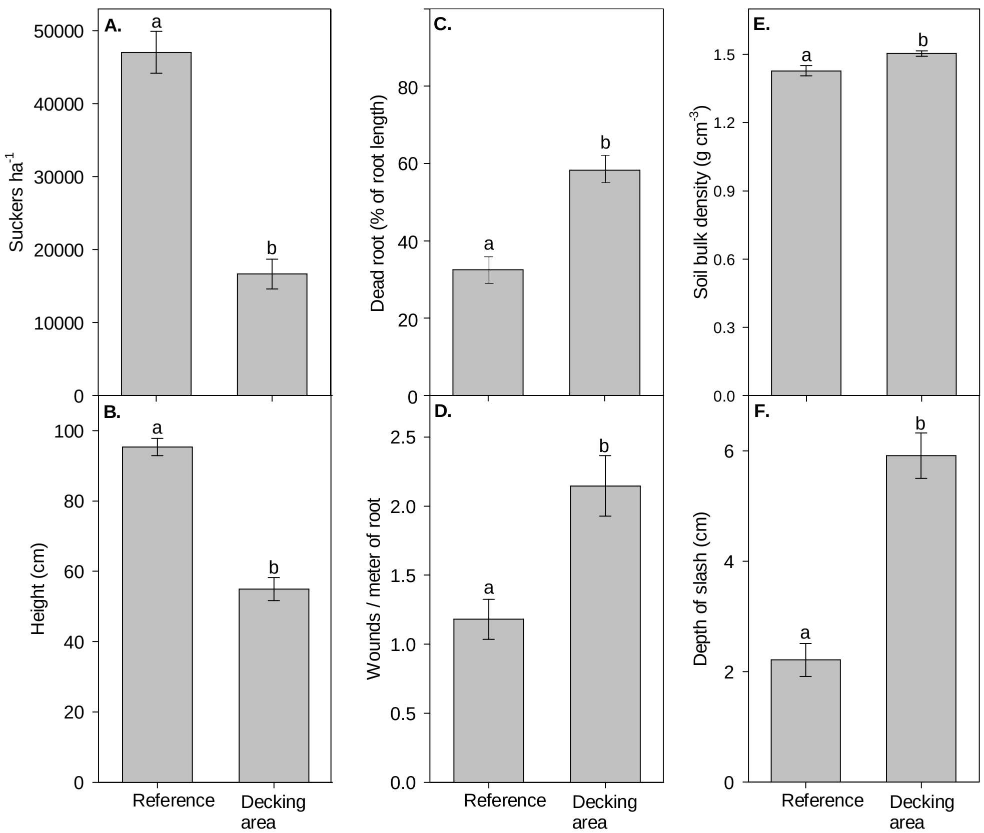

Figure 2-1: Comparison between logged areas that were minimally disturbed by harvest activity (reference) and decking areas. (A) Sucker density of aspen. (B) First year height growth of the leading suckers. (C) Percent dead roots by root length. (D) Density of wounds greater than 1 cm^2 on aspen roots. (E) Bulk density of the top 10 cm of mineral soil. (F) Depth of slash such as bark and branches. Different letters indicate statistically significant differences for each graph (p<0.05), and the lines represent standard error.

2.3.2 Impact of season of log deck building

Building log decks during a summer harvest had a significant negative impact on sucker densities and amount of living roots compared to fall built log decks (Table 2-3). Suckering on decking areas harvested in summer which had 3 to 5 months of log storage prior, had half the density of suckers (7,574 stems ha^{-1}) compared to fall harvest with a similar period of log storage (16,472 stems ha^{-1}; Figure 2-2A). Season of establishing log decks did not affect the height of suckers. First year height of the leading suckers for both treatments was approximately 45 cm (Figure 2-2B). Condition of the root system in decking areas was different between the two treatments. Two summers after logging, 85% of the root length was dead in summer harvested sites compared to 50% in fall harvested sites (Figure 2-2C).

Table 2-3: One-way ANOVAs and means separation test results for comparisons made between the three log deck storage treatments: summer - short storage (summer) with fall - short storage (fall) and fall – short storage (short) with fall - long storage (long).

Response variable	Source of variation	df	F-ratio	p-value	Comparison (p-value)	
					summer-fall	short-long
1)Sucker density	Treatment	2	3.50	0.0479	0.0148	0.4658
(reference area density)	Covariate	1	8.08	0.0095		
2)First year height	Treatment	2	3.74	0.0393	0.8864	0.0352
3)Dead root	Treatment	2	5.88	0.0087	0.0187	0.7973
4)Root wounding	Treatment	2	1.56	0.2325		
5)Soil bulk density	Treatment	2	0.03	0.9726		
6)Slash depth	Treatment	2	0.07	0.9321		

Root wounding, soil bulk density, and slash load were not affected by season of log deck building. The trend, however, was for more wounds in the fall-harvested sites (2.9 wounds m^{-1}) compared to summer decks (1.9 m^{-1}) (Figure 2-2D). Mean bulk density was 1.50 g cm^{-3} (Figure 2-2E) and slash depth was about 6.1 cm for both treatments (Figure 2-2F).

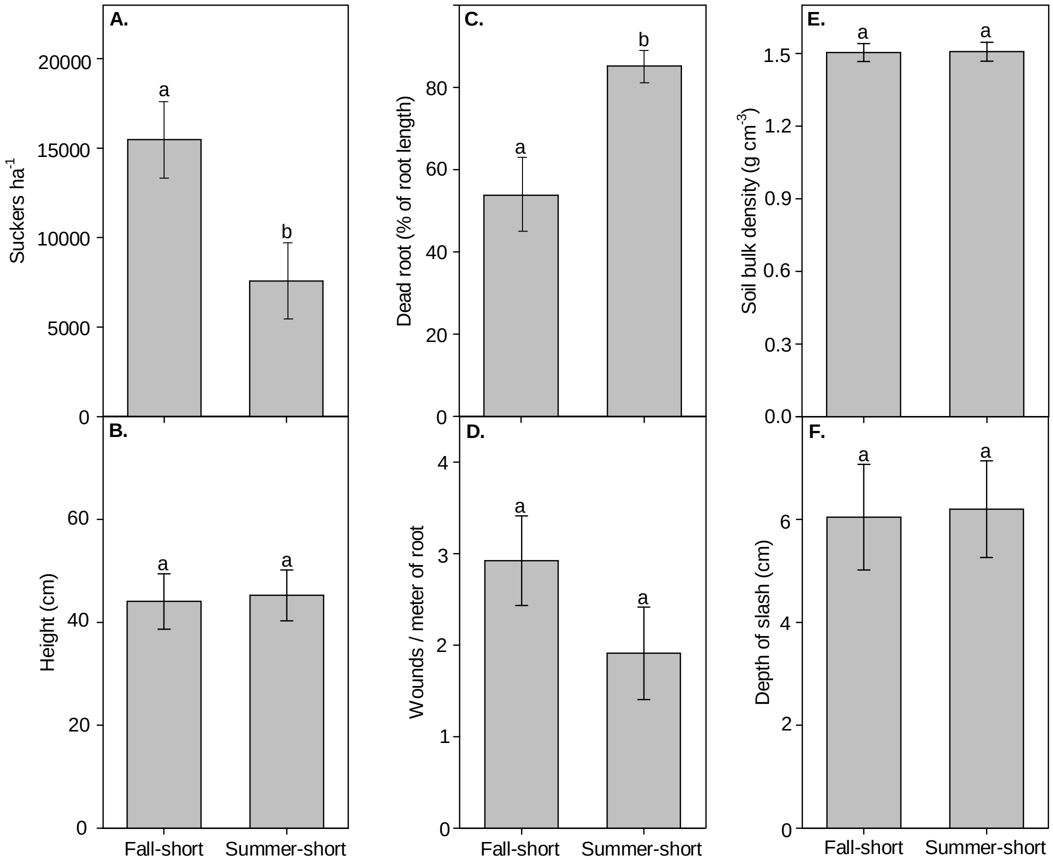

Figure 2-2: Comparison between log decks that were built after an early summer harvest followed by 3 to 5 month of log storage (summer-short storage) compared to decks that were built during a fall harvest and hauled after a similar storage period (fall-short storage). (A) Sucker density of aspen. (B) First year height growth of the leading suckers. (C) Percent dead roots by root length. (D) Density of wounds greater than 1 cm^2. (E) Bulk density of the top 10 cm of mineral soil. (F) Depth of slash such as bark and branches. Different letters indicate statistically significant differences for each graph ($p<0.05$), and the lines represent standard error.

