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Regeneration dynamics of planted seedling-origin aspen (*Populus tremuloides* Michx.)

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Abstract Aspen (*Populus tremuloides* Michx.) is a foundational tree species of the North American boreal forest. After disturbance, clonal aspen stands quickly achieve canopy closure by sending up numerous clonal shoots (root suckers) from their lateral root system. Controlled aboveground disturbance will commonly induce prolific root suckering and thereby increase stem density in clonal aspen stands, but it is unclear if increases in stem density will be observed in planted seedling-origin aspen stands. The objectives of this study were to determine (1) overall root suckering response of planted aspen to aboveground disturbance; (2) if different cut heights of the stem or infliction of root damage impact the number of root suckers produced. We found that planted aspen regenerated readily after disturbance, averaging five root suckers per cut tree. However, individual response was highly variable, ranging from zero to 29 root suckers per root system. Of the cut trees, 75% produced at least one root sucker and 60% produced at least one stump sprout. Cutting trees close to the soil surface produced more root suckers than leaving a 25 cm stump. While root system size (mass and length) was well correlated with aboveground measures of planted aspen, root suckering was not related to root system size. As a result of increased forest reclamation efforts in the boreal forest region the planting of aspen has become a more common practice, necessitating a better understanding of the regeneration dynamics and root suckering potential of these planted and seedling-origin aspen forests.

Keywords Planted aspen seedlings · Root suckering · Stump sprouting · Forest recovery, disturbance

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Introduction

Aspen (*Populus tremuloides* Michx.) is a wide-ranging tree species and is considered to be a foundational species in many areas of the North American continent (DeByle and Winokur 1985; Peterson and Peterson 1992). As an early successional species, aspen is able to rapidly occupy sites after disturbance, particularly through its ability to spread and reproduce vegetatively through root sprouts (root suckers) (Schier and Smith 1979; Bartos and Meuggler 1981; Peterson and Peterson 1992; Frey et al. 2003). This regeneration strategy (where many new stems may develop from a shared root system), among other properties, has made aspen a focal species for reclamation and restoration projects, particularly across its boreal range (Macdonald et al. 2012). Over the past 30 years, and particularly the last 15–20 years, aspen seedlings have been planted on reclamation sites in the boreal forest region (Government of Alberta 2013). The increasing focus on planting aspen has prompted questions surrounding the ability of these planted seedling-origin stands to regenerate after above-ground disturbance, and whether stem densities at the stand level will be sufficient to recover the forest (Macdonald et al. 2012).

Aspen is a well-studied species, and naturally regenerated clonal stand attributes have been studied in all age classes, from root sucker establishment to over-mature or dying forest stands (Bartos et al. 1991; Peterson and Peterson 1992; Frey et al. 2003, 2004). In the recent past the forest sector, particularly in Canada, have viewed aspen as a competitor to species that are more commercially valuable (Miller 1996), and numerous studies have focussed on how to decrease or inhibit aspen regeneration (Bell et al. 1999; Pitt et al. 2003; Greifenhagen et al. 2005; Pitt and Bell 2005). While these studies have sought to reduce aspen abundance, they have also demonstrated how cutting and timing of harvest can be used to manipulate regeneration density—via root suckering and stump sprouting—in clonal-origin stands (Bell et al. 1999; Mundell et al. 2008). In natural clonal aspen stands, full stem removal has consistently resulted in significant regeneration through root suckering (Farmer 1962; Schier 1978; Bates et al. 1993; Grewal 1995; Frey et al. 2003) while the retention of some stems may have a negative impact on regeneration (Huffman et al. 1999; Mulak et al. 2006). Removal of the aboveground portion of the stem disrupts the hormonal balance between the root and shoot, which stimulates the development of root suckers on the root system (Eliasson 1971; Schier 1972, 1975). In younger stands, the cutting of stems can also produce stump sprouts, which are thought to suppress the production of new root suckers from the parent clonal root system (Sterett and Chappell 1967; Eliasson 1971; Mulak et al. 2006; Wan et al. 2006). Furthermore, earlier research on vegetation management has shown that the ratio of root suckers to stump sprouts can be manipulated in young stands by altering the height at which trees are cut, as well as when they are cut (Bates et al. 1993; Bell et al. 1999; Mulak et al. 2006).

