

University of Alberta

Natural Recovery of Upland Boreal Forest Vegetation on a Hummocky Peat-Mineral Mix Substrate in the Athabasca Oil Sands Region, Alberta

by

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ABSTRACT

This research investigated the natural recovery of upland boreal forest vegetation on a peat-mineral mix substrate in the Athabasca Oil Sands Region, Alberta.

Three sites, aged 26 to 34 years, were assessed to determine effects of substrate (pH, electrical conductivity, texture), topography, slope, aspect, hummock size, litter depth, tall shrub and tree stem densities, canopy cover, and tree ages on community composition and cover of upland boreal vegetation.

Environmental variables that had the most influence on the plant communities were substrate texture (clay), tree canopy cover, and tall shrub stem density. The plant communities, which likely developed from early successional lowland communities, most closely approximate an upland boreal mixedwood forest in transition from an early to mid successional stage. Community development was concluded to be a product of measured environmental variables, with unmeasured factors such as propagule dispersal, germination conditions, and initial species composition also playing important roles.

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I. INTRODUCTION

1. Background

Vegetation has been defined as a system of largely spontaneously growing plants (van der Maarel 2005). By this definition, a field planted with a crop is not vegetation; however, the non seeded plants surrounding the crop are vegetation. Vegetation ecology, also called synecology, is the study of plant cover and its relationship with the environment. It is a complex undertaking to study vegetation ecology because of the temporal and spatial variation of plants and the intricate interactions with the abiotic and biotic factors of their environment (van der Maarel 2005).

Vegetation in the boreal forest has been subjected to considerable stress due to a marked increase in oil extraction activities. Over the last 40 years, the mixedwood forest in the Athabasca Oil Sands Region (AOSR), which is located in northeastern Alberta, Canada, has been subjected to intense and extensive development, and will continue to be for the foreseeable future. This development has centered around open pit mining of oil sands where surface minable oil sands located 0 to 50 m below the soil surface (Mossop 1980), are accessed by removing overlying vegetation and soil, thereby creating large scale disturbances including large pits, overburden piles, tailings dykes, and by-products such as sulphur blocks and fine tailings. Alberta Environment and the Alberta Energy and Utilities Board regulate these disturbances and require that they be reclaimed to diverse, self sustaining boreal forest with equivalent land capability similar to that of the surrounding region (Alberta Environmental Protection 1998, Oil Sands Vegetation Reclamation Committee 1998).

Challenges associated with reclamation in the AOSR include growing season constraints, limited supply of native seed, competition from non-native species, loss of soil and organic matter, slow growth and accumulation of peat, slow soil development, altered water tables, and decreased viability of the soil seed bank. Plant species for revegetation must be adapted to the local climate and soils, which can be saline or sodic and water limiting. In the short term, revegetation is required to prevent erosion and reduce invasion by undesirable species. In the

long term, it must provide for efficient soil nutrient and water cycling, establishment of a diversity of early, mid, and late successional native plant species, addition of organic matter, and wildlife habitat.

To date, reclamation efforts in the AOSR have centered on the addition of top soil or salvaged pre-disturbance soil to create a suitable plant growth medium and to provide a source of native plant propagules that can facilitate natural recovery of vegetation in the disturbed areas. Peat and LFH have been used as substrate amendments and caps, with LFH being more successful in the short term because of its greater quantity and diversity of propagules and greater amount of woody material (Mackenzie and Naeth 2009). However, quantities of LFH available for use in reclamation are limited. A peat mineral mix is more readily available, and its larger quantities mean it can cover a larger area, thus facilitating reclamation and revegetation to a greater extent. However, peat is also in short supply for long term reclamation of large AOSR areas.

Oil sands reclamation studies have investigated effects of the depth of peat and mineral soil treatments on the growth of *Elymus trachycaulus* (Link) Gould ex Shinnars (slender wheatgrass) and *Pinus banksiana* Lamb. (jack pine) (Danielson et al. 1983); reclamation of saline composite tailings using peat and *Hordeum vulgare* L. (common barley) (Renault et al. 2003); using forest floor material as a reclamation amendment (McMillan 2005, Mackenzie and Naeth 2009); factors that affect reclamation success of a tailings storage facility (Burgers 2005); soil water and nutrient regimes in reclaimed upland slopes (Leatherdale 2008); species richness on reclamation treatments with different decay classes of peat (Hemstock 2008); quality of organic matter in different reclamation practices compared to undisturbed conditions (Turcotte et al. 2009); and plant diversity and functioning of ecosystem processes across several different reclamation treatments (Rowland et al. 2009). However, no research has explicitly investigated the potential for natural recovery of upland boreal forest vegetation on a salvage peat-mineral mix substrate.

Natural recovery may facilitate revegetation and reclamation of the oil sands, and may address some of the challenges in reclaiming large expanses of disturbed land. Natural recovery relies on the residual soil propagule bank and/or seed dispersal from adjacent areas to revegetate disturbed sites. Native propagules

reduce resources needed to reclaim, and may be better adapted to local site conditions than introduced propagules, thereby increasing germination and establishment. Natural recovery enhances plant species diversity by providing local propagules for species that are not commercially available or are only available at great cost. Local seed that is readily wind dispersed onto disturbed sites is often of early successional species that facilitate establishment of later successional species. However, little is known about how naturally recovered plant communities will develop or the timeline required to successfully reclaim an oil sands mined site using natural recovery.

This research is a product of the unintentional natural recovery of mixedwood boreal forest vegetation on three peat mineral mix stockpiles, and the vision and drive of the people who recognized the potential of these sites to contribute to the natural recovery knowledge base. It is an investigation into the possibility of long term success of natural recovery of mixedwood boreal forest vegetation on a peat mineral mix substrate. Results from this research will have direct applications to reclamation in the AOSR and will contribute to the complex science of the study of vegetation ecology.

2. The Canadian Boreal Forest Ecosystem

2.1 Extent and geography

The boreal forest is a circumpolar ecosystem covering approximately 11% of the earth's land surface and 8% of forested areas (Bonan and Shugart 1989, Alberta Environmental Protection 1998). In Canada, the boreal forest is the largest ecosystem, covering approximately 58% of the land base (Natural Resources Canada 2004, Anielski and Wilson 2005) (Figure 1.1). It occurs in a northwesterly direction from the Atlantic coast to northern British Columbia and the Yukon, in some places approximately 2,000 km wide. The boreal forest northern limit is defined by a transition to tundra, sometimes called the continental arctic tree line which coincides with the frontal zone between arctic and southern air masses (Larsen 1980). The southern limit of the boreal forest is generally characterized by a transitional zone, called the aspen parkland, which is a gradation from coniferous boreal forest, to deciduous forest, to grassland (Larsen 1980).

Land contours are rolling to mountainous, with large expanses of flat black spruce muskeg. Rivers, lakes, wetlands, and other small water bodies abound (Lawrence 1988). These water bodies and wetlands provide atmospheric and climate stabilization through carbon storage and sequestration and by absorbing high volumes of water during floods and slowly releasing it to the atmosphere (Anielski and Wilson 2005).

2.2 Climate

In Canada, the boreal forest climate is characterized by strong seasonal variation with short, moderately warm summers and long, extremely cold and dry winters. Long term climate averages coincide with boreal forest northern and southern boundaries (Bonan and Shugart 1989). The Köppen Climate Classification System, devised by Vladimir Köppen in 1918, uses air temperature and precipitation data to classify world climates (Strahler and Strahler 1989), where climate boundaries coincide approximately with major vegetation boundaries. According to this classification, the boreal forest climate is cold and snowy with a cool, short summer. The average temperature of the coldest month is $< -10^{\circ}\text{C}$, and that of the warmest month is $> 10^{\circ}\text{C}$. Fewer than four months of the year have mean temperatures $> 10^{\circ}\text{C}$. There is no dry season and the winter is cold and moist (Strahler and Strahler 1989). Average annual precipitation is 455.5 mm, of which 342.2 mm is rainfall and 155.8 mm is snowfall (Environment Canada 2009).

2.3 Soils

The type of soil that develops in any given region of the boreal forest depends on type of parent material underlying the soil (acidic or calcareous), the vegetation that grows in the area (coniferous or deciduous), water drainage, and natural disturbances such as fire, flooding, and insect outbreaks. Six orders of soil are found in the boreal forest: Podzols, Luvisols, Brunisols, Regosols, Gleysols, and Organics, the most common being Podzols. While each soil order does not possess characteristics unique to the boreal forest region, the characteristics that are most representative of these northern soils are a thick organic layer on the surface of the soil, and development of Ae and Bf horizons (Larsen 1980).

2.4 Vegetation

Vegetation of the western Canadian boreal forest can loosely be classified into two associations, upland and lowland. Within these associations, much variation exists, based on topography, climate, and soil characteristics (Larsen 1980). The following is a general description of species found in each association.

Tree species in the upland vegetation association include *Picea glauca* (Moench) Voss (white spruce), *Populus tremuloides* Michx. (trembling aspen), *Populus balsamifera* L. (balsam poplar), and *Betula papyrifera* Marsh. (paper birch). *Abies balsamea* (L.) Mill. (balsam fir), *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir), *Pinus contorta* Douglas ex Loudon (lodgepole pine), and *Pinus banksiana* Lamb. (jack pine) are less common, being found in areas with specific topographic or soil characteristics (Rowe 1972). Understory species include *Viburnum edule* (Michx.) Raf. (low bush cranberry), *Rosa* spp. L. (rose), *Ribes* spp. L. (currant and gooseberry), *Prunus* spp. L. (cherry), *Mertensia paniculata* (Aiton) G. Don (tall bluebells), *Fragaria* spp. L. (strawberry), *Pyrola* spp. L. (wintergreen), *Chamerion angustifolium* (L.) Scop. (fireweed), *Calamagrostis canadensis* (Michx.) P. Beauv. (marsh reedgrass), *Cornus canadensis* L. (bunchberry), *Mitella nuda* L. (bishop's cap), *Viola* spp. L. (violet), and *Linnaea borealis* L. (twinline). Non-vascular species include *Hylocomium splendens* (Hedw.) Schimp., *Ptilium crista-castrensis* (Hedw.) De Not., *Pleurozium schreberi* (Brid.) Mitt., *Pylaisiella polyantha* (Hedw.) Grout, *Dicranum* spp. Hedw., *Aulacomnium palustre* (Hedw.) Schwägr., *Orthotrichum* spp. Hedw., *Polytrichum juniperinum* Hedw., *Drepanocladus* spp. (Müll. Hal.) G. Roth, *Brachythecium* spp. Schimp., *Mnium* spp. Hedw., and *Thuidium recognitum* (Hedw.) Lindb. (Larsen 1980).

