The role of microtopography in the expression of soil propagule banks on reclamation sites

by

Katharine Olegovna Melnik

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

Master of Science

in
LAND RECLAMATION AND REMEDIATION

Department of Renewable Resources
University of Alberta

Abstract

Legacy propagule banks of salvaged topsoils are excellent sources of plant propagules for reclamation of mine sites. However, prior studies show that less than 50% of species found in original propagule banks actually establish. We hypothesize that the expression of this legacy propagule bank is limited by a lack of diversity of microsites and appropriate growing conditions. In an operational-scale field experiment we manipulated topographical characteristics and substrate materials and explored early vegetation establishment on an east- and south-facing slope. Three different site treatments with different microtopographic characteristics: (i) levelled surface, (ii) parallel ridges, and (iii) large loose piles were created using salvaged upland and lowland forest floor soil material.

Placing materials in loose hills and providing heterogeneity in substrates more than doubled plant abundance, species richness, and increased the proportion of species that require higher soil moisture. However, the site' s overall slope aspect had a modulating effect on microtopographic treatments, with the greatest treatment effect on species richness and plant abundance occurring on the east-facing slope, while the greatest effect of treatment on the proportion of species requiring higher soil moisture was observed on the south-facing slope. Lower micro-elevations and northern microaspects of the microtopographic structures had higher soil water content, species richness and plant abundance. Micro-elevation had the greatest effect on expression of vegetation on hills constructed from cover soil salvaged from upland forests, while microaspect affected vegetation the most on hills constructed from cover soil salvaged from low-lying areas. Variability in microtopography and substrate can create favourable growing conditions that help express a wider range of species from the legacy propagule bank at operational scale.

Preface

Data of chapter 2 and 3 were used in a publication Melnik K, Landhäusser SM, Devito K (in press) "The role of microtopography in the expression of soil propagule banks on reclamation sites", *Restoration Ecology*, doi: 10.1111/rec.12587. I supervised research operations, conducted the greenhouse study, collected and analysed data and prepared the manuscript. S.M. Landhäusser conceived the research idea, designed the experiment, interpreted data, and contributed to the manuscript. K. Devito contributed to the experimental design, interpreted data, and edited the manuscript.

Dedicated to my parents, Oleg Melnik and Larisa Melnic.

Thank you for always supporting and inspiring me.

Acknowledgements

I would like to thank my supervisor, Dr. Simon Landhäusser, for his support and guidance through all the steps of my degree. Thanks to his insight, mentoring and enthusiasm about research I learned a great deal about research and scientific writing, and developed invaluable professional skills. Thank you to Dr. Kevin Devito and Dr. Scott Nielsen for serving on my committee, and for sharing their knowledge and insight.

I would like to express my gratitude to Rob Vassov for assisting with overseeing research site construction, and providing unwavering support with logistics of the field research. Thank you to Clayton Dubyk for providing assistance and support with snow surveys. I thank Fran Leishman for assisting with soil sample collection, coordinating resources, and helping me accomplish my research goals by providing valuable ideas and advice. Thank you to Trevor Kent, Rebecca Fyfe, Craig Mutch, Dilveer Dhillon, Jessica Grenke, Lynnette Allemand, Larisa Melnic, Oleg Melnik, Andrew Shaman, Rob Hetmanski, Mika Little-Devito, Trevor De Zeeuw, Alana Benoit and the rest of the Landhäusser research group for your help during exciting and not-so-exciting times in the field, greenhouse and the lab, as well as for great conversations and moral support in the office. Thank you to Hugh Wallace, Oleg Melnik, Amanda Melnik, Chantal Dings-Avery, Graeme Harper and Kyle Le for reading my thesis and sharing your thoughtful comments and suggestions. I would like to express my gratitude to my family, friends and my partner Hugh for being there with me every step of the way, believing in me and supporting me throughout this journey.

Funding for this project was provided by the Natural Sciences and Engineering Research Council of Canada and the Collaborative Research and Training Experience Program, TransAlta

Corporation, Land Reclamation International Graduate School, and Canada's Oil Sands Innovation Alliance through Canadian Natural Resources Limited, Imperial Oil Resources Limited, Shell Canada, Suncor Energy, and Syncrude Canada Limited.

Table of Contents

List of Tables

List of Figures

Chapter 1: Introduction

1.1 Industrial disturbance and forest reclamation

On a global scale, industrial, agricultural and infrastructure development has claimed 46% of our forested areas. (Bryant et al. 1997). Although the rate of deforestation has declined in recent years, on average 3.3 million hectares of forests per year were still lost between 2010 and 2015. As the scale and importance of the issue is recognized, reclamation of previously forested landscapes has become a priority for policy makers (Jacobs et al. 2015). Reclamation strategies differ depending on the post-deforestation land use, with mining providing practitioners with one of the most challenging scenarios. While mining amounts to a relatively small fraction of disturbed land, it creates some of the most severe disturbances that destroy ecosystem function, as it requires the removal of soil overlaying the resource along with all the plants and animals, or results in their burial (Cooke & Johnson 2002). Mining is a temporary landuse, and reclamation and revegetation of affected areas after the completion of resource extraction is an important part of the mine closure process, which aims to return the land to a resilient, sustainable state (Cooke & Johnson 2002).

In Alberta, the largest area affected by mining is located within the Boreal Forest Natural Region. The region covers 58% of the province (381,000 km^2), spans most of northern Alberta and a small portion of the central Alberta (Natural Regions Committee 2006), and consists of upland forests and low-lying wetlands. The region experiences long very cold winters with average temperatures below -10°C during at least four months, and short warm summers with average temperatures exceeding 15°C during only one or two months. Mean annual temperature is -0.2°C, mean annual precipitation is 469mm (Natural Regions Committee 2006). Dominant soils are Luvisols and Brunisols on upland areas, and Gleysols and Organic soils in wetlands (Natural Regions Committee 2006). The dominant tree species are aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) (Natural Regions Committee 2006), and the understory includes species such as bearberry (*Arctostaphylos uva-ursi*), blueberry (*Vaccinium myrtilloides*), Labrador tea (*Ledum groenlandicum*), green alder (*Alnus crispa*) and low-bush cranberry (*Viburnum edule*) (Beckingham & Archibald 1996).

Understory vegetation is an important component of boreal forests, as it is responsible for the majority of plant biodiversity, and it significantly contributes to the primary net productivity of the region. Although the combined mass of understory vegetation is relatively low compared to that of trees, understory plants turn over much more rapidly and their combined net primary productivity is comparable to the net primary productivity of trees (Nilsson & Wardle 2005). Additionally, understory vegetation prevents invasive species colonization and interference with tree seedling establishment. It is important to conserve understory species diversity, as diverse vegetation cover enhances ecosystem productivity and sustainability (Tilman et al. 1996), and facilitates recovery following disturbance (Frank & McNaughton 1991; Peterson et al. 1997). While initial revegetation efforts focused on establishing vegetation cover regardless of species origin and function, reclamation practices have evolved with the focus shifted to utilizing species native to the area and to reclaiming the disturbed areas to a landuse similar to the original (Macdonald et al. 2015). While planting trees is often seen as a priority in previously forested landscapes (Löf et al. 2012), a diverse vegetative cover containing species found in the original forests must also be established on the site in order to facilitate the development of a self-sustaining forest ecosystem.

1.2 Salvaged cover soil materials

Soil materials salvaged from previously forested areas proved to be a great source of seeds and vegetative fragments of many forest understory species (Mackenzie & Naeth 2010). In order to obtain this species-rich soil, the reclamation process must begin before commencing mining. After trees are cleared from the site that is intended for development, topsoil materials are salvaged and are either stockpiled for future use, or are used immediately on a site that is being reclaimed at the time. Topsoils salvaged from different forest types differ in the propagules they contain, and in chemical and physical properties (Mackenzie & Naeth 2010).

In northern Alberta, cover soil is usually salvaged from either lowland forests and has a thick organic peat horizon, or from upland forests with a thin organic LFH (litter-fibre-humic) horizon. The lowland peat-rich material is high in organic matter and is called peat-mineral mix (PMM), while the material salvaged from upland forests contains a high percentage of mineral soil and is called forest floor material (FFM). PMM has significantly higher water retention capacity, higher level of organic matter and lower porosity than FFM (Walczak & Rovdan 2002). The chemical properties of the FFM cover soil are more suitable for vegetation establishment, including higher levels of potassium and phosphorus, lower electrical conductivity (Mackenzie 2013), and a greater amount of micronutrients such as Fe, Mn, Zn and Cu (Haynes & Swift 1985). However, PMM is more readily available for reclamation in northern Alberta due to the prevalence of low-lying wet areas and the resulting decreased rates of organic layer decomposition., (Natural Regions Committee 2006). While there is an overlap in species composition between the FMM and PMM propagule banks, FFM tends to contain more species adapted to drier, upland conditions, while PMM tends to have more species adapted to high-moisture conditions of lowland sites. Understory species common on upland sites where FFM is salvaged include blueberry, bearberry, bog cranberry (*Vaccinium vitis-idaea*), Labrador tea, cream-colored vetchling (*Lathyrus ochroleucus*), low-bush cranberry. Understory species common to low-lying areas where PMM is salvaged include Labrador tea, cloudberry (*Rubus chamaemorus*), bog cranberry, small bog cranberry (*Vaccinium oxycoccos*), meadow horsetail (*Equisetum pratense*) and sedges (*Carex* spp.) (Beckingham & Archibald 1996).

1.3 Challenges and operational approaches

In order for the propagules found in cover soils to be expressed on reclamation sites, desirable growing conditions must be present. Edaphic factors such as soil water content, solar radiation levels, soil and air temperature, and available nutrients are important variables that determine the eventual success of each species. Seeds of different species require different levels of these factors to germinate (Harper & Benton 1966). Natural sites tend to have a high diversity of available microsites and are able to satisfy the growing requirements of many diverse species (Beatty 1984), while conventionally created reclamation sites often lack microhabitat heterogeneity. Additionally, forests harbour higher-moisture, lower temperature, wind and solar radiation exposure conditions, and experience less fluctuation in moisture and temperature compared with treeless reclamation sites (Chen et al. 1993). Propagules found in forest soil likely require the availability of diverse microsites, and the presence of some sheltered microsites containing higher moisture and lower temperatures for their successful expression on reclamation sites. Previous research has shown that variability in available growing conditions resulting from surface roughness and microtopographic heterogeneity can facilitate vegetation establishment and increase species diversity (Lundholm & Larson 1998; Macdonald et al. 2015).

Additionally, the presence of sheltered microsites can facilitate vegetation establishment on high-stress sites (Fowler 1986; Valenzuela et al. 2016).

One of the methods to increase microsite heterogeneity and ensure the presence of sheltered microsites on reclamation sites is to construct microtopography. Microtopographic structures can be created via techniques such as mounding and trenching, which have already been used for centuries to facilitate the survival of planted tree species by removing competing vegetation, reducing soil bulk density (Sutton 1993; Löf et al. 2012), and creating elevated planting areas in water-logged areas (Löf et al. 2012; Bannister et al. 2013; Born et al. 2015). More recently, it was discovered that by diversifying the available microsites, mounding can also increase the richness and abundance of colonizing herbaceous vegetation on reclamation sites. Biederman & Whisenant (2011) demonstrated that creating mounds during grassland restoration increases the number of seeded and unseeded prairie species. Gilland & Mccarthy (2014) showed that on broadleaf forest reclamation sites, mounds constructed on sites with abundant soil moisture increase species richness and abundance by reducing soil bulk density and creating elevated areas. It is likely that introducing microtopographic heterogeneity on boreal forest reclamation sites will benefit the colonizing vegetation by providing some sheltered moist microsites on otherwise dry sites, and by diversifying the available growing environments.

Another way of creating microsite heterogeneity is by alternatively placing contrasting cover soils. While it is a common reclamation practice to apply the same substrate across the entire site, creating a mosaic of soil materials with contrasting textures, water retention capacity, organic matter content, bulk density and porosity could be beneficial for satisfying diverse growing requirements of different species (Macdonald et al. 2015). Since FFM and PMM cover soils differ in their physical and chemical properties (as discussed earlier), interchangeably placing these cover soils would introduce a high level of substrate heterogeneity. Placing both of these cover soils can also expand the range of species available for germination on the site, as the propagule banks of the two materials differ from one another (Mackenzie & Naeth 2010). Lastly, since the supply of forest floor material in northern Alberta is more limited than that of peat mineral mix, using PMM along with FFM can potentially allow practitioners to use FFM more efficiently by applying it over a larger area.

1.4 The chapters ahead

Creating microtopographic structures on boreal forest reclamation sites has the potential to facilitate the expression of propagules contained in salvaged and placed cover soils. The overall objective of this thesis is to evaluate the capacity of treatments with different levels of microtopographic heterogeneity to increase species richness and abundance of vegetation establishing from soil propagule banks, and to determine which microsites within these treatments provide the most desirable growing conditions.

Chapter 2 presents the results of a study comparing vegetation expression among three cover soil placement techniques with varying levels of microtopography, to determine which technique is most facilitative for vegetation establishment. This study examined species richness, plant abundance, the expression of three species functional habitat types (i.e. forest species with an affinity for higher soil moisture (moisture-loving), forest species associated with understories, or disturbance and open canopy associated species) and edaphic factors across the three cover soil placement techniques.

Chapter 3 contains an in-depth examination of differences in vegetation expression among various microtopographic positions on constructed small hills, aiming to determine the positions most conducive to vegetation establishment. Species richness, plant abundance, the expression of three species functional types, as well as edaphic factors were evaluated for each microsite position.

Chapter 4 summarizes the main finding of the previous two chapters and discusses them in the context of related studies, reports management implications, outlines limitations of this research and recommends future research.

Chapter 2: The role of microtopography in the expression of soil propagule banks on reclamation sites*

2.1 Introduction

Natural forests often provide a broad range of microsites that vary in size, substrates, and climatic and edaphic conditions that result in heterogeneities in the abundance and composition of vegetation. Much of that variation is driven by variables such as topographic heterogeneity at the landscape and microsite scale, and is modified by factors such as canopy composition and closure, and coarse woody debris (Beatty 1984; Cornett et al. 1997). Plant species vary widely in their prerequisites for establishment, growth, and survival (Harper & White 1974). Greater heterogeneity in resource availability and conditions (i.e. microsite diversity) in a given area increases the likelihood that resource requirements of a greater array of species can be satisfied, and should lead to increased overall species richness and diversity (Nichols et al. 1998; Bartels & Chen 2010).

Surface mining creates severe disturbances in forest regions, as it requires the complete removal of surface soil and overburden material that cover the resource. After mining activities have ceased, many mined areas require the reconstruction of forests including facilitating the restoration of basic ecological functions (Macdonald et al. 2012). While planting trees remains a key aspect contributing to restoring ecological function within the post-disturbed forest landscape, the establishment of a diverse understory is considered an essential part of the recovery of forest ecosystem functions (Jacobs et al. 2015; Macdonald et al. 2015). In many forest ecosystems, the understory plant community is one of the greatest contributors to

* Portions of this chapter have been included in the publication Melnik K, Landhäusser SM, Devito K (in press) The role of microtopography in the expression of soil propagule banks on reclamation sites. Restoration Ecology. doi: 10.1111/rec.12587

ecosystem species richness, where it can provide a range of functional types and traits that support all trophic levels (Nilsson & Wardle 2005; Gilliam 2007).

Establishing species-rich plant communities in reclaimed forest understories is a challenge that requires the availability of a diverse array of plant propagules (seeds and vegetative fragments) in combinations with the appropriate growing conditions (Macdonald et al. 2012, 2015). Salvaged forest soils placed on reclamation sites can be a valuable source of native plant propagules (Tacey & Glossop 1980; MacKenzie & Quideau 2010), but establishment success of the array of species contained in this material is determined by the specific growing requirements of each species (i.e. the species specific recruitment niche) (Harper & White 1974; Dalling & Hubbell 2002). Water and nutrient availability, and climatic conditions, such as soil and air temperature, are important factors influencing seed germination and establishment (Harper and Benton 1966, Silvertown 1999). Of those factors, adequate water availability is a crucial driver of germination and early establishment success for many species (Rodriguez-Iturbe 2000; Bhattacharjee et al. 2008). Surface microtopography is an important factor for vegetation establishment (Klug-Pümpel 1982, Frouz et al. 2011), as it can affect the distribution of soil moisture, and increase the availability of sheltered microsites that benefit germination and establishment of plants from seeds by protecting them from high respiration rates, early and late frosts, and herbivory (Elmarsdottir et al. 2003; Schott et al. 2014).

Compared to natural forests, forest reclamation sites provide a unique opportunity to explore some of the fundamental hypotheses that relate plant richness to microsite heterogeneity and resource availability, because the climatic and edaphic impacts on initial resource availability are mostly independent of historical site conditions in these constructed landforms. In addition, reconstruction of these sites allows for the creation of a variety of landscape and microscale topographical features through variations in soil surface microtopography (Biederman & Whisenant 2011) and substrate types (Hutchings et al. 2003; Ojekanmi & Chang 2014). The role of microtopography in the re-development of forest understory communities has not yet been explored in boreal forest reclamation settings, but this approach has been successfully applied in temperate forest, wetland and grassland restoration projects (Ewing 2002; Bruland & Richardson 2005; Biederman & Whisenant 2011; Frouz et al. 2011). It is possible that increasing microtopographic variability on upland forest reclamation sites may prove to be a valuable strategy for facilitating ecosystem recovery and species diversity.

In this study, we explored the impact of microsite heterogeneity on the expression of the propagule bank that is contained in salvaged and placed surface cover soils in reclamation areas. We hypothesized that on upland forest reclamation sites, surface soil treatments that provide a greater range of microtopographic and substrate variability will conserve higher species richness, plant abundance, and a greater range of species functional types relative to that originally contained in the propagule bank. The specific objectives of this research were: (1) to evaluate how slope aspect and microtopographic surface treatments will affect the early expression of the initial propagule bank (i.e. abundance, richness and early community compositions) and explore these responses in relation to edaphic conditions (i.e. snow accumulation, soil water availability, bulk density, and soil temperature) at the site scale and (2) to examine in more detail the effect of microtopographic elevation (micro-elevation) of microtopographic features on the propagule bank expression, and explore this in response to soil water availability, bulk density, and soil temperature at the microsite level.

2.2 Materials and methods

2.2.1 Study area

Research was conducted on an oil sands mining lease (Canadian Natural Resources Albian Sands) located 70 km north of Fort McMurray, Alberta, Canada (lat. 57°15'N, long. 111°23'W) within the Central Mixedwood natural forest subregion (Natural Regions Committee 2006). The average annual temperature is 0.2 °C, with monthly January and July temperatures of -17.4 °C and 17.1 °C , respectively. Average annual precipitation and potential evapotranspiration is 465 mm and 518 mm, respectively (Marshall et al. 1999). Snow fall (November to April) is about 30% of annual precipitation, and the average frost-free period is 97 days. During the year of the study, 2015, the average annual daily temperature was 3.4°C and average daily temperature over the growing season (May 15 to August 31) was 17.5 °C. The total annual and growing season precipitation in 2015 was 26% (310 mm) and 55% (126 mm) lower than the long-term average, respectively (Environment Canada 2015, Figure A1).

Study sites were established on a south-facing and east-facing slope of a large hill landscape feature that was constructed from the overburden material overlaying the ore. The landscape feature was contoured in the summer of 2014, and subsequently capped with two different salvaged cover soils: a peat mineral mix (PMM) and forest floor material (FFM). PMM is a mixture of peat and some of the underlying mineral soil salvaged from black spruce (*Picea mariana*) dominated lowland forests, with the mineral content varying greatly among PMM materials depending on salvage depth. The FFM is a mixture of upland organic forest LFH soil horizons and underlying mineral A and B soil horizons salvaged to a depth of about 30 cm. The upland forest stands were dominated by jack pine (*Pinus banksiana*) with lesser components of trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*). The understory was dominated by dwarf shrubs *Vaccinum* spp. and lichen (*Cladonia* spp. and *Cladina* spp.). The soil was an Eluviated Dystric Brunisol that developed in this area on course textured, acidic, glaciofluvial outwash parent materials. The organic forest floor was approximately 5 cm thick and of a mor humus form. Both the PMM and the FFM were salvaged in April 2014 and temporarily stockpiled in several large piles until late fall of 2014.

