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Trembling aspen root suckering and stump sprouting response to above ground disturbance on a reclaimed boreal oil sands site in Alberta, Canada

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Abstract

Trembling aspen (*Populus tremuloides* Michx.) is an important early successional species in the boreal region that commonly regenerates via root suckering and, to a lesser extent, stump sprouting after aboveground disturbance such as harvesting or wildfire. However, the response of aspen to disturbance on reclaimed oil sands sites is not known. To determine the suckering and sprouting response of 6-year-old seedling origin aspen growing on a reclamation site, we destructively sampled 87 individual trees in May 2017. Trees were selected across two soil types, forest floor-mineral mix and peat-mineral mix, and three height classes, 100–199 cm, 200–299 cm, and > 300 cm. In August 2017, we returned to each cut tree to assess the type (sucker vs. stump sprout) and abundance of regeneration. Aspen readily responded to disturbance; however, responses were highly variable between trees, ranging from zero to 47 suckers and zero to 42 sprouts. Trees growing on peat-mineral mix were 7.8 times more likely to produce at least one sucker and generally had a higher abundance of suckers. Tree height was also positively correlated with suckering probability and abundance, while competition from surrounding vegetation decreased the probability and abundance of suckering, especially when cover of competing species was greater than 52.5%. The probability of stump sprouting was not affected by soil type or tree size, but did decrease with increases in tree competition. Overall, trembling aspen respond vigorously to disturbances on mine reclamation sites which is a promising sign of resilience for these novel and young ecosystems.

Keywords *Populus tremuloides* · Root suckering · Forest regeneration · Land reclamation · Resiliency · Disturbance

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Introduction

Trembling aspen (*Populus tremuloides* Michx.) is a widespread, early successional species in Alberta's boreal forests (DeByle and Winokur 1985; Downing and Pettapiece 2006; Peterson and Peterson 1992). As an early successional species, it is able to respond quickly to disturbances through its ability to reproduce vegetatively through root suckers (Schier and Smith 1979; Bartos et al. 1991; Peterson and Peterson 1992). The quick development of aspen root suckers after disturbance provides many benefits useful for forest regeneration, which can also be applied to land reclamation. Root suckers develop leaves quickly which mitigate water stress by reducing solar radiation to the forest floor and early litter production from aspen suckers aids in the development of a surface organic layer of soil that is commonly lost after disturbance (Rowland et al. 2009). These two factors are also important on reclaimed areas, as they encourage the development of a natural understory and soil–plant nutrient cycle (Pinno and Errington 2015).

Root suckers are generally produced when a disturbance removes or kills the above ground portions of the tree (Frey et al. 2003). The mortality or removal of the aboveground portions of the tree causes an imbalance between two hormones, auxin and cytokinin, within the tree, initiating sucker growth (Farmer 1962; Eliasson 1971; Schier 1972; Steneker 1974). Auxin is produced in the twigs and buds of the trees and is transported to the roots where it promotes root growth and inhibits sucker growth (Eliasson 1971; Hicks 1972; Schier 1972). Cytokinins, on the other hand, are produced at the root tips and are transported towards the stem, and are known to initiate root suckering on many plants by counteracting the activity of auxin (Peterson 1975; Hicks 1972; Thimann 1977). Therefore, mortality or removal of the above ground portion of a tree will stop auxin production, causing an increase in the cytokinin:auxin ratio, initiating root sucker growth (Winton 1968; Wolter 1968). In stands less than 25 years old, removal of stems can also produce stump sprouts; however, this is not seen as a primary source of reproduction in aspen (Heeney et al. 1980). Younger trees are able to produce stump sprouts because they possess dormant buds around the stump collar, but as a tree matures these buds are lost (Tredici 2001). Dormant collar buds allow young trees to sprout to survive under a variety of stressful conditions (e.g. herbivory, site exposure, pathogens, and desiccation) (Tredici 2001). Generally, species that produce stump sprouts only have a single stump sprout survive to maturity (Keim et al. 2006; Lockhart and Chambers 2007).

The response of aspen root suckering to disturbances in natural stands is substantial, with regeneration one year post fire reaching as high as 240,000 stems ha^{-1} (Wang 2003) and over 69,000 stems ha^{-1} being regenerated one year after harvest (Mundell et al. 2008). Suckers also undergo self-thinning almost immediately after establishment with high mortality of root suckers. Several long-term studies have shown that regardless of initial sucker abundance, after about 5 years of self-thinning stands generally have similar long-term average densities of around 20,000 stems ha^{-1} (Steneker 1974; Bella 1986; Perala 1984).

The role of tree height in relation to the number of root suckers produced after disturbance has not been directly studied. However, we can assume that taller trees have more extensive root systems that would allow them to produce more root suckers and stump sprouts. King and Landhäusser (2018) found that large diameter (DBH = 6.4 cm) aspen trees had significantly larger root systems compared to small diameter (DBH = 4.4 cm) aspen trees, and as a result produced more root suckers. Larger root segments can also store greater amounts of carbohydrates, which is a limiting factor for suckering (Wachowski et al. 2014). Root carbohydrate reserves are relied upon for maintenance (respiration) of surviving root tissue and the regeneration of new stem, leaf, and root tissue until the suckers are able to produce enough energy for these processes on their own (Lambers et al. 2002).

In terms of tree and stand age, suckering has been observed in stands of varying ages (20–150 years); with older trees (≥ 80 years) often producing fewer suckers than younger trees because their root systems are typically beginning to decay (Maini 1968; Peterson and Peterson 1992); although some young stands have also been found to have high amounts of root decay (DesRochers and Lieffers 2001). There has been some evidence of trees < 20 years old producing root suckers. Horton and Maini (1964) observed root suckering in a 5 year old clonal aspen stand that had been slashed; while King and Landhäusser (2018) observed root suckering in planted aspen seedlings that were 8 and 12 years old. However, root suckering potential of young aspen seedlings that established naturally has not been studied.

Since aspen more commonly reproduce vegetatively via root suckers, they are considered a clonal species, and are studied as such. However, some research has shown that aspen are more frequently revegetating disturbed areas sexually via seed than previously thought (Stefani et al. 2018; Krasnow and Stephens 2015). Disturbed areas, such as mine land reclamation sites, provide ideal conditions for aspen seeds to germinate, having exposed soil and less competition for resources such as water, nutrients, and light. These conditions are not often found in natural forests, even after disturbance, which is why seedling-origin aspen have been understudied (Jelinski and Cheliak 1992). Disturbance could affect seedling-origin aspen differently than clonal aspen. Removing the stem of a seedling could cause a greater response from the root system because it is dependent on the apical dominance of a single stem; whereas cutting a single stem that belongs to a clonal root system would have much smaller effects on apical dominance. On the other hand, seedlings also have much smaller root systems, and could suffer after a disturbance because of smaller carbohydrate reserves. King and Landhäusser (2018) studied sprouting response to disturbance in planted seedlings and suggested that the response of these seedling-origin stands over a wider range of site conditions represents a critical knowledge gap.

Soil properties, including temperature, moisture, pH and nutrients, can also effect root suckering in aspen (Frey et al. 2003). Warmer soil temperatures (12 °C and above) have been considered to be the most important factor for sucker initiation (Fraser et al. 2002) as higher soil temperatures degrades auxin and promotes cytokinin synthesis, stimulating sucker initiation (Schier et al. 1985; Hungerford 1988). The effects of soil nutrients, pH, and moisture on sucker initiation have not received as much attention (Frey et al. 2003) but it can be hypothesized that increases of nutrient availability and/or pH that is commonly seen after wildfires stimulates the initiation of root suckering (Frey et al. 2003). Both very dry and water-saturated growing conditions have been found to reduce sucker initiation (Horton and Maini 1964; Schier et al. 1985). Sucker initiation on water-saturated sites is limited due to a lack of oxygen, and excess water promotes early root mortality and decay (Frey et al. 2003). Vegetative competition, especially from grasses, can also significantly reduce suckering in aspen (Landhäusser and Lieffers 1998). Not only is there competition for resources, but a thick litter layer of grass can insulate the ground, reducing soil temperatures (Hogg and Lieffers 1991; Landhäusser and Lieffers 1998).

The two most commonly used soils in oil sands mine reclamation are forest floor mineral mix (FFMM) and peat mineral mix (PMM). These soils have very different properties that could influence aspen suckering and sprouting (Howell et al. 2016; Tremblay 2017). It has been shown that natural aspen seedlings establish and grow faster on PMM than on FFMM because of its high water holding capacity (Pinno and Errington 2015; Tremblay

2017). Therefore, the trees on PMM should be more robust and should be capable of producing greater amounts of suckers and stump sprouts. Trees growing on PMM should also have an advantage because there is generally less understory competition, particularly from grass and forb species, found on these sites. PMM also warms faster in the spring compared to FFMM (Tremblay 2017), likely due to less vegetation, which should allow greater sucker initiation on PMM. Nutrient availability and water holding capacity are also greater on PMM (Howell et al. 2016), creating more ideal conditions for sprout initiation. Overall, PMM seems to be better suited for sucker and sprout initiation compared to FFMM.

In Alberta, reclamation of an oil sands mine requires the re-establishment of a self-sustaining ecosystem, consisting of native species (Alberta Environment and Sustainable Resource Development 2013). In order to meet this goal, various criterion need to be met including that reclaimed ecosystems display characteristics of resilience to disturbances. However, there are many questions surrounding the ability of young, seedling-origin aspen stands to regenerate after disturbance, and whether stem densities at the stand level will be sufficient to recover the forest (Macdonald et al. 2012). To the best of our knowledge, suckering of seedling origin aspen in young stands has not previously been studied. Determining the sprouting response of aspen after a disturbance on a reclamation site is a good first step when determining the resilience of a constructed ecosystem. Therefore, the overarching objective of this study is to determine if young aspen, which established on a reclamation site via seed, are capable of showing resiliency. Specifically, the two research questions asked in this study include:

1. Does tree size or environmental conditions (soil type and competition) have an effect on whether or not root suckers and stump sprouts are initiated?
2. If root suckers are initiated, what factors affect abundance of root suckers?

Methods

Study area

This study took place on an oil sands mine located approximately 75 km northwest of Fort McMurray, Alberta, Canada (57°20′N, 111°49′W) in the Central Mixedwood Natural Subregion (Downing and Pettapiece 2006). The natural forest in the area is characterized by trembling aspen dominated stands mixed with balsam poplar (*Populus balsamifera* L.), white birch (*Betula papyrifera* Marsh.), white spruce [*Picea glauca* (Moensch) Voss], and balsam fir [*Abies balsamea* (L.) Mill.]. Black spruce (*Picea mariana* Mill.) bogs and fens are also prevalent on the landscape. Upland soils are predominantly Gray Luvisols, while lowland soils are Organic (Soil Classification Working Group 1998); both of these soils are commonly used in land reclamation as the basis of common reclamation soils (see below). The average temperature of the warmest month is 17.1 °C and the average temperature of the coldest month is −17.4 °C, mean annual precipitation is 419 mm (Fort McMurray 1981–2010 Environment Canada climate normal).

The reclamation area used in this study is an 88.6 ha overburden dump, constructed in 2011, and capped with two different reclamation cover soils, forest floor mineral mix (FFMM) and peat mineral mix (PMM). Soil types were placed in four blocks (2 blocks of each soil type) of approximately 22 ha each. FFMM is derived from upland forest soils, mainly Gray Luvisols mentioned above, and consists of the surface organic layers (LFH) and the underlying mineral soil (A and B horizons) salvaged to a maximum total depth of 30 cm. PMM is derived from Organic soils and consists of peat and underlying mineral soil salvaged at an approximate 60:40 ratio of peat:mineral (Errington and Pinno 2016). Many soil properties differ between these two soil types (Table 1). Both FFMM and PMM soils used on the reclamation area were salvaged in the winter of 2010–2011 and directly placed to a depth of 0.5 m over 1.5 m of suitable (non-saline) subsoil. In the first growing season a cover crop of annual barley (*Hordeum vulgare*) and white spruce seedlings were planted at a density of 1500 seedlings per hectare. Deciduous trees, such as trembling aspen and balsam poplar established naturally via seed from surrounding forests, the closest of which is located 300 m northeast of the reclamation area (Pinno and Errington 2015). Aspen has established on site at an density of 3455 stems ha^{-1} on FFMM and 9485 stems ha^{-1} on PMM (Tremblay 2017) by age 5 with 96% of the aspen originating from sexual reproduction (seedling origin), not from vegetative reproduction (Stefani et al. 2018).

Vegetation cover was different between soil types (Table 1) with average total vegetation cover on FFMM of 72% compared to 59% on PMM ($p = 0.02$). There was also significantly higher tree ($p < 0.01$) and invasive forb ($p = 0.02$) cover on PMM, while FFMM had significantly higher shrub ($p < 0.01$), native forb ($p = 0.02$), grass ($p < 0.01$), herbaceous (grass, native forb, and invasive forb cover combined; $p < 0.01$), and total ($p = 0.02$) cover. For more information about this study site please see: Pinno and Errington (2015), Tremblay (2017), and Stefani et al. (2018). These studies looked at aspen seedling establishment, aspen growth across soil types, and the effects of soil type on aspen and their associated below ground microbiome on this same study site.

Field methods

To examine aspen regeneration via root suckers in different reclamation soils and competition levels, 87 tree centered plots were established across the site in the summer of 2017, using a stratified random sampling design. Forty-four plots were established in the PMM soil treatments, and 43 plots were established in the FFMM soil treatments. Plots represented a gradient of aspen tree sizes and competing vegetation across the treatment types. Twenty-nine of the selected trees were between 100 and 199 cm tall, 30 between 200 and 299 cm tall, and 28 > 300 cm tall. Each selected tree was cut down in May of 2017 at 2.5 cm above the ground. Trees were cut in May to mimic spring wildfires that are common in the region due to readily available dry fuel (Kochtubajda et al. 2017). A tree cookie was also taken from each cut aspen to confirm tree age; all cut trees were 6 years old. In August of 2017, a 3.99 m radius (50 m^2) plot was established around each cut aspen in order to count the number of root suckers and stump sprouts produced by each tree. Root suckers were defined as sprouts originating from roots and stump sprouts were defined as sprouts originating from the stump collar of the tree. Excavated 8 m tall planted aspen had root systems with a radius of 5 m (King and Landhäusser 2018); therefore our natural seed origin aspen with a maximum height of 4.6 m would have comparable root systems. Root suckers were easily identifiable, as they had larger leaves and greener stems compared to seed-origin aspen of similar size. Overall plant composition was determined within each 3.99 m radius plot. Percent of each functional group present was evaluated: trees, shrubs, invasive forbs, native forbs, grass, and bryophytes. At each plot, one sucker was randomly excavated to confirm origin and the root depth and diameter on the proximal side of origin was measured.

Table 1 Basic soil characteristics of reclamation soils, including total carbon (TC), total nitrogen (TN), pH, bulk density (Db) at 5–10 cm, volumetric water content (VWC) at 12 cm, and temperature; reporting means with standard error in brackets (n = 6)

	TC (%)	TN (%)	pH	D_b (g cm^{-3})	VWC (%)	June temperature (°C)	Grass (%)	Invasive forb (%)	Native forb (%)	Shrub (%)	Tree (%)	Bryo-phyte (%)
FFMM	2.61 (0.29)	0.12 (0.01)	7.59 (0.12)	1.18 (0.03)	19.70 (1.95)	13.1	34	8	16	9	5	0
PMM	8.07 (1.98)	0.25 (0.07)	6.01 (0.52)	0.94 (0.20)	35.87 (2.40)	15.2	10	19	10	3	13	2

Soil data is taken from previous studies performed on the same reclamation site (Howell et al. 2016; Tremblay 2017). Average percent cover of vegetation functional groups from data collected in this study (n = 87)

Data analysis

All data was analyzed using R software (R Core Team 2018, Boston, MA). Since the response variables of number of root suckers produced and number of stump sprouts produced were over-dispersed count data and could not be transformed, negative binomial models were used. Data analyses for root suckers and stump sprouts were performed separately; however both response variables underwent the same statistical testing. First, to determine the effects of the site selector variables, soil type (FFMM and PMM) and tree height classes, a negative binomial model was used (*glm.nb* command in R 3.1.4; R 2018) with soil and height classes as the only two explanatory variables and the number of root suckers produced as the response variable. We then ran an analysis of deviance (*anova* command in R 3.1.4; R 2018). Height was chosen over stump diameter to represent tree size classes because it created stronger models and was consistently the more significant variable.

Secondly, logistic models (*glm* command in R 3.1.4; R 2018) were used to determine what explanatory variables (soil type, tree height, and vegetation cover) had an effect on the probability of a cut stem producing at least one sucker. To do this, count data was transformed into binary presence/absence data. Models were selected based on the lowest AIC score. Odds ratios for each significant variable were calculated by transforming the beta value; e^{β}. Pseudo R^2 values were calculated using the *rms* package (Version 5.1-1; Harrell 2017).

Thirdly, zero-truncated negative binomial models were used to determine what explanatory variables had an effect on the abundance of root suckers produced by trees that showed sucker initiation. Beta values were transformed to integer values, 10^{β}, to more easily understand the magnitude of effects. These zero-truncated models were not carried out on the stump sprout data because only one stump sprout is expected to survive. To determine threshold values for the significant variables found in our models regression tree analyses were performed using the *mvpart* package (Version 1.1-1; Therneau and Atkinson 2004).

Lastly, to understand the differences in ground cover between the two different soil types a MANOVA was performed on the vegetation cover data, by functional group (trees, shrubs, invasive forbs, native forbs, grasses). Tree and shrub cover were added up to calculate woody cover; invasive forbs, native forbs, and grasses were added up to calculate herbaceous cover. All functional groups were added together to calculate total cover at a plot. Here vegetation data were log transformed in order to meet the assumption of data normality.

Results

Responses in aspen root suckering was highly variable, ranging from 0 to 47 stems produced in PMM and 0 to 7 stems produced in FFMM for each cut tree. Of the 87 trees cut, 63% produced at least a single root sucker, 86% on PMM, and 40% on FFMM. Sucker producing roots were found at depths ranging from 0.5 to 6 cm below the soil surface, the mean depth was 1.6 cm with no difference between soil types ($p = 0.95$). On both soil types large trees had larger sucker producing roots (0.95 cm in diameter). However, medium and small trees on PMM had larger roots compared to the medium

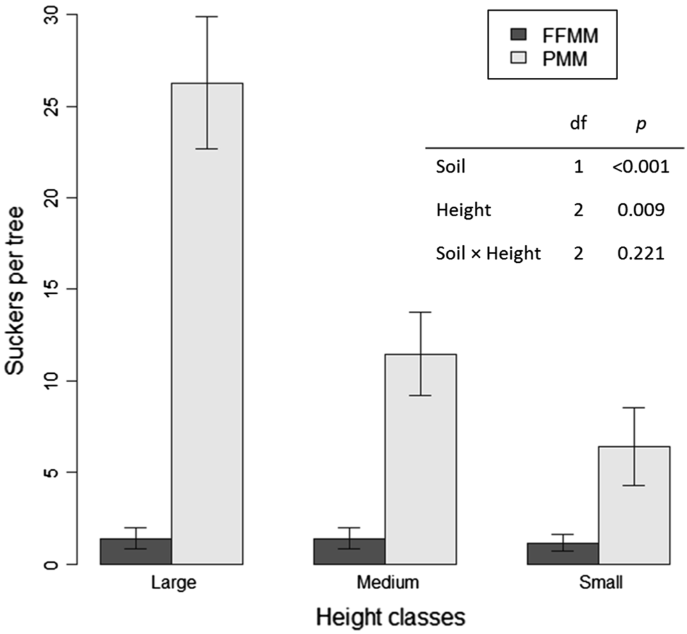

Fig. 1 The average number of suckers produced (stems/ha) by large (> 300 cm), medium (200–299 cm), and small (100–199 cm) trees on the different soil types

Table 2 Logistic regression model parameters of soil, height with increments of 1 cm, and total cover with increments of 1% relating to the presence/absence of suckers produced by aspen trees

Variable	Odds ratio	β	SE	p
Soil—PMM	7.75	2.047	0.608	< 0.001
Height	1.01	0.008	0.004	0.035
Total Cover	0.96	− 0.041	0.014	0.004
Pseudo $R^2 = 0.402$				

Odds ratio pertains to how much more likely a tree is to produce at least one root sucker with each increment increase of a parameter, there were no significant interactions

and small trees on FFMM. On PMM, average root size was 0.60 cm for medium trees and 0.71 cm for small trees, while on FFMM medium trees had a root size of 0.45 cm and 0.48 cm for small trees.

There was a significant difference in the number of root suckers produced on each soil type ($p < 0.01$), with more suckers being produced on peat, compared to forest floor ($p < 0.01$) (Fig. 1). On PMM, large trees (> 3 m tall) produced significantly more suckers than small trees (1–1.99 m tall; $p < 0.01$), while there was no significant difference in the amount of suckers produced between large trees and medium trees (2–2.99 m tall; $p = 0.06$) or medium and small trees ($p = 0.27$). On FFMM, there were no significant differences found between tree height and the number of suckers produced ($p = 0.94$). Finally, we found no significant interaction between soil type and tree height.