There were no differences in sucker densities or height growth between the reference areas (non-decking areas) of these two treatments (Table 2-4). Sucker density (44,313 stems ha^{-1}) and height growth (92 cm) were similar to the average of all reference areas in Figure 2-2A&B.

Table 2-4: One-way ANOVA results for the comparison between the paired reference areas of each of the log deck treatments.

Response variable	d.f.	F-ratio	p-value
Sucker density	2	0.29	0.7500
First year height	2	0.64	0.5383

2.3.3 Impact of log storage duration after a fall harvest

Density of aspen suckers and condition of the root system was not affected by the duration of log storage after a fall harvest (Table 2-3). A mean density of 19,641 stems ha^{-1} was found on long storage areas (11 months) compared to 16,472 stems ha^{-1} for short storage (1.5 to 3 months; Figure 2-3A). First year height growth of leading suckers was different between the two treatments with taller suckers being on sites with long storage of logs (62 cm compared to 43 cm for the short storage; Figure 2-3B). Condition of the root systems was similar between the long and short storage. Approximately half of the roots were dead in both treatments (Figure 2-3C).

Log storage duration did not affect root wounding, soil bulk density, or slash (Table 2-3). Each treatment had 2 to 3 wounds m^{-1} of root (Figure 2-3D). Soil bulk density was on average 1.50 g cm^{-3} (Figure 2-3E) and slash was about 6 cm deep (Figure 2-3F).

There were no differences between reference areas (non-decking areas) of these two treatments (Table 2-4), and sucker density and height growth were approximately equal to the overall average of all reference areas in Figure 2-1A&B (47,431 stems ha^{-1} and 96 cm).

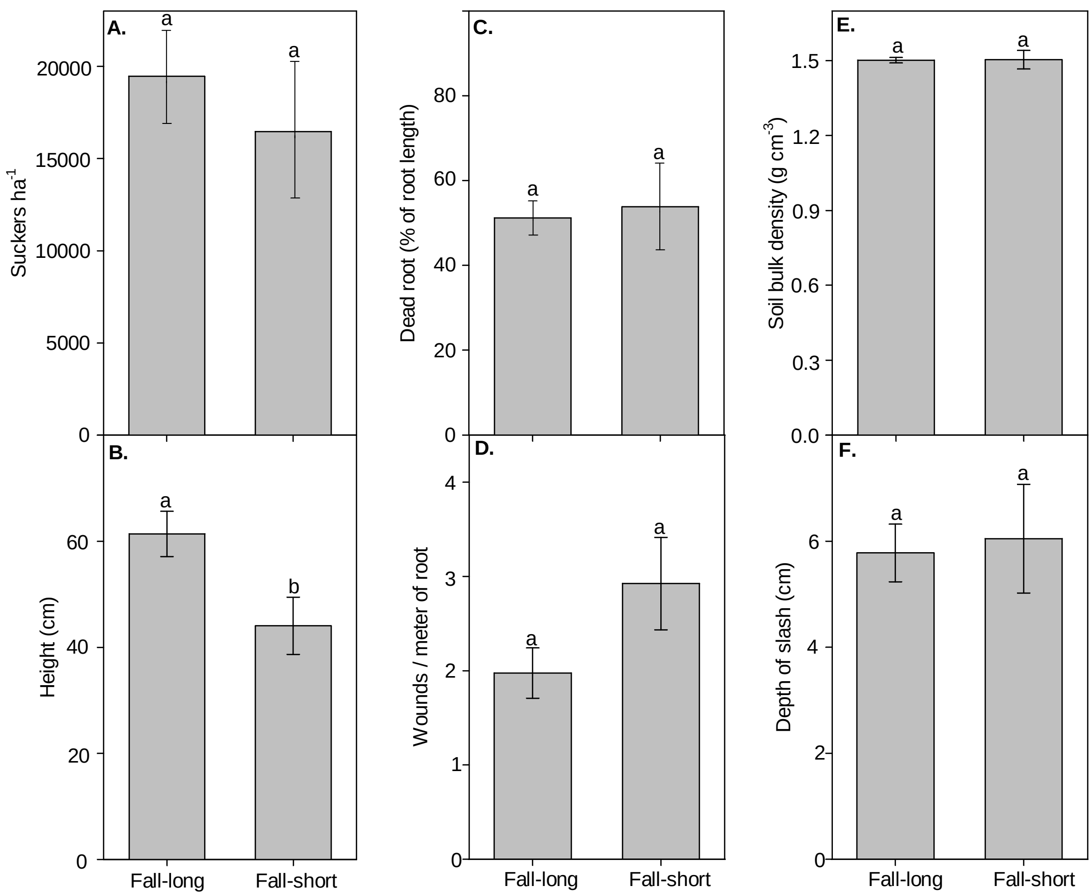

Figure 2-3: Comparison between decks with 11 months of log storage after a fall harvest (fall-long storage) compared to decks where the logs were removed 1.5 to 3 months after a fall harvest (fall-short storage). (A) Sucker density of aspen. (B) First year height growth of the leading suckers. (C) Percent of dead roots by root length. (D) Density of wounds greater than 1 cm^2. (E) Bulk density of the top 10 cm of mineral soil. (F) Depth of slash such as bark and branches. Different letters indicate statistically significant differences for each graph ($p<0.05$), and the lines represent standard error.

2.4 Discussion

Season of log-deck building had a substantial impact on aspen regeneration. Areas where log decks were built during a summer harvest and stored until the upcoming fall had half the density of aspen suckers compared to decking areas constructed in the fall and hauled shortly thereafter. The decrease in aspen regeneration on decking areas in the summer months has typically been attributed to increases in soil compaction and root wounding due to harvesting occurring on unfrozen and wetter soil conditions (Bates et al. 1993). These factors have been linked to increased root death (Bella 1986; Shepperd 1993) which would cause a decrease in sucker density (DesRochers and Lieffers 2001); however, soil compaction and root wounding were similar between the summer and fall treatments (Figure 2-2). Additionally, poor regeneration after summer logging has often been linked to low root carbohydrate reserves in the summer (Bates et al. 1993; Landhäusser and Lieffers 2002), but there were no differences in sucker density and height growth between the controls of the summer and fall treatments suggesting that season of harvest had little direct impact on sucker density; this is supported by other studies (Mundell et al. 2008, Mulak et al. 2006). As well, slash depths were not different between the fall and summer treatments (Figure 2-2), and were likely not factor in the decrease in regeneration observed on decking areas which had log deck built after a summer harvest.

The cause of poor regeneration on the summer decking areas is likely related to the log deck itself. Even though summer built log decks were stored longer than the fall built log decks, but this was probably not a factor. Earlier removal of the log deck in the fall would not have impacted the root system or later suckering because the root system was dormant at the time of removal (e.g. DesRochers et al. 2002; Table 2-1). The presence or absence of the log deck would likely have had no effect. Poor regeneration was likely due to the seasonal timing of log deck building. The fall built log deck was placed on dormant roots while the summer built log deck was placed on the root system at a time when soil temperatures were high and when suckering naturally occurs. Suckers produced were either unable to emerge from the soil as the log deck acted as a physical barrier, or if they did, they were in darkness and unable to photosynthesize. The warm soil conditions caused high root respiration (DesRochers et al. 2002), and the inability of suckers to photosynthesize would have depleted carbohydrate reserves, which has been linked to the death of portions of aspen root systems and poor sucker growth (eg. DesRochers and Lieffers 2001; Landhäusser and Lieffers 2002). This likely explains the large die-off of roots in the summer decking area and the poor suckering in general (Figure 2-2C).