2.2.2 Study design

After placing and leveling a 35-cm base layer of PMM as a cover soil over the constructed landscape feature in October of 2014, five blocks (100 × 100 m each) were established on the south facing and the east facing aspects of the landscape feature (Figure 2.1). In each block, three microtopographic treatments (control, ridged, and hilled) were randomly assigned to 30×100 m areas with a 3-m buffer between them (Figure 2.1A). In the control treatment, a 15-cm layer of FMM was placed over the PMM base layer and levelled using a D6 Caterpillar® bulldozer, which is a representation of the current operational practice (Figure 2.1B). The ridged treatment was constructed in the same manner as the control, but tracks of a D8 Caterpillar® bulldozer were used to create deep surface soil ridges by driving the machine perpendicular to the slope in parallel lines (Figure 2.1C). To minimize the compaction of the base layer, this was done in early spring (March 2015) when the underlying overburden and PMM layer were still frozen while the surface FFM layer had already thawed. Ridges were 0.4 to 0.8 m high, 1.5 m wide and located approximately 1 to 2 m apart. The hilled treatment was constructed after the base layer had frozen. Using a D6 Caterpillar® bulldozer, stockpiled PMM or FFM cover soils were selected randomly and pushed from the upper slope to the lower slope and placed as unconsolidated hills into off-set rows evenly distributed in each treatment plot (Figure 2.1D). The hills had approximately oval bases (approximately 3.5 m wide and 5.5 m long), were 1.5 m tall, and spaced approximately 1.5 meters apart.

2.2.3 Vegetation and edaphic variable assessment

To assess the vegetation in the three microtopographic treatments, 15 vegetation sampling quadrats (1×1 m) were randomly placed along an 80-m transect running parallel with the slope and located in the center of each microtopographic treatment plot (total of 30 transects). The location of each quadrat relative to the position (micro-elevation) on a microtopographic feature in the hilled and the ridged treatments was also noted (i.e. between-hill, toe, slope and crest in the hilled treatment, and trough and ridge in the ridged treatment (Figure 2.1E). At the microtopographic treatment level, all possible micro-elevation positions were represented in each transect of each plot to allow the overall effect of microtopographic position within the microtopographic features to be evaluated.

Vegetation was assessed in early- to mid-August 2015. In all sampling quadrats plants were identified to species and the number of individuals of each species was determined. Soil water content and soil temperature were measured at a six-cm depth in the center of each vegetation sampling quadrat three times during the growing season (May 16, June 9, and August 10, 2015) using a hand-held mobile TDR (time domain reflectometry) probe (POGO, Stevens Water Monitoring Systems, Inc. Portland, Oregon, U.S.A.). To assure the accuracy of the water content values, the TDR probe was calibrated for each cover soil in the laboratory after the field season to convert the measured soil water content into actual soil water content. Soil for this purpose was collected from five microsite types in the field - levelled surface of the control, trough in the ridged treatment, and FFM hill, PMM hill and between hills in the hilled treatment. Three samples (height=12 cm, diameter=15.05 cm, volume=2.13 L) were collected in different blocks from each of the microsite types. To collect a sample, soil was cored with a soil corer (diameter=15.05 cm) to the depth of 12 cm, the corer was carefully extracted and placed into a water-tight cylindrical container to preserve the structure, and transported to the lab for calibrations. Soil samples were then saturated with water and allowed to dry out for 2 months. During the drying period, the water content of every sample was measured with the TDR probe, and the total weight of the container and the sample was recorded (Weitz et al. 1997). Measurements were initially taken every second day, with the frequency gradually decreasing as the drying rates declined. After the TDR probe readings remained unchanged for 2 weeks, the soil was extracted from the containers and oven-dried, after which the soil and each container were weighed. The actual water content at each measurement time was calculated by subtracting the container weight and the soil dry weight from the total weight. A linear model was then built for each soil type to predict the actual water content from the measured water content (both R^2=0.89):

$$Actual\ water\ content_{FFM} = 0.02226 + 0.89080\ \times\ \text{Measured water content}_{FFM} \quad (1)$$

and

$$Actual\ water\ content_{PMM} = 0.04796 + 0.82308\ \times\ \text{Measured water content}_{PMM}, \quad (2)$$

where in both Eqs. (3) and (4) actual water content and measured water content are in %. Depending on whether a microsite contained primarily FFM or primarily PMM, the respective model was used to convert soil water content of each microsite measured in the field into actual water content.

Snow surveys were conducted during the first growing season to determine how microtopographic treatments and the overall slope aspect influenced snow accumulation and the resulting snow water equivalent (SWE). The surveys took place between February 17 and February 20, 2015 when the accumulated snow pack was near its peak (Figure A2). Snow depth data were collected in three replicates of only the control and the hilled treatment on the south and east-facing slope, as the ridged treatment had not yet been constructed. Snow depth was measured with a ruler every 2 m on either side of a 100 m long transect placed in the center of each treatment plot (30 transects) parallel with the direction of the slope. Snow density (g/cm^3) was determined at three randomly located points for a range of snow depths (at 1-cm depth intervals) on each slope aspect. Snow density was not correlated to snow depth on either slope aspect (both $p>0.79$). Snow water equivalent (SWE, g/cm^2) was calculated by multiplying average snow density by each snow depth on the respective slope aspects (Elder et al. 1998; Jonas et al. 2009).

Soil bulk density was measured at three random locations per microsite position per treatment plot: three random samples from the control treatment plots, three samples each from the ridge and trough positions in the ridged treatment, and three samples each from the slope position (all south hill aspect) of FFM hills and PMM hills, and from the between-hill position in the hilled treatment plots. Soil bulk density samples were collected by hammering a cylindrical metal ring of known volume into the soil (inside diameter 7.22 cm, height 7.75 cm, volume 317.3 cm^3), carefully extracting it, then drying and weighing the sample (Blake 1965).

2.2.3.1 Initial propagule bank of salvaged FFM and PMM cover soils

To explore the inherent propagule bank (seed and vegetative bud bank) of the two different cover soils used in this study, 18 bulk soil samples were collected in August 2014 from the salvaged

PMM and FFM stockpiles. Each bulk soil sample consisted of three soil cores (3.3 L, 14.5 cm diameter, 20 cm tall), with two cores collected from the top 20 cm of the stockpile surface and a third taken at a 20 cm depth.

Plant propagules in the soil samples were concentrated to approximately 30% (3 L) of the original bulk sample to increase the likelihood of germination/sprouting as outlined by Ter Heerdt et al. (1996). Concentrated samples were spread onto a weed free potting soil mix (Sunshine LA4 mix potting soil with 55-65% sphagnum peat, perlite, dolomitic limestone, gypsum, wetting agent), and placed in plant trays (51×26 cm) at a 2-cm thickness. Rhizomes and other vegetative propagules separated during sieving were placed and covered in a layer of potting soil mix and incubated separately. The trays were incubated in the greenhouse at a 16-hour photoperiod with day and night temperatures set to 21 °C and 15 °C, respectively, and relative humidity set between 50% and 75%. The trays were watered every one to three days using an automatic misting system to maintain moist soil conditions. As soon as plants could be identified, they were counted and removed from the incubation trays; plants that initially could not be identified were transplanted into separate pots to allow for further development. After new plants stopped appearing in the seed trays, irrigation was paused for 1 week to allow the soil to dry slightly and was disturbed by lightly raking the soil surface to encourage maximum possible germination (Ter Heerdt et al. 1996). The incubation of the propagule bank study was terminated after 16 weeks when no new germinants were observed. Since the propagule banks yielded very low numbers of viable vegetative fragments, the number of germinants and sprouted vegetative propagules were combined for each bulk sample for the subsequent analysis.

2.2.4 Data analysis

All data analyses were performed in The R Project for Statistical Computing (R Core Team 2015). Prior to performing analysis of variance (ANOVA) procedures, datasets were tested to ensure that assumptions of normality and equality of variances of the residuals were met. Post-hoc pairwise comparisons of least-squares means with no *p*-value adjustment were then performed for each significant main affect and interactions to determine which treatment combinations were different from the others.

2.2.4.1 Propagule bank study:

The propagule bank study in the greenhouse was set up as a completely randomized design with cover soil as the treatment effect (FFM and PMM). The experimental unit for the propagule bank study was a tray (containing the bulked subsamples). The emerged plant species were assigned into one of three functional types associated with disturbance (includes ruderal and grassland species), forests, and moist habitats. The assignment was based on the preferred habitat types of each species described in the Flora of Alberta (Moss & Packer 1983, Table 2.1). Non-metric multidimensional scaling (NMDS) analyses using Bray-Curtis dissimilarity coefficients based on the number of individuals of each species was performed to visualize the differences between the communities in the two cover soils and the three microtopographic treatments. A one-way MANOVA was also performed to compare the communities in the two cover soils and the three microtopographic treatments. Species area saturation curves constructed using the specaccum function (Oksanen et al. 2016) and fitted by reciprocal function (Colwell & Coddington 1994) indicated that potentially 78% and 82% of the species were detected in the FFM and PMM cover soil, respectively (Figure 2.2) and that this study sufficiently represents the actual number of species in the propagule bank.

2.2.4.2 Slope aspect and microtopographic treatments:

To determine the effect of microtopographic treatments and slope aspects on response variables, two-way ANOVA was used on transect species richness, plant abundance, proportion of functional type, soil water content, snow water equivalent, and soil bulk density at the treatment scale with the data being averaged at the treatment plot-level (transect) (Table A1). Plant abundance was transformed with $\log_{10}$ and species richness was transformed with Box-Cox transformation using packages car and geoR (Fox & Sanford 2011; Ribeiro & Diggle 2016) to achieve normality. For soil temperature, the effect of microtopographic treatments separately within a given slope aspect (One-way ANOVA) could be examined, as operational constraints allowed only one aspect to be measured in a given day. Soil temperature was averaged at the treatment plot level and blocked in time to minimize bias due to changing temperatures over the day (Table A1). Indicator species characterizing each of the three field treatments were determined based on their indicator values (Dufrêne & Legendre 1997) at $p<0.01$ by using labdsv package (Roberts 2016).

2.2.4.3 Micro-elevation study:

Two-way ANOVAs were performed to explore the effect of micro-elevation position with slope aspect on quadrat species richness, plant abundance, soil water content and soil bulk density (Table A2). The influence of micro-elevation position was analysed as a randomized block design, and thus, hilled and the ridged microtopographic treatments were analyzed separately. Each of the 15 experimental quadrats along the transects in the ridged treatment was classified by its microtopographic position: trough or ridge. In the hilled treatment, the 15 quadrats along each transect were classified by their micro-elevation positions: between-hill, toe, slope, and crest. These positions were used for all measured variables apart from soil bulk density measurements, which were only collected in the between-hill and slope positions on either a FFM or PMM hill. All the measured variables were averaged for each microelevation position in each treatment plot and the data were analyzed as a split-block design. In the ridged treatment, slope aspect (south-facing and east-facing) and micro-elevation (trough and ridge) were the two fixed factors. In the hilled treatment, slope aspect (south-facing and east-facing) and micro-elevation (between-hill and slope for soil bulk density; between-hill, toe, slope, and crest for the other variables) were the two fixed factors. In the hilled treatment, plant abundance was transformed with square-root transformation.

2.3 Results

2.3.1 Species and community composition

The two cover soils in the greenhouse study differed in their number of species and abundance of propagules in the initial propagule bank. The propagule bank of the FFM cover soil material contained a total of 213 individuals (205 individuals from seed and 8 individuals from vegetative fragments) while the PMM cover soil material contained a total of 1439 (1433 individuals from seed and 6 individuals from vegetative fragments). The average propagule density in the FFM was 1.2±1.2 (SD) propagules/L, while the propagule density in PMM was on average 8.0±8.2 (SD) propagules/L. Overall, the FFM and PMM cover soils contained 21 and 28 species, respectively. The FFM and PMM cover soils had similar numbers of species that were forest-associated (8 for FFM and 11 for PMM; see species assignment to functional types in Table 2.1) and disturbance-associated (10 for FFM and 8 for PMM). However, the PMM cover soil contained more species associated with high soil moisture (3 for FFM and 9 for PMM). When combining the initial FFM and PMM propagule bank, the total initial seedbank had 35 species, of which 7 were unique to the FFM cover soil and 14 were unique to the PMM cover soil. This is in contrast to the total of 58 species that were found in the field study after the first growing season, of those 23 species (40%) had also been present in the initial propagule bank (Figure 2.3).

The hilled treatment had the highest species richness compared to the ridged and the control (Table 2.2). While the three microtopographic treatments had similar numbers of species that either originated from the initial propagule bank found in the greenhouse study (~11 species) or were shared among the three treatments (~24 species), the hilled treatment had more species unique only to this treatment (11 species) compared to two and four for the other two treatments (Table 2.2, species unique to treatment listed in Table 2.3). The hilled treatment contained the highest number of species associated with high-moisture habitats and forests, while the number of species associated with disturbance was similar among the three microtopographic treatments (Table 2.2).

Based on species richness and abundance, the early community composition differed among the three microtopographic treatments and the initial propagule banks of the two cover soils ($p<0.001$) (Figure 2.4). The plant communities developed from the initial PMM and FFM propagule banks differed from each other and also from the communities observed in three microtopographic treatments in the field ($p<0.001$ for all). However, within microtopographic treatments, the early plant community in the hilled treatment differed from the communities in the ridged and the control ($p=0.001$ for both), while the latter two had similar early community composition ($p=0.123$). The indicator species analysis revealed that the field treatments were dominated by disturbance-associated native and introduced species such as *Chenopodium berlandieri* and *Melilotus alba*. The initial propagule bank of FFM cover soil was dominated by forest-associated species such as *Rubus idaeus*, and the initial propagule bank of PMM cover soil was dominated by moisture-loving species such as *Ranunculus sceleratus.*

2.3.2 Slope aspect and microtopographic treatments

Average species richness and plant abundance varied with microtopographic treatment, but not with slope aspect. However, there was a slope aspect by treatment interaction (both $p<0.030$) (Table A1). The hilled treatment had higher species richness on the east-facing slope compared to the south-facing slope, while there was no difference between slope aspects in the control and ridged treatments (Figure 2.5A and B). On the east-facing slope, average species richness and plant abundance was higher in the hilled treatment compared to the control and the ridged treatments. A different trend was observed on the south-facing slope, where species richness was highest in the control and lower in the ridged treatments, with no difference in plant abundance between microtopographic treatments.

The proportion of species associated with high soil moisture contained in total species pool was also influenced by the microtopographic treatments and not slope aspect, but with a significant slope aspect by treatment interaction (p=0.013) (Figure 2.5C). The control treatment had a lower proportion of species that require higher soil moisture (moisture-loving) on the south-facing slope compared to the east-facing slope, while there was no impact of slope aspect in the ridged and hilled treatments (Figure 2.5C). However, on the east-facing slope, the proportion of moisture-loving species was highest in the hilled compared to the ridged treatment, while on the south-facing slope the control had the lowest proportion of moisture-loving species (Figure 2.5C). The proportion of forest- and disturbance-associated species was unaffected by slope aspect and microtopographic treatments (all $p>0.08$, see Table A1).

Average soil water content differed with microtopographic treatment (p=0.001), but not slope aspect (p=0.889). There was also a slope aspect by treatment interaction (p=0.047). On the east-facing slope, average soil water content was higher in the hilled treatment compared to the control and the ridged treatment, while on the south-facing slope soil water content did not differ among microtopographic treatments (Figure 2.5D). The slope aspect and microtopographic treatments had no impact on average snow accumulation (both p>0.138); however, it needs to be considered that snow accumulation was only measured in the hilled and control treatments (see methods). Soil temperature was not affected by microtopographic treatments (p=0.880), while average soil bulk density differed among the microtopographic treatments (p<0.001). The control treatment had the highest average bulk density, followed by the ridged treatment and the hilled treatment with 1.45 ± 0.02, 1.34 ± 0.02 and 1.03 ± 0.02 g/cm^3, respectively.

2.3.3 Micro-elevation

In the ridged treatment, micro-elevation position (ridge vs trough) affected average species richness, plant abundance, soil water content and soil bulk density (all p<0.03; see Table A2-A). In the ridged treatment, species richness, plant abundance, soil water content and soil bulk density was higher in troughs than on ridges (Figure 2.6). Soil temperature was not affected by the micro-elevation position within the ridged treatment (data not shown).

In the hilled treatment, the different microtopographic positions (Figure 2.1E) had an effect on species richness, plant abundance and soil water content (all p<0.017; see Table A2-B). Here, species richness and plant abundance was higher at the toe and the between-hill position compared to the slope and crest position (Figure 2.7A, B). Soil water content was also highest in the between-hill and the toe position (p<0.001, Figure 2.7C). Soil temperature was not affected by hill micro-elevation position (p=0.999).

2.4 Discussion

The results of this study indicate that the creation of diverse microsite conditions in reclamation areas is a valuable tool in forest restoration that can improve the diversity of species initially establishing on the site. We had hypothesized that the increased microtopographic heterogeneity and the range of microclimatic conditions and gradients result in increased early species richness and establishment. Since the hilled and the ridged treatments provided greater microtopographic heterogeneity we expected increased richness in both. However, only the hilled treatment with the selectively placed hills appeared to create a range of conditions that was conducive to greater species richness and plant abundance early on. Beneficial for forest re-development and restoration, this greater species richness also resulted in plant communities with overall larger numbers of early and later successional forest-associated species that were different from the ridged and control treatments (Table A1). This treatment also provided favourable (i.e. relatively higher soil moisture) conditions on the harsher and drier south-facing slope, which allowed for the establishment of proportionally more species that prefer higher soil moisture conditions. This is in contrast to the somewhat reduced topographical variation provided by the ridged treatment, which had little or no positive effect on plant abundance or species diversity and was often comparable to the control. Our results agree with those from other studies (Dhillion 1999; Biederman & Whisenant 2011; Frouz et al. 2011), which showed that naturally occurring and constructed mounds had a positive effect on the species richness and abundance of plants in the restoration of temperate forest and grassland ecosystems, and also increased the growth and survival of artificially seeded species (Ewing 2002). Further, increasing microtopographic variability has also been shown to increase vegetation richness in wetlands by providing unique conditions that suit a wider range of species (Bruland & Richardson 2005; Lieffers et al. 2017).

Although both the hilled and the ridged treatments increased microtopographic heterogeneity, several important differences appeared to have encouraged more effective overall vegetation expression and recruitment of a larger range of plants in the hilled treatment. The effectiveness of the microtopographic features might have been influenced by their size and shape, the soil placement technique, and the location of the contrasting cover soil materials. The larger size of the microtopographic features in the hilled treatment likely resulted in greater range of growing conditions with more sheltered microsites favourable for early plant establishment. The size of the microtopographic features might have also influenced the capture of long-distance dispersed seeds from sources adjacent to the site (Titus & del Moral 1998; Farrell et al. 2012), as a large percentage of the species found on the sites were not detected in the initial seed bank. Casual observations in the field revealed that the loose placement of the cover soil in the hilled treatment could have resulted in greater fine-scale microtopographic heterogeneity, which have been shown to increase species diversity in restored grasslands (Deák et al. 2015). Additionally, the loose placement of soil, the presence of exposed PMM at the surface, and limited heavy-machinery passes in the hilled treatment, compared to the control and the ridged, resulted in the lower bulk densities measured in this treatment. This is consistent with previous research, which has shown soil compaction from one or two additional bulldozer passes can significantly reduce vegetation expression and regeneration (Zenner et al. 2007; Mundell et al. 2008). However, while the ridged treatment also contained some exposed PMM and had overall lower average soil bulk density than the control, plant abundance and richness in the ridged treatment was similar or even lower than the control. The poor performance of the ridged treatment may be due to high soil bulk density found in the troughs, which were comparable to the control. This and the potential of shedding of water from the ridges into the troughs might have led to high water accumulation in the troughs during spring snowmelt and sporadically during rain events through the growing season. Casual observations in the field revealed that there was very little or no standing water in the control and the hilled treatments, while the troughs contained standing water in early spring and after heavy rainfalls, which could have adverse effects on germination and early establishment of germinants arising form the propagule bank.