Tree species found in the lowland vegetation association include *Picea mariana* (Mill.) Britton, Sterns and Poggend. (black spruce) and *Larix laricina* (Du Roi) K. Koch (tamarack). Understory species include *Ledum groenlandicum* Oeder (Labrador tea), *Salix* spp. L. (willow), *Betula* spp. L. (birch), *Vaccinium uliginosum* L. (bog blueberry), *Vaccinium vitis-idaea* L. (lingonberry), *Vaccinium oxycoccus* L. (small bog cranberry), *Rubus chamaemorus* L. (cloudberry), *Hedysarum* spp. L. (sweetvetch), *Listera borealis* Morong (northern twayblade), *Habenaria* spp. Willd. (orchid), *Parnassia palustris* L. (grass of Parnassus), *Geocaulon lividum* (Richardson) Fernald (false toadflax), *Moneses uniflora* (L.) A. Gray (one-

flowered wintergreen), *Pyrola* spp. (wintergreen), *Linnaea borealis*, *Equisetum* spp. L. (horsetail), *Eriophorum* spp. L. (cottongrass), and *Carex* spp. L. (sedge). Non-vascular species include *Sphagnum* spp. L. (peat moss), *Hylocomium splendens*, *Pleurozium schreberi*, *Aulacomnium palustre*, *Tomenthypnum nitens* (Hedw.) Loeske, and *Drepanocladus* spp. (Larsen 1980).

2.5 Disturbance ecology

Spatial and temporal heterogeneity are important in understanding ecosystem processes. Disturbance has been recognized as an important generator of heterogeneity within an ecosystem (Johnson and Gutsell 1994), whether naturally or anthropogenically induced.

Fire is the dominant natural disturbance in the boreal forest (Weber and Flannigan 1997, Bridge et al. 2005). The Canadian boreal region averages 5,000 reported ignitions per year and is characterized by high intensity, high rate of spread, crown fires (Gutsell 1995). Despite the large number of annual fires, only approximately 3% burn an area over 200 ha. However, large fires account for almost all large scale impacts in the boreal forest and are responsible for more than 97% of the area burned (Burton et al. 2008), with crown fires accounting for most of the area burned (Bergeron et al. 2004). In Canada, stand replacing crown fires burn approximately 2 million ha (0.5% of forest area) each year and typical fire cycles are 75 to 150 years depending on the local fire regime (de Groot et al. 2003).

Localized fire regimes vary widely and have changed in the last 200 years due to human activities on the landscape. Land clearing and burning for agricultural fields changed the fire cycle in localized areas during the early 1900s when colonization began (Bergeron et al. 2004). Climate change is expected to increase fire intensity, fire severity (depth of burn), and fire season length in the Canadian boreal forest region. This predicted fire regime change is expected to affect the annual area burned (Weber and Flannigan 1997, de Groot et al. 2003).

Weather, fuels, and landform patterns influence fire regime variability and its impacts. This combination of factors has generated the diversity of ecosystem composition, structure, productivity, and habitat characteristic of the boreal

(Burton et al. 2008), which then provides varied habitat for fauna and has influenced human use of the forest (Murphy 1995).

In North American boreal forests, tree species have adapted to recurrent fire by storing seed in the canopy, re-sprouting from roots, producing large quantities of wind dispersed seed (i.e. shade-intolerant pioneer species), or regular seed release to establish seedlings in the understory of post-fire stands (i.e. shade tolerant, late successional species). Thick, fire resistant bark is a rare survival strategy to protect the parent trees (de Groot et al. 2003).

Insect disturbances are widespread in the Canadian boreal forest (Bergeron et al. 2004). Spruce budworm, *Choristoneura fumiferana* (Clemens) causes the greatest disturbance to coniferous trees in the eastern boreal forest (Johnson et al. 2003). Unlike a fire disturbance, which does not appear to be age dependent (Johnson 1992), a spruce budworm outbreak has been related to stand age (MacLean 1980).

Other disturbances that have significant impacts at a local or regional scale in some boreal forests include herbivory, disease, wind throw, flooding, landslides, avalanches, and climate change. Disturbances directly or indirectly associated with humans also play a large role in forest dynamics (e.g. timber harvesting) (Weber and Flannigan 1997, Engelmark 1999).

3. Vegetation Dispersal

3.1 Vascular

Vascular plants are divided into three large groups: seedless vascular plants (e.g. ferns, horsetails), gymnosperms (e.g. cycads, ginkgo, conifers), and angiosperms (e.g. flowering plants such as apples, roses, grasses). Seedless vascular plants lack seeds, but have vascular tissue, xylem, and phloem. These plants reproduce through spores, and require water during the fertilization period of their reproductive cycle. Gymnosperms (from Greek, meaning naked seed) produce seeds that lack a protective enveloping structure such as a fruit and do not require water during any part of their reproductive cycle. Angiosperms (from Greek, meaning seed in a vessel), the plants that most influence human life,

reproduce through seeds, but differ from gymnosperms in that they produce a flower (Raven et al. 1999).

Two main types of vascular plant dispersal are vegetative expansion and seed and spore dispersal. Dispersal, disturbance size, and predisturbance species composition determine regeneration composition, density, and patchiness of regenerating communities (Greene et al. 1999). In both vegetative expansion and seed and spore dispersal, a range of dispersal methods are responsible for local (e.g. vegetative growth, seeds settling close to the parent plant under conditions of light wind) and long distance (e.g. fragmentation and transport of the parent plant during a flood, seed transport by strong winds and vertebrates) dispersal (Clark et al. 1999).

Plant species distribution across the landscape is strongly affected by vegetative reproduction pattern and fate of individuals produced by vegetative reproduction. There are several types of vegetative expansion, including rhizomes, stolons, buds, tillering, suckering, layering, and fragmentation (Luken 1990). Some plant species depend on vegetative expansion as a means of reproduction. Three species in the North American boreal forest (*Populus tremuloides*, *Populus balsamifera*, and *Betula papyrifera*) have the capacity to sprout from buds near the root collar. The two *Populus* species can also reproduce from roots, known as suckering. This ability to regenerate in situ in large disturbances gives a great advantage to these species (Greene et al. 1999). For example, *Populus tremuloides* has been noted to expand through the extension of root suckers up to 21 m from the nearest bole. The average distance that root suckers are found from the parent plant is 5 m (Greene et al. 1999).

Darwin (1859) argued that adaptations for seed dispersal and accidental means of long distance transport are of importance to plants. Cain et al. (2000) argued that long distance (> 100 m) seed dispersal is of critical importance as it influences many aspects of plant biology, including colonization, population dynamics, evolution of populations, metapopulation dynamics, biological invasions and dynamics, and diversity of ecological communities. Because the landscape is inherently patchy, many plant populations are separated by hundreds of meters or more. For such species, seed dispersal is the only way for populations to colonize empty but suitable habitat. Dispersal can occur through

wind, water, fauna, and self dispersal (Howe and Smallwood 1982, Luken 1990, Schupp 1993). Since most seeds move short distances (zero to several tens of meters), unusual events that move seeds long distances are of critical importance (Cain et al. 2000). Clark et al. (1999) reported that seed dispersal up to 10 km is possible for many species during severe storms and when transported by frugivorous birds and bats, and large vertebrates, such as bears and foxes. Schupp (1993) discussed the importance of the effectiveness of vertebrate seed dispersers to the success of future plant reproduction.

3.2 Non-vascular

Bryophytes are the only haploid land plants. They are currently classified as a polyphyletic group, composed of mosses (Bryophyta), liverworts (Marchantiophyta), and hornworts (Anthocerotophyta). Although each group is different in structure, they correspond in life cycles and are all spore producing plants that require water during their reproductive cycle (Frahm 2008). They differ from vascular plants in that they lack xylem and phloem (Raven et al. 1999). Bryophytes disperse a single cell with a haploid genome (a spore), usually in masses. Spores are produced in sporangia, ranging in size from 7 to 200 μm . They are released in quantities between several hundred thousand to several million, and can be lifted into the atmosphere by warm air and distributed by global air currents (Frahm 2008).

Locally, the dominant method of dispersal for bryophytes is through gametophyte fragments (McDaniel and Miller 2000) or specialized asexual reproductive structures such as gemmae (Kimmerer 1994). However, most long distance dispersal occurs through spores (Miles and Longton 1992), which are ejected from the capsule by specialized structures when the sporophyte reaches maturity and appropriate environmental conditions are present (Schofield 2001). Consistent with studies indicating spores are capable of traveling long distances, van Zanten (1978) found a strong positive correlation between spore longevity and size of distributional area. Frahm (2008) reported that spores can keep their viability for more than 100 years. Genetic analysis of the ubiquitous moss *Ceratodon purpureus* (Hedw.) Brid. suggests ongoing intercontinental dispersal (Miller and McDaniel 2004). Muñoz et al. (2004) and Frahm (2008) both

concluded that direction dependent long distance wind dispersal is responsible for intercontinental transport of bryophyte spores in the southern hemisphere.

Miller and McDaniel (2004) sampled mortar walls containing calcium carbonate along a highway in the Adirondack Mountains of New York and found the walls contained nearly twice as many species as native acidic bedrock sites. The closest location of bedrock containing calcium carbonate to the sample locations was approximately 5 km distant. This, in combination with the differences between the native flora and that was found on the mortar walls indicated that the calcicoles in the highway samples emigrated from distant locations.

In a study of land reclaimed from the sea in the Netherlands, Bremer and Ott (1990) concluded some bryophyte species established from sources 10 to over 100 km distant. Van Zanten (1978) showed that species with broad distributions often have spores that are tolerant of long storage and temperature extremes, both of which are advantageous adaptations when traveling long distances in unknown environmental conditions. For species with specific habitat requirements and suitable sites separated by long distances, selection may favour individuals with highly dispersible spores (Miller and McDaniel 2004).

Parsons et al. (2008) found bryophyte spores can be dispersed by *Pteropus conspicillatus* (spectacled flying fox) in the Wet Tropics bioregion, northeastern Australia. They analyzed flying fox feces and discovered bryophyte fragments that were viable when grown in culture. Parsons et al. (2008) reported bryophyte dispersal via an animal gut (endozoochory); studies also referred to bryophyte dispersal by adhering to animals (epizoochory) (Kimmerer 1994), and dispersal of spores by flies (entomophily) (Goffinet and Shaw 2004).

4. Soil Seed Bank

Soil seed banks are herein defined as all viable propagules (seeds and vegetative structures) on and under the soil surface. A. Peter first drew attention to the soil seed bank in 1893 (Granström 1982), stating that the existence of a viable, buried seed bank in forest soils was common knowledge among foresters in Germany at that time. Since then, there have been many studies relating to seed banks, highlighting the importance of this part of the forest ecosystem.

Seed banks are considered a storage mechanism of genetic variation. A larger genetic variation in the seed bank than in the present community may have consequences for the persistence of communities. Genetic variability could facilitate evolutionary change in response to the environment, or conversely it could act as a genetic load if it is adapted to past environmental conditions (Grandin 1998).

Soil seed banks play an important role in community dynamics (Hills and Morris 1992) as they are instrumental in regeneration of new populations (Leck et al. 1989). The characteristics, longevity, and number of seeds in the soil are determined by seed inputs and outputs. Inputs include seed rain, which is a function of plant density and per capita seed release. Outputs include losses to parasitism, predation, physical destruction, decay, dormancy, and germination (Luken 1990, Mackenzie 2004). Seed bank dynamics are dependent on seed dispersal, sources, predation, decay, soil type, and soil conditions (Hills and Morris 1992).

An early successional seed bank is hypothesized to be larger than a later successional seed bank (Donelan and Thompson 1980, Grandin 1998) because early successional species produce more seeds than late successional species, and seeds of early successional species tend to be longer lived than those of late successional species. Thus, seed bank size and longevity should decrease with successional change and time as species replacement occurs and seeds of early successional species are lost from the seed bank.