While there is extensive knowledge on the aboveground portion of aspen in response to disturbance, very little is known about the root system development of planted aspen and its response to disturbance and leaf area development (Landhäusser and Lieffers 2002). The root system structure of mature clonal aspen stands has been studied in some detail (Day 1944; Strong and La Roi 1983a, b; DesRochers and Lieffers 2001a, b; Snedden 2013), but there are still significant gaps in our understanding of rooting dynamics of planted seedling-origin aspen. The depth and size of the root system will likely have a significant impact on the ability of roots to sucker, and the spatial distribution of root suckers. Earlier research has shown that aspen roots are concentrated in the top 5–20 cm of soil (Strong and La Roi 1983a, b; Snedden 2013) and root sucker emergence is unlikely from soil depths greater than 20 cm (Wachowski 2012; Wachowski et al. 2014). Further, Steneker (1976) determined that stand age did not affect root suckering potential, however, this was observed in natural clonal-origin stands, which most likely had a much older (and larger) connected clonal root system. Disturbance to the root system—such as severing or scarification of roots—has been found to induce root suckering (Shepperd 1996; Fraser et al. 2004; Kabzems and Haeussler 2005); however, these injuries cannot be too severe (Renkema et al. 2009). In addition, clonal-origin aspen stands have extensive parent root systems that may also be connected through intra- and inter-clonal grafts (DesRochers and Lieffers 2001a, b; Jelínková et al. 2009; Snedden 2013). These grafted root sections may persist even after the original parent tree has died off, and may assist in the transfer of resources between clones and ramets (Desrochers and Lieffers 2001a); indeed, a larger root system may lead to a greater amount of resources available for resprouting. Since seedling-origin aspen are individual genotypes that have individual root systems, it is unclear if these genetically diverse aspen stands will respond to aboveground disturbance in similar patterns to clonal stands that have already gone through selective pressures by enduring one or more disturbance cycles in their lifetime (Kemperman 1977; Perala 1978).

The objective of this study is to determine how planted aspen respond to above-ground disturbance, and whether root sucker numbers vary by different cutting heights of the stem or by inflicting root damage. We explore the role of individual root system size in the production of root suckers, and whether the number of stump sprouts affects the root sucker regeneration of planted aspen. We hypothesize that trees cut lower to the ground will have greater root sucker numbers, while higher cut trees will have more stump sprouts and fewer root suckers. We further predict that the root system size will have a significant and positive effect on the number of root suckers produced. Our study was located on two stands (on one site)—a stand with larger diameter trees and a stand with smaller diameter trees—and we hypothesize that larger trees will have more extensive root systems, which will produce a greater number of root suckers. Additionally, we anticipate that severed root systems will produce similar root sucker numbers to root systems attached to a stump.

Methods

Study site

This study was carried out at the University of Alberta Ellerslie Research Station, Edmonton, Alberta (N53°24″44″; W113°32″31″). The research station is located in the central parkland ecoregion (Natural Regions Committee 2006) on a Malmo silty clay loam (fine textured), which is an Eluviated Black Chernozem developed from a lacustrine parent geological material (Bowser et al. 1962). Weather data were collected from the University of Alberta South Campus weather station, 9 km due north of the Ellerslie Research Station. Precipitation in the 2015 growing season totalled 145 mm (leaf out April 1st until harvest, August 28th, 2015). During the 2015 growing season, average maximum daily temperature was 20.6 °C and average minimum daily temperature was 8.1 °C. The long-term average maximum and minimum temperatures in this region are 18.8 and 6.4 °C respectively. The long-term average amount of precipitation at this site for these months is 289 mm, making the 2015 growing season both warmer and drier than average (Alberta Agriculture and Forestry 2016). Precipitation in the 2016 growing season (April 1st until plot measurements on August 18th, 2016) totalled 365 mm, with an average maximum daily temperature of 20.7 °C and an average minimum daily temperature of 8.8 °C, making 2016 wetter and warmer than average.

Two planted aspen stands were established on one site in 2003 and 2007. The 12 year old stand (larger diameter at breast height stand, LD) occupied an area of approximately 0.06 ha, was planted at a density of 10,000 stems ha^{-1}, average DBH of 6.4 ± 5.4 cm in 2015. The 8 year old stand (smaller diameter at breast height stand, SD) occupied an area of 0.04 ha and was planted at 29,000 stems ha^{-1}; stem DBH averaged 4.4 ± 0.7 cm in 2015 (Table 1). The large difference in tree size between the two stands was most likely a result of the initial planting density; however, because both stands were also planted 4 years apart we cannot separate the age effect from the density effect. Thus tree size, average diameter, and age were considered in combination when comparing trees from the large and small diameter stands (LD or SD respectively) (Table 1). Since both stands were in close proximity to each other and planted on a level, formerly cultivated field, soil conditions were considered homogeneous across the stands.

Both stands had closed canopies with negligible understory vegetation. However, to control the potential spread of species that could become competitive (e.g., *Cirsium arvense*), an herbicide (Glyphosate, Roundup, Monsanto, St. Louis, MO, USA) was applied by spot-application, as directed by the product label, using a hand sprayer prior to root suckering. Only healthy dominant or codominant canopy trees were selected for this study in both stands. Trees with evidence of hypoxylon canker, bark deformations, or evidence of wood boring insects were not used, nor were trees with more than one bole. The DBH of all dominant and codominant trees was measured in each stand prior to treatment tree selection to ensure that an equal range of tree diameters were captured in the study.