Aside from the lower soil bulk density, the loose and rough placement of cover soil in the hilled treatment resulted in greater exposure of PMM base layer compared to the other two treatments, and increased germination success of the propagules that occur in PMM cover soil. The hilled and the ridged treatments were expected to have higher soil water content because of increased snow accumulation and redistribution as a result of the microtopographic features (Elder et al. 1991). However, in our study the microtopographic features did not result in higher average snow retention, and therefore did not contribute to higher soil water content via snow accumulation. The higher soil water content observed in the hilled treatment was likely the result of higher infiltration capacity of the loosely placed soil resulting in reduced run-off (Appels et al. 2011), and a greater exposure of PMM with its higher water holding capacity (Walczak & Rovdan 2002) at the soil surface. Lastly, the increased overall soil water availability in the PMM and between-hill positions was likely a major factor in facilitating the establishment of species that require higher moisture availability. At an early stage, forest reclamation sites are treeless and the surface soil is exposed to higher evaporation rates than forested stands with a canopy (Chen et al. 1993; Geiger et al. 2009; von Arx et al. 2013). This exposure was further aggravated in this study due to the below-average precipitation during the sampling year. Adequate soil moisture levels that are crucial during seed germination and initial seedling development (Harper & White 1974; von Arx et al. 2013) might not have been reached, which is supported by the limited expression (65%) of the initial propagule bank in the field study.

2.4.1 Micro-elevation position

The presence of different micro-elevation positions in the hilled and ridged treatments produced heterogeneity that was reflected in the increased spatial variability in species and plant abundance within the treatments. The effect of micro-elevation in the hilled treatment was more pronounced on the east-facing slope. Differences in edaphic conditions across the various micro-elevation positions were likely the driving factor for the spatial heterogeneity in species richness and plant abundance. Vegetation expression is strongly tied to soil water content (Harper & White 1974; von Arx et al. 2013), but establishing plants also benefit from sheltered conditions occurring with micro-elevation even if soil water content remains unchanged (Elmarsdottir et al. 2003; Schott et al. 2014; Valenzuela et al. 2016). For example, the low-lying between-hill and toe micro-elevation positions in the hilled treatment, and the trough position in the ridged treatment had not only higher soil water content but were likely more sheltered from the sun and wind compared to micro-elevation positions located on the slope and crests of the hills and ridges.

Overall our results suggest that the effect of topographical variation on plant abundance and the richness of species will also depend on the overall slope aspect, which would have implications for landscape feature construction and the use of microtopographic treatments in forest restoration. Even though the differences in edaphic conditions that we measured on both slope aspects were relatively small (likely a result of the limited monitoring or an overall dry year), the level of environmental stress was most likely higher on the south aspect where the energy input is greater particularly at higher latitudes (Holland & Steyn 1975). This suggests that increased microtopography should be more valuable on sites that are exposed to greater stress conditions (i.e. south-facing vs. east-facing slopes in northern latitudes). However, in our study the positive effect of the hilled treatment on the overall plant abundance and species richness was highest on the east-facing slope. This might indicate that the greater stress conditions experienced on the south-facing slope reduced the overall impact of the microtopographic treatment on plant abundance and species richness. This observation is supported by earlier work, which suggests that microrelief might have the greatest positive effect on vegetation at moderate-stress sites, and negligible or even negative effect at sites with high or low environmental stresses, respectively (Loneragan & del Moral 1984). An important implication of this result is that slope aspect on which the reclamation area is located should be accounted for when selecting techniques for achieving specific revegetation objectives.

Tables

Table 2.1. Species assignment to functional types according to each species' preferred habitat as indicated by Moss & Packer (1983), and their prevalence in the initial propagule bank (PB), control field treatment (C), hilled field treatment (H), or ridged field treatment (R). Abbreviation with no asterisk indicates the presence of species in up to 25% of samples, one asterisk indicates the presence of species in 25-50% of samples, two asterisks indicate the presence of species in 50-75% of samples, and three asterisks indicate the presence of species in over 75% of samples.

Species	*Functional type*	*Prevalence*
Achillea millefolium	forest	C
Achillea sibirica	forest	C
Actaea rubra	forest	H
Agropyron trachycaulum	forest	C*, H, R
Agrostis scabra	forest	PB*, C, H, R
Alnus tenuifolia	high-moisture	PB
Aster borealis	high-moisture	H
Axyris amaranthoides	disturbance	C, H, R
Beckmannia syzigachne	high-moisture	C
Betula papyrifera	forest	PB
Calamagrostis canadensis	forest	C, H, R
Carex spp.	high-moisture	PB***, C*, H*, R*
Chenopodium berlandieri	disturbance	PB, C, H** R

Species	*Functional type*	*Prevalence*
Chenopodium capitatum	disturbance	H, R
Cornus canadensis	forest	PB
Cornus stolonifera	forest	C, R
Corydalis aurea	forest	C, H, R
Crepis tectorum	disturbance	PB, C, H, R
Dracocephalum parviflorum	forest	H
Epilobium angustifolium	forest	PB*, C, H, R
Epilobium ciliatum	high-moisture	PB*, C, H
Equisetum arvense	forest	PB, C, H, R
Erigeron canadensis	disturbance	PB, H
Galium trifidum	high-moisture	PB, H, R
Geranium bicknelii	forest	PB, C*, H, R*
Hordeum jubatum	disturbance	C, H
Impatiens noli-tangere	forest	R
Juncus balticus	high-moisture	PB
Lathyrus ochroleucus	forest	C, H, R
Ledum groenlandicum	forest	PB
Lepidium densiflorum	disturbance	PB
Maianthemum canadensis	forest	PB
Matricaria matricarioides	disturbance	C
Medicago sativa	disturbance	C, H, R

Species	*Functional type*	*Prevalence*
Melilotus alba	disturbance	C** H*, R*
Melilotus officinalis	disturbance	C, R
Mentha arvensis	high-moisture	H
Mitella nuda	forest	PB
Picea glauca	forest	PB, H
Plantago major	disturbance	C, R
Poa palustris	forest	C, H, R
Polygonum aviculare	disturbance	C, H, R
Polygonum convolvulus	disturbance	C, H*, R
Polygonum lapathifolium	disturbance	C, H*, R
Potentilla norvegica	disturbance	PB*, C, H, R
Prunus pensylvanica	forest	C, H, R
Ranunculus sceleratus	high-moisture	PB*, H, R
Ribes oxyacanthoides	forest	PB
Ribes spp.	forest	H
Rorippa palustris	high-moisture	PB, C, H, R
Rubus idaeus	forest	PB*, C, H, R
Rubus pubescens	forest	PB
Salix discolor	high-moisture	H
Salsola pestifer	disturbance	C, H
Scutellaria galericulata	high-moisture	H

Species	*Functional type*	*Prevalence*
Smilacina spp.	forest	H
Sonchus spp.	disturbance	PB, C, H*, R
Sphenopholis intermedia	high-moisture	PB
Symphyotrichum ciliolatum	forest	PB, C
Taraxacum officinale	disturbance	PB, C, H, R
Trientalis borealis	forest	H
Trifolium hybridum	disturbance	PB, C*, H, R
Typha latifolia	high-moisture	PB, R
Urtica dioica	forest	PB*, H
Vaccinium myrtilloides	forest	PB
Vicia americana	forest	C, H, R
Viola adunca	forest	H, R

Table 2.2. The total number of species in the three microtopographic treatments, and of those the number of species that were either contained in the initial propagule bank, were unique to or shared with treatments.

Microtopographic treatment	***Number of Species***						
	Total	*Contained in propagule bank*	*Unique to treatment*	*Shared among treatments*	*Associated with high moisture*	*Associated with forests*	*Associated with disturbance*
Control	39	12	4	23	4	15	19
Hilled	47	12	11	24	9	20	18
Ridged	37	10	2	25	5	15	17

Table 2.3. A list of species absent from germination trials of the propagule bank and unique to each of the three microtopographic treatments.

Microtopographic treatment	*Species unique to the microtopographic treatment*
Control	*Achillea millefolium, Achillea sibirica, Beckmannia syzigachne, Matricaria matricarioides*
Hilled	*Actaea rubra, Aster borealis, Dracocephalum parviflorum, Erigeron canadensis, Mentha arvensis, Ribes* spp., *Salix discolor, Scutellaria galericulata, Trientalis borealis, Urtica dioica, Picea glauca*
Ridged	*Impatiens noli-tangere, Typha latifolia*

Figures

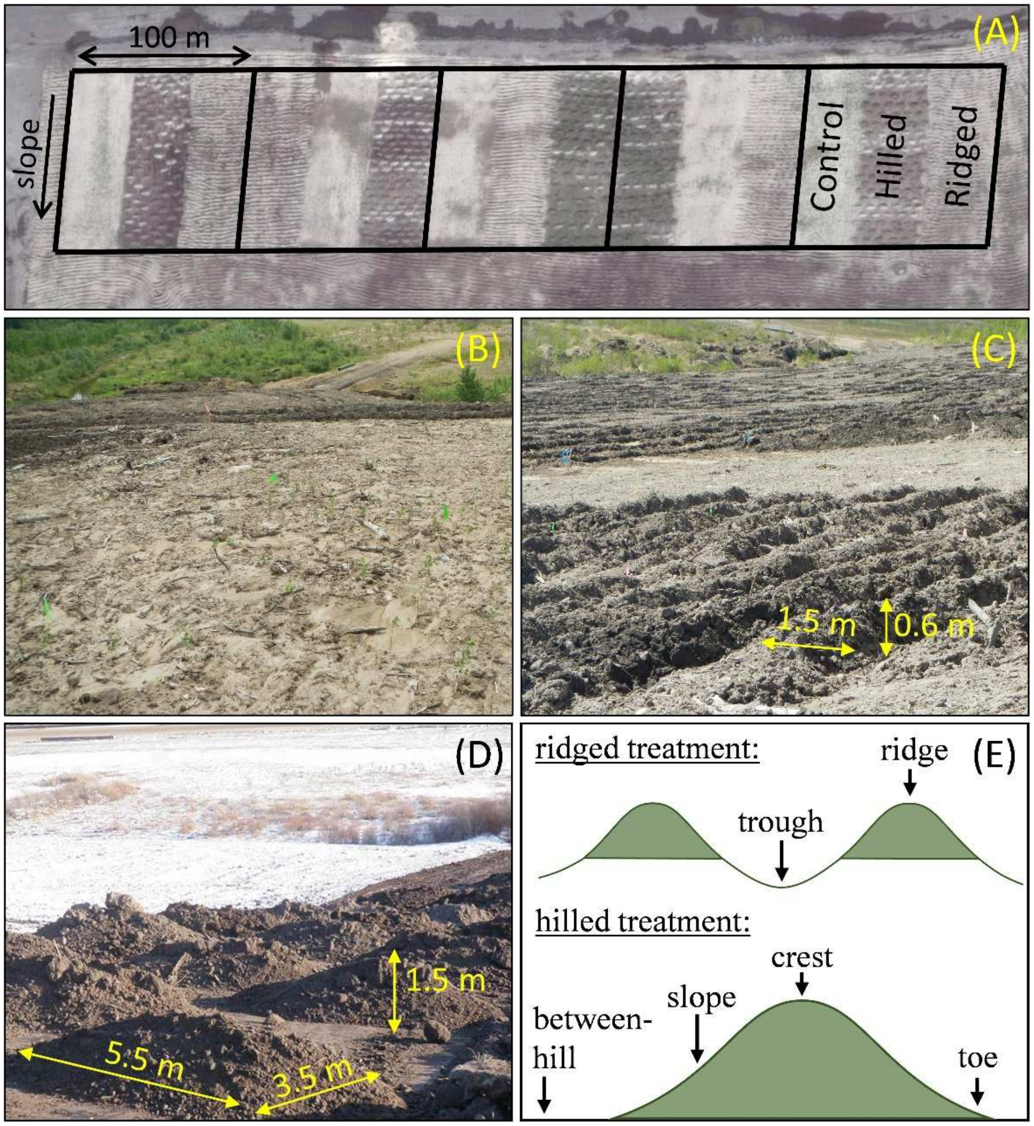


Figure 2.1. Aerial view of one of the two slope aspects containing five blocks, with the control, hilled, and ridged microtopographic treatments replicated in each block (A); photographs of the control (B), ridged (C), and hilled (D) treatment plots; and diagrammatic representation of the micro-elevation positions identified on topographic features in the ridged and the hilled treatments (E).

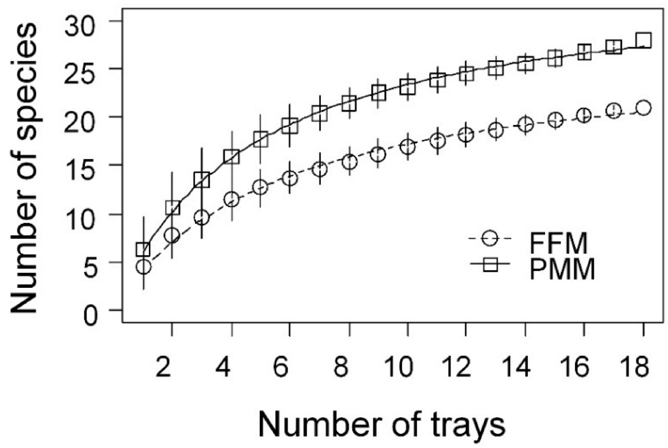


Figure 2.2. Species area curves for the propagule bank expression of FFM and PMM cover soils in the greenhouse, with reciprocal functions fitted to the data points. Error bars indicate a standard error of the mean.

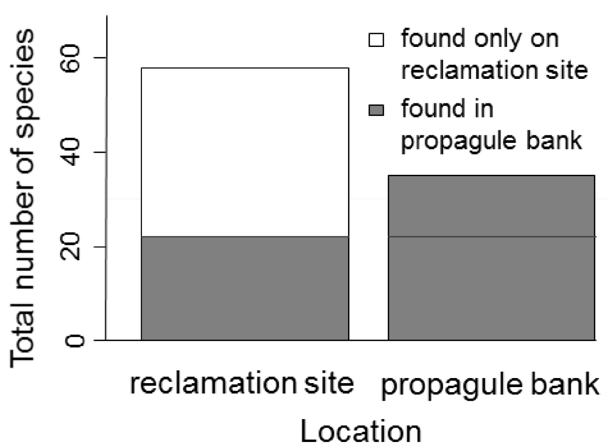


Figure 2.3. The total number of species found on the reclamation site and in the initial propagule bank of the FFM and PMM cover soils. The colors indicate whether the species were discovered in the initial propagule bank, or whether they were only detected on the reclamation site.

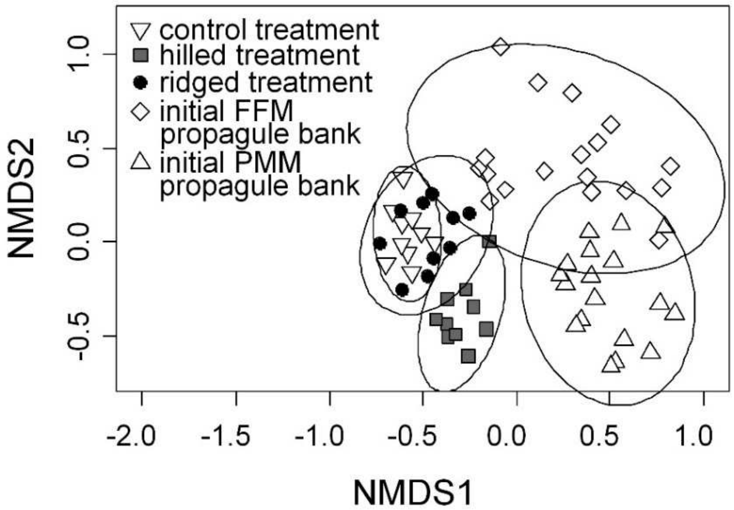
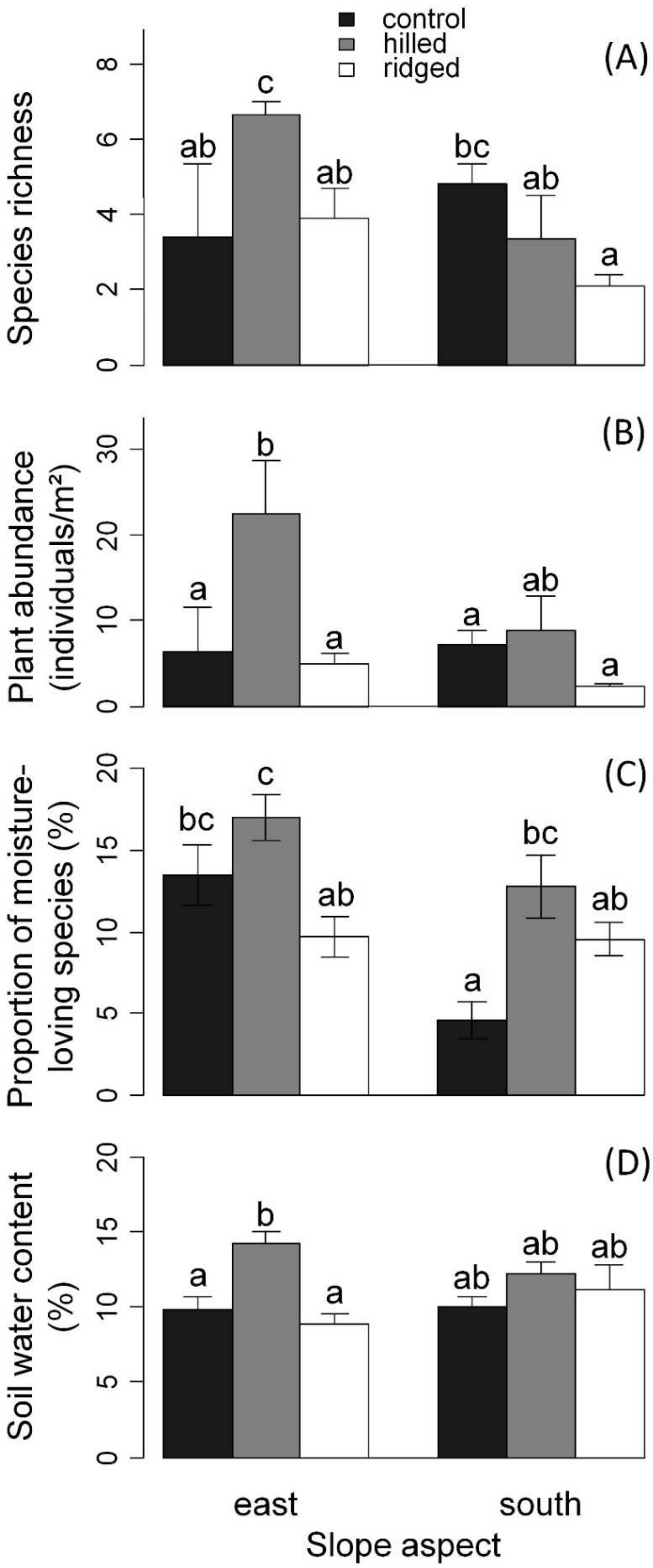


Figure 2.4. Non-metric multi-dimensional scaling (NMDS) analysis comparing the community composition of the initial Forest Floor Material (FFM) and Peat Mineral Mix (PMM) propagule bank in the greenhouse with the three microtopographic treatments after one growing season in the field. The same FFM and PMM cover soil material was used in the greenhouse and in the field study. Ellipses indicate 95% probability of distributions.



control
hilled
ridged
(A)
Species richness
(B)
Plant abundance (individuals/m²)
(C)
Proportion of moisture-loving species (%)
(D)
Soil water content (%)
east
south
Slope aspect

Figure 2.5. Average species richness (A), plant abundance (average number of individuals per m^2) (B), proportion of species that are associated with high soil moisture (moisture-loving) over the total species number (C), and soil water content (D) in the three microtopographic treatments within the two slope aspects (n=5 transects). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE ($\alpha<0.05$).