Seed numbers rapidly decrease with soil depth. Few seeds are found below 15 cm; those beyond this depth are not likely viable (Luken 1990). Most viable seed occurs in the top 5 cm of soil, with the remainder in the top 5 to 10 cm of mineral soil (Mackenzie 2004). Several studies (Moore and Wein 1977, Granström 1986, Hills and Morris 1992) found seed viability decreased with increasing soil depth. Moore and Wein (1977) found most seedlings emerged from the top 0 to 2 cm of organic matter and the upper layers of mineral soil in all of their study sites.

4.1 Vascular seed bank

Dormancy is the condition when viable seed fails to germinate, even under

optimal conditions (Leck et al. 1989, Luken 1990). Dormancy may be present when the seed leaves the parent plant or it can be created by lack of resources; it may depend on fluctuations in light, temperature, water, soil, burial depth, and other environmental conditions (Mackenzie 2004). Some seeds require a period of cold stratification; therefore, germination does not occur in the same season the seed was produced. Some seeds have hard seed coats that must be broken or removed before germination can occur (Luken 1990). Dormancy is important as it determines whether a seed will be an input or an output (Mackenzie 2004).

Germination is the continuation of growth by the embryonic plant in the dormant seed (Hills and Morris 1992). It requires resources and stimuli to break seed dormancy (Luken 1990). These conditions can be found on the soil surface and in the soil. An inverse relationship exists between germination and depth of seed in the soil (Baskin and Baskin 2001). Disturbances to the soil such as tillage, excavation, tree throw, and soil fauna activity can bring seeds to the surface exposing them to favourable conditions that promote germination, or seeds can be buried deeper in the soil, where they remain dormant for long periods, or will not germinate at all due to unfavourable conditions (Baskin and Baskin 2001).

Natural regeneration in forests can occur without the assistance of the seed bank by vegetative propagules capable of reproducing asexually through axillary and adventitious buds under variable conditions (Mackenzie 2004). Parts of plants capable of asexual reproduction include rhizomes, stolons, stems, branches, bulbs, tubers, and root suckers (Luken 1990). Clonal propagation is an important means of population increase. The production of vegetative propagules is often limited by the patchy availability of light in forests and the physiological ability of the plant to produce tissues required for vegetative reproduction (Wijesinghe and Wigham 1997). Vegetative propagules are influenced by their proximity to the regenerating population, their size, health, and abundance.

4.2 Non-vascular diaspore bank

The occurrence of bryophyte propagules in boreal forest soils has been mentioned in studies of forest seed banks (Granström 1982, 1986). These studies suggested that the bryophyte diaspore bank functions similarly to the vascular seed bank, promoting plant colonisation. Jonsson (1993) confirmed this,

stating that the bryophyte diaspore bank allows species to survive unfavourable periods; facilitates rapid colonisation after disturbance; and influences post-disturbance species composition and diversity.

Jonsson (1993) collected soil from a boreal forest in Sweden immediately after the soil had been experimentally disturbed; 31 bryophyte taxa germinated from the samples. He found that dominant life strategies in the diaspore bank were colonist and short lived shuttle species, compared to perennial species that dominated the undisturbed forest floor; and that species reproduced through spores, gemmae, and fragments, indicating the importance of each of these methods of reproduction.

The diaspore bank is of great importance for the colonisation of bryophytes after soil disturbance in boreal forests; it is an important factor responsible for the high bryophyte diversity observed in naturally disturbed patches in boreal forests (Jonsson 1993). Early successional species dominance in the diaspore bank demonstrated by Jonsson (1993) corresponds well with patterns observed in vascular seed banks (Moore 1980, Henderson et al. 1988, Lavorel et al. 1991).

Several studies have indicated the ability of bryophyte spores and gemmae to survive in the soil over long periods of time (Bristol 1916, During and ter Horst 1983, Whitehouse 1984). For example, spores of the moss *Physcomitrium sphaericum* (Ludw.) Fuernr. may persist in lake shore mud until optimum conditions (extreme drought), which occur at 30 to 40 year intervals, permit germination and reproduction (Furness and Hall 1981).

5. Plant Community Development

Plant community development is often referred to as succession. However, succession research and discussion tends to focus on plant community changes in structure, function, and composition, neglecting the inherent changes in a soil system that accompanies plant community development. Thus a brief review of soil-plant interrelationships is necessary to preface the discussion of succession.

5.1 Soil-plant relationships

The interface between soil and air forms the biosphere, which supports life on

earth (Larsen 1980). Soil is composed of minerals, bacteria, organic matter, air, and water (Clark et al. 2006). Soil formation is influenced by climate, organisms, relief, parent material, and time (Strzemeski 1975). Plants interact with soil above and below ground, with the majority of interactions occurring below ground. Root system dynamics are important in maintaining biological and chemical equilibria in the soil. Roots of higher plants are a vital functional component of below ground systems as they are one of the main soil forming agents and interact with nearly all soil components (Cheng and Kuzyakov 2005). Although plant roots are not solely responsible in determining soil activities, they are the main factor (Zobel 2005). Soil-plant interactions occur on macro, meso, and micro scales.

At the macro scale, plants contribute to development of an organic horizon on the soil surface through litter deposition. As litter builds up on the soil surface, organic materials underneath are decomposed, and eventually become soil. Plants on slopes or other unstable areas can reinforce and cover soil, thus reducing or preventing erosion, especially during high intensity precipitation events. Plant roots are strong in tension but weak in compression; soil is weak in tension but strong in compression; together they create complementary strength. Root permeated soil can be considered a composite material similar to reinforced concrete; like re-bar, roots transmit stresses beyond the immediate shear zone, providing strength to the soil. Older, dense root systems produce larger increases in soil strength than younger, finer root systems (Collison et al. 2005).

Soil can affect above and below ground plant growth. Root biomass can be altered by soil nutrients, temperature, and water. In nutrient poor soils, plants require more root surface area or depth. Friable soil is amenable to the development of smooth, cylindrical roots, and compacted soil can lead to gnarled, stubby roots that can limit access to water and nutrients. Compaction may be ameliorated by decreased bulk density and increased porosity below the compacted zone (Tresder et al. 2005). Soil that is too porous may inhibit roots from making contact with the solid and liquid phases of soil to extract available nutrients or water (Passioura 1991). If roots can access sufficient water and nutrients, adverse soil conditions can cause the plant to send inhibitory signals to the leaves.

At the meso scale, soil-plant interrelationships are mainly rhizospheric

processes, those directly influenced by roots and occurring in the vicinity of the root surface. Among the benefits of rhizosphere processes are enhanced nutrient acquisition, conditioning of soil pathways for root growth, and improvement to soil structure and chemical environment (Cheng and Kuzyakov 2005).

Roots contribute substantially to ecosystem carbon budgets, providing carbon compounds to the soil through epidermal sloughing and death. Roots affect decomposition of soil organic matter (Tresder et al. 2005). Depending on substrate conditions and species, root effects on rate of decomposition can range from negative 70% to as high as 330% above an unplanted control (Cheng and Kuzyakov 2005). Anthropogenic disturbances such as elevated carbon dioxide and land use change can modify carbon cycling in soils by altering root contributions to below ground carbon pools (Tresder et al. 2005).

Roots remain mixed in soil throughout decomposition and are important in soil aggregation. Roots influence clay platelet orientation, stabilize structural units $\geq 2 \mu\text{m}$ in diameter, and contribute to combining aggregates $\geq 200 \mu\text{m}$ in diameter (Goss and Kay 2005). Mucilages released by the root cap and epidermis link particulate organic residues with mineral fragments. Microorganisms in the rhizosphere use plant mucilage as a substrate, then secrete their own mucilage, which combines with plant mucilage and stabilizes finer aggregates. Water extraction is important in formation and stabilization of aggregates. It helps to draw particles together so additional bonding can occur between aggregates, and reduces the destabilizing effects of abiotic stresses such as the freeze-thaw process (Goss and Kay 2005). Soil aggregate size affects plant growth, which in turn affects litter production and further soil nutrient cycling. Donald et al. (1987) and Misra et al. (1988) found that maize, cotton, and corn grow better in pots with small aggregates (1 to 16 mm) than pots with larger aggregates. They concluded that a non-nutritional signal from the roots affected the growth of the shoots.

Micro scale interactions are important in the soil-plant continuum. Roots of approximately 80% of land plants are colonized by arbuscular mycorrhizal (AM) fungi. These fungi function as extensions of the roots and influence plant growth and soil quality, including soil structural development and maintenance. A major function of AM fungi is to transport nutrients from the soil to the roots. AM fungi can extend hyphae up to several centimeters away from the root into the soil,

thereby accessing a much greater volume of soil than the roots alone (Wright 2005). Tisdall (1991) presented evidence that AM fungal hyphae contribute to binding micro aggregates (0.02 to 0.25 mm) into macro aggregates (> 0.25 mm) through polysaccharides produced by the fungi. Hyphae may work in conjunction with roots to create physical and chemical conditions that bind soil particles through physical entanglement (Wright 2005). Glomalin is a hydrophobic compound that is insoluble in its natural state (Wright et al. 1996). Apparently produced exclusively by AM fungi, it acts like a glue to bind aggregates together.

5.2 Succession

All plant communities change as they age, through plant species replacements, shifts in population structure, and changes in availability of resources such as light and nutrients (Luken 1990). This process of change is called succession: the sequence of one thing following another in time (Korner 2005). Succession is an open system where plant species can move into the community from surrounding areas (Connell 1979); it is the change in composition or structure of a community, sometimes following a disturbance. Successional stage of a community is a typical combination of traits expressed by the plant community (Grandin 1998) and is defined by the species present in it.

Primary succession occurs when vegetation development begins on a newly formed bare substrate with low fertility and no vegetation or reproductive propagules present to begin colonization (Glen-Lewin and van der Maarel 1992). Secondary succession occurs when vegetation is replaced following a disturbance that disrupts or eradicates existing vegetation (Higginbotham 1981, Glen-Lewin and van der Maarel 1992, Bazzaz 1996). In secondary succession, the soil is developed and a seed bank and propagules are present for colonization of the disturbance.

Early successional species are colonizers, capable of growing under marginal conditions. They characteristically produce many small seeds at regular intervals, have low shade tolerance, a short life span, fast rates of growth and photosynthesis, and high water consumption (Korner 2005). They have broader, more overlapping niches than late successional species (Bazzaz 1996), and are classified as r-selected species (MacArthur and Wilson 1967). Early successional

species in the boreal forest include *Salix* spp., *Betula* spp., *Populus* spp. L. (poplar), and *Chamerion angustifolium*.

Late successional species produce few large seeds at erratic intervals, have relatively low photosynthesis and resource acquisition rates (Bazzaz 1996), and are classified as k-selected species (MacArthur and Wilson 1967). Late successional species in the boreal forest include *Abies balsamea*, *Picea* spp. A. Dietr. (spruce), *Vaccinium myrtilloides* Michx. (blueberry), *Vaccinium oxycoccus*, *Habenaria* spp., and *Oryzopsis asperifolia* Michx. (aspen ricegrass).

Mid successional species are often difficult to identify and classify because of the gradual shift in species composition during succession. They are more shade tolerant than early successional species, compete with early successional species through allelopathy, produce many seeds at regular intervals, and have a longer life span. However, they are shorter lived, less shade tolerant, and produce more seeds than late successional species.