In contrast to the season of log deck construction, duration of log storage appeared to have little effect on aspen sucker density on the decking area when constructed in the fall (Figure 2-3A). The treatments used to assess duration of log storage did have different time-spans for sucker regeneration and could have affected the results; the short storage had two years of growth while the long storage had only one year before measurements were taken. Self-thinning of aspen suckers can occur between the first and second season in high density situations where losses of 25% are not uncommon (Peterson et al. 1989). However, in regenerating stands where initial sucker densities are low, e.g. less than 20 000 stems/ha, thinning is minimal in the second year (Krasny and Johnson 1992; David et al. 2001). The slightly higher sucker densities on the long compared to the short storage sites can likely be explained by some thinning occurring in the short storage, but it is probable that sucker densities on the long storage areas would have been comparable to the densities on short storage areas if it had had one more season of growth. Heights between treatments may have been impacted by the different age of suckers as shoot dieback may have occurred after the first year (Peterson and Peterson 1992) in the short storage sites; thus explaining the reduced height growth in the fall-short storage compared to the fall-long storage treatment (Figure 2-3B).

In the fall harvest, the presence of the log deck likely did not have an incremental impact on aspen regeneration for several reasons. Mundell et al. (2008) showed when aspen is cut in late summer, there was no root suckering before the following growing season. Therefore, it can be assumed that the root system did not sucker under the log decks in the fall and deplete their carbohydrate reserves as suggested for the summer decking areas. However, these root systems also did not sucker under the log deck the following growing season as we did not find any two-year-old suckers on these decking areas. The likely reason that the root system failed to sucker in the summer under the deck was related to the insulating nature of the log deck, coupled with greater freezing during the prior winter (Lieffers and van Rees 2002). Typically snow acts as an insulating layer and can prevent the ground from freezing deeply (eg. Zhang et al. 2008). However in the case of a log deck we propose that the snow likely accumulated on top of the log deck, but since the ends of the deck remained open, there was a break in the insulating layer. As a result cold air moved between the logs and contacted the ground resulting in a deeper penetration of frost into the ground. In the spring, the ground around the log deck melted and soil temperatures increased; however under the log deck, soil temperature remained low as the deck intercepted radiation that would typically warm the soil. For example Lieffers and Van Rees (2002) recorded that soils froze earlier under a loose layer of coarse slash that had intercepted snow; these areas also remained cool over the following growing season. As soil temperatures in the boreal forest are already cool (Strong and Leggat 1992) the log deck could have prevented soils from reaching the 9° C necessary for suckers to grow (Landhäusser et al. 2006). Further, cool soils decreased root respiration (DesRochers et al. 2002). Consequently, root carbohydrate reserves could remain relatively unchanged and suckering potential could be expected to be sustained once the log deck was removed.

As long-term storage of log decks failed to have an impact on aspen regeneration when constructed in the fall, the hypothesis that leachates from these logs could affect aspen regeneration (Conlin 2001) can be negated. Height of suckers was actually greater after long-term storage of the log deck compared to the short–term storage. Similarly, Landhäusser et al. (2007) found relatively little impact of the leachates generated from 4 cm of chipping debris from aspen and it appears that the leachates from a deck of logs does not reach the threshold that damages aspen regeneration.

Even without the effects of log deck storage, regeneration on decking areas was poor, and this reinforces the large body of literature showing poor aspen regeneration on landing areas (Bates et al. 1993; Navratil 1996; Berger et al. 2004; MacIssac et al. 2006; Zenner et al. 2007). While many studies have implicated soil compaction for low sucker densities (Bates et al. 1993; Shepperd 1993; Stone and Elioff 1998), they observed increases in bulk density of 10-30%, i.e., much greater than the 5% we observed in our study. Small increases in bulk densities like the 5% we observed have been found to actually increase sucker density while decreasing height growth (Stone 2001; Kabzems and Haeussler 2005). Root wounding in this study was much lower than that observed by Shepperd (1993) on skid trails, while our density of wounds was similar to that of Fraser et al. (2004), who actually saw an increase in sucker density with that degree of wounding. Although, root wounding does allow for the entry of decay causing fungi which can reduce height growth (Basham 1988) as observed in the fall short-storage treatment which had increased wounding and decreased height growth (Note the author has no logical explanation for the increase in wounding found for in the fall short-storage treatment). Therefore, wounding may not have impacted sucker density, but it could have resulted in a decrease in sucker height that was observed.

Slash depth is likely one of the main causes of low sucker density in this study. The reduction of sucker density in our study is consistent with the results of Corns and Maynard (1998) and Landhäusser et al. (2007) who saw 30-50% reductions in sucker density with a chipping residue depth of 4-10cm because the residue acted as a barrier to sucker emergence. The slash on decking areas was similar to chipping residues as it was composed of a thick interwoven layer of bark and small branches and likely had a similar effect. Also, slash has an insulating effect which keeps soil temperatures low and will negatively influence height growth of the sucker regeneration (Bella 1986; Lavertu et al. 1994).

While slash depth likely had a significant influence on sucker density, increased soil bulk density and wounding can not be ruled out as causes detrimental to aspen regeneration. Soil compaction and root wounding (Shepperd 1993; Bates et al. 1993) are dependent on soil conditions such as texture and moisture content during landing construction and skidding operations (Shepperd 1993; McNabb et al. 2001). Unfavourable soil conditions appear not to have been a significant factor in our study, but under different conditions, compaction and root wounding may have a larger impact.

In conclusion, building and storage of log decks during the growing season significantly reduced regeneration densities below the suggested minimum of 15, 000 to 30 000 stems ha^{-1} (David et al. 2001), and storing logs should be avoided during summer logging operations. On the other hand, log deck storage after a fall or winter harvest into July of the following growing season had little incremental impact on aspen regeneration beyond other disturbances during harvest. The amount of interwoven slash left on decking areas even after the clean-up may be a major factor limiting aspen regeneration. This mat of debris should be carefully removed during reclamation of the decking area. However, care must be taken to remove debris without excessive removal or damage to the aspen root system as a result of blading too deep. In addition, avoiding excessive soil compaction or direct damage to the root system during operation would likely improve aspen regeneration in these problem areas; consequently logging on frozen ground should be the preferable option.

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Chapter 3: Suckering response of aspen to simulated log storage and traffic-induced-root wounding[†]

3.1 Introduction

Aspen (*Populus tremuloides* Michx.) regeneration by root suckering is dependent upon the physiological condition of the parent root system as well as environmental conditions surrounding these roots (Frey et al. 2003). Conditions include hormonal balance, carbohydrate content, root damage, and soil temperature, strength, and aeration. During harvest, machine traffic can damage the root system and change soil conditions (Bates et al. 1993; Shepperd 1993; Berger et al. 2004; Zenner et al. 2007), and log storage has been speculated to reduce soil temperature and root carbohydrate reserves (Renkema et al. 2009). As a result, on heavily-impacted areas such as roads, landings, and skid trails, aspen regeneration is often poor, or in some instances does not occur at all (e.g. Bates et al. 1990; MacIssac et al. 2006). To improve regeneration in these problem areas it needs to be determined how changes in site conditions due to harvest activities affect the parent root system and subsequent suckering density and vigour.