The probability of a cut stem producing at least one root sucker was significantly influenced by soil type, tree height, and total competition. The probability of root sucker

Table 3 Zero-truncated negative binomial model parameters of soil, height with increments of 1 cm, and total cover with increments of 1% relating to the abundance of suckers produced by aspen trees, there were no significant interactions

Variable	β	SE	*p*
Soil—PMM	1.433	0.221	< 0.001
Height	0.005	0.001	< 0.001
Total Cover	−0.014	0.004	< 0.001
Pseudo $R^2 = 0.583$			

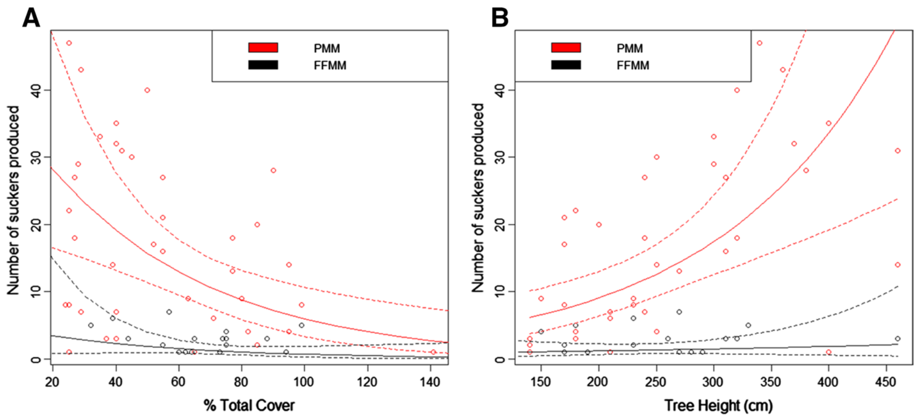

Fig. 2 **a** Observed number of suckers produced over a range of total ground cover (%) on both soil types with a fitted zero-truncated negative binomial GLM curve (solid line) and 95% confidence bands (dotted lines). **b** Observed number of suckers produced over a range of tree heights (cm) on both soil types with a fitted zero-truncated negative binomial GLM curve (solid line) and 95% confidence bands (dotted lines)

initiation was 7.8 times greater on PMM compared to FFMM (Odd ratio in Table 2). Taller trees also had a higher probability of producing root suckers; with each 10 cm increment increase in height the probability of a tree producing a sucker increases by 10%. Vegetation competition reduced suckering; with each 10% decrease in surrounding total cover increasing odds of suckering by 10%. Total cover was used instead of each vegetation functional group to simplify models because all functional groups were found to have significant negative effects on sucker production. Models made with total cover also had a better fit compared to models using all the functional groups. Since total vegetation cover was used some sites have > 100% cover, this is due to overlap of the different functional groups. There were no significant interactions found between variables in this model.

When suckers were present, the same three factors of soil type, tree height, and total competition had an effect on sucker abundance (Table 3). On average, trees growing on PMM produced 27 more root suckers than a similar sized tree cut on FFMM. Regardless of soil type, larger trees also tended to produce more suckers, with each increment increase of 10 cm in tree height producing 10 more suckers (Fig. 2). Competition decreased sucker abundance with each increment increase of 10% in total cover there are 10 fewer suckers produced (Fig. 2).

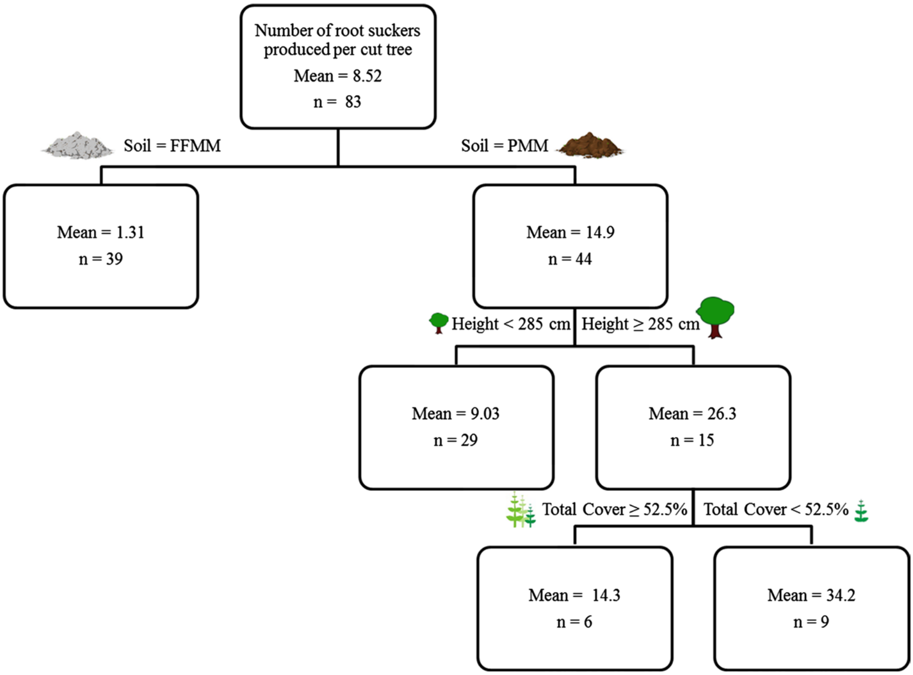

Fig. 3 Regression tree analysis showing the conditions needed for different levels of root suckering, the most favorable conditions are on the far right and the least favorable are on the far left

There are many thresholds that create more (far right side) or less (far left side) optimal aspen root suckering conditions (Fig. 3). Soil type creates the first threshold, with mean suckers produced on FFMM being only 1.31, providing the least optimal conditions. On PMM soil, tree height was the most important factor for abundant root suckering. Trees 285 cm tall or greater produced the most root suckers. Total understory vegetation cover also affects the abundance of suckers, with trees having less than 52.5% surrounding competition producing the most root suckers. The most optimal conditions for producing root suckers, of a tree growing on PMM being more than 285 cm tall and having less than 52.5% of total competition, was rare in our sampling design with only 9 trees meeting these conditions.

Stump sprouting also varied greatly, ranging from 0 to 11 produced on FFMM and 0 to 42 produced on PMM per cut stem. 89% of the trees cut on PMM, and 72% of trees cut on FFMM produced stump sprouts. However, neither soil type ($p=0.66$) nor tree height ($p=0.37$) had a significant effect on whether or not stump sprouts were produced. Competing vegetation, however, did reduce sprouting with the probability of a cut aspen to produce a stump sprout dropping by 5% per each 10% increment increase in tree cover ($p=0.01$; Table 4). Any cut tree with ≥40% surrounding tree cover did not produce any stump sprouts. Tree cover, in this case, was the only vegetation cover type to have an effect on stump sprout initiation, therefore total vegetation cover was not used. Consequently, the best fit model only used tree percent cover. The model also showed a significant interaction between soil type and tree cover, showing that on PMM soil suckers were 1.7 times more affected by tree cover ($p=0.04$).

Table 4 Logistic regression model parameters of soil, height with increments of 1 cm, and total cover with increments of 1% relating to the presence/absence of stump sprouts produced by aspen trees, likelihood ratio pertains to how much more likely a tree is to produce at least one stump sprout with each increment increase of a parameter

Variable	Odds ratio	β	SE	*p*
Tree cover	0.54	−0.623	0.254	0.014
Soil—PMM: tree cover	1.69	0.525	0.251	0.036
Pseudo $R^2 = 0.444$				

Discussion and conclusions

Aspen that have established on a reclamation area via seed responded readily to an above ground disturbance, through both root suckering and stump sprouting. Soil type, total plant cover, and tree height all had significant effects when it came to both root sucker initiation and abundance. Soil type had one of the largest effects on root suckering with greater sucker initiation and abundance on PMM. However, soil type also directly affects competition and tree size, which may magnify its significance (Mackenzie and Naeth 2010; Pinno and Errington 2015; Tremblay 2017). It is known that understory vegetation establishes much more readily on FFMM compared to PMM (Mackenzie and Naeth 2010; Naeth et al. 2013), and our results showed the same (72% total cover on FFMM and 59% total cover on PMM). Previous studies have shown that aspen establishment and growth is significantly greater on PMM compared to FFMM (Pinno and Errington 2015; Tremblay 2017) with less competition from other vegetation thought to be one of the main reasons for this. Higher amounts of competition from surrounding vegetation also had a large negative effect on root sucker initiation and abundance, with trees growing on PMM being 7.8 times more likely to initiate suckers and producing approximately 27 more suckers on average compared to trees growing on FFMM. Landhäusser et al. (2007) saw similar results with a 30% decrease in aspen root sucker emergence with the presence of *Calamagrostis canadensis* ([Michx.] Beauv.), likely due to the roots from the competing vegetation acting as a barrier to suckers as well as decreased soil temperatures from leaf litter insulating the soil. Pinno and Errington (2015) found that at vegetation covers greater than 51% aspen seedling establishment was reduced. This is similar to our results where competition levels greater than 52.5% reduced root sucker abundance. These results could indicate that a competition level of around 50% is the threshold for optimal aspen establishment either by seed or sucker.

Tree size was also very important for sucker initiation and abundance. We found that taller trees tended to produce more root suckers, especially on PMM. Larger trees should produce more root suckers, as they have larger root systems. King and Landhäusser (2018) observed that larger planted aspen seedlings (DBH of 6.4 ± 5.4 cm) had larger root systems and produced more root suckers compared to smaller planted seedlings (DBH of 4.4 ± 0.7 cm), matching our findings. Most aspen suckers originate from roots that are 0.5–2.5 cm in diameter, and are within the first 12 cm of the soil surface (Horton and Maini 1964; DesRochers and Lieffers 2001; Wachowski et al. 2014). All our sucker producing trees had roots producing suckers within the top 6 cm of soil across both soil types; smaller trees did have smaller diameter roots, which could explain why overall small trees produced fewer root suckers. On FFMM, we found that the sucker producing roots of small and medium trees were smaller than 0.5 cm on average. As suckers grow, they deposit wood onto the parent root meaning these roots were likely even smaller at the time of disturbance (DesRochers and Lieffers 2001). Therefore, small and medium sized trees on FFMM likely produce fewer sprouts because the average sucker producing root size is outside of the optimum range.

Soil properties such as temperature, moisture, and nutrients could have also played a small role in root sucker initiation and abundance. PMM soil on our site does warm up as fast in the spring compared to FFMM (Table 1), likely due to less leaf litter insulating the soil. Warmer soil temperatures have been considered the most important environmental factor for controlling sucker initiation, as high temperatures facilitate auxin degradation and promote cytokinin synthesis (Schier et al. 1985; Hungerford 1988). PMM on our site also has a greater water holding capacity compared to FFMM. Poor soil water holding capacity has been linked to an increase in aspen sucker mortality, as it reduces the trees capacity to withstand dry spells (Jacobi et al. 1998). Greater amounts of nutrients are also found in PMM due to its high organic matter content (Howell et al. 2016). The effects of soil nutrients on root sucker initiation have been understudied (Frey et al. 2003); however nutrient rich PMM does promote more robust trees compared to FFMM (Tremblay 2017). More robust trees have larger root systems and greater carbohydrate stores, which would allow them to produce more suckers (King and Landhäusser 2018; Wachowski et al. 2014). Further research should be conducted to determine the full effects of soil properties on root suckering of aspen growing on reclamation soils.

Stump sprouting was common among all soil and tree size classes (84% of all trees) but was reduced by surrounding tree cover, particularly on PMM. It is unclear why only competition from surrounding trees, and no other vegetation, had an effect on sprout initiation. However, Tredici (2001) suggests that stump sprouts require very high amounts of light in order to develop into effective replacement stems. Therefore, it could be possible that the shading impacts caused by high levels of tree cover had an effect on sprout initiation. Shading from smaller understory vegetation may not have had as great as an effect on sprout initiation because the sprouts originate slightly above ground level, keeping them above small plants. Since the disturbance took place during the spring, many understory species would not have been well enough established to be significant light competitors. Given the size of the trees that underwent disturbance (bole diameters ranging from 1 to 6 cm), it was expected that they would produce stump sprouts. Previous research has found that all temperate angiosperm trees will sprout in high percentages from stumps between 5 and 15 cm in diameter (Tredici 2001).

Overall, the aspen seedlings growing on this reclamation area were resilient to disturbance with 89% of the trees cut responding by either producing root suckers, stump sprouts, or both. Our disturbance treatment, however, was very different from fire, the most likely and most destructive disturbance to affect a reclamation area. It is difficult to say how these trees would respond if the reclamation area were to burn. Fire would destroy the competing understory vegetation that interferes with root sucker initiation and could add beneficial nutrients to the soil, promoting root suckering (Frey et al. 2003). On the other hand, fire could consume the sucker producing roots found within the first 6 cm of the soil, severely hampering root sucker production. Although our disturbance treatment was different from common disturbances found in the boreal, this study still identified important drivers that can affect root sucker regeneration in seedling origin aspen growing on reclamation areas. As this study focused on regeneration potential of aspen seedlings immediately following disturbance, further studies are needed to identify the vigor and survival rates of aspen suckers on reclaimed areas over multiple years. This is an important next step in understanding the resiliency of aspen growing on a reclaimed boreal oil sands site.

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