University of Alberta

The effects of soil nutrition, temperature, mechanical site preparation and wildfire on trembling aspen (*Populus tremuloides* Michx.) root suckering

by

Erin Cristine Fraser

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Abstract

The objective of this thesis was to examine some of the drivers of trembling aspen (*Populus tremuloides* Michx.) root suckering. In order to accomplish this, three studies were completed. The first study examined the effects of maximum daily soil temperature on aspen suckering in a controlled chamber experiment. Results showed that temperatures between 12° and 20°C did not affect the number of suckers initiated per root, but did affect the time required for sucker initiation. In a second growth chamber study, $CaSO_4$ or NH_4NO_3 was applied to sections of aspen root. These nutrients did not affect numbers of suckers produced, but sucker dry weight was significantly increased by both nutrients. Finally, a field-based study investigated the effects of mechanical site preparation (MSP) and subsequent wildfire on aspen suckering. Results showed that MSP can successfully stimulate aspen suckering and that microsites where the parent root system was disturbed but not seriously damaged generated the greatest number of suckers. Also, this study indicated that fire after the first growing season can successfully be used to improve suckering.

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CHAPTER I

General Introduction

Trembling aspen regeneration

Trembling aspen (*Populus tremuloides* Michx.) is a deciduous tree species that is widely distributed throughout North America (Perala 1990). This species is able to reproduce via seed dispersal, however vegetative regeneration through root sucker production is the more common means of reproduction (Barnes 1966, Steneker 1976, Kemperman 1978). Consequently, aspen stands are often clones of genetically identical above-ground individuals that are connected through a shallow root system (Day 1944, Strong and LaRoi 1983). During the life cycle of a healthy aspen stand root suckers typically appear in the understory on a regular basis, however the new stems are generally weak and short-lived (Schier and Smith 1979). Following a severe disturbance like clearcut harvesting or wildfire, however, aspen usually regenerates prolifically (Bartos and Mueggler 1981, Bartos and Mueggler 1982, Crouch 1983, Brown and DeByle 1987) and can produce over 100 000 suckers per hectare in the first growing season (Schier and Smith 1979, Bella 1986).

Trembling aspen suckering is controlled by several factors, the first of which is apical dominance. Apical dominance is the inhibition of subapical bud development by an apical bud (Farmer 1962, Eliasson 1971). In aspen, the hormone auxin has been identified as the primary mechanism of apical dominance (Wickson and Thimann 1958, Farmer 1962, Eliasson 1971, Schier 1972, Schier 1981). Auxin is produced in the crown and is constantly transported to the root system (Farmer 1962, Eliasson 1971, Schier

1972). Cytokinin, another hormone that is produced in the root tips, is also thought to be involved in apical dominance (Wickson and Thimann 1958, Winton 1968, Wolter 1968, Schier 1981). It is thought that the balance between auxin and cytokinin in the root system is the critical factor for sucker suppression or initiation (Schier et al. 1985, Doucet 1989). When aspen stems are removed or killed, auxin no longer enters the root system and cytokinin no longer exits, thus the hormonal balance is upset (Eliasson 1971). This loss of hormonal equilibrium appears to signal previously suppressed buds to release, thereby initiating suckers. The removal of apical dominance is critical for aspen regeneration. Steneker (1974) concluded that it was the most important factor in aspen suckering when he noted that on sites where apical dominance was removed, there was approximately three times the aspen density compared to sites where apical dominance was maintained, even though site conditions were otherwise highly favourable for suckering.

Injury to the parent root system has also been identified as an important factor for aspen regeneration, and this has been linked to apical dominance. It is thought that severing or girdling parent roots eliminates or reduces the flow of auxin within the injured root (Farmer 1962, Maini and Horton 1966a). However, this relationship is not clear as the majority of aspen root wounding studies have been done under field conditions where there are many other confounding factors. Nevertheless, a number of experiments have shown that treatments that disturb the parent root system tend to dramatically increase sucker numbers compared to undisturbed areas (Zehngraff 1946, Zillgitt 1951, Maini and Horton 1966a, Weingartner 1980, Alban et al. 1994, Lavertu et al. 1994, Frey 2001).

Soil temperature has also been identified as an important part of aspen sucker initiation (Steneker 1974, Steneker 1976, Peterson and Peterson 1992, Peterson and Peterson 1995). It is thought that higher soil temperatures not only speed up internal metabolic processes, but also contribute to the degradation of auxin (Schier et al. 1985), however this theory has not been rigorously investigated. Nevertheless, previous laboratory experiments have reported that the number of aspen suckers produced on a given root section increase with increasing temperature up to a maximum temperature of approximately 30°C (Horton and Maini 1964, Maini and Horton 1966b, Gifford 1967, Zasada and Schier 1973). However, these studies often used constant temperatures throughout the experimental period (Horton and Maini 1964, Maini and Horton 1966b, Gifford 1967), which do not reflect natural conditions. Further, several studies incubated small (8-10cm) root sections (Maini and Horton 1966b, Gifford 1967, Zasada and Schier 1973), which may have affected sucker survival over the experimental period (Perala 1978). Soil temperature has also been noted to affect aspen suckering under field conditions. Maini and Horton (1966a) and Hungerford (1988) observed significant increases in suckering over controls related to higher average daily soil temperatures during the period of sucker initiation (June and July). However, the temperature increases observed by Hungerford (1988) following prescribed burning were relatively minor (2-3°C during June and July), yet the treated areas generated 4.5-15 times more suckers than the untreated control sites. This seems to indicate that soil temperature alone was not responsible for the remarkable increase in aspen suckering following treatment. Instead, injury to the parent root system or increased soil nutrient availability may have been contributing factors.

Disturbances such as prescribed burning and mechanical site preparation have been reported to increase the availability of nutrients immediately following treatment (Ahlgren and Ahlgren 1960, Feller 1982, van Cleve and Dyrness 1983, Macadam 1987, Vitousek et al. 1992, Schmidt et al. 1996). There have been no reports of nutrients affecting the rate of aspen suckering but high nutrient levels have been observed to increase aspen growth rates in laboratory experiments (Gifford 1967, Lu and Sucoff 2001). Also, in a field-based study Frey (2001) observed a significant correlation between soil calcium and magnesium availability and aspen sucker density, percent cover and total stem height.

Once suckers have been initiated, the carbohydrate reserves in the parent root system are critical for early growth and development. The number of suckers initiated per root is independent of root carbohydrate reserves (Tew 1970, Schier and Zasada 1973), however the number of suckers appearing above the soil surface would likely be related to reserve levels. Suckers are wholly dependent on root reserves until they begin photosynthesizing (Schier and Zasada 1973). Consequently, at the start suckers are entirely dependent on carbohydrate reserves for energy as they grow through the soil profile to the surface (Schier and Zasada 1973).

Trembling aspen management

Due to the necessity of removing apical dominance for successful aspen suckering, it is generally recommended that aspen stands be clearcut to ensure prolific regeneration (Zehngraff 1947, Stoeckeler and Macon 1956, Steneker 1976, Schier and Smith 1979, Doucet 1989, Peterson and Peterson 1992, Stone 1997). In fact, Schier and

Smith (1979) found that partial cut areas where 67% of the stand basal area was removed generated only 42% of the aspen suckers after one year than areas that were clearcut. This pattern was maintained over time as after 12 years, the clearcut areas still had double the number of suckers as the partially cut sites (Schier and Smith 1979).

Following harvesting, some sites do not regenerate successfully even though apical dominance has been broken (Darrah 1991, Peterson and Peterson 1992). Regeneration failure can be especially prevalent if soils are compacted during harvesting (Bates et al. 1993) or if highly competitive vegetation (e.g. *Calamagrostis canadensis* (Michx.) Beauv.) establishes quickly (Landhäusser and Lieffers 1998). Mechanical site preparation (MSP) has been proposed as a treatment option that may alleviate some of these constraints and increase aspen regeneration following timber harvesting. Several studies have tested the effects of forest floor removal and/or disturbance to the parent root system on the promotion of trembling aspen and have found that when applied prior to the first growing season, these treatments can dramatically increase sucker numbers (Zehngraff 1946, Zillgitt 1951, Maini and Horton 1966a, Weingartner 1980, Alban et al. 1994, Lavertu et al. 1994, Frey 2001). In fact, these studies demonstrated that aspen suckering following treatment can be up to 12 times greater than in untreated control areas (Zehngraff 1946). However, some of these previous studies used treatments that are not commonly utilized in operation forestry (e.g. hand raking and agricultural disking) (Zehngraff 1946, Zillgitt 1951, Maini and Horton 1966a, Alban et al. 1994, Lavertu et al. 1994), which may make the results less applicable to forest managers. Further, previous studies did not differentiate between the regeneration successes of different microsites created with MSP.

