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Kevin N. Renkema

Simon M. Landhausser

Victor J. Lieffers

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Suckering response of aspen to traffic-induced-root wounding and the barrier-effect of log storage

Kevin N. Renkema [*], Simon M. Landhäusser, Victor J. Lieffers

Centre for Enhanced Forest Management, Department of Renewable Resources, University of Alberta, 4-42 Earth Sciences Building, Edmonton, AB T6G 2E3, Canada

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ABSTRACT

In a growth chamber, we tested how the seasonal timing of placing a physical barrier (simulating a possible effect of log storage) and inflicting root damage impacted aspen (*Populus tremuloides* Michx.) root systems and their suckering capability. Roots from 4-year-old saplings were used, and one half of these root systems had the above-ground portion cut in the winter (dormant) while the other half was cut during the growing season in the summer. Damage was inflicted to the roots by driving a large farm tractor over them, and a covering treatment was applied using a polystyrene board to prevent suckers from emerging from the soil. Soil temperatures for the winter-cut root systems were kept at 5 °C over the growing season, using a water bath, while for the summer-cut root systems soil temperatures were maintained at 17 °C over the growing season. In the winter-cut root systems, both log storage and root wounding caused a 40% reduction in living root mass and carbohydrate reserves, as well as reducing sucker numbers and their growth performance. In the summer-cut root systems log storage and root wounding reduced living root mass by approximately 35% as well as sucker growth, but had less of an impact on the number of suckers produced.

1. Introduction

Aspen (*Populus tremuloides* Michx.) regeneration by root suckering is dependent upon the physiological condition of the parent root system as well as the environmental conditions surrounding these roots (Frey et al., 2003). These conditions include hormonal balance, carbohydrate content, root damage, soil temperature, and soil 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; MacIsaac 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 impact of soil compaction on aspen suckering has been widely studied (Bates et al., 1993; Shepperd, 1993; Zenner et al., 2007). 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). Soil compaction can also lead to root wounding although wounding can occur without soil compaction (Shepperd, 1993). Wounding affects the hormonal balance of the root system producing an increase in suckering density and growth (Farmer, 1962; Lavertu et al., 1994; Fraser et al., 2004). However, severe wounding can cause a reduction in suckering due to extensive fragmentation of the root system which limits the suckers access to resources (Zahner and DeByle, 1965) or allows for disease to attack and weaken the root system (Basham, 1988). Studies suggesting that soil compaction with root wounding is detrimental to suckering have rarely examined the root system and do not differentiate between the impacts of wounding and soil compaction (Bates et al., 1993; Zenner et al., 2007) while studies that have looked at the direct impact of wounding used shovels or hand tools to simulate root damage by severing or scraping the aspen roots (Farmer, 1962; Fraser et al., 2004). No studies have directly examined aspen roots impacted by heavy machine traffic and the effect on subsequent suckering performance. Looking at the root systems will help isolate the effects of root wounding from soil compaction and give a better understanding of the impacts of harvesting on subsequent aspen regeneration.

Log storage and its impacts on aspen suckering have also received minimal attention. This is surprising because storage of

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[*] Corresponding author. Tel.: +1 780 492 277; fax: +1 780 492 2771.
E-mail address: renkema@ualberta.ca (K.N. Renkema).

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log decks can cause large reductions in suckering (Renkema et al., 2009) and affect a significant portion (6–8%) of a harvested area (MacIsaac 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 was due to the effect of the log decks on soil temperature. For example, a log deck built during the winter maintains low soil temperature during the growing season due to its insulating ability which slows root respiration (DesRochers et al., 2002) and prevents suckering under the log deck (Landhäusser et al., 2006). Thus, cool soils under the deck allow roots to conserve carbohydrate reserves for longer survival, leading to better suckering and growth once the log deck is removed. In contrast, a log deck built in the summer has warmer soils underneath the deck 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 suckering, once the log deck is removed, could be poor. However; these hypotheses, that the impacts of log storage are largely due to its barrier effects and influence on soil temperature, have never been tested.

The effects of log storage and wounding of parent roots may also interact with each other. For example, 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 wounding may become more detrimental to the root system covered by log decks as it is less able to respond defensively to the root 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.