Numerous theories of succession have evolved and undergone significant alterations during the last century. Successional theory began with the idea of predictable, unidirectional, community oriented succession that leads to a regional climax (Clements 1916), then changed to individual species based environmentally random succession (Gleason 1926). These two theories described ecosystem disturbance as an uncommon, extrinsic phenomenon to the community, and therefore not integral to succession (Cook 1996). A polyclimax theory of succession was proposed (Tansley 1935, Whittaker 1953), which was in conflict with earlier theories. Some believed succession is best understood at the patch level (Watt 1947). The initial floristics model stated that all species that will be part of successional communities are present early in the sequence of changes (Egler 1954). It emphasized the importance of chance events contributing propagules for colonization, compared to earlier theories that emphasized the importance of plant reaction in the environment and competition between plants (Cook 1996).

Three alternative theories of succession (facilitation, tolerance, inhibition) were proposed (Connell and Slatyer 1977). Facilitation is succession where plant species prepare the way for other species; unlike the Clementsian view, it does

not emphasize a high level of community organization with internal positive feedback mechanisms. Tolerance is succession in which plant species entering the community after the initial colonists are established must be capable of surviving under conditions of low resource availability. The efficiency with which these resources are used will dictate which species dominate the community. Inhibition is succession in which established species prevent invasion and growth of potential competitors during the entire successional process. A paradigm shift from mono climax theory to multi climax theory and multi directional succession pathways occurred in the 1980s and 1990s (Finegan 1984, McCook 1994, Cook 1996). McCune and Cottam (1985) suggested that in some situations, a climax community is unattainable, due to external influences on the community.

5.3 Vascular succession

Boreal forest plant species diversity is relatively low compared to ecosystems such as rainforests. It does, however, have a high diversity of species traits, known as functional diversity (Wirth 2005). This implies a number of functional groups or functional types. Gitay and Noble (1997) reviewed functional types and define a functional group as a “group of species which perform similarly in an ecosystem based on a set of common biological attributes”. Van der Maarel (2005) defined a functional type as “a group of species sharing certain morphological characteristics”. Smith and Huston (1989) and Wilson (1999) believe the concept of functional type to be analogous to the term guild. The diversity of functional groups in the boreal forest has created a mosaic of species and communities throughout the entire ecosystem.

The boreal forest is characteristically a disturbance forest (Rowe 1961). It does not fit the classical climax mold in which the plant community progresses through a definable series of plant associations that terminates with one community type dominated by the same species each time the process is initiated and completed. Climax in the boreal forest is not limited to a typical closed canopy spruce dominated forest, but ranges from open sphagnum dominated peatland to closed canopy forest along topographic and environmental gradients. This pattern is cyclical, and encompasses all phases of regeneration in every community of the climax pattern (Larsen 1980). “The ecosystem as a whole may be in a steady

state even if the individual stands are not" (Sprugel 1976). Differences in boreal species composition from north to south and east to west result in different regional successional patterns (Larsen 1980).

Many processes control variables affecting direction of succession in the boreal forest (Van Cleve and Viereck 1981). The typical successional pathway is dependent upon fire frequency, with frequent fires favouring resprouting, shade intolerant, early successional species. These species include *Populus* spp., *Betula* spp., *Chamerion angustifolium* and others that readily establish in full sunlight (Mackenzie 2004). As these early successional species die, openings in the community are created, releasing resources for the next successional species, which would be shade tolerant. Frequent disturbances in the boreal forest, such as fire and insect outbreaks, keep the community in early to mid successional status (Mackenzie 2004).

In isolated areas where frequency of disturbance is low, communities of later successional species can be found and are referred to as climax communities. A climax community is an assemblage of self replacing species (Connell 1979) that have reached a stable end point in the final stage of succession. Barring any major disturbance, the species composition of this community will not change substantially; early and mid successional species are excluded through competition with late successional species. There are four dominant climax tree species in the boreal forest: *Pinus banksiana* on dry sandy sites; *Picea glauca* on mesic sites; and *Picea mariana* and *Larix laricina* on wet sites.

5.4 Non-vascular succession

Bryophyte communities are much slower than vascular plant communities to establish and change after disturbance. Bryophyte diversity and cover peaks later than that of vascular plants, and increases with time (Hart and Chen 2006). Bryophyte succession is partly driven by species composition in the overstory. Broadleaf stands tend to support vascular communities; conifer stands favour the establishment of bryophytes; and mixedwood stands support an intermediate understory community (Hart and Chen 2006).

Following a fire disturbance, bryophyte species are a small component of the

initial community because of their inability to grow rapidly in response to increased resources and intense competition from vascular plants (Hart and Chen 2006). However, bryophyte cover increases with time after fire (Nygaard and Odegaard 1999). Small canopy gaps due to wind throw increase throughfall precipitation, which promotes the growth of bryophytes (Økland et al. 1999). Frego (1996) found that *Pleurozium schreberi* is effective at occupying small forest floor gaps because of its abundant propagules and relatively rapid growth. Rees and Juday (2002) found a few post-fire specialists following a fire in an upland boreal forest in Alaska. These species were *Ceratodon purpureus*, *Marchantia polymorpha* L., and *Leptobryum pyriforme* (Hedw.) Wilson.

Following forest harvesting, understory diversity increases in response to resource availability and colonisable microsites (Rees and Juday 2002). Bryophyte diversity increases following forest harvesting at a much slower rate than vascular plants and may require five to six years to double (Tellier et al. 1995). Nevertheless, bryophyte cover, particularly by feather mosses, is often much higher following harvesting than after fire (Rees and Juday 2002).

Fenton and Bergeron (2006) studied bryophyte succession in a black spruce forest in northwestern Quebec and found feather mosses were replaced by shade and desiccation tolerant hummock *Sphagnum* species, which were replaced by faster growing, hollow *Sphagnum* species. These changes were related to increased light availability and upward water movement into the forest floor.

Bryophyte community structure and composition on fallen decaying trees are influenced by species, decay stage, bark cover, pH, and wood density and texture (Kushnevskaia et al. 2007). Four stages of succession occurred on decaying spruce trees in a boreal forest in northwestern Russia. The first stage is characterized by dominating epiphytic species. The second stage, characterized by the spread of established species and colonization of new species, had the greatest species richness; the number of generalist, epigeous and epixylic species increasing in relative abundance. In the third stage, epigeous species dominated; relative abundance of epiphytic, epixylic, and generalist species and overall species richness decreased. The fourth stage was characterized by vascular species spread and decreased bryophyte species richness.

6. Natural Recovery

Natural recovery is the natural re-establishment of plants on disturbed land. It relies on revegetation from the soil seed bank or invasion from adjacent lands (Powter 2002). The benefits of natural recovery are many (del Moral and Walker 2007, Li et al. 2009, Rowland et al. 2009). Relative to current reclamation practices, it requires reduced resources to reclaim a disturbed site and enhances diversity by supplying seeds of species that are not commercially available. Native propagules in the seed bank are better adapted to local conditions than species that may be imported from other areas within the province or country. Natural recovery allows the plant community to develop through succession, which may in turn enhance the redevelopment of ecosystem functions and processes. The developing plant community more closely resembles a natural community and is more aesthetically pleasing than a traditionally reclaimed area.

Natural recovery has several disadvantages (Skrindo 2005, del Moral and Walker 2007, Skrindo and Halvorsen 2008). It is a slow process, often taking many decades to return to the pre-disturbance community. A return to pre-disturbance conditions is not guaranteed, however, as many factors can influence the trajectory of community development, including type of disturbance, anthropogenic interference, and invasion of undesirable species from adjacent areas. Sometimes it is necessary to accept the development of a modified community when pre-disturbance conditions are not attainable. Natural recovery can leave disturbed land in a bare and impoverished state for long periods of time, which can alter community development and ecosystem processes.

Under natural conditions, biological processes repair disturbed ecosystems through natural recovery. Disturbance is an integral part of the physical and biological process on earth, and natural recovery facilitates the continued health of the planet. In many cases, however, it is not possible or desirable to wait for natural recovery that may not happen or may produce unwelcome results. The key to meeting the challenges posed by a disturbance is in understanding the intricacies of natural recovery (del Moral and Walker 2007). Large bodies of literature are dedicated to studying recovery of the Canadian and circumpolar boreal forest following fire, harvesting, and insect outbreaks. However, little

research has been dedicated to the natural recovery of boreal forest vegetation following a severe anthropogenic disturbance such as oil sands mining.

Harvey and Brais (2002) found that careful logging operations in the south eastern boreal forest of Quebec resulted in higher disturbance levels in skid trails, which favoured the establishment of *Larix laricina*, *Rubus idaeus* L., and graminoids. Kembell et al. (2006) found that winter logging activities favoured establishment of tall shrubs; greater disturbance to the forest floor caused by fire resulted in lower establishment of shrubs; and low shrub coverage in spruce budworm damaged stands resulted from lower light conditions due to a combination of slow opening of the canopy and the retention of non-host tree canopy. Nguyen-Xuan et al. (2000) observed a greater abundance of pioneer species after fire and a greater abundance of residual species after clear cutting. Differences in vegetation composition observed between burned and logged stands appear to mainly reflect differences in the amount of forest floor removed by each disturbance type. In a study that used different intensities of ground disturbance to judge rate and success of natural recovery of boreal vegetation, Rydgren et al. (1998) found that the least severe disturbances displayed the fastest recovery and that the length of the successional path increased with increasing disturbance severity and size. Vascular plant species richness was higher three years after disturbance than before disturbance, while the opposite was true for bryophytes. Many species recovered by discrete recovery mechanisms. Species that were abundant in intact forest floor vegetation recovered primarily by resprouting from intact rhizomes and clonal in-growth. Other species recovered through germination from the soil propagule bank or propagule dispersal into the disturbed areas. These collective results support the hypothesis that forest floor disturbance is an important element in the dynamics of boreal forest regeneration.

Pugachev et al. (2004) investigated natural recovery of land disturbed by gold mining activities on the Chukchi Peninsula. They found that 12 to 20 years after cessation of mining activities overburden rock dumps supported *Salix* communities with a continuous ground vegetation layer consisting of grasses, *Carex* spp., *Eriophorum* spp., *Equisetum* spp., and green mosses. Conversely, pebble dumps facilitated little recovery of plant cover due to poor water supply

and low fine soil particle content. They concluded that recovery of plant cover depended primarily on the content of fine particles in the surface layer of mining altered substrates and the distance from the undisturbed plant communities, which serve as a source of colonizing propagules.

Aggressive non-native plants, sometimes known as weeds, can potentially reduce the abundance and diversity of native plants, and in some situations even threaten the survival of native species. However, control of aggressive non-native species during natural recovery does not always result in enhanced recovery of the native species (Reid et al. 2009). Removing them can result in no response in the plant community, colonization by other non-native species, recolonization by the removed species, colonization by both native and non-native species, or only by native species. When non-native species control is considered as a method to enhance natural recovery, control sites should be selected based on degree of degradation, where less degradation is better. Activities that facilitate the recovery of native plants should also be considered.

7. Oil Sands Development / Mining

Alberta oil reserves, second in proven reserves only to Saudi Arabia, are found mostly in oil sands deposits. Alberta oil sands, containing 173 billion barrels of recoverable oil, are located in three major areas of northern Alberta beneath approximately 140,000 km² (Figure 1.2) (Government of Alberta 2009).