The effect of soil compaction on aspen suckering has been widely studied, but less is known about the effects of root wounding and log deck storage. Soil compaction decreases the ability of aspen roots to grow because it increases soil resistance to penetration (Ruark et al. 1982; Standish et al. 1988) and reduces soil aeration which in turn increases root mortality as oxygen for respiration is limited (Landhäusser et al. 2003). As a result of soil compaction on the aspen

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root system, suckering is often minimal (Bates et al. 1993). With respect to root wounding, past studies have used shovels or hand tools to simulate root damage by severing or scraping aspen roots, and this type of damage has been found to increase density and height growth of suckers due to changes in the root's hormonal balance (Farmer 1962; Lavertu et al. 1994; Fraser et al. 2004). Other studies that have examined machine traffic have focused on aspen stands 10 years after harvesting (Shepperd 1993) and examined how root wounding affects the spread of diseases and decay (Basham 1988; Pankuch et al. 2003). However, no studies have directly examined aspen roots impacted by heavy machine traffic and the effect on subsequent suckering performance. Looking directly at the root systems will help isolate effects of root wounding and give a better understanding of the impacts of root wounding on subsequent aspen regeneration.

Log storage and its impact on aspen suckering have only been studied by Renkema et al. (2009 – Chapter 2). This is surprising because storage of log decks can cause large reductions in suckering (Renkema et al. 2009) and affect a significant portion (6-8%) of a harvested area (MacIssac et al. 2006). In a field study Renkema et al. (2009) found that log decks built in the fall had less impact on suckering than log decks built in the summer. They hypothesized that the seasonal effect is due to the impact of the log deck on soil temperature. For example, a log deck built during the winter maintains low soil temperature during the growing season due to its insulation ability which slows root respiration (DesRochers et al. 2002) and prevents suckering under the log deck.

Thus, cool soils under the deck allow roots to conserve carbohydrate reserves for longer survival, and lead to better suckering and growth once the log deck is removed. In contrast, a log deck built in the summer initially has warmer soils underneath it, which results in much higher respiration rates (DesRochers et al. 2002) that could significantly deplete carbohydrate reserves. Additionally, the warmer soils encourage suckering, but any suckers that do emerge under the log deck are unable to photosynthesize and resupply root carbohydrate reserves (Landhäusser and Lieffers 2002). Thus, once the log deck is removed, suckering is poor. However, these hypotheses have never been tested.

The effects of log storage and root wounding may also interact with each other. Prolonged log storage may weaken the ability of a damaged root system to repair and defend itself against decay fungi (e.g. Shigo 1984). As a result, the impact of traffic may become more detrimental to a root system covered by log decks as it is less able to respond defensively to the damage caused by the traffic.

The objectives of this growth chamber study were to evaluate how aspen regeneration and parent root survival are related to the simulated effect of log storage and traffic-induced-root wounding as influenced by (i) winter harvest with subsequent coverage of the soil during the following growing season and chilling the soil to 5°C, and (ii) summer harvest with subsequent coverage of the soil over the remaining part of the growing season but maintaining soil temperature at 18° C.

3.2 Methods

3.2.1 Plant Material

One hundred aspen (*Populus tremuloides* Michx.) saplings were used. They were grown from seed collected from open-pollinated aspen trees in Edmonton, Alberta. When the seedlings were one-year-old they were transplanted into rectangular pots (16 cm wide x 15 cm deep x 57 cm long); a single seedling was planted 8 cm from one end of each pot which had been filled with a 3:1 mixture of sand to peat. Transplanted seedlings were grown outside at the University of Alberta (Edmonton, AB) for three additional years. The seedlings were regularly watered and fertilized using a commercial fertilizer (20-20-20, N-P-K) with chelated micronutrients and grown to the sapling stage (~1 m in height; Table 1). During winters the pots were covered with 30 cm of loose straw and buried in the snow to prevent frost damage to the roots. Similar potted saplings were used by Landhäusser et al. (2007) which allowed a dense and laterally spread root system with root sizes up to 20 mm in diameter to develop, and the sand-peat mixture allowed for easy extraction of the roots for examination.

3.2.2 Treatments

The study was separated into two experiments. The first experiment began after a winter-cut (removal of the above ground portion) of the saplings and the second after a summer-cut. Each experiment followed a 2 × 2 factorial design with treatments being simulated log storage (no-storage and storage) and root wounding by machine traffic (non-wounded and wounded). The work was divided into two experiments because the duration and conditions in the log-storage treatment were not comparable between the winter and summer-cut studies.

3.2.2.1 Winter-cut

The sequence of application and duration of the treatments are depicted in Figure 1A. In October 2007, 50 out of the 100 saplings were randomly assigned to the winter-cut. Ten saplings were sampled to take pretreatment measurements. The other 40 saplings were cut off at the soil surface, and the root wounding treatment was applied to half of these root systems (20) while the other half was left untreated (non-wounded).

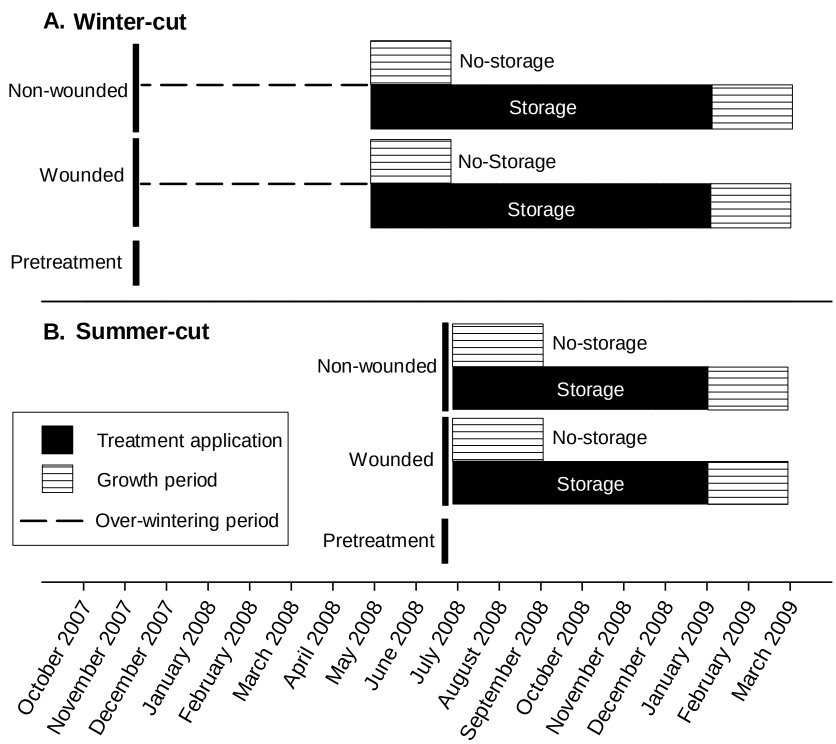

Figure 3-1: Timeline of the application of the treatments: wounding and storage for (A.) winter-cut (B.) summer-cut. The width of each box indicates the duration of treatment application while the height indicates the relative number of root systems to which the treatment was applied.

For the wounding treatment the root mass and bound soil of 20 root systems were removed from their pots and placed side-by-side to form a 57 cm-wide by 320 cm long, continuous bed of soil and roots, on a hard road surface. Two 320 cm long pieces of lumber 5 cm high and 10 cm wide were placed under this bed, and a logging chain was looped on top of the root systems. This setup was used to simulate crushing and shearing damage to roots that occurs during machine operations on unfrozen ground (Zenner et al. 2007). A 7130 Case International Magnum farm tractor that exerted an approximate ground pressure of 63 KPa, which is similar to skidders (William and Neilson 2000), then made 6 passes over the root systems. Based on a preliminary study, six tractor passes caused a 70% reduction in root mass typical of heavily trafficked skid trails and landings (Shepperd 1993). No significant soil compaction occurred as a result of the machine traffic; this was judged by the fact that soil volume appeared to increase when roots and soil were placed back into the pots. Subsequently, all root systems (non-wounded and wounded) were covered with a 2 cm layer of forest floor material obtained from a local aspen stand in Edmonton, Alberta to inoculate the soil with microorganisms typical of natural field conditions. Root systems were overwintered outside by covering them with 30 cm of loosely packed straw and burying them in the snow.