2. Methods

2.1. Plant material

One hundred aspen (*P. tremuloides* Michx.) saplings were used in this study. They were grown from seed collected from open-pollinated aspen trees in Edmonton, Alberta. When the seedlings were 1-year-old they were transplanted into rectangular pots (16 cm wide × 15 cm deep × 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. The transplanted seedlings were grown outside at the University of Alberta (Edmonton, AB) for 3 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 the 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 for a dense and laterally spread root system with root sizes up to 20 mm in diameter to develop, and the sand-peat mixture made the roots easy to extract for examination.

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 the treatments being coverage simulating a physical barrier (no-coverage and coverage) and root wounding by machine traffic (non-wounded and wounded). The separation of the study into two experiments was because the duration and conditions in the coverage treatment were not comparable between the winter-cut and summer-cut.

Table 1

Pretreatment measurements (mean ± SE) from 10 pretreatment root systems/saplings for the winter-cut and summer-cut segments ($n = 10$).

	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 ± 2.3^{b}
Height (cm)	122 ± 14^{b}	151 ± 22^{a}
Stem dry mass (g)	54 ± 21^{a}	69 ± 31^{a}

Different letters indicate statistical differences between the winter-cut versus summer-cut material.

2.2.1. Winter-cut

The sequence of application and duration of the different treatments are depicted in Fig. 1A. In the fall (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). For the wounding treatment the root masses and bound soil were removed from their pots and placed side-by-side to form a 57 cm-wide by 320 cm-long continuous bed on a hard road surface. Two 320 cm long pieces of lumber 5 cm-high and 10 cm-wide were placed lengthwise under this bed and a heavy logging chain was looped three times on top; these features were used to induce the crushing and shearing processes typical of logging operations. A 7130 Case International Magnum farm tractor, exerting a ground pressure of 63 kPa—similar to loaded skidders (William and Neilson, 2000), made 6 passes over the root systems (based on a preliminary study, 6 tractor passes caused a 70% death of root mass typical of heavily trafficked skid trails and landings (Shepperd, 1993)). No significant soil compaction occurred as a result of the root wounding treatment judged by a visible increase in soil volume 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 in order to inoculate the pots with natural bacteria and fungi. Root systems were then overwintered outside by covering them with 30 cm of 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 h of light at 18 °C, 7 h 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 coverage treatments (no-coverage and coverage). The 20 root systems assigned to no-coverage were given 9 weeks to sucker and grow. The coverage treated root systems were tightly fitted with a 2.5 cm thick sheet of polystyrene board that was pressed firmly against the soil surface and affixed to the pot. The bottom of the pots were sealed and placed in a water bath (as described by Landhäusser et al., 2003) to maintain soil temperatures at 5 °C. The 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 the root systems were moved outside to overwinter covered with 30 cm of straw and buried in

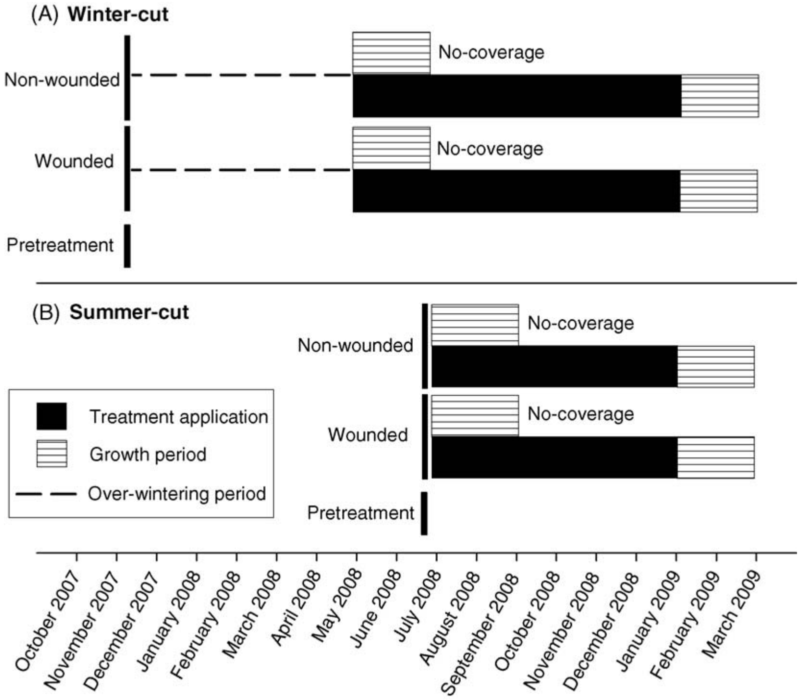

Fig. 1. Timeline of the application of the treatments: root wounding and coverage for (A) winter-cut (B) summer-cut. The width of each box indicates the duration of treatment application while the height indicates the relative number of root systems to which the treatment was applied.

snow. In January 2009 the root systems were brought back into the growth chamber and allowed to sucker and grow for 9 weeks under the same growth chamber conditions as described before and with ambient soil temperatures.