The first mention of Canadian oil sands was in 1719 when a Cree native assisting fur traders brought samples of oil sands to the Hudson's Bay post at Fort Churchill. In 1790 Scottish explorer Alexander Mackenzie provided the first recorded detailed description of the Athabasca oil sands. In 1883, G.C. Hoffman, of the Geological Survey of Canada, successfully attempted to separate bitumen from oil sands by introducing hot water to the sand. Based on the design of Karl Clark, an oil sands separation plant was built in railway yards in the Athabasca region in 1924, and in 1928 Karl Clark and his associate Sidney Blair were granted a Canadian patent for their hot water separation process. Two years later, in 1930, entrepreneur Robert Fitzsimmons made the first sale of commercially produced bitumen in Edmonton. Because technology did not yet

exist to upgrade the bitumen, it was used as fence post dip, roof tar, and pavement (Energy Resources Conservation Board 2006).

Canadian oil sands operations began in 1967, following research and development that started in the early 1900s. The Alberta Research Council, established by the provincial government in 1921, supported early research on separating bitumen from sand and other materials, and demonstration projects continued throughout the 1940s and 1950s. The Great Canadian Oil Sands Company, later renamed Suncor Energy, began commercial production in 1967 at 12,000 barrels per day (Humphries 2008). In 1974 the Alberta Oil Sands Technology and Research Authority was established to research in situ oil sands technologies (Energy Resources Conservation Board 2006). In 1978 the Energy Resources Conservation Board approved Syncrude's proposal to build a \$1 billion plant at Mildred Lake to produce up to 129,000 barrels per day (Humphries 2008). Imperial Oil began commercial production at Cold Lake in 1985. In 1999 Shell Canada began production at its Muskeg River Mine. In 2003 the Athabasca Oil Sands Project, a joint venture between Shell, ChevronTexaco, and Western Oil Sands, became operational and began producing 118,000 barrels per day. The next year the Energy and Utilities Board issued approvals for the Shell Canada Jackpine mine and the Canadian Natural Resources Horizon project (Energy Resources Conservation Board 2006). As of January 2009, 91 oil sands projects are operating in Alberta. Of these, five are open pit mining operations and the remainder use in situ recovery methods (Government of Alberta 2009).

8. Oil Sands Reclamation

Currently, 500 km² are disturbed by mining activities in the AOSR (Government of Alberta 2009). Current guidelines require disturbed land in the AOSR to be reclaimed to productive, maintenance free, self sustaining ecosystems with land capabilities equivalent to or better than the pre-mining environment (Oil Sands Vegetation Reclamation Committee 1998). Reclamation in the oil sands is a 30 to 40 year process; only a small percentage of the area disturbed by mining activities has been reclaimed. In March 2008, the Alberta government issued its first reclamation certificate to Syncrude Canada Ltd. for a 104 ha piece of land known as Gateway Hill, approximately 35 km north of Fort McMurray.

Early reclamation research in the oil sands focused on suitable substrate and capping prescriptions, dewatering of tailings sands, and ability of selected species to grow in tailings materials. Recently there has been an increase in reclamation and revegetation research. Studies have investigated reclamation of saline composite tailings using peat and barley (Renault et al. 2003); quality of organic matter in different reclamation practices compared to undisturbed conditions (Turcotte et al 2009); using forest floor as a reclamation amendment (McMillan 2005); using LFH to facilitate native plant community development (Mackenzie 2004, Mackenzie and Naeth 2009); and soil water and nutrient regimes in reclaimed upland slopes (Leatherdale 2008).

Hemstock (2008) found reclamation treatments with fibric peat had lower species richness and cover than those with mesic and humic peat. She attributed this difference to fibric peat being less decomposed and more acidic than mesic and humic peat. She suggested the lower pH of fibric peat deters plant establishment and reduces the rate of nitrogen mineralization, which limits plant growth.

In a study examining reclaimed slopes of a tailings storage facility, Burgers (2005) found that 5 and 10 years after reclamation began, plant communities were composed primarily of early successional species. Salinity and soil water did not affect reclamation success; however, sodicity, soil nutrient deficiencies, and inadequate depth of amendment soil did.

Elymus trachycaulus and *Pinus banksiana* both grew better in shallow (5 cm deep) peat overburden over oil sands tailings compared to the same depth of a deep mineral overburden over the same tailings (Danielson et al. 1983). Both species developed extensive root systems in the tailings sand layer below the four overburden treatments tested. However, when the depth of the peat overburden treatment was increased to 15 cm, both species exhibited a decrease in growth, whereas they exhibited favourable effects when the depth of the deep mineral overburden treatment was increased to 15 cm. Differences in growth under different depths of overburden treatment were attributed to a decrease of available phosphorous and suppressed iron and manganese uptake under the thicker peat overburden. They found that when peat was combined with the deep mineral overburden, *Elymus trachycaulus* showed no effect, but shoot production of *Pinus banksiana* was reduced.

In a comparison of different reclamation treatments to natural ecosystems, Rowland et al. (2009) found that the pH of the reclaimed areas was consistently higher than that of the natural areas. This was attributed to the inherently high pH of the parent material used in the capping. In all reclamation treatments, nitrogen was at or above the natural range. Plant diversity on reclamation treatments appeared stable before declining with advancing canopy closure at about age 31 to 35, at which point understory species began to disappear. They concluded that treatments that used a repeatedly fertilized peat-mineral mix, or a peat-mineral mix fertilized once and with underlying subsoil over clean overburden, were developing into functioning forest soils capable of supporting ecosystem processes that mimic those of the natural boreal forest.

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10. Figures



Figure 1.1. Map showing the extent of the Canadian boreal forest (<http://www.cpawsyukon.org/>).



Figure 1.2. Map showing the location of the Athabasca Oil Sands Region within Alberta, Canada (<http://www.grandsespaces.ch/>).

II. NATURAL RECOVERY OF UPLAND BOREAL FOREST VEGETATION ON A HUMMOCKY PEAT-MINERAL MIX SUBSTRATE IN THE ATHABASCA OIL SANDS REGION, ALBERTA

1. Introduction

Vegetation in the boreal forest has been subjected to considerable stress due to a marked increase in oil extraction activities. Over the last 40 years, the mixedwood forest in the Athabasca Oil Sands Region (AOSR), which is located in northeastern Alberta, Canada, has been subjected to intense and extensive development, and will continue to be for the foreseeable future. This development has centered around open pit mining of oil sands where surface minable oil sands located 0 to 50 m below the soil surface (Mossop 1980), are accessed by removing overlying vegetation and soil and creating large scale disturbances including large pits, overburden piles, tailings dykes, and by-products such as sulphur blocks and fine tailings. Alberta Environment and the Alberta Energy and Utilities Board regulate these disturbances and require that they be reclaimed to diverse, self sustaining boreal forest with equivalent land capability similar to that of the surrounding region (Alberta Environmental Protection 1998, Oil Sands Vegetation Reclamation Committee 1998).

Challenges associated with reclamation in the AOSR include growing season constraints, limited supply of native seed, competition from non-native species, loss of soil and organic matter, slow growth and accumulation of peat, slow soil development, altered water tables, and decreased viability of the soil seed bank. Plant species for revegetation must be adapted to the local climate and soils, which can be saline or sodic and water limiting. In the short term, revegetation is required to prevent erosion and reduce invasion by undesirable species. In the long term, it must provide for efficient soil nutrient and water cycling, establishment of a diversity of early, mid and late successional native plant species, addition of organic matter, and provision of wildlife habitat.

To date, reclamation efforts in the AOSR have centered on the addition of top soil or salvaged pre-disturbance soil to create a suitable plant growth medium and to provide a source of native plant propagules that can facilitate natural

recovery of the vegetation in the disturbed areas. Peat and LFH have been used as substrate amendments and caps, with LFH being more successful in the short term because of its greater quantity and diversity of propagules and greater amount of woody material (Mackenzie and Naeth 2009). However, quantities of LFH available to be used in reclamation are limited. A peat mineral mix is more readily available, and its larger quantities mean it can cover a larger area, thus facilitating reclamation and revegetation to a greater extent. However, peat is also in short supply for long term reclamation of large AOSR areas.

Recently there has been an increase in reclamation research in the oil sands focussing on responses of planted / seeded plant species to various reclamation treatments. Studies have investigated effects of the depth of peat and mineral soil treatments on the growth of *Elymus trachycaulus* (Link) Gould ex Shinnars (slender wheatgrass) and *Pinus banksiana* Lamb. (jack pine) (Danielson et al. 1983); reclamation of saline composite tailings using peat and *Hordeum vulgare* L. (common barley) (Renault et al. 2003); using forest floor material as a reclamation amendment (McMillan 2005, Mackenzie and Naeth 2009); factors that affect reclamation success of a tailings storage facility (Burgers 2005); soil water and nutrient regimes in reclaimed upland slopes (Leatherdale 2008); species richness on reclamation treatments with different decay classes of peat (Hemstock 2008); quality of organic matter in different reclamation practices compared to undisturbed conditions (Turcotte et al. 2009); and plant diversity and functioning of ecosystem processes across several different reclamation treatments (Rowland et al. 2009). However, no research has explicitly investigated the potential for natural recovery of upland boreal forest vegetation on a salvage peat-mineral mix substrate.

Natural recovery may facilitate revegetation and reclamation of the oil sands, and may address some challenges in reclaiming large expanses of disturbed land. Natural recovery relies on the residual soil propagule bank and/or seed dispersal from adjacent areas to revegetate disturbed sites. Native propagules reduce the resources needed to reclaim disturbed areas, and may be better adapted to local site conditions than introduced propagules, thereby increasing germination and establishment of native propagules. Natural recovery enhances plant species diversity by providing local propagules for species that are not commercially

available or are only available at great cost. Local seed that is readily wind dispersed onto disturbed sites is often of early successional species that facilitate establishment of later successional species. However, little is known about how naturally recovered plant communities will develop or the timeline required to successfully reclaim an oil sands mined site using this strategy.

This research is a product of the unintentional natural recovery of mixedwood boreal forest vegetation on three peat-mineral mix substrate stockpiles, and the vision and drive of the people who recognized the potential of these sites to contribute to the natural recovery knowledge base. It is an investigation into the possibility of long term success of natural recovery of mixedwood boreal forest vegetation on a peat mineral mix substrate. Results from this research will have direct applications to reclamation in the AOSR and will contribute to the complex science of the study of vegetation ecology.

2. Research Objectives and Hypotheses

2.1 Objectives

The objective of this research was to assess the potential of natural recovery as a viable option for large scale reclamation in the Athabasca Oil Sands. Specific objectives were:

- To assess species composition of boreal forest vegetation that has been growing on a mineral peat mix substrate for 26 to 34 years.
- To determine if there is a relationship between vascular species cover and composition and the pH, electrical conductivity, and texture of the substrate.
- To determine if there is a relationship between vascular species cover and composition and micro and macro topographic characteristics.
- To determine if there is a relationship between non-vascular species composition and macro topographic characteristics.
- To determine the successional status of the vegetation on the study sites.