In April 2008, once air temperatures rose above 5 °C, all root systems were brought into a growth chamber with 17 hours of light at 18 °C, 7 hours of dark at 16 °C, and a relative humidity of 60%. Half of the non-wounded and wounded root systems were assigned to one of the log storage treatments (no-storage and storage). The 20 root systems assigned to no-storage were given 9 weeks to sucker and grow. The storage treated root systems were covered with a 2.5 cm thick sheet of polystyrene board that was pressed firmly against the soil surface and affixed to the pot using plastic ties that were wrapped around the pot and board. The bottom of these pots were sealed to prevent water leakage and placed in a water bath (as described by Landhäusser et al. 2003) to maintain the soil temperature at 5 °C. The soil temperature of 5°C was based on an estimate from Lieffers and van Rees (2006) which describes the impact of slash on summer soil temperature when it is placed during the winter. These root systems remained in the water bath for 7 months until outside air temperatures were below 5 °C in November 2008. Then the polystyrene board was removed and root systems were moved outside where they were covered with 30 cm of loosely packed straw and buried in snow to overwinter. In January 2009 the root systems were brought back into the growth chamber and allowed to sucker and grow for 9 weeks (Figure 3-1A) under the same growth chamber conditions as described before but with ambient soil temperatures.

3.2.2.2 Summer-cut

In late July 2008 after full leaf out and during early shoot expansion, the remaining 50 saplings were assigned to the summer-cut (Fig. 1B). Ten saplings were sampled to make pretreatment measurements. The remaining root systems (40) were cut at the soil surface and assigned to a root wounding treatment (non-wounded or wounded). Twenty root systems were wounded - as described for the winter-cut saplings, and the wounded and non-wounded root system were immediately brought into a growth chamber with 17 hours of light at 18 °C, 7 hours of dark at 16 °C, and a relative humidity of 60%. The root systems were covered with a 2 cm layer of forest floor material obtained from a local aspen stand in Edmonton, Alberta.

Once in the growth chamber half of the non-wounded and half of the wounded root systems were assigned to the no-storage level of the log storage treatment and given 9 weeks to sucker and grow. The remaining root systems were subjected to the storage level of the log storage treatment and covered with a 2.5 cm thick sheet of polystyrene board pressed firmly against the soil surface and affixed to the pot as described for the winter-cut. Soil temperature was maintained at ambient air temperature conditions. In September 2008, the storage treated root systems were uncovered and placed outside to condition them for winter. To overwinter, root systems were covered with 30 cm of loosely packed straw and buried in the snow. In January 2009 they were brought back into the growth chamber to sucker and grow for 9 weeks under the same growth chamber conditions.

During the treatment periods all root systems (winter-cut and summer-cut) were watered when needed and randomly relocated in the water baths or growth chamber to minimize effects caused by differences in the water bath or growth chamber. During suckering any sucker that emerged within 1 cm from the stump of the original sapling was removed. This was done to encourage suckering from the root system and avoiding excessive stump sprouting because stump sprouts are not typical of mature stands regenerating after harvest (Peterson and Peterson 1992).

3.2.3 Measurements

For the 10 pretreatment saplings from both the winter-cut and summer-cut experiments, root collar diameters were taken just above the soil surface (two measurements rotated 90° apart were averaged), heights were measured from the soil surface to the base of the apical bud, and stem dry mass was determined by removing any leaves and cutting the stem at the soil surface and oven drying it until at constant weight. Root systems were washed clean of soil under gentle stream of running water. A 10 cm wide slice of the root system was taken from each sapling to be used for sugar and starch concentration analysis (see below). The remaining roots were oven dried at 68 °C, weighed, and added to the mass of roots taken for carbohydrate sampling to determine total mass of living roots.

For the remaining root systems, after the suckering and growth period of nine weeks had ended, suckers and roots were harvested. All suckers that emerged from the surface of the soil were counted and their heights measured. Each sucker was cut off at the soil surface (the portion of the sucker remaining below the soil was included as part of the root system) and dried at 68 °C until constant mass to calculate an average dry mass per sucker.

Roots were carefully washed clean of soil under gentle stream of running water. Suckers that had not emerged from the soil surface but had expanded more than 5mm from the root system were counted for each root system. Fine roots (<2 mm in diameter) were separated from coarse roots and discarded.

Living coarse roots were separated from dead coarse roots (roots were considered dead when they were dark in color and a blackened interior was revealed by partial removal of the phloem) and dried separately at 68 °C. The dry mass of living roots and dead roots was used to calculate the percentage of living (coarse) roots. Root samples for determining root carbohydrate content were taken as described for the pretreatment measurements: a 10 cm wide slice of roots (living and dead) from the middle section of the potted root system was used for analysis (see below). If all roots were completely blackened and presumably dead, carbohydrate content was considered zero and not analyzed (e.g. DesRochers and Lieffers 2001).

Carbohydrate analysis involved placing the root samples immediately into a drying oven at 100 °C for one hour, and then 68 °C for 3 days. After drying, root sections were ground in a Wiley-Mill until they passed through a 40 mesh screen. Total soluble sugars and starch were extracted and analyzed according to Chow and Landhäusser (2004). Soluble sugars were extracted three times using hot 80% ethanol and then analyzed by reacting the extract with phenol-sulfuric acid and measuring it colourimetrically. Following sugar extraction, starch was digested with α-amylase and amyloglucosidase and glucose equivalents were determined colourimetrically with peroxidase-glucose oxidase-o-dianisidine. Total non-structural carbohydrate reserve (TNC) of roots was calculated as a sum of the concentration per dry mass of sugar and starches.

3.2.4 Data analysis

Pretreatment data for sapling root collar diameter, height, stem dry mass, living root mass, and sugar, starch, and TNC content were compared between the winter-cut and summer-cut saplings using a t-test in SAS (SAS 9.1, SAS Institute, Cary, NC). Data met the assumption of normality using the Shapiro-Wilk test. Significance for all test was based on an alpha value of $p=0.05$.

Measurements made on suckers and root systems after the 9 week suckering and growth period were analyzed separately for the winter-cut and the summer-cut. For each season of cut, data were analyzed as a completely randomized 2 × 2 factorial design. The model tested was

$$Y = \mu + A + B + AB + \varepsilon ,$$

where Y was the response variable (percentage living roots, TNC, number of suckers, number of non-emerged suckers, sucker height, and total dry mass (stems and leaves) standardized per sucker), μ was the population mean, A was the effect of root wounding, B was the effect of log storage, and ε was the random error. A two-way ANOVA using the GLM procedure in SAS was used to test the model. An LSD means comparison test was used to examine the interactions if they were significant. While not all the residuals of the response variables met the assumptions of normality based on the Shapiro-Wilk test, all met the assumption of homogeneity of variances based on a Levene's test. Moreover, data could not be transformed to meet the assumption of normality, so it was also analyzed using the Kruskal-Wallis non parametric test (not presented). For all variables the non-parametric test gave the same results as the ANOVA.

3.3 Results

3.3.1 Pre-treatment conditions

Winter-cut saplings had an average of 105 g living root mass and there were no dead roots. Total non-structural carbohydrate content of roots was 38.5 % of dry mass comprised of soluble sugars (23.1 % root dry mass) and starch (15.1 % root dry mass; Table 3-1). Summer-cut saplings grew in the spring before they were cut, and they were taller than the winter-cut saplings. Root mass and root TNC concentrations were not different from the winter-cut saplings but were in different forms, with 11.8 % being soluble sugar and 24.5 % being starch (Table 3-1).

Table 3-1: Pretreatment measurements (mean ± SE) from the 10 pretreatment root systems/saplings for the winter-cut and summer-cut segments (n=10). Different letters indicate statistical differences between the winter-cut versus summer-cut material ($p<0.05$).