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 h of light at 18 °C, 7 h 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-coverage level of the coverage treatment and given 9 weeks to sucker and grow. The remaining root systems were subjected to coverage and a tightly fitted 2.5 cm thick sheet of polystyrene board was pressed firmly against the soil surface and bound to the pot. Soil temperature was maintained at the ambient air temperature. In September 2008, the coverage treated root systems were uncovered and placed outside to condition them for winter. To overwinter, root systems were buried in straw and in the snow in November 2008. In January 2009 they were brought back into the growth chamber to sucker and grow for 9 weeks under the same growth chamber conditions described earlier.

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 of position in the chamber. During the suckering period, any sucker that emerged within 1 cm from the stump of the original sapling was removed to encourage suckering from the root system and avoiding excessive stump sprouting which occurs on younger stems; stump sprouts are not typical of mature stands regenerating after harvest (Peterson and Peterson, 1992).

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, cutting the stem at the soil surface, and oven drying it until at constant weight. The root systems were washed clean of soil under gentle stream of running water. A 10 cm wide slice taken from the middle section of the root system of each plant was 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 the total mass of living roots.

For the remaining root systems after the suckering period of 9 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.

The root systems were then 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 5 mm from the root system were counted. Fine roots (<2 mm in diameter) were separated from the coarse roots. 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 the living roots and dead roots was used to calculate the percent living 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. If all roots for the potted root system 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 1 h, and then 68 °C for 3 days. After drying, the 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 a sum of the concentration per dry mass of sugar and starches.

2.4. Data analysis

Pretreatment data for root collar diameter, sapling height, stem dry mass, living root mass, and sugar, starch, and TNC content between winter-cut and summer-cut saplings were analyzed using a *t*-test in SAS (SAS 9.1, SAS Institute, Cary, NC). The data met the assumption of normality using the Shapiro–Wilk test.

Measurements made on suckers and root systems after the 9-week 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

$$Y = +A + B + AB +$$

where Y was the response variable (ratio of dead to 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 coverage, and ε was the random error. A two-way ANOVA using PROC GLM in SAS was used to test the model. A LSD means comparison test was used to examine differences between treatments. 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. For all variables the non-parametric test gave the same results as the above-described ANOVA, so only the ANOVA was presented. In all tests, significance was based on an alpha of 0.05.

3. Results

3.1. Pretreatment conditions

Winter-cut saplings had on average 105 g of living root mass and there were no dead roots. Total non-structural carbohydrate content of roots was 38.5% (root dry mass) comprised of soluble sugars (23.1% root dry mass) and starch (15.1% root dry mass; Table 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 TNC was in different forms, with 11.8% (root dry mass) being soluble sugar and 24.5% (root dry mass) being starch (Table 1).

3.2. Winter-cut

Coverage and root wounding significantly impacted the amount of living aspen roots and their TNC content (Table 2). Nearly all roots survived (99%) when the root systems were subject to no-coverage and non-wounded. Adding coverage caused a drop in percent living roots to 72%, and wounding resulted in 51% of the roots being alive. Coverage plus wounding resulted in 2% of the roots surviving (Fig. 2A). A similar trend was observed for TNC; root systems with no-coverage and non-wounded had a TNC content of 29% (root dry mass). Coverage resulted in TNC content of 20%, and for wounded roots it was 19%, while for coverage combined with wounding, TNC content of the roots was 7% (Fig. 2B).

The number of suckers produced as well as their height and dry mass was affected by both coverage and root wounding (Table 2). With no-coverage, non-wounded root systems produced 9.2 suckers with a height of 12 cm and dry mass of 0.84 g per sucker. With coverage, non-wounded roots had 4.9 suckers and were 4 cm tall and 0.27 g per sucker. Wounding resulted in 3.6 suckers at a height of 4 cm and a mass of 0.21 g per sucker, while coverage with wounding completely inhibited suckering (Fig. 3A–C).