Treatments

Treatments were applied at the individual tree level in 2015 and at the stand level in 2016. To explore the impact of planting density and disturbance type on root suckering and stump sprouting of planted aspen trees, four different disturbance treatments (treatments) were applied on May 29th, 2015 to 40 trees in each stand (total of 80 trees, n = 10 per treatment × stand combination). The treatments were: (1) trees with no treatment (Control); (2) trees that had all lateral roots severed to a soil depth of 20 cm (Severed); (3) trees that had the stem removed at ground level (0 cm) (Low Cut); and (4) trees that had the stem removed 25 cm above ground level (High Cut). Treatments 3 and 4 were applied

Table 1 Average initial stand and study tree characteristics (± SD) for the large diameter (LD) and small diameter (SD) stand

Stand type	Stand				Study trees (n = 40)		
	DBH (cm)	Density (stems ha^{-1})	Basal area (m^2 ha^{-1})	Age (years)	Height (m)	DBH (cm)	Leaf area (m^2)
LD	6.4 ± 5.4	29,000	79	12	9.9 ± 1.4 **a**	7.1 ± 2.2 **a**	6.8 ± 4.7 **a**
SD	4.4 ± 0.7	10,000	49	8	8.0 ± 0.9 **a**	4.6 ± 0.9 **b**	4.1 ± 2.0 **b**

While 40 individual trees were selected for this study in each stand, the stand characteristics were based on averages measured on all trees in the entire stand. Letters indicate significance differences between study trees in the LD and SD stand type ($\alpha < 0.05$)

using a handsaw and stems were cut just above the root collar (Low Cut) or 25 cm above the root collar (High Cut). For the Severed treatment, a sharpened, flat-headed spade, followed by a narrow handsaw, was used to sever all roots to a depth of 20 cm in a radius of 10 cm around the bole of each tree. The 20 cm depth was chosen to ensure that all roots with the potential to produce emergent root suckers would be severed (Strong and La Roi 1983a, b; Wachowski 2012; Wachowski et al. 2014). The treated trees were left to regenerate over the growing season (May 29–August 13), and their root systems were excavated at the end of the growing season to assist in the accurate count of root sucker regeneration, and to provide a measure of root system extent.

To understand the root suckering dynamics across the two stands, and to relate total basal area to root suckering density, all ($\sim$ 1700) trees were cut in the winter of 2016 at approximately 5–10 cm above the ground. The total basal area of each stand was determined by measuring the basal diameter of each cut tree at this time. The stands were left to regenerate for one growing season (April 13 2016–August 18 2016). Root suckering and stump sprouting were assessed in late August 2016 by measuring the root sucker and stump sprout density and their heights in 10 m^2 circular plots (1.78 m radius) on both stands (LD $n = 5$, SD $n = 4$). A metal stake was used for the plot center, and plots were randomly placed throughout the two stands but did not overlap.

Measurements

To assess root suckering of each individual tree, the root systems of all 80 treatment trees (including Control trees) were carefully excavated in late August 2015 and were evaluated for root sucker initiation and development. Root systems were excavated by gently loosening the soil around the bole of the tree with a pitchfork and then carefully removing the soil from the lateral roots using hand trowels. Each lateral root greater than 0.5 cm in diameter, and originating within the top 20 cm of the soil, was collected; each individual root was traced, and the root and all root suckers attached to that root were collected. All roots were followed as far as possible or until the root dipped below a soil depth of 20 cm. Collected roots that were less than 0.5 cm in diameter were combined for the whole root system and added to the total root system weight of the individual. Where root suckers were present in the vicinity and general direction of a root, the root was followed until it could be determined that the root sucker was or was not from that particular root system. Roots and root suckers were stored in bags and kept moist and cool in the field. Stump sprouts were collected separately. All roots and sprouts were brought back to the lab at the end of each day and were stored at 4 °C until processing in the lab. Once in the lab, total root length was measured and coarse root volume was estimated using the water displacement method (Harrington et al. 1994). These measures allowed us to calculate total root surface area (Eq. 1). Total coarse root dry mass was measured after drying samples to constant weight at 70 °C. The relationships between tree diameter and root mass, and between root mass and root length from the individual trees were used to estimate area-based root length and root mass of the stands.