Fire has also been proposed as a tool for aspen management. Trembling aspen has been considered to be dependent upon fire for successful regeneration (DeByle et al. 1987, Bonan and Shugart 1989). However, due to the control of wildfires and the fact that many regions do not have extensive prescribed burning programs, fire does not currently play a major role in aspen regeneration after harvesting (DeByle et al. 1987). Nevertheless, following a fire site conditions are typically very favourable for aspen suckering. The forest floor thickness is typically reduced (Horton and Hopkins 1966, Perala 1974, Brown and DeByle 1987, Bonan and Shugart 1989), which tends to increase the proportion of roots that will produce suckers (Schier and Campbell 1978). Further, the established aspen stems are generally killed without extensive injury to the parent root system (Horton and Hopkins 1966, Bonan and Shugart 1989), which removes the influence of apical dominance. Consequently, burning has been observed to generate a greater number of aspen suckers than clearcutting alone (Perala 1974) or clearcutting followed by light intensity scarification (Maini and Horton 1966a). However, it is currently not known whether fire can be used successfully following the first growing season. Root carbohydrate levels would be reduced following the first season of growth because the developing suckers use these reserves to support their initial development (Schier and Zasada 1973). Consequently, the ability of the root system to allocate reserves to sucker growth may be compromised and it is not known whether this would seriously impact sucker regeneration.

The objective of thesis was to examine some of the drivers of aspen root suckering. This study used both laboratory and field-based studies. The objectives of the laboratory experiments were to assess suckering of aspen root sections harvested from northern clones in relation to: (*i*) accumulated degree-days and daily maximum soil temperatures and (*ii*) available calcium and nitrogen. Accumulated degree-days were selected as a measure of suckering response to temperature because they are a measurement that combines temperature and time and degree-days have been demonstrated to be a reliable indicator of plant growth rates (Environment Canada 1982). The objectives of the field portion of this thesis were to assess the suckering response of trembling aspen to various site preparation treatments commonly used in forestry operations (disc trenching, drag scarifying and blading) and to examine the regeneration responses in the different microsites created by each treatment following the first and second growing seasons. A large wildfire, however, burned 80% of the MSP study sites at the beginning of the second growing season. Consequently, only limited second year data was available. However, regeneration data from the first growing season following the fire are also presented.

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CHAPTER II

Soil nutrition and temperature as drivers of root suckering in trembling aspen (*Populus tremuloides* Michx.)[1]

Introduction

The primary means of trembling aspen (*Populus tremuloides* Michx.) regeneration is through vegetative root suckers (Barnes 1966, Maini and Horton 1966a, Steneker 1976, Kemperman 1978). Initial sucker production and growth can be very rapid and under favourable conditions over 100 000 stems per hectare establish in the first growing season (Schier and Smith 1979). In natural systems, stand-replacing disturbances such as wildfire typically lead to prolific aspen regeneration (Bartos and Mueggler 1981, Brown and DeByle 1987). Regeneration after harvesting of aspen stands, however, has not always been as successful, especially on logged sites with vigorous grass establishment or heavy machine trafficking (Darrah 1991, Bates et al. 1993, Landhäusser and Lieffers 1998).

The increase in soil temperature that follows a major disturbance has been thought to be the major environmental condition necessary for sucker initiation. Controlled laboratory experiments have reported that the number of aspen suckers produced on a given root section increases with increasing temperature up to a maximum temperature of approximately 30°C (Horton and Maini 1964, Maini and Horton 1966b, Gifford 1967, Zasada and Schier 1973). However, several of these experiments used constant temperatures throughout the course of the experiment (Horton and Maini 1964, Maini

[1] A version of this chapter has been submitted for publication in the Canadian Journal of Forest Research

and Horton 1966b, Gifford 1967). Other studies utilized short (8-10cm) root segments (Maini and Horton 1966b, Gifford 1967, Zasada and Schier 1973), which may have affected sucker survival over the experimental period (Perala 1978).

A number of field-based studies have also examined the relationship between aspen suckering and soil temperature. Hungerford (1988) noted a 4.5 to 15-fold increase in suckering over controls related to 2-3°C higher average daily soil temperatures during June and July following prescribed burning. Further, in a study of mechanical site preparation and aspen regeneration, there was a 3-fold increase in sucker numbers following treatments that raised average daily soil temperature by 1°C and daily maximum temperatures by 2.5°C in the rooting zone (Chapter III). The fact that only slight increases in soil temperature were related to large changes in suckering suggests that temperature is not the sole driver of aspen suckering.

Disturbances such as burning and mechanical site preparation have been reported to increase the availability of nutrients, such as nitrogen and calcium, immediately following treatment (Ahlgren and Ahlgren 1960, Feller 1982, van Cleve and Dyrness 1983, Macadam 1987, Vitousek et al. 1992, Schmidt et al. 1996). There have been no reports of nutrients affecting rate of suckering but once established, suckers exposed to higher levels of NPK grew taller and had larger new root systems in their first season of growth compared to those grown with fewer available nutrients (Gifford 1967). Also, in a field-based study Frey (2001) observed a significant correlation between soil calcium availability and aspen sucker density, percent cover and total stem height.

The objectives of this study were to assess suckering of aspen root sections harvested from northern clones in relation to: (*i*) accumulated degree-days and daily maximum soil temperatures and (*ii*) available calcium and nitrogen.

Materials and Methods

Plant material and storage conditions

Root samples were collected from 12 clones within an area of mature, pure aspen near Alder Flats, Alberta (52°58'N, 114°59'W). Clones were healthy, at least 20m from roads and other disturbances and at least 50m apart. Collection sites were assumed to be individual clones because previous studies in the area have indicated that aspen clones in the region are small (unpublished data). Root samples for the temperature experiment were collected in the early winter (December 8, 2000) and in the spring just prior to leaf out (May 3, 2001), with winter and spring samples harvested from different clones. At each collection date, 10 root segments (30cm long, 0.5 to 2.0cm diameter) were carefully excavated by hand from each site, for a total of 120 root segments per collection date. Following excavation, the root sections were stored at –2°C until planting. Storage time varied for each collection date; the winter samples were stored for 39 to 83 days and the spring samples for 19 to 63 days (Table 2-1).

Root sections for the nutrient experiment were harvested as for the spring-collected samples above. Nine segments were harvested from each of 12 clones, for a total of 108 root samples. Samples were stored at -2°C for 35 days before planting.

Temperature experiment

For each collection, root segments were incubated in the dark at five temperature regimes: 12/8°, 14/8°, 16/8°, 18/8° and 20/8°C high/low temperatures, with 14/10-hour high/low cycles. A base temperature of 8°C was selected because it represents field conditions observed in aspen cutovers near Slave Lake, Alberta during the period of aspen sucker initiation (early June). During the suckering period, day temperatures fluctuated among microsites, but night temperatures returned to approximately 8°C (Chapter III). Each temperature regime was assigned to one of five-0.2 m^3 incubation chambers (Percival Scientific Inc. Perry, IA). Each chamber contained three shelves 25cm apart and each shelf held four 40 x 7cm trays. For each collection date, the entire experiment was replicated in two runs. In each run, the trays were randomly assigned to a shelf and the trays were moved to a different shelf every day to minimize potential spatial temperature differences within each incubation chamber. For the second run, each chamber was re-randomized and programmed with a new temperature regime.

Root segments were gently washed with cold water, all fine roots were removed and a small (2cm) piece was removed from the end of each root segment for analysis of total non-structural carbohydrates. The weight, length and diameter of each root section were recorded prior to planting. One root segment from each collection site was randomly selected and planted in each tray, for a total of 12 root sections per temperature. Root segments were planted approximately 2cm deep in vermiculite, watered as necessary (approximately once per week) and no additional nutrients were added. One Hobo® H8 temperature data logger (Onset Computer Corp. Bourne, MA) was located within three trays per incubation chamber to monitor the vermiculite temperature throughout the course of the experiment.

The root sections were incubated at their respective temperatures for a varying number of days, until all reached approximately 124 degree-days using 8°C as a base temperature. Degree-days were obtained by summing the (average temperature - base temperature) x number of days in the experimental period. Degree-days were calculated from a base temperature of 8°C for the purpose of the experimental design because this represented nighttime temperatures in the field at the time of suckering. Thus, incubation was 62 days at 12/8°, 41 days at 14/8°, 31 days at 16/8°, 25 days at 18/8° and 21 days at 20/8°C. It has been demonstrated that aspen sucker production at 20°C reaches a maximum at approximately 20-24 days (Maini and Horton 1966b), therefore it is reasonable to assume that the root sections would not have generated additional suckers following the experimental period used in this study. At the end of this time, non-suckering roots were incubated for an additional 2 weeks but there was no further suckering. Degree-days above 5°C were also calculated after the experiment because at this temperature aspen roots have little metabolic activity (DesRochers 2000) or root growth (Landhäusser and Lieffers 1998, Wan et al. 1999). Every two days the root sections were assessed for sucker initiation and carefully reburied. After a root section began suckering, it was left undisturbed for the remainder of the experiment.