The number of non-emerged suckers (suckers that did not emerge from the soil surface) was affected by coverage and the interaction between root wounding and coverage (Table 1). Root systems with no-coverage and which were non-wounded produced 4.1 non-emerged suckers, and with coverage, root systems had 6.0 non-emerged suckers. Wounded root systems had 12.6 non-emerged suckers. Coverage and wounded root systems produced 1.0 non-emerged suckers (Fig. 3D).

3.3. Summer-cut

Coverage and root wounding had an impact on the percentage of living roots (Table 2). No-coverage and non-wounded root systems remained completely alive (100% living roots), when subjected to cover 73% of the roots were living, with wounding 61%

Table 2
Summary of p-values from the ANOVA for the winter-cut and summer-cut.

Effect	Response variable					
	Percent living root	TNC	Number of suckers	Height	Dry mass per sucker	Non-emerged suckers
Winter-cut						
Wounding	<0.0001	<0.0001	0.0025	0.0006	0.0013	0.4159
Coverage	0.0003	0.0001	0.0197	0.0019	0.0041	<0.0001
Wounding × coverage	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
Coverage	<0.0001	<0.0001	0.0085	<0.0001	<0.0001	<0.0001
Wounding × coverage	0.0594	0.1039	0.0486	0.1031	0.0046	<0.0001

The response variables tested were root wounding and coverage as well as their interaction term.

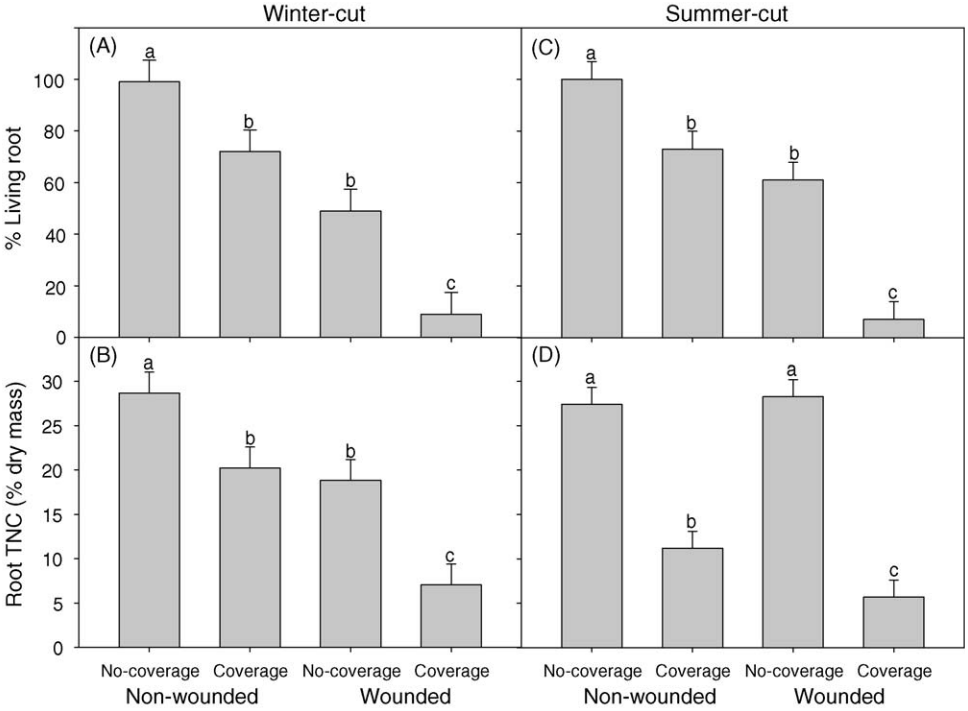

Fig. 2. The impact of root wounding and coverage on the percent of living roots and the root total non-structural carbohydrates (TNC) at the termination of the experiment for root systems that were summer-cut (A and B) and winter-cut (C and D). Different letters indicate a significant difference ($p < 0.05$) and the lines indicate standard error.

of the roots were living, and wounding and coverage combined resulted in 7% of the roots being alive (Fig. 2C). TNC content of the root system followed a different trend, where TNC was affected by coverage but not root wounding (Table 2). The TNC content of no-coverage and non-wounded root systems was 27% (root dry mass) while covered roots had 11%. Wounding had little effect compared to no treatment (28%). Coverage with wounding resulted in a TNC content of 6% (Fig. 2D).