	Winter	Summer
Living root (g)	105 ± 15^{a}	99 ± 15^{a}
Root TNC (% dry mass)	38.5 ± 1.4^{a}	36.3 ± 1.4^{a}
Root sugar (% dry mass)	23.1 ± 0.1^{a}	11.8 ± 0.1^{b}
Root starch (% dry mass)	15.1 ± 1.3^{b}	24.5 ± 1.3^{a}
Root collar diameter (mm)	16.2 ± 3.0^{a}	$13.6\pm2.3.4^{b}$
Height (cm)	122 ± 14^{b}	151 ± 22^{a}
Stem dry mass (g)	54 ± 21^{a}	69 ± 31^{a}

3.3.2 Winter-cut

Simulation of log storage and root wounding significantly impacted the amount of dead aspen roots and their TNC content (Table 3-2). Nearly all roots survived (99 %) when the root systems were subject to no-storage and were non-wounded. Applying storage caused the percent of living roots to drop to 72 %, and wounding to 51 %. Storage plus wounding resulted in 9 % of the roots surviving (Figure 3-2A). A similar trend was observed for TNC (Table 3-2). With no-storage and no root wounding, the TNC content of roots after the growth period was 29 % (of root dry mass). Storage resulted in a TNC content of 20 % and for wounded roots it was 19 %, while for storage combined with wounding, TNC content of the roots was 7 % (Figure 3-2B).

Table 3-2: Summary of p-values from the ANOVA for the winter-cut and summer-cut. The response variables tested were traffic induced root wounding (wounding) and simulated log deck storage (storage) including their interaction term.

	Effect	**Response variable**					
		% living root	**TNC**	**Number of Suckers**	**Height**	**Dry mass / sucker**	**Non-emerged suckers**
Winter-cut	Wounding	<0.0001	<0.0001	0.0025	0.0006	0.0013	0.4159
	Storage	0.0003	0.0001	0.0197	0.0019	0.0041	<0.0001
	Wounding*Storage	0.4426	0.4833	0.8300	0.2667	0.1595	<0.0031
Summer-cut	Wounding	<0.0001	0.2276	0.1036	<0.0001	<0.0001	<0.0001
	Storage	<0.0001	<0.0001	0.0085	<0.0001	<0.0001	<0.0001
	Wounding*Storage	0.0594	0.1039	0.0486	0.1031	0.0046	<0.0001

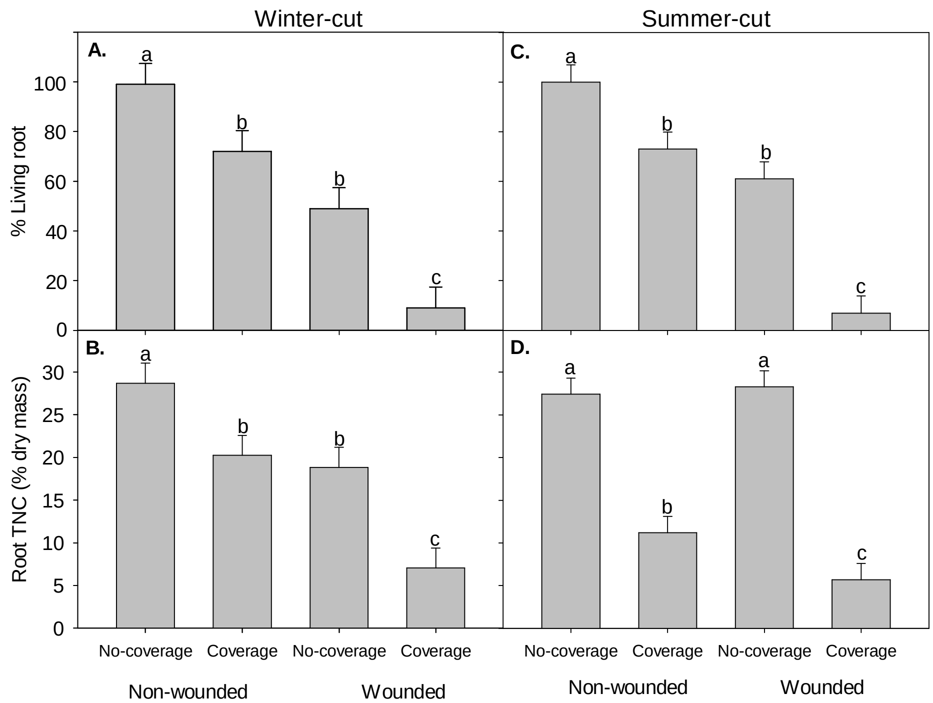

Figure 3-2: The impact of traffic induced root wounding and simulated log storage on the percentage of living roots (A,C) and root TNC (B,D) at the termination of the experiment for root systems that were summer-cut (A, B) and winter-cut (C, D). Different letters indicate a significant difference (p<0.05), and the lines indicate standard error.

The number of suckers produced as well as their height and mass were affected by both log storage and root wounding (Table 3-2). With no-storage, non-wounded root systems produced an average of 9.2 suckers with an average height of 12 cm and dry mass of 0.84 g per sucker. With storage, 4.9 suckers grew from each root system with a height of 4 cm and at a mass of 0.27 g per sucker. Wounded roots with no-storage produced 3.6 suckers at a height of 4 cm and a mass of 0.21 g per sucker, while wounding with storage completely inhibited suckering (Figure 3-3AB&C).