2.2 Hypotheses

Hypotheses were developed after reconnaissance trips to the research sites and are as follows:

- Texture will not influence total (vascular and non-vascular) plant species cover.
- Electrical conductivity and pH will not influence total plant species cover.
- Micro topographic characteristics (1 x 1 quadrat position, hummock size, degree of slope, aspect, litter depth) will not influence total species cover.
- Macro topographic characteristics (hummock sizes, aspect), canopy cover, shrub and tree densities, and tree ages will not influence total species composition.
- Canopy cover will influence non-vascular species composition.
- Overall, development of plant communities on each site is a result of random factors that may include soil propagule bank dynamics, species dispersal, initial floristics, climatic conditions, and inter-species competition.

3. Materials and Methods

3.1 Site history and descriptions

The Suncor Energy Inc. mine is located approximately 20 km north of Fort McMurray in the Boreal Forest Ecozone (Natural Resources Canada 2007) in the Athabasca Oil Sands Region (AOSR) of Alberta (Figure 2.1). The Boreal Forest Ecozone is characterized as a continental, relatively humid climate, with cold winters and moderately warm summers (Natural Resources Canada 2007). It receives an average annual precipitation of 455.5 mm per year, of which 342.2 mm falls as rain and 155.8 cm as snow (Environment Canada 2009). The average temperature of the coldest month is < -10 °C, and > 10 °C in the warmest month. Fewer than four months of the year have mean temperatures > 10 °C (Strahler and Strahler 1989). Dominant soils in the area are Brunisols, Gleysols, Luvisols, and Mesisols (organic) (Crown and Twardy 1975). Wetlands and peat bogs make up 25 to 50% of the territory. The forest is dominated by *Picea glauca* (Moench) Voss (white spruce), *Populus tremuloides* Michx. (trembling aspen), *Larix laricina* (Du Roi) K. Koch (tamarack), *Pinus banksiana*, and *Abies balsamea* (L.) Mill. (balsam fir) (Natural Resources Canada 2007).

Three study sites were selected on the Suncor Energy Inc. mine (Figure 2.2). Each site is a stockpile composed of a peat-mineral soil mix (substrate) that was

salvaged from unrecorded locations on the mine site prior to oil sands extraction activities. The substrate was transported to the three stockpile locations in 50 to 75 ton trucks and dumped with the intention of placing as much substrate on the stockpile as possible (Tuttle 2008). Thus substrate depth varies from 1 to 5 m. The stockpiles were not recontoured or revegetated, as the substrate was intended for use in future reclamation. The substrate was not used and native vegetation established without human influence or interference.

Site 1 (Waste Area 5) is approximately 4 ha in size and triangular in shape (Figure 2.3). It is located on the west side of the mine, above the original level of the land on a large tailings dyke, south of Dyke 2E and west of Pond 1A. It is the oldest of the three study sites, stockpiled in winter 1975 (Tuttle 2008). The slopes surrounding Site 1 were traditionally reclaimed with *Picea* spp. A. Dietr. (spruce) and *Caragana arborescens* Lam. (Caragana), and a *Bromus inermis* Leyss. (smooth brome), *Medicago sativa* L. (alfalfa), *Melilotus officinalis* (L.) Lam. (yellow sweet clover) reclamation mix (Shopik and Klym 1978). Topography ranges from small to large hummocks and there is no standing water.

Site 2 (Crane Lake) is approximately 20 ha in size (Figure 2.4). It is located on the west side of the mine, on the original level of land, south of Pond 5, west of Pond 2/3, and directly adjacent to the newly reconstructed northbound Highway 60. It surrounds Crane Lake, which is an impoundment of water drained from the surrounding dykes and retained by the stockpiled substrate. The lake supports a diversity of waterfowl, insect, and animal life. Site 2 is the second oldest of the three sites; material was placed in winter 1976 and 1982-83 (Tuttle 2008). Topography ranges from flat to hummocks over 3 m in height. Small pools of standing water can be found in the southern portion of the site.

Site 3 (Waste Area 16) is approximately 6 ha in size and square in shape (Figure 2.5). It is located on the west side of the mine, above the original level of the land on a large tailings dyke, west of Pond 2/3 and south of Waste Area 14. It is the youngest of the three sites, stockpiled in late winter 1983 (Tuttle 2008). The slopes to the west and south were revegetated with *Picea* spp., *Caragana arborescens*, and a *Bromus inermis*, *Medicago sativa*, *Melilotus officinalis* reclamation mix (Anonymous 1983). Topography ranges from relatively flat undulations to large hummocks. Large pools of standing water can be found in

several locations on site edges. The interior is mostly dry; a few pockets of wet ground can be found in the northwest portion of the site.

3.2 Experimental approach and design

The research is ex post facto (after the fact research), in that the sites were not designed as a replicated experiment, but will be used to characterize naturally occurring plant species and their associated substrate (soil) and topographic characteristics. Ex post facto research is “research in reverse”; instead of beginning with independent variables and subjecting them to different treatments to bring about different responses, an ex post facto experiment begins with groups that have already been subjected to a treatment(s) and searches in retrospect for the factor(s) that brought about the response(s) (Cohen et al. 2000). The main weakness of this type of investigation is the lack of control of independent variables, and therefore lack of randomization. Conclusions are limited to stating relationships. It is not possible to know for certain if the causative factor has been included or even identified, therefore relationships between two variables do not establish cause and effect.

Knowledge gained will be a productive means to generate new hypotheses of successional trajectories as they relate to management of disturbed systems. The three research sites are the only ones of their kind in the AOSR, preventing typical experimental replication and direct comparisons among these sites due to differences in age, location, size, and construction history.

Reconnaissance surveys were conducted in May and June 2007 to visually assess general topographic and vegetation patterns and site variability to aid in experimental design. Based on reconnaissance data, sites were stratified into edge and interior locations (Figure 2.6). Several species seen in the edge decreased in abundance to almost zero approximately 15 m from the edge of the site; thus the edge stratification was set at 15 m wide.

Prior to plot establishment, a Garmin 12 Personal Navigator GPS unit with an accuracy of 15 m was used to map site boundaries. Coordinates were used to create a boundary map for each site at a 1:2000 scale. Randomly generated numbers were used as GPS coordinates for plots and incorporated into their

respective maps (Figure 2.7). Twenty plots were selected for each stratification at each site, the final number based on species area curves for each site. Each plot consisted of a 5 x 5 m quadrat with a 1 x 1 m quadrat nested in one corner. GPS navigation was not possible in the dense canopied site interiors, so a compass and 50 m measuring tape were used. A bearing to the first plot was taken from a site map; the required distance and bearing were navigated until the plot location was reached. Edge plots were located with randomly generated numbers using boundary maps and the measured circumference of each site. At each plot the closest and largest living tree or tall shrub was flagged and became a permanent plot marker. Interior plots were oriented to cardinal directions; edge plots were oriented such that one corner of the plot was 5 m from hummock edges.

3.3 Vegetation and ground cover

Species area curves based on vascular species richness were used to determine number of quadrats sampled per site. A total of 38 quadrats were sampled in Site 1 (21 interior, 17 edge) (Figure 2.8a, 2.8b); 50 in Site 2 (28 interior, 22 edge) (Figure 2.9a, 2.9b); and 47 in Site 3 (27 interior, 20 edge) (Figure 2.10a, 2.10b). Prior to data collection, pictures of the undisturbed plot were taken from the permanent corner marker, in each cardinal direction and diagonally across the plot. Additional pictures were taken of site anomalies or interesting features.

In 1 x 1 m quadrats, plant species were identified in growth form categories: lichens, mosses, sedges, grasses, forbs, low shrubs (< 150 cm tall), tall shrubs (> 150 cm tall, < 5 cm diameter at breast height, 135 cm), and trees (> 5 cm diameter at breast height, 135 cm). Vascular plants were identified to genus and species if possible. If they were not identifiable to genus and if there were more than five plants of the unknown species in the quadrat, a sample was collected for later identification. Percent canopy cover of each species (excluding tall shrubs and trees), bare ground, exposed rock, and litter were visually estimated.

A ruler was used to measure litter depth in five locations in each 1 x 1 m quadrat; one measurement on each side of the quadrat and one in the center. The ruler was worked into the litter to the point at which resistance from the humus layer was reached and depth was recorded. The observer was careful not to compress or push away the litter. The average of the five measurements was recorded.

The 5 x 5 m quadrats were systematically walked through, beginning around the edges then back and forth across the quadrat. All species were identified and species not present in their respective 1 x 1 m quadrats were recorded. Stem counts of low shrub, tall shrub, and tree species were taken to estimate productivity and assess community structure and regeneration of woody species. *Rubus idaeus* L. (wild red raspberry) stems were not counted because of the very high stem numbers (100s) in many quadrats.

Bryophyte samples were collected from 5 x 5 m quadrats. Samples were taken from substrates < 30 cm from the ground surface, including mineral soil, organic matter, litter, rocks, decomposing deadfall, and tree trunk bases. Samples were placed in a paper bag, labelled, air dried, then sorted into piles of species similar in appearance without microscopic examination. Reference samples for each pile and any unknown species were identified by two moss experts. Several samples per pile were checked by a moss expert for quality control.

3.4 Topography, slope, aspect, and canopy cover

A modified version of the topography classification system in Beckingham and Archibald (1996) was used to describe topographic position of the 1 x 1 m quadrat relative to the quadrat position on a hummock. Topography was classified as top, crest, upper, mid, lower, toe, saddle, depression, or flat (Figure 2.11, Table 2.1). The size of the hummock the quadrat was located on was described relative to other hummocks across the site. Quadrat aspect was measured with a Suunto compass by holding the compass perpendicular to the average plane of the ground. If the quadrat was located on top of a hummock, on a flat area, or in a depression, aspect was recorded as zero. Each aspect measurement was converted to 2 continuous variables (east west aspect and north south aspect) between -1 and 1 to allow for easier interpretation in the statistical analyses. To convert to east west aspect, the measurement was converted to radians, and then converted again using sine. To convert to north south aspect, the measurement was converted to radians and then converted again using cosine. Degree of slope was determined using a Suunto clinometer. A reference point at the same eye height as the observer was chosen at the bottom of the hummock and the clinometer was compared against this point.

Northing and easting coordinates and elevation were recorded with the same GPS unit used to map site boundaries.

In each 5 x 5 m quadrat, topography was described relative to that across the site. Average aspect was measured with a compass; if the quadrat contained 2 hummocks average aspect was estimated; if the quadrat had a slope, slope direction was taken as the average aspect; if the quadrat was on a flat spot no aspect was recorded. Canopy cover was measured with a Forest Densiometers Model A spherical convex densiometer following Montana Cooperative Wildlife Research Unit field protocols (Martin et al. 1997) (number of dots on the mirror covered by canopy were counted, divided by 96, and multiplied by 100 to obtain % covered overhead area). Four measurements were taken facing northwest, northeast, southeast, and southwest then averaged. Canopy cover estimation was calibrated between observers several times during data collection.

3.5 Tree cores

A core was taken from the largest individual of each tree species in each 5 x 5 m quadrat. Cores were taken with a 5 mm diameter Mora increment borer. After removal from the tree, the core was pushed into a plastic drinking straw which was taped closed and labelled. Cores were dried in the straws for several months.