Coverage and its interaction with root wounding affected the number of suckers produced (Table 2) while coverage and wounding as well as their interaction affected the number of non-emerged suckers and dry mass per sucker (Table 2). Wounded root systems with coverage produced few suckers (0.3 suckers; Fig. 3E), while there were no differences in numbers of suckers (mean of 9.7) among the remaining treatments. For non-emerged suckers, the number produced per root system was increased when wounded with no-coverage (12.0), and the remaining treatments produced fewer (1.7 for non-wounded with no-coverage, 1.4 for non-wounded with coverage, and 1.2 for wounded with coverage; Fig. 3H). Dry mass was 1.09 g per sucker for no-coverage treated root system that were non-wounded (Fig. 3G) and dropped significantly for the remaining treatments (0.18 g per sucker for cover, 0.21 g per sucker for wounding, and 0.01 g per suckers for coverage with wounding).

Sucker height growth was affected by coverage and root wounding but not by their interaction (Table 2). With no-coverage, non-wounded root system grew suckers 15 cm, and with coverage their growth was 6 cm. Wounded root systems produced suckers with an average height of 5 cm, and coverage with wounding produced suckers with a height of 0.2 cm (Fig. 3F).

4. Discussion

Both coverage and root wounding had significant negative effects on the aspen root system, the recovery of root carbohydrates after suckering, and the number and growth of suckers produced. The combination of coverage and root wounding nearly eliminated aspen regeneration in both the winter- and summer-cut. Root wounding caused the death of a large portion of the root system (Fig. 2), but despite the root death there was a large increase in the number of non-emerged suckers (Fig. 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 here was caused by machine traffic and not by hand; in the wounding treatment growth rates of the suckers was suppressed and many of the initiated suckers were unable to reach the soil surface after 9 weeks of growth. The severe root wounding caused by machine traffic completely killed sections of the root which likely reduced the hormonal stimulation of suckering from 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; Lieffers and Van Rees, 2002). Thus, the importance of an intact root system for sucker growth and the need to limit root wounding during harvest is demonstrated in this study.

Coverage also caused an increase in mortality of the aspen root system and led to a reduction of root carbohydrate reserves (Fig. 2), which decreased the growth of suckers (Fig. 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 coverage treatment (Fig. 3) likely because sucker numbers are more strongly related to the hormonal balance of the root system (Farmer, 1962; Schier, 1973, 1981) than to the carbohydrate reserves (Schier and Zasada, 1973). The reduction in suckering that did occur can possibly be attributed to the loss of root area (less fine root growth) due to carbohydrate exhaustion in the root systems from respiration (DesRochers and Lieffers, 2001; Lieffers and Van Rees, 2002). The main effect of log storage on the

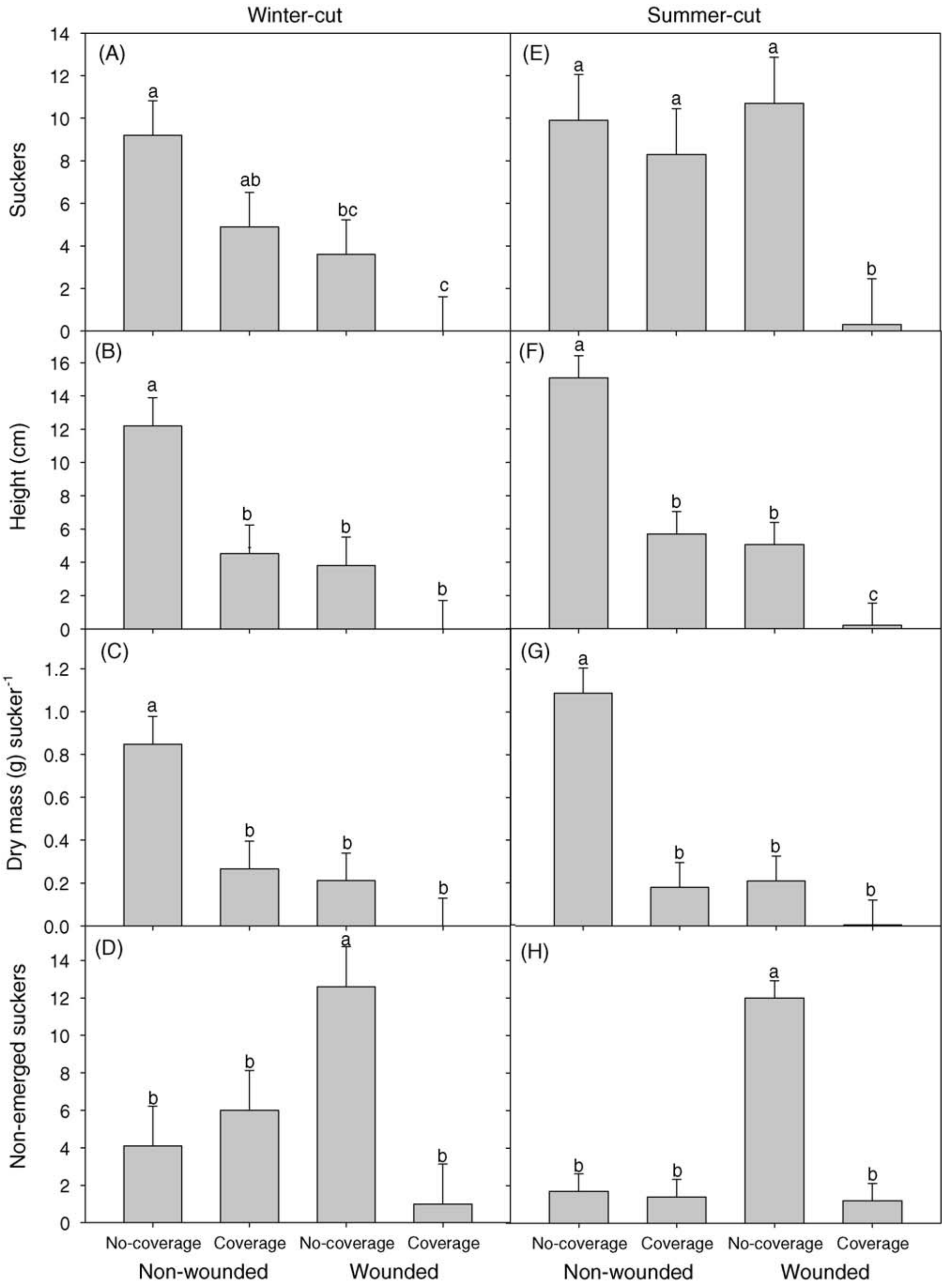

Fig. 3. The impact of root wounding and coverage on the number of suckers produced from each root system (A and E), the height of the suckers (B and F), the dry mass of the suckers (C and G), and the number of suckers that did not emerged from the soil surface (non-emerged) (D and H) for the winter-cut (A–D) and winter-cut (E–H). Different letters indicate a significant difference ($p < 0.05$) and the lines indicate standard error.

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 coverage and wounding on numbers of suckers; however, in the summer-cut, the additive effects were less pronounced. Wounding alone in the summer-cut had relatively little impact on sucker numbers (Fig. 3E), likely through stimulation of suckering by hormones produced after wounding on an actively growing root system. However the covering of the wounded root systems likely negated any hormonal benefits to suckering related to wounding during the growing season (Schier, 1981); the coverage gave fungi and bacteria a period to attack and weaken the wounded root system resulting in much lower numbers of emerged suckers, thus resulting in an interaction between coverage and wounding.

Initially we had hypothesized that a physical barrier applied in the summer would have a more negative impact than one applied in the winter based on the field observations of Renkema et al. (2009), where summer storage was more detrimental to suckering than winter storage. However, this growth-chamber study showed that winter-cutting with coverage and maintenance of soil temperatures of 5 °C was equal or possibly slightly more negative to aspen regeneration (Fig. 3) than summer-cutting with coverage and soils of 18 °C. The inconsistency between studies may be due two reasons: (1) our coverage 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 warmer soil temperatures used in our experiments might have caused higher respiration rates (DesRochers et al., 2002), depleted root carbohydrates, caused the suckers from the winter-cut to not have enough resources to emerge, and thus evened out the differences between the winter and summer-cut. (2) The root systems we used were from 4-year-old saplings compared to mature trees in logged stands.

In conclusion, both root wounding and coverage (i.e. the simulation of the physical barrier and soil temperature effects of log storage) were detrimental to the survival of aspen parent root systems, and thus inhibited suckering and growth after the 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. Coverage 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 soil temperatures (e.g. 5 °C) over the normal growing period, there was a large decline in suckering. However the combination of root wounding and physical barriers that prevented suckering had the most dramatic effect on aspen root systems, killing most of the root systems and eliminated the regeneration potential regardless of the timing of the cut. To avoid the negative impacts of wounding and coverage from log storage on aspen regeneration the ideal solution would be for logging and hauling to occur in frozen conditions; here root damage would be minimal and logs would be removed before the next growing season otherwise they would impede the emergence of suckers.

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