Equation 1. Calculation for the surface area of a root, using the equation for calculating the surface area of a truncated cone

$$\begin{aligned} \textbf{\textit{S}}\textit{lant}\,\textbf{\textit{H}}\textit{eight} &= \sqrt{\textit{length}^2 + (\textbf{\textit{Bottom}}\,\textbf{\textit{R}}\textit{adius} - \textbf{\textit{Top}}\,\textbf{\textit{R}}\textit{adius})^2} \\ \textit{Surface Area} &= \pi \times (\textbf{\textit{BR}} + \textbf{\textit{TR}}) \times \textit{slant height} \end{aligned} \tag{1}$$

Statistical methods

All data were analyzed using R-Studio (R Core Team 2016, Boston, MA). For parametric analyses, assumptions of normality and homoscedasticity were tested using the Shapiro–Wilks test and Levene's Test. If data did not meet the assumptions, other statistical approaches such as transformation or non-parametrical analyses were applied (see below). Our study was divided into two field seasons. In the first field season (2015) the disturbance treatments were applied and response measurements taken at the individual tree level; the experimental trees in both stands were sufficiently spaced and thus we considered each tree an independent experimental unit, and stand was treated as a fixed factor in this analysis. By analyzing stand as a fixed, rather than random, factor, we were able to use stand as a proxy for differences in tree size. The methods for the first growing season (2015) assessed the relationships between the four disturbance treatments and the two stands on root sucker production, where the response of the individual tree is of interest. To determine the effect of treatment and stand on root sucker production of individual trees, a generalized linear model following a Poisson distribution was fitted, as the count data did not meet the assumptions of normality; pairwise comparisons were determined with the general linear hypothesis testing function with Fisher's least squared difference (LSD test) and an α adjustment with Hommel's method from the multcomp package (Hothorn et al. 2008). The effect of disturbance treatment and stand on stump sprout production was determined using a two-way ANOVA; Fisher's LSD test with a Bonferroni adjustment was used for the post hoc pairwise comparisons. To determine (1) if the pooled High and Low Cut (Cut) trees produced more root suckers than the roots of Severed trees; and (2) if the Cut trees produced more total sprouts (root suckers and stump sprouts combined) than the Severed trees, data were log + 1 transformed and two-way ANOVAs with treatment and stand as main effects were used. To test if the production of stump sprouts inhibited the production of root suckers at the individual tree level, Spearman's Rank Correlation was used to test the correlation between root sucker and stump sprout production in the High and Low Cut treatments. Finally, simple linear regressions were used to test the relationships between total root sucker and stump sprout production, and between the total root length for the High Cut and Low Cut treatments; root sucker and stump sprout values were log + 1 transformed. To explore differences between the stands in average total root length and weight of trees, the non-parametric Kruskal–Wallis test by ranks was used. Non-linear regression models were fitted to assess the relationships between root mass and DBH, and root mass and root length.

In the second field season (2016) one treatment (clearfelling) was applied to both stands (LD and SD): all results were based on the 10 m^2 regeneration plot measurements within the two stands. We realize the significant limitation of this approach to assess the regeneration of planted seeding-origin aspen beyond the individual scale (see above); however, we believe that this is the first attempt of its kind that assesses the suckering ability at a somewhat larger scale. To test for differences in root sucker and stump sprout regeneration between the LD and SD stands t-tests or Mann–Whitney–Wilcoxon tests were used; the impact of stump sprouting on root suckering was measured with a Spearman's Rank Correlation.

Results

The root suckering response of trees was highly variable among individuals, and ranged from 0 to 29 root suckers per tree. Despite this variability, treatments had a significant effect on root sucker production ($\chi^2_{3,76} = 417.35$, $p < 0.001$), but this response differed between the large diameter (LD) and small diameter (SD) stands (treatment × stand interaction $\chi^2_{3,72} = 397.47$, $p < 0.001$). In both the LD and SD stands, the Low Cut treatment produced the greatest number of root suckers per tree ($\bar{x} = 7.5$), while the Control treatment had the fewest (Fig. 1). The High Cut and Severed treatments produced similar numbers of root suckers but fewer than in the Low Cut treatment; however, the number of root suckers in the High Cut and Severed treatments were approximately two times higher in the LD stand than in the SD stand (Fig. 1). Stand had a significant effect on the amount of stump sprouts produced; however, cut height had no effect on the production of stump sprouts ($F_{1,36} = 0.30$, $p = 0.59$) (Fig. 2). The smaller diameter trees (the SD stand) produced three times more stump sprouts ($\bar{x} = 4.5$) than the larger diameter trees (the LD stand ($F_{1,36} = 6.25$, $p = 0.02$).