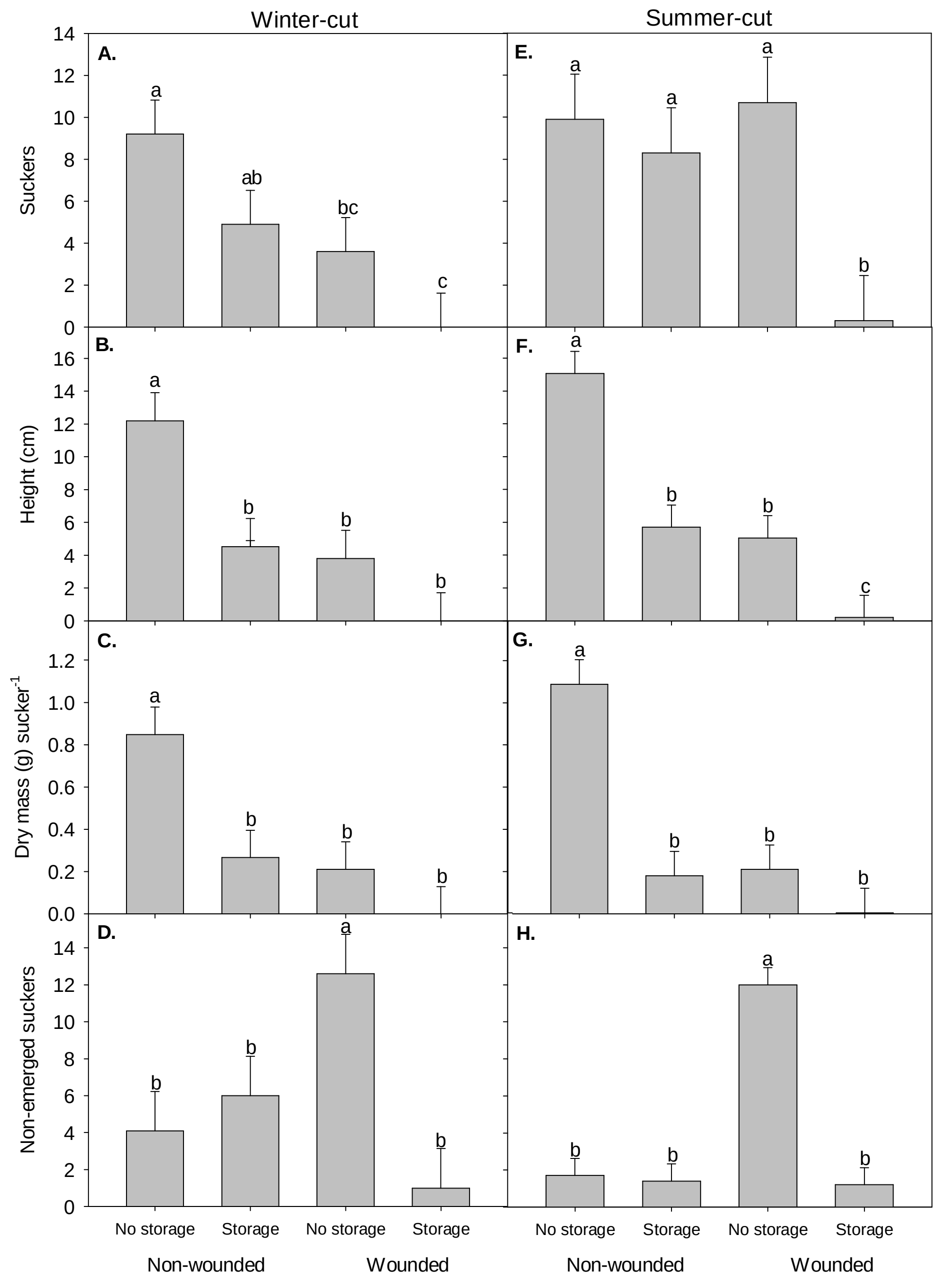

Figure 3-3: The impact of traffic induced root wounding and simulated log storage on the number of suckers produced from each root system (A,E), the height of the suckers (B,F), the dry mass of the suckers (C,G), and the number of suckers that did not emerge from the soil surface (D,H) for the winter-cut (A, B, C, D) and summer-cut (E, F,G,H). Different letters indicate a significant difference ($p<0.05$), and the lines indicate standard error.

The number of non-emerged suckers (suckers that did not emerge from the soil surface) was affected by log storage and the interaction between root wounding and storage (Table 3-2). Non-wounded root systems with no-storage had 4.1 non-emerged suckers. With storage, non-wounded root system produced 6.0 non-emerged suckers. When the root system was wounded with no-storage an average of 12.6 non-emerged suckers were observed. Storage and wounded treated root systems produced 1.0 non-emerged suckers (Figure 3-3D).

3.3.3 Summer-cut

Simulation of log storage and root wounding impacted the percentage of living roots (Table 3-2). Non-wounded root systems with no-storage had all living roots (100 %), but when subjected to storage, the percentage of living roots was reduced to 73 %. Wounded root systems with no-storage had 61 % living roots, similar to the storage treated root systems. Combined, wounding and storage resulted in only 7 % living roots (Figure 3-2C). TNC content of the root system followed a different trend, where TNC was affected by storage but not by root wounding (Table 3-2). Non-wounded root systems with no-storage had a TNC content of 27 % (by root dry mass) while storage treated roots had 11 %. Wounding had little effect as the root systems had 28 % TNC content, but wounding and storage together resulted in a significantly reduced TNC content of 6 % (Figure 3-2D).

Storage and its interaction with root wounding affected the number of suckers produced while wounding and storage as well as their interaction affected the number of non-emerged-suckers and dry mass per sucker (Table 3-2). Wounded root systems with storage produced few suckers (0.3 suckers; Figure 3-3E), while there were no differences in numbers of suckers (mean of 9.7) among the remaining treatments. The number of non-emerged suckers was increased for the wounded root systems with no-storage (12.0 non-emerged suckers per root system; Figure 3-3H) while the remaining treatments produced fewer (approximately 1.4). Dry mass was 1.09 g per sucker for the non-wounded root systems with no storage (Figure 3-3G) and dropped significantly for the remaining treatments (0.18 g per sucker for non-wounded root systems with storage, 0.21 g per sucker for wounded root systems with no-storage, and 0.01 g per sucker for wounded root systems with storage).

Sucker height growth was affected by root wounding and log storage but not by their interaction (Table 3-2). Non-wounded root system without storage grew suckers with an average height of 15 cm, and with storage the height was 6 cm. Wounded root systems with no-storage had suckers with an average height of 5 cm and with storage the height was 0.2 cm (Figure 3-3F).

3.4 Discussion

Both root wounding and simulated log storage (barriers that prevent emergence of suckers) had significant negative effects on the health of the root systems, recovery of root carbohydrates after suckering, and the number of suckers produced, as well as their growth rate. The combination of root wounding and log storage nearly eliminated aspen regeneration in both the winter-cut and summer-cut root systems. Root wounding caused death of a large portion of the root system, but despite the root death there was a large increase in the number of non-emerged suckers (Figure 3-2&3). This stimulation of suckering is consistent with Fraser et al. (2004) who suggested that damage to the root system affects the hormonal conditions of the parent root, which can lead to increased sucker production. However, unlike the study by Fraser et al. (2004) the wounding was caused by machine traffic not by hand, and it did not increase the growth rates of the suckers produced, as many of the initiated suckers were unable to reach the soil surface after nine weeks of growth. The severe root wounding caused by machine traffic completely killed sections of the root which likely reduced the hormonal stimulation of cytokinin production needed for shoot elongation (Peterson 1975; Schier 1981) and limited access to resources (carbohydrates, water, nutrients) necessary for the developing suckers (Zahner and Debyle 1965; Fraser et al. 2002; Landhäusser and Lieffers 2002).

Simulated log storage caused an increase in the mortality of the parent root system and led to a reduction of root carbohydrate reserves (Figure 3-2), which decreased the growth of suckers (Figure 3-3). The importance of root carbohydrate reserves for aspen sucker growth has been well established (Schier and Zasada 1973; Landhäusser and Lieffers 2002). However, unlike growth, the number of suckers was not affected as much by the simulated storage (Figure 3) likely because sucker numbers are more strongly related to the hormonal balance of the root system (Farmer 1962; Schier 1973&1981) than to carbohydrate reserves (Schier and Zasada 1973). The reduction in suckering that did occur can possibly be attributed to the loss of root area due to carbohydrate exhaustion from respiration (DesRocher and Lieffers 2001; Landhäusser and Lieffers 2002). Thus, the main effect of log storage on the number of suckers was related to loss of root area rather than decline in root carbohydrates *per se.*

There were differences in the number of suckers that emerged, between the winter-cut and summer-cut experiments. For the winter-cut, there was an additive effect of storage and wounding on numbers of suckers; however, in the summer-cut, the additive effects were less pronounced (Figure 3-3) as wounding had little impact on suckering. The reasons for this difference between the winter and summer experiments may relate to the prolonged overwintering period (stored over two dormant seasons) endured by the winter-cut root systems (Figure 3-1). This longer overwintering may have given fungi a longer incubation period to attack the root system, and thus worsened the effects of root wounding. In addition, the overwintering period may have influenced hormonal balance, which is important for suckering (Schier 1981). The summer-cut did not have an extended storage period; thus suckering and the replenishment of root carbohydrate reserves was less affected by wounding. However, when simulated log storage was added to root wounding it caused a large decrease in suckering for the summer-cut, which resulted in the interaction between storage and wounding.

Initially we had hypothesized that summer applied storage with warm soil temperatures would have a greater negative impact than winter applied storage with cold soil temperatures as was suggested by the field observations of Renkema et al. (2009). However, this growth-chamber study showed that winter-cutting and subsequent storage was equal or possibly more negative than summer-cutting and subsequent storage (Figure 3-2 & 3-3). The inconsistency between studies may be due two reasons. (1) The storage treatment for the winter-cut storage period had a soil temperature of 5 °C. This temperature was based on the findings of Lieffers and van Rees (2002) who measured summer-soil-temperatures under slash piles; however, it is possible that log decks which are denser with a greater biomass could keep soil temperatures cooler than 5 °C over summer. The soil temperatures used in our experiments might have caused higher respiration rates (DesRochers et al. 2002), depleted root carbohydrates, and increased fungal activity (eg. Ross 1976) which may have caused suckers from the winter-cut to not have adequate resources to emerge from the soil. (2) The root systems used were from four-year-old saplings compared to mature trees in logged stands which can react differently to disturbances (eg. Peterson and Peterson 1992). Thus, as a result of these inconsistencies, there was not a clear difference between the winter-cut and summer-cut in this study.