Nutrient experiment

Three root segments from each clone were randomly selected and assigned to one of three treatments: addition of calcium ($CaSO_4$), nitrogen (NH_4NO_3) or distilled water only (control). Each root was gently washed with water, all fine roots were removed and each was measured for length, diameter and weight. A small (2cm) section was removed for total non-structural carbohydrate analysis. Each root was planted approximately 2cm deep in perlite in a 40 x 7cm plastic tray. The root sections were grown for 47 days in a fully controlled growth room at a temperature regime of 18/10°C high/low temperatures with 12/12-hour high/low cycles under a light intensity of 350-400 μmol $m^{-2} \cdot s^{-1}$. The trays were randomly assigned a position within the growth room and were moved every four days to minimize potential spatial differences in the growing environment.

Nutrients dissolved in distilled water were applied every four days. The $CaSO_4$ was applied at a rate equivalent to 400 kg of Ca/ha and the NH_4NO_3 at 200 kg of N/ha, as these levels reflect conditions often encountered following a stand-replacing disturbance (Personal Communication, Scott Chang University of Alberta 2001). Each tray received 0.25 litres of nutrient solution per application, and the control received 0.25 litres of distilled water. Every eight days, each root section was flushed with 0.5 litres of distilled water prior to application of the nutrient solution in order to remove any solid nutrient accumulation.

Sample measurement and tissue analysis

At the termination of each experiment, roots were rinsed with water and the number of suckers was recorded. In the nutrient experiment, all suckers were removed and dried at 68°C for 2 days for dry weight measurement.

For the determination of total non-structural carbohydrates, all root samples were cut into small pieces and oven-dried at 68°C for at least two days. Dried tissues were ground with a Wiley mill to pass a 40-mesh screen, and stored in air-tight containers in the dark at 20°C. Sugars were extracted with hot ethanol (85%) three times. Sugar concentrations were then determined colorimetrically using phenolsulfuric acid (Smith et al. 1964). Remaining starch was then solubilized by sodium hydroxide and hydrolyzed to glucose by an enzyme mixture of α-amylase (ICN 190151, from *Bacillus licheniformis*) and amyloglucosidase (Sigma A3514, from *Aspergillus niger*) for 41 hours, then measured colorimetrically using glucose oxidase/peroxidase-o-dianisidine solution (Sigma Glucose Diagnostic Kit 510A). Absorbance readings for sugar and starch contents were converted to percent of root dry weight.

Statistical analysis

The temperature experiment was analyzed as a randomized block design with two blocks, one for each collection season (Multilocation trial, SAS® System for Mixed Models). The runs were designated as blocks within each collection season because storage time was a potential source of suckering variation. Within each block, there were 5 temperature treatments (12/8°, 14/8°, 16/8°, 18/8° and 20/8°C). As there was no significant season x treatment interaction (P=0.249), the collection seasons were ignored and the data was analyzed as a randomized block design with four blocks and five treatments. In this study, there were four blocks (runs) per treatment and 12 samples per replicate.

The nutrient experiment tested a single factor-nutrient addition ($CaSO_4$, NH_4NO_3 and control). In this study, there were three treatments, 12 blocks (clones) per treatment and 3 samples per block.

The response variables in the temperature experiment were the number of suckers produced per root, the number of suckers per cm^2 of root surface area, the number of degree-days required for sucker initiation (base temperatures of 5° and 8°C) and the number of days to sucker initiation. In the nutrient experiment, the number of suckers produced per root, the number of suckers per cm^2 of root surface area and the dry weight per sucker were the response variables tested.

Response variables for both the temperature and nutrient experiments did not meet the assumptions of normal distribution or equality of variance, so the variables were natural log transformed. The number of suckers per root and the number of suckers per cm^2 of root surface area were transformed $\ln(x + 1)$. To test for treatment effects, ANOVA procedures using the mixed model in release 8.1 of SAS® (SAS Institute Inc. Cary, NC) were performed for the temperature experiment and the general linear model was used for the nutrient experiment. Trend analysis in the temperature experiment was completed with orthogonal comparisons, multiple comparisons in the nutrient experiment were done with the lsd test and a significance level of $\alpha=0.05$ was used for all response variables.

Results

Average sugar concentration was 12.9% and average starch concentration was 0.6%. No relationships were found between sugar and/or starch content and the measured response variables.

Temperature did not have a significant effect on the number of suckers produced per cm^2 of root surface area (P=0.558), but there was a trend for reduced suckering at 12°C (Fig. 2-1a). There was also no temperature effect detectable on the total number of suckers per root (P=0.801).

Sucker initiation was delayed at 12°C compared to the warmer regimes (P=0.018); roots grown at 12° required 12 additional days to initiate suckers than those grown at 20°C (Fig. 2-1b).

Root sections grown under warmer temperature regimes required significantly more degree-days (base temperature 8°C) to initiate suckers than those grown at cooler temperatures (P=0.050). The root sections grown under the 20/8° temperature regime required an average of 70 degree-days to initiate suckering, compared to 47 days at 12/8°C (Fig. 2-2a). When degree-days were based on a temperature of 5°C, however, the time to sucker initiation was not different among the temperature treatments (P=0.819). On average, approximately 113 degree-days were needed for sucker initiation (Fig. 2-2b).

Trend analysis for the temperature experiment indicated that there was no significant relationship for the number of suckers generated per cm^2 of root surface area (P=0.129), the number of days required for sucker initiation was a linear relationship ($P<0.0001$), the number of degree-days required for sucker initiation at a base temperature of 8°C was a quadratic relationship (P=0.003) and the number of degree-days necessary for sucker initiation at a base of 5°C showed no significant relationship ($P=0.166$).

Application of $CaSO_4$ or NH_4NO_3 did not affect the number of suckers produced per cm^2 of root surface area ($P=0.655$, Fig. 2-3a) or the number of suckers per root section ($P=0.435$). The addition of nutrients, however, increased the dry weight per sucker ($P=0.024$). The average dry weight per sucker was approximately 2.5 times greater following the addition of $CaSO_4$ or NH_4NO_3 compared with no nutrient addition (Fig. 2-3b).

Discussion

The results of this study suggest that soil temperature alone is not the sole environmental driver of aspen suckering following a stand-replacing disturbance, as the tested temperature regimes did not affect the number of suckers produced. While very low soil temperatures (e.g. 5°C) have been shown to inhibit aspen metabolism (DesRochers 2000) and root growth (Landhäusser and Lieffers 1998, Wan et al. 1999), there was little difference in sucker production for the 12° to 20°C range of maximum temperatures used in this study. Further, there does not appear to be a minimum threshold temperature for aspen suckering between 12° and 20°C. These results disagree with earlier experiments (see Introduction); however, our study was different in several ways. First, our experiment was designed to reduce the influence of date of sucker initiation. Our study and Maini and Horton (1966b) demonstrated that root segments grown in warm soils produce suckers earlier than those grown in cooler soils. Therefore, if root sections in all temperature regimes were incubated for the same length of time, those grown under warmer conditions would have more time to generate suckers before the conclusion of the experiment. To alleviate this concern, our study allowed root sections in cooler regimes to grow longer than in warmer regimes. Additionally, all initiated suckers were counted on each root section instead of just those that had attained a minimum height. Furthermore, our study used variable diurnal temperatures to more closely mimic natural conditions.

When calculated from a base temperature of 5°C, aspen roots begin to sucker at approximately the same number of degree-days across regimes ranging from 12/8° to 20/8°C. This relationship was not evident when degree-days were calculated from a base temperature of 8°, likely because some aspen root growth occurs at 8°, but not at 5°C (Wan et al. 1999). Time of emergence has also been correlated with accumulated degree-days in wheat, barley and rice (e.g. Ma and Smith 1992, Rickman and Klepper 1995).

It has been suggested that the degradation of auxin at high temperatures, and the corresponding reduction in hormonal control over suckering, is the primary mechanism behind increased aspen suckering at warmer soil temperatures (Schier et al. 1985, Hungerford 1988). The temperature at which auxin uptake and transport is reduced varies by species, however it tends to occur at temperatures greater than 20°C (Gregory and Hancock 1955, Morris 1979, Huberman et al. 1997). As our study did not use temperatures greater than 20°C, it is unlikely that auxin degradation occurred. Further, since soil temperatures in the rooting zone in northern climates usually do not exceed 20°C at any time during the growing season (Tryon and Chapin 1983, Hogg and Lieffers 1990), auxin degradation likely does not play a role in aspen suckering in these forests.