To determine if cutting of stems produced more root suckers or total sprouts than root severing, root sucker and total sprout production of individual trees was compared between the Severed and Cut (combined High Cut and Low Cut treatments) treatments in both the LD and SD stands. There was no difference in the production of root suckers ($F_{1,56} = 0.964$, $p = 0.33$) or total sprouts (sum of root suckers and stump sprouts) ($F_{1,56} = < 0.001$, $p = 0.98$) between the two stands. However, based on the initial tree volume, the SD produced approximately 12.2 root suckers per m^3 of initial aboveground mass, compared to the LD producing 8.5 root suckers per m^3 of aboveground mass. The number of root suckers produced in the Cut and Severed treatments was not statistically different ($F_{1,56} = 2.470$, $p = 0.12$) (Fig. 3a), but showed a trend for greater root sucker production in the Cut treatment. The trees in the Cut treatment had an average of 8 sprouts per tree, approximately four times higher than in the Severed treatment ($F_{1,56} = 9.726$, $p = 0.003$) (Fig. 3b).

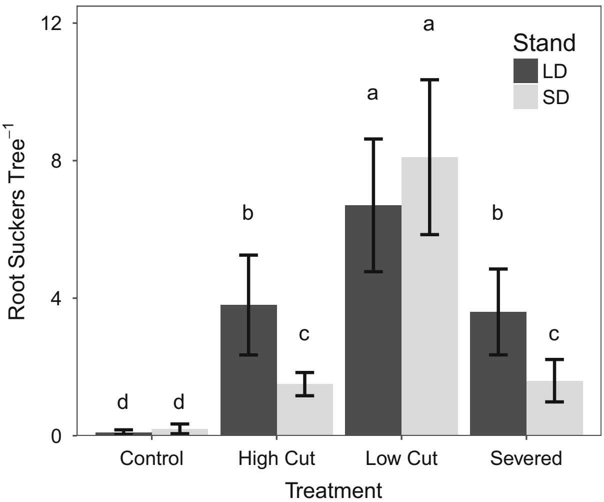

Fig. 1 Average root sucker production in response to stand and treatments (Control, High Cut, Low Cut, and Severed). The large diameter (LD) stand was planted at 10,000 stems ha^{-1} and the small diameter (SD) stand was planted at 29,000 stems ha^{-1}. Error bars represent standard deviation and different letters indicate significant differences ($\alpha < 0.05$) (n = 10)

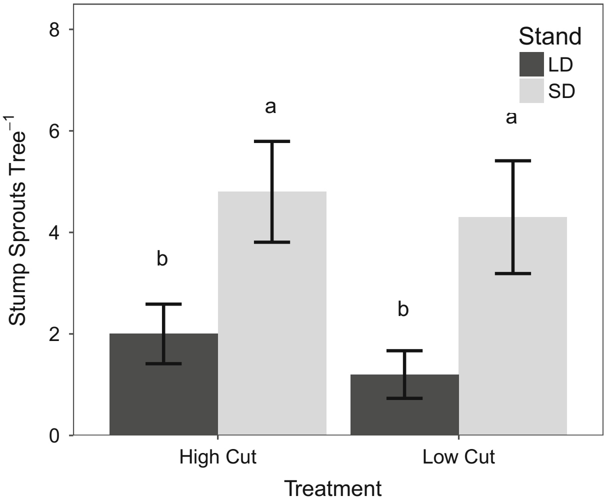

Fig. 2 Average stump sprout production in response to stand and cutting treatment (High Cut and Low Cut only). The large diameter (LD) stand was planted at 10,000 stems ha^{-1} and the small diameter (SD) stand was planted at 29,000 stems ha^{-1}. Error bars represent standard deviation and different letters indicate significant differences ($\alpha < 0.05$) (n = 10)

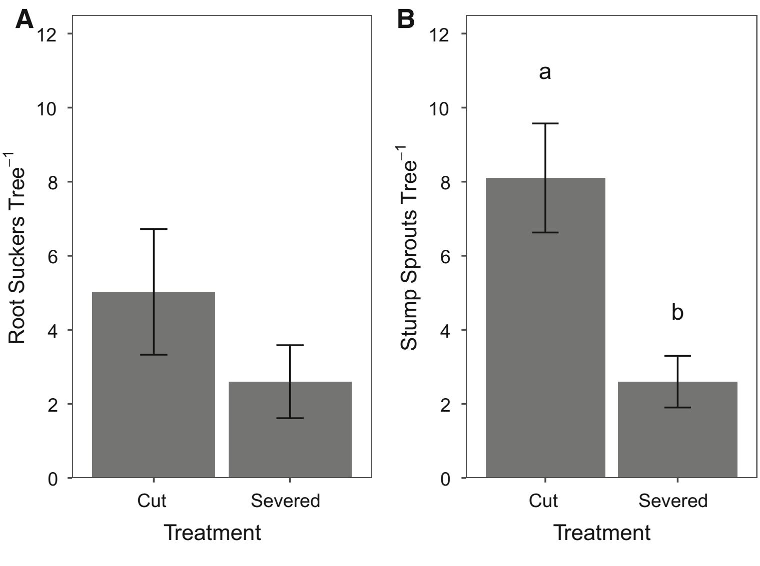

Fig. 3 Average root sucker (**a**) and sprout (root suckers and stump sprouts combined) (**b**) production per tree. The Cut treatment is the High Cut and Low Cut treatments pooled (see text). Error bars represent standard deviation and different letters indicate significant differences ($\alpha < 0.05$) (n = 40 for Cut and n = 20 for Severed)