In conclusion, root wounding by machine traffic with forced delays in suckering brought about by surface barriers (i.e. simulated log decks) were detrimental to the survival of aspen parent root systems, and thus inhibited suckering and growth after removal of the barrier. Root wounding damaged and killed portions of the root system and reduced sucker growth but initiated the formation of more sucker buds, presumably due to hormonal changes as a result of wounding. Log storage due to its barrier effect reduced the TNC reserves of root systems, thereby limiting their ability to provide the energy for sucker growth. Furthermore, even when soils were held at cool temperatures (e.g. 5°C) over the normal growing period, there was a large decline in suckering. Logging and hauling in frozen conditions would largely eliminate these problems.

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Chapter 4: General conclusions

4.1 Research summary

Aspen regeneration was assessed in response to disturbances common to log decking areas such as log deck building and storage, soil compaction, root damage, and slash accumulation. The field study in chapter 2 assessed the effects of season of building of decks (summer or fall), and duration of log storage (1.5-3 months or 11 months after a fall harvest) as well as the impacts of root wounding, soil bulk density, and slash load on aspen regeneration. It was found that log decks built in the summer and stored for 3 to 5 months caused significant root death and a 50% reduction in sucker regeneration density, but a log deck built in the fall and stored for a similar length of time had little impact on parent root survival and associated sucker regeneration density. Additionally, it was found that when logs from a fall built log deck were stored for up to 11 months and over a full growing season, the impact on regeneration was minimal.

Slash likely had a significant effect on aspen regeneration on these decking areas compared to root wounding and soil bulk density. Slash was nearly three times thicker on decking areas than less disturbed areas, and it consisted of a nearly impenetrable mat of bark, twigs, and small branches. Only a small difference in soil bulk density and root wounding between decking areas and minimally disturbed harvested areas was observed, and the small difference that was observed would likely have had little effect on aspen regeneration. Soil bulk density and root wounding were less of a factor because the slash may have moderated the effects of machine traffic (Akay et al. 2007).

The controlled growth-chamber study in chapter 3 evaluated the mechanisms proposed in chapter 2 of how the timing of log storage affects aspen parent root systems and suckering as well as examining the effects of traffic-induced-root wounding after a summer and winter harvest. The results of this study showed that log storage with root wounding was detrimental to the survival of the parent root system, total non-structural root carbohydrate (TNC) reserves, and the growth of aspen suckers. Both seasons of cut had similar responses for these variables; however, for the summer-cut, storage and wounding had little impact on the number of suckers produced. For the winter harvesting this was not true as storage and wounding alone caused a decrease in the number of suckers produced.

The effects of log storage in the controlled, growth-chamber study (chapter 2) and field study (chapter 3) were not consistent as expected. Season had little effect in the growth-chamber study, and summer harvesting with subsequent storage performed similar to the winter-cut, while in the field study a fall harvest with subsequent storage clearly performed better then the summer treatment. The lack of seasonal difference in the growth chamber study may be due to warmer soil temperatures (5 °C) used to simulate the impact of log storage after a winter harvest. As well, smaller and younger roots were used in the growth chamber study compared to the field study where much older and larger roots were present. The smaller roots (2 cm in diameter) in the growth chamber may have been less affected by cold soil temperatures than larger roots in the field study (eg. DesRochers et al. 2002). Lastly, the seasonal storage periods were longer in the growth chamber study (3-6 months) than in the field study (1.5-5 months) which may have decreased any seasonal effects.

While root wounding was not considered a major factor in the poor growth of aspen in the field study (chapter 3) it had a significant impact in the growth-chamber study (chapter 2). The differences may be, as previously, due to the root sizes; the mature aspen stand in field study had much thicker roots than root systems used in the growth chamber study where the largest roots were 2 cm in diameter, allowing them to be more easily damaged. As well, in the field study a thick layer of slash may have protected the root systems from damage (Akay et al. 2007) and overrode the effects of root damage. Lastly, the growth chamber study had a much longer period between harvest and suckering (up to 16 months) compared to the field study (maximum 11 months). This period may have allowed for fungi to attack the root system and affected the hormonal balance of the root system negating any sucker stimulating effects of root wounding (eg. Fraser et al. 2004).

4.2 Management Implications

To ensure that a healthy mature stand of 500-700 stems ha^{-1} of aspen can eventually develop, its has been recommended that a minimum of 15 000 to 30 000 suckers ha^{-1} are needed one year after harvest (Krasny and Johnson 1992; David et al. 2001). As found in chapters 2&3, log storage, machine traffic, and slash accumulation can prevent stands from reaching these densities on decking areas. However, from these studies several suggestions for managing harvest activities to lessen the impact on aspen regeneration can be deduced.

Avoiding the building of log decks and prolonged storage of logs by cutting, skidding, delimbing, and immediate hauling, also known as hot-logging, is an obvious solution. However, hot-logging may not always be possible due to unsuitable hauling conditions or wood flow to the mill. For these situations, harvesting with storage over the winter months until the following summer may be an option. Evidence from chapters 2&3 suggests the impact on suckering may be lessened provided that soil temperatures under the log deck remain around freezing (below 5 °C) and storage does not exceed a year. In contrast, building decks in summer followed by a several month storage period should be avoided.

Limiting damage to the root systems and soil structure caused by traffic will further improve sucker regeneration. Ensuring that the soil is frozen prior to harvesting will reduce the impact of traffic on aspen regeneration (Bates et al. 1993; Berger et al. 2004; Mundell et al. 2008). Harvesting on unfrozen soils in the winter and summer may be unavoidable. In these situations care should be taken to avoid wet soils as they are more prone to rutting leading to increased root damage (Shepperd 1993: Stone and Elioff 1998&2000) and soil compaction (McNabb et al. 2001). There is evidence that placing a thick layer of slash or organic matter over the soil can protect the roots and soil from damage (McNabb 1994; Akay et al. 2007).

Although slash may reduce the impacts of machine traffic, a thick layer (approximately 5 cm) can prevent suckers from emerging from the soil surface (Chapter 2; Landhäusser et al. 2007). Removing this slash after harvest is important. While slash clean-up on decking areas does typically occur, it usually only removes the larger branches and logs and leaves behind the finer branch and bark debris. This debris, which can be compacted by traffic into an interwoven mat, and needs to be removed during clean-up. Care in this operation would be required because digging too deeply could also damage the root system, and not digging deep enough would leave too much debris. Another option would be to adopt a different operations model such as cut-to-length where the tree is processed at the stump, and there is not a single site where heavy debris accumulates.

4.3 Future research

As log storage has received minimal attention in the past, much is still unknown. Therefore, several areas require further research:

1. The soil temperature under a log deck throughout the year is not known. The studies in chapters 2&3 assumed that a log deck had a similar but more drastic effect than a slash pile on soil temperatures; preventing summer soil temperatures from rising above 5 °C when the log deck was built during a period of cold soil temperatures (Lieffers and van Rees 2006). Knowing the actual effect of log decks on soil temperatures would provide a clearer picture of the mechanism and impact of log deck storage on aspen regeneration. Along with this, determining if there is a minimum temperature needed for a given storage period to ensure suckering occurs once the log deck is removed. This would be useful information for managing log deck storage.

2. Measuring root carbohydrates during the storage period as well as after the log deck storage period (prior to a growth period) would allow for a better understanding of the effects of log storage on carbohydrate reserves. Carbohydrate measurements may help determine if suckering is limited primarily by a loss of carbohydrates or if another factor such as hormones are affecting suckering.

3. Re-examining the influence of slash (small branch and bark debris), root damage, and soil compaction could be useful in concretely determining their individual contribution to aspen regeneration. Looking at how these disturbances correspond to the number of suckers produced and their height growth could help determine thresholds of slash thickness for aspen management.

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