A Dado blade mounted on a table saw was used to cut a 3 x 5 mm groove down the center of hemlock window jamb moulding. Cores were cut out of straws with a utility knife then glued into the moulding groove with approximately 5 cm between cores. Once the glue dried, a band saw was used to cut the moulding into small pieces containing one core. Cores were sanded with a Makita belt sander using 120 grit sandpaper, then by hand using progressively finer sandpaper (180, 220, 320, 400, 600 grits) to create a smooth surface for counting core rings. Rings were counted under a Swift Stereo Zoom Eighty Eight dissecting microscope with a fixed 2x magnification power. A Wild-Heerbrugg M3 dissecting microscope was used to recount 50 random cores under a higher power. Several cores had rings that could not be seen under lower magnification, so all cores were recounted under 16x magnification power with the Wild-Heerbrugg microscope.

3.6 Substrate

Electrical conductivity (EC) and pH were selected as representative chemical properties of the substrate. Soil pH is probably the single most important chemical characteristic of a soil. It is considered a “master variable” and can be used as a proxy to estimate other chemical characteristics of the soil (Bloom 2000, Brady and Weil 2002). EC was chosen as an indirect measurement of salt content because parent material in the study region is known to have a high salt content (Crown and Twardy 1975). Salt affected soils adversely affect plants because of concentration of salts (salinity) in the soil solution and concentrations of specific ions, especially sodium (sodicity) (Brady and Weil 2002). Total organic matter, nutrient availability, water content, and temperature were considered but not sampled because of spatial and temporal variability.

Three plots were randomly selected in each site for reconnaissance substrate sample collection, in which EC and pH were measured. Observations were recorded, such as water in the quadrat, presence of fungal hyphae, pebbles or stones, and pictures were taken. Using a 4 cm diameter Dutch auger, two samples (approximately 375 cm³) were collected in each 5 x 5 m quadrat, one on a hummock and one in a hollow. Litter was removed from the surface before taking the sample from 0 to 15 cm.

Samples were placed in Ziploc bags and weighed at the end of the day. A DiST 4 waterproof conductivity tester calibrated with a 1413 µS solution according to the manufacturer’s instructions was used to measure field EC (Hanna Instruments 2001a). A pHep HI 98107 pocket sized pH meter calibrated with pH 7, 4, and 10 buffer solutions according to the manufacturer’s instructions was used to measure field pH (Hanna Instruments 2001b).

For each sample, 30 mL of substrate was measured into a 50 mL plastic beaker, after hand crushing aggregates > 2 mm in diameter. The sample was placed in a 100 mL plastic jar with a screw lid and a 1:2 substrate to water ratio was created by adding 30 mL of distilled water with a 50 CC syringe. The jar was shaken 100 times for thorough mixing of substrate and water. Immediately after shaking, the conductivity tester was used to measure EC according to the manufacturer’s instructions (Hanna Instruments 2001a). Sample pH required measurement 15

minutes after shaking to allow substrate particles to settle, leaving a layer of free water above the substrate in which to place the pH meter electrode (Soil Quality Institute 1998). The pH meter was used according to manufacturer's instructions (Hanna Instruments 2001b). After both EC and pH readings, meter electrodes were thoroughly rinsed with distilled water between samples.

Each substrate sample was weighed again in the laboratory, oven dried at 100 °C for 24 hours then weighed to determine water loss. Using the same procedures and instruments as in the field, EC and pH were measured to determine changes due to variable water content of the substrate in the field.

Five substrate samples were taken from each plot, one in each corner and one in the center for texture descriptions. Vegetation growing immediately on or within the vicinity (approximately 30 cm) of the sampling location was recorded as forbs, grasses, and sedges. Prior to collecting the substrate, all vegetation and litter were cleared from the surface. Litter was defined as organic material that contained identifiable pieces of plants, such as a piece of a leaf, equivalent to the mesic class of litter according to the Canadian System of Soil Classification (Soil Classification Working Group 1998). A handful of substrate from the top 5 cm was visually classified as organic, mineral, or mix. The dominant and less common particle types in the sample were identified using hand texturing.

3.7 Statistical analyses

Only data collected in the interior quadrats of each site were analyzed. Data collected in the edge quadrats were used to complete species lists. Unknown species that occurred only once in the interior quadrats of any of the three sites were not included in statistical analyses. Prior to analyses, all percent cover data collected in the 1 x 1 m interior quadrats were log transformed to prevent over-emphasis of dominant species (McCune and Grace 2002). Each analysis was completed for three scales of sampling within the interior quadrats: 1 x 1 quadrats, 5 x 5 quadrats, and moss samples.

To determine if distinct community types existed in each site, data were subjected to cluster analysis to produce groupings of quadrats with similar species composition using R: A Language and Environment for Statistical

Computing, version 2.9.1 (R Development Core Team 2009). Clustering was performed via hierarchical agglomerative clustering, using Bray-Curtis distance as the community distance measure and Ward's minimum variance as the agglomerative method, which attempts to find compact, spherical clusters. The resulting dendrogram from each cluster analysis was cut at successively finer levels, each to a maximum of 10 levels. After each cut, group membership was written to a file that included environmental data. Each membership file was run against the related species data using indicator species analysis (ISA). By calculating indicator values and testing their significance for each species at each clustering level, the most ecologically meaningful number of clusters was chosen. The ISA iteration that resulted in the lowest average probability for the indicator value averaged across all species was chosen as the optimal stopping point.

Multi-Response Permutation Procedure (MRPP) was then used to determine if significant differences existed between groups defined by cluster analysis, using Bray-Curtis distance as the community distance measure. If MRPP gave a significant p-value (< 0.05), groups produced at this level of clustering in each of the three research sites were defined as community types. Using MRPP, pair-wise comparisons between each community type were performed. A Bonferroni corrected alpha was used for each set of comparisons. Group comparisons that resulted in an alpha lower than the corrected alpha and an A value > 0.2 were deemed significantly different from one another. The A value is the chance corrected within group agreement. In other words it is a numerical description of the dispersion between two community types (or the homogeneity within groups) when compared to the random expectation. It is common for A values to be < 0.1 . An A value of > 0.3 is quite high (McCune and Grace 2002). The A value of 0.2 was chosen as a relatively high value for pair wise comparisons because the majority of the comparisons showed an A value less than that. Species composition of each group was then analyzed, and species that had an indicator value > 0.45 were noted as characteristic of that group. If no species in the group had an indicator value of 0.45, a lesser value was chosen as the threshold value.

Following cluster analyses, a detrended correspondence analysis (DCA) was performed for each site using CANOCO (ter Braak and Šmilauer 2002). Gradient length, which measure beta diversity in community composition along the

individual ordination axes (Lepš and Šmilauer 2003), was used to determine what type of ordination should be used. If the value of the largest gradient was > 4 , a unimodal method was used. If the value was < 3 , a linear method was used. For values between 3 and 4, either method of ordination could work equally well (Lepš and Šmilauer 2003).

Both unimodal and linear ordination methods were used (Table 2.2). Canonical correspondence analysis (CCA) was chosen as the unimodal method and redundancy analysis (RDA) was chosen. Both analysis types were run using CANOCO (ter Braak and Šmilauer 2002). RDA analysis is analogous to CCA, except that it is based on a linear model of species responses (McCune and Grace 2002). In both types of analyses, automatic forward selection was used to determine which environmental variables explained the most variance within the data. Only significant environmental variables were used in the final ordination. RDA analyses were scaled by inter-sample distances and centered by species. CCA analyses were scaled by inter-sample distances using Hills scaling, which increases the interpretability of the ordination diagram (McCune and Grace 2002, Lepš and Šmilauer 2003); centering was not required for this analysis type. No post transformations were applied to the species scores of either analysis type. RDA and CCA ordination axes were tested for significance using a Monte Carlo Permutation Test under a reduced model (to reduce the chance of making a Type I error) and 499 permutations. Ordination diagrams included species with correlation values for the first and second axes > 0.5 and species with indicator values > 0.45 . Environmental vectors were scaled to 5 times their original length.

4. Results and Discussion

4.1 Substrate

Substrate texture in Site 1 was relatively homogeneous; with few exceptions, the five samples in 5 x 5 quadrats were dominated by organic matter, with sand being sub-dominant. Textures in Sites 2 and 3 were more variable, ranging from pure organic matter to various combinations of particle types. Few quadrats in either site had the same texture in each of the five samples. The majority of quadrats contained a range of dominant and sub-dominant texture types. This

variability is assumed to have been caused during substrate excavation and dumping. Due to the many combinations and different relative dominances of substrate types within each quadrat no analyses were performed on these data.

Field electrical conductivities (EC) were < 0.75 dS/m, and, with the exception of one measurement, laboratory measurements were < 0.85 dS/m (Table A1).

These values are at the low end of the range that can be expected in the boreal forest (Gobran and Clegg 1996, Soon et al. 2000). Since there were no numerical differences in EC among locations no statistical analyses were performed and no relationship with vegetation could be discerned.

Field pH ranged from 5.3 to 7.8, and laboratory measurements ranged from 5.1 to 7.7. Lower pH values were generally associated with samples dominated by organic matter, and values closer to neutral were associated with samples dominated by mineral soil (Table A1). The pH in a bog is generally less than 4.6, and ranges from 5.5 to 7.0 in fens (Johnson et al. 1995). Niva et al. (2006) found that pH of boreal forest soil ranged from 4.4 to 5.1. The pH of Brunisols falls around 5.5 (Soil Classification Working Group 1998). Generally, pH increases with depth in the soil profile (Uchida et al. 1998). Overburden material in the region has a pH range of 7.1 to 8.0 (Fung and Macyk 2000), and when mixed with salvaged surface organic matter can produce a more basic material than is found in undisturbed sites. On the research sites, coarse mixing of the subsoil and organic matter has created a patchy substrate with distinct pockets of mineral soil and organic matter, which is the reason for the different pH measurements. As the measured pH values fall within normal ranges for the substrate types, testing for relationships between sampled substrate chemical properties and vegetation was not conducted.

4.2 Plant community composition

Species richness across sites was relatively high compared to general reclamation sites in the area. A total of 90 species were found in Site 1, 120 in Site 2, and 126 in Site 3 (Tables A2, 2.3). Due to lack of flowering structures, several identifications were done to genus only, potentially increasing the number of species present in each site.

Vascular plant species numbers were lower than typical for an undisturbed upland boreal forest plant community. Generally, vascular and non-vascular species found on the sites (Table A2) were as expected for upland and lowland habitats in mixedwood boreal forests (Rowe 1972, Larsen 1980). Species found on site that were not characteristic of the boreal forest included *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass), *Phleum pratense* L. (timothy), *Sonchus arvensis* L. (perennial sow thistle), *Chenopodium* spp. L. (goosefoot), and *Medicago sativa* L. (alfalfa). These species are non-natives associated with anthropogenic disturbances. Some are cosmopolitan (e.g. *Sonchus arvensis*), while others are found out of their typical range (e.g. *Agropyron cristatum*).

4.3 1 x 1 quadrats

Most environmental variables were similar across all three sites. Aspect ranged from 0 to 350 degrees, averaging 178 degrees, which is due south. Slopes ranged from 0 to 27 degrees, averaging 12 degrees, and topography class ranged from 0 to 7 (Tables A3, 2.4). Ground cover was dominated by litter (average 94% cover, 3.4 cm deep), with < 1% cover of bare ground and rocks (Table A3). Substrate texture class was more variable than other environmental parameters. In Site 1 it was class 4 in all quadrats. In Sites 2 and 3 it ranged from 0 to 4; average classes were 2 and 3, respectively (Table A3, 2.5). Topographic variability was high among all sites with Site 1 being the least variable.

Cluster analysis and ISA distinguished several community types in each site and in all sites combined (Table 2.6). MRPP distinguished significant differences among several of the community types; however, with the exception of one comparison in Site 3, the low A values suggested an overlap in species composition, which means the differences may not be strong enough to distinguish different communities (Table 2.7). Thus, based on these analyses there were no distinct community types in Sites 1, 2, or all sites combined at this sampling scale. In Site 3, community types 2 (upland forb #1) and 4 (wet forb), and 4 and 6 (upland forb #2) showed strong and significant differences (Table 2.7). Community types 2 and 6 were not significantly different. These results were supported by general field observations. Several comparisons in Sites 2 and 3 yielded relatively high A values, although p-values were greater than the

respective corrected alpha (Table 2.7). This may be a result of the relatively small sample size in these sites (McCune and Grace 2002); sample sizes may not be large enough to fully capture differences between these community types.

RDA for Site 1 revealed that neither the first canonical axis nor all axes combined were significant descriptors of the relationship between species composition and environmental variables (Table 2.8). Forward selection in RDA gave the same results (Table 2.9), therefore no ordination is included.

RDA, cluster analysis, and ISA combined indicated that at this sampling scale Site 1 is homogeneous and no environmental variables sampled explained variations in vegetation. Environmental variables that were not sampled, such as long term soil water and / or temperature, may differentiate plant communities; or perhaps no environmental variables will differentiate the plant communities. The homogeneous organic substrate, topography, and time may have led to the homogeneous state of the plant community. Initial community composition may have played a large role in the current composition. Due to the origins of the substrate, the seed bank would have contained propagules of hydrophilic species that theoretically would have emerged the growing season following substrate placement. As the substrate drained, growing conditions would become less ideal for these species, and eventually they would die; this can be inferred from *Betula papyrifera* Marsh. (paper birch) and *Salix* spp. L. (willow) snags throughout the site. If the developing substrate was conducive to establishment and growth of the dominant understory species, *Rubus idaeus*, and if a propagule source in relatively close proximity was available, it might have arrived on site and firmly established before propagules of other upland species arrived and began to establish. *Rubus idaeus* is a competitive and adaptive species that thrives in soils with high nitrogen (Tilman 1987, Jobidon 1993, Pitcairn et al. 1998). High nitrogen in the substrate during this establishment time would favour *Rubus idaeus* and further disadvantage other species. A combination of the above explanations may be responsible for the site homogeneity.

In Sites 2, 3, and all sites combined, Monte Carlo permutation test results in CCA indicated that for each ordination the first canonical axis and all axes combined were significant (Table 2.8). CCA results indicated that 7.1 % to 22.8% of the variation in the species data was explained by both canonical axes, and species-

environment correlations were strong (Table 2.10), as confirmed by eigenvalues for each axis in the ordinations (Figures 2.12, 2.13, 2.14). Forward selection in CCA found several significant environmental variables in each site (Table 2.9).

Significant environmental variables in Site 2, as determined by forward selection in CCA, were clay (axis 1, correlation = 0.989) and large sized hummocks (axis 2, correlation = 0.991), both of which showed strong correlations with the ordination axes (Table 2.9). Several of the species associated with clay were wetland species (e.g. *Carex* spp., *Salix* spp. (low shrub), and *Betula pumila* L. (low shrub)) (Figure 2.12). Visual observations and texture analysis of substrate samples from wet depressions in this site showed that clay was common in depressions, possibly preventing water from draining quickly, thereby sustaining a wetter plant community. Species associated with large sized hummocks were *Cornus sericea* L. (low shrub) and *Taraxacum officinale* F.H. Wigg. However, it is not clear why these species showed this association. The associations of community types with environmental variables appear irrelevant as none of the communities were significantly different.

In Site 3, forward selection in CCA determined that significant environmental variables were east west aspect (axis 2, correlation = -0.816), tree canopy cover (axis 1, correlation = 0.708), clay (axis 1, correlation = -0.449), medium sized hummocks (axis 1, correlation = -0.604), and sand (axis 1, correlation = 0.458) (Table 2.9, Figure 2.13). East-west and not north-south aspect as a significant predictor of the relationship between species and environmental variables may be due to construction techniques. Dumping substrate at the eastern (western) end of the stockpile and continually dumping westward (eastward) may have influenced hummock shape, making them oblong in a north-south direction. This would have created longer east and west sides of hummocks, biasing the overall aspect. Community types 2 (characterized by *Rubus idaeus* (low shrub)) and 6 (characterized by *Fragaria virginiana* Duchesne) were associated with higher canopy cover and sand, and community type 4 (characterized by *Melilotus officinalis* and moss) was associated with low canopy cover, medium size hummocks, and more east than west facing slopes (Figure 2.13).

Rubus idaeus, the dominant understory species in Site 3, is adapted to a closed canopy during its dormant seed state, and readily germinates under optimal

conditions (increased light, water, nitrate availability) (Jobidon 1993). Without knowing when *Rubus idaeus* established, it is impossible to know what germination conditions were at that time. *Rubus idaeus* may have arrived on site via wind and bird transport when trees were establishing and the canopy had not yet formed, or it may have arrived in the soil seed bank. There would have been ample sunlight, and if *Rubus idaeus* established before most water drained from the saturated substrate, there would have been ample water. Without canopy cover, the soil would have warmed and microorganisms would have a flush of activity, converting organic nitrogen to mineral nitrogen, hence increasing plant available nitrogen. Soil nitrate can increase in the first 3 years following forest cover removal, which favours establishment of *Rubus idaeus* (Jobidon 1993). Pitcairn et al. (1998) found that *Rubus idaeus* showed preference for areas with higher nitrogen, and Tilman (1987) found that *Rubus idaeus* increased significantly along a gradient of increasing nitrogen. Jobidon (1990) found that after logging disturbance, many eastern coniferous forest sites in Canada were rapidly recolonized by *Rubus idaeus*.

Fragaria virginiana is known to frequent both closed canopy and open habitats (Moss 2000); it is therefore not unexpected to find it under denser canopy.

Melilotus officinalis is an introduced weed species that thrives in disturbed, high light conditions, so it would be found in quadrats with lower canopy cover. Since bryophytes were not collected exclusively in 1 x 1 m quadrats, it is impossible to know if species characterizing community type 4 in Site 3 display a greater affinity for higher light conditions.

In all sites combined, forward selection in CCA found that clay (axis 1, correlation = 0.840), mid slope position of quadrats (Axis 1, correlation = 0.271), and upper slope position of quadrats (axis 2, correlation = 0.932) were significant environmental variables (Table 2.9, Figure 2.14). Species associated with clay included *Carex* spp., *Equisetum arvense* L., and *Betula pumila* (low shrub). As in Site 3, these wetland species may be associated with this substrate texture because it may be preventing water drainage, thus supporting a wetter plant community. It is not known why upper and mid slope quadrat positions were chosen as significant environmental variables, or why the significant variables in this ordination differ from the significant variables in ordinations for Sites 2 and 3.

The associations of community types with environmental variables appear irrelevant as none of the communities were significantly different.

4.4 5 x 5 quadrats

Aspect across all three sites ranged from 0 to 350 degrees, averaging 114 degrees, which is east southeast. Topography class ranged from 1 to 7 (Tables A4, 2.4) and canopy cover ranged from 14.6 to 94.8%, averaging 61.5% (Table A4). In Sites 1 and 2, tall shrub stem density ranged from 0 to 27, averaging 7 stems per 25 m², or 2,800 stems per ha. In Site 3, tall shrub stem density ranged from 3 to 78, averaging 20 stems per 25 m², or 8,000 stems per ha. Tree stem density across all three sites ranged from 0 to 15 stems, averaging 5 stems per 25 m², or 2,000 stems per ha. No studies have determined tall shrub or tree stem density in a situation similar to this one. Following three large forest fires near Watson Lake, YT, maximum density of *Populus tremuloides* reached 50,000 stems per ha within 20 years post fire, averaging 5,500 stems per ha (Johnstone et al. 2004). Relative stem densities of all boreal tree species remained the same throughout the 20 year observation period. Between 10 and 19 years post fire, *Populus tremuloides* density decreased markedly, and by year 19, it had thinned to below that observed in year 5. These results contrast what is occurring on the sites in this study, where, based on lack of observed *Populus tremuloides* snags, density is likely not decreasing, even 34 years after substrate placement. This may be due to differences in conditions between the research sites in this study and the ones in the study conducted by Johnstone et al. (2004). Site 1 tree ages ranged from 16 to 32 years, averaging 25.8 years; Site 2 ages ranged from 13 to 28 years, averaging 19 years; Site 3 ages ranged from 12 to 22 years, averaging 17.6 years. Initial tree establishment on each site was delayed between 2 and 5 years, which is likely the time it took for many propagules to arrive.

Tree species characteristic of wet lowlands were relatively absent (Table A5), most notably *Picea mariana* (Mill.) Britton, Sterns and Poggenb. This species would theoretically have been present in the original plant community, given that the substrate contains high amounts of undecomposed peat and was saturated at placement. Propagules for the three *Larix laricina* trees sampled likely came from the seed bank. The oldest individual (30 years), and the only one on Site 1,

would have germinated at approximately the same time as *Populus tremuloides* and *Populus balsamifera* L. (balsam poplar). The other two individuals (17 and 18 years, Site 3) had delayed germination compared to *Populus tremuloides* and *Populus balsamifera*. Soil temperature and water and light availability would have been relatively high, creating ideal germination conditions (Duncan 1954). Assuming optimal conditions and knowing the substrate came from lowlands, *Larix laricina* could be expected to have had a greater presence. However, without knowing the original community composition before disturbance, it is not possible to determine if this species had high or low germination. Given the substrate origins, and only three individuals in the 5 x 5 quadrats, the presence of this species is likely lower than in the original community. If *Larix laricina* did exhibit a greater presence in the original community then perhaps conditions for germination were not ideal on either Site 1 or 3. This species exhibits relative dormancy and low seed quality (Duncan 1954, Brown 1982), which could explain why only a few individuals were observed. Relative dormancy was proposed after observations were made that as dormancy was released, the temperature range permissive for germination widened until it was maximal. Conversely, as dormancy was induced, the range of temperatures over which germination could occur narrowed until it was no longer possible (Allen et al. 2007).

Salix spp. ranged in age from 15 (Sites 2 and 3) to 26 (Site 1) years, averaging 18.9 years. Health and vigour were not directly assessed, but visual observations indicate *Salix* spp. were struggling to survive under the *Populus* canopy. Many cored individuals had numerous dead branches and sparse canopies, and dead individuals were observed in all three sites. Many individuals of this genus may exhibit younger ages because they are secondary growth; older trees likely died as the substrate drained and have been replaced by secondary growth. *Betula papyrifera*, generally found on well drained but moist sites (Johnson et al. 1995), was entirely absent from Sites 1 and 2. Many snags were seen and recorded, but no live trees were seen. In Site 3, 9 individuals were cored (14 trees), ranging in age from 12 to 20 years. Visual observations indicate this site is more mesic than the other two, and is therefore more amenable to continued growth of this species. *Betula papyrifera* recruitment in Site 3 (140 low shrubs, 53 tall shrubs) further supports this conclusion. This species may be responding similarly to *Salix* spp., where older trees died and were replaced with younger trees (or not

replaced in Sites 1 and 2). This species did not appear to be thriving and may eventually disