Plant Community Dynamics on Soil Islands in Oil Sands Reclamation

by

Kaitlyn Elizabeth Trepanier

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in

Forest Biology and Management

Department of Renewable Resources
University of Alberta

Abstract

Oil sands mining is a significant disturbance in the Canadian boreal forest. One objective for reclamation after mining is to create a self-sustaining ecosystem, which includes establishing a native plant community. For this thesis, study one evaluates the different plant assembly mechanisms, including seed bank, seed rain, vegetative expansion, and competition. Study two determines the optimal size, shape, and configuration of soil patches to increase plant richness on a new reclamation design known as “Islands.” This technique integrates islands of higher diversity forest floor mineral mix (FFMM) within a matrix of lower diversity peat mineral mix (PMM). Plant communities were sampled after Year 2 and Year 5, along with assembly mechanisms. The initial plant community had greater cover and diversity on FFMM compared to PMM but was dominated by non-native forbs. Initial plant cover and diversity differences were linked to the seed bank, which had 5x more seeds in the FFMM. Over time, the plant community shifted to native species and by Year 5 had a total cover of 40% in both soil types. The similarity in the plant community development over time was due to species originating from seed rain and biotic dispersal. Over time native species originating from the seed bank are also contributing to the community due to late germination. Seed rain was similar across both soil because a large portion of the species were wind-dispersed early-successional species**.** Biotic-dispersed late-successional species were also established on both soil types by Year 5, potentially due to an increase of favorable habitat conditions over time. There is evidence of native forb vegetative expansion from the FFMM into the surrounding PMM up to 2 m. Finally, competition emerges as a potential factor with a decrease in non-native forbs associated with an increase in total vegetative cover. For study two, there was no optimal size or shape of islands that allows for increased species richness or expansion. For example, 10 islands ranging in size from 541 to

7348 m^2 hall had a richness of 63 species. Overall, multiple factors are involved in structuring plant communities on reclamation sites, but it appears that there is a general convergence in the plant communities between soil types over time.

Preface

This study was initiated by Ruth Errington and Bradley Pinno in 2015 and overtaken by myself in May of 2019. Ruth Errington collected data in 2015, 2016, and by myself in 2019. The data analysis and interpretion was completed by myself. I was responsible for the research design and data collection in 2019, analysis, and manuscript composition. Brad Pinno was involved with the research design, contributed to the analysis, and manuscript edits.

The following thesis, "Plant Community Dynamics on Soil Islands in Oil Sands Reclamation." was presented in a poster presentation in 2019 in Montana, USA at the American Society of Mining and Reclamation (ASMR) Annual Meeting and in 2020 at the University of Alberta at the Forestry Industry Lecture. No part of this thesis has been previously published.

Acknowledgments

The completion of my graduate work and thesis would not have been possible without the help and support from my family, friends, colleagues, and mentors. I would like to first thank and extend my gratitude to my supervisor, Dr. Bradley Pinno. Thank you for accepting me as a graduate student, guiding me through this project, and allowing me to be the lead lab coordinator and organize the logistics for multiple projects. You have taught me to be a stronger researcher in all aspects. I would also like to thank Charles Nock and my external examiner Ellen Macdonald for being on my committee and putting in your time and effort.

I would also like to thank my fellow graduate students, especially my Silviculture Laboratory group. You helped me in one way or another, whether it was offering support, encouragement, providing feedback on presentations, and reviewing my written work. Special thanks to Sanatan Das Gupta, Jennifer Buss, Stephanie Jean, and Laureen Echiverri for your continued support with data analysis.

Support and funding for this research study were provided by Canadian Natural Resource Limited, Natural Resources Canada, and the Alberta Conservation Association. Laboratory work in 2015 and 2016 was completed by the Canadian Natural Resource team lead by Ruth Errington. In 2019, Dani Degenhardt from Natural Resource Canada provided help and resources to make my project possible, thank you! Field and laboratory work were completed with the help of Brea Burton, Matthew Anderson, and Sofia Toledo. Thank you!

Lastly, thank you to my family and friends for your support and encouragement to complete this fantastic opportunity over the last two years. This would not have been possible without you.

Table of Contents

Abstract ii
Preface iv
Acknowledgments v
List of Tables vii
Table of Figures viii
1.1 Introduction 1
    1.1.1 Plant community dynamics 1
    1.1.2 Boreal forest region 1
    1.1.3 Surface Mine Reclamation 2
    1.1.4 Reclamation 2
    1.1.5 Plant Assembly 4
    1.1.6 Island Reclamation 11
    1.1.7 Research Questions 13
1.2 Methods 14
    1.2.1 Research Area 14
    1.2.2 Field Methods 15
        1.2.2.1 Study one 15
        1.2.2.2 Study two 17
    1.2.3 Statistical Methods 18
1.3 Results 23
    1.3.1 Plant community composition 23
    1.3.2 Mechanisms causing community change over time 24
    1.3.3 FFMM islands 29
1.4 Discussion 29
1.5 Conclusion 40
    1.5.1 Research Summary 40
    1.5.2 Research Applications 42
    1.5.3 Study Limitations and Future Research 43
Literature Cited 71
Appendix 81
    A.1 Soil Properties 81
    A. 2 Supplemental Material 83

List of Tables

Table 1. Soil characteristics for FFMM and PMM. Values are means (standard error)............... 46

Table 2. PermANOVA results with mean values (standard errors) for number of seedlings germinated from the seed bank functional groups comparing FFMM and PMM with depths of 0-5 cm and 5-10 cm... 47

Table 3. Total cover (%) of species originating from each assembly mechanism (seed bank, seed rain, and other dispersal), leaf litter, and bare soil. Values are averages (standard error) for each soil type and year. Total proportion of cover (%) are separated by year and soil type for each assembly mechanism. 48

Table 4. Total cover (%) of each functional group (native forbs, graminoids, non-native forbs, shrubs, and trees) originating from the assembly mechanism (seed bank, seed rain, and biotic dispersal). Values are averages (standard error) for each soil type and year. Total proportion of cover (%) are separated by year and soil type for each assembly mechanism. 49

Table 5. PermANOVA comparing counts (standard error) of seedlings emerging from the seed rain samples for all species and by functional groups (native forbs, non-native forbs, and graminoids), and dispersal mechanisms of native forbs (gravity, vegetative, and wind)............ 50

Table 6. RTEI results were testing the percent cover of functional groups (graminoid, non-native forbs, and native forbs), dispersal mechanisms for native forbs (wind, gravity, and vegetative), and an example species for vegetative dispersal (Fragaria virginiana) in FFMM and PMM 0-4, 10, 15, and 20 m. Significant values were percentiles, the bolded ones are considered significantly different between the FFMM and PMM locations. p < 2.5 (significantly less than the FFMM) and p > 97.5 (significantly higher than the reference). 51

Table 7. Species-area curve model fitting for functional groups (graminoid, non-native forb, shrub, and native forb) showing AICc, weight, and adjusted r² for each curve type. Curve models shown below have passed validation checks and are ranked based on the best fit. Curve types: Loga= logarithmic, koba= Kobayashi, asymp= asymptotic, negexpo= Negative exponential, weibull= Cumulative Weibull 3 par, mmf= Morgan-Mercer-Flodin. 52

Table of Figures

Fig. 1. Diagram of reclamation sites plant assembly over time and soil type. In 2015 the seed bank and seed rain is expected to play a large role on the FFMM with reduced on PMM. By Year 2 most of the cover on the FFMM will be from the seed bank and seed rain compared to PMM will mainly be influenced by seed rain. Over time we expect to see competition to play a role in structuring the plant community on both soil types. By 2019 we expect species that established from the FFMM seed bank to expand into the PMM with continual addition from seed rain and biotic dispersal to develop trees and woody species on the PMM. As we move into the future there is a convergence of both the overstory and understory.. 53

Fig. 2. Map of the 9.5-hectare overburden island reclamation site on an oil sand mine Northwest of Fort McMurray, Alberta Canada. The points represent transect locations.............................. 54

Fig. 3. Transect with 1x1m plant quadrats extending 5 m into the FFMM and 20 m into the PMM at each FFMM island. Black boxes are soil collection locations, light grey boxes are PMM 1x1m plant quadrats, and dark grey boxes are FFMM 1x1m plant quadrats... 55

Fig. 4. Average cover of different functional groups (a=native forb, b=non-native forb, c=graminoid, d=total shrub, e=tree, and f=total cover) in Year 2 (n=10) and Year 5 (n=35) in FFMM and PMM. Significant letters are based on permANOVA results showing the interaction over time and between soil types. Values are means with standard error bars............................ 56

Fig. 5. 2D NMDS of plant species cover a) Year 2 and b) Year 5. The variance explained by the two axes was a) 32.4% with a minimum stress value of 0.331, b) 31.7% with a minimum stress value of 0.428. The vectors represent the 15 most frequent plant species found within the site at Year 2 and Year 5. 57

Fig. 6. Average seedling count for functional groups (forbs, graminoid, and non-native forbs) at depths of 0-5 cm and 5-10 cm for FFMM and PMM in the seed bank. Values are means with standard error bars.. 58

Fig. 7. Total cover from species originating from the seed bank, seed rain, and biotic dispersal, bare soil, and leaf litter in Year 2 and Year 5 in both soil types.. 59

Fig. 8. The total proportion of cover (%) in Year 2 and Year 5 on FFMM and PMMM. The proportions are given for species originating from different assembly mechanisms (seed bank, seed rain, and other dispersal) and the functional groups (native forbs, non-native forbs, graminoids, shrubs, and trees) present within each mechanism. 60

Fig. 9. Seedling count of seed rain for functional groups (native forbs, non-native forbs, and graminoids) in Year 1 for FFMM and PMM (n=14 for each soil type). 61

Fig. 10. Average cover (%) of species by functional group (a=native forb, b=non-native forb, and c=graminoid) at 0 - 4, 10, 15, and 20 m distances into the PMM (n=35 transects) from the FFMM (average of 5 plots per transects). Standard error bars included and significant letters are based on RTEI results 62

Fig. 11. The average cover (%) (standard error) for native forbs by their different dispersal mechanisms: a) gravity, b) vegetative, c) wind, and d) *Fragaria virginiana* (as an example of a vegetatively reproducing species) at 0 - 4, 10, 15, and 20 m distances into the PMM (n=35 transects) from the FFMM (average of 5 plots per transect). Significant letters are based on RTEI results. 63

Fig. 12. Pearson's correlation comparing native forb cover (%) to non-native forb cover (%) in FFMM and PMM. a) Year 2 (df=9) and b) Year 5 (df=34). 64

Fig. 13. Pearson's correlation comparing graminoid cover (%) to native forb cover (%) in FFMM and PMM. a) Year 2 (df=9) and b) Year 5 (df=34). 65

Fig. 14. Pearson's correlation comparing non-native forb cover (%) to graminoid forb cover (%) in FFMM and PMM. a) Year 2 (df=9) and b) Year 5 (df=34). 66

Fig. 15. Species area curve of 26 FFMM islands for: a) native forb species (Asymptotic curve r^2=0.28), b) non-native forb species (Power curve r^2=0.06), c) graminoid species (Power curve r^2=0.03), and d) shrub species richness (Kobayashi curve r^2=0. 06). 67

Fig. 16. Pearson's correlation between species richness and the perimeter: area ratios of 26 FFMM islands for native forb species, non-native forb, graminoid, and shrub species richness (df= 25). 68

Fig. 17. Percent cover of native forb species that use vegetative dispersal at locations 0, 1, and 2 m away from FFMM Islands into adjacent PMM; islands are ordered by area (m^2). 69

Fig. 18. Percent cover of native forb species that use vegetative dispersal at locations 0, 1, and 2 m into the PMM from the FFMM at each island; islands ordered by perimeter-area ratio. 70

1.1 Introduction

1.1.1 Plant community dynamics

Plant communities play an integral role in the ecological function of a forest. When plant diversity is high, it allows for improved recovery and stability of an ecosystem (De Grandpré and Bergeron, 1997; Tilman, 1996). These communities are significant components and drivers for diversity, nutrient cycling, overstory succession, and providing food and habitat for a vast range of species (Hobbie, 1992; Pinno and Errington, 2015; Millennium Ecosystem Assessment, 2005). At any spatial and temporal scale, plant communities reflect the combined effects of functional groups, regeneration processes, biotic interactions, and resource availability (Grubb, 1977; Macdonald and Fenniak, 2007; Díaz and Cabido, 2001). The change in plant structure and composition over time, with associated changes in biotic and abiotic factors, is known as community dynamics (Hart and Chen, 2006). The long-term dynamics of both plant succession and disturbance are essential in developing and understanding a functioning ecosystem, as well as in determining the future successional trajectory of a forest ecosystem (Mclntosh et al. 2016; Seagle and Shugart, 1985).

1.1.2 Boreal forest region

The boreal is one of the world's largest bioclimatic regions encompassing a variety of climates, soils, and plant assemblages (Brandt, 2009; Brandt et al. 2013). In Canada, the boreal region accounts for more than three-quarters of the country's forest, while occupying 58% of Alberta (Millennium Ecosystem Assessment, 2005). It is defined as a mosaic of deciduous, mixed-wood, and coniferous forests, surrounded by extensive wetlands in low-lying areas (Dhar et al. 2018; Downing and Pettapiece, 2006). The boreal forest has adapted to disturbance regimes in such a way that plant communities have become disturbance dependent (Hart and Chen, 2006). The cause, type, severity, frequency, extent, and pre-disturbance plant species may influence the patterns of plant community succession (Hart and Chen, 2006; Macdonald and Fenniak, 2007).

1.1.3 Surface Mine Reclamation

Energy extraction is yet another sizeable anthropogenic disturbance in Alberta's boreal forest, specifically, the oil sands, which underlie 142,200 km^2 (Government of Alberta, 2018b). Within the oil sands region, minable surface area equals about 4,800 km^2 and currently the area cleared or disturbed for oil sands mining is equal to about 895 km^2 (Government of Alberta, 2018b). Disturbances resulting from open-pit mining go beyond the severity of both natural disturbances and forest harvesting. The oil sand deposits are concentrated in Northern Alberta within the Athabasca, Cold Lake, and Peace River regions (Government of Alberta, 2018b). Open-pit mining is used when bitumen reserves are shallow enough (up to 75 m) to extract (Governmental of Alberta, 2018b). The disturbance extends past the mineable area as it also includes areas for infrastructure, bitumen processing, and other associated developments. The environmental issues caused by mining are substantial since the ecological footprint is relatively large across Alberta's boreal forest.

1.1.4 Reclamation

Land reclamation following mining involves the re-establishment of a self-sustaining ecosystem through the creation of soil profiles using salvaged soil material and surface organic matter (Alberta Environment and water, 2012). The initial steps before mining in land reclamation include harvesting all timber and surface soils are salvaged from the site (Alberta Environment and water, 2012). Following mining, current reclamation operations involve constructing landforms from overburden of either lean oil sands (<10% oil), Pleistocene glacial deposits, Cretaceous silts, shales, and sandstones (MacDonald et al. 2012). After re-contouring the land, reclamation practices entail placing a layer of suitable subsoil, which is capped with a cover soil (Alberta Environment and water, 2012).

There are two main cover soil types used to cap mineral soil in oil sands reclamation: forest floor-mineral mix (FFMM) and peat-mineral mix (PMM). FFMM is a limited resource of upland based soil salvage that aims to create an appropriate mix of organic forest floor layer and underlying soil material (A and B horizon) to preserve soil quality and seeds/propagules (Alberta Environment and Water, 2012). FFMM results in greater plant richness and soil microbial community (Macdonald et al. 2015). PMM is a mixture of lowland peat deposits and underlying mineral soil, consisting of a ratio of 60:40 peat to soil volume (Alberta Environment and Water, 2012) and is widely used as cover soil material, as large portions of the mining footprint are lowland peat bogs and fens. PMM makes up the majority of volume required for mine reclamation now and into the future (Alberta Environment and Water, 2012). The characteristics of PMM makes it ideal for tree and woody species establishment due to its high nitrogen mineralization rates, organic matter content, water holding capacity, and surface roughness (Pinno and Hawkes, 2015; Pinno and Errington, 2015). Reclamation soils are often used in combinations and layered on a single landform to provide a soil-cover design (Mackenzie, 2011). However, the combination of FFMM and PMM on a single landform is not widely used. The mixing and layering of both soil types were reported to be similar to PMM alone, but the combination of FFMM in patches surrounded by PMM could optimize the benefits of both soil types (Mackenzie and Quideau, 2012; McMillan et al. 2007).

The Government of Alberta's policy requires that a disturbed mine site should be reclaimed to equivalent land capacity (Government of Alberta, 2018a). Thus, the general goal in mine reclamation is to return the land to a self-sustaining boreal forest ecosystem while creating conditions that support long-term successional development (Dhar et al. 2019; Government of Canada, 2016; Macdonald et al. 2015). A self-sustaining ecosystem includes various ecosystem components such as soil, plants, wildlife, along with processes like primary productivity and nutrient cycling. To obtain these various ecosystem functions, an essential and widely used target in reclamation is plant communities (Dhar et al. 2018).

Plant communities change rapidly during the early development years. Therefore, it is vital to monitor the progression of communities across reclamation areas of different soil types. Monitoring plant communities on reclaimed areas will help determine if plant dynamics are following similar trajectories as natural ecosystems. Land reclamation practices are used to meet post-mining land use goals; however, there is still information that is lacking in plant community dynamics on reclamation sites that use a configuration of FFMM islands surrounded by a matrix of PMM. Understanding how various soil configurations on reclamation sites can influence plant community dynamics is an essential step in developing new methods and targets for oil sands reclamation (Dhar et al. 2018).

1.1.5 Plant Assembly

One obstacle in the boreal forest following mining is the re-establishment of a diverse native plant community. In this study, we use a sequence approach to characterize the change in vegetation community over time on FFMM and PMM. The sequence approach was done by examining the successional processes, i.e., seed bank, seed rain, biotic dispersal, plant expansion, and competition. Many reclamation techniques rely on approaches of passive natural regeneration and planting seedlings of desired tree species. Relying on passive reclamation increases the challenges and uncertainties associated with the re-establishment of vegetation on reclamation sites on both FFMM and PMM. Uncertainties on both soil types include variability associated with germinating buried seeds or vegetation material, seed dispersal, plant expansion, competition, availability of microsites, and resource availability (e.g., nutrients and water) (Jones and Landhäusser, 2018; Macdonald et al. 2012; Mackenzie and Naeth, 2010). Over time plant community dynamics are influenced by both the aboveground (e.g., life-history of species, competition, litter deposition) and belowground properties (e.g., soil pH, nutrients, and moisture) (McIntosh et al. 2016; Nilsson and Wardle, 2005). Thus, there is a need to understand the mechanisms behind the establishment of vegetation during reclamation. The first step in this process is to describe the patterns that emerge over time and link these to management practices.

Seed bank

With large scale disturbances, such as open-pit mining, the plant community is altered and succession is reset (Luzurianga et al. 2005). With the plant community being reset, regeneration of plants from the seed bank becomes significantly more important (Luzurianga et al. 2005). The seed bank is expected to play a dominant role in early composition, but the longer-term role is unknown. In recent years there has been an increase in planting native understory species in addition to tree seedlings on reclamation sites; however, a vast majority of native species are not commercially available (Cumulative Environmental Management Association, 2012; Alberta Environment, 2010). Furthermore, the seed bank plays a significant role in community dynamics as they are instrumental in the regeneration of natural plant communities that cannot be obtained by planting. Luzurianga et al. (2005) found with the removal of the seed bank that aboveground plant densities were 12.2-fold lower than plots with an untouched seed bank. In the boreal forest, many species regenerate vegetatively from roots and rhizomes; therefore, when referring to the seed bank, it also includes the entire propagule bank.

Salvaged cover soil is a significant resource for initially establishing plant communities following disturbance (Mackenzie and Naeth, 2010). FFMM is known for providing a seed bank that has a unique source of seeds and plant propagules, which have a higher potential to develop onto upland reclamation sites (Alberta Environment and Water, 2012; McMillan et al. 2007). The potential source of native propagules on the FFMM exists within the thin organic horizon of litter (L), fragmented and fermenting litter (F), and humus (H) in upland forests (Buss et al. 2020; Mackenzie and Naeth, 2010). LFH contains abundant seeds for replanting following a disturbance, providing species that are adapted to upland conditions (Mackenzie and Naeth, 2010). In contrast, the seed bank for lowland derived PMM cover soil contains mainly peatland-associated species that are suited to hydric conditions; therefore, the species carried in the soil may not be suited to conditions on reclaimed upland sites (Macdonald et al. 2012; Macdonald et al. 2015). The main benefits of using PMM are not from the seed bank, but rather in its positive effect on establishment and initial growth rates of trees and woody species (Pinno and Hawkes, 2015; Pinno and Errington, 2015).

Salvaging and placement success of the seed bank is strongly influenced by depth and placement method (Mackenzie and Naeth, 2010). The organic and upper mineral soil horizons are an essential source of seed and plant propagules for both upland forest plant communities and peatland-associated species (Naeth et al. 2013; Mackenzie and Naeth, 2010). Deep salvage will dilute the seed bank by mixing surface layers (containing seeds and propagules) with deeper mineral soil, differing overall abundance and composition represented in the seed bank to varying depths (Alberta Environment and Water, 2012; Mackenzie and Naeth, 2010). Direct placement involves removing the soil from nearby unmined forest donor sites and placing it directly onto a reclamation area preserves the seed bank (Naeth et al. 2013). Direct placement is the preferred method over stockpiling (Koch et al. 1996; Rokich et al. 2000) and was used in this study.

Dispersal

The dynamics of plant species after initial colonization are driven in part by sexual (seed) and asexual reproduction (clonal fragments and vegetative expansion) (Silvertown, 2008). Dispersal can come from on-site (referred to as nucleation) when early-successional plant species establish in the patches that expand outward or by seed dispersal (Yarranton and Morrison, 1974). Seed-based reproduction is generally more effective because it is associated with rapid colonization and widespread dispersal distance compared to vegetative expansion following a high severity disturbance (Silvertown, 2008). Incoming seed rain species are generally seed-based wind dispersing species that have a continual input in an area, which plays a critical role in the aboveground community during the early stages of succession (Matlack, 1987; Corbin et al. 2016; Robinson and Handel, 2000). On reclamation sites, wind-dispersed species are either trees or early successional species (Corbin et al. 2016; Gallagher et al. 2011). Previous studies have emphasized that adjacent patches or remnant plants act as a local wind-dispersed seed source and distance to those sources strongly determine the amount of seed rain coming into the reclamation site (Bochet et al. 2007; Mola et al. 2011). Initially, species that utilize wind-dispersal are anticipated to initially be found on both FFMM and PMM due to increased available seedbed, decreased competition, and vegetation barriers (Corbin et al. 2016; Robinson and Handel, 2000).

Safe seedbeds are critical for the establishment of plant species and one of the key factors is surface roughness. Surface roughness has been identified as an important site characteristic that improves seed retention, germination, microsites, and reducing evaporation (Bradshaw, 2000; Mackenzie and Naeth, 2010; Pinno and Errington, 2015). Surface roughness is generally higher on PMM compared to FFMM; however, the conditions on the PMM vary (Jones and Landhausser, 2018; Pinno and Errington, 2015). PMM has been found to display hydrophobic properties at the soil surface, potentially leading to seed desiccation and reduced germination success of seeds that were retained on PMM seedbeds (Leatherdale et al. 2012; Pinno and Errington, 2015). The establishment of woody species, especially tree and woody species, will likely be higher on PMM from wind-dispersed (e.g., *Populus sp., Salix sp*) or animal dispersed species (e.e., *Ribes sp*., *Cornus sericea*) which need a constant supply of available water (Pinno and Errington, 2015). Therefore, it is important to note that seedling establishment is strongly dependent on soil conditions such as surface roughness and soil moisture.

Plant recruitment through vegetation expansion generally occurs at the patch edges due to the combination of higher species richness within the patch, facilitation effects, or disturbed habitat margin (Jones and Landhausser, 2018; Kettenring et al. 2016). Vegetative expansion from plant patches commonly expands into recently disturbed areas in the boreal forest (Rydgren et al. 2004). Previously applied nucleation restoration has often found that species using above and belowground vegetative structures have a relatively slow rate of expansion into surrounding area (Jones and Landhausser, 2018; Robinson and Handel, 2000; Silvertown, 2008). However, species expansion into PMM from FFMM may potentially benefit from belowground rather than aboveground vegetative expansion due to greater access to resources (high water holding capacity and nitrate availability) (Mackenzie and Naeth, 2010). The reproductive structure belowground will be less exposed to the harsh surface conditions and increased desiccation than seeds and stolons that disperse aboveground (Mackenzie and Naeth, 2010).

As the disturbed ecosystem increases in complexity, seed dispersal through biotic (mainly birds and mammals) interactions become important for the development of late-successional fruiting and woody species (Rey Benayas et al. 2008; Corbin et al. 2016; Robinson and Handel, 2000). Morphological adaptations of seeds have developed to increase dispersal to allow for biotic movement, including the use of barbs, hooks, and colorful seed coats (Chambers and MacMahon, 1994). The biotic movement of seeds into disturbed areas contributes to the efficient dispersal of large-seeded species and improves germination capacity by partially digesting the seed coats (Matlack, 1994). Biotic dispersed species tend to increase over time with the establishment of a canopy and favorable habitat conditions causing the attraction of birds and other mammal species that might disperse seed (Cole et al. 2010; Zahawi et al. 2012; Zahawi and Augspurger, 2006). Biotic dispersal is critical for the long-term maintenance and development of plant communities and can account for a large proportion of the total seeds dispersed (40-85%) (Corbin et al. 2016; Zahawi and Augspurger, 2006).

In mature natural and harvested forests, the tree canopy has a strong influence on the understory plant community altering, the understory light, soil nutrients, pH, and forest floor heterogeneity (Hart and Chen, 2006). Closed canopy forests over time are less likely to be invaded by early successional species than a cleared open area because they create a barrier for wind-dispersed species and out shade intolerant species (Hart and Chen, 2006). Canopy closure changes microsite conditions from exposed to sheltered creating habitat, which will potentially increase the presence of biotic movement throughout the reclamation site (Mackenzie and Naeth, 2010).

In the boreal forest, most woody species do not establish from the seed bank but rather from outside sources, showing the influences of the broader landscape on the successional success on reclamation sites as yearly as 4 years post disturbance (Corbin et al. 2016; Robinson and Handel, 2000). Seed inputs onto highly disturbed reclamation sites may be altered due to the location of the site to remnant forest, surrounding disturbed areas, or altered behavior of seed-dispersing animals (Cole et al. 2010). In such circumstances, new recruitment may be derived from seeds found within the soil or from species found within distant remnant patches, which will affect the ability of seed rain and seed-dispersing animals to utilize the landscape (Cole et al. 2010).

Competition

There are two large impacts on the structuring of the plant community: competition and facilitation. Some species may switch between competitive or facilitative depending on the life history and successional stage (MacDougal and Turkington, 2005; Walker and Del Moral, 2009). Competition by the dominant plant species limits the abundance and reproduction of many species; however, many of these species may also be facilitating species survival by filling a specific niche (MacDougal and Turkington, 2005).

Undesirable, native, or non-native species that impact ecological, economic, and management objectives (Alberta Environment, 2010). Non-native and invading graminoid species establishment on disturbed sites is an ongoing management issue worldwide. The problem arises when those species dominate to the point where the desired native plant community is altered. Non-native species typically have high rates of reproduction, spread rapidly, and are highly adaptable. Many non-native species in the boreal are fast-growing annuals, short-lived perennials, or biennial non-woody ruderals leading them to potentially being outcompeted by native perennials overtime (Alday et al. 2011; Forster and Tillman, 2000). In addition to non-native species, native graminoid species have also been known to be a competitor to the desired plant community. Graminoids can outcompete forbs and trees through light competition, snow press damage from standing litter, low soil temperatures, and nutrients

(Landhäusser and Lieffers, 1998); however, graminoid species have also been shown to facilitate plant recruitment. In a seed addition experiment, the highest survival of seeds occurred in the summer when graminoid cover reduced heat stress on the seeds (MacDougal and Turkington, 2005). In the boreal forest, *Calamagrostis canadensis* is a common native grass species that is a strong competitor because of its ability to colonize and dominate disturbed areas from seed or rhizomes (Landhäusser and Lieffers, 1998).

An overabundance of non-native or dominating graminoid species can delay succession and obstruct native plant assembly, so having these on reclamation sites may not be desirable. Long term effects of competitive non-native and graminoid species on reclamation sites are relatively unknown. It is unknown whether they act as drivers that negatively impact ecosystem development or if they are acting as a temporary placeholder in the early stages of succession (MacDougall and Turkington, 2005; Gingras-Hill et al. 2018). Within the early stages of succession, non-natives and graminoids can act as pioneer species, which can help accelerate pedogenic development and facilitate the establishment of plant species in the long run (Gingras-Hill et al. 2018). These interactions are dependent on cover soil as FFMM plant richness is often higher than PMM, leading to increased competition on FFMM (Gingras-Hill et al. 2018). Over time with an increase in diversity and a decrease in available seedbed competition may become a stronger influence in structuring the plant community.

1.1.6 Island Reclamation

In current reclamation practices, soils are placed in relatively large homogeneous patches of each soil type. These large blocks of individual soil types may not be providing optimal use of limited reclamation soil resources. A significant operational challenge associated with this is how to maximize the ecological benefits of both soil types across the landscape. The island reclamation approach was adapted from elements of both natural disturbance and active reclamation, to influence the rate and direction of natural succession to sustain biological diversity (Bradbury, 2004; Corbin and Holl, 2011). Following a forest fire, unburnt patches of plant species are common. Similarly, forest harvesting patches are often left as a technique to provide a “lifeboat” or colonizing center to species post-disturbance (Bradbury, 2004). These ideas are now being implemented in reclamation, such as island reclamation. A potential strategy of “Island” reclamation for the boreal forest is the translocation and strategic placement of the valuable upland FFMM surrounded by a matrix of lowland PMM. Various iterations of this technique have been used in restoration studies, including applied nucleation using islands of forests or planted trees. Generally, islands of larger sizes had higher densities of plant species (Corbin et al. 2016; Robinson and Handel, 2000; Zahawi and Augspurger, 2006) and seed bank translocation from forested areas (Jones and Landhausser, 2018; Pinno et al. 2016).

The size of islands is generally a good indicator to quantify species richness and occurrence (Bradbury, 2004). The increase in species happens for two main reasons: first, as more individuals are sampled, there is a higher chance of encountering additional species (Scheiner, 2003), and second, larger areas will have environmental heterogeneity; therefore, containing additional species in specific niches (Scheiner, 2003). Thus, larger areas tend to have more species present (Pinno et al. 2016). The size of the islands effect of species richness will be determined using species-area curves (SAC), which will develop the relationship between a specified area and the number of species found within that area (Scheiner, 2003). Islands species-area curves are used to determine the minimum area needed for a desirable species community (Humphreys and Kitchener, 2010; Scheiner, 2003). Within island reclamation, SAC will be able to determine whether the creation of larger homogenous patches or several smaller patches will be beneficial to create a desirable plant community.

The FFMM islands aim to re-develop a plant community from the seed bank that contains many species adapted to upland conditions, which will expand into the surrounding landscape. The effectiveness of these patches is dependent on size, shape, and spatial arrangement can help in determine the length of time it takes for a specific species to colonize in the surrounding area (Bradbury, 2004; Pinno et al. 2016). Island shape (perimeter-area ratio), is important as vegetative reproduction becomes a greater proponent to the expansion of the plant community into the surrounding PMM; however, this is yet to be studied (Alberta Environment and Water, 2012). Thus, studying the effect of shape on plant expansion and richness is key to understanding and enhancing reclamation methods. The distance of the gap between islands is an important factor for the rate of plant filling in gaps within the PMM. Small gaps are colonized more rapidly than larger ones, particularly due to higher clonal ingrowth densities (Bullock et al. 1995; Rydren et al. 1998).

1.1.7 Research Questions

The overall aim of this research is to explore plant community assembly on various soil designs (material type and configuration) on upland reclamation areas following oil sands mining. Study one examines three questions: 1) what is the initial plant community on each soil type, 2) how does it change over time, and 3) what plant community assembly mechanisms cause this, including seed bank, seed rain, vegetative expansion, and competition? Study one is laid out in the conceptual framework depicted in Fig. 1. Study two examines: 1) what is the effect of FFMM islands on the plant community, including the optimal size, spacing, and configuration of these islands.

1.2 Methods

1.2.1 Research Area

The research took place at an oil sands mine approximately 75 km northwest of Fort McMurray, Alberta, Canada (57.3377 ˚N -111.7552 ˚W) within the Boreal Mixedwood ecological area, which is a mosaic of upland forest and extensive wetlands (Natural Regions Committee, 2006). FFMM soil comes from upland areas consisting of trembling aspen (*Populus tremuloides)* and white spruce (*Picea glauca*) mixedwood (Natural Regions Committee, 2006). Common upland understory species in this area include wild rose (*Rosa acicularis),* bunchberry *(Cornus canadensis),* twinflower *(Linnaea borealis),* and lily-of-the-valley *(Maianthemum canadense)* (Errington and Pinno, 2015). Upland soils are predominantly Gray Luvisols, which have a forest floor layer (LFH) overlaying the mineral soil (Natural Regions Committee, 2006; Soil Classification Working Group, 1998). PMM comes from organic soils found in wetlands vegetated by black spruce (*Picea mariana*) with an understory of Labrador tea (*Rhododendron groenlandicum*), dwarf birch (*Betula pumila var. glandulifera*), cloudberry (*Rubus chamaemorus*), and sedges (*Carex sp*.) (Beckingham et al. 1996; Natural Regions Committee, 2006; Soil Classification Working Group, 1998). The study location experiences short cool summers and long cold winters (Natural Regions Committee, 2006). The average temperature of the warmest month is 17.0˚C and -21.9˚C for the coldest month with a mean annual precipitation of 365.7 mm (Government of Canada, 2019).

The 19-ha reclamation site was created in the spring of 2015 on mine overburden material constructed to form a tailings dyke (Fig.2). The overburden for this site was made up of a mixture of Clearwater clay, interburden material, and some Pleistocene clays (Alberta Environment and Water, 2012). Subsoil was placed above the overburden at a depth of 1 m because the underlying oilsands substrates are generally devoid of or low in nutrients and may be sodic, saline, or contain hydrocarbons (Naeth et al. 2013). The final capping material was upland FFMM and lowland PMM at a depth of 0.25 m. The reclamation site was one area with various shaped and sizes of FFMM islands surrounded by PMM. The FFMM and PMM soil characteristics were measured in July of 2019 (A. 1). Volumetric water content and soil temperatures were 6.9% and 0.8˚C higher in the PMM than FFMM, while pH was similar between soil types (Table 1). Nutrient supply rates were determined using PRS probes in an aerobic incubation (A. 1). There was a higher nutrient supply rate in the FFMM of Ca^{2+}, Mg^{2+}, K^{+}, and PO_4^{3-}, and similar supply rate for NO_3-N and NH_4-N in both soil types (Table 1). Spruce seedlings were planted on both soil types, all other plants established naturally on-site.

1.2.2 Field Methods

Vascular plants were identified to species level in the field; if unidentifiable, a sample was collected for later identification. Plant species were grouped into growth form categories: native forbs, graminoids (grasses, rushes, and sedges), non-native forbs, shrubs, and trees. The native forbs were further grouped based on their primary dispersal mechanisms: vegetative, wind, and gravity dispersed (Moss and Packer, 1994; Tannas, 2001, 2003, 2004). Vegetative species were any species that use asexual reproduction, including rhizomes, stolons, and suckers, as their primary method of dispersal. Wind-dispersed species were identified based on the adaptation of their seeds, such as wings, pappus, or bristles. Gravity-dispersed species were those that do not use vegetative reproduction and have no adaptations on the seed. 2015 will be referred to as Year 1, 2016 as Year 2, and 2019 as Year 5.

1.2.2.1 Study one

The plant community was sampled in Year 2 and Year 5 on both soil types. Species richness and abundance was characterized by functional groups (native forbs, non-native forbs, graminoids, shrubs, and trees). The initial, final, and change to plant community were then related to plant community assembly mechanisms, i.e., seed bank, seed rain, biotic dispersal, vegetative expansion, and competition.

Plant sampling

Transects were placed at each island and along the large homogeneous patch of FFMM perpendicular to the boundary separating FFMM islands from the surrounding PMM. Each transect was a total of 25 m in length, initiating 5 m inside the FFMM and extending 20 m perpendicular into the surrounding PMM (Jones and Landhäusser, 2017) (Fig. 3). Quadrats of 1-m² were established every meter from 0-5, 10, 15, and 20 m from the soil interface inside PMM (n = 8) and 0-5 m inside the FFMM (n = 5) (Fig. 3). Within each 1-m² quadrat, percent cover was collected for each plant species. Bare soil (proxy for available seedbeds) was determined by the total average plant cover -100% in Year 2 and in Year 5 bare soil was determined by the total average plant cover plus total average leaf litter cover -100%. The transects were established in locations where the 20 m plot was at least a minimum of 20 m away from any other FFMM islands. 10 transects were measured in Year 2 (n=10), and those 10 transects were re-measured with an additional 25 transects in Year 5 (n=35).

Seed Bank and Seed Rain

Seed bank samples were collected in late May of Year 1 from 28 locations, 14 in each soil type, located 10 m from any soil boundary. The depths that were collected were 0-5 cm and 5-10 cm. At each sampling location, five seed bank samples were collected from each depth. Samples were collected in 10 cm PVC tubes for a pooled sample volume of 2026 cm^3.

To assess seed rain, seed traps were placed in the spring of Year 1 and collected in the fall of Year 1 at 10 transects. The seed traps were placed at 0, 3, 5, 10, 15, and 20 m along transects in both soil types. The ten transects that were chosen for the seed rain were placed on islands large enough to extend up to 20 m into the FFMM. Each seed trap consisted of a greenhouse flat (27.79 cm W x 54.46 cm L x 6.20 cm D) with a liner of artificial turf at the base of the tray. The seed traps were installed into the ground, so the top of the tray remained flush with the surrounding ground.

Once in the lab, both seed bank and seed rain samples were sieved using a 4 mm sieve to ensure samples were uniform and to remove large, non-seed debris such as wood, rocks, and coarse roots. The samples were then wet sieved through 500 and 212 µm sieves. Following sieving, greenhouse trays were pre-filled with potting soil to approximately ¾ of the height and packed down firmly to provide an even surface for placement. The concentrated samples of either seed bank or seed rain were then evenly spread at a thickness of 0.5 cm or less into the greenhouse trays. Control trays were filled with potting soil to determine the potential species coming from the potting mix or aerially through the ventilation system. The control trays were placed throughout the treatment trays to account for approximately 10% of the area. No seedlings germinated from the control flats. The trays were placed in the greenhouse and monitored every two or three days for four months. Trays were watered daily with an automatic irrigation system. Seedlings were identified to the species level when maturity was reached, counted, and then removed. When no seedling emergence was recorded for more than a week, the samples were mixed to ensure buried seeds were not prevented from germinating and then re-monitored for another two weeks.

1.2.2.2 Study two

FFMM island surveying

For the FFMM islands, species-area curves were developed based on plant species richness in areas ranging from 366 – 7,348 m² (Fig. 2). The first island design is a total area of 9 ha comprised of 22 FFMM islands of varying sizes (366-1908 m²) and configuration within a PMM soil matrix. Additionally, within the larger continuous patches of FFMM, we sectioned off four areas, ranging in size from 4417- 7348 m² (Fig. 2).

Plant composition of the 26 FFMM islands, excluding planted seedlings, was assessed in June to August in Year 5 using a walk around survey. The walk around survey consisted of two individuals systematically searching along parallel and adjacent linear transects covering the entire island (Henderson, 2009). Flags marked the outside boundary, while GPS tracks determined the area covered inside to eliminate double sampling (Zhang et al. 2014). Flagging and GPS tracks ensure there was a fixed distance of 2-4 m between observers (Henderson, 2009). The search effort of islands was based on a time-limited survey. Zhang et al. (2014) found the optimal search effort for a 2500 m² site in the boreal region of northeast Alberta requires about 1 hour to sample 90% of total vegetation species. Due to a variation in size, any island below 2500 m² had a search effort of one hour; the search effort was altered for sizes larger than 2500 m². For example, 5000 m² island would be surveyed for two hours.

1.2.3 Statistical Methods

All data analysis was done using R software (version R.3.1.1, R Core Team, 2019) unless otherwise specified. The plant species were categorized into dispersal assembly mechanisms such as seed bank, seed rain, and biotic dispersal and was based on percent cover by functional group within each category. The data was non-normal distribution based on the Shapiro-Wilk normality test and residual plots (quantile-quantile, residuals vs. fitted values, and residual histograms).

Plant community composition

Community compositions at Year 2 and Year 5 were quantified based on functional group cover. The average percent cover was calculated by transects for each functional group in FFMM and PMM over Year 2 and Year 5. A permutational analysis of variance (permANOVA) using the *lmPerm* package (version 2.1.0; Wheeler and Torchiano, 2016) with Tukey's HSD Post Hoc test was used. Blocking was not a significant factor for the differences in soil type at Year 2 and Year 5, therefore was not used in the analysis. Bare soil (seed bed availability) and leaf litter in Year 2 and Year 5 on both soil types were compared using permANOVA with Tukey's HSD Post Hoc test.

To explore the effect of soil type on plant community composition at Year 2 and Year 5, Bray-Curtis distance and interpreted using Non-metric multidimensional scaling (NMDS) ordinations. NMDS was run on non-transformed binary data of species percent cover in each plot to show patterns of species composition clearly.

Mechanisms causing community change over time

Seed bank and seed rain were measured by count of seedlings of species abundance and richness for each functional group and were compared between soil types (and depth for seed bank) using permANOVA with Tukey's HSD Post Hoc test. This allowed us to determine where the seeds were coming from initially for both soil types.

If species occurred in both the seed bank and seed rain, they were excluded from the seed rain aboveground community. The removal of shared species from the seed rain was to ensure that species establishing from the seed bank and spreading seed within the first growing season were not recounted for as the seed rain. The separation of species allows us to determine species that are truly originating from the seed rain. Species that were not found in either the seed bank or seed rain but still occurred in the aboveground plant community were classified as having biotic dispersal. We are classifying these species as biotic dispersal but some of the species use other dispersal strategies such as wind or gravity. The importance of species originating from seed rain, seed bank, and biotic dispersal in Year 2 and Year 5 we looked at richness and abundance using a permANOVA with Tukey's HSD Post Hoc. Blocking was not significant in the analysis, therefore was not sued for the analysis on differences in soil type at Year 2 and Year 5. Each mechanism of dispersal was separated by species originating through that mechanism and then further separated into functional groups to allow us to determine where functional groups are originating and developing into what soil types over time. A proportional graph will show the influence of each mechanism and where each functional group is originating from in the aboveground community.

Plant expansion was assessed by calculating mean cover for each functional group at each distance in the PMM and the FFMM. Expansion analysis was done for each functional group, native forb dispersal mechanisms (gravity, wind, and vegetative), and an example of a vegetative expansion species (*Fragaria virginiana*) in year 5. The expansion was quantified using the randomization test of edge influence (RTEI), which is an excel macro program with blocking. RTEI compares the average edge distance values (PMM) to the average reference values (FFMM) using randomizations blocking by transect (Harper and Macdonald, 2001, 2002, 2011). RTEI was based on $\alpha = 0.05$ using a two-tailed test and 1000 permutations. Significant values were based on $p < 2.5$ being significantly less than the reference, and $p > 97.5$ being significantly higher than the FFMM. Plant expansion is determined by how similar the mean cover is in the PMM plant community at each distance is to the plant community in the FFMM.

Competition was determined based on species co-occurrence and Pearson’s correlation. Species co-occurrence patterns were analyzed using a probabilistic co-occurrence model. This analysis aims to determine the amount to which the communities contain species that were positively, negatively, and randomly associated with one another (Griffth et al. 2016). Positive associations occur when the observed frequency of co-occurrence is significantly larger than expected, negative associations were smaller than expected, and random associations have no significant difference and were approximately equal to expected. This analysis was conducted using the R package “cooccur 1.3" on species presence-absence (Griffth et al. 2016). The analysis produces a summary statistic on all pairwise species comparisons and the probability of co-occurring more or less frequently than by their observed frequency (Griffth et al. 2016). Analysis of species co-occurrence in Year 5 by soil type considered 3828 pair combinations of species where 919 pairs (24.01%) of species pairs were removed from the analysis because their expected co-occurrence was <1 (share less than one site). If the species pairs had negative interactions between native vs. non-native forbs or native vs. graminoids than positive interactions would lead us to believe there is competition occurring.

Pearson’s correlation was used to compare the cover of various functional groups to one another (native forbs to non-native forbs, non-native forbs to graminoids, and native forbs to graminoids) in Year 2, Year 5 and on both soil types. Negative correlations indicate competition, while positive correlations indicate facilitation or no interaction.

FFMM Islands

FFMM island species-area curves were based on species richness in areas from 366-7925m^2. Species-area curves will determine the optimal size of islands for native forbs, non-native forbs, graminoids, and shrubs. Fit and comparisons of species areas curve models were completed using multimodel inference with the sars R package (sars 1.2.1, Matthew et al. 2019; Tjørve, 2003). The multimodel SAR produced outputs that contain successfully fitted models, models that were removed due to failing validation tests (tests of normality and homoscedasticity of the residuals), criterion weights, and weights of successfully fitted models. Models were selected based on the lowest AIC score and criteria weight for both area and perimeter to area ratio. The criteria model weights were determined based on model rank according to some criteria (e.g., Akaike's information criterion, AIC) and the criterion values converted into weights (i.e., the conditional probabilities for each of the n models) (Matthew et al. 2019).

To determine the optimal shape of islands, Pearson's correlation was used to compare the perimeter-area ratio of the richness in each functional group. If there is a positive correlation between perimeter-area ratio and richness would indicate a certain shape of islands that would be optimal for increasing richness.

To determine if island size has an effect on the rate of vegetative expansion, Pearson's correlation was used to compare island area (m^2) to the vegetative expansion of native forb cover (%) into the surrounding PMM at 0, 1, and 2 m. A positive correlation between vegetative expansion and island area would suggest a certain island area range that would be optimal for increasing the rate of expansion into surrounding PMM. The optimal spacing of the islands was assessed based on the rate of plant expansion and Year 5 plant community composition. Based on plant expansion, slow expansion rates from islands would potentially need to be closer together. Based on Year 5 aboveground plant cover, if PMM is similar to FFMM, the islands can be further apart.

1.3 Results

1.3.1 Plant community composition

Over five years, there has been an increase in total vegetation cover and richness in both soil types (Fig. 4f) despite different starting conditions. Total cover in Year 2 was higher ($p<0.001$) on FFMM (27.6%) compared to PMM (3.8%) (Fig. 4f); but by Year 5 was not different by soil type (FFMM = 44.8%, PMM = 42.9%, $p = 0.189$). Cover increased differentially between soil types with an average increase of 17.2% on FFMM and 39.1% on PMM. Bare soil (a proxy for seedbed availability) differed by year and soil type. In Year 2, on FFMM bare soil was 72.4 %, and on PMM 95.9% ($p<0.001$), but decreased over time to 5% on FFMM and 20.8% on PMM ($p<0.001$) in Year 5. Leaf litter in Year 2 had a total cover of <1% ($p=1$) in both soil types. By Year 5 leaf litter increased to 50.2% on the FFMM and 36.3% on PMM ($p<0.001$).

Beyond the total plant cover, there were different temporal responses by functional groups. Native forbs increased in percent cover from Year 2 to Year 5 by 15.4% on FFMM ($p<0.001$) and by 19.3% on PMM ($p<0.001$) such that cover of native forbs was similar between soil types in Year 5 (FFMM = 19.7%, PMM = 18.8%, $p=0.894$) (Fig. 4a). Non-native forb cover was initially different between FFMM (20.9%) and PMM (1.4%) ($p<0.001$) (Fig. 4b). However, non-native forb cover decreased on the FFMM by 13% and increased on the PMM by an average of 6.3% between Year 2 and Year 5 such that by Year 5, there was no significant difference between them (FFMM=7.8%, PMM=7.7%, $p=0.99$) (Fig. 4b). Graminoid cover in Year 2 was similar between soil types (FFMM = 2.0%, PMM = 0.33%, $p=0.32$); however, over time there was a differential increase in cover by soil type (FFMM = 9.9%, PMM = 5.9%, $p<0.001$) resulting in a higher graminoids cover on FFMM than PMM in Year 5 ($p<0.001$) (Fig. 4c). Shrub cover was minimal in Year 2 ($p=0.99$) and slightly increased in Year 5 by 1.2% on the FFMM (p=0.20) and 1.45% on the PMM (p=0.014) (Fig. 4d). Non-planted tree cover was minimal in Year 2 and increased over time on PMM (5% increase, p<0.001) but not on FFMM (1% increase, p=0.99) (Fig. 4e).

The plant community described by the NMDS duplicates the same relationship between soil types and functional groups, as seen in Fig.4 (Fig. 5). For both years the NMDS explained a low proportion of variance (Year 2= 32.4%, Year 5=31.7%) (Fig. 5). At Year 2, non-native forbs were negatively correlated with axis 1 suggesting a higher abundance on the FFMM (e.g., *Melilotus albus* and *Sonchus uliginosus*). By Year 5, we see more overlap between FFMM and PMM. At Year 5, the loadings in the NMDS suggest that PMM was associated with higher abundance of certain non-native forbs (*Crepis tectorum*) and *Populus tremuloides*. Graminoids are positively correlated to axis 1 indicating they have a higher abundance on FFMM compared to PMM (*Calamagrostis canadensis*).

1.3.2 Mechanisms causing community change over time

Seed bank

Based on the seedlings germinated from all seed bank samples, there was a total emergence of 2,135 seedlings representing 55 species (FFMM = 51 species, PMM = 29 species). For all three categories (native forbs, graminoids, and non-native forbs) more seedlings emerged from FFMM than from PMM (FFMM = 86.3%, PMM = 13.7% of total seedlings, p<0.001) (Table 2; Fig. 6). By functional group, there were more seedlings in all groups in the FFMM compared to PMM (p<0.001) (Table 2; Fig. 6). For non-native forbs there were 13 species emerging from FFMM and 10 from PMM (FFMM = 13%, PMM = 12.7% of total seedlings germinated by soil type) (Table 2; Fig. 6). For native forbs there were 26 species emerging from FFMM and 11 from PMM (FFMM = 40.5%, PMM = 27.7% of total seedlings germinated by soil type) (Table 2; Fig. 6). For graminoids there were 11 species emerging from FFMM and 7 from

PMM (FFMM = 46.5%, PMM = 59.6% of total seedlings germinated by soil type) (Table 2; Fig. 6). Soil type had similar seedling emergence at both soil depths ($p>0.41$) (Table 2; Fig. 6).

There was a change between Year 2 and Year 5 in terms of the component of the aboveground plant community that originated from the seed bank in both soil types. Initially in the aboveground plant community, species originating from the seed bank account for 25.9% of total cover on FFMM (34 species, 93.6% of total proportion of cover) and 2.8% of total cover on PMM (30 species, 73.9% of total proportion of cover) ($p<0.001$) (Table 3; Fig. 7; Fig. 8). The aboveground community originating from the seed bank in Year 2 consisted mainly of non-native and native forbs. Non-native forbs originating from the seed bank had a total cover of 21.9% on FFMM (79.2% of total proportion of cover) and 1.6% of total cover on PMM (42.9% of total proportion of cover) ($p<0.001$) (Table 4; Fig. 7; Fig. 8). Native forbs originating from the seed bank had a total cover of 2.8% on FFMM (10.2% of total proportion of cover) and 0.9% of total cover on the PMM (23.2% of total proportion of cover) ($p=0.466$) (Table 4; Fig. 7; Fig. 8). Graminoids accounted for less than 2% of total cover and less than 8% of total proportion of cover on both soil types ($p=0.835$) (Table 4; Fig.7; Fig. 8).

Over time cover of species originating from the seed bank remains similar on the FFMM accounting for 28.5% of total cover (34 species, 63.6% of total proportion of cover) ($p=0.663$) and increasing on the PMM accounting for 18.7% of total cover (35 species, 43.5% of total proportion of cover) ($p<0.001$) (Table 3; Fig. 7; Fig. 8). There was a change in seed bank originating species from being dominated by non-native forbs to native plants. Non-native species originating from the seed bank decreased in total cover by 14.6% on the FFMM (decreasing by 63% of total proportion of cover, $p<0.001$) and increasing by 5% of total cover on PMM (decreasing by 27.3% of total proportion of cover) (Table 4; Fig.7; Fig. 8). Native forbs originating from the seed bank increased in total cover by >10% on both soil types (increasing on FFMM by 18.3% of total proportion of cover, decreasing on PMM by 6% of total proportion of cover) ($p<0.001$) (Table 4; Fig.7; Fig. 8). Graminoids increased ($p<0.001$) in total cover by 7.3% on FFMM (increase by 14.8% of total proportion of cover) and on PMM by 4.5% of total cover (increase by 3.3% of total proportion of cover) (Table 4; Fig.7; Fig. 8).

Seed Rain

Seed rain samples had a total emergence of 32,811 individual seedlings from all samples, representing 68 species (FFMM = 62 species, PMM = 50 species) with total seedling emergence similar between soil types (FFMM = 49%, PMM = 51% of total seedlings, $p=1$) (Table 5; Fig. 9). Based on all seedlings emerged, 62.3% used wind-dispersal and 35.6% used gravity dispersal. Out of the 68 total species, there were 27 native forbs (30% of total seedlings germinated), 10 graminoid species (27% of total seedlings), 18 non-native forbs (43% of total seedlings), and 2 tree species (<1% of total seedlings) (Table 5; Fig. 9). Seed rain for both non-native forbs and native forbs was similar between both soil types ($p>0.08$), while graminoids were more abundant in the PMM ($p=0.055$) (Table 5; Fig. 9).

In the aboveground plant community, seed rain originating species in Year 2 account for an total cover less than 2% on both soil types, however, they account for 4.5% of total proportion of cover on FFMM (10 species) and 16.8% of total proportion of cover on PMM (8 species) ($p=0.991$) (Table 3; Fig. 7; Fig. 8). The vast majority of establishing species from seed rain were native forbs (Table 4; Fig. 8).

Over time there was an increase of seed rain originating species ($p<0.001$) of total cover to 11.6% on FFMM (17 species, 25.9% of total proportion of cover) and PMM to 15.2% of total cover (14 species, 35.3% of total proportion of cover) ($p=0.007$) (Table 3; Fig. 7; Fig. 8). The increase of seed rain originating species is mainly from native forbs on both soil types and tree species on PMM. Native forbs originating from the seed rain increased in total cover by 8.6% on FFMM (17.6% of total proportion of cover) and 6.8% on PMM (3.4% of total proportion of cover) ($p=0.019$) (Table 4; Fig. 7; Fig. 8). Trees increased in total cover by 5% on PMM ($p<0.001$) and did not significantly increase on FFMM ($p=0.991$) (Table 4; Fig. 7; Fig. 8). Graminoid, non-native forbs, and shrubs account for a total cover <2% and <4% of total proportion of cover on both soil types ($p>0.991$) (Table 4; Fig. 7; Fig. 8).

Biotic dispersal

In the aboveground plant community in Year 2, species originating from biotic dispersal mechanisms account for an total cover of 0.5% on FFMM (11 species, 2% of total proportion of cover) and 0.4% of total cover on PMM (13 species, 9.4% of total proportion of cover) ($p=0.999$) (Table 3; Fig.7; Fig. 8). Over time in the aboveground plant community, there was an increase of species originating from biotic dispersal in both soil types ($p<0.001$) to an total cover of 4.7% on FFMM (32 species, 10.4% total cover) and 9.1% of total cover on PMM (33 species, 21.2% total cover) ($p<0.001$) (Table 3; Fig.7; Fig. 8). The shift in the community from biotic dispersal is mainly due to native forbs; other functional groups had a total cover <0.89% and <2% of total proportion of cover on both soil types ($p>0.256$) (Table 4; Fig. 7; Fig. 8). Native forbs increased on both soil types ($p<0.001$) by 3.6% of total cover on FFMM (increasing by 7.6% of proportion of cover) and by 7.4% of total cover on PMM (increased by 10.3% of proportion of cover) ($p<0.001$) (Table 4; Fig.7; Fig. 8).

Plant Expansion

Plant dispersed species in Year 2 had a total cover of 1.6% on the FFMM and 0.4% on PMM ($p=0.928$), over time they increased ($p<0.001$) to 14.2% on FFMM and 12.5% on PMM ($p=0.326$). Although the overall cover is different between soil types, there appears to be no movement of species from FFMM into PMM for graminoids (RTEI $p=0.1$) or non-native forbs (RTEI $p>2.8$) (Table 6; Fig. 10). For native forbs, movement from FFMM into PMM varies by dispersal mechanism with no expansion for gravity (RTEI $p>0.54$) or wind (RTEI $p>5.29$) dispersed species (Table 6; Fig. 11). However, for native forbs with vegetative reproduction, there was an average dispersal from FFMM into PMM of 1 m, although this varied for individual species (Table 6; Fig.11). For example, *Fragaria virginiana* expanded out to 2 m from the FFMM into the PMM (Table 6; Fig. 11).

Plant competition

Analysis of species co-occurrence in Year 5 by soil type showed that 73.35% of all species pairs were random, and only 1.7% of species potential pair associations were significant. The total number of positive associations were slightly higher than the number of negative associations (26 positive compared to 23 negative) (A.1).

Based on the correlation analysis among functional groups, FFMM showed no significant interactions between any of the functional group cover (%) comparisons in either year ($p>0.05$) (Fig. 12; Fig. 13; Fig 14). By comparison, in Year 2 on PMM, all functional group comparisons showed a positive correlation ($p<0.011$). In Year 5 on PMM, only native forbs and non-native forb cover continued to be positively correlated ($p=0.015$) (Fig.12), but there were no relationships among other functional groups (Fig.13; Fig. 14).

1.3.3 FFMM islands

FFMM Islands had a total species richness of 140 species: 66 native forbs, 17 non-native forbs, 26 graminoids, 25 shrubs, and 6 trees. The 2 islands with the highest species richness have an area of 5659 m^2 (84 species) and 7348 m^2 (71 species) compared to the island with the lowest richness having an area of 811 m^2 (40 species). The remaining islands fell between these with species richness of 47-66 species.

Species-area curves were generally very weak. The best relationship was from native forbs using the asymptotic curve ($p<0.001$, $r^2=0.35$). All other species groups had r^2 values less than 0.06 (Table 7; Fig. 15). There was no relationship between the perimeter-area ratio and species richness for shrubs, graminoids, and non-native forbs ($p>0.244$), however native forbs showed a marginal and weak negative relationship ($p=0.058$, $r=-0.377$) (Fig. 16).

The rate of native forb vegetative expansion from different islands showed no correlation between size and rate of expansion at 0m, 1m, or 2m ($p>0.734$, 0 m $r=-0.070$, 1 m $r=0.070$, 2 m $r=0.028$) (Fig. 17). Perimeter-area ratio and the rate of native forb expansion at 0m, 1m, and 2m showed no correlation ($p>0.734$, 0 m $r=-0.066$, 1 m $r=0.070$, 2 m $r=0.028$) (Fig. 18).

1.4 Discussion

Study one demonstrates that the seed bank initially is the main driver of the plant community with greater cover on FFMM compared to PMM. Over time, multiple drivers shift the plant community resulting in the convergence of the plant community between both soil types, as depicted in Fig. 1. Reclamation soils are highly disturbed, having all plants removed. Therefore, it is beneficial to reclamation practices to determine how the plant community changes over time and what assembly mechanisms are causing the shift. The initially plant communities are distinct on both soil types, with FFMM early-successional non-native communities originating from the seed bank where PMM had almost no cover. Five years after material placement, plant communities are comparable in cover and shifted to a more native community on both soil types. The seed bank is still the largest contributor to the plant community on both soil types due to delayed germination and slow growth rates of native species. Seed rain and biotic dispersal are the next largest contributors with the addition of trees and other late-successional species on both soil types. Vegetative expansion from FFMM into surrounding PMM plays a smaller role in the convergence of plant cover on both soil types, with plants moving up to 2 m after five years. Competition does not seem to be a large contributor in shifting the community over time because there is still adequate available seedbeds and resources likely limiting competition. The results of study two indicate that five years after placement, island size and shape did not show any optimal configuration to increase species richness or vegetative expansion. The island technique is still a beneficial tool for reclamation, combining plant-rich FFMM with plant-poor PMM promotes the development and dispersal of species into adjacent areas but the size and shape of islands appears to be a relatively minor factor.

Seed bank

The seed bank plays a critical role in the establishment of the aboveground plant community on both the FFMM and PMM. However, FFMM had 5x more seed and 2x higher diversity compared to PMM. The increase of seed bank found within the FFMM is due to the LFH layer on the donor site having a dense seed bank (Buss et al. 2020; Mackenzie and Naeth, 2010; Macdonald et al. 2015). The initial plant community reflected the seed bank by having a 10x higher cover on the FFMM compared to the PMM. Initially, non-native forb species originating from the seed bank were the largest contributor to the aboveground community. Non-native species are highly adaptable and have rapid expansion, while acting as pioneer species; thus, they develop into the community first. Non-native species is why we see species originating from the seed bank accounting for 93% and 74% of the total proportion of cover on FFMM and PMM, respectively in Year 2. With that said, other studies found low amounts of non-native species within natural forest seed banks and an increase of those species in reclamation soils (Buss et al. 2020; Bellairs and Bell, 1993; Jauni et al. 2015). Therefore, the non-native forbs in the seed bank are likely originating from either after clearcutting or from contamination during removal or movement of soil (Knapp et al. 2016; Moore, 1980).

Seed bank originating non-native species dominated the plant community initially, over time there is a shift to native species originating seed bank dominating the plant community. At Year 5, species originating from the seed bank increased in absolute cover. Still, they decreased in total proportional cover because of the increase of seed rain and biotic dispersal originating species contributing to the community. The seed bank is still the largest contributor to the aboveground community, accounting for 64% and 43% of the total proportion of cover on FFMM and PMM, respectively. Native species are now the dominant functional group representing 28.6% and 16.7% of the total proportion of plant cover. Most of these native species were found within the initial vegetation community at Year 2 at very low frequency and cover. These species then increased over time, likely due to the facilitation by non-native species and the continuous establishment by seed (e.g., *Potentilla norvegica*, *Plantago major,* and *Rubus idaeus),* and growth of individual perennial plants (Tannas, 2001). Also, a small portion of the species within the seed bank can have an extended dormancy, which could lead to the delayed establishment (e.g., *Betula papyrifera, Cornus canadensis, and Mentha arvensis*) (Greene et al. 1999; Tappeiner and Alaback, 1998).

Based on species richness, about 65% of the species from the seed bank express themselves in the initial aboveground community on both FFMM and PMM. This rate increased to about 70% by Year 5. Melnik et al. (2018) also found 65.7% of species found within the seed bank expressing themselves within the aboveground community on a similar reclamation site. However, within various disturbances and ecosystems, the similarity between the seed bank and the aboveground community is not very high (Buss et al. 2020; Shang et al. 2016). In forested communities, there tends to be a lower similarity between the seed bank and aboveground plant community compared to disturbed sites (Grandin, 2001; Hopfensperger, 2007; Mackenzie and Naeth, 2010). Forested communities after a disturbance tend to have pioneer species that produce persistent seeds that remain in the seed bank, but do not establish years later because they are shade-intolerant (Grandin, 2001; Hopfensperger, 2007). Rico-Gray and Garcia-Franco (1992) found on slash and burn sites, shortly after there is higher similarity and with succession similarity decreases. The increased similarity shortly after a disturbance is likely due to increased light triggering germination (Grandin, 2001; Hopfensperger, 2007; Rico-Gray and Garcia-Franco, 1992). Dissimilarities can occur when species produce numerous seeds, leading to overrepresentation in the seed bank (Eriksson and Eriksson, 1997; Shang et al. 2016).

Most of the forb species establishing from the seed bank are upland species, such as *Fragaria virginiana*, *Vicia americana*, and *Geum macrophyllum*. Hydrophilic species such as *Typha latafolia, Juncus balticus*, and *Vaccinium vitis-idea* are absent in the aboveground community but are found in the seed bank, particularly in the wetland derived PMM. Species translocated from cold and wet environments to warmer and well-drained landscapes may not be able to establish into the community (Mackenzie and Naeth, 2010). Most of the graminoid species in the aboveground community originate from the seed bank (*Calamagrostis canadensis*, *Agrostis scabra*, and *Carex sp*.). These graminoid species are the most abundant below and above ground because they produce many seeds each season and can remain dormant in the seed bank (Buss et al. 2020; Fyles, 1988; Lieffers and Macdonald, 1993). The only tree species establishing through the seed bank was *Betula papyrifera,* as this species is one of the only boreal tree species that has a seed dormancy that can extend beyond one year (Greene et al. 1999).

Seed rain

Seed rain was similar across both soil types and the majority of species found within the seed traps were early successional forbs and wind-dispersed, similar to other results on disturbed areas (Jones and Landhäusser, 2018; Winterhalder 1996, Robinson and Handel 2000, Corbin et al. 2016). Seed rain had little impact on the initial plant community, but its impact increased over time to account for 20% of the total vegetation cover by Year 5. Similar to what we found, other studies have consistently shown wind-dispersed species being evenly spread across the site (Corbin et al. 2016; Jones and Landhäusser, 2018; Robinson and Handle, 2000). The initial even spread of seed rain species from the seed traps on both soil types is likely due to the low vegetation cover and high seedbed availability. Over time there is a continual addition of these wind-dispersed species, which was seen through the increase of cover and richness from seed rain originating species in the aboveground community. With more time, an increase of vegetative barriers, and a decrease of available microsites the potential for seed rain originating species to establish may be reduced (Hart and Chen, 2006). Adjacent patches and remnant plants act as local seed sources and strongly influenced the type of plant species establishing across the site. Colonization rates on disturbed sites can be strongly influenced remnant patches that are in close proximity and in some instances, colonization relies entirely on those species (Bochet et al. 2007; Mola et al. 2011).

In addition to herbaceous species, the vast majority of the non-planted trees (mainly *Populus tremuloides* and *Populus balsamifera*) and *Salix* species establishing on site are from seed rain. Tree and shrub species establishing from seed rain is common because their seeds are not viable within the seed bank and are adapted for wind-dispersal (Greene et al. 1999; Gallagher et al. 2011; Corbin et al. 2016). Studies on abandoned mine and landfill sites have found with no planting the dominant tree species were all wind-dispersed (Gallagher et al. 2011; Corbin et al. 2016). Most tree and shrub species found on the reclamation site were established from the seed rain onto the PMM. Since, PMM creates ideal conditions for seedling establishment compared to FFMM due to its greater water holding capacity, organic matter, surface roughness, and reduced vegetation competition (Pinno and Errington, 2015). These conditions cause beneficial alterations and microclimatic effects such as temperature and evaporation, increasing trapped seeds, and creating microsites (Bradshaw, 2000).

Biotic dispersal

A variety of forb and shrub species were found throughout the site that did not originate from either the seed bank or seed rain. Many of these species require biotic dispersal by birds and mammals within the boreal forest (Matlack, 1994). Birds, in particular, have been observed as a predominant dispersal method in other island reclamation studies (Cole et al. 2010; Zahawi and Augspurger, 2006; Zahawi et al. 2012). At Year 2, biotic dispersed species were very low; however, over time, the proportion of total vegetation cover based on biotic dispersed species increased by 8.4% and 11.8% on FFMM and PMM, respectively. Recruitment patterns of biotic dispersed species were higher on the PMM, which was different from another study that found recruitment patterns were not concentrated in or around the tree patches (Corbin et al. 2016). The increase in the tree and shrub canopy in the PMM establishes favorable conditions to attract birds and other mammals that might disperse seed, compared to FFMM (Cole et al. 2010; Zahawi and Augspurger, 2006; Zahawi et al. 2012). Our study found a combination of late-successional fruit-bearing woody species (*Ribes sp*., *Sheperdia canadensis*, *Arctostaphyos uva-ursi*), native forb species (*Trifolium pratense, Rubus pubescens, Galium triflorum*), and graminoids *(Leymis innovates, Elymus canadensis)* potentially establishing through biotic dispersal. Many studies looking at patches have demonstrated that the establishment of species through animal-dispersal tends not to be desirable late-successional species but rather early-successional and other small-seeded species (Corbin et al. 2016; Zahawi et al. 2013). In contrast, Robinson and Handel. (2000) found new woody recruitment appeared to establish within the first couple of years following reclamation. The increased recruitment of the late-successional shrubs being concentrated on the PMM is beneficial since the conditions created by the peat are favorable for the establishment of woody species (Pinno and Hawkes, 2015; Pinno and Errington, 2015). Native species and late-successional shrubs establishing from biotic dispersal are contributing to the species pool early on, which is a positive sign for the vegetation community and reclamation practices.

The proximity to the remnant forest will affect the ability of seed-dispersing animals to move through the landscape (DeClerck et al. 2010). The reclamation site is located beside a river with remnant forests on two sides, leading to a continual dispersal of late-successional species. In contrast, Jones and Landhäusser. (2018) found limited evidence of biotic dispersal on a similarly aged oil sands reclamation site. However, their site was isolated in the center of a large mine with no intact forest for several kilometers, which may have limited availability for biotic dispersal of late-successional fruit-bearing species. By comparing both studies that are similar in age and island technique, we can see the importance of distance to remnant forests when using a passive reclamation technique to increase the ability of biotic movement through the reclamation site.

Plant expansion

Vegetative expansion from native forbs accounts for the largest proportion of dispersal, although overall, there was a slow rate of expansion into the surrounding PMM. The bulk of species and the largest variety of species expanding from the FFMM into the PMM were native forbs since most of the non-native and graminoid species use wind or gravity dispersal strategies. Native forb species are generally expanding at a slow rate into the PMM with the dispersal of on average up to 2 m after 5 years. Jones and Landhäusser (2018) found similar rates of vegetative expansion from FFMM into PMM from an average of less than 2 m to a maximum of 4 m. The main species showing vegetative expansion were species using stolons (*Fragaria virginiana*). *Fragaria virginiana* per individual plants may produce one to four stolons a season and non-branching stolons will root when in contact with moist substrate up to 1 m from the parent plant (Angevine, 1983). The expansion of *Fragaria virginiana* is slow because stolons decay by late summer, losing the connections between nodes (Angevine, 1983). The slow expansion of vegetative species from intact areas into recently disturbed areas is commonly observed (Corbin et al. 2016; Rey Benayas et al. 2008; Winterhalder 2004). The cover of each species using vegetative reproduction is generally low on the FFMM, leading to the lower expansion ability. Species using vegetative reproduction tend to have slow rates of dispersal. Therefore, the potential for being outcompeted by species with high rates of reproduction and expansion ability is high. PMM typically has a high water-holding capacity, which may contribute to vegetative dispersal, particularly those species utilizing belowground expansion (rhizomes) (Mackenzie and Naeth, 2010). In contract, species using aboveground reproduction, such as stolons, will be more susceptible to desiccation. The slow rate of expansion as a result of the use of vegetative dispersal has been identified as one of the limitations of using patches in reclamation (Robinson and Handel, 2000).

Competitive interactions

The vegetation community after 5 years has a random structure indicated by limited positive and negative co-occurrence patterns (73% random) as is the norm during the initial years after reclamation (Dhar et al. 2018; Zaplata et al. 2013). Competition will likely play a larger role in structuring the vegetation community in the future. Currently, there are adequate available seedbeds and resources, thereby limiting that amount of competition occurring.

Non-native forb species cover was initially high on FFMM but decreased over time. On PMM, non-native species were initially low and increased over time. This is in agreement with other studies that have shown higher non-native cover on FFMM within 1 to 3 growing seasons compared to PMM (Errington and Pinno, 2015; Mackenzie and Naeth, 2010). By year 5, other studies have found that PMM had a higher non-native cover (Forsch, 2014). The initial spike of non-native forb species on FFMM indicates that these species are exploiting initial resources, higher nutrient concentrations, and lower moisture content (Alday et al. 2011; Buss et al. 2018; Gingras-Hill et al. 2018). Non-native forbs on FFMM do not appear to be having a negative impact on the vegetation community; instead, they are acting as a niche filler and potentially facilitating the establishment and growth of native forbs. For example, one of the non-native forbs colonizing the site was *Melilotus alba,* which as a nitrogen-fixing legume would presumably produce large amounts of soil organic matter, increase nitrogen mineralization, increase shade reducing seed desiccation, and increase pollinators presence, thus facilitating the development of native species (Foster and Tilman, 2000; Spellman et al. 2015; Tilman and

Wedin, 1991). The decrease of non-native forbs on the FFMM is likely due to competition. The life history of the non-native species found on the FFMM is generally fast-growing annuals or biennials, which were found to be displaced by slower-growing long-lived perennial native species. The decrease of non-natives over time is likely due to the ability of native species to be superior competitors for limited soil nitrogen (Foster and Tilman, 2000). The initial spike did not occur on PMM because a large proportion of the species were only found within the FFMM seed bank. Over time the increase of non-native forbs was because the site was never fully occupied (with a mean cover of 40%) with roughly 20% bare soil for available seedbeds. Thus, processes of competitive interactions had little influence on the total vegetation community since there was still room for development on the PMM. The same trend present on the FFMM in time may occur on the PMM; however, non-native forbs do not seem to have a negative impact on the vegetation community across the site.

Graminoid species cover, particularly *Calamagrostis canadensis,* generally increases following a disturbance in the boreal forest and can impede the development of forbs and trees (Landhäusser and Lieffers, 1998; Landhäusser et al. 2007). However, there was no direct evidence of competition between graminoids and other plant functional groups on either soil type. In some cases, with the emergence of native perennial grasses, all native forb species were reduced to 10% cover, but they primarily have been shown to impact the development of tree species (Brown and Bugg, 2001; Henkel-Johnson et al. 2015; Landhäusser et al. 2007). After five years, graminoid cover remained higher on FFMM than PMM, which could be why there is a lower tree cover on FFMM.

FFMM islands

The focus of the island reclamation design was to quantify the optimal size and configuration of high diversity FFMM islands. However, FFMM islands did not indicate a particular size or shape associated with increased species richness. Wardle and Jonsson (2014) in Sweden's boreal forest studied island found within lakes. They found that island size only showed a modest response to the aboveground plant community after 14 years post-disturbance (Wardle and Jonsson, 2014). An initial study of the same FFMM islands found a positive relationship between island size and species richness (Pinno et al. 2016). Pinno et al. (2016) determined that the initial island size that would be 671 m^2 to reach 75% (32 species) of species found within the largest island. Their number was similar to the number of species found in a nearby aspen-dominated mixed wood stand that was disturbed by fire (Li et al., 2014; Pinno et al. 2016). However, the initial study likely reflected the seed bank community within the islands, but over time, the study reflects the seed bank but also seed rain and biotic dispersal. My study on the same site over time did not show the same trend in species-area curves. For example, to achieve the same 75% of total species from the largest island (63 species) would be achieved at 10 islands ranging in size from 541 to 7348 m^2. Island size seems to be important in the early development of the vegetation community, while over time is not as significant on establishing the community.

Island size and shape did not seem to influence vegetation expansion or alter species richness. Patch shape determines the length of patch edge that is directly in contact with the surrounding environment so patches with a higher ratio of edge to interior have a greater proportion of plants in the edge habitat compared to patches with a low ratio (Collinge, 1996). Moen and Jonsson. (2003) suggested that when using smaller islands, a lower perimeter-area ratio should be used to increase interior conditions. Island shape may not have been as critical to my study as both soil types offered high quality growing conditions. However, on other island reclamation sites that may have lower propagule richness PMM soil having a lower perimeter-area ratio may be necessary for reducing the edge effects on the FFMM species. Islands need to be able to facilitate the development of native species as they emerge from the seed bank. Making islands with a higher perimeter-area ratio may increase exposure and decrease the vigor of emerging plants. However, by increasing the perimeter-area ratio, this may enhance the ability for expansion of pioneer species to facilitate the development of other species in the future. The rate of expansion into the surrounding PMM was not influenced by island size or shape. Making islands too large may limit the dispersal of species that utilize vegetative expansion and non-wind-dispersed seeds.

1.5 Conclusion

1.5.1 Research Summary

In the boreal forest, oil sands mining creates a large-scale disturbance on Alberta's landscape that will need to be reclaimed. Reclamation practices must create sites that allow for a self-sustaining ecosystem to develop, which includes establishing a native plant community. The island reclamation technique was developed to combine pre-disturbance plant-rich upland FFMM within otherwise plant-poor lowland PMM. This technique was used to promote the development and dispersal of understory species into adjacent areas, while allowing for tree establishment on PMM in conditions with reduced competition. The main objective of this research was to explore plant community assembly mechanisms on various soil designs (material type and configuration) on an upland reclamation site over time. The first study examined a sequenced approach to characterize the change in plant community over time on FFMM and PMM by examining the assembly mechanisms, i.e., seed bank, seed rain, biotic dispersal, vegetative expansion, and competition. The second study evaluated the effect of island size, shape, and configuration on the plant community.

Initially saw the seed bank was critical in the establishment of species initially with 5x more seeds within the FFMM seed bank, which was reflected by 10x higher cover in the aboveground community in Year 2 compared to PMM. The initial aboveground colonization on the FFMM was from non-native species originating from the seed bank. In addition to the seed bank, the next largest mechanisms influencing the initial plant community was seed rain and biotic dispersal. Over time on the FFMM, there was a shift in the seed bank originating species to a native forb and graminoid community. This shift away from non-natives was due to the life cycle of non-native forbs, competition, and facilitation. With the addition of seed rain and biotic dispersed species by year 5, the aboveground community was similar on both soil types. Seed rain from seed traps was similar across both soil types; this was because 62% of the species use wind-dispersal. Wind-dispersed tree species originating from seed rain that established on the PMM due to the preferable seedbed conditions, including surface roughness, organic matter, and increased soil moisture. Biotic-dispersed species established on both soil types, potentially due to an increase of favorable habitat conditions over time. Therefore, in the future, post canopy closure, the plant community will increase in structure and have additional shifts towards a late-successional community. By year 5, native forbs using vegetative dispersal were expanding into the PMM up to 2 m from the FFMM islands. The development and expansion of plant species from the FFMM islands into the surrounding PMM was not strongly influenced by island size or shape; however, it is critical to have both soil types separated on the reclamation site when developing an understory and overstory. These results create a better understanding of the successional trajectory and plant assembly mechanisms, which will lead to a self-sustaining ecosystem.

1.5.2 Research Applications

The results of this research demonstrated the benefits of strategically utilizing directly placed upland FFMM as it is a limited resource with an abundant seed bank within an abundant resource of lowland PMM. The seed bank is one of the most important components in developing the aboveground vegetation community; therefore, methods in reducing the degradation of the seed bank is critical. The non-native species found in the seed bank were likely due to contamination during salvage and placement. Determining how non-native species are contaminating the seed bank could lead to developing operational methods to prevent contamination.

Seed rain and biotic dispersal were the next largest factors in the development of a native community. Developing reclamation sites that are located near remnant patches of vegetation or perhaps older reclamation when possible will enhance native seed rain and biotic dispersal into the reclamation site. These dispersal mechanisms are key in the long-term success of the site since a large portion of late-successional boreal species are not found within the seed bank (Fyles, 1989). To enhance those mechanisms, there are potential landscape planning designs that could be put into practice. Some of them include: reclaim sites closer to the outside of the claim first, leaving some patches around the mine, or stagger reclamation to allow for reclamation areas to have an increased structure then reclaim the sites adjacent. Having trees and other materials such as coarse woody debris or bird nests on-site will also increase habitat, therefore, increasing the potential of biotic late-successional dispersed species.

Due to the low availability of propagule rich FFMM having many smaller islands that have low perimeter: area ratios (round or square in shape) surrounded by PMM can achieve high rates of species richness in the FFMM islands. We found the separation of the soil types to be essential in the establishment of the understory and overstory. Having FFMM islands still allows for the understory species to establish from the seed bank while separating the PMM, there is a greater chance of tree seedling survival and recruitment due to the specific seedbed conditions and reduced competition. Over time the canopy will reduce shade-intolerant and wind-dispersed species allowing for the increase of late-successional species. In terms of operational constraints of the island reclamation approach, future reclamation areas can be less structured without a predetermined layout of islands. Creating increased island structure is time-consuming and expensive due to surveying and equipment costs, as well as operator hours and expertise. Another potential method could be randomly dumping loads of FFMM within a matrix of PMM that may serve to recreate the critical aspects of the islands, which includes propagule-rich islands, conservation of limited FFMM soil, and increased landform diversity (Pinno et al. 2016).

1.5.3 Study Limitations and Future Research

The variation within the FFMM islands and potentially other island reclamation sites could be due to the differences between donor sites, the quality of soil collected, and how the soil was placed. In my study, seedbed conditions were generally favorable on both soil types, which is why we saw overall a high diversity by Year 5. The study was initially divided into multiple sections occurring over multiple years and at varying locations. Therefore, there was no replication between the seed bank, seed rain, and aboveground vegetation community. A direct comparison between the mechanisms and the aboveground vegetation community cannot be made. From the initial placement of long-term sampling plots, having one design for multiple aspects may be beneficial to enhance repetition and directly link all components of vegetation assembly.

When initially placed the islands where not officially marked out on the ground, therefore, after 5 years the FFMM island boundary was not distinct due to vegetation and soil movement. The full vegetation survey of the islands was based on GPS files used to stake out the islands for the operator originally. Due to operator constraints during placement, there was potential for the initial mixing of soil at the boundary or placing over the boundary. In the future, when continual monitoring is being conducted, some method of marking out the sections may be beneficial to remain on site.

Future reclamation projects should move towards a long-term monitoring plan before salvage to after reclamation is completed. One of the critical components that are often missing when studying reclamation sites is information about the donor site. Completing surveying on pre-salvage for the above and belowground vegetation community and soil conditions would enhance the ability to allocate resources to sites with potentially lower quality soil and seed bank conditions.

Further research into understanding how various assembly mechanisms directly impact the vegetation community in the longer-term on different types of FFMM and PMM configurations would be vital in determining if passive reclamation and current practices are efficient in creating a self-sustaining ecosystem. Understanding how species are establishing and dispersing on-site and the methods behind increasing dispersal rates would be instrumental for passive reclamation. Thus, including studies on the effect of canopy cover, nest boxes, and coarse woody debris effect on enhancing habitat to increase the rate of biotic plant dispersal would help in potentially reducing costs and increase desirable species. Analysis of early successional development on functional groups based on their dispersal or life-history strategies and the role of colonization processes improves our understanding of post-reclamation vegetation dynamics. Increasing our understanding of plant community assembly would allow us to help identify stages in reclamation where it might be important in guiding future reclamation strategies. Therefore, further research and monitoring of the long-term effects of non-native and graminoid species on vegetation communities on reclamation sites are essential to developing management practices.

In addition to the research listed above, continued monitoring of the FFMM islands and surrounding PMM should also be conducted. In this study, we saw no optimal size or shape of islands that would increase species richness; however, over time, with succession island size and shape may become significantly more important for richness of the vegetation community. Studies looking at smaller FFMM islands with a reduced structure or other various configurations are of particular interest because it would determine if this technique would show similar results in different locations.

Overall, reclamation studies need to move away from a single short-term survey to a long-term multi-discipline approach. Vegetation establishment is one factor of a self-sustaining ecosystem; therefore, an ecosystem approach would help in understanding how each component influences each other, which will lead to more effective reclamation practices.

Tables

Table 1. Soil characteristics for FFMM and PMM. Values are means (standard error).

	FFMM	PMM	*p*
Soil pH	6.7 (0.11)	6.6 (0.11)	0.850
Volumetric water content (%)	17.6 (1.14)	24.5 (1.14)	**<0.001**
Soil temperature (°C)	14.3 (0.21)	15.1 (0.21)	**0.005**
Calcium (µg/10 cm^2 /7 days)	2165.6 (96.72)	1857.1 (129.63)	**<0.001**
Magnesium (µg/10 cm^2 /7 days)	405 (19.41)	377.6 (14.97)	**<0.001**
Potassium (µg/10 cm^2 /7 days)	47 (13.76)	31.3 (5.79)	**<0.001**
Phosphorous (µg/10 cm^2 /7 days)	1.3 (0.13)	0.7 (0.08)	**<0.001**
Nitrate (µg/10 cm^2 /7 days)	31.5 (10.51)	18.65 (8.92)	0.430
Ammonium (µg/10 cm^2 /7 days)	1.5 (0.31)	1.09 (0.57)	0.210

Table 2. PermANOVA results with mean values (standard errors) for number of seedlings germinated from the seed bank functional groups comparing FFMM and PMM with depths of 0-5 cm and 5-10 cm.

		p	FFMM 0-5cm	FFMM 5-10cm	PMM 0-5cm	PMM 5-10cm
Native Forb	Soil Type	**<0.001**	22.29 (6.71)	27.14 (8.60)	2.14 (0.59)	3.21 (1.03)
	Depth	0.706				
	Soil x Depth	1.00				
Graminoid	Soil	**<0.001**	26.21 (3.77)	35.21 (9.76)	7.00 (2.53)	5.64 (1.40)
	Depth	0.980				
	Soil x Depth	0.271				
Non-Native Forbs	Soil	**<0.001**	7.64 (2.44)	10.50 (3.12)	1.07 (0.30)	1.76 (0.60)
	Depth	0.408				
	Soil x Depth	0.726				

Table 3. Total cover (%) of species originating from each assembly mechanism (seed bank, seed rain, and other dispersal), leaf litter, and bare soil. Values are averages (standard error) for each soil type and year. Total proportion of cover (%) are separated by year and soil type for each assembly mechanism.

	Total cover (%)				Total Proportion of Cover (%)			
	Year 2		Year 5		Year 2		Year 5	
	FFMM	PMM	FFMM	PMM	FFMM	PMM	FFMM	PMM
Seed Bank	25.85 (8.09)	2.82 (0.62)	28.46 (2.19)	18.66 (1.15)	93.55	73.85	63.58	43.45
Seed Rain	1.24 (0.37)	0.64 (0.12)	11.63 (1.35)	15.17 (1.35)	4.48	16.75	25.98	35.33
Biotic Dispersal	0.54 (0.23)	0.36 (0.13)	4.67 (0.98)	9.11 (1.01)	1.97	9.39	10.44	21.22
Bare Soil	72.37 (7.67)	95.9 (0.95)	5.00 (1.32)	20.8 (1.99)				
Leaf Litter	0	0.28 (0.31)	50.24 (2.23)	36.26 (1.12)				

Table 4. Total cover (%) of each functional group (native forbs, graminoids, non-native forbs, shrubs, and trees) originating from the assembly mechanism (seed bank, seed rain, and biotic dispersal). Values are averages (standard error) for each soil type and year. Total proportion of cover (%) are separated by year and soil type for each assembly mechanism.

		Total Cover (%)				Total Proportion of Cover (%)			
		Year 2		Year 5		Year 2		Year 5	
		FFMM	PMM	FFMM	PMM	FFMM	PMM	FFMM	PMM
Native Forbs	Seed Bank	2.83 (0.73)	0.88 (0.24)	12.78 (1.39)	7.16 (0.73)	10.23	23.15	28.56	16.68
	Seed Rain	1.11 (0.37)	0.52 (0.12)	9.66 (1.42)	7.31 (0.80)	4.01	13.6	21.59	17.03
	Biotic	0.18 (0.08)	0.29 (0.11)	3.75 (0.61)	7.66 (0.82)	0.64	7.53	8.39	17.83
Graminoid	Seed Bank	1.14 (0.48)	0.30 (0.09)	8.46 (0.96)	4.84 (0.43)	4.11	7.95	18.9	11.26
	Seed Rain	0.06 (0.03)	0.02 (0.01)	0.36 (0.07)	0.45 (0.07)	0.2	0.41	0.80	1.05
	Biotic	0.34 (0.18)	0.03 (0.02)	0.52 (0.11)	0.89 (0.13)	1.25	0.67	1.16	2.06
Non-Native Forbs	Seed Bank	21.89 (6.50)	1.63 (0.01)	7.22 (0.99)	6.66 (0.61)	79.21	42.75	16.13	15.5
	Seed Rain	0.05 (0.05)	0.00	0.37 (0.10)	0.81 (0.28)	0.19	0.00	0.83	1.90
	Biotic	0.02 (0.01)	0.03 (0.02)	0.13 (0.05)	0.49 (0.21)	0.08	0.65	0.29	1.15
Shrubs	Seed Rain	0.00	0.00	0.92 (0.37)	1.46 (0.33)	0.01	0.05	2.06	3.39
	Biotic	0.00	0.02 (0.01)	0.27 (0.15)	0.08 (0.03)	0.00	0.54	0.61	0.18
Tree	Seed Rain	0.02 (0.02)	0.1 (0.02)	0.31 (0.10)	5.14 (0.84)	0.07	2.70	0.69	11.97

Table 5. PermANOVA comparing counts (standard error) of seedlings emerging from the seed rain samples for all species and by functional groups (native forbs, non-native forbs, and graminoids), and dispersal mechanisms of native forbs (gravity, vegetative, and wind).

		p	FFMM	PMM
Functional groups	Total	1.00	265.57 (151.47)	276.25 (110.98)
	Native Forbs	0.962	79.22 (37.75)	83.28 (26.01)
	Non-Native	0.084	160.05 (138.43)	72.45 (38.34)
	Graminoids	0.055	26.32 (22.23)	120.52 (135.22)
Dispersal mechanisms for Native Forbs	Gravity	1.00	2.38 (1.92)	6.58 (15.22)
	Vegetative	**0.020**	7.47 (15.34)	0.30 (0.29)
	Wind	1.00	69.35 (50.62)	76.40 (35.50)

Table 6. RTEI results were testing the percent cover of functional groups (graminoid, non-native forbs, and native forbs), dispersal mechanisms for native forbs (wind, gravity, and vegetative), and an example species for vegetative dispersal (Fragaria virginiana) in FFMM and PMM 0-4, 10, 15, and 20 m. Significant values were percentiles, the bolded ones are considered significantly different between the FFMM and PMM locations. $p < 2.5$ (significantly less than the FFMM) and $p > 97.5$ (significantly higher than the reference).

		FFMM	0m		1m		2m		3m		4m		10m		15m		20m	
		Mean (SE)	Mean (SE)	*p*	Mean (SE)	*p*	Mean (SE)	*p*	Mean (SE)	*p*	Mean (SE)	*p*	Mean (SE)	*p*	Mean (SE)	*p*	Mean (SE)	*p*
Functional Groups	Graminoid	9.89 (4.98)	7.13 (0.78)	**0.1**	6.59 (0.78)	**0.10**	4.77 (0.61)	**0.10**	5.43 (0.72)	**0.10**	5.69 (0.78)	**0.10**	6.51 (1.44)	**0.10**	6.11 (1.28)	**0.10**	4.69 (0.70)	**0.10**
	Non-Native	7.88 (5.26)	7.79 (1.66)	51.4	6.23 (0.74)	3.15	6.97 (0.86)	16.15	8.47 (1.11)	17.05	6.17 (0.59)	3.35	9.71 (1.21)	96.40	7.16 (1.45)	26.20	9.36 (1.64)	91.30
	Native Forb	19.67 (9.93)	21.06 (2.19)	76.7	18.21 (2.23)	19.75	16.50 (1.55)	2.80	20.73 (2.23)	71.55	18.21 (2.14)	25.50	17.84 (2.68)	20.00	19.69 (2.03)	54.30	18.41 (2.40)	28.70
Native Fob Dispersal Mechanisms	Vegetative	15.50 (9.63)	15.77 (1.96)	57.2	12.24 (1.52)	**0.9**	12.64 (1.81)	**2.1**	10.40 (1.41)	**0.1**	10.77 (1.59)	**0.2**	10.63 (2.06)	**0.2**	10.34 (2.06)	**0.2**	10.81 (2.01)	**0.3**
	Wind	8.25 (6.79)	7.19 (1.10)	20.95	7.21 (1.02)	20.1	7.69 (0.88)	34.4	7.57 (1.14)	34.2	7.16 (1.27)	20.5	7.10 (1.02)	21.1	5.29 (0.98)	0.2	6.83 (0.99)	12.9
	Gravity	0.31 (0.25)	0.54 (0.11)	99.25	0.59 (0.13)	99.8	1.20 (0.34)	100	0.74 (0.24)	100	0.54 (0.11)	99.65	0.69 (0.10)	99.9	0.70 (0.19)	99.9	0.71 (0.13)	100
Example of a Vegetative Dispersal Species	*Fragaria virginiana*	0.88 (0.30)	1.66 (0.69)	95.75	1.21 (0.51)	80.6	0.34 (0.13)	**2.40**	0.07 (0.06)	**0.10**	0.07 (0.06)	**0.10**	0.29 (0.20)	**1.20**	0.14 (0.14)	**0.15**	0.16 (0.10)	**0.10**

Table 7. Species-area curve model fitting for functional groups (graminoid, non-native forb, shrub, and native forb) showing AICc, weight, and adjusted r^2 for each curve type. Curve models shown below have passed validation checks and are ranked based on the best fit. Curve types: Loga= logarithmic, koba= Kobayashi, asymp= asymptotic, negexpo= Negative exponential, weibull= Cumulative Weibull 3 par, mmf= Morgan-Mercer-Flodin.

Functional Group	Curve Type	Weight	AICc	r^2 Adj
Graminoid	power	**0.22**	**39.7**	**0.03**
	loga	0.13	37.77	0.03
	koba	0.21	39.77	0.03
	monod	0.11	41.08	-0.02
	asymp	0.06	42.11	0.004
	negexpo	0.05	42.49	-0.08
	weibull	0.05	42.16	-0.01
	mmf	0.05	42.16	-0.01
Non-Native Forb	power	**0.23**	**41.86**	**0.06**
	loga	0.22	42.02	0.06
	koba	0.22	42.02	0.06
	monod	0.11	43.31	0.01
	asymp	0.06	4.46	0.03
	mmf	0.06	44.68	0.02
	weibull	0.06	44.68	0.02
	negexpo	0.04	45.65	-0.08
Shrub	koba	**0.19**	**58.9**	**0.06**
	loga	0.19	58.9	0.06
	power	0.18	58.92	0.06
	monod	0.16	59.16	0.05
	negexpo	0.1	60.13	0.02
	asymp	0.06	61.14	0.04
	weibull	0.05	61.58	0.03
	mmf	0.05	61.64	0.02
Native Forb	asymp	**0.33**	**78.98**	**0.35**
	power	0.22	79.77	0.28
	koba	0.16	80.46	0.26
	loga	0.16	80.46	0.26
	weibull	0.06	82.59	0.25
	mmf	0.06	82.59	0.25

Figures

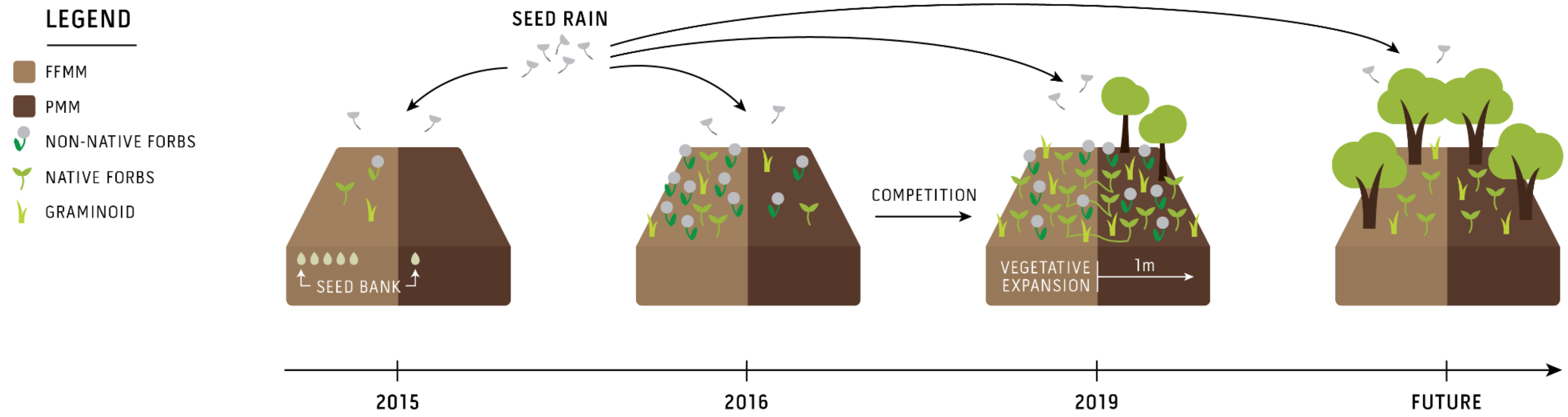


Fig. 1. Diagram of reclamation sites plant assembly over time and soil type. In 2015 the seed bank and seed rain is expected to play a large role on the FFMM with reduced on PMM. By Year 2 most of the cover on the FFMM will be from the seed bank and seed rain compared to PMM will mainly be influenced by seed rain. Over time we expect to see competition to play a role in structuring the plant community on both soil types. By 2019 we expect species that established from the FFMM seed bank to expand into the PMM with continual addition from seed rain and biotic dispersal to develop trees and woody species on the PMM. As we move into the future there is a convergence of both the overstory and understory.

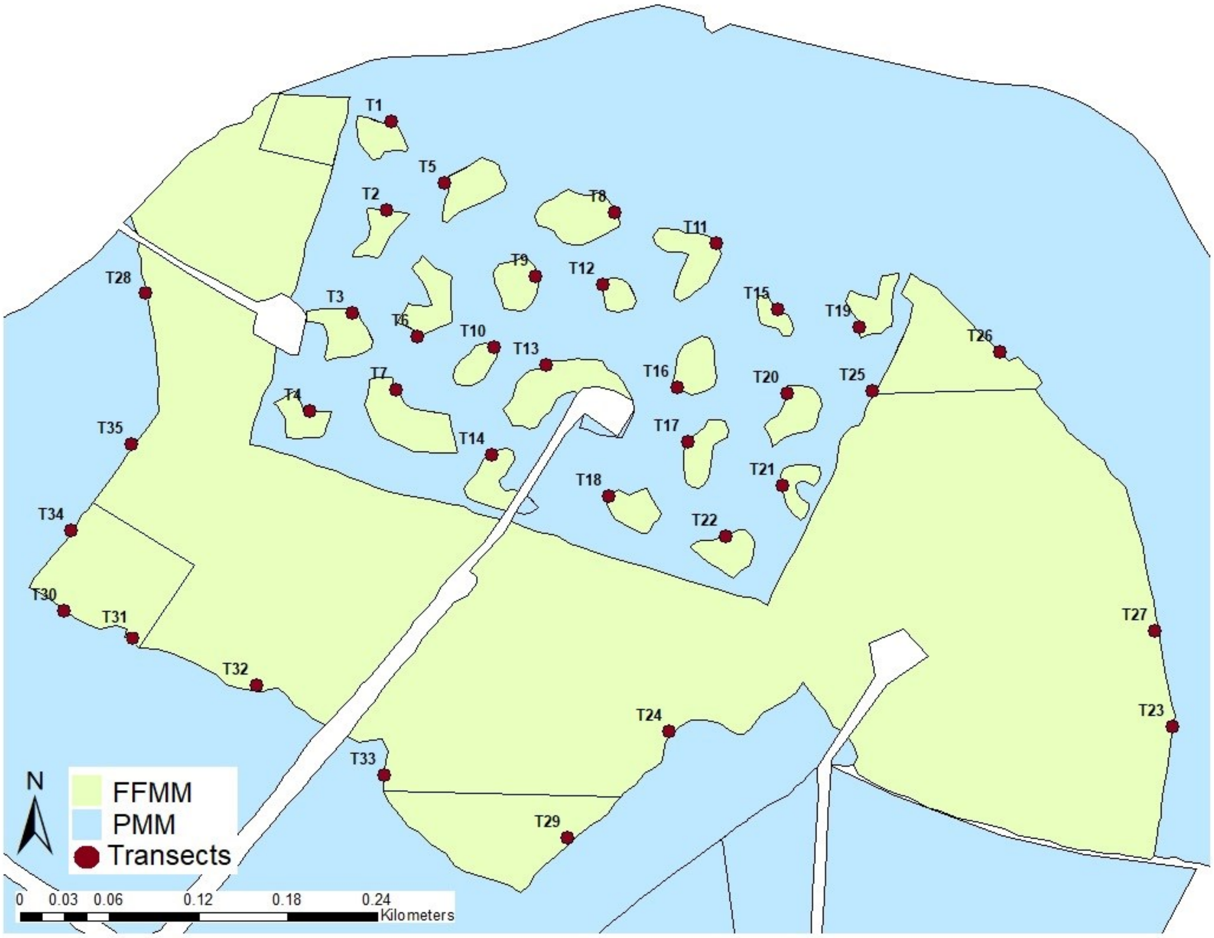


Fig. 2. Map of the 9.5-hectare overburden island reclamation site on an oil sand mine Northwest of Fort McMurray, Alberta Canada. The points represent transect locations.

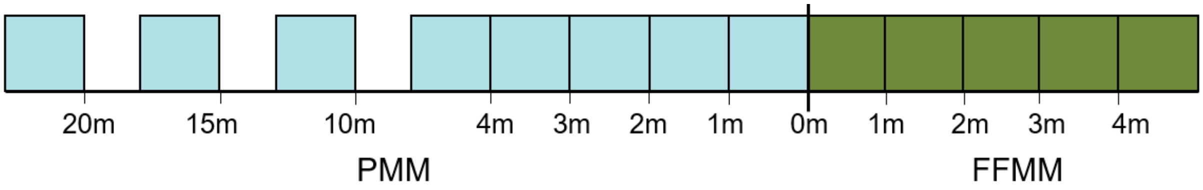


Fig. 3. Transect with 1x1m plant quadrats extending 5 m into the FFMM and 20 m into the PMM at each FFMM island. Black boxes are soil collection locations, light grey boxes are PMM 1x1m plant quadrats, and dark grey boxes are FFMM 1x1m plant quadrats.

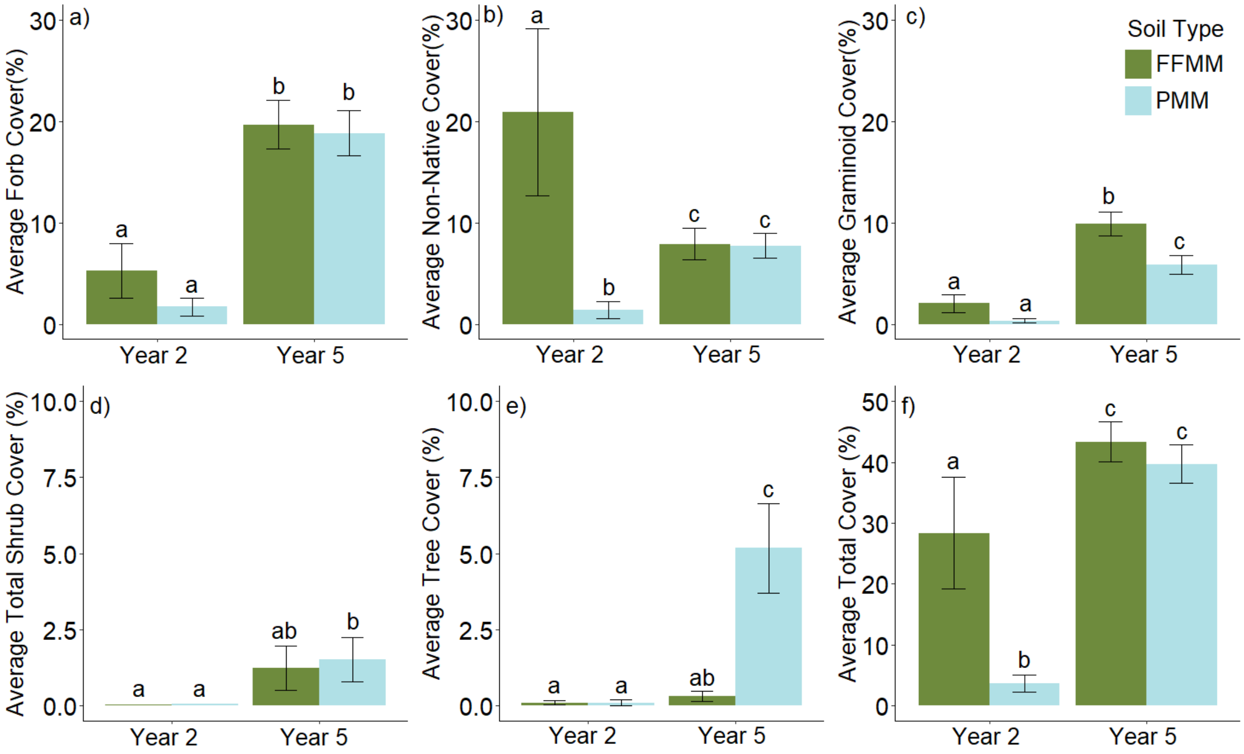


Fig. 4. Average cover of different functional groups (a=native forb, b=non-native forb, c=graminoid, d=total shrub, e=tree, and f=total cover) in Year 2 (n=10) and Year 5 (n=35) in FFMM and PMM. Significant letters are based on permANOVA results showing the interaction over time and between soil types. Values are means with standard error bars.

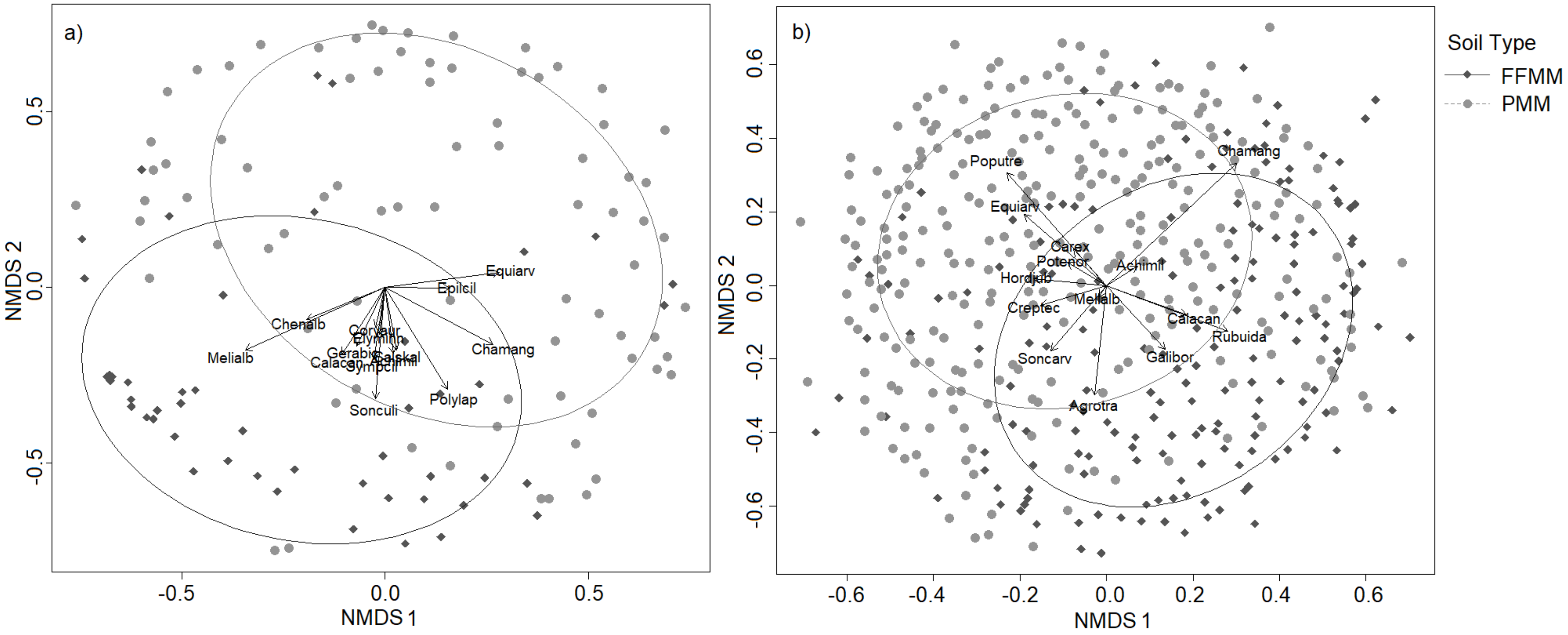


Fig. 5. 2D NMDS of plant species cover a) Year 2 and b) Year 5. The variance explained by the two axes was a) 32.4% with a minimum stress value of 0.331, b) 31.7% with a minimum stress value of 0.428. The vectors represent the 15 most frequent plant species found within the site at Year 2 and Year 5.

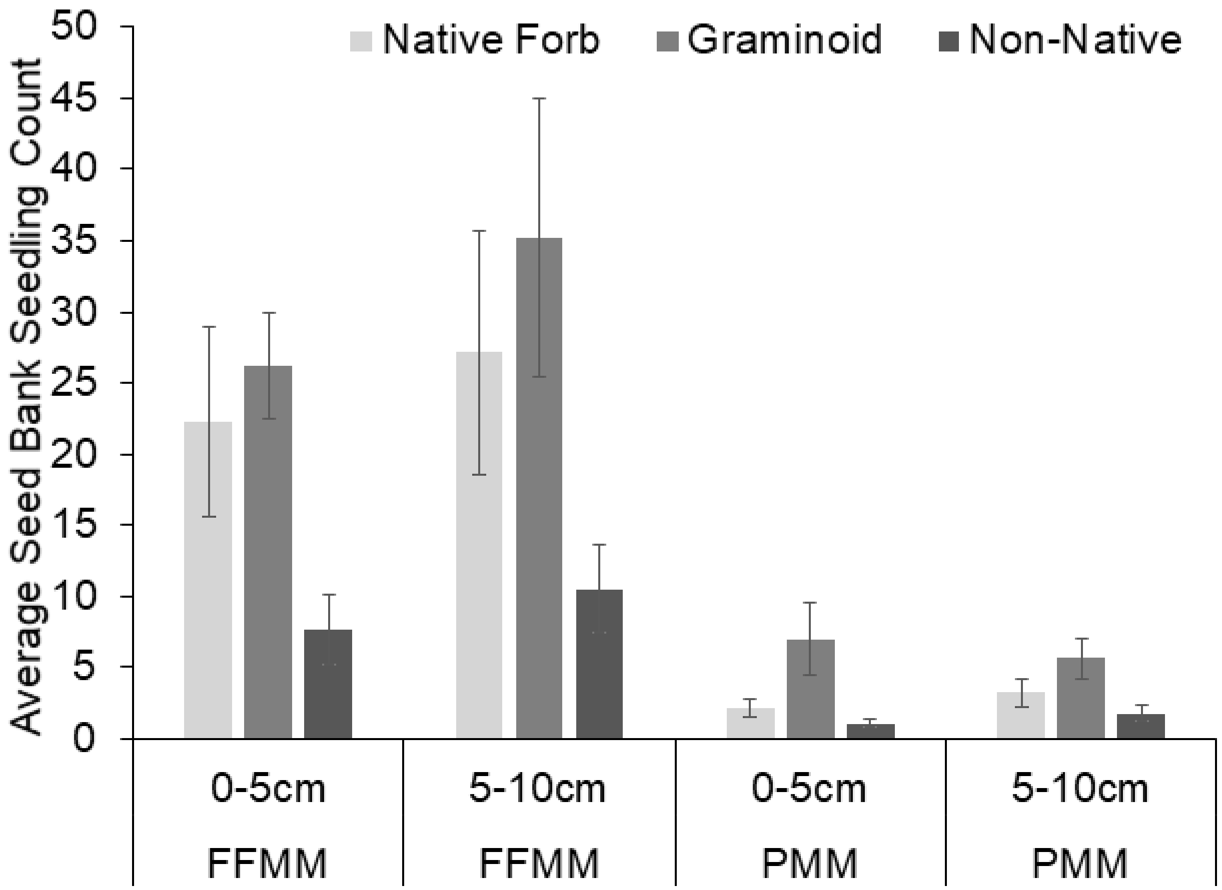


Fig. 6. Average seedling count for functional groups (forbs, graminoid, and non-native forbs) at depths of 0-5 cm and 5-10 cm for FFMM and PMM in the seed bank. Values are means with standard error bars.

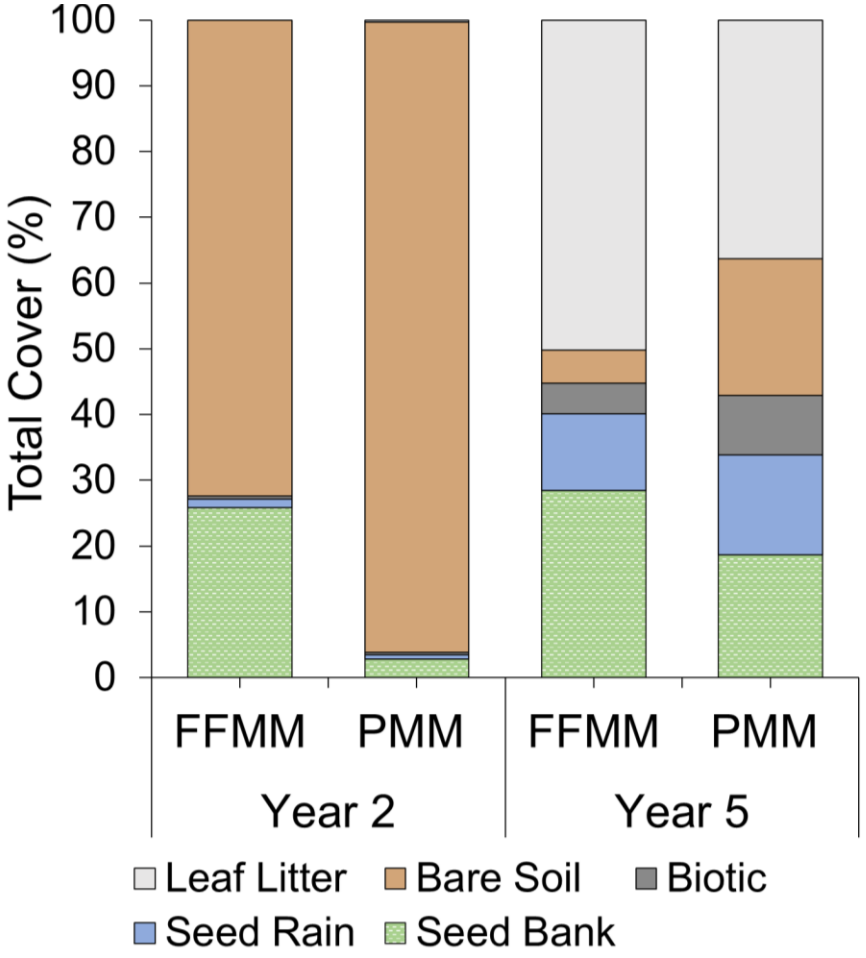


Fig. 7. Total cover from species originating from the seed bank, seed rain, and biotic dispersal, bare soil, and leaf litter in Year 2 and Year 5 in both soil types.

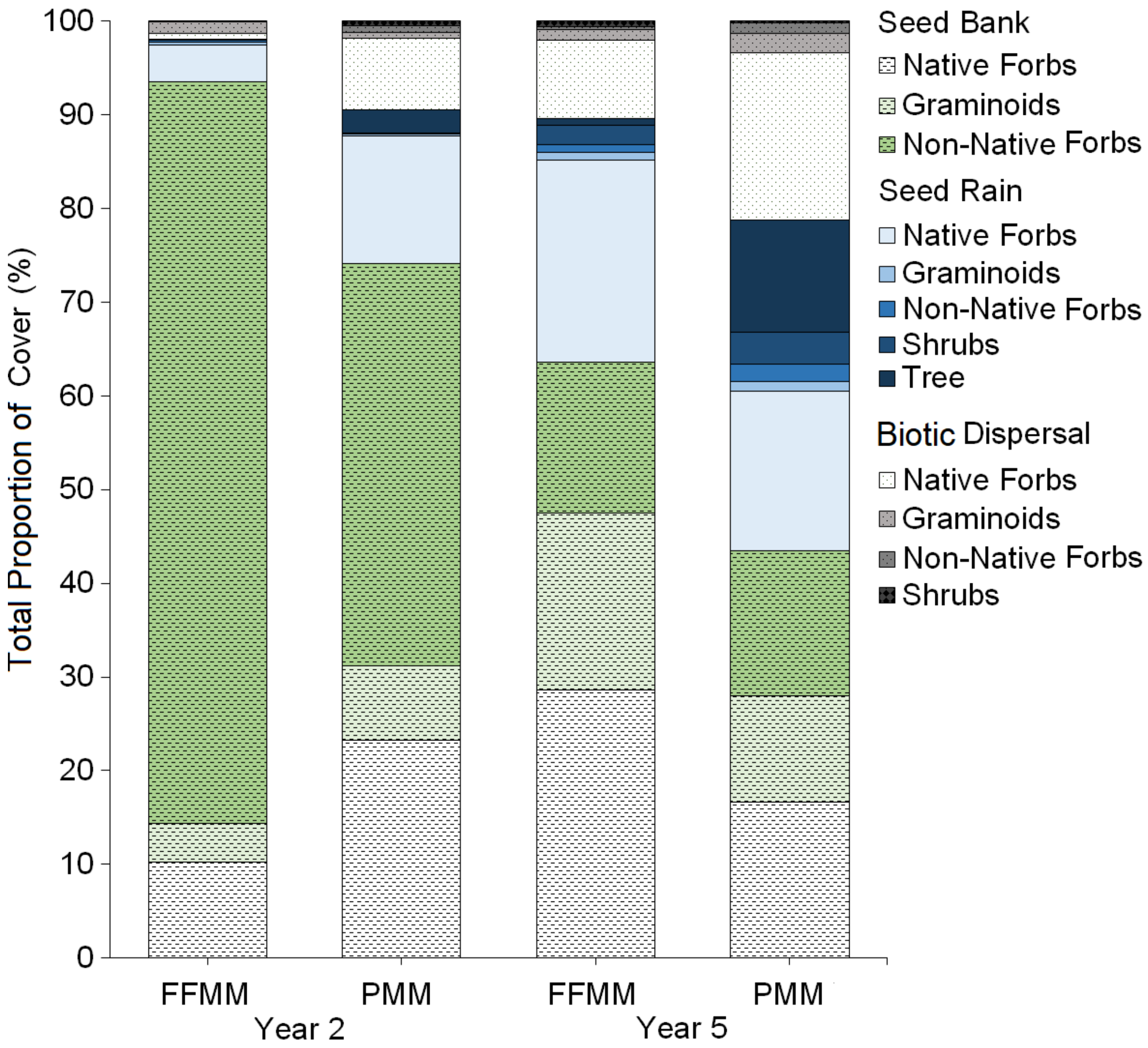


Fig. 8. The total proportion of cover (%) in Year 2 and Year 5 on FFMM and PMMM. The proportions are given for species originating from different assembly mechanisms (seed bank, seed rain, and other dispersal) and the functional groups (native forbs, non-native forbs, graminoids, shrubs, and trees) present within each mechanism.

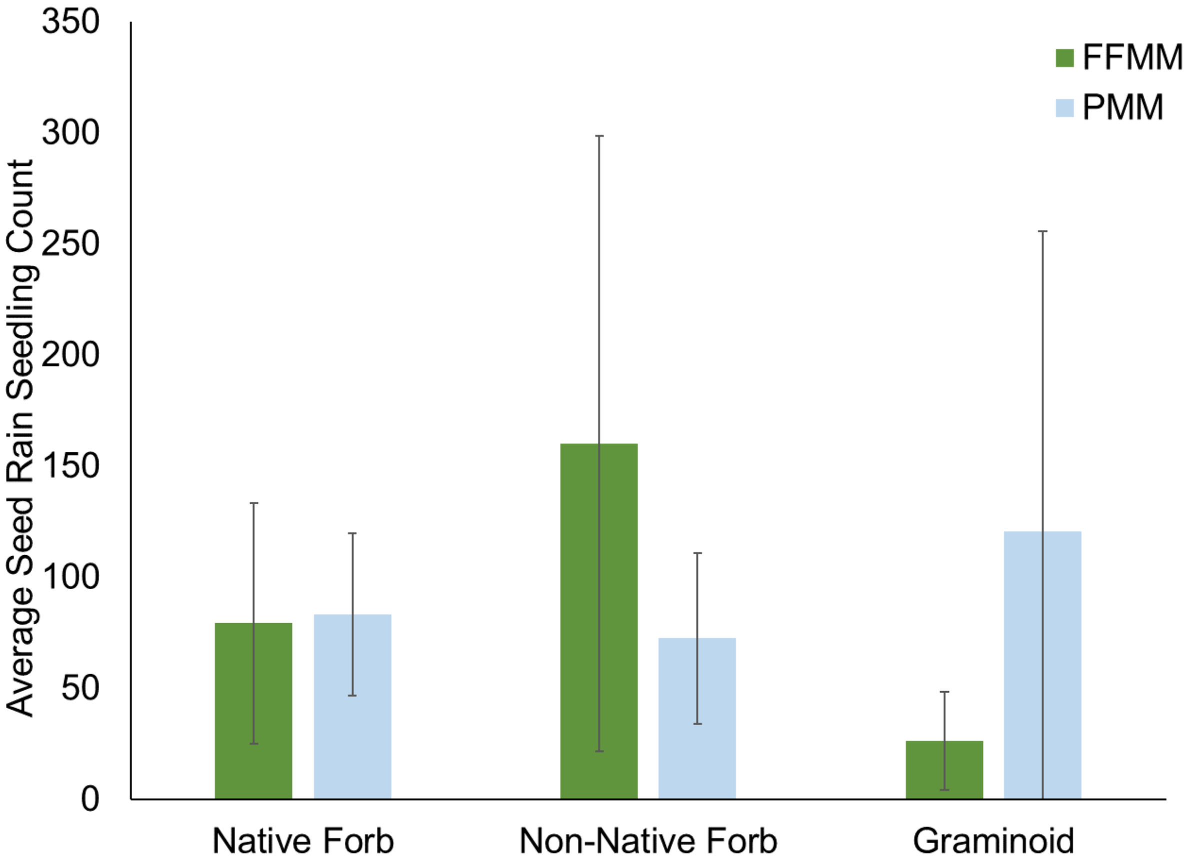


Fig. 9. Seedling count of seed rain for functional groups (native forbs, non-native forbs, and graminoids) in Year 1 for FFMM and PMM (n=14 for each soil type).

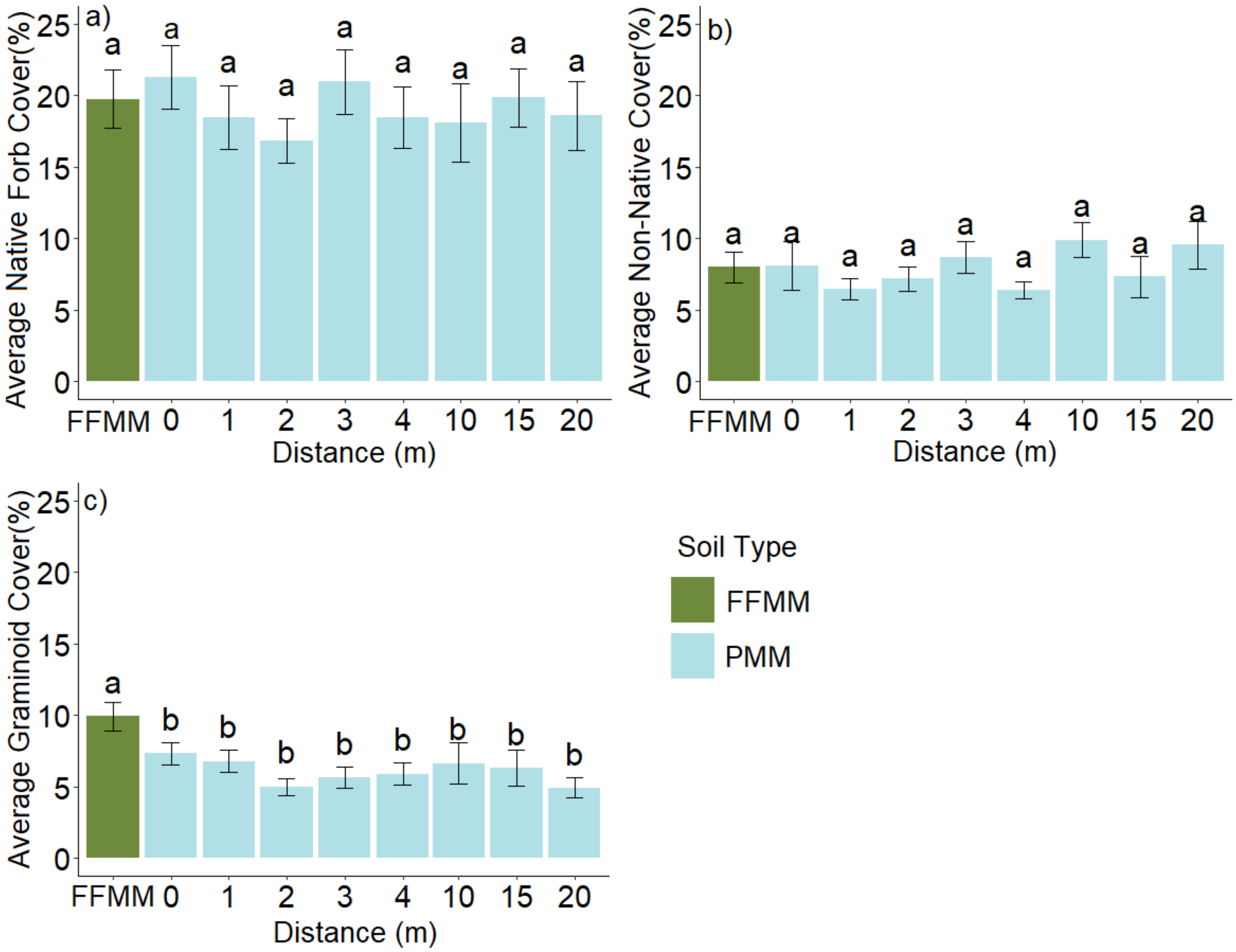


Fig. 10. Average cover (%) of species by functional group (a=native forb, b=non-native forb, and c=graminoid) at 0 - 4, 10, 15, and 20 m distances into the PMM (n=35 transects) from the FFMM (average of 5 plots per transects). Standard error bars included and significant letters are based on RTEI results.

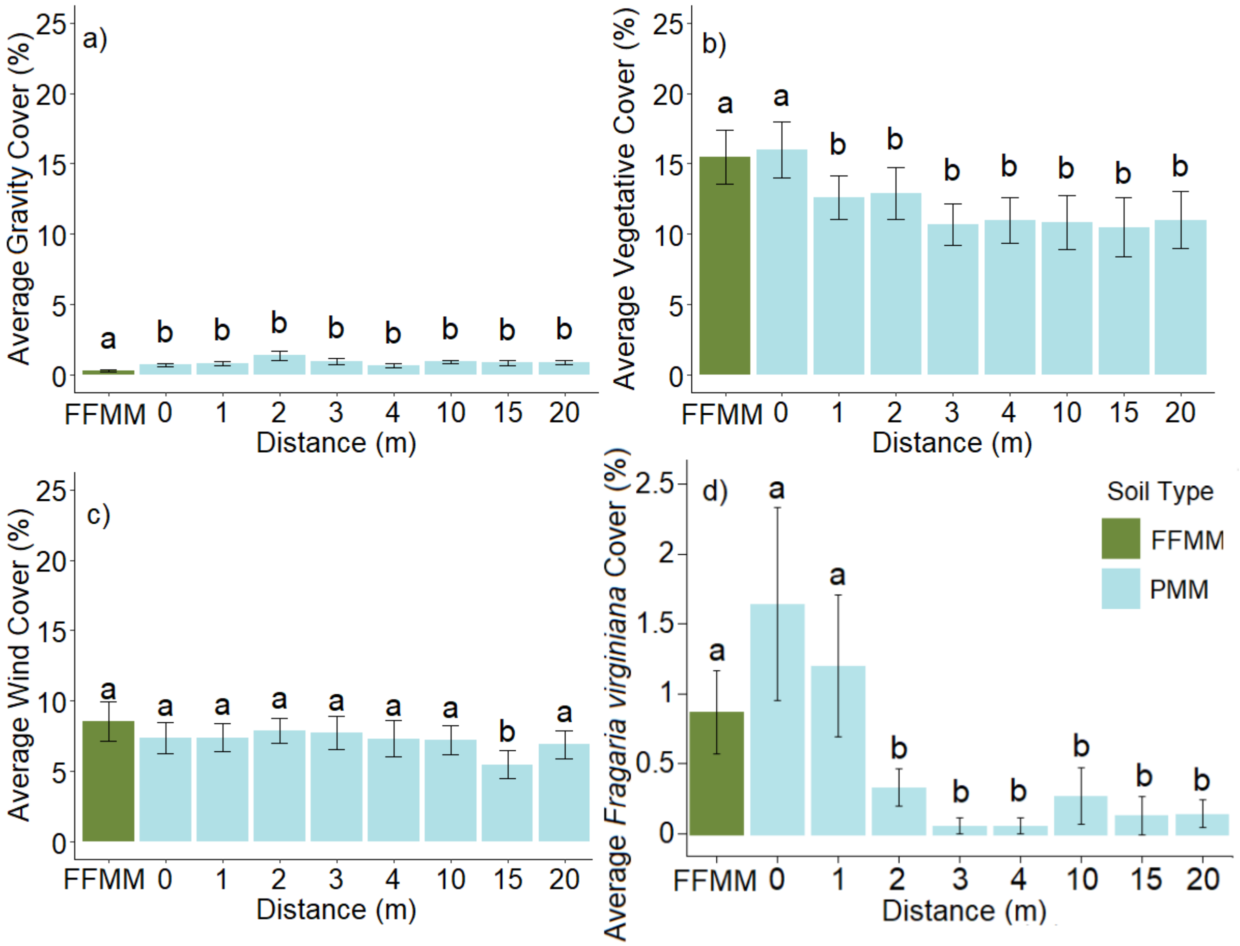


Fig. 11. The average cover (%) (standard error) for native forbs by their different dispersal mechanisms: a) gravity, b) vegetative, c) wind, and d) *Fragaria virginiana* (as an example of a vegetatively reproducing species) at 0 - 4, 10, 15, and 20 m distances into the PMM (n=35 transects) from the FFMM (average of 5 plots per transect). Significant letters are based on RTEI results.

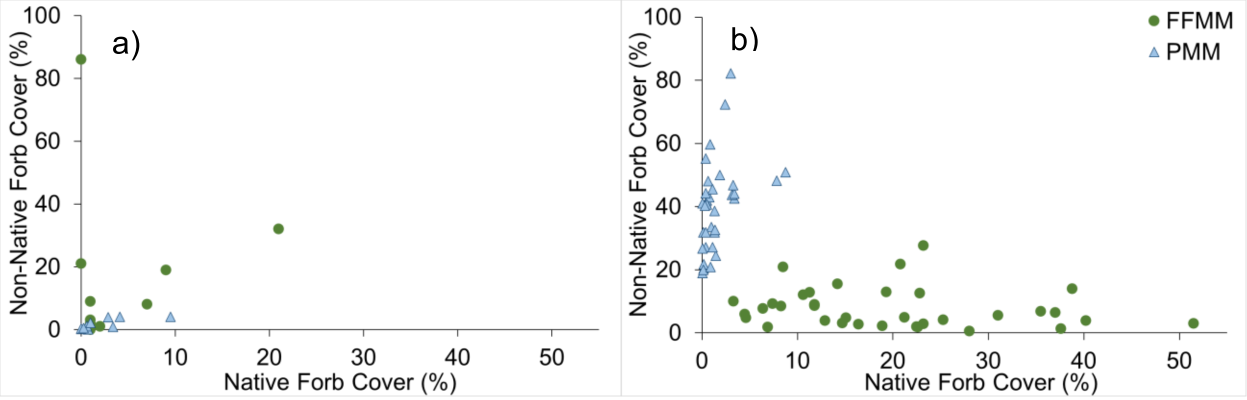


Fig. 12. Pearson's correlation comparing native forb cover (%) to non-native forb cover (%) in FFMM and PMM. a) Year 2 (df=9) and b) Year 5 (df=34).

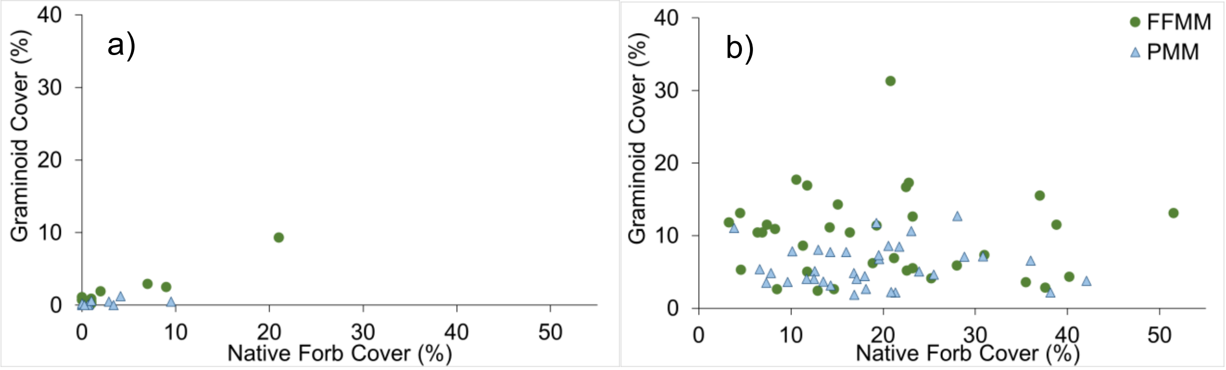


Fig. 13. Pearson’s correlation comparing graminoid cover (%) to native forb cover (%) in FFMM and PMM. a) Year 2 (df=9) and b) Year 5 (df=34).

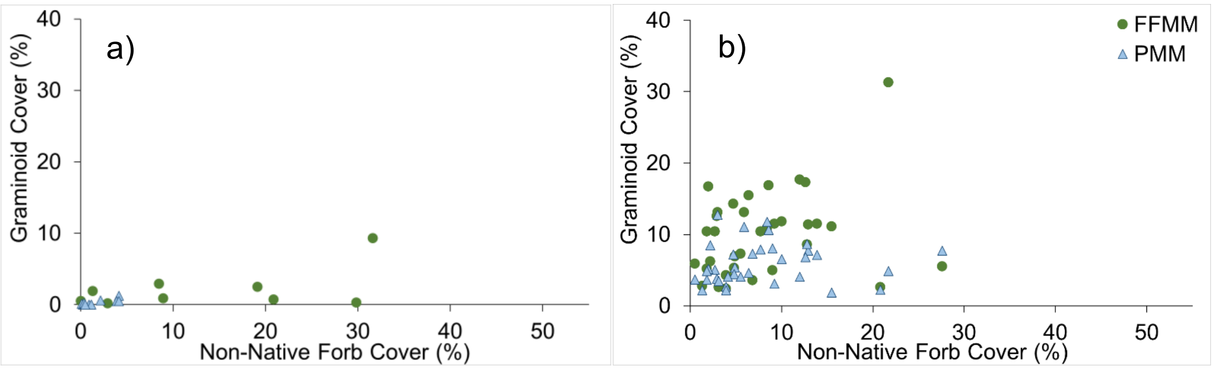


Fig. 14. Pearson's correlation comparing non-native forb cover (%) to graminoid forb cover (%) in FFMM and PMM. a) Year 2 (df=9) and b) Year 5 (df=34).

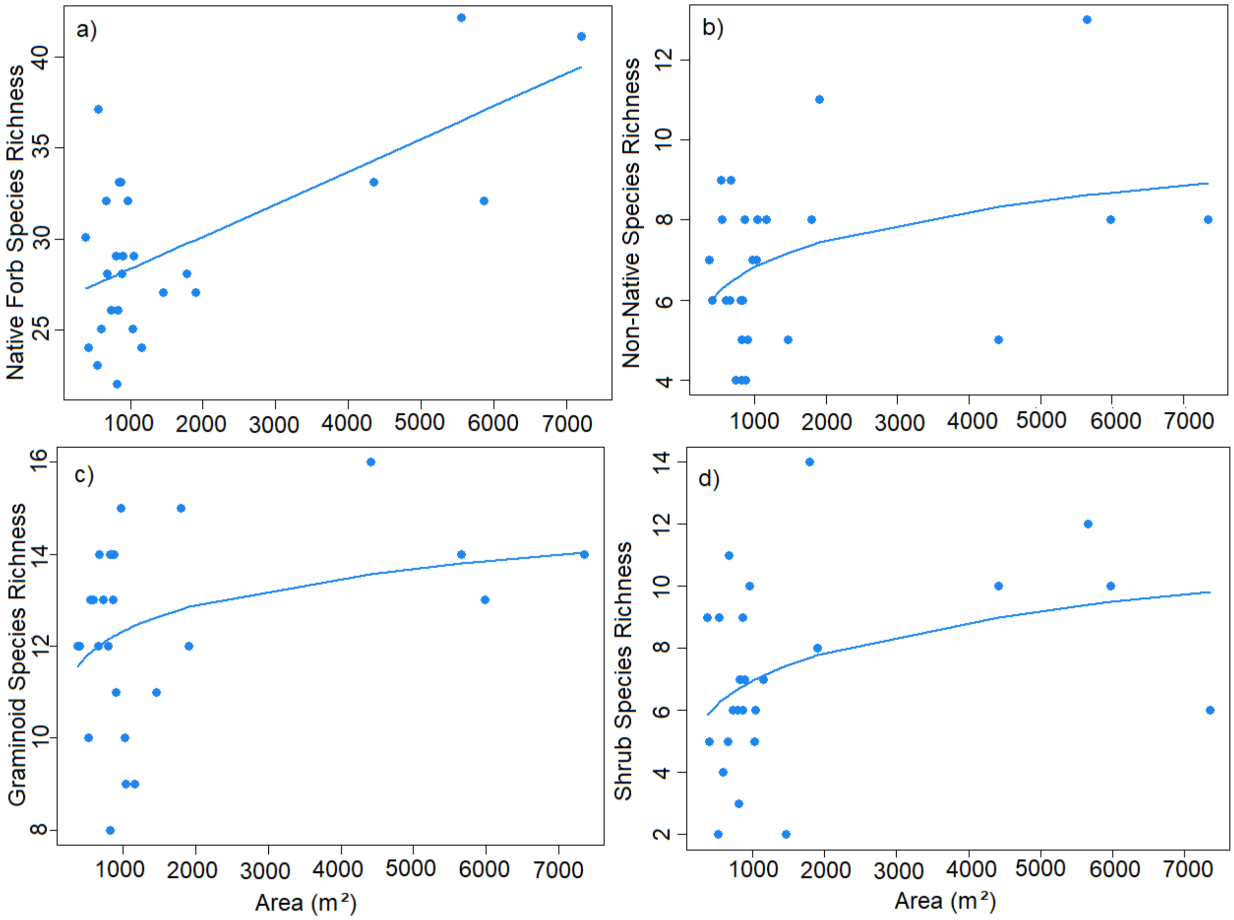


Fig. 15. Species area curve of 26 FFMM islands for: a) native forb species (Asymptotic curve r^2=0.28), b) non-native forb species (Power curve r^2=0.06), c) graminoid species (Power curve r^2=0.03), and d) shrub species richness (Kobayashi curve r^2=0. 06).

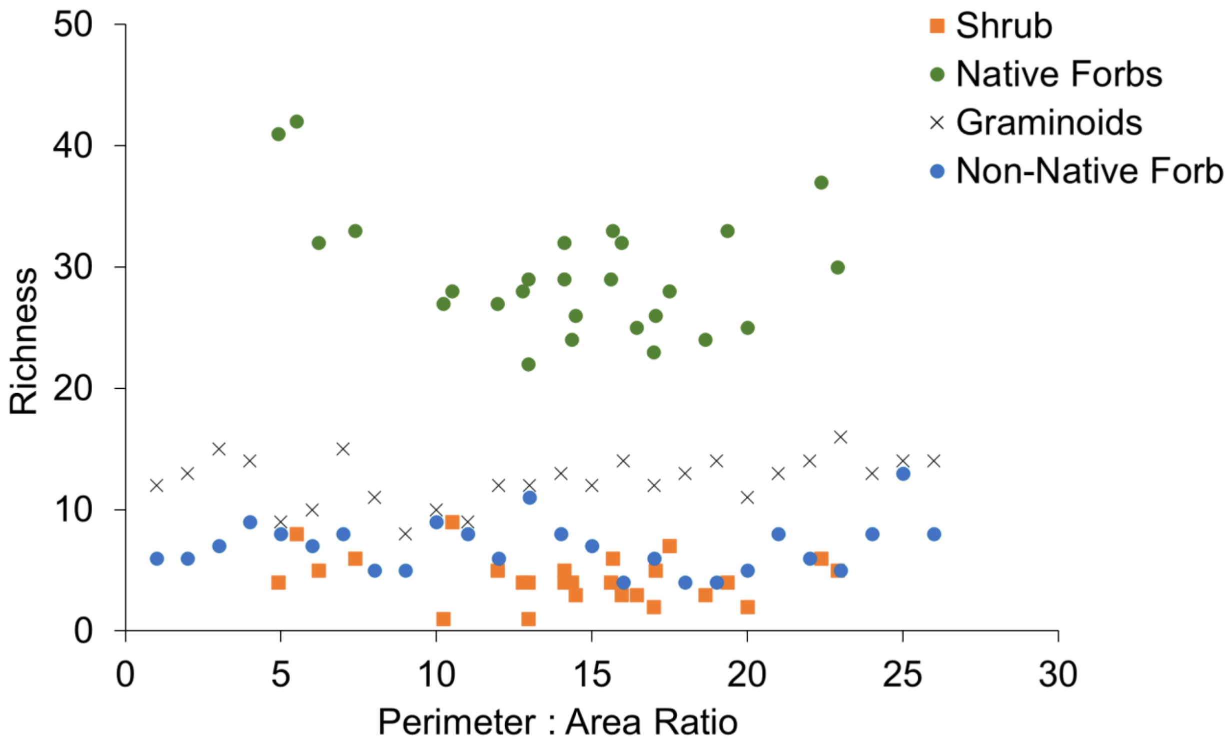


Fig. 16. Pearson’s correlation between species richness and the perimeter: area ratios of 26 FFMM islands for native forb species, non-native forb, graminoid, and shrub species richness (df= 25).

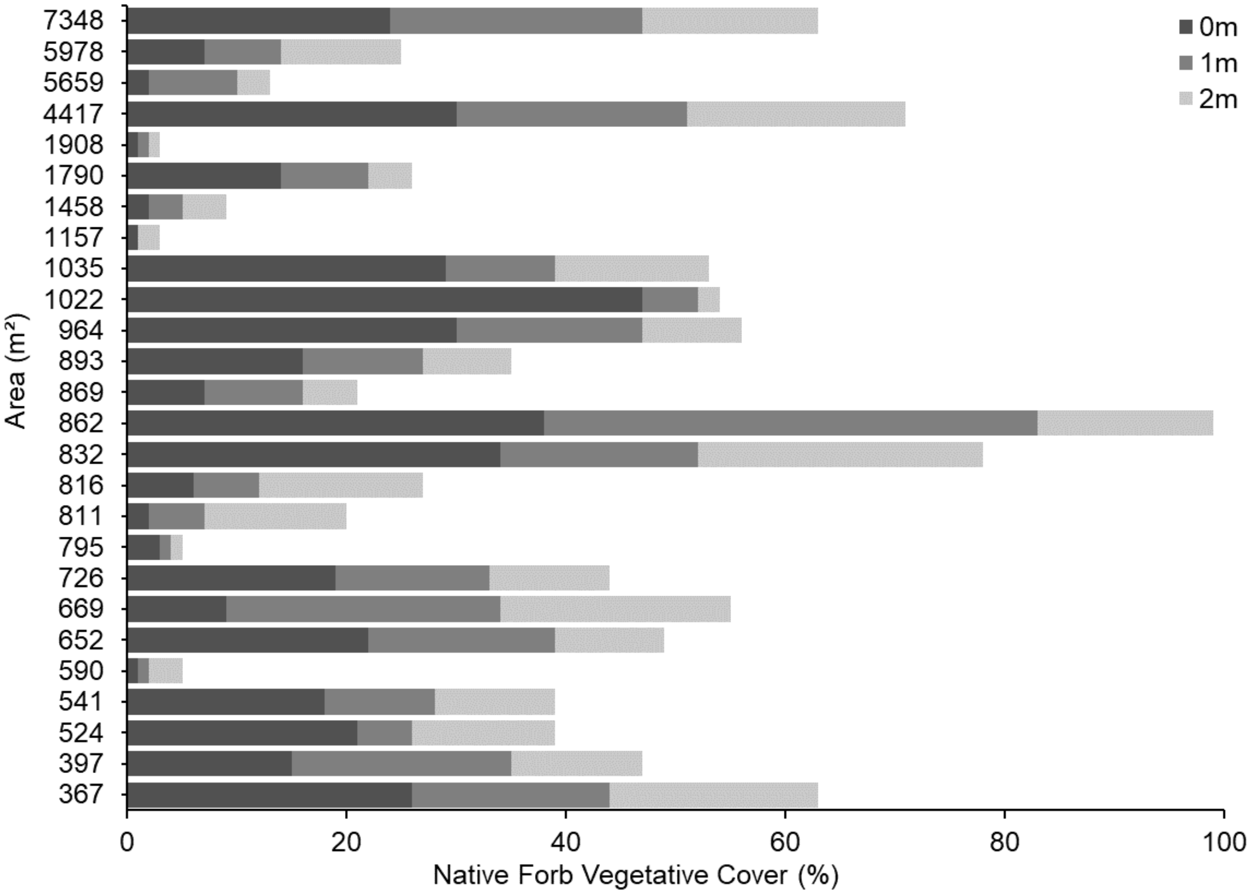


Fig. 17. Percent cover of native forb species that use vegetative dispersal at locations 0, 1, and 2 m away from FFMM Islands into adjacent PMM; islands are ordered by area (m²).

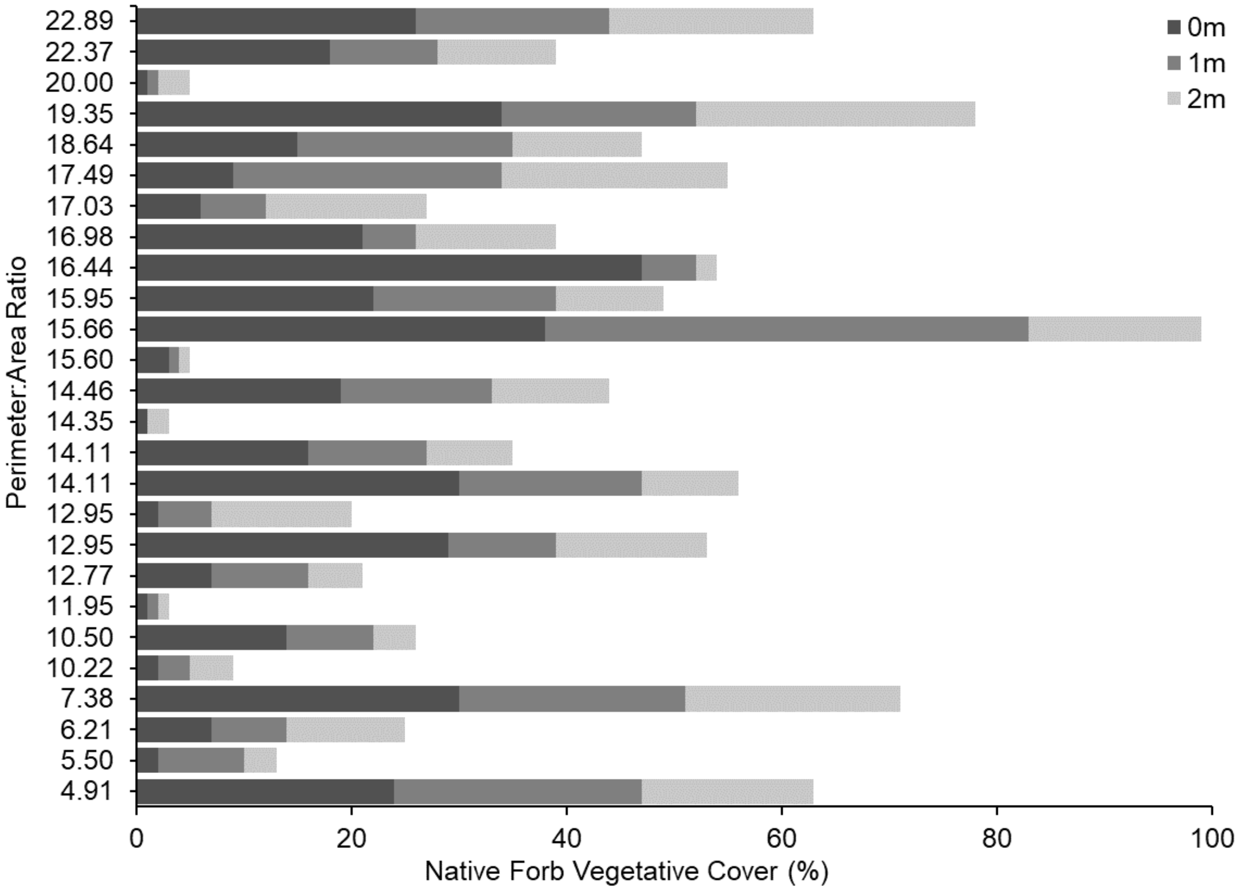


Fig. 18. Percent cover of native forb species that use vegetative dispersal at locations 0, 1, and 2 m into the PMM from the FFMM at each island; islands ordered by perimeter-area ratio.

Literature Cited

Alday, J.G., Pallavicini, Y., Marrs, R.H., Martínez-Ruiz, C., 2011. Functional groups and dispersal strategies as guides for predicting plant dynamics on reclaimed mines. Plant Ecol. 212, 1759–1775. https://doi.org/10.1007/s11258-011-9947-6

Alberta Environment, 2010. Guidelines for Reclamation to Forest Plant in the Athabasca Oil Sands Region. Prepared by the Terrestrial Subgroup of the Reclamation Working Group of the Cumulative Environmental Management Association, Fort McMurray, Alberta.

Alberta Environment and Water, 2012. Best Management Practices for Conservation of Reclamation Materials in the Mineable Oil Sands Region of Alberta, Direct. 1-161. https://doi.org/978-1-4601-0048-6

Angevine, M.W., 1983. Variations in the Demography of Natural Populations of the Wild Strawberries *Fragaria vesca* and *F. virginiana*. J. Ecol. 71, 959. https://doi.org/10.2307/2259605

Beckingham, J.D., Corns, I.G.W., Archibald, J.H., 1996. Field guide to ecosites of west-central Alberta. Vancouver, British Columbia.

Bellaris, S.M., Bell, D.T., 1993. Restoration of species-rich shrubland plant following mining in western Australia. Restor. Ecol. 231-240. https://doi.org/10.1111/j.1526-100X.1993.tb00032.x

Bochet, E., García-fayos, P., Tormo, J., 2007. Road slope replant in semiarid mediterranean environments. Part I: Seed dispersal and spontaneous colonization. Restor. Ecol. 15, 88–96. https://doi.org/10.1111/j.1526-100X.2006.00193.x

Brandt, J.P., 2009. The extent of the North American boreal zone. Environ. Rev. 17, 101–161. https://doi.org/10.1139/A09-004

Brandt, J.P., Flannigan, M.D., Maynard, D.G., Thompson, I.D., Volney, W.J.A., 2013. An introduction to Canada's boreal zone: ecosystem processes, health, sustainability, and environmental issues. Environ. Rev. 21, 207–226. https://doi.org/10.1139/er-2013-0040

Bradbury, S., 2004. Understory plant communities in boreal cutblocks with different sizes and numbers of residual tree patches. Can. J. For. Res. 34, 1220–1227. https://doi.org/10.1139/x04-010

Bradshaw, A., 2000. The use of natural processes in reclamation - Advantages and difficulties. Landsc. Urban Plan. 51, 89–100. https://doi.org/10.1016/S0169-2046(00)00099-2

Brown, C.S., Bugg, R.L., 2001. Effects of established perennial grasses on introduction of native forbs in California. Restor. Ecol. 9, 38–48. https://doi.org/10.1046/j.1526-100X.2001.009001038.x

Bullock, J.M., Clear Hill, B., Silvertown, J., Sutton, M., 1995. Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species. Oikos, 72, 273-282.

Buss, J., Pinno, B.D., Quideau, S., 2020. A comparison between stockpile and boreal forest seed banks and plant communities. Restor. Ecol.

Buss, J., Stratechuk, K., Pinno, B.D., 2018. Growth and competition among understory plants varies with reclamation soil and fertilization. Ecol. Process. 7. https://doi.org/10.1186/s13717-018-0123-y

Chambers, J.C., MacMahon, J.A., 1994. A day in the life of a seed: Movements and fates of seeds and their implications for natural and managed systems. Annu. Rev. Ecol. Syst. 25, 263–292. https://doi.org/10.1146/annurev.es.25.110194.001403

Cole, R.J., Holl, K.D., Zahawi, R.A., 2010. Seed rain under tree islands planted to restore degraded lands in a tropical agricultural landscape. Ecol. Appl. 20, 1255–1269.

Collinge, S.K., 1996. Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. Landsc. Urban Plan. 36, 59–77. https://doi.org/10.1016/S0169-2046(96)00341-6

Corbin, J.D., Holl, K.D., 2012. Applied nucleation as a forest restoration strategy. Forest. Ecol. Manag. *265*, 37–46. https://doi.org/10.1016/j.foreco.2011.10.013

Corbin, J.D., Robinson, G.R., Hafkemeyer, L.M., Handel, S.N., 2016. A long-term evaluation of applied nucleation as a strategy to facilitate forest restoration. Ecol. Appl. 26, 104–114. https://doi.org/10.1890/15-0075.1/suppinfo

Cumulative Environmental Management Association, 2012. Criteria and Indicators Framework for Oil Sands Mine Reclamation Certification.

DeClerck, F.A.J., Chazdon, R., Holl, K.D., Milder, J.C., Finegan, B., Martinez-Salinas, A., Imbach, P., Canet, L., Ramos, Z., 2010. Biodiversity conservation in human-modified landscapes of Mesoamerica: Past, present and future. Biol. Conserv. 143, 2301–2313. https://doi.org/10.1016/j.biocon.2010.03.026

De Grandpre, L.E., Bergeron, Y., 2016. Diversity and Stability of Understorey Communities Following Disturbance in the Southern Boreal Forest. Biol. Conserv. 85, 777–784.

Dhar, A., Comeau, P.G., Karst, J., Pinno, B.D., Chang, S.X., Naeth, A.M., Vassov, R., Bampfylde, C., 2018. Plant community development following reclamation of oil sands mine sites in the boreal forest: a review. Environ. Rev. 298, 1–13. https://doi.org/10.1139/er-2017-0091

Dhar, A., Comeau, P.G., Vassov, R., 2019. Effects of cover soil stockpiling on plant community development following reclamation of oil sands sites in Alberta. Restor. Ecol. 27, 352–360. https://doi.org/10.1111/rec.12858

Díaz, S., Cabido, M., 2001. Vive la différence: Plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2

Eriksson, Å., Eriksson, O., 1997. Seedling recruitment in semi-natural pastures: The effects of disturbance, seed size, phenology and seed bank. Nord. J. Bot. 17, 469–482. https://doi.org/10.1111/j.1756-1051.1997.tb00344.x

Errington, R.C., Pinno, B.D., 2015. Early Successional Plant Community Dynamics on a Reclaimed Oil Sands Mine in Comparison with Natural Boreal Forest Communities. Ecoscience 22, 133–144. https://doi.org/10.1080/11956860.2016.1169385

Forsch, K.B.C., 2014. Oil sands reclamation using woody debris using LFH mineral soil mix and peat mineral soil mix cover soils: impacts on select soil and plant properties. M.Sc. thesis, Department of Renewable Resources, University of Alberta, Edmonton, Alta. doi:10.7939/R39G5GM3P.

Foster, B.L., Tilman, D., 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. Plant Ecol. 146, 1–10. https://doi.org/10.1023/A:1009895103017

Fyles, J.W., 1989. Seed bank populations in upland coniferous forests in central Alberta. Can. J. Bot. 67, 274–278. https://doi.org/10.1139/b89-039

Gallagher, F.J., Pechmann, I., HolZafel, C., Grabosky, J., 2011. Altered Vegetative Assemblage Trajectories Within an Urban Brownfield. Environ. Pollut. 159, 1159-1166. https://doi.org/10.1016/j.envpol.2011.02.007

Gingras-Hill, T., Nwaishi, F.C., Macrae, M.L., Price, J.S., Petrone, R.M., 2018. Ecohydrological functioning of an upland undergoing reclamation on post-mining landscape of the Athabasca oil sands region, Canada. Ecohydrol. 11, 1. doi: 10.1002/eco.1941.

Government of Alberta, 2018a. Oil Sands Facts and Stats. https://www.alberta.ca/oil-sands-facts-and-statistics.aspx (accessed 1 October 2018).

Government of Alberta, 2018b. Alberta Regulations 115/1993. In Environmental Protection and Enhancement Act. http://www.qp.alberta.ca/documents/Regs/1993_115.pdf (accessed 4 December 2018).

Government of Canada, 2016. Oil Sands Extraction and Processing. https://www.nrcan.gc.ca/energy/oil-sands/18094 (accessed 2 October 2018).

Government of Canada, 2019. Canadian Climate Normals 1981-2010 Station Data. https://climate.weather.gc.ca/climate_normals/results_1981_2010_e.html?searchType=stnProv&lstProvince=AB&txtCentralLatMin=0&txtCentralLatSec=0&txtCentralLongMin=0&txtCentralLongSec=0&stnID=2704&dispBack=0 (accessed 22 April 2020).

Grandin, U., 2001. Short-term and long-term variation in seed bank/vegetation relations along an environmental and successional gradient. Ecography (Cop.). 24, 731–741. https://doi.org/10.1111/j.1600-0587.2001.tb00534.x

Greene, D., Zasada, J., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., Simard, M., 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29, 824–839.

Griffith, D.M., Veech, J.A., Marsh, C.J., 2016. Cooccur: Probabilistic species co-occurrence analysis in R. J. Stat. Softw. 69, 1–17. https://doi.org/10.18637/jss.v069.c02

Grubb, P.J., 1977. The Maintenance of Species-Richness in Plant Communities: The Importance of the Regeneration Niche. Biol. Rev. 52, 107–145. https://doi.org/10.1111/j.1469-185X.1977.tb01347.x

Harper, K.A., Macdonald, S.E., 2001. Structure and composition of riparian boreal forest: New methods for analyzing edge influence. Ecology. 82, 649–659. https://doi.org/10.1890/0012-9658(2001)082[0649:SACORB]2.0.CO;2

Harper, K.A., Macdonald, S.E., 2002. The critical values program for assessing edge influence. ESA. 83, 61-62.

Harper, K.A., Macdonald, S.E., 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. Ecosphere. 2, 1-17. https://doi.org/10.1890/es11-00146.1

Hart, S.A., Chen, H.Y.H., 2006. Understory plant dynamics of North American boreal forests. CRC. Crit. Rev. Plant Sci. 25, 381–397. https://doi.org/10.1080/07352680600819286

Henderson, D.C., 2009. Occupancy survey guidelines; prairie plant species at risk.

Henkel-Johnson, D., Macdonald, S.E., Bork, E.W., Thomas, B.R., 2016. Influence of weed composition, abundance, and spatial proximity on growth in young hybrid poplar plantations. For. Ecol. Manage. 362, 55–68. https://doi.org/10.1016/j.foreco.2015.11.010

Hobbie, S.E., 1992. Effects of plant species on nutrient cycling. Trends Ecol. Evol. 7, 336–339. https://doi.org/10.1016/0169-5347(92)90126-v

Hopfensperger, K.N., 2007. A review of similarity between seed bank and standing vegetation across ecosystems. Oikos 116, 1438–1448. https://doi.org/10.1111/j.2007.0030-1299.15818.x

Humphreys, A.W.F., Kitchener, D.J., 2010. The Effect of Habitat Utilization on Species-Area Curves: Implications for Optimal Reserve Area. J. Biogeogr. 9, 391–396.

Jauni, M., Gripenberg, S., Ramula, S., 2015. Non-native plant species benefit from disturbance: a meta-analysis. Oikos. 124, 122-129.

Jones, C.E., Landhäusser, S.M., 2018. Plant recolonization of reclamation areas from patches of salvaged forest floor material. Appl. Veg. Sci. 21, 94–103. https://doi.org/10.1111/avsc.12350

Kettenring, K.M., Mock, K.E., Zaman, B., McKee, M., 2016. Life on the edge: reproductive mode and rate of non-native *Phragmites australis* patch expansion. Biol. Invasions. 18, 2475–2495. https://doi.org/10.1007/s10530-016-1125-2

Koch, J.M., Ward, S.C., Grant, C.D., Ainsworth, G.L., 1996. Effects of bauxite mine restoration operations on topsoil seed reserves in the jarrah forest of Western Australia. Restor. Ecol. 4, 368–376.

Knapp, S., Stadler, J., Harpke, A., Klotz, S., 2016. Dispersal traits as indicators of plant dynamics in long-term old-field succession. Ecol. Indic. 65, 44–54. https://doi.org/10.1016/j.ecolind.2015.10.003

Landhäusser, S.M., Lieffers, V.J., 1998. Growth of *Populus tremuloides* in association with Calamagrostis canadensis. Can. J. For. Res. 28, 396–401. https://doi.org/10.1139/x98-006

Landhäusser, S.M., Mulak, T.L., Lieffers, V.J., 2007. The effect of roots and litter of *Calamagrostis canadensis* on root sucker regeneration of *Populus tremuloides*. Forestry. 80, 481–488. https://doi.org/10.1093/forestry/cpm035

Leatherdale, J., Chanasyk, D.S., Quideau, S., 2012. Soil water regimes of reclaimed upland slopes in the oil sands region of Alberta. Can. J. Soil Sci. 92, 117–129. https://doi.org/10.4141/CJSS2010-027

Lieffers, V.J., Macdonald, E.S., Hogg, E.H., 1993. Ecology of and control strategies for *Calamagrostis canadensis* in boreal forest sites. Can. J. For. Res. 23, 2070-2077. https://doi.org/10.1139/x93-258

Luzuriaga, A.L., Escudero, A., Olano, J.M., Loidi, J., 2005. Regenerative role of seed banks following an intense soil disturbance. Acta Oecol. 27, 57–66. https://doi.org/10.1016/j.actao.2004.09.003

Macdonald, S.E., Fenniak, T.E., 2007. Understory plant communities of boreal mixedwood forests in western Canada: Natural patterns and response to variable-retention harvesting. For. Ecol. Manage. 242, 34–48. https://doi.org/10.1016/j.foreco.2007.01.029

Macdonald, S.E., Landhäusser, S.M., Skousen, J., Franklin, J., Frouz, J., Hall, S., Jacobs, D.F., Quideau, S., 2015. Forest restoration following surface mining disturbance: challenges and solutions. New For. 46, 703–732. https://doi.org/10.1007/s11056-015-9506-4

Macdonald, S.E., Quideau, S., Landhäusser, S.M., 2012. Rebuilding boreal forest ecosystems after industrial disturbance, in: Vitt, D.H., Bhatti, J.S., (Eds.), Restoration and Reclamation of Boreal Ecosystems. Cambridge Press Cambridge, United Kingdom, pp. 123-160.

MacDougall, A.S., and Turkington, R., 2005. Are non-native species the drivers or passengers of degraded ecosystems? Ecology. 86, 42–55. doi:10.1890/04-0669.

Mackenzie, D.D., Naeth, M.A., 2010. The role of the forest soil propagule bank in assisted natural recovery after oil sands mining. Restor. Ecol. 18, 418–427. https://doi.org/10.1111/j.1526-100X.2008.00500.x

Mackenzie, M.D., Quideau, S.A., 2012. Laboratory-based nitrogen mineralization and biogeochemistry of two soils used in oil sands reclamation. Can. J. Soil Sci. 92, 131–142. https://doi.org/10.4141/CJSS2010-070

Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in Eastern North America. Am.J. Bot. 75,1491-1502.

Matthews, T.J., Triantis, K.A., Whittaker, R.J., Guilhaumon, F., 2019. sars: an R package for fitting, evaluating and comparing species–area relationship models. Ecography (Cop.). 42, 1446–1455. https://doi.org/10.1111/ecog.04271

McIntosh, A.C.S., Macdonald, S.E., Quideau, S.A., 2016. Understory plant community composition is associated with fine-scale above- and below-ground resource heterogeneity in mature lodgepole pine (Pinus contorta) forests. PLoS One. 11, 1–17. https://doi.org/10.1371/journal.pone.0151436

McMillan, R., Quideau, S.A., MacKenzie, M.D., Biryukova, O., 2007. Nitrogen Mineralization and Microbial Activity in Oil Sands Reclaimed Boreal Forest Soils. J. Environ. Qual. 36, 1470. https://doi.org/10.2134/jeq2006.0530

Melnik, K., Landhäusser, S.M., Devito, K., 2018. Role of microtopography in the expression of soil propagule banks on reclamation sites. Restor. Ecol. 26, S200–S210. https://doi.org/10.1111/rec.12587

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Synthesis. Washington, DC.

Moen, J., Jonsson, B.G., 2003. Edge effects on liverworts and lichens in forest patches in a mosaic of boreal forest and wetland. Conserv. Biol. 17, 380–388. https://doi.org/10.1046/j.1523-1739.2003.00406.x

Mola, I., Jiménez, M.D., López-Jiménez, N., Casado, M.A., Balaguer, L., 2011. Roadside Reclamation Outside the Replant Season: Management Options under Schedule Pressure. Restor. Ecol. 19, 83–92. https://doi.org/10.1111/j.1526-100X.2009.00547.x

Moore. P.D., 1980. Soil seed banks. Nature. 284, 123-124.

Moss, E.H., Packer, J., 1994. Flora of Alberta, second ed. Toronto, Ontario.

Naeth, M.A., Wilkinson, S.R., Mackenzie, D.D., Archibald, H.A., Powter, C.B., 2013. Potential of LFH Mineral Soil Mixes for Reclamation of Forested Lands in Alberta. Oil Sands Research and Information Network Report No. TR-35, pp 1- 64.

Natural Regions Committee, 2006. Natural Regions and Subregions of Alberta, Government of Alberta. https://doi.org/Pub. No. T/852

Nilsson, M.C., Wardle, D.A., 2005. Understory Plant as a Forest Ecosystem Driver: Evidence from the Northern Swedish Boreal Forest. Front Ecol. Environ. 3, 421-428. https://www.jstor.org/stable/3868658.

Pinno, B.D., Errington, R.C., 2015. Maximizing natural trembling aspen seedling establishment on a reclaimed boreal oil sands site. Ecol. Restor. 33, 43–50. https://doi.org/10.3368/er.33.1.43

Pinno, B.D., Hawkes, V.C., 2015. Temporal trends of ecosystem development on different site types in reclaimed boreal forests. Forests. 6, 2109–2124. https://doi.org/10.3390/f6062109

Pinno, B.D., Sherr, I., Errington, R.C., Shea, K., 2016. Islands – Soil Patches and Plant Community Dynamics on a New Oil Sands Reclamation Design. J. Am. Soc. Min. Reclam. 2016, 28–44. https://doi.org/10.21000/JASMR16010028.

R Core Team, 2019. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-proje ct.org/

Rey Benayas, J.M., Bullock, J.M., Newton, A.C., 2008. Creating woodland islets to reconcile ecological restoration, conservation, and agricultural land use. Front. Ecol. Environ. 6, 329–336. https://doi.org/10.1890/070057

Rico-Gray, V., Garciá-Franco, J.G., 1992. Vegetation and Soil Seed Bank of Successional Stages in Tropical Lowland Deciduous Forest. J. Veg. Sci. 3, 617–624. https://doi.org/https://doi.org/10.2307/3235828

Robinson, G.R., Handel, S.N., 2000. Directing Spatial Patterns of Recruitment during an Experimental Urban Woodland Reclamation. Ecol. Appl. 10, 174. https://doi.org/10.2307/2640994

Rokich, D.P., Dixon, K.W., Sivasithamparam, K., Meney, K.A., 2000. Topsoil handling and storage effects on woodland restoration in Western Australia. Restor. Ecol. 8, 196–208.

Rydgren, K., Økland, R.H., Hestmark, G., 2004. Disturbance severity and community resilience in a boreal forest. Ecology 85, 1906–1915. https://doi.org/10.1890/03-0276

Scheiner, S.M., 2003. Six types of species-area curves. Glob. Ecol. Biogeogr. 12, 441–447. https://doi.org/10.1046/j.1466-822X.2003.00061.x

Seagle, S.W., Shugart, H.H., 1985. Faunal Richness and Turnover on Dynamic Landscapes: A Simulation Study. J Biogeogr. 12, 499-508. https://www.jstor.org/stable/2844905

Shang, Z., Yang, S., Wang, Y., Shi, J., Ding, L., Long, R., 2016. Soil seed bank and its relation with above-ground vegetation along the degraded gradients of alpine meadow. Ecol. Eng. 90, 268–277. https://doi.org/10.1016/j.ecoleng.2016.01.067

Silvertown, J., 2008. The evolutionary maintenance of sexual reproduction: Evidence from the ecological distribution of asexual reproduction in clonal plants. Int. J. Plant Sci. 169, 157–168. https://doi.org/10.1086/523357

Soil Classification Working Group, 1998. The Canadian System of Soil Classification, Third ed. Ottawa, Canada.

Spellman, K. V., Schneller, L.C., Mulder, C.P.H., Carlson, M.L., 2015. Effects of non-native Melilotus albus on pollination and reproduction in two boreal shrubs. Oecologia 179, 495–507. https://doi.org/10.1007/s00442-015-3364-9

Tannas, K.E., 2001. Common Plants of the Western Rangelands – Volume 1: Grasses and Grass-Like Species, first ed. Lethbridge, Alberta.

Tannas, K.E., 2003 Common Plants of the Western Rangelands – Volume 2: Trees and Shrubs, first ed. Lethbridge, Alberta.

Tannas, K.E., 2004 Common Plants of the Western Rangelands – Volume 3: Forbs, first ed. Lethbridge, Alberta.

Tappeiner, J.C., Alaback, P.B., 1989. Early establishment and vegetative growth of understory species in the western hemlock-Sitka spruce forests of southeast Alaska. Can. J. Bot. 67, 318–326. https://doi.org/10.1139/b89-046

Tilman, D., 1996. Biodiversity: Population Versus Ecosystem Stability. Ecology. 77, 350-363. https://doi.org/10.2307/2265614

Tilman, D., Wedin, D., 1991. Dynamics of Nitrogen Competition Between Successional Grasses. Ecology 72, 1038–1049.

Tjørve, E., 2003. Shapes and Functions of Species-Area Curves: A Review of Possible Models. J Biogeogr. 30, 827-835. https://www.jstor.org/stable/3554616.

Walker L, R., Del Moral, R., 2009. Lessons from primary succession for restoration of severely damaged habitats. Appl. Veg. Sci. 12, 55–67. https://doi.org/10.1111/j.1654-109X.2009.01002.x

Wardle, D.A., Jonsson, M., 2014. Long-term resilience of above- and belowground ecosystem components among contrasting ecosystems. Ecology. 95, 1836–1849. https://doi.org/10.1890/13-1666.1

Western Ag, 2019. PRS Technology Analysis. https://www.westernag.ca/innovations/technology/analysis_units (accessed Febuary 14, 2019)

Wheeler, B., Torchiano, M., 2016. lmPerm: Permutation Tests for Linear Models. https://CRAN.R-project.org/package=lmPerm

Winterhalder, K., 1996. Environmental degradation and rehabilitation of the landscape around Sudbury, a major mining and smelting area. Environ. Rev. 4, 185–224. https://doi.org/10.1139/a96-011

Winterhalder, K., 2004. the Relative Merits of Native Transplant Plugs and Topsoil Islands in the Enhancement of Understory Biodiversity on Reclaimed Minelands. J. Am. Soc. Min. Reclam. 2004, 2042–2060. https://doi.org/10.21000/jasmr0402042

Yarranton, G.A., Morrison, R.G., 1974. Spatial dynamics of a primary succession: Nucleation. Journal of Ecology 62, 417–428.

Zahawi, R.A., Augspurger, C.K., 2006. Tropical forest restoration: Tree islands as recruitment foci in degraded lands of Honduras. Ecol. Appl. 16, 464–478. https://doi.org/10.1890/1051-0761(2006)016[0464:TFRTIA]2.0.CO;2

Zahawi, R.A., Holl, K.D., Cole, R.J., Reid, J.L., 2013. Testing applied nucleation as a strategy to facilitate tropical forest recovery. J. Appl. Ecol. 50, 88–96. https://doi.org/10.1111/1365-2664.12014

Zaplata, M.K., Winter, S., Fischer, A., Kollmann, J., Ulrich, W., 2013. Species-driven phases and increasing structure in early-successional plant communities. Am. Nat. 181. https://doi.org/10.1086/668571

Zhang, J., Nielsen, S.E., Grainger, T.N., Kohler, M., Chipchar, T., Farr, D.R., 2014. Sampling plant diversity and rarity at landscape scales: Importance of sampling time in species detectability. PLoS One 9. https://doi.org/10.13

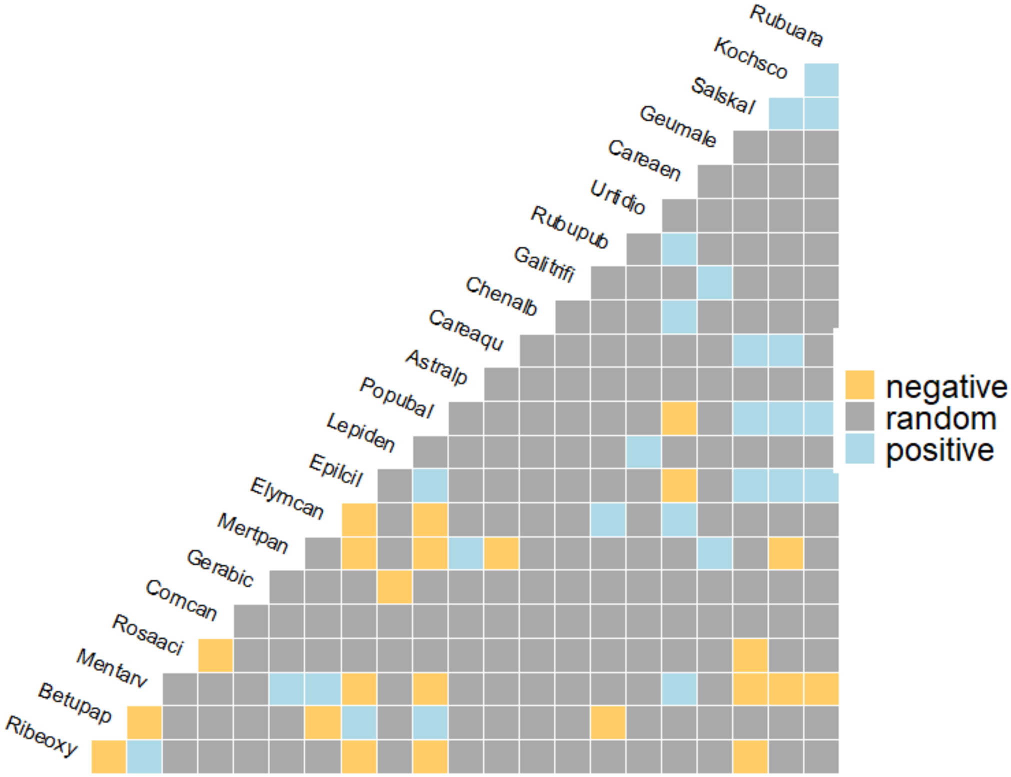
Appendix
A.1 Soil Properties

Soil measurements were conducted on all transects at 5 m in FFMM and PMM to obtain general soil and site characteristics at Year 5. Volumetric soil water (FieldScout TDR 300, Spectrum Technologies Inc., Aurora, IL), soil temperature (Fisher Scientific digital thermometers), and pH (400 meter, Field Scout, Spectrum Technologies Inc., Aurora, IL) was conducted in July within a short period (3-5 days) to minimize variation (Macdonald and Fenniak, 2007; Pinno et al. 2016). All volumetric soil water, soil temperature, and pH measurements were not performed on days with heavy rain and completed 24 hours after a rain event, to examine differences in dry soil (Macdonald and Fenniak, 2007). Volumetric soil water content was repeated three times at each 5 m plot to acquire an average reading (Pinno et al. 2016). Thermometers were left in the ground to stabilize for 2-3 minutes before the reading was taken. Thermometers, volumetric water content, and pH meter were placed at a depth of 12 cm to ensure readings are at the same depth.

Plant Root Simulator (PRS™) probes were used to measure soil nutrient (Ca^{2+}, Mg^{2+}, K^{+}, P, NO_3^{-}, and NH_4^{-}) (Western Ag Innovations Inc., Saskatoon, Saskatchewan, Canada). Soil samples were incubated in the lab to quantify the potential nutrient supply rate under controlled moisture conditions and temperature. 1 L of soil from 0-15 cm depth was collected outside of the 1 m² quadrat at 5 m on both the FFMM and PMM of 28 transects (Fig.2). Lab incubation methods were based on the Western Ag sampling protocol and the United States Department of Agriculture soil moisture protocol (Western AG Innovations, 2018). PRS probes were pre-incubate for 24 hours to reach a temperature between 18-21 ˚C. A homogeneous soil sample was created by removing large clumps, rocks, and woody debris. From the homogeneous mixture, 700 g was measured. Before the PRS probes were inserted, the sample needs to reach field capacity (FC), which is the amount of water that soil can hold after the downward water movement has stopped. Once the samples reached FC, the sample was placed into bags, squared off into the bottom 2/3 rds. Two pairs of anion/cation PRS probes installed into the bag, leaving 1 cm of soil on both sides of the membrane. The probed samples were placed into bins, with some light exposure occurring on the top layer of the soil. The soil was checked to determine if the soil remained at FC and in contact with the membrane. The probes were collected after seven days of burial, cleaned thoroughly with reverse osmosis water, placed into clean Ziploc bags, and sent to Western Ag Innovations for analysis.

A hierarchical generalized mixed-effect model was used to compare nutrients between FFMM and PMM (lme4 package version 1.1-19), while random effects of transect location were included. A Poisson distribution was used on Ca^{2+}, Mg^{2+}, and K^+ due to the left-skewed distribution of the data. A Gamma distribution was used on the following nutrients NH_4+, NO_3^-, and P due to the left-skewed and fractional values. Analysis of general soil characteristics (pH, volumetric soil water content, and temperature) was done using a hierarchical generalized mixed-effect model, and random effects include transect location (lme4 package version 1.1-19). Volumetric water content and temperature used Gaussian distribution, while pH used Gamma distribution based on the skewed data.

A. 2 Supplemental Material



A.2.1. Potential significant pairwise species associations based on probabilistic model of co-occurrence analysis. Abbreviations of species are the first four digest of the genus and the first 3 digest of the species.

A. 2.2. Four most abundant species found within each functional group (FG) and soil type in the seed bank, seed rain, Year 2, and Year 5 above-ground plant. Species nomenclature follows the Flora of Alberta and Common Plants of the Western Rangelands (Moss and Packer, 1994; Tannas, 2001, 2003, 2004).

FG	Soil	Seed Bank	Seed Trap	Year 2	Year 5
Graminoids	FFMM	*1. Typha latifolia* *2. Carex sp.* *3. Calamagrostis canadensis* *4. Agrostis scabra*	*1. Agrostis scabra* *2. Carex sp.* *3. Hordeum jubatum* *4. Poa palustris*	*1.Calamagrostis canadensis* *2. Agropyron trachycaulum* *3. Elymus innovates* *4. Agrostis scabra*	*1.Calamagrostis canadensis* *2. Agropyron trachycaulum* *3. Elymus innovatus* *4. Poa palustris*
	PMM	*1. Carex sp.* *2. Typha latifolia* *3. Agrostis scabra* *4. Calamagrostis canadensis*	*1. Agrostis scabra* *2. Carex sp.* *3. Hordeum jubatum* *4. Agropyron sp.*	*1.Calamagrostis canadensis* *2. Agropyron trachycaulum* *3. Elymus innovates* *4. Agrostis scabra*	*1.Calamagrostis canadensis* *2. Agropyron trachycaulum* *3. Poa palustris* *4. Elymus innovatus*
Native Forbs	FFMM	*1. Potentillia norgegica* *2. Epilobium ciliatum* *3. Plantago major* *4. Galium boreale*	*1. Epilobium ciliatum* *2. Chamerion angustifolium* *3. Erigeron canadensis* *4. Plantago major*	*1. Epilobium angustifolium* *2. Potentillia norvegica* *3. Achillea millefolium* *4. Corydalis aurea*	*1. Chamerion angustifolium* *2. Equisetum arvense* *3. Rubus idaeus* *4. Achillea millefolium*
	PMM	*1. Potentillia norvegica* *2. Epilobium ciliatum* *3. Aquiligia brevistyla*	*1. Epilobium ciliatum* *2. Chamerion angustifolium* *3. Potentillia norvegica*	1. *Chamerion angustifolium* *2. Potentillia norvegica* *3. Geranium bicknellii*	*1. Chamerion angustifolium* *2. Equisetum arvense* *3. Rubus idaeus*

		4. Plantago major	*4. Erigeron canadensis*	4. *Achillea millefolium*	*4. Achillea millefolium*
Non-Native Forbs	FFMM	*1. Chenopidium album* *2. Polygonum lapathifolium* *3. Sonchus sp.* *4. Crepis tectorum*	*1. Polygonum lapathifolium* *2. Matricaria matricarioides* *3. Polygonum arenestrum* *4. Crepis tectorum*	*1. Melilotus alba* *2. Sonchus sp.* *3. Polygonum lapathifolium* *4. Chenopidium album*	*1. Sonchus sp.* *2. Melilotus alba* *3. Crepis tectorum* *4. Taraxacum officinale*
	PMM	*1. Chenopodium album* *2. Rorippa palustris* *3. Polygonum lapathifolium* *4. Urtica dioica*	*1. Polygonum lapathifolium* *2. Sonchus sp.* *3. Chenopodium album* *4. Crepis tectorum*	*1. Melilotus alba* *2. Sonchus sp.* *3. Polygonum lapathifolium* *4. Chenopidium album*	*1. Sonchus sp.* *2. Melilotus alba* *3. Crepis tectorum* *4. Taraxacum officinale*

A. 2.3. List of all identified species along with their functional group (FG), the dispersal mechanism (DM) for native forbs (V=vegetative, W=wind,G=gravity) and soil type (FFMM and PMM), if they were present in the seed bank, seed rain, and in 2016 (year 2) or2019 (year 5) above ground cover. FG included (F=native forb, G=graminoid, I=non-native forb, S=shrub, T=Tree). Species nomenclature follows the Flora of Alberta and Common Plants of the Western Rangelands (Moss and Packer, 1994; Tannas, 2001, 2003, 2004)

				Seed Bank		Seed Trap		Year 2		Year 5	
Scientific Name	FG	DM	AM	FFMM	PMM	FFMM	PMM	FFMM	PMM	FFMM	PMM
Achillea millefolium L.	F	V	SB	X	X	X	X	X	X	X	X
Agrostis scabra Wild.	G	W	SB	X	X	X	X	X	X	X	X
Aquilegia brevistyla Hook.	F	V	SB	X	X	X				X	X
Calamagrostis canadensis (Michx.) P. Beauv.	G	W	SB	X	X	X	X	X	X	X	X
Carex aquatilis Wahlenb.	G		SB	X	X	X	X		X	X	X
Carex siccata Dewey	G		SB	X	X	X	X	X	X	X	X
Carex spp.	G		SB	X	X	X	X	X	X	X	X
Chenopodium album L.	I	G	SB	X	X	X	X	X	X	X	X
Chenopodium capitatum (L.) Asch.	I	G	SB	X	X	X	X	X	X		
Conyza canadensis (L.) Cronquist var. *canadensis*	F	W	SB	X	X	X	X				
Epilobium ciliatum Raf.	F	W	SB	X	X	X	X	X	X	X	X
Geranium bicknellii Britton	F	G	SB	X	X	X		X	X	X	X
Geum macrophyllum Willd.	F	G	SB	X	X	X	X			X	X
Plantago major L.	F	G	SB	X	X	X	X	X		X	X
Poa palustris L.	G		SB	X	X	X	X	X	X	X	X
Polygonum lapathifolium L.	I		SB	X	X	X	X	X	X		
Potentilla norvegica L.	F	G	SB	X	X	X	X	X	X	X	X
Ranunculus sceleratus L.	F	G	SB	X	X	X					
Rorippa palustris (L.) Besser	I		SB	X	X	X	X	X			
Sonchus L.	I	W	SB	X	X	X		X	X	X	X
Typha latifolia L.	G	W	SB	X	X	X	X				
Betula papyrifera Marsh.	T		SB	X	X					X	X
Chenopodium L.	I	G	SB	X	X						
Salsola kali L.	I		SB	X	X			X	X		X
Achillea sibirica Ledeb.	F	V	SB	X		X		X		X	X
Astragalus alpinus L.	F	V	SB	X		X		X		X	X
Cornus canadensis L.	F	V	SB	X		X					X

				Seed Bank		Seed Trap		Year 2		Year 5	
Scientific Name	FG	DM	AM	FFMM	PMM	FFMM	PMM	FFMM	PMM	FFMM	PMM
Crepis L.	I	W	SB	X		X	X	X	X	X	X
Dracocephalum parviflorum Nutt.	F	W	SB	X		X		X	X		
Elymus trachycaulus (Link) Gould ex Shinners ssp. *trachycaulus*	G		SB	X		X	X	X	X	X	X
Fragaria virginiana Duchesne	F	V	SB	X		X	X	X		X	X
Galium boreale L.	F	V	SB	X		X		X	X	X	X
Juncus bufonius L.	G		SB	X		X	X				
Lactuca serriola L.	I		SB	X		X	X				
Lepidium densiflorum Schrad.	I		SB	X		X	X	X	X	X	X
Matricaria discoidea DC.	I		SB	X		X	X	X			
Melilotus alba (L.) Lam.	I		SB	X		X	X	X	X	X	X
Poa pratensis L.	G		SB	X		X		X	X	X	X
Rubus idaeus L.	F	V	SB	X		X	X	X	X	X	X
Senecio L.	I		SB	X		X	X			X	
Symphyotrichum ciliolatum (Lindl.) Á. Löve & D. Löve	F	W	SB	X		X	X	X	X	X	X
Vicia americana Muhl. ex Willd.	F	V	SB	X		X		X	X	X	X
Viola adunca Sm.	F	G	SB	X		X	X	X	X	X	X
Viola renifolia A. Gray	F	G	SB	X		X	X			X	X
Argentina anserina (L.) Rydb.	F	V	SB	X							
Bidens cernua L.	F	W	SB	X							
Galium trifidum L.	F	V	SB	X			X	X	X	X	X
Mentha arvensis L.	F	V	SB	X						X	
Moehringia lateriflora (L.) Fenzl	F	V	SB	X							
Phleum pratense L.	G		SB	X							
Stellaria longifolia Muhl. Ex Willd.	F	V	SB	X					X	X	X
Polygonum arenastrum Jord. Ex Boreau	I		SB		X	X	X	X	X		

				Seed Bank		Seed Trap		Year 2		Year 5	
Scientific Name	FG	DM	AM	FFMM	PMM	FFMM	PMM	FFMM	PMM	FFMM	PMM
Bassia scoparia (L.) A.J. Scott	I		SB		X			X	X	X	X
Cirsium arvense (L.) Scop.	I		SB		X					X	X
Comarum palustre L.	F	G	SB		X						
Vaccinium vitis-idaea L.	F	V	SB		X		X				
Carex deflexa Hornem.	G		SR			X	X				
Chamerion angustifolium (L.) Holub ssp. *angustifolium*	F	W	SR			X	X	X	X	X	X
Collomia linearis Nutt.	F	G	SR			X	X			X	
Corydalis aurea Willd.	F	W	SR			X	X	X	X		
Epilobium palustre L.	F	W	SR			X	X				
Eriophorum L.	G		SR			X	X				
Hordeum jubatum L.	G		SR			X	X	X	X	X	X
Populus balsamifera L.	T		SR			X	X			X	X
Populus tremuloides Michx.	T		SR			X	X	X	X	X	X
Salix bebbiana Sarg.	S		SR			X	X	X	X	X	X
Taraxacum officinale F.H. Wigg.	I		SR			X	X			X	X
Urtica dioica L.	F	G	SR			X	X		X	X	X
Vaccinium oxycoccos L.	F	V	SR			X	X				
Astragalus americanus (Hook.) M.E. Jones	F	V	SR			X				X	X
Lathyrus ochroleucus Hook.	F	V	SR			X		X	X	X	X
Medicago sativa L.	I		SR			X				X	X
Oxytropis deflexa (Pall.) DC.	F	V	SR			X				X	
Piptatheropsis pungens (Torr.) Romasch., P.M. Peterson & R.J. Soreng	G		SR			X				X	X
Polygonum convolvulus L. var. *convolvulus*	I		SR			X		X		X	X
Rosa acicularis Lindl.	S		SR			X		X	X	X	X
Vaccinium myrtilloides Michx.	S		SR			X		X		X	X

				Seed Bank		Seed Trap		Year 2		Year 5	
Scientific Name	FG	DM	AM	FFMM	PMM	FFMM	PMM	FFMM	PMM	FFMM	PMM
Beckmannia syzigachne (Steud.) Fernald	G		SR				X	X	X		
Bromus ciliatus L.	G		SR				X	X		X	X
Epilobium leptophyllum Raf.	F	W	SR				X				
Solidago L.	F	W	SR				X			X	
Carex aenea Dewey	G		BD					X	X	X	X
Elymus innovatus (Beal) Pilg.	G		BD					X	X	X	X
Equisetum arvense L.	F	V	BD					X	X	X	X
Hieracium umbellatum L.	I	W	BD					X	X		X
Petasites frigidus (L.) Fr. var. *palmatus* (Aiton) Cronquist	F	V	BD					X	X	X	X
Rubus pubescens Raf. var. *pubescens*	F	O	BD					X	X	X	X
Trifolium L.		O	BD					X	X	X	X
Alopecurus aequalis Sobol.	G		BD					X			
Elymus canadensis L.	G	O	BD					X		X	X
Mertensia paniculata (Aiton) G. Don	F	V	BD					X		X	X
Scutellaria galericulata L.	F	G	BD					X		X	X
Tripleurospermum perforatum (Mérat) M. Lainz	I		BD					X		X	X
Betula pumila L.	S		BD						X		X
Chenopodium rubrum L.	I		BD						X		
Dasiphora fruticosa (L.) Rydb.	S		BD						X		
Equisetum sylvaticum L.	F	V	BD						X	X	X
Galium triflorum Michx.	F	V	BD						X	X	X
Rubus chamaemorus L.	F	V	BD						X	X	X
Salix myrtillifolia Andersson	S		BD						X		
Arctostaphylos uva-ursi (L.) Spreng.	S	O	BD							X	X
Carex aurea Nutt.	G		BD							X	X
Cornus sericea L. ssp. *sericea*	S	O	BD							X	X
Deschampsia cespitosa (L.) P. Beauv.	G	W	BD							X	X

				Seed Bank		Seed Trap		Year 2		Year 5	
Scientific Name	FG	DM	AM	FFMM	PMM	FFMM	PMM	FFMM	PMM	FFMM	PMM
Equisetum fluviatile L.	F	V	BD							X	X
Equisetum hyemale L.	F	V	BD							X	X
Equisetum pratense Ehrh.	F	V	BD							X	X
Fragaria vesca L.	F	V	BD							X	X
Geum aleppicum Jacq.	F	V	BD							X	X
Ribes glandulosum Grauer	S	O	BD							X	X
Ribes hudsonianum Richardson	S	O	BD							X	X
Ribes oxyacanthoides L.	S	O	BD							X	X
Ribes triste Pall.	S	O	BD							X	X
Rubus arcticus L.	F	V	BD							X	X
Shepherdia canadensis (L.) Nutt.	S	O	BD							X	X
Symphoricarpos albus (L.) S.F. Blake	S	O	BD							X	X
Symphyotrichum ciliolatum (Lindl.) Á. Löve & D. Löve	F	W	BD								X
Symphyotrichum puniceum (L.) Á. Löve & D. Löve var. *puniceum*	F	W	BD							X	X
Trifolium hybridum L.	I	O	BD							X	X
Trifolium pratense L.	I	O	BD							X	X

Appendix 4. List of all identified species on the FFMM islands with functional group (FG). FG included (F=native forb, G=graminoid, I=non-native forb, S=shrub, T=Tree). Species nomenclature follows the Flora of Alberta and Common Plants of the Western Rangelands (Moss and Packer, 1994; Tannas, 2001, 2003, 2004).

Species	FG
Achillea millefolium L.	F
Achillea sibirica Ledeb.	F
Agrostis scabra Wild.	G
Alnus viridis (Chaix) DC.	S
Amelanchier alnifolia (Nutt.) Nutt. ex M. Roem.	S
Anemone canadensis L.	F
Aquilegia brevistyla Hook.	F
Aralia nudicaulis L.	F
Arctostaphylos uva-ursi (L.) Spreng.	S
Arnica chamissonis Less.	F
Astragalus alpinus L.	F
Astragalus americanus (Hook.) M.E. Jones	F
Axyris amaranthoides L.	F
Bassia scoparia (L.) A.J. Scott	I
Beckmannia syzigachne (Steud.) Fernald	G
Betula papyrifera Marsh.	T
Bromus ciliatus L.	G
Calamagrostis canadensis (Michx.) P. Beauv.	G
Carex magellanica Lam. ssp. *irrigua* (Wahlenb.) Hultén	G
Carex praticola Rydb.	G
Carex aenea Dewey	G
Carex aquatilis Wahlenb.	G
Carex atherodes Spreng.	G
Carex aurea Nutt.	G
Carex bebbii Olney ex Fernald	G
Carex deflexa Hornem.	G
Carex rossii Boott	G
Carex siccata Dewey	G
Carex spp.	G
Carex utriculata Boott	G
Chamaedaphne calyculata (L.) Moench	S
Chamerion angustifolium (L.) Holub ssp. *angustifolium*	F
Chenopodium album L.	I
Cirsium arvense (L.) Scop.	I
Collomia linearis Nutt.	F
Comarum palustre L.	F
Cornus canadensis L.	F

Cornus sericea L. ssp. *sericea*	S
Corydalis aurea Willd.	F
Crepis sp. L.	I
Deschampsia cespitosa (L.) P. Beauv.	G
Dracocephalum parviflorum Nutt.	F
Elymus canadensis L.	G
Elymus innovatus (Beal) Pilg.	G
Elymus trachycaulus (Link) Gould ex Shinners ssp. *subsecundus* (Link) Á. Löve & D. Löve	G
Elymus trachycaulus (Link) Gould ex Shinners ssp. *trachycaulus*	G
Epilobium ciliatum Raf.	F
Equisetum arvense L.	F
Equisetum fluviatile L.	F
Equisetum hyemale L.	F
Equisetum pratense Ehrh.	F
Equisetum sylvaticum L.	F
Erigeron philadelphicus L.	F
Eurybia conspicua (Lindl.) G.L. Nesom	F
Fragaria vesca L.	F
Fragaria virginiana Duchesne	F
Galium boreale L.	F
Galium trifidum L.	F
Galium triflorum Michx.	F
Gentianella amarella (L.) Börner	F
Geranium bicknellii Britton	F
Geum aleppicum Jacq.	F
Geum macrophyllum Willd.	F
Geum triflorum Pursh	F
Hieracium umbellatum L.	I
Hordeum jubatum L.	G
Juncus bufonius L.	G
Lactuca serriola L.	I
Larix laricina (Du Roi) K. Koch	T
Lathyrus ochroleucus Hook.	F
Lathyrus venosus Muhl. ex Willd.	F
Ledum groenlandicum Oeder	S
Lepidium densiflorum Schrad.	I
Lonicera dioica L.	S
Lonicera involucrata (Richardson) Banks ex Spreng.	S
Maianthemum canadense Desf.	F
Medicago sativa L.	I
Melilotus alba (L.) Lam.	I
Mentha arvensis L.	F

Mertensia paniculata (Aiton) G. Don	F
Oxytropis deflexa (Pall.) DC.	F
Packera paupercula (Michx.) Á. Löve & D. Löve	F
Parnassia palustris L.	F
Petasites frigidus (L.) Fr. var. *palmatus* (Aiton) Cronquist	F
Petasites frigidus (L.) Fr. var. *sagittatus* (Banks ex Pursh) Cherniawsky	F
Petasites frigidus (L.) Fr. var. *vitifolius* (Greene) Cherniawsky	F
Picea glauca (Moench) Voss	T
Pinus banksiana Lamb.	T
Piptatheropsis pungens (Torr.) Romasch., P.M. Peterson & R.J. Soreng	G
Plantago major L.	F
Poa palustris L.	G
Poa pratensis L.	G
Polygonum aviculare L.	I
Polygonum convolvulus L.	I
Polygonum lapathifolium L.	I
Populus balsamifera L.	T
Populus tremuloides Michx.	T
Potentilla norvegica L.	F
Rhinanthus minor L.	F
Ribes americanum Mill.	S
Ribes glandulosum Grauer	S
Ribes hudsonianum Richardson	S
Ribes lacustre (Pers.) Poir.	S
Ribes oxyacanthoides L.	S
Ribes triste Pall.	S
Rosa acicularis Lindl.	S
Rubus arcticus L.	F
Rubus chamaemorus L.	S
Rubus idaeus L.	S
Rubus pubescens Raf. var. *pubescens*	S
Rumex aquaticus L. var. *fenestratus* (Greene) Dorn	F
Salix bebbiana Sarg.	S
Salix exigua Nutt.	S
Salsola kali L.	I
Scutellaria galericulata L.	F
Shepherdia canadensis (L.) Nutt.	S
Sibbaldiopsis tridentata (Aiton) Rydb.	F
Sisyrinchium montanum Greene	F
Sium suave Walter	F
Solidago L.	F
Solidago missouriensis Nutt.	F
Stachys palustris L.	F

Stellaria longifolia Muhl. Ex Willd.	F
Stellaria longipes Goldie	F
Symphoricarpos albus (L.) S.F. Blake	S
Symphyotrichum ciliolatum (Lindl.) Á. Löve & D. Löve	F
Symphyotrichum puniceum (L.) Á. Löve & D. Löve var. *puniceum*	F
Taraxacum officinale F.H. Wigg.	I
Trientalis borealis Raf.	F
Trifolium hybridum L.	I
Trifolium pratense L.	I
Tripleurospermum perforatum (Mérat) M. Lainz	I
Urtica dioica L.	F
Vaccinium myrtilloides Michx.	S
Viburnum edule (Michx.) Raf.	S
Viburnum opulus L.	S
Vicia americana Muhl. ex Willd.	F
Viola adunca Sm.	F
Viola renifolia A. Gray	F