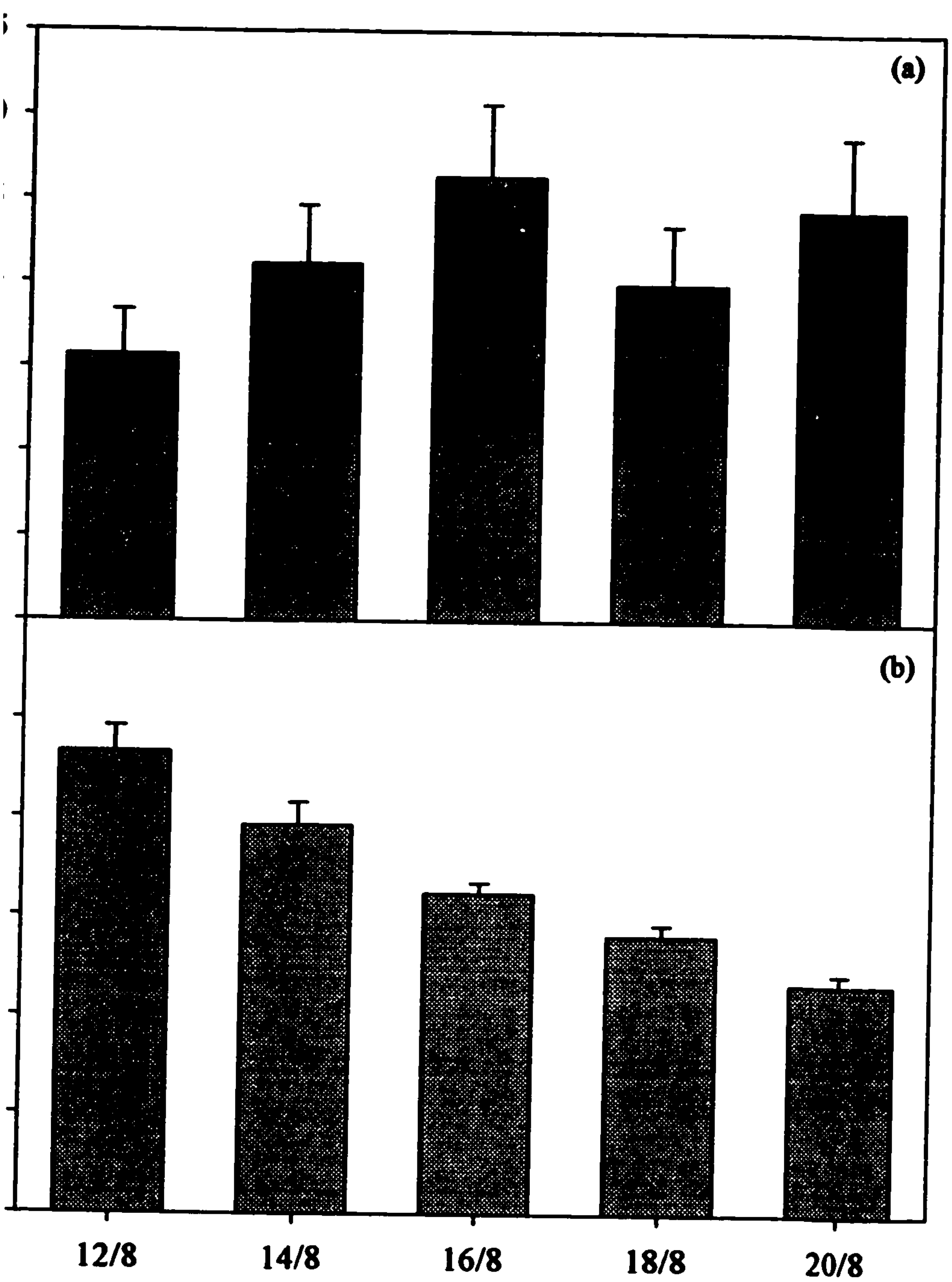
The addition of $CaSO_4$ and NH_4NO_3 did not affect the number of suckers produced, however these nutrients significantly increased sucker dry weight. Both nitrogen and calcium are known to affect growth and photosynthesis in plants (Kimmins 1997, Lambers et al. 1998). However, since the root sections were harvested from one of the best growing sites in the region (Canada Land Inventory 2000), it is unlikely that they were under severe nutrient deficiency at the time of collection. Secondly, the increased sucker growth was not likely related to an increase in carbon fixation from photosynthesis. The root sections were incubated for only 47 days, so the largest suckers did not spend more than 2-3 weeks above the perlite surface. Bigtooth aspen (*Populus grandidentata* Michx.) leaves require approximately 2 weeks to become a source as opposed to a sink of metabolites (Donnelly 1974), therefore it is unlikely that the new leaves significantly contributed to carbon fixation. Instead, we suggest that growth was driven by the mobilization of stored reserves from the parent root. In the particular case of $CaSO_4$ addition, there may have been an increase in cell elongation and growth due to the reported stimulating effect of Ca on auxin-induced cell elongation in plants (de la Fuente and Leopold 1973, Poovaiah and Veluthambi 1985, Raghothama et al. 1985, Reddy et al. 1988, Brummell and MacLachlan 1989, Yang and Poovaiah 2000). The demands for growth were likely supported by stored reserves in the parent root. It is also feasible that the S in $CaSO_4$ increased initial sucker size in a similar fashion, as there is some evidence that S addition can increase initial plant growth rates (Singh and Chaudhari 1995, Zhao et al. 1999).

It is likely that soil temperature and nutrient availability work together to encourage aspen suckering under field conditions. Soil temperature and mineralization rates tend to increase following a stand-replacing disturbance (Binkley 1984, Weber 1990a, Weber 1990b, Prescott 1997, Prescott et al. 2000), as does the rate of plant nutrient uptake (Lambers et al. 1998). Therefore, it is reasonable to assume that more nutrients are available to and taken up by the parent root system following a disturbance. Considering that high nutrient availability increases initial shoot growth rates, suckers initiated under nutrient rich conditions would likely emerge from the soil surface sooner and would start photosynthesizing before slower growing competitors on more nutrient poor sites. Consequently, fast growing suckers would be more likely to out-compete other vegetation species, possibly leading to higher rates of survival in the first growing season. This relationship may explain the results obtained in field studies that observed prolific aspen suckering following disturbance, despite a minimal increase in soil temperature. Nevertheless, further research is needed to test this relationship, possibly using more natural root systems with their fine roots attached.

These results may have implications for the management of trembling aspen following harvesting. It has long been assumed that soil temperature is the most critical environmental factor controlling aspen suckering and initial growth (Steneker 1974, Steneker 1976, Peterson and Peterson 1992, Peterson and Peterson 1995). Our results, however, demonstrate that nutrient availability stimulated the initial growth of aspen suckers. Treatments that tend to increase nutrient release (e.g. prescribed burning, mechanical site preparation or perhaps fertilization) would likely promote aspen growth.

Table 2-1: Days of storage at -2°C prior to planting for aspen root segments incubated in each temperature regime in each collection season

Temperature regime (high/low °C)	Days			
	winter samples		spring samples	
	run 1	run 2	run 1	run 2
12 / 8	39	43	19	19
14 / 8	39	62	19	42
16 / 8	39	66	19	46
18 / 8	39	72	19	52
20 / 8	39	83	19	63



lumber of suckers per cm^2 of root surface area (a) and number of days
sucker initiation (b) at various high/low temperature regimes for segments of

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CHAPTER III

The effects of mechanical site preparation and subsequent wildfire on trembling aspen (*Populus tremuloides* Michx.) regeneration[2]

Introduction

Trembling aspen (*Populus tremuloides* Michx.) is a shade intolerant deciduous tree species that typically regenerates through vegetative root suckers (Perala 1990). As a result, aspen often forms clones of genetically identical individuals that are connected through a shallow root system (Day 1944, Strong and LaRoi 1983). Following stand-replacing disturbances such as wildfire or clearcut harvesting, aspen usually regenerates prolifically via root suckering (Bartos and Mueggler 1981, Bartos and Mueggler 1982, Crouch 1983, Brown and DeByle 1987) and can produce over 100 000 suckers per hectare in the first growing season (Schier and Smith 1979, Bella 1986). However, in some regions aspen fails to fully regenerate following harvesting (Darrah 1991), especially if soils are compacted during harvesting (Bates et al.1993) or if competitive vegetation (e.g. *Calamagrostis canadensis* (Michx.) Beauv.) establishes quickly (Landhäusser and Lieffers 1998).