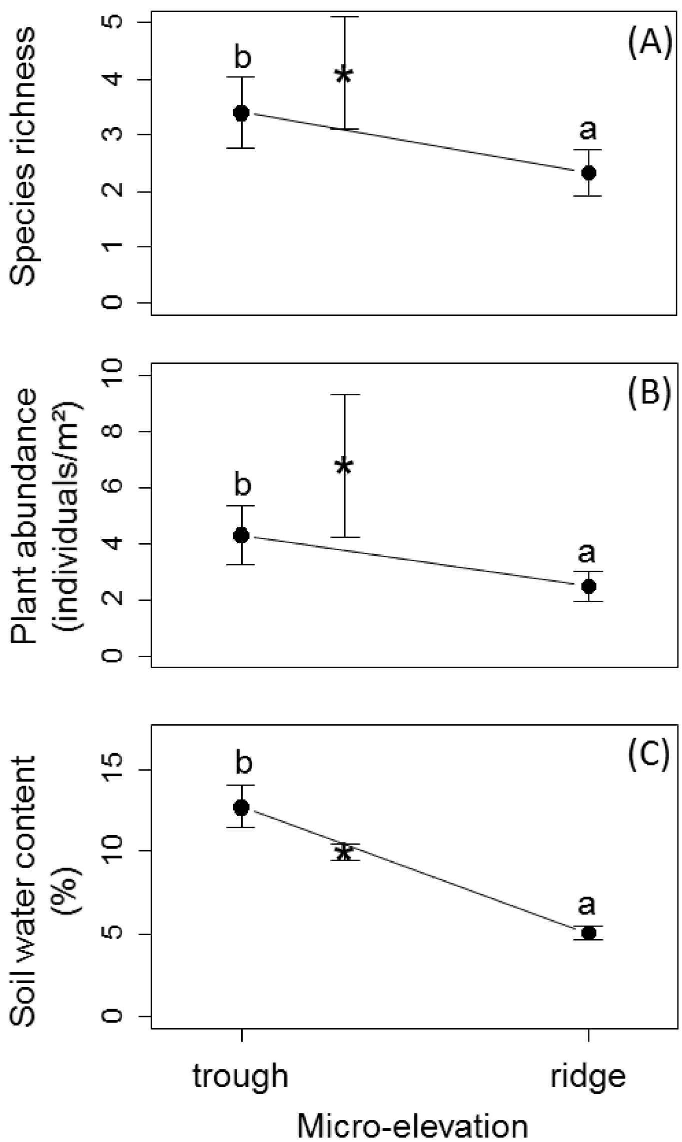


Figure 2.6. The average species richness per m^2 (A), number of individuals (B), and soil water content (C) in response to two micro-elevation positions (trough and ridge) within the ridged treatment (n=10). For comparison, an asterisk was added to indicate the average for these response variables in the control treatment. Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

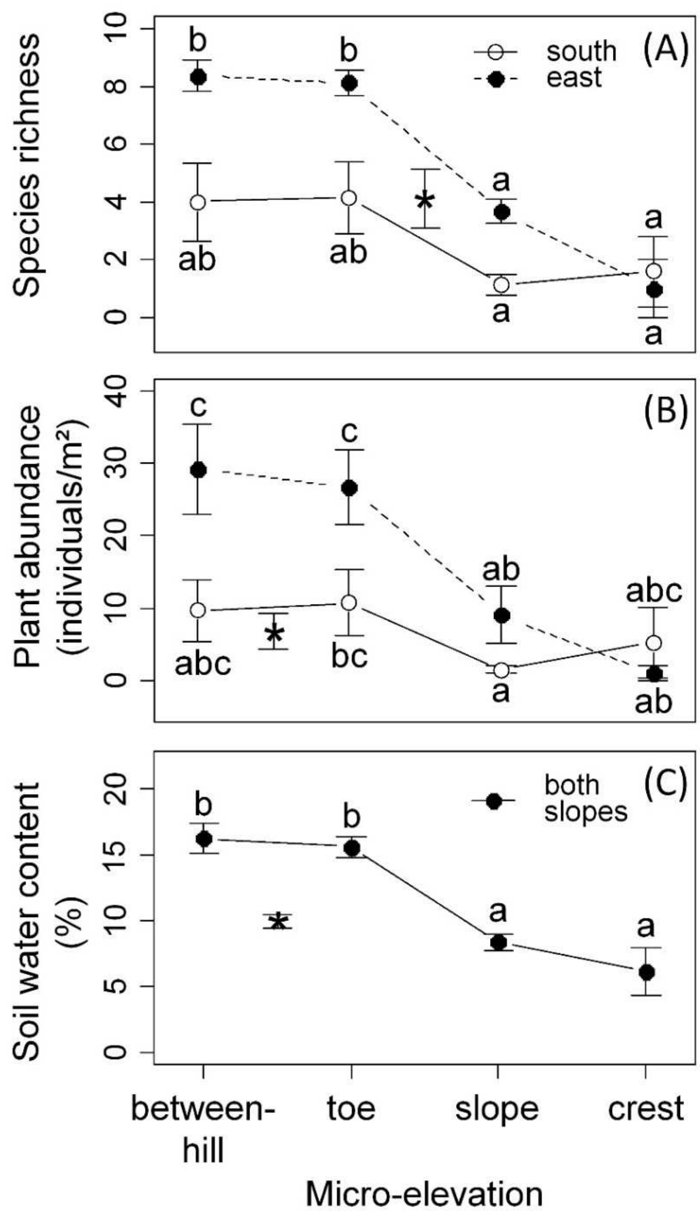


Figure 2.7. The average species richness per m^2 (A), and number of individuals (B) in response to four micro-elevation positions (between-hill, toe, slope, crest) by slope aspect (east and south slope aspects shown separately due to significant micro-elevation position-slope aspect interactions) within the hilled treatment (n=5). The soil water content (C) in response to four micro-elevation positions, averaged across both slope aspects (east and south slope aspects are combined, as there was no significant microtopographic position-slope aspect interaction)

(n=10). For comparison, a star symbol was added to indicate the average for these response variables in the control treatment. Bars with different letters indicate differences among treatment means. Error bars indicate ± SE ($\alpha<0.05$).

Chapter 3: Microtopographic position alters the expression of vegetation from soil propagule banks*

3.1 Introduction

Soil propagule banks found in salvaged soils can be a valuable resource for reclaiming post-mining sites, as they contain seeds and vegetative fragments of species characteristic to the area and can give rise to a diverse vegetation cover. It is important to create conditions that facilitate the expression of vegetation from soil propagules banks as early as the first growing season, as the newly established vegetation can provide a source of new propagules and create shelter for subsequent plant establishment (Chapter 2; Ren et al. 2008). Presence of microtopographic formations such as small hills, ridges, and depressions on the soil surface can provide a range of growing conditions and increase the likelihood that plant propagules will encounter conditions favourable for their germination and growth (see chapter 2). Microtopographic variability has been shown to increase vegetation richness and abundance in natural areas (Lundholm & Larson 1998) and on reclamation sites (Ewing 2002; Bruland & Richardson 2005; Biederman & Whisenant 2011; Brown & Naeth 2014; Gilland & Mccarthy 2014; also see Chapter 2). The potential of microtopographic treatments to promote the expression of desirable species can likely be increased by maximizing the availability of suitable microhabitats for their establishment. However, limited information is available on the preferred microhabitats of species contained in the propagule banks on upland boreal forest reclamation sites.

The two topographical factors that likely affect vegetation expression at the micro scale are elevation (micro-elevation) and aspect (microaspect), as they influence local microsite conditions

* Portions of this chapter have been included in the publication Melnik K, Landhäusser SM, Devito K (in press) The role of microtopography in the expression of soil propagule banks on reclamation sites. Restoration Ecology. doi: 10.1111/rec.12587

including soil water content and light availability. Micro-elevation affects soil water content via gravitational movement of water, preferential snow accumulation in low-lying areas (Beatty 1984), and/or changes in evaporative demand with lower micro-elevations often being more sheltered from the wind and sun. Microaspect can also affect soil water content through wind exposure and solar radiation input, with lee sides and north aspects (in the northern hemisphere) of constructed mounds retaining more soil moisture due to shelter from wind (Biederman & Whisenant 2011; Bhattacharjee et al. 2008) and solar radiation (Kutiel et al. 1998; Katra et al. 2007).

The specific effect of micro-elevation and microaspect on vegetation establishment will depend on the growing requirements of species present in the soil propagule banks, and on the overall conditions of the site. In areas susceptible to spring flooding, more forest understory species were shown to establish on microtopographic structures than at low micro-elevation positions with excessive soil moisture (Beatty 1984). On the contrary, on moisture-limited prairie and forest reclamation sites, low-lying areas at the bases of mounds or between mounds were most conducive to vegetation expression (Biederman & Whisenant 2011; also see Chapter 2). As for microaspect, it was shown that lee sides of constructed mounds with higher moisture and lower fluctuations in moisture produced higher richness and density of seeded plants when compared with windward sides (Biederman & Whisenant 2011). However, no information is available on whether vegetation expression generally differs between aspects of microtopographic features.

Differences in physical and chemical properties of cover soils also influence the response of vegetation expressions to microtopographic position by influencing vegetation response to variables, such as soil water content. The importance of soil water content for vegetation depends on physical properties such as soil texture, structure, porosity and organic matter content (Saxton

& Rawls 2006; Bhattacharjee et al. 2008). Additionally, vegetation response to microtopographic position also depends on the species present in the soil propagule bank, since growing requirements vary among species (Oomes & Elberse 1976). Soils originating from upland sites generally contain propagules adapted to mesic conditions, while soils salvaged from low-lying sites with abundant moisture can be expected to contain more species that favor microsites with higher soil water content. As a result, propagules contained in soils salvaged from low-lying areas might have a higher affinity for low-lying, north-facing microsites, and south-facing microsites will be dominated by ruderal disturbance species not contained in the original seed bank.

The overall slope aspect of a larger topographic feature (i.e. overburden dump) can also influence how vegetation develops in the different microtopographic positions. Similarly to the microtopographic positions, the growing conditions and environmental stresses can differ between the aspects of a topographic feature. This is due to variable levels of solar energy input and wind exposure, and it has been shown that site productivity and levels of environmental stress can influence the effect of microtopographic heterogeneity on vegetation expression. For instance in subalpine meadows, the presence of microrelief had no effect on species richness at sites with low productivity and high environmental stresses, a positive effect at sites with moderate productivity, and a negative effect at highly productive sites (Loneragan & Moral 1984).

The purpose of this study is to evaluate the effect of microtopographic position on upland forest reclamation structures constructed from contrasting soil materials on vegetation establishment. In particular, this study examines the effects of slope aspect, cover soil, micro-elevation and microaspect on species richness, plant abundance, the expression of species from propagule banks, and edaphic factors on an upland reclamation site. This knowledge could facilitate the inclusion of microtopography in reclamation practices to maximize the availability of appropriate microhabitats for the establishment of a larger range of species, and could enable a higher-efficiency use of seeds, planting stock and seed-rich cover soils by placing them in the most favourable microhabitats.

3.2 Materials and methods

The research site is located on Canadian Natural Resources Albian sands lease in northeastern Alberta on the south-facing and the east-facing slopes of a large reconstructed landscape feature made from overburden material. Two contrasting cover soils – forest floor material (FFM) salvaged from upland forests and peat-mineral mix (PMM) salvaged from low-lying areas – were used in the soil re-construction of the site. To reconstruct the surface soil, a 35 cm-thick layer of PMM was placed and levelled over the overburden material within each research plot in October of 2014. Ten 30m × 100m research plots were established on the landscape feature (five plots on the south-facing slope, five plots on the east-facing slope), which was done after the PMM layer froze to minimize compaction of the base layer. To contour the cover soil surface for this study, FFM and PMM cover soils were selected randomly and pushed from the respective stockpiles located on the upper slope of the landscape feature downslope using a Caterpillar® D6 bulldozer in December of 2014. This procedure formed evenly spaced unconsolidated piles (small hills) of cover soil material over the PMM base layer in the plots. The resulting hills formed off-set to rows to limit free passage of water downslope, consisted of either FFM or PMM, were 1.5 m tall, had approximately oval bases (3 m wide and 5 m long), and were located approximately 3 meters away from each other (Figure 2.1D in Chapter 2).

Sampling quadrats (see below) were established at different microtopographic positions to examine the effect of microtopographic position and cover soil on early establishment of colonizing vegetation and some edaphic factors. Three FFM hills and three PMM hills were selected in each plot, with one hill of each cover soil located at the top of the plot, one – in the middle, and one – at the bottom of the plot. Before the treatment was constructed, a propagule bank study (described in Chapter 2) was conducted to determine what seeds and vegetative propagules were initially present in the FFM and PMM cover soils used in the construction of the plots.

3.2.1 Edaphic and vegetation assessments

To assess vegetation expression and edaphic factors at various microtopographic positions on hills made from the two cover soils, nine sampling quadrats (0.5×0.5 m) were established on each experimental hill, with one quadrat at the crest position, four quadrats at the slope positions in the four cardinal directions, and four quadrats at the toe positions in the four cardinal directions (Figure 3.1). Vegetation was assessed in early- to mid-August 2015. In each sampling quadrat, plants were identified to species and the number of individuals of each species was determined. The vegetation was classified into three functional types: species associated with moist habitats, disturbance and forests. These functional types were assigned according to the habitat each species was most commonly found in according to Moss & Packer (1983) (refer to Methods in Chapter 2). In the field, the expression of each functional type was calculated as a proportion of each functional type in the initial propagule bank (propagule bank expression) and as a proportion of each functional type found on each hill (hill-based expression). Propagule bank-based expression was calculated by dividing the number of species belonging to a functional type in each quadrat by the total number of species of this functional type discovered in the initial propagule bank. Hill-based expression was calculated by dividing the number of species belonging to a functional type in each quadrat by the total number of species of this functional type discovered on the entire hill where the quadrat was located.

Soil water content and soil temperature were measured in the center of each sampling quadrat (Figure 3.1) using a hand-held mobile TDR probe (POGO, Stevens Water Monitoring Systems, Inc. Portland, Oregon, U.S.A). These measurements were conducted three times during the growing season (May 18, 2015; June 10, 2015; August 11, 2015). To assure the accuracy of the water content values, the TDR probe was calibrated for each cover soil separately (refer to Chapter 2 for details on the calibration procedure). Snow surveys were conducted before the first growing season, February 17 to February 20, 2015, to determine how microtopographic position, cover soil and the overall slope aspect influenced snow accumulation and the snow water equivalent (SWE). Snow depth data were collected on the experimental hills in three plots on each of the two slope aspects. Snow depth was measured with a ruler in the center of each sampling quadrat (Figure 3.1). Snow density (g/cm3) was determined at three randomly located points for a range of snow depths (at 1-cm depth intervals) on each slope aspect. Snow water equivalent (SWE, g/cm^2) was calculated by multiplying average snow density by each snow depth on the respective slope aspects (Elder et al. 1998; Jonas et al. 2009) (see Chapter 2 for more details).

3.2.2 <u>Data manipulation, visualization and analysis</u>

Data visualization and analysis were performed in The R Project for Statistical Computing (R Core Team 2015). The experimental design for micro-elevation and microaspect analyses was a split-block experimental design, where each treatment plot was treated as a block. Prior to performing analysis of variance (ANOVA) procedures, datasets were tested to ensure that assumptions of normality and equality of variances of the residuals were met, and if the assumptions were not met, data were transformed. If a significant micro-elevation effect, microaspect effect or a significant interaction was detected, post-hoc pairwise comparisons of least-squares means with no *p*-value adjustment were performed to determine which positions were different from the others.

3.2.2.1 Micro-elevation scale

To explore the effect of micro-elevation position, cover soil and slope aspect on species richness, plant abundance, propagule bank-based expression, hill-based expression, soil water content, soil temperature and snow water equivalent, data were analysed as a randomized split-block design with slope aspect (south-facing and east-facing), cover soil (FFM and PMM) and micro-elevation (toe, slope and crest) as three fixed factors. Measurements of response variables at each micro-elevation were averaged across four cardinal directions, and across three hills per cover soil per plot. Three-way ANOVAs were performed to analyze the effect of slope aspect, cover soil and micro-elevation on all response variables aside from soil temperature (Table A3-A). For soil temperature, a two-way ANOVA was performed to evaluate the effect of cover soil and micro-elevation on each slope aspect; the effect of slope aspect could not be evaluated because operational constraints allowed only one aspect to be measured in a given day. Soil temperature measurements were blocked in time to minimize bias due to changing temperatures over the day. Species richness, propagule bank-based expression of forest functional type and hill-based expression of forest functional type were transformed with $\log_{10}$ transformation; plant abundance was transformed with square-root transformation; and propagule bank-based expression of moisture-loving functional type, propagule bank-based expression of disturbance functional type and hill-based expression of disturbance functional type were transformed with Box-Cox transformation.

Non-metric multidimensional scaling (NMDS) analysis using Bray-Curtis dissimilarity coefficients was performed based on the number of individuals of each species to visualize the differences between the communities at the toe, slope and crest positions. A two-way MANOVA was also performed to determine the effect of cover soil and micro-elevation position on the community composition (Table A3-B). If a significant micro-elevation effect was detected, one-way MANOVAs were performed to determine whether there were differences between the toe and slope, slope and crest, or toe and crest positions, separately for PMM hills and for FFM hills.

3.2.2.2 Microaspect scale

To explore the effect of microaspect, cover soil and slope aspect on species richness, plant abundance, propagule bank-based expression, hill-based expression, soil water content, soil temperature and snow water equivalent, data were analysed as a randomized split-block design with slope aspect (south-facing and east-facing), cover soil (FFM and PMM) and microaspect (N, E, S, W) as three fixed factors. For this analysis, only quadrats at hill slope positions were analyzed after being averaged for each cardinal direction across three hills of each cover soil in each plot. Three-way ANOVAs were performed to analyze the effect of slope aspect, cover soil and microaspect on all the measured variables aside from soil temperature (Table A4-A). For soil temperature, a two-way ANOVA was performed to evaluate only the effect of cover soil and microaspect, as operational constraints allowed only one aspect to be measured in a given day. Soil temperature measurements were blocked in time to minimize bias due to changing temperatures over the day. Propagule bank-based expression of forest functional type was transformed with Box-Cox transformation.

Non-metric multidimensional scaling (NMDS) analysis using Bray-Curtis dissimilarity coefficients was performed based on the number of individuals of each species to visualize the differences between the communities at the north, south, east and west microaspects. A two-way MANOVA was also performed to determine the effect of cover soil and microaspect on the community composition (Table A4-B).

3.3 Results

The initial PMM propagule bank contained a greater total number of species compared to the initial FFM propagule bank, and each propagule bank contained a number of species that did not occur in the other propagule bank (PMM and FFM contained 14 and 7 such species, respectively; see Chapter 2). However, many of the species unique to only FFM or PMM initial propagule bank did not establish under field conditions, and the species detected in the initial propagule bank and also found in the field were quite similar between FFM and PMM cover soils, with only two unique to FFM, and only five unique to PMM (Table 3.1). Additionally, 67% of the species found in the FFM initial propagule bank was expressed in the field, compared to 61% of the species in the PMM propagule bank. The total number of species across all treatment plots expressed in the field (whether originating from the initial propagule bank or recruited in the field) on PMM hills was only greater by three compared to FFM hills, of which one was associated with moist habitats and two were forest-associated (Figure 3.2).