Root sucker and stump sprout production were not correlated with each other in either cut treatment in 2015; this may indicate that stump sprouting was not inhibiting the production of root suckers. The relationship between the two sprout types was insignificant for both the Low Cut treatment (r = 0.43, n = 40, $p = 0.058$) and the High Cut treatment (r = 0.33, n = 40, $p = 0.156$).

The excavation of individual root systems in 2015 allowed us to determine average root system size differences between trees in the SD and LD stands. On average, trees in the LD stand had greater root mass ($F_{1,78} = 17.15$, $p < 0.001$) and greater root length ($F_{1,78} = 9.27$, $p = 0.003$) than trees in the SD stand (Fig. 4). There were relationships between root characteristics and initial tree size (Table 2); but there were no significant relationships between root characteristics (surface area, length, mass) and root sucker production. No relationships between total root length and root sucker production ($r^2 = 0.07$, n = 40, $p = 0.079$) and stump sprout production ($r^2 = 0.001$, n = 40, $p = 0.82$) were detected.

In winter 2016, the basal area of all trees in the LD stand (590) and SD stand (1137) were measured. The LD stand, with a stem density of 10,000 stems ha^{-1}, had a basal area equivalent to 79 m^2 ha^{-1} while the higher density (29,000 stems ha^{-1}) SD stand had a basal area of 49 m^2 ha^{-1}. After clearfelling in 2016, the LD stand produced significantly more root suckers (t = 3.88, n = 5, $p = 0.012$) that were 23% taller than root suckers in the SD stand ($t_{3057} = 7.04$, $p < 0.001$, Table 3). The SD stand produced significantly more stump sprouts after clearfelling (t = 8.0, n = 5, $p < 0.001$), but there was no corresponding increase in stump spout height ($t_{756} = 1.15$, $p = 0.24$, Table 3). As in 2015, there was no association between root suckering and stump sprouting in the SD or LD stands in 2016 after clearfelling (LD r = 0.32, n = 4, $p = 0.59$; SD r = − 0.49, n = 4, $p = 0.50$).

Discussion

Planted aspen regenerated readily after above ground disturbance through both root suckering and stump sprouting; however, the root suckering response was highly variable, and ranged from zero root suckers to a maximum of 29 root suckers per root system, with an average of five root suckers per cut tree in 2015. Of our cut trees, 75% produced at least one root sucker and 60% produced at least one stump sprout. Although there are no

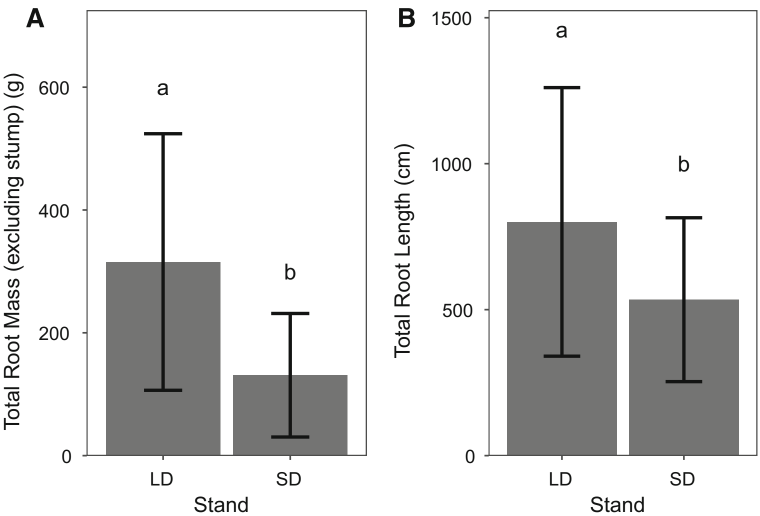

Fig. 4 Average root weight (**a**) and average root length (**b**) per tree in the large diameter (LD) and small diameter (SD) stands. Error bars represent standard deviation, and different letters indicate significant differences ($\alpha < 0.05$) (n = 40)

Table 2 Regression equations and r^2 values for four different relationships used to estimate stand level root mass and length

	Relationship	Slope equation	r^2	*p*
1	Power relationship between total root mass (excluding stump) and DBH (cm)	$y = 6.3762x^{1.9505}$	0.52	< 0.001
2	Power relationship between total root length and total root mass (excluding stump)	$y = 77.497x^{0.3515}$	0.33	0.014

The two power relationships are based on the measured root system mass (1) and length (2), collected in August 2015 in both the large diameter (10,000 stems ha^{-1}, LD) and SD stands (n = 80)

Table 3 Height and density of root suckering and stump sprouting following clear cutting in April 2016 in both the small diameter (SD, 29,000 stems ha^{-1}) and large diameter (LD, 10,000 stems ha^{-1}) stands

Stand	Root suckers		Stump sprouts		Estimated root system size	
	Regeneration (stems ha^{-1})	Average height (cm)	Regeneration (stems ha^{-1})	Average height (cm)	Total length (m ha^{-1})	Total weight (kg ha^{-1})
Large diameter	40,380 ± 6264 a	59 ± 44 a	3000 ± 1811 a	67 ± 43 a	81,856	5700
Small diameter	26,025 ± 665 b	48 ± 37 b	15,225 ± 2212 b	64 ± 45 a	130,743	3639

Standard deviation (±) reported for all 2016 measures, and different letters indicate significant differences within columns ($\alpha < 0.05$) (n = 5 for LD, n = 4 for SD)

independent data available on the root suckering potential of planted aspen after cutting, our values are very similar to aspen that had established from seed after a fire in Arizona and produced voluntary root suckers without aboveground disturbance (Fairweather et al. 2014). In that study 61% of seedlings produced root suckers, ranging from 1 to 39 root suckers per ortet with an average of 5.4 root suckers (Fairweather et al. 2014).

The second year of our study assessed the stand-wide response of the LD and SD stands to clearfelling; the average number of root suckers per root system produced decreased to four in the large diameter (LD) stand and to one in the small diameter (SD) stand. The number of root suckers produced after clearfelling should be viewed with caution; due to the limiting size of our study site and the sampling design. The values from 2016 are however interesting, as they provide values for average root sucker and stump sprout height after the above canopy has been removed, as well as give an idea of regeneration density at a greater stand scale. Compared to clonal-origin stands, the root suckers produced in our study after the whole stand was cut were relatively short, averaging only 55 cm in height. Root suckers arising from established clonal stands can reach over 200 cm in the first growing season (Peterson and Peterson 1992). The trees were cut prior to leaf flush in the 2016 growing season and the timing of cutting has been shown to have little impact on the number of suckers being produced (Mundell et al. 2008); however, the reserve status of the root system at that time of the year could have affected the height growth of root suckers in the 2015 growing season (Schier and Zasada 1973; Landhäusser et al. 2006). It is interesting that a significant proportion of individual aspen root systems did not produce any root suckers. This response might be related to the large genotypic variability in planted aspen (Fairweather et al. 2014). The expression of genotypic variation has been observed in a multitude of traits in aspen including: carbon allocation to roots and shoots, and root turnover (King et al. 1999); canopy decline and mortality (Schier and Campbell 1980; St Clair et al. 2010); root sucker production (Zufa 1971; Schier and Campbell 1980); and concentrations of both phenolic compounds and tannins, which affect both the decomposition rate of leaves, and the degree of herbivory (Osier and Lindroth 2001; Lindroth et al. 2002).

Cutting trees at the surface (Low Cut) in our experiment produced more suckers than leaving a 25 cm stump (High Cut) across the two stands; this pattern is similar to observations in clonal-origin stands (Bell et al. 1999). However, counter to our results, Bell et al. (1999) found that the number of stump sprouts increased with height of cut. In our study, the smaller diameter stems produced more stump sprouts than the large diameter stems, which is consistent with findings in clonal aspen where more stump sprouts were observed in both young or smaller diameter trees (Heeney et al. 1980; DeByle and Winokur 1985; Mulak et al. 2006). However, we also observed a significant stand by treatment interaction, which was observed in both the high and low cut treatments in LD and SD stands; this may be related to the age of the trees and/or the difference in diameter of trees located in each site; however, since the planting density also influenced the diameter of our trees we cannot separate the density effect from stand age. It has been hypothesized that the presence of stump sprouts may also prevent the formation of root suckers in aspen (Sterett and Chappell 1967; Eliasson 1971; Mulak et al. 2006). Our study showed no evidence of root sucker suppression by stump sprouts in either 2015 or 2016. Interestingly, we found that the cut stump height had a significant effect on the amount of root suckers but not on the number of stump sprouts. Similar results have been observed in smaller aspen seedlings where dormant seedlings that were debuded (i.e., stems were unable to grow new shoots and leaves) or had half of their stems cut off, produced significantly fewer root suckers than seedlings that were cut close to the ground (Wan et al. 2006). The authors concluded that the stem had an influence on root sucker production, most likely a process driven by plant hormones. Severing all lateral roots to a depth of 20 cm from the main stem of the established aspen resulted in root sucker regeneration on the severed roots. However, in these young trees the root sucker density from the severed roots tended to be lower than in the cut trees with intact root systems. Interestingly, the trees with severed lateral root systems remained alive throughout the growing season and, other than the overall anchorage of the trees, the severing did not appear to have any ill effects on the same-year performance of these individuals.

Although the root system size (mass and length) was not a significant determinant of the root suckering ability of individual planted aspen, root system size may still have played a role in the root suckering of planted aspen at the stand level. Our results indicate that after clearfelling, the root systems in the LD stand, where individual root systems were significantly greater, produced more root suckers than in the SD stand. This might suggest that there is a relationship between root system size and root suckering that our experimental design, i.e., limited to one stand, were not able to capture. Also our study was potentially limited by the conditions of that particular site where the root systems of the trees appeared to be somewhat constrained with average individual lateral roots extending less than 1 m in length. We have observed average lateral root lengths of over 3 m in 4 year old aspen trees on some boreal reclamation sites. The role site conditions play on the expression of the lateral root system in planted and seedling-origin aspen are unclear, but may be significant drivers of regeneration potential of planted aspen seedlings.

Root grafts are commonly observed in clonal aspen root systems (Desrochers and Lieffers 2001a; Jelínková et al. 2009; Snedden 2013), but were generally lacking in our stands. Of the 80 excavated trees with 423 individual roots, only one root graft was observed between two trees, indicating that root systems of planted aspen are isolated even as the stand develops. This is interesting as root grafts and their role in resource sharing of carbohydrates, nutrients and water are important aspects in the reproduction, growth and stand dynamics of clonal aspen stands (Debyle 1963; Eis 1972; DesRochers and Lieffers 2001a). Functional root grafts can connect different clones or individuals and allow for the transport of nutrients and water between clones (Desrochers and Lieffers 2001b; Fraser et al. 2006; Jelínková et al. 2009). The presence of root grafts in planted stands may effectively increase the extent of the root system size, which could have a positive impact on their ability to resprout. Given the high planting density of the LD and SD stands, it is surprising that overlapping root systems did not result in more root connections. Root grafting was found to be common in high density *Pinus contorta* Doug. (seedling-origin) stands (Fraser et al. 2006) of a comparable age and spacing to our trees (Fraser et al. 2005). The reason for a lack of interconnection is puzzling, but might be due to intraspecific belowground competition between a greater number of individuals (different genoptypes), generally not deemed a significant factor in clonal aspen stand dynamics. The occurrence of grafting among seedling-origin pines varied with tree age (Fraser et al. 2005), so it is possible that adequate time for grafting to occur may not have elapsed in our stands. If the root systems of planted aspen continue to be independent at the stand level, it is conceivable that the growth and regeneration dynamics of these stands will change when compared to clonal-origin stands, particularly when above and below ground intraspecific competition plays a greater role.

Conclusions and management implications

The large variability in the regeneration potential among aspen seedling genotypes—with about 25% of the seedlings not producing any suckers—is a very interesting outcome of this study, which has significant implications for the regeneration dynamics of planted aspen stands. Currently aspen is planted on boreal reclamation and restoration sites at relatively low densities (1500–1800 stems ha^{-1}); the large variability in root sucker regeneration observed in our study suggests that this planting density may lead to patchy regeneration and open site conditions after above-ground disturbance. A delay in canopy closure during regeneration may have further consequences for the future trajectory of these regenerating forests. Natural aspen stands of clonal-origin have been observed to reach high leaf area indices (LAI) indicative of canopy closure in as little as 4 years after disturbance, capturing the site successfully by supressing early successional, ruderal, and competitive herbaceous species (Pollard 1970, 1971; Pinno et al. 2001). Delayed canopy closure may provide opportunities for competitive grass and forb species to become established and dominate sites, which may further impede the re-development of an aspen canopy (Landhäusser and Lieffers 1998; Frey et al. 2003; Bockstette et al. 2017).

Although parts of this study are somewhat limited by the study design, our research identified some important drivers and challenges that can impact root sucker regeneration in planted seedling-origin aspen stands. Regeneration in these planted aspen stands appears to be related to the type of aboveground disturbance; the age and density of the planted seedling-origin stand; and the extent and size of the lateral root system, which may be modulated by the soil and site conditions. In light of the increasing deployment of aspen seedlings throughout its range, further studies are needed that explore the suckering regeneration and stand dynamics of these seedling-origin stands over a wider range of stand and site conditions.

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