Mechanical site preparation (MSP) has been proposed as a treatment option that may alleviate some of these issues and increase aspen regeneration following timber harvesting. Several studies have tested the effects of forest floor removal and/or disturbance to the parent root system on the promotion of aspen suckering and have found that when applied prior to the first growing season, these treatments can

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[2] A version of this chapter has been submitted for publication in New Forests

dramatically increase sucker numbers (Zehngraff 1946, Zillgitt 1951, Maini and Horton 1966, Weingartner 1980, Alban et al. 1994, Lavertu et al. 1994, Frey 2001). In fact, these studies demonstrated that aspen suckering following treatment can be up to 12 times greater than in untreated control areas (Zehngraff 1946). However, some of these previous studies used treatments that are not commonly utilized in operational forestry (e.g. agricultural disking and hand raking) (Zehngraff 1946, Zillgitt 1951, Maini and Horton 1966, Alban et al. 1994, Lavertu et al. 1994), which may make the results less applicable to forest managers. Further, previous studies did not differentiate between the regeneration successes of different microsites created with MSP.

Fire has also been proposed as a tool for aspen management. Historically, trembling aspen was considered to be dependent upon fire for successful regeneration (DeByle et al. 1987, Bonan and Shugart 1989). However, due to the control of wildfires and the fact that many regions do not have extensive prescribed burning programs, fire does not currently play a major role in aspen regeneration (DeByle et al. 1987). Nevertheless, site conditions are normally very favourable for aspen suckering following burning. The forest floor thickness is typically reduced (Horton and Hopkins 1966, Perala 1974, Brown and DeByle 1987, Bonan and Shugart 1989), which tends to increase the proportion of roots that will produce suckers (Schier and Campbell 1978). Consequently, prescribed burning has been observed to generate a greater number of aspen suckers per hectare than clearcutting alone (Perala 1974) or clearcutting followed by light intensity scarification (Maini and Horton 1966).

The objectives of this study were to assess the suckering response of trembling aspen to various MSP treatments commonly used in forestry operations (disc trenching, drag scarifying and blading) and to examine the regeneration responses in the different microsites created by each type of treatment following the first and second growing seasons. A large wildfire, however, burned 80% of the study sites at the beginning of the second growing season. Consequently, only limited second year data was available. However, regeneration data from the first year following the fire are also presented.

Materials and methods

Site description

Four cutblocks 10-20 ha in size located near Slave Lake, Alberta (55°17'N; 114°46'W) were used in this study. Each cutblock was clearcut during the winter of 1999/2000 with a fellerbuncher and grapple skidder. Prior to harvest, the stand composition on each cutblock was at least 90% trembling aspen, with minor components of balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* (Moench) Voss) and paper birch (*Betula papyrifera* Marsh.). Each cutblock was flat or slightly north facing, had thick (>15cm) organic layers, grey luvisol soils and was in the lower foothills natural ecoregion, low bush cranberry-aspen ecosite (e2) (Beckingham et al. 1996).

Study design

Ten 90 x 60m sites were located within the four cutblocks. Each site was uniform in slope and aspect and each was located at least 15m from the cutblock edge. Each site was divided into four 15 x 60m treatment strips, with a 10 x 60m buffer separating each treatment strip. Each of the four treatments (disc trenching, drag scarifying, blading and untreated control) was randomly assigned to one strip within each site, for a total of 10 replicates per treatment.

Post harvest treatments

The three site preparation treatments were carried out with the same prime mover, a John Deere™ 740 skidder (Deere and Company Inc. Moline, IL) between May 3-10, 2000. The disc trenching was done with rear mounted hydraulic discs, the drag scarifying used sharkfin barrels that were approximately 160 x 50cm and 2/3 filled with liquid $CaCl_2$ and the blading treatment utilized the straight blade mounted on the front of the skidder. The control strips were left undisturbed, with no additional vehicle traffic.

The objectives of the site preparation treatments were to cause varying levels of organic layer removal and disturbance to the aspen parent root system. Specifically, the disc trenching created trenches approximately 30cm deep and 50cm wide, with an elevated berm about 70cm across on one side and an undisturbed mid-trench area approximately 80cm wide on the other. There was extensive severing of the parent root system along the edges of the trenches and within the trenches, the top 30cm of soil and the roots it contained was completely removed. On the berms, the undisturbed root system was buried beneath approximately 20cm of material. In the mid-trench area, the parent root system was undisturbed, although severed on both sides. The drag scarifying treatment created discontinuous barrel paths that were approximately 30cm wide. Within these paths, the organic layer had been disturbed and some scuffing and severing injuries were inflicted on parent roots within the top 5cm of mineral soil. The target for the blading treatment was removal of 1/3 to 1/2 of the organic layer. However, due to the difficulty of carrying out this treatment, a number of different microsites were created. There were shallow scrapes where a portion of the duff layer was removed, deep scrapes where mineral soil was exposed and piles of material where the skidder blade had been lifted, mostly around stumps. As a result, injury to the parent root system was variable across the blading treatment. In the shallow scrapes, there were limited scuffing injuries to the parent roots at the duff-mineral soil interface. In the deep scrapes, the root system in the top 5-20cm of mineral soil was extensively scraped or removed. Under the piles, the parent roots were undisturbed, but buried beneath 20-50cm of material.

At the beginning of the second growing season, an intense wildfire burned 8 of the 10 MSP sites. This fire was discovered on May 23, 2001 and burned approximately 113 000 ha over the next several weeks. The MSP sites were likely burned during the first week of June. This fire was particularly intense as conditions were extremely dry and it occurred following leaf out. Further, this fire burned off the entire forest floor in many areas and as a result, a large proportion of the shallow aspen roots were killed or severely injured.

Field assessments

Immediately following the MSP treatments, 2 Hobo® H8 temperature data loggers (Onset Computer Corp. Bourne, MA) were buried in the upper rooting zone in each treatment strip, for a total of 20 data loggers per treatment. The data loggers were buried in the following microsites: shallow scrapes in the blading, barrel paths in the drag scarifying, berms and mid-trench areas in the disc trenching and undisturbed areas in the control.

Additionally, slash levels were measured immediately following treatment. Three 10m transect lines were randomly located across each control strip. Two 1m sections of the transect line were randomly selected and each piece of slash intersecting this portion of the transect line was counted and assigned to one of three diameter classes: <0.6cm, 0.6-2.5cm and 2.5-7.6cm. Pieces that were greater than 7.6cm in diameter were individually measured and recorded along the entire 10m transect line. The volume of slash on each control strip was calculated:

[1] $$V = n\left[\frac{\pi^2 d_q^2}{8L}\right]\alpha$$

where V is the volume of slash, n is the number of pieces tallied per diameter class, d_q is the quadratic mean diameter of each diameter class or individually measured piece, L is the length of the sample line and α is the correction term for non-horizontal orientation bias (Brown and Roussopoulos 1974). This formula was applied to each diameter class and each piece of slash greater than 7.6cm in diameter individually and then the values were summed for each plot. The average slash loading was calculated at 88 m^3 per ha prior to treatment over all MSP sites.

In late August of the first growing season, the MSP sites were assessed for regeneration success using two different techniques. First, an overall assessment of sucker density for the 60 x 15m strips was obtained using standard regeneration survey techniques. Circular plots, 1.78m radius, were located approximately every 8m down the centre of each strip. There were 5 plots per strip, for a total of 50 per treatment. The total number of trembling aspen suckers was recorded in each plot, as was the height of the tallest aspen.

Secondly, regeneration success was assessed in specific microsites. Microsites were: trenches, berms, and mid-trench areas in the disc trenching, shallow scrapes, deep scrapes, and piles in the blading, barrel paths in the drag scarifying and undisturbed areas in the control. Due to the different microsite shapes, two different plot forms were used. The first was 71 x 71cm (0.5m^2) and this was used for all microsites in the disc trenching, blading and control. The second form was 25 x 100cm (0.25m^2) and was used for the barrel paths in the drag scarifying. In each case, the plot form was flipped two or four times within the same microsite to make a total plot size of 1m^2. The trench microsite plots in the disc trenching included the trench and approximately 15cm on each side of the trench. The other microsite plots assessed the centre of the particular microsite and did not include any transitional areas between microsites. Each microsite plot was located in the closest acceptable microsite relative to the plot centre of the regeneration plot. Five plots per microsite were done in each treatment strip, for a total of 50 plots per microsite. The number of aspen suckers was recorded, along with the height of the tallest aspen. Additionally, the largest fully developed leaf was collected from the tallest aspen in each plot for leaf size measurement with a LI-COR™ model 3100 area meter (LI-COR Biosciences Ltd. Lincoln, NE).

Both the regeneration and microsite plots were supposed to be re-measured following the second growing season, however the wildfire burned 8 of the 10 sites. As a result, only the two unburned sites were reassessed for second year data. In these sites, both the regeneration and microsite plots were repeated and the same information was collected in late August following the techniques used in the first growing season. In the burned sites, only the control treatment strips were assessed for aspen regeneration.

To monitor soil temperature following the fire, 10 temperature data loggers were buried in the upper rooting zone in early June in burned non-site prepared areas and five data loggers were buried in an unburned clearcut area that was harvested during the winter of 2000/2001.

Statistical analysis

This study was analyzed as a randomized block design testing a single factor- site preparation treatment. Each MSP site was designated as a block, so there were 10 blocks for the first growing season data, 2 blocks for the second year data and 8 blocks for the data collected on the burned sites. In all cases, there were five samples per treatment in each block. The response variables in this study were the number of suckers per ha and the average dominant sucker height following each MSP treatment. The number of suckers per ha, the average dominant sucker height and the average leaf size were also assessed for each microsite within each treatment. Following the second season of growth, the same response variables were assessed as in year one in each MSP treatment as well as in each microsite. For the sites burned in the fire, the response variables tested were the number of suckers per ha and the average dominant sucker height.

The soil temperature data was analyzed as a one-way analysis of variance and the response variables tested were the average, maximum and minimum daily soil temperatures.

The height and leaf area data conformed to the assumptions of normality and equality of variance, however the number of suckers per ha in the both the regeneration and microsite plots did not. Consequently, the sucker density data was natural log transformed. To test for treatment effects, ANOVA procedures using the general linear model in release 8.1 of SAS® (SAS Institute Inc. Cary, NC) were performed. Multiple comparisons were done with the lsd test and a significance level of $\alpha=0.05$ was used for all response variables.

Results

Average daily soil temperature was not affected by site preparation treatment ($P=0.759$), however both average daily maximum ($P=0.001$) and minimum ($P=0.009$) temperatures were affected. On a monthly basis, the blading had the highest maximum temperatures during June and July and the lowest minimum soil temperatures throughout the growing season (Fig. 3-1a and 3-1b). On average, the soil temperature in the blading was 2.5° higher during the day and 1.5°C lower at night compared to the other treatments.

The fire did not affect average daily soil temperature ($P=0.865$), however both average daily maximum ($P<0.0001$) and minimum ($P<0.0001$) temperatures were significantly affected. When analyzed on a monthly basis, the burned sites were 2-3°C higher during the day and 1-2°C cooler at night than the unburned areas (Fig. 3-2a and 3-2b).

The site preparation treatments significantly increased the overall number of suckers per ha compared to the untreated control areas following the first growing season ($P<0.0001$). The disc trenching produced 86 100 suckers per ha, the blading 75 800, the drag scarifying 50 680 and the control generated 27 840 aspen suckers per ha (Fig. 3-3a). There was no difference in average dominant sucker height among treatments (P=0.638); all were approximately 95cm tall one growing season following treatment (Fig. 3-3b).

Following the wildfire, aspen regeneration averaged 59 325 stems per hectare (Fig. 3-3a) and average dominant sucker height was 83cm (Fig. 3-3b) following one season of growth.

Microsites significantly affected the number of suckers generated in the first growing season (P<0.0001). The trenches in the disc trenching, shallow scrapes in the blading and the barrel paths in the drag scarifying generated the greatest number of suckers, while the piles in the blading and the control produced the fewest (Fig. 3-4a).

There was also a significant difference between the dominant sucker heights in each microsite (P<0.0001). The trenches in the disc trenching and the shallow scrapes in the blading produced the tallest suckers at approximately 80cm, whereas the berms in the disc trenching and the piles in the blading generated the shortest suckers at approximately 34cm (Fig. 3-4b).

Average leaf size was also significantly affected by microsite (P<0.0001). The trench microsite in the disc trenching and the shallow scrape in the blading produced suckers with the largest leaves at about 38cm^2, while suckers from the piles in the blading had the smallest leaves (16cm^2, Fig. 3-4c).

For the two MSP sites surviving to the second growing season, no difference was detected in the number of suckers per ha (P=0.827) or average dominant sucker height (P=0.467) among site preparation treatments in the regeneration plots. On average, mortality was negligible and the suckers grew approximately 50cm to a total maximum height of about 140cm across all treatments. There was also no difference in either aspen density (P=0.742) or average dominant sucker height (P=0.310) among microsites in the microsite plots. In these plots, the suckers grew an average of 24cm and had an average mortality of 23%.

Discussion

This study found that mechanical site preparation could dramatically increase aspen suckering following timber harvesting. These results concur with earlier studies which found that treatments that reduced the forest floor thickness and/or injured the parent root system lead to increased suckering relative to untreated control areas (Zehngraff 1946, Zillgitt 1951, Maini and Horton 1966, Weingartner 1980, Alban et al. 1994, Lavertu et al. 1994, Frey 2001). Further, this study demonstrated that microsites where the parent root system was disturbed but not extensively damaged (e.g. shallow scrapes in blading, barrel paths in drag scarifying) resulted in greater suckering than those where the root system was undisturbed (e.g. mid-trench in disc trenching, control) or severely damaged (e.g. deep scrapes in blading).

It has generally been assumed that soil temperature is the most important environmental factor driving aspen suckering following a stand-replacing disturbance (Steneker 1974, Steneker 1976, Peterson and Peterson 1992, Peterson and Peterson 1995). However, in our study there were no significant differences in average daily soil temperatures and there were differences of only 2.5° and 1.5°C in daily maximum and minimum temperatures among treatments, respectively. Since aspen suckering on root segments has been observed to be relatively insensitive to small changes in daily maximum temperature between 12° and 20°C (Chapter II), the minor changes in soil temperature that followed MSP would likely not account for the large differences in sucker numbers. Instead, other factors may be involved in sucker initiation and early growth under field conditions. Injury to the parent root system of living trees has been noted to stimulate aspen suckering under controlled conditions (Farmer 1962) and it has also been speculated that it would promote suckering in the field following harvesting (Maini and Horton 1966, Steneker 1974, Shepperd 1996). It has been proposed that injury to the root system prevents or reduces the flow of sucker inhibiting hormones within the roots, thus encouraging the formation of suckers (Farmer 1962, Maini and Horton 1966). As the majority of aspen roots are contained within the top 12cm of mineral soil (Kemperman 1978, Schier and Campbell 1978), treatments that disturb this portion of the soil profile would likely reduce the flow of hormones and lead to an increase in aspen suckering. However, excessive disturbance has been shown to be detrimental to aspen growth and survival (Steneker and Walters 1971, Perala 1978), which corresponds with the results from our microsite plots. It is also possible that nutrient availability affects aspen suckering following MSP. Soil nutrient availability tends to increase immediately following site preparation (Vitousek et al. 1992, Schmidt et al. 1996) and high soil nutrient status has been observed to increase initial aspen growth rates (Gifford 1967, Lu and Sucoff 2001, Chapter II). Therefore, it would be logical to expect that the increase in nutrient availability that typically follows MSP could lead to an increase in initial aspen growth rates.

The control plots in the eight burned sites generated approximately 60 000 suckers per ha in the first season of growth (second season after logging), which was similar to the number stimulated by MSP carried out immediately following harvesting and was approximately double the number generated following no site preparation. The average dominant sucker height, however, was lower following the fire than after MSP (83 vs. 95cm). The developing suckers use stored root carbohydrate reserves for initial growth (Tew 1970, Schier and Zasada 1973), so it is likely that the reserves were lower following the fire than immediately after MSP. Consequently, the ability of the root system to allocate reserves to sucker growth may have been compromised following the fire.

These results have implications for aspen management following timber harvesting. This study demonstrates that mechanical site preparation can successfully be used to regenerate aspen stands. While it is not necessary to treat all aspen cutblocks prior to suckering, those sites with thick organic layers or high brush hazards could benefit from MSP treatment. However, these results also demonstrate that certain microsites are more conducive to suckering than others. Treatments that disturb the parent root system, without seriously damaging it, would likely be the best treatment options. This study also shows that aspen regeneration could be promoted with fire even after the first growing season following harvesting. Consequently, if aspen regeneration is inadequate following the first season of growth, forest managers could carry out a prescribed burn (or perhaps MSP) prior to the second growing season and expect better suckering, provided the parent root system remains viable.

This study also has implications for mixedwood management. In the Canadian prairie provinces, trembling aspen and white spruce generally dominate mixedwood stands (Rowe 1972). When spruce regeneration is desired following harvesting on mixedwood sites, cutblocks are typically mechanically site prepared and planted with spruce (Day and Bell 1988, Navratil et al. 1991, Lieffers and Beck 1994). However, the choice of site preparation is critical to ensure a balance between spruce and aspen regeneration. Our results as well as previous studies have demonstrated that aspen regeneration is most vigorous following treatments that disturb but do not remove the forest floor. Consequently, if some control over aspen were desired in order to allow for spruce regeneration, the moderate intensity treatments would likely be inappropriate choices. Instead, it would be more beneficial to straight plant spruce seedlings without site preparation or to carry out a more intense treatment that would seriously disturb the aspen parent root system in small areas but not seriously injure it over an entire cutblock. This could include treatments such as mixing, however this approach has not been tested on an operational basis.

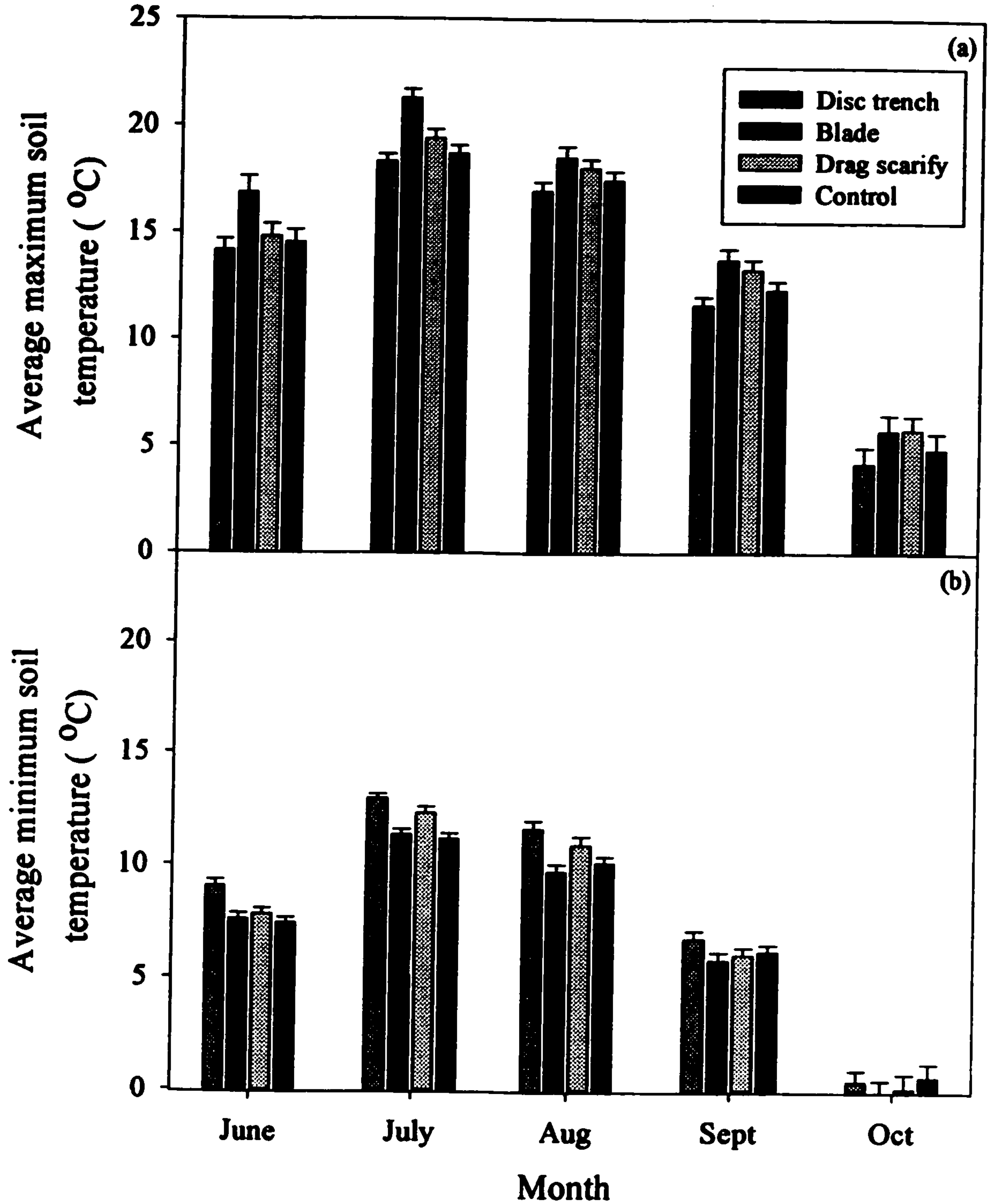

Figure 3-1: Average monthly maximum (a) and minimum (b) soil temperatures in the rooting zone during the first growing season after mechanical site preparation

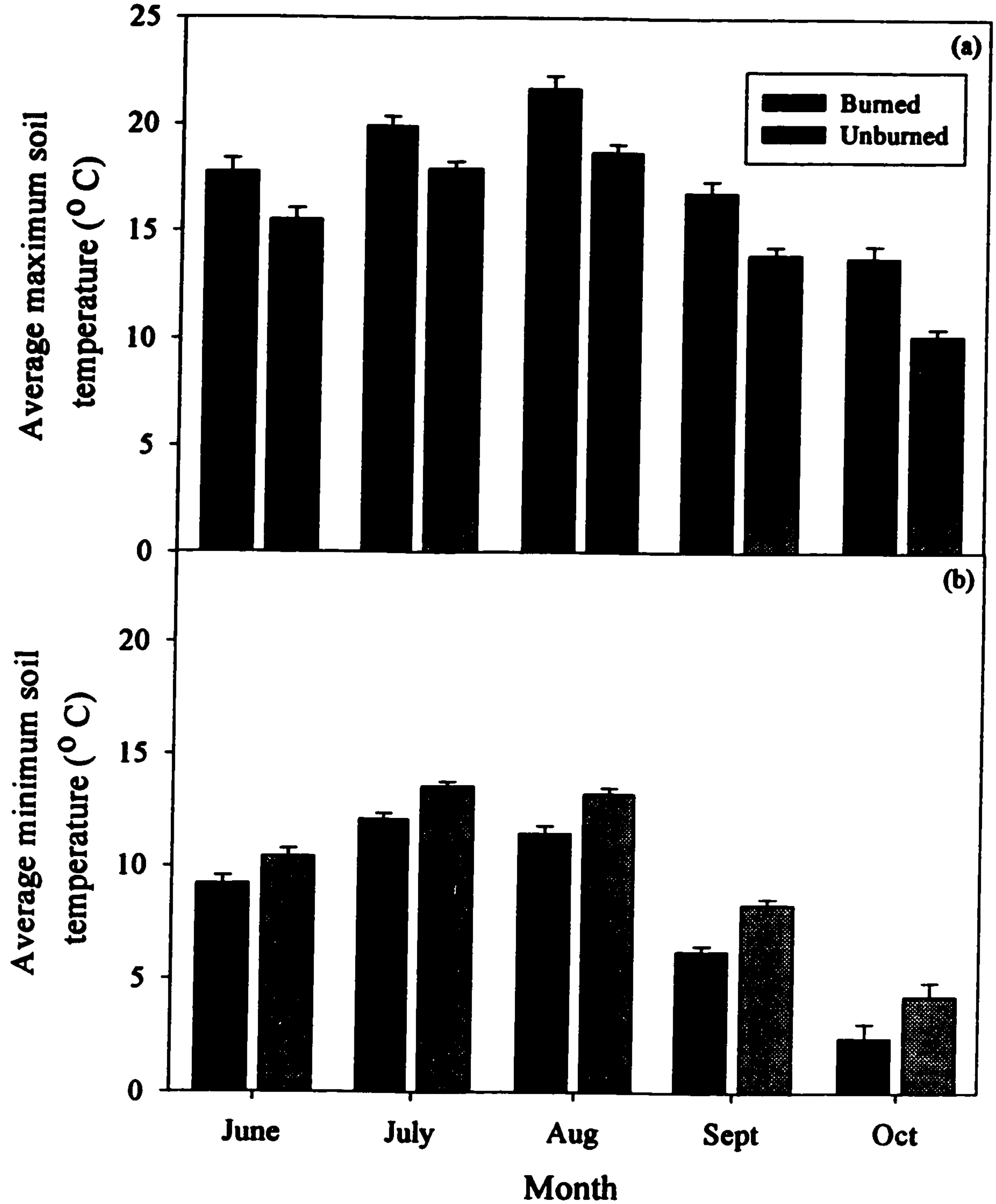

Figure 3-2: Average monthly maximum (a) and minimum (b) soil temperatures in the rooting zone during the first growing season after a wildfire in burned and unburned areas

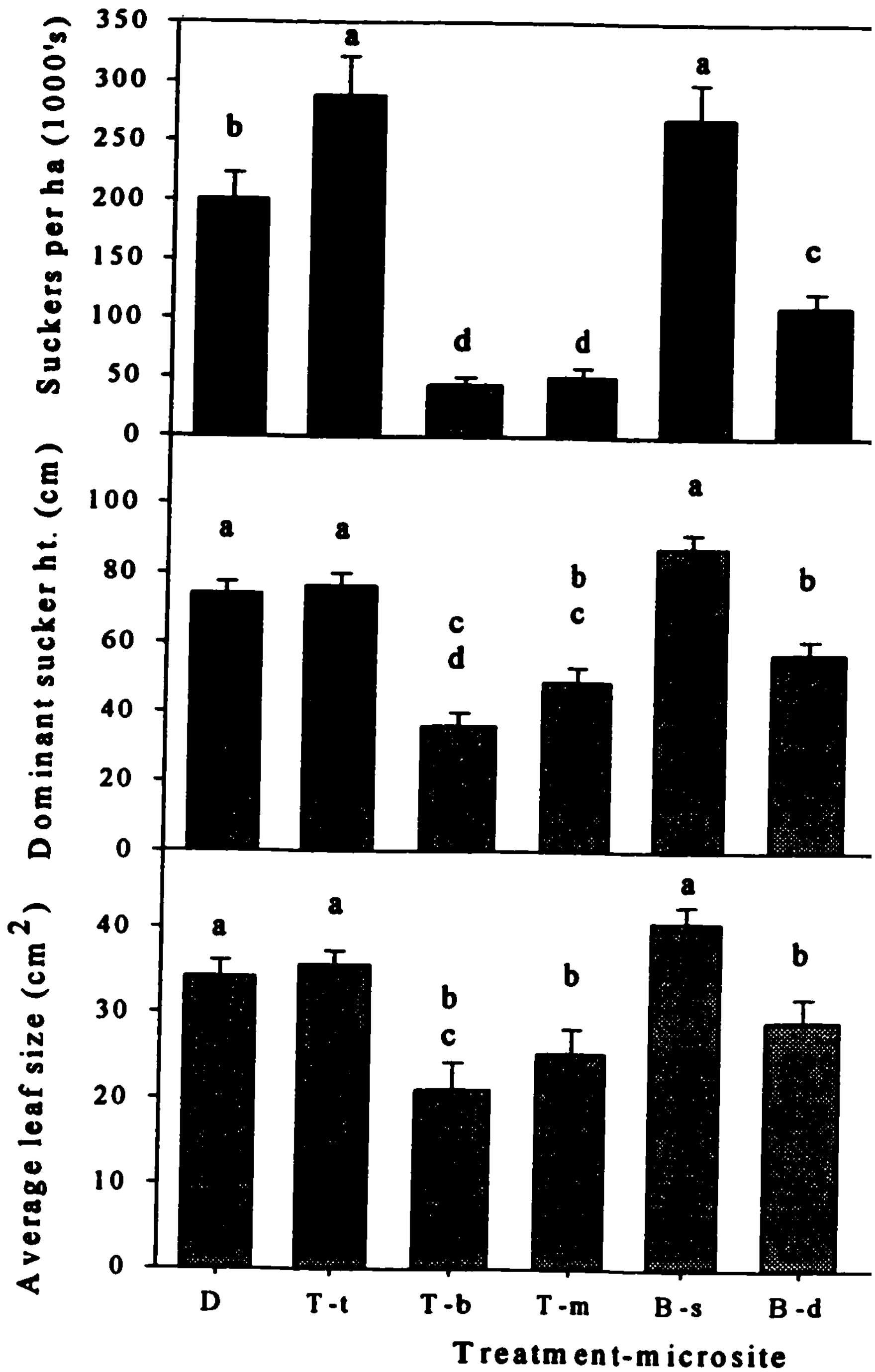

Figure 3-4: Number of suckers per hectare (a), average dominant sucl
average leaf size (c) in microsite plots following the first growing sea:
mechanical site preparation. Legend: D: drag scarify-barrel path, T-t:
T-b: disc trench-berm, T-m: disc trench-mid trench, B-s: blade-shallo
blade-deep scrape, B-p: blade-pile, C: control

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CHAPTER IV

Research summary, implications and future work

In general, trembling aspen (*Populus tremuloides* Michx.) regenerates prolifically following a stand-replacing disturbance. In some instances, however, aspen fails to produce a fully stocked stand of suckers. In the past, this failure to regenerate was often attributed to low soil temperatures. Results from Chapter II, however, demonstrated that suckering may not be as inhibited by cold soil as previously thought. These results showed that sucker production was not affected by small changes in daily maximum soil temperatures between 12° and 20°C. Additionally, there was no evidence of a minimum threshold temperature for aspen suckering in the temperature range tested. This suggests that soil temperature is not the main environmental driver of aspen suckering in the field when maximum daily temperatures exceed 12°C. Further, soil nutrition appears to exert a greater influence than previously thought on initial sucker development. There have been no previous reports of nutrients affecting aspen suckering. However, results from Chapter II indicated that $CaSO_4$ or NH_4NO_3 addition significantly increased sucker dry weight, and this was attributed to the mobilization of stored carbohydrate reserves from the parent root. An increase in initial sucker growth rates could be important under field conditions because suckers initiated under nutrient rich conditions would likely emerge from the soil surface sooner than other species. These suckers, therefore, may be able to out-compete other vegetation species, leading to higher rates of survival in the first growing season.

A forest management option that has been proposed for aspen management is mechanical site preparation (MSP). MSP has been reported to increase soil nutrient availability following treatment (Vitousek et al. 1992, Schmidt et al. 1998). MSP can also help alleviate some other common limiting factors for aspen suckering, including vigorous establishment of competitive vegetation (von der Gonna 1992). Results from Chapter III demonstrated that MSP could be used successfully for aspen regeneration when applied before the first growing season after harvesting. However, the results from this study also showed that some microsites are more conducive to suckering than others. Areas where the forest floor was disturbed and the parent root system was only slightly injured, but not extensively damaged, generated significantly more suckers than microsites where the root system was either undisturbed or severely injured.

Prescribed burning has also been proposed as an aspen management tool. Following a fire, site conditions are generally thought to be very favourable for suckering because the forest floor thickness is typically reduced (Horton and Hopkins 1966, Perala 1974, Brown and DeByle 1987, Bonan and Shugart 1989) and the availability of soil nutrients tends to increase (Ahlgren and Ahlgren 1960, Feller 1982, van Cleve and Dyrness 1983, Macadam 1987). However, it was not known whether fire could successfully be used following suckering in the first growing season. Results from Chapter III, however, showed that fire could be a viable treatment option even when applied in the second year after logging. However, the average dominant sucker height was lower following the fire (second season after logging) compared to suckers initiated immediately after harvesting and MSP. This may have been due to reduced root carbohydrate reserve levels following first year sucker production and second year leaf formation since the fire occurred during leaf out.

The results from this thesis have impacts for aspen management following timber harvesting. The results indicate that soil temperature may not be the sole environmental driver for aspen suckering and that soil nutrition may play a larger role in initial sucker development than previously thought. Consequently, forest management options such as MSP and prescribed burning would likely promote aspen, as they both tend to increase nutrient availability immediately following treatment. While it would not be necessary to treat all aspen cutblocks prior to suckering, those sites with thick organic layers or high brush hazards could benefit from treatment. Further, this thesis also demonstrated that aspen could be successfully regenerated with fire even after the first growing season following harvesting. Consequently, if aspen regeneration is inadequate following the first season of growth, forest managers could carry out a prescribed burn prior to the second growing season and expect improved suckering, as long as the parent root system remains viable.

While this study did address some of the drivers of aspen suckering, there are still a number of research areas that require future work.

1) The maximum and minimum temperature thresholds for aspen suckering of northern clones should be identified. Previous studies incubated short root sections at various temperatures for the same period of time, which may have overestimated the number of suckers produced at higher temperature regimes (see Chapter II). Consequently, the minimum temperature threshold that has been

identified for aspen suckering (14°C) (Maini and Horton 1966, Hungerford 1988) may not accurately reflect the response of aspen suckers in the field.

2) The effects of nutrient addition on the suckering of natural root systems, with fine roots intact, should be examined. Natural root systems may react differently than the root sections used in this thesis because the ability of roots to take up nutrients would obviously be increased by the presence of fine roots.

3) The issue of root wounding should be addressed. To date, there have been no studies that have isolated the effects of root wounding on aspen suckering. Previous researchers have commented on this question (Maini and Horton 1966, Weingartner 1980, Lavertu et al. 1994, Frey 2001). However, these studies were conducted in the field where there were many other confounding factors. As a result, it is currently not known whether injury to the root system actually stimulates suckering or whether another factor that typically accompanies root disturbance (e.g. increased nutrient availability, increased soil aeration, reduced competition from other vegetation species) is the mechanism that promotes suckering.

4) The viability of carrying out MSP following the first growing season should be examined. Since burning appears to promote suckering when applied in the second growing season, it would be logical to expect a similar response with MSP. If this option were feasible, forest managers would have another treatment alternative to address inadequate first year aspen suckering.

5) The long-term growth and productivity impacts of MSP and prescribed burning should be identified. It is currently not known whether certain microsites (e.g.

trenches in disc trenching) would be detrimental to the long-term growth of a stand, if nutrients may become limiting over time or whether root injuries created by MSP could offer an entry point for pathogens. Before treatments like MSP and prescribed burning are implemented on a large scale for aspen regeneration, it would be valuable to know whether these treatments are beneficial beyond the first few growing seasons.

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