3.3.1 <u>The effect of slope aspect, cover soil and micro-elevation on vegetation expression and edaphic factors</u>

Cover soil and micro-elevation had a significant effect on species richness and plant abundance (Table A3-A). Both species richness and plant abundance were higher on PMM hills than on

FFM hills, and at the toe position compared with slope and crest positions (Figure 3.3). Overall, the propagule bank-based expression and hill-based expression of moisture-loving, forest and disturbance functional types were highest at the toe position compared to the slope and crest positions (Figure 3.4 and Figure 3.5). The effect of micro-elevation on propagule bank-based expression of moisture-loving and disturbance functional types varied depending on the cover soil used (significant cover soil by micro-elevation interaction, Table A3-A). The proportion of moisture-loving species to the initial propagule bank was greatest at the toe position of FFM hills compared to the slope and crest positions, while on PMM hills it was greater at the toe than at the crest, while the slope did not differ from the toe or the crest (Figure 3.4). For disturbance-associated species, the proportion of species found relative to the propagule bank was also greatest at the toe position of FFM hills compared to the other two positions while no difference was detected between the three micro-elevations on PMM hills. For forest-associated species the proportion of species found relative to the propagule bank was greater at the toe compared to the slope and crest positions on both FFM and PMM hills (Figure 3.4). The expression of the propagule bank relative to the total amount of species found on each hill in each functional type responded similarly to the expression relative to the initial propagule bank, where the greatest number of species associated with higher soil moisture, forest and disturbance was highest at the toe position compared to the slope and crest positions (Figure 3.4 and Figure 3.5). The impact of micro-elevation on hill-based expression of the propagule bank for disturbance-associated species varied depending on the cover soil and on the overall slope aspect (significant cover soil by micro-elevation interaction and slope aspect by micro-elevation interaction, Table A3-A). On FFM hills, hill-based expression of disturbance functional type decreased sharply from toe position to slope and crest positions, while on PMM hills this decline was less pronounced

(Figure 3.5). Additionally, the decline in hill-based expression of disturbance functional type from toe position to slope and crest positions was more pronounced on the east-facing slope than on the south-facing slope (Figure 3.5).

Community composition differed between the south-facing and east-facing slopes, between hills constructed from FFM and hills made from PMM, and among the three micro-elevation positions (Table A3-B). In particular, on FFM hills the plant community at the toe position was different from those at the slope and crest positions (both $p<0.001$), but slope position did not differ from the crest position ($p=0.249$) (Figure 3.6A). On PMM hills, toe was different from slope and crest positions (both $p<0.008$), and while the difference between slope and crest positions was not statistically significant ($p=0.073$), there seems to be a gradual change in community composition with increasing micro-elevation, (Figure 3.6B), while on the FFM hills this trend is not apparent.

Overall, soil water content was greatest on hills constructed from PMM cover soil compared with hills made from FFM cover soil; however, the impact of micro-elevation on soil water content varied depending on the overall slope aspect and the cover soil used (slope aspect by cover soil by micro-elevation interaction, Table A3-A). On the south-facing slope, the toe position of the FFM hills was wetter than the toe of the PMM hills, while there was no difference at the toe positions between the two cover soils on the east slope (Figure 3.7A). In addition, on the south-facing slope, the slope and crest positions had similar moisture conditions, with soil water content at these positions being higher on PMM hills than on FFM hills. On the east-facing slope, slope and crest positions of FFM hills had similar soil water content, while on PMM hills the slope position was wetter than the crest (Figure 3.7A). On the east facing slope, the difference in soil water content between toe and crest was similar between cover soils, although the water content on PMM hills changed more gradually with micro-elevation than on FFM hills.

On the south-facing slope, the difference in water content across micro-elevations was more dramatic for FFM hills than for PMM hills.

The impact of micro-elevation on snow water equivalent varied depending on the overall slope aspect (significant slope aspect by micro-elevation interaction, Table A3-A). On the east-facing slope, snow water equivalent was greatest at the toe position, lower at the slope, and lowest at the crest position (Figure 3.7B). On the south-facing slope, snow water equivalent was greatest at the toe position, and equally low at the slope and the crest positions. Lastly, soil temperature on either slope aspect was not affected by cover soil or micro-elevation (Table A3-A).

3.3.2 The effect of slope aspect, cover soil and microaspect on vegetation expression and edaphic factors

Cover soil and microaspect had a significant effect on species richness, plant abundance, and soil water content (Table A4-A, Figure 3.8). A slope aspect by cover soil by microaspect interaction was observed for species richness (Table A4-A, Figure 3.8A). Overall, species richness was greatest on hills constructed with PMM compared with hills made from FFM on the east-facing slope, while on the south slope the two cover soils had no effect on species richness. On the east-facing slope, the north and south microaspects had higher species richness when hills were constructed with PMM cover soil, while the west microaspect had the lowest richness when hills were constructed with FFM cover soil. However, species richness did not differ among microaspects on the south-facing slope regardless of cover soil. Greater plant abundance was observed on the north microaspects than on the west microaspects, while plant abundance on the south and east microaspects did not differ from both the north and west microaspect (Figure 3.8B). Plant abundance also varied with cover soil but responded differently depending on the slope aspect (cover soil by slope aspect interaction Table A4-A). On the east-facing slope, plant abundance was higher on PMM hills than on FFM hills, while on the south-facing slope plant abundance did not differ between the two cover soils (data not shown). Microaspect did not affect the community composition on PMM or FFM hills (Table A4-B).

The effect of microaspect on propagule bank-based expression of moisture-loving functional type varied depending on the slope aspect and the cover soil used (significant slope by cover soil by microaspect interaction, Table A4-A): on the east-facing slope, the propagule bank-based expression was greater on the north microaspect of FFM hills compared to all microaspects of PMM hills. Overall, the proportion of moisture-loving species to the initial propagule bank was greater on the north microaspect than on the south microaspect; however, it was not different across microaspects within either FFM or PMM hills on either slope aspect (data not shown). For forest- and disturbance-associated species, the proportion of species found relative to the propagule bank was not affected by microaspect, while the effect of slope aspect varied depending on the cover soil used (significant slope by cover soil interaction, Table A4-A). The propagule bank-based expression of forest and disturbance functional types on the east-facing slope was higher on FFM hills, but did not differ between the two cover soils on the south-facing slope (Figure 3.9). Lastly, greater overall propagule bank-based expression of disturbance functional type occurred on FFM hills than on PMM hills (Figure 3.9).

Overall, the expression of the propagule bank relative to the total amount of species found on each hill in the moisture-loving functional type responded similarly to the expression relative to the initial propagule bank, where the greatest number of species associated with higher soil moisture was higher on the north microaspect than on the south and west microaspects (data not shown). Additionally, the effect of microaspect on hill-based expression of moisture-loving functional type varied depending on the slope aspect and the cover soil used (significant slope by cover soil by microaspect interaction, Table A4-A): on the south slope, the hill-based expression of moisture-loving functional type was greater on the north microaspect of PMM hills than on the north and south microaspects of FFM hills (data not shown). The effect of microaspect on hill-based expression of disturbance functional type varied depending on the cover soil used (significant cover soil by microaspect interaction, Table A4-A): on FFM hills it was similar across microaspects, while on PMM hills it was greater on the north microaspect than on the west microaspect (Figure 3.10). The expression of forest functional type relative to the total number of forest-associated species found on each hill did not differ with slope aspect, cover soil or microaspect (Table A4-A).

Soil water content varied depending on the slope aspect (slope aspect by microaspect interaction, Table A4-A, Figure 3.11A). On the east-facing slope, soil water content was higher on the west compared to the east and south microaspects, while on the south-facing slope, the north microaspect had higher soil water than the east, south and west microaspects. Soil water content also varied with cover soil, with a slope aspect by cover soil interaction (Table A4-A) (not shown). On the east-facing slope, soil water content was higher on PMM hills compared to FFM hills, while on the south-facing slope, soil water content did not differ between the two cover soils. Microaspect significantly affected snow water equivalent (Table A4-A), which was highest on the north, lower on the west and lowest on the south microaspects, with the snow water equivalent on the east microaspect being similar to that at the west and the south microaspects (Figure 3.11B). Lastly, soil temperature on either slope aspect was not affected by cover soil or microaspect (Table A4-A).

3.4 Discussion

3.4.1 Micro-elevation

Elevation differences in the hilled treatment created spatial variability in species richness, plant abundance and the expression of vegetation functional types across micro-elevation positions. On both FFM and PMM hills, the toe position produced vegetation communities different from those at the slope and crest positions, the greatest number of species and individuals, the greatest hill-based expression of species associated with moist habitats, forests and disturbance, and the greatest propagule bank-based expression of species associated with moist habitats and forests. On FFM hills only, the toe position also produced the greatest propagule bank-based expression of disturbance-associated species. These results indicate that low, sheltered micro-elevation positions were more favourable for vegetation expression than the elevated positions on the constructed hills. Moreover, selectively planting and seeding species at lower micro-elevations can increase plant establishment on water-limited upland reclamation sites.

The spatial heterogeneity in species richness, plant abundance and the expression of functional types in our study was likely driven by differences in edaphic conditions modulated by climate. Soil water content is a key factor in plant establishment (Harper & White 1974; von Arx et al. 2013), and is generally highest at low micro-elevations on microtopographic structures (Bo et al. 2014; Born et al. 2015; Klug-Pümpel 1982). However, previous research has shown that the position most favourable for vegetation establishment can change depending on the local site conditions and the growing requirements of the species present on a site. For instance, on sites with abundant soil moisture or with fine-textured soils that significantly slow down infiltration, low micro-elevations may contain excess soil water and negatively impact the establishing upland vegetation (Klug-Pümpel 1982; Gilland & Mccarthy 2014). However, if the present vegetation is adapted to wetland conditions, the lowest micro-elevations with standing water may be the most productive (Bruland & Richardson 2005). Research conducted on moisture-limited upland sites suggests that low microtopographic positions at the toes of hills and mounds are generally more conducive to plant establishment and growth (Lorio & Hodges 1971; Biederman & Whisenant 2011). Further, the low lying micro-elevation positions in this study not only had higher soil water content, but were also likely more sheltered from the sun and wind, which has also been shown to facilitate plant establishment under harsh growing conditions (Elmarsdottir et al. 2003; Schott et al. 2014). In this study, the propagule banks originated from upland and lowland forests and contained species likely adapted to sheltered, higher-soil moisture conditions than those commonly found on the newly built upland reclamation sites lacking canopy cover (Chen et al. 1993). As a result, the edaphic conditions at low micro-elevations were likely the closest to the preferred growing conditions of the majority of the species present on the site.

3.4.2 Microaspect

The presence of different microaspects in the hilled treatment also resulted in increased spatial variability in species richness, plant abundance, and the expression of moisture-loving and disturbance functional types on the constructed hills. Species richness and plant abundance were greatest on the north microaspects, particularly on the south-facing slope, while the west microaspects did poorly most likely due to the greater sun exposure at the warmest part of the day. The propagule bank-based expression of moisture-loving functional type was higher on the north microaspect than on the south microaspect across both cover soils. Additionally, on PMM hills the hill-based expression of the moisture-loving functional type was greatest on the north microaspect and lowest on the south microaspect, while the hill-based expression of the disturbance functional type was greatest on the north microaspect and lowest on the south and west microaspect. It appears that the drier soil and greater solar exposure on the south microaspect were least conducive to the expression of moisture-loving vegetation, and the greater sun exposure during the warmest part of the day on the west microaspect was least conducive to the expression of the disturbance-associated vegetation. Furthermore, soil water content was highest on the north microaspect of hills on the south-facing slope, while the west microaspect was the wettest on the east-facing slope. It is not clear if these differences in soil moisture are due to accumulated runoff from up slope and/or shading. Nonetheless, it appears that plant abundance and the propagule bank-based expression of moisture-loving and disturbance functional types not only increased in response to high soil water content (highest on upslope-facing microaspects: i.e. west on the east-facing slope and north on the south-facing slope), but also the reduced solar radiation input (lowest on the north slope aspect) on these exposed sites. These findings suggest that creating microtopographic structures with large north and south microaspects on reclamation sites can increase the heterogeneity in vegetation distribution and provide desirable north-facing microaspects for overall plant establishment, and in particular for the expression of species adapted to moist habitats from soil propagule banks.

3.4.3 <u>**The effect of cover soil on the effects of micro-elevation and microaspect**</u>

Overall the results of this study indicate that the cover soil from which microtopographic structures are constructed can modify the effect of the microtopographic position on plant abundance, the richness of species, and the expression of moisture-loving, forest and disturbance functional types. For instance, on hills constructed from FFM cover soil the propagule bank-based expression of disturbance functional type was greatest at the toe, while on hills constructed from PMM it was the same across all micro-elevations. Additionally, species richness, plant abundance, the expression of species functional types, overall community compositions, and the soil water content responded more sharply to increases in micro-elevation on FFM hills, and gradually on PMM hills. It is likely that the steep drop-off in soil water content with increasing micro-elevation on hills constructed from FFM cover soil was the driving factor for larger differences in vegetation expression across micro-elevations on FFM hills, as vegetation expression is strongly tied to soil water content (Harper & White 1974; von Arx et al. 2013). The FFM cover soil with its lower organic matter content, high content of mineral soil, and coarser texture likely had a lower matric potential than the PMM cover soil (Walczak & Rovdan 2002), leading to the observed abrupt drop-off of soil water content from the toe position to slope and crest positions on hill constructed from FFM. A possible implication of this result is that when constructing hills from FFM, less elevation is required to achieve heterogeneity in microsite conditions. On the other hand, when PMM material is used, maximizing the availability of sheltered mesic toe microsites can have the additional benefit of encouraging the establishment of forest-associated species from soil propagule banks, while not substantially affecting the expression of disturbance-associated species.

The cover soil used in the construction of microtopographic structures can also alter the effect of microaspect on the expression of species functional types. While vegetation response to micro-elevation was strongest on hills constructed from FFM cover soil, variables such as the hill-based expression of moisture-loving and disturbance functional types responded to microaspect only on PMM hills. Soil water content followed the same pattern across the different microaspects on hills constructed from FFM and PMM cover soils, but it is likely that the response of vegetation to soil water content changed depending on the soil texture (Bhattacharjee et al. 2008) and the levels of environmental stress on each cover soil (Loneragan & del Moral 1984). It has been shown that the effect of microrelief on vegetation can be negligible at low-productivity sites with high environmental stresses, is positive at moderate-stress sites, and could potentially have negative effects at low-stress sites (Loneragan & del Moral 1984). This might indicate that lower soil water content on hills constructed from FFM cover soil resulted in greater stress conditions experienced on these hills, leading to a reduced overall effect of microaspect on the expression of moisture-loving and disturbance functional types. Another possible explanation is that since the PMM cover soil originated from moist lowland forests, its propagule bank potentially contained species that were less adapted to abundant sun exposure and low soil water content, and the subtle differences in these variables across the microaspects were enough to trigger a vegetation response. However, although the initial FFM and PMM propagule banks were substantially different, the species actually expressed in the field were quite similar between hills constructed from FFM and PMM cover soils.

Overall, the results of this study indicate that creating microtopographic heterogeneity on upland forest reclamation sites can provide microsites that are sheltered from sun and wind, contain greater soil moisture, and are favourable for plant establishment. It appears that on newly constructed small hill surface structures one to two meters in height, micro-elevation was generally a more important driver for vegetation expression than microaspect. This study also indicated that the magnitude of vegetation responses to microtopographic position may differ depending on the physical properties of the cover soil, such as organic matter content and soil texture, as well as on the species present in the soil propagule bank. The results of this study show that there were greater differences in vegetation responses between the toe and crest micro-elevation positions on hills with greater mineral soil content than on hills with greater peat content, and that species adapted to moist habitats were generally more sensitive to the microtopographic position than forest- or disturbance-associated species. While the significance of vegetation response to the microtopographic position depended on the cover soils and the functional type, the pattern was similar across the two cover soils and the three functional types examined, with low-lying and north-facing microhabitats generally producing the highest abundance of individual plants and species.

Tables

Table 3.1. The total number of species contained in the initial propagule banks of FFM and PMM cover soils, displaying the total number of species in the propagule bank, the number of species expressed in the field and shared between both initial propagule banks or unique to one propagule bank for each cover soil, and the number of species absent in the field that were shared between initial propagule banks of both cover soils or unique to one cover soil.

Initial propagule bank	*Number of species*				
	Total	*Expressed in the field (shared)*	*Expressed in the field (unique)*	*Absent in the field (shared)*	*Absent in the field (unique)*
FFM	21	12	2	2	5
PMM	28	12	5	2	9

Figures

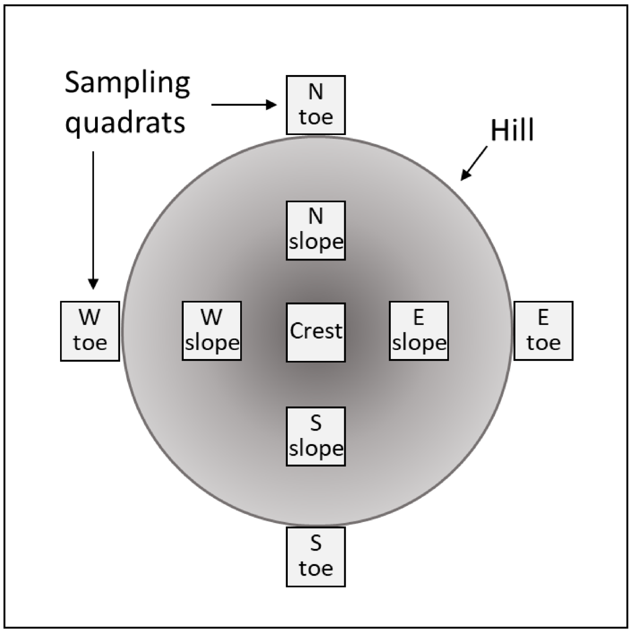


Figure 3.1. Schematic representation (view from above) of sampling quadrats (50 cm×50 cm) established on selected hills for vegetation and edaphic assessments.

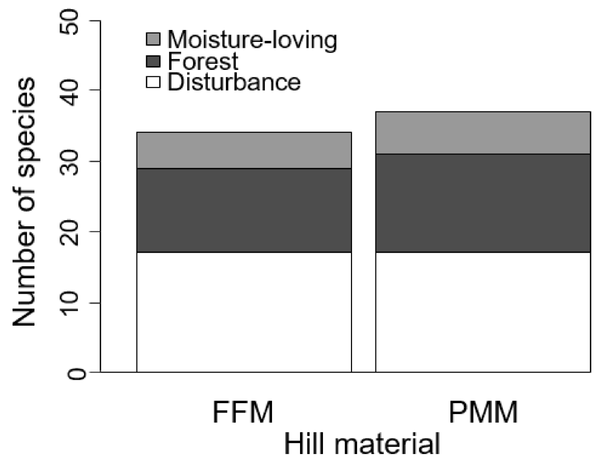


Figure 3.2. The total number of species discovered on the field site on FFM (forest floor material) and PMM (peat-mineral mix) hills that are associated with higher soil moisture (moisture-loving), forest, or disturbance.

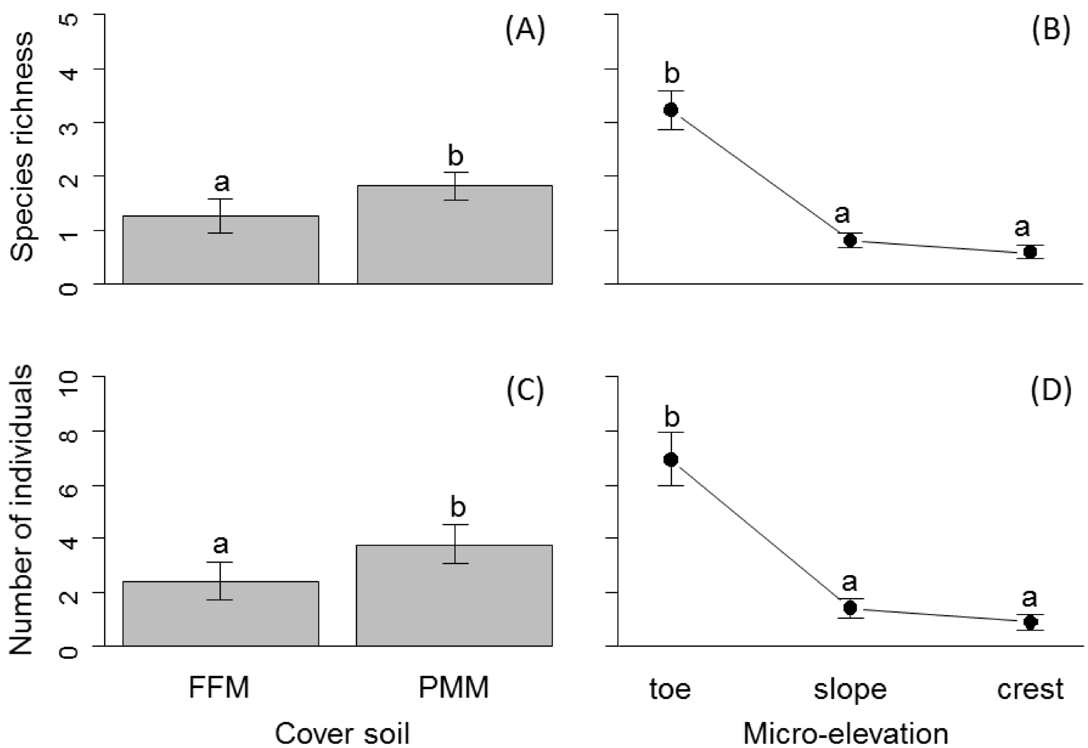


Figure 3.3. The average species richness in response to cover soil (n=10) (A) and micro-elevation (n=10) (B) averaged across both slope aspects (east and south); and the average number of individuals in response to cover soil (n=10) (C) and micro-elevation (n=10) (D) averaged across both slope aspects. Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

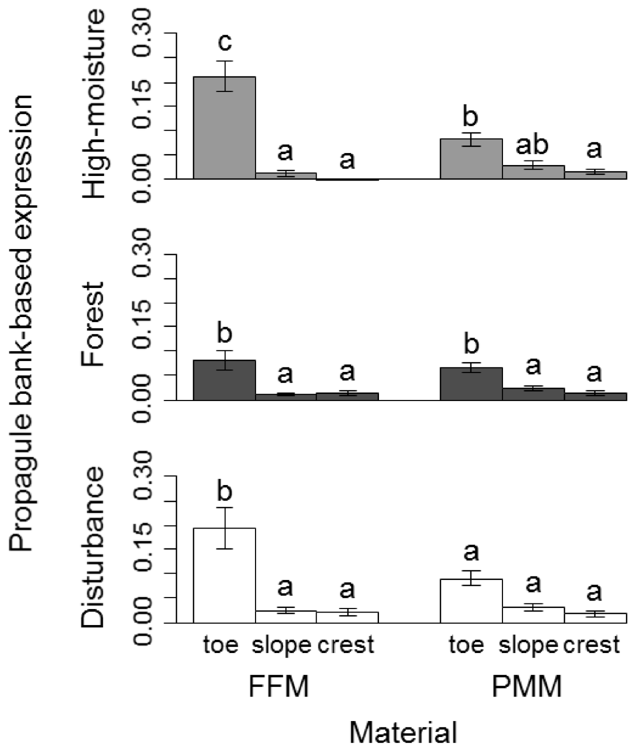


Figure 3.4. Average proportional expression of each functional type' s richness relative to its richness in the initial propagule bank, in response to cover soil and micro-elevation (n=10). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

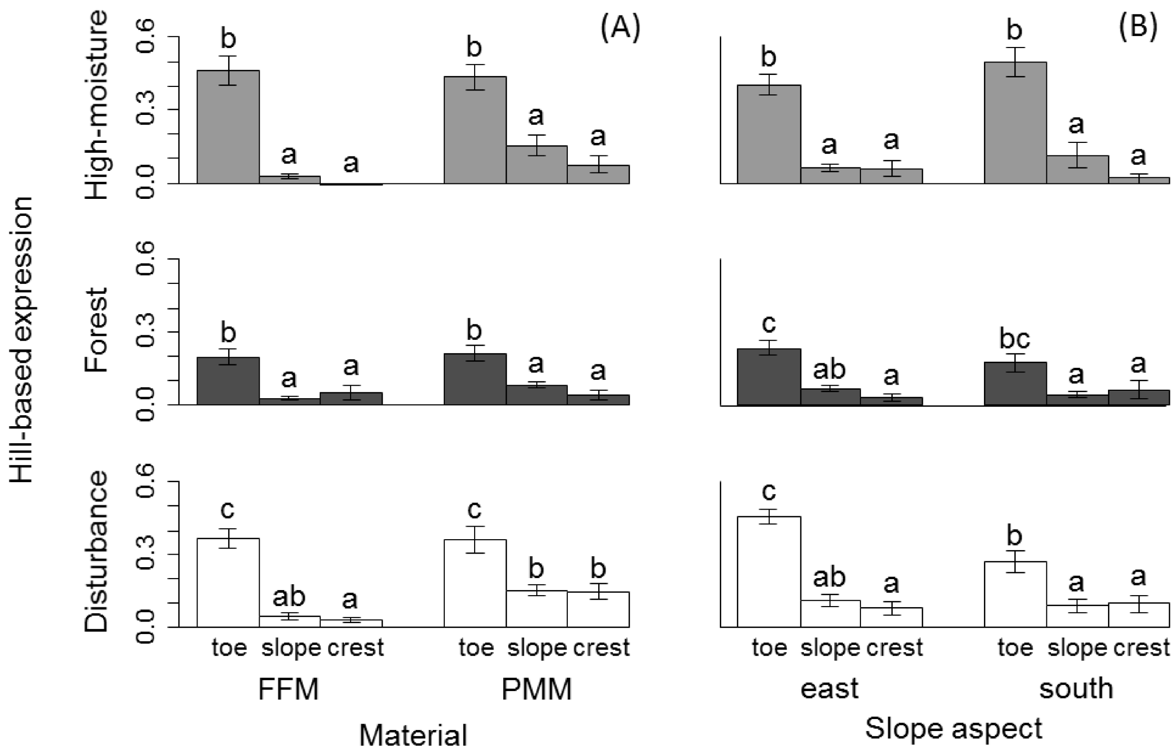


Figure 3.5. Average proportional expression of each functional type' s richness relative to its richness on each hill, in response to cover soil and micro-elevation (n=10) (A) and in response to slope aspect and micro-elevation (n=5) (B). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

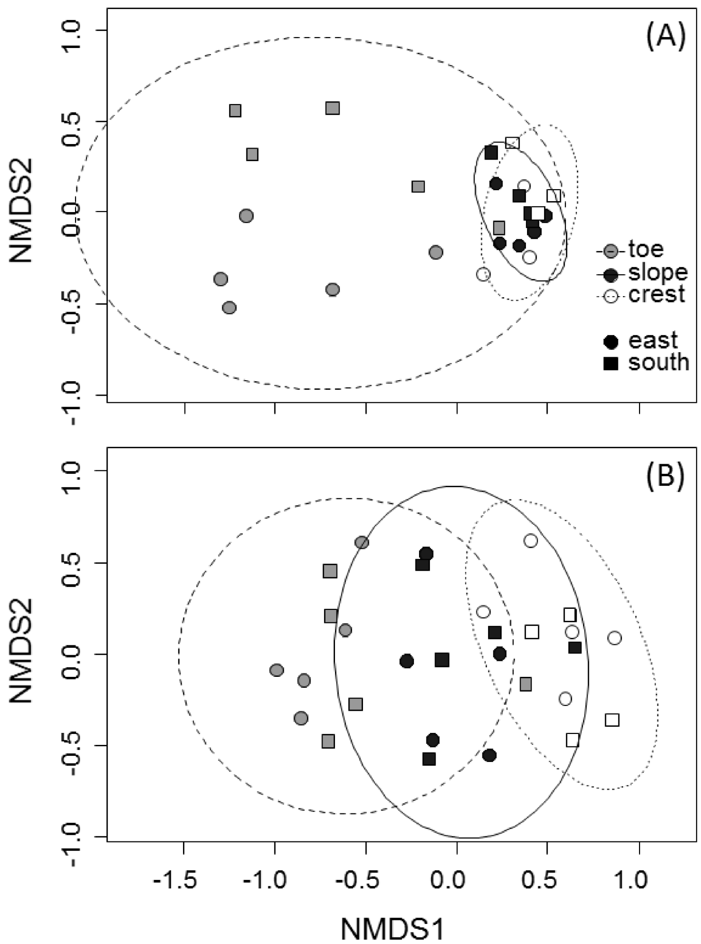
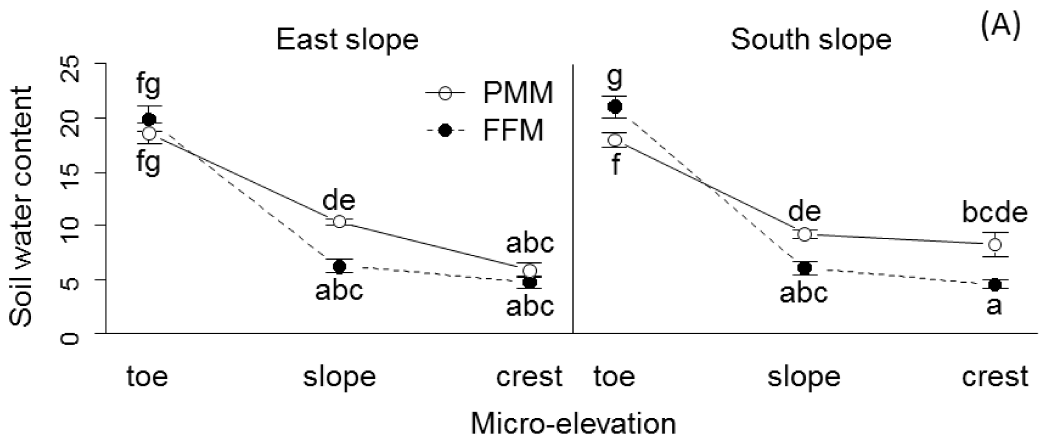


Figure 3.6. Non-metric multi-dimensional scaling (NMDS) analysis comparing the community composition at toe, slope and crest micro-elevations (the south and east-facing slopes are combined) on hills made from FFM (forest floor material) cover soil (A) and PMM (peat-mineral mix) cover soil (B). Ellipses indicate 95% probability of distributions.



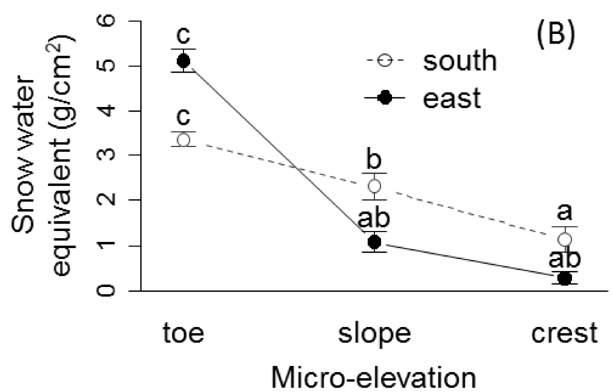


Figure 3.7. Average soil water content (A) in response to slope aspect, cover soil and microaspect (n=5); and average snow water equivalent (B) in response to slope aspect and micro-elevation averaged across FFM (forest floor material) and PMM (peat-mineral mix) cover soils (n=6). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

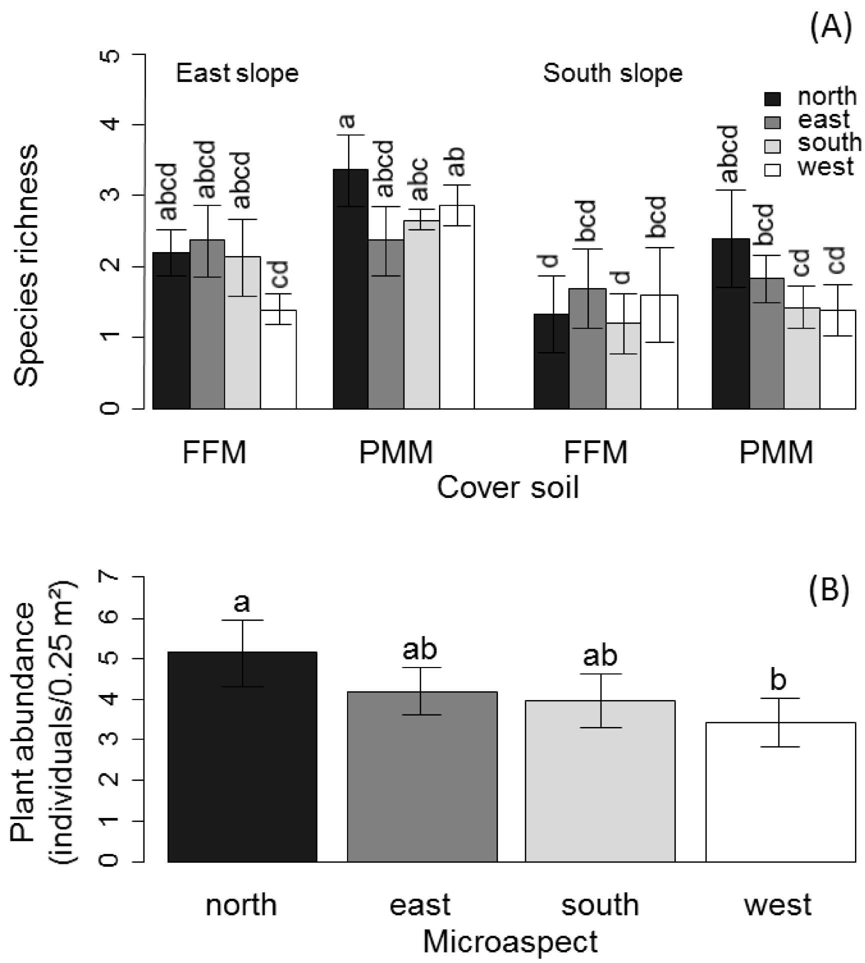


Figure 3.8. Average species richness (A) in response to slope aspect, cover soil and microaspect (n=5); and average plant abundance (B) in response to microaspect (n=10). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

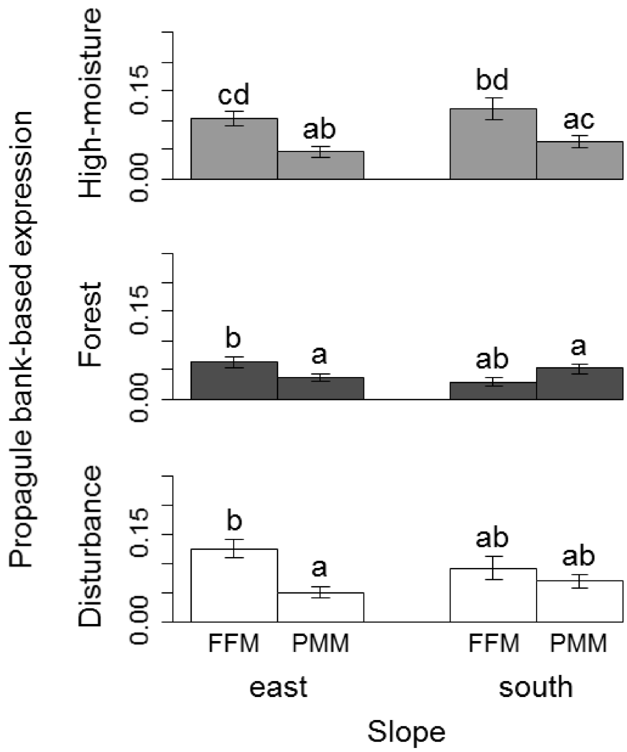


Figure 3.9. Average propagule bank-based expression of each functional type in response to slope aspect and cover soil (n=5). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

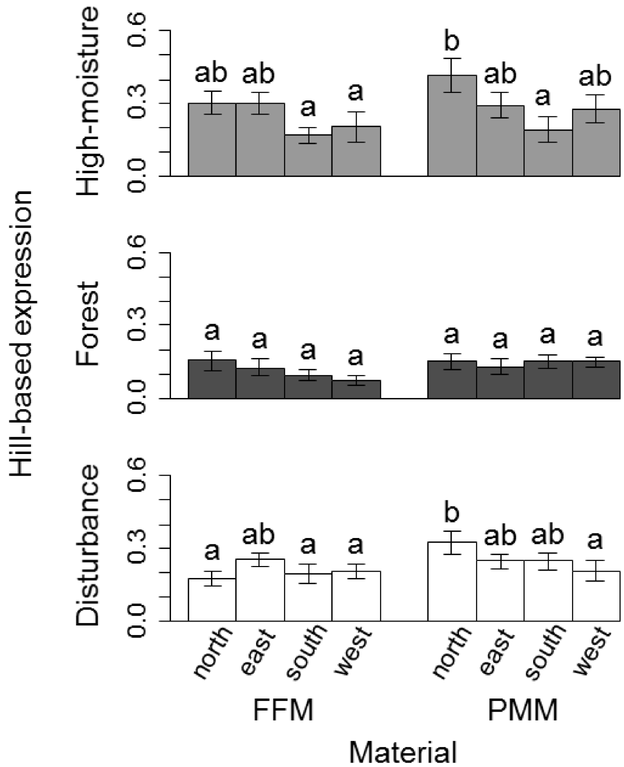


Figure 3.10. Average hill-based expression of each functional type in response to cover soil and microaspect (n=10). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

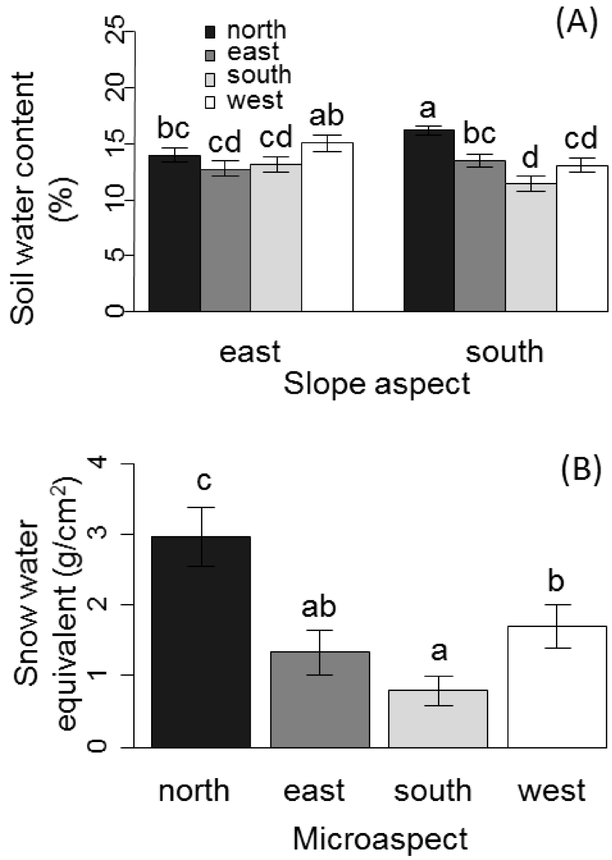


Figure 3.11. Average soil water content (A) in response to slope aspect and microaspect (n=5); and average snow water equivalent (B) in response to microaspect on both slope aspects (n=6). Bars with different letters indicate differences among treatment means. Error bars indicate ± SE (α<0.05).

Chapter 4: Synthesis and future research

4.1 Research overview

Re-establishing the herbaceous and shrub layers is integral to the revegetation of previously forested areas disturbed by industrial development. Topsoil transfer and placement provides propagules and a growth medium, but the presence of desirable growing conditions for the wide range of species present in these soil propagule banks is also crucial for vegetation establishment. The main objective of my thesis was to evaluate how artificially created microtopography affects the early expression of the initial propagule banks on upland reclamation sites. My specific objectives were to examine how slope aspect and different microtopographic surface treatments affect vegetation expression, and to identify the most favourable microsites for plant establishment on microtopographic features constructed from two contrasting cover soils.

In the first study, I evaluated the role of microsite heterogeneity on early vegetation expression on two slope aspects in an operational-scale experiment. In the second study, I examined how the microtopographic position on small hills constructed from two contrasting cover soils on two slope aspects affect early vegetation expression. It was hypothesized that species richness and abundance of vegetation arising on the site would be higher in treatments with greater microtopographic heterogeneity, because the resulting variability in microsite conditions will better satisfy the diverse growing requirements of different species within a small area. The results of the first study demonstrate that artificially created microtopography produces microsites with diverse growing conditions, and can encourage vegetation expression on upland forest reclamation sites. Out of the three treatments examined, creating small hills (~1.5 m in height) by loosely piling contrasting capping materials resulted in highest plant abundance, species richness, vegetation similarity with the soil seedbank, and the recruitment of forest-specific plants. Interestingly, creating parallel ridges on the soil surface also increased the diversity of microsite conditions, but did not increase species richness and had a negative effect on plant abundance compared to the current operational practice. It is likely that the size and shape of the microtopographic structures, the types of produced micro-elevation positions, the soil placement technique, soil bulk density, and the utilized cover soil also have a substantial effect on vegetation expression. The hilled treatment had the largest microtopographic structures, loosely placed soil with lowest soil bulk density and the most surface roughness, and the greatest amount of exposed PMM (peat-mineral mix) cover soil at the surface.

In the second study, I examined how microtopographic position on hills constructed from two cover soils affected the expression of species associated with moist habitats, forests and disturbance. Micro-elevation effects were the strongest on FFM (forest floor material) hills, while microaspect effects were the strongest on PMM hills. While I hypothesized that microtopography would facilitate the expression of many species due to increased diversity of growing conditions, it appears that species generally preferred the same microsites produced by the microtopographic structures. Overall, I found that depending on the cover soil and the functional type, vegetation was either unaffected by microtopographic position, or preferred low-lying, north-facing positions on the hills, which provided moister, more sheltered conditions. This implies that microtopographic structures were beneficial not necessary due to the heterogeneity of conditions they generate, but because they enabled the existence of microhabitats desirable for most species and absent from the levelled plots.

Another important result of the two studies was that the effect of microtopographic treatments on early plant communities can be modulated by site topography, and that the impact of microtopographic position can be affected by the cover soil. The hilled treatment positively affected plant abundance and species richness on the east-facing slope, while increasing the proportion of species requiring higher soil moisture on the south-facing slope. Micro-elevation had the greatest effect on vegetation expression on hills constructed from FFM than on hills constructed from PMM, while microaspect affected vegetation the most on hills constructed from PMM. The observed differences in vegetation response to microtopographic heterogeneity between south- and east-facing slopes were likely caused by the differences in stress levels due to differences in sun exposure. The observed differences in response to microtopographic position between hills constructed from FFM and PMM cover soils likely occurred due to differences in water retention capacity of the two cover soils, which occurred because FFM and PMM differed in organic matter content and soil texture.

The two studies reveal how microtopographic structures constructed on forest reclamation sites can influence the early expression of vegetation from the initial soil propagule banks. The presented results indicate that microtopography and presence of contrasting substrates are important for the reestablishment of a diverse vegetation layer on sites with previously removed topsoil.

4.2 Applications for reclamation

Revegetation of upland reclamation sites with forest-adapted species presents challenges, and this research demonstrated that constructed microtopography has the capacity to facilitate the revegetation process by providing sheltered, moist microsites favourable for the expression of many species present in soil propagule banks. While all three evaluated techniques resulted in some vegetation expression, the results suggest that piling salvaged forest floor materials to create an uneven surface, and utilizing contrasting material types can increase species richness and plant abundance compared to standard operations. Additionally, the hilled treatment can create a wider range of microsite conditions, allowing species with different ecological niches to establish. However, the overall site conditions must be evaluated and accounted for in regards to specific revegetation objectives for the area, as the relative effect of the microtopographic treatments can change depending on the conditions at the reclamation site. The hilled treatment provided the additional benefit of reducing equipment hours (personal communication R. Vassov), as it did not require consequent levelling of the soil surface. Meanwhile, the ridged treatment required more equipment hours compared to standard operations, but resulted in similar vegetation expression compared to the operational control.

I observed that proportionally more species were expressed on the upland reclamation sites from the cover soil salvaged from an upland forest (FFM) compared with the cover soil originating from a low-lying forest (PMM), likely because a greater proportion of the species enclosed in the upland cover soil were adapted to the site conditions. If FFM is limited it is possible that including a few sporadic hills of FFM among the PMM hills could provide the initial source of adapted species, which would disperse seeds across the site. Meanwhile, a cover soil from a low-lying area may also give rise to species adapted to the reclamation site conditions as long as these species are present in the propagule bank. Additionally, introducing some high-organic-matter-content cover soil from low-lying areas to upland reclamation sites along with upland cover soil could increase soil water retention and encourage vegetation expression.

If a reclamation site contains microtopographic variability and is seeded with target plant species, I recommend placing seeds in low-lying areas, and if they must be placed at elevated positions on microtopographic structures, more shaded (north and east) microaspects are recommended. This preferential placement will likely increase the number of successfully established individuals, as low-lying areas and more shaded microaspects have been shown to be the most desirable for plant establishment. Although the research presented in this thesis was conducted on an upland boreal forest reclamation site, the same principles are likely applicable on other sites where moisture levels are lower than the ideal growing conditions of the species of interest.

4.3 Study limitations and future research

The research presented in this thesis was conducted at an operational scale, and sheds light on how treatments with varying levels of microtopographic heterogeneity and the microsite positions within these treatments affect vegetation expression in a real-life setting. Operational-scale trials produce results that can be readily applied in reclamation practice; however, at the same time operational constraints can present some limitations for research. Due to limited availability of FFM for treatment construction, the hilled treatment contained hills constructed from FFM and hills constructed from PMM atop the PMM base layer, while the ridged and control treatments only contained a layer of FFM atop the PMM base layer. This led to one of the main limitations of this research, which was that the hilled treatment not only had the greatest level of microtopographic heterogeneity than the ridged and control treatments, but also had the greatest amount of exposed PMM at the soil surface. The greater amount of exposed PMM in the hilled treatment likely resulted in more soil water available for the developing vegetation, and could have contributed plant species absent from the FFM initial propagule bank. As a result, the effect of microtopographic heterogeneity in this study cannot be separated from the effect of exposed PMM cover soil. In the future, it would be interesting to evaluate the effect of microtopographic heterogeneity across different microtopographic treatment constructed with the same cover soil.

Due to differences in soil placement techniques, soil bulk density differed across the three treatments, being lowest in the hilled treatment, moderate in the ridged treatment, and greatest in the control. Soil bulk density is known to affect vegetation establishment (Sweigard et al. 2007), and it is possible that these differences contributed to differences in vegetation expression across treatments. Future research projects could examine how different levels of microtopographic heterogeneity affect vegetation expression at a consistent soil bulk density, to separate the effects of these two variables.

The presented research study evaluated vegetation response to treatments and microtopographic positions at the end of the first growing season and presents important information regarding initial vegetation communities on the site. However, vegetation is dynamic on newly-constructed reclamation sites, and further monitoring is required to assess long-term treatment effects. Future vegetation assessment at this research site would identify a more long-term effect of treatments and microtopographic positions on vegetation communities, and would reveal how communities change going forward from the baseline numbers presented here. Future assessments could also evaluate the response of mosses, lichens and fungi to treatments and microtopographic positions.

Future reclamation projects could benefit from research into what microtopographic positions are most favourable for the establishment of specific commercially available boreal understory species (such as *Arctostaphylos uva-ursi*, *Cornus canadensis*, *Viburnum edule* and *Vaccinium* spp.) and tree species (such as *Pinus contorta* var. *latifolia*, *Picea glauca*, and *Populus tremuloides*) that may be seeded or planted on reclamation sites. It is possible that the preferences of some important boreal species will be different from the general trends presented in this thesis, and this additional research will allow for the most efficient use of seeds and planting stock. It would also be interesting to evaluate if trees with their larger root systems are able to take advantage of the greater soil water content at the lower micro-elevation positions even when planted higher up. There are many ways to construct microtopographic structures on reclamation sites, and experimenting with various sizes, shapes and spacing of microtopographic structures would allow to develop a technique optimal for encouraging vegetation establishment. Lastly, it would be beneficial to conduct microtopographic trials on flat ground and on north- and west-facing slopes, to determine how microtopography affects vegetation expression in these environments.

Literature cited

Appels WM, Bogaart PW, van der Zee SE (2011) Influence of spatial variations of microtopography and infiltration on surface runoff and field scale hydrological connectivity. Advances in Water Resources 34:303-313

Bannister JR, Coopman RE, Donoso PJ, Bauhus J (2013) The importance of microtopography and nurse canopy for successful restoration planting of the slow-growing conifer *Pilgerodendron uviferum*. Forests 4:85-103

Bartels SF, Chen HY (2010) Is understory plant species diversity driven by resource quantity or resource heterogeneity? Ecology 91:1931-1938

Beatty SW (1984) Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology 65:1406-1419

Bhattacharjee J, Taylor JP, Smith LM, Spence LE (2008) The importance of soil characteristics in determining survival of first-year cottonwood seedlings in altered riparian habitats. Restoration Ecology 16:563-571

Beckingham JD, Archibald JH (1996) Field guide to ecosites of Northern Alberta. Canadian Forest Service, Northwest region, Northern Forestry Centre

Biederman LA, Whisenant SG (2011) Using mounds to create microtopography alters plant community development early in restoration. Restoration Ecology 19:53-61

Blake GR (1965) Bulk Density. Pages374-390. In: Black CA, Evans DD, White JL, Ensminger LE, Clark FE (eds) Methods of Soil Analysis, Part I. American Society of Agronomy. Madison, Wisconsin

Bo Y, Zhu Q, Zhao W (2014) Characteristics of soil moisture in relation to microtopography in the loess region of northern shaanxi, China. Journal of Environmental Biology 35:741-749

Born J, Bagchi R, Burslem D, Nilus R, Tellenbach C, Pluess AR, Ghazoul J (2015) Differential responses of dipterocarp seedlings to soil moisture and microtopography. Biotropica 47:49-58

Brown RL, Naeth MA (2014) Woody debris amendment enhances reclamation after oil sands mining in Alberta, Canada. Restoration Ecology 22:40-48

Bruland GL, Richardson CJ (2005) Hydrologic, edaphic, and vegetative responses to microtopographic reestablishment in a restored wetland. Restoration Ecology 13:515-523

Bryant D, Nielsen D, Tangley L (1997) The last frontier forests: ecosystems and economies on the edge. Issues in Science and Technology 14:85-87

Chen J, Franklin JF, Spies TA (1993) Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. Agricultural and Forest Meteorology 63:219-237

Cooke JA, Johnson MS (2002) Ecological restoration of land with particular reference to the mining of metals and industrial minerals: A review of theory and practice. Environmental Reviews 10:41-71

Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society B: Biological Sciences 345:101-118

Cornett MW, Reich PB, Puettmann KJ (1997) Canopy feedbacks and microtopography regulate conifer seedling distribution in two Minnesota conifer-deciduous forests. Ecoscience 4:353-364

Dalling JW, Hubbell SP (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. Journal of Ecology 90:557-568

Deák B, Valkó O, Török P, Kelemen A, Miglécz T, Szabó S, Szabó G, Tóthmérész B (2015) Microtopographic heterogeneity increases plant diversity in old stages of restored grasslands. Basic and Applied Ecology 16:291–299

Dhillion SS (1999) Environmental heterogeneity, animal disturbances, microsite characteristics, and seedling establishment in a *Quercus havardii* community. Restoration Ecology 7:399-406

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67:345-366

Elder K, Dozier J, Michaelsen J (1991) Snow accumulation and distribution in an alpine watershed. Water Resources Research 27:1541-1552

Elder K, Rosenthal W, Davis RE (1998) Estimating the spatial distribution of snow water equivalence in a montane watershed. Hydrological Processes 12:1793-1808

Elmarsdottir A, Aradottir AL, Trlica MJ (2003) Microsite availability and establishment of native species on degraded and reclaimed sites. Journal of Applied Ecology 40:815-823

Environment Canada (2015) Daily Data Report for January 2015 - Mildred Lake, Alberta http://climate.weather.gc.ca/historical_data/search_historic_data_e.html (accessed 21 July 2016)

Ewing K (2002) Mounding as a Technique for Restoration of Prairie on a Capped Landfill in the Puget Sound Lowlands. Restoration Ecology 10:289-296

Farrell C, Hobbs RJ, Colmer TD (2012) Microsite and litter cover effects on seed banks vary with seed size and dispersal mechanisms: implications for revegetation of degraded saline land. Plant Ecology 13:1145-1155

Fowler NL (1986) Microsite requirements for germination and establisment of three grass species. American Midland Naturalist 115:131-145

Fox J, Sanford W (2011) An {R} Companion to Applied Regression, Second Edition. SAGE Publications, Thousand Oaks. California

Frank DA, McNaughton SJ (1991) Stability increases with diversity in plant communities: empirical evidence from the 1988 Yellowstone drought. Oikos 62:360-362

Frouz J, Kalčík J, Velichová V (2011). Factors causing spatial heterogeneity in soil properties, plant cover, and soil fauna in a non-reclaimed post-mining site. Ecological Engineering 37:1910-1913

Geiger R, Aron RH, Todhunter P (2009) The Climate Near the Ground. Rowman & Littlefield Publishers, Lanham, Maryland

Gilland KE, Mccarthy BC (2014) Microtopography influences early successional plant communities on experimental coal surface mine land reclamation. Restoration Ecology 22:232-239

Gilliam FS (2007) The Ecological Significance of the Herbaceous Layer in Temperate Forest Ecosystems. BioScience 57:845-858

Harper JL, White J (1974) The demography of plants. Annual Review of Ecology and Systematics 5:419-463

Harper JL, Benton RA (1966) The behaviour of seeds in soil. II. The germination of seeds on the surface of a water supplying substrate. Journal of Ecology 54:151-166

Haynes RJ, Swift RS (1985) Effects of liming on the extractability of Fe, Mn, Zn and Cu from a peat medium and the growth and micronutrient uptake of highbush blueberry plants. Plant and Soil 84:213-223

Holland PG, Steyn DG (1975) Vegetational Responses to Latitudinal Variations in Slope Angle and Aspect. Journal of Biogeography 2:179-183

Hutchings MJ, John EA, Wijesinghe DK (2003) Toward understanding the consequences of soil heterogeneity for plant populations and communities: Underground processes in plant communities. Ecology 84:2322-2334

Jacobs DF, Oliet JA, Aronson J, Bolte A, Bullock JM, Donoso PJ, Landhäusser SM, Madsen P, Peng S, Rey-Benayas JM, Weber JC (2015) Restoring forests: what constitutes success in the twenty-first century? New Forests 46:601-614

Jonas T, Marty C, Magnusson J (2009) Estimating the snow water equivalent from snow depth measurements in the Swiss Alps. Journal of Hydrology 378:161-167

Katra I, Blumberg DG, Lavee H, Sarah P (2007) Topsoil moisture patterns on arid hillsides - Micro-scale mapping by thermal infrared images. Journal of Hydrology 334:359-367

Klug-Pümpel B (1982). Effects of microrelief on species distribution and phytomass variations in a *Caricetum curvulae* stand. Vegetatio 48:249-254

Kutiel P, Lavee H, Ackermann O (1998) Spatial distribution of soil surface coverage on north and south facing hillslopes along a Mediterranean to extreme arid climatic gradient. Geomorphology 23:245-256

Lieffers VJ, Caners RT, Ge H (2017) Re-establishment of hummock topography promotes tree regeneration on highly disturbed moderate-rich fens. Journal of Environmental Management 197:258-264

Löf M, Dey DC, Navarro RM, Jacobs DF (2012) Mechanical site preparation for forest restoration. New Forests 43:825-848

Loneragan WA, del Moral R (1984) The influence of microrelief on community structure of subalpine meadows. Bulletin of the Torrey Botanical Club 111:209-216

Lorio PL, Hodges JD (1971) Division S-7 forest and range soils. Soil Science Society of America Journal 35:795-800

Lundholm JT, Larson DW (1998) Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. Ecography 26:715-722

Macdonald SE, Quideau SA, Landhäusser SM (2012) Rebuilding boreal forest ecosystems after industrial disturbance. Pages123-161 In: Vitt D, Bhatti J (eds) Restoration and Reclamation of Boreal Ecosystems: Attaining Sustainable Development. Cambridge University Press, Cambridge, United Kingdom

Macdonald SE, Landhäusser SM, Skousen J, Franklin J, Frouz J, Hall S, Jacobs DF, Quideau S (2015) Forest restoration following surface mining disturbance: challenges and solutions. New Forests 46:703-732

Mackenzie DD (2013) Oil sands mine reclamation using boreal forest surface soil (LFH) in northers Alberta. University of Alberta

Mackenzie DD, Naeth MA (2010) The role of the forest soil propagule bank in assisted natural recovery after oil sands mining. Restoration Ecology 18:418-427

MacKenzie MD, Quideau SA (2010) Laboratory-based nitrogen mineralization and biochemistry of two soils used in oil sands reclamation. Canadian Journal of Soil Science 44:131-142

Marshall IB, Schut PH, Ballard M (1999) A national ecological framework for Canada: attribute data. Environmental Quality Branch, Ecosystems Science Directorate, Environment Canada and Research Branch, Agriculture and Agri-food Canada, Ottawa, Ontario/Hull.

Moss EH, Packer JG (1983) Flora of Alberta: a manual of flowering plants, conifers, ferns, and fern allies found growing without cultivation in the Province of Alberta, Canada. University of Toronto Press

Mundell TL, Landhäusser SM, Lieffers VJ (2008) Root carbohydrates and aspen regeneration in relation to season of harvest and machine traffic. Forest Ecology and Management 1:68-74

Natural Regions Committee (2006) Natural Regions and Subregions of Alberta. Compiled by D.J. Downing and W.W. Pettapiece. Government of Alberta. Pub. No. T/852

Nichols WF, Killingbeck KT, August PV (1998) The influence of geomorphological heterogeneity on biodiversity II. A landscape perspective. Conservation Biology 12:371-379

Nilsson M, Wardle D (2005) Understory vegetation as a forest ecosystem drive: evidence from the northern Swedish boreal forest. Frontiers in Ecology and the Environment 8:421-428

Ojekanmi AA, Chang SX (2014) Soil Quality Assessment for Peat–Mineral Mix Cover Soil Used in Oil Sands Reclamation. Journal of Environment Quality 43:1566

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2016) Vegan: community ecology package. R package version 2.3-3 https://CRAN.R-project.org/package=vegan

Oomes MJM, Elberse WT (1976) Germination of six grassland herbs in microsites with different water contents. The Journal of Ecology 64:745-755

Peterson G, Allen CR, Holling CS (1998) Ecological resilience, biodiversity, and scale. Ecosystems 1:6-18

R Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/

Ren H, Yang L, Liu N (2008) Nurse plant theory and its application in ecological restoration in lower subtropics of China. Progress in Natural Science 18:137-142

Ribeiro PJ, Diggle PJ (2016) geoR: Analysis of geostatistical data. R package version 1.7-5.2 https://CRAN.R-project.org/package=geoR

Roberts DW (2016) Ordination and Multivariate Analysis for Ecology. R package version 1.8-0 https://CRAN.R-project.org/package=labdsv

Rodriguez-Iturbe I (2000) Ecohydrology: a hydrologic perspective of climate-soil-vegetation dynamics. Water Resources Research 36:3-9

Saxton K, Rawls W (2006) Soil water characteristic estimates by texture and organic matter for hydrologic solutions. Soil Science Society of America Journal 70:1569-1578

Schott KM, Karst J, Landhäusser SM (2014) The role of microsite conditions in restoring trembling aspen (*Populus tremuloides* Michx) from seed. Restoration Ecology 22:292-295

Silvertown J (1999) Seed ecology, dormancy, and germination: a modern synthesis from Baskin and Baskin. American Journal of Botany 86:903-905

Sutton RF (1993) Mounding site preparation: A review of European and North American experience. New Forests 7:151-192

Sweigard R, Burger J, Zipper C, Skousen J, Barton C, Angel P (2007) Low compaction grading to enhance reforestation success on coal surface mines. Appalachian Regional Reforestation Initiative, US Office of Surface Mining. Forest Reclamation Advisory Number 3

Tacey WH, Glossop BL (1980) Assessment of topsoil handling techniques for rehabilitation of sites mined for bauxite within the jarrah forest of western Australia. The Journal of Applied Ecology 17:195-201

Ter Heerdt GNJ, Verweij GL, Bekker RM, Bakker JP (1996) An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. Functional Ecology 10:144-151

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718-720

Titus JH, del Moral R (1998) Seedling establishment in different microsites on Mount St. Helens, Washington, USA. Plant Ecology 134:13-26

Valenzuela P, Arellano EC, Burger JA, Becerra P (2016) Using facilitation microsites as a restoration tool for conversion of degraded grasslands to *Nothofagus* forests in Southern Patagonia. Ecological Engineering 95:580-587

von Arx G, Graf Pannatier E, Thimonier A, Rebetez M (2013) Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. Journal of Ecology 101:1201-1213

Walczak R, Rovdan E (2002) Water retention characteristics of peat and sand mixtures. International Agrophysics 16:161-165

Weitz AM, Grauel WT, Keller M, and Veldkamp E (1997) Calibration of time domain reflectometry technique using undisturbed soil samples from humid tropical soils of volcanic origin. Water Resources Research 33:1241-1249

Zenner EK, Fauskee JT, Berger AL, Puettmann KJ (2007) Impacts of skidding traffic intensity on soil disturbance, soil recovery, and aspen regeneration in north central Minnesota. Northern Journal of Applied Forestry 24:177-183

Appendix

Table A1. Results of ANOVAs at microtopographic treatment plot level, showing *p*-values for the effect of slope aspect (*df*=1), treatment (*df*=2), and slope aspect by treatment interaction (*df*=2). Bold values indicate statistical significance at $\alpha = 0.05$.

Response variable	*Slope aspect (S)*	***Microtopographic Treatment (M)***	*S × M*
Species richness	0.066	**0.015**	**0.007**
Plant abundance	0.256	**0.016**	**0.030**
Proportion of moisture-loving spp.	**0.017**	**0.001**	**0.013**
Proportion of forest-specific spp.	0.388	0.329	0.956
Proportion of disturbance-specific spp.	0.083	0.432	0.543
Soil water content	0.889	**0.001**	**0.047**
Snow water equivalent	0.691	0.138	0.062
Soil bulk density	0.187	**<0.001**	0.724
Soil temperature	N/A	0.880	N/A

Table A2. Results of ANOVAs at micro-elevation level, within the ridged microtopographic treatment (A) and the hilled microtopographic treatment (B). Displayed are *p*-values for the effect of slope aspect (*df*=1), micro-elevation (*df*=3), and slope aspect by micro-elevation interaction (*df*=3). Bold values indicate statistical significance at $\alpha = 0.05$.

		Hill or Ridge	
Response variable	*Slope aspect (S)*	***Micro-elevation (ME)***	*S × ME*
(A)			
Species richness	0.076	**0.008**	0.244
Plant abundance	0.106	**0.019**	0.311
Soil water content	0.272	**<0.001**	0.124
Soil bulk density	0.701	**0.030**	0.423
Soil temperature	N/A	0.607	N/A
(B)			
Species richness	**0.005**	**<0.001**	**0.047**
Plant abundance	**0.030**	**<0.001**	**0.031**
Soil water content	**0.029**	**<0.001**	0.527
Soil bulk density	0.175	**<0.001**	**0.032**
Soil temperature	N/A	0.834	N/A

Table A3. Results of ANOVAs (A) and MANOVA (B) showing *p*-values for the effect of slope aspect (east and south, *df*=1), cover soil (FFM and PMM, *df*=1), micro-elevation (toe, slope and crest positions, *df*=2), and their interactions on vegetation expression and edaphic factors. Bold values indicate statistical significance at $\alpha = 0.05$.

			Hill				
Response variable	*Slope aspect (S)*	*Cover soil (C)*	***Micro-elevation (ME)***	*S×C*	*S×ME*	*C×ME*	*S×C×ME*
(A)							
Species richness	0.181	**<0.001**	**<0.001**	0.635	0.240	0.072	0.928
Plant abundance	0.170	**<0.001**	**<0.001**	0.497	0.153	0.171	0.654
Soil water content	0.798	**<0.001**	**<0.001**	0.934	0.065	**<0.001**	**0.009**
Soil temperature (east-facing slope)	N/A	0.272	0.869	N/A	N/A	0.595	N/A
Soil temperature (south-facing slope)	N/A	0.256	0.971	N/A	N/A	0.950	N/A
Snow water equivalent	0.790	0.836	**<0.001**	0.345	**<0.001**	0.743	0.681

			Hill				
Response variable	*Slope aspect (S)*	*Cover soil (C)*	***Micro-elevation (ME)***	*S×C*	*S×ME*	*C×ME*	*S×C×ME*
Propagule bank-based expression (moisture-loving)	0.9033	0.0772	**<0.001**	0.5934	0.5037	**<.0001**	0.325
Propagule bank-based expression (forest)	0.4359	0.9438	**<0.001**	0.0988	0.4249	0.3734	0.0617
Propagule bank-based expression (disturbance)	0.6393	0.1088	**<0.001**	0.1423	0.5516	**0.0307**	0.4443
Hill-based expression (moisture-loving)	0.464	0.058	**<0.001**	0.653	0.178	0.114	0.343
Hill-based expression (forest)	0.388	0.309	**<0.001**	0.935	0.222	0.385	0.354
Hill-based expression (disturbance)	0.188	**<0.001**	**<0.001**	0.393	**0.025**	**0.007**	0.174
(B)							
Community composition	**<0.001**	**0.006**	**<0.001**	0.340	0.095	0.364	0.866

Table A4. Results of ANOVAs (A) and MANOVA (B) showing *p*-values for the effect of slope aspect (east and south, *df*=1), cover soil (FFM and PMM, *df*=1), microaspect (north, east, south and west, *df*=3) and their interactions on vegetation expression and edaphic factors. Bold values indicate statistical significance at $\alpha = 0.05$.

			Hill				
Response variable	*Slope aspect (S)*	*Cover soil (C)*	***Microaspect (MA)***	*S×C*	*S×MA*	*C×MA*	*S×C×MA*
(A)							
Species richness	0.196	**<0.001**	**0.012**	**0.042**	0.400	**0.018**	**0.037**
Plant abundance	0.192	**<0.001**	**0.004**	**0.003**	0.059	0.064	0.100
Soil water content	0.834	**0.035**	**<0.001**	**0.040**	**<0.001**	0.945	0.092
Soil temperature (east-facing slope)	N/A	0.635	0.641	N/A	N/A	0.889	N/A
Soil temperature (south-facing slope)	N/A	0.319	0.742	N/A	N/A	0.992	N/A
Snow water equivalent	0.098	0.504	**<0.001**	0.839	0.383	0.482	0.206

			Hill				
Response variable	*Slope aspect (S)*	*Cover soil (C)*	***Microaspect (MA)***	*S×C*	*S×MA*	*C×MA*	*S×C×MA*
Propagule bank-based expression (moisture-loving)	0.498	**<0.001**	**0.021**	0.964	0.357	0.720	**0.047**
Propagule bank-based expression (forest)	0.420	0.947	0.269	**0.001**	0.909	0.422	0.640
Propagule bank-based expression (disturbance)	0.825	**<0.001**	0.634	**0.028**	0.688	0.272	0.203
Hill-based expression (moisture-loving)	0.277	0.119	**0.001**	0.193	0.610	0.526	**0.016**
Hill-based expression (forest)	0.175	0.080	0.462	0.319	0.998	0.343	0.946
Hill-based expression (disturbance)	0.054	**0.006**	0.194	0.375	0.549	**0.009**	0.163
(B)							
Community composition	**0.001**	0.082	0.508	0.387	0.742	0.998	0.762

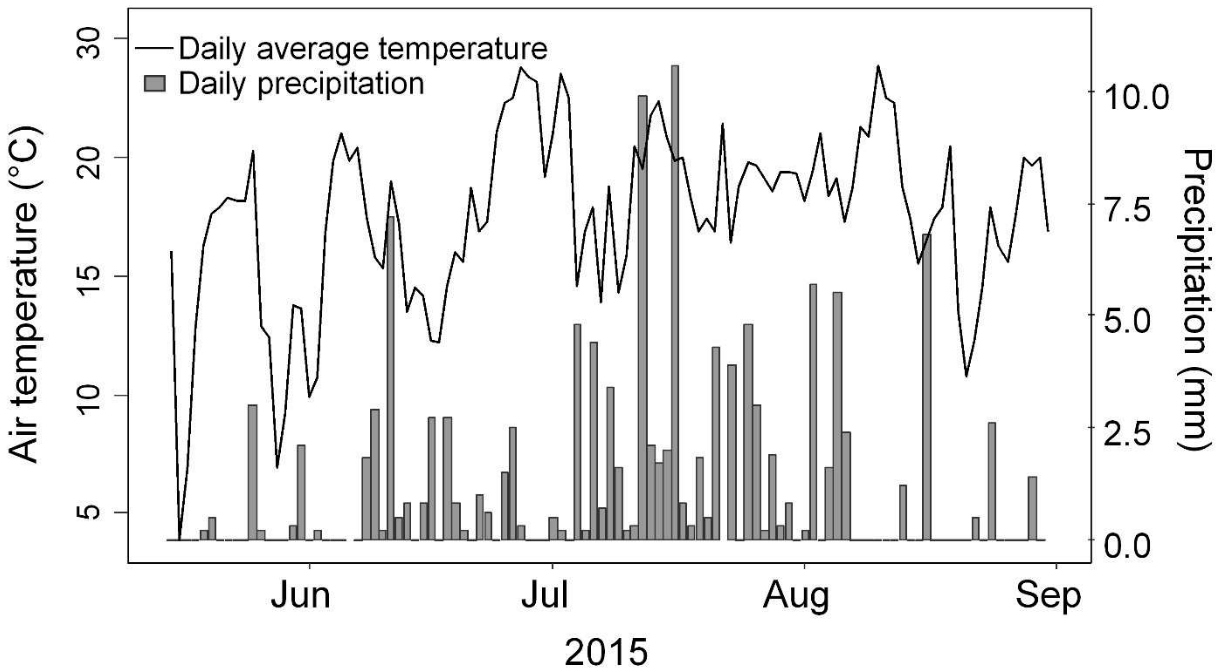


Figure A1. Daily average air temperature and daily precipitation during the 2015 growing season (May 15, 2015 to August 31, 2015, Environment Canada 2015).

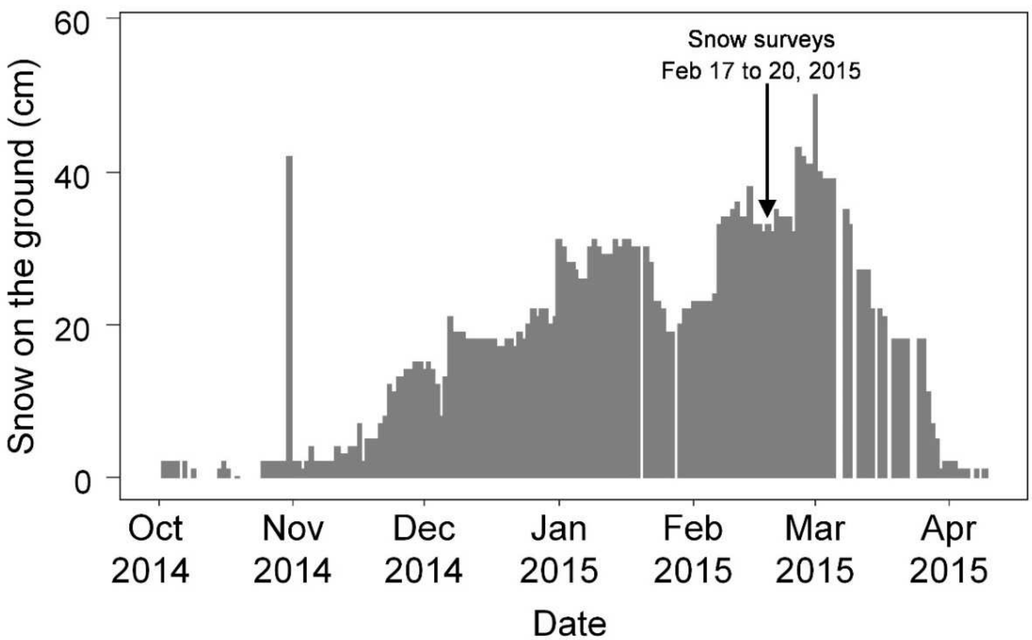


Figure A2. Snow accumulation during 2014/2015 winter period indicating the timing of snow surveys (Environment Canada 2015).

Figure A3. A control treatment plot in the foreground with the hilled treatment plot in the background at the end of the first growing season in August 2015.

Figure A4. Overview of the treatment plots on the south-facing slope in early spring 2015 before the first growing season following treatment construction. Photo credit: Rob Vassov.

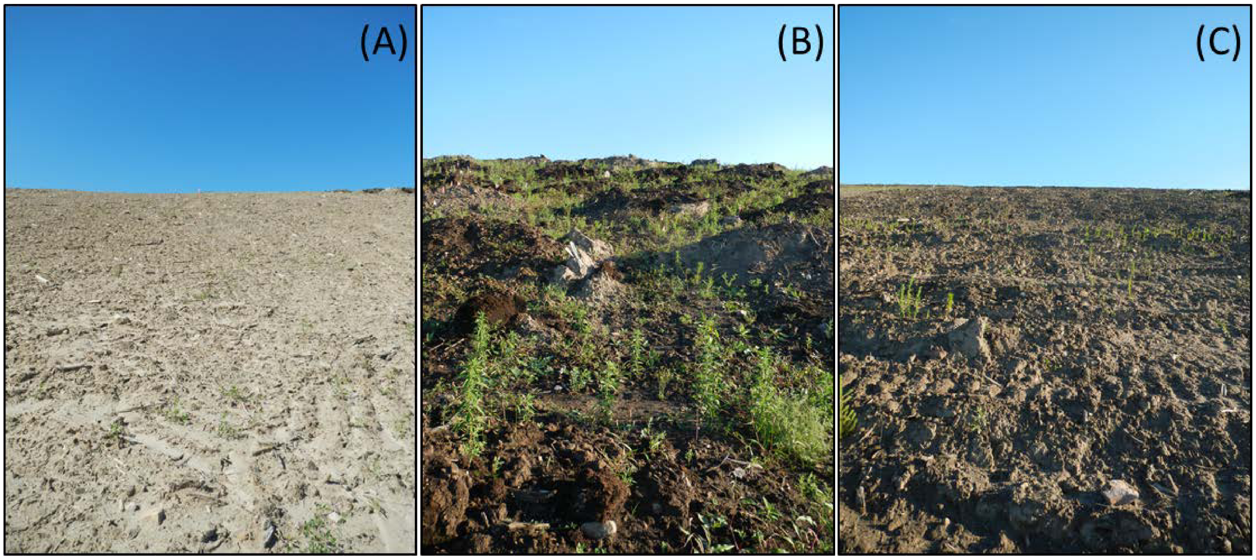


Figure A5. Control (A), hilled (B) and ridged (C) treatment plots at the end of the first growing season in August 2015.

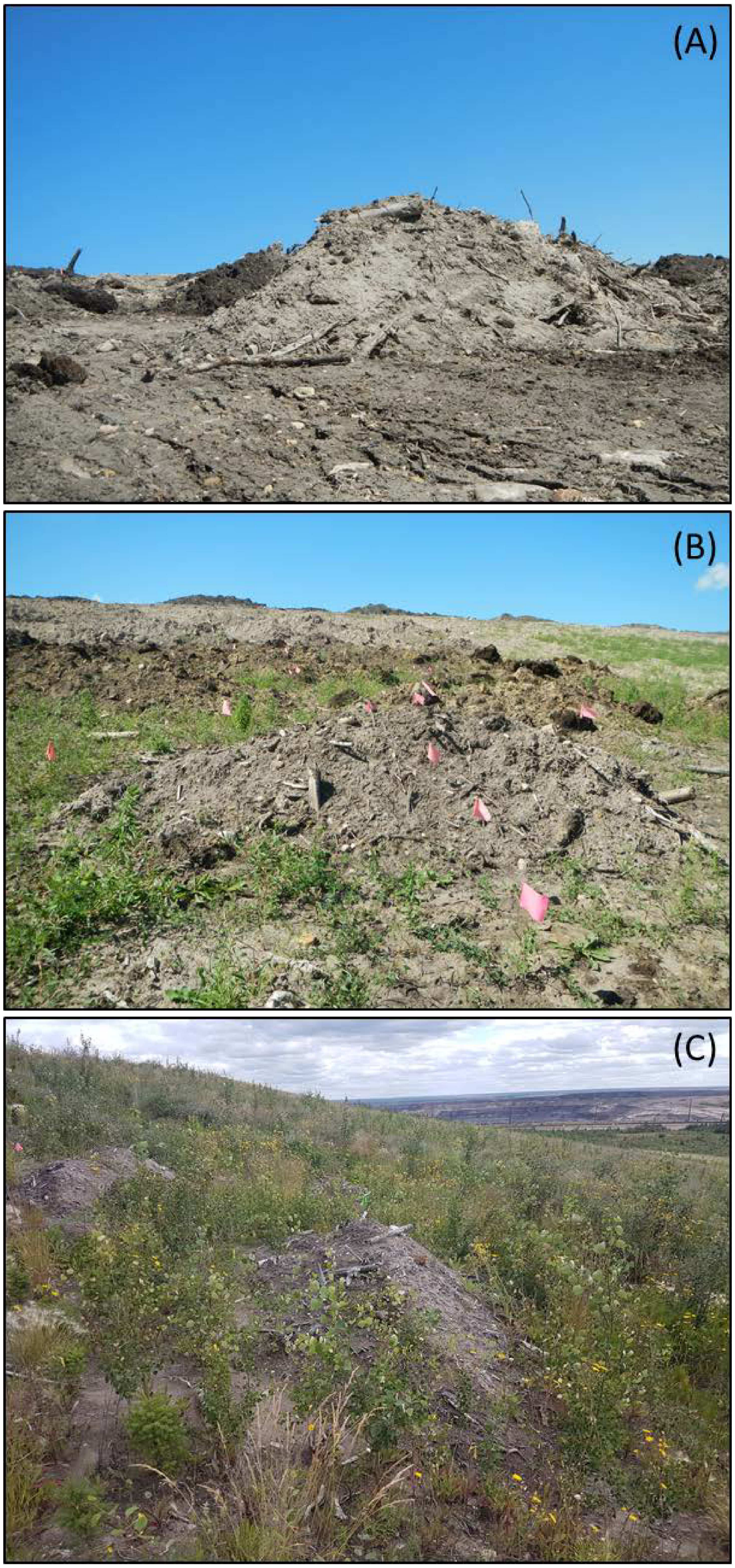

(A)
(B)
(C)

Figure A6. A hill in the hilled treatment before the first growing season in March 2015 (A), at the end of the first growing season in August 2015 (B), and at the end of the third growing season in August 2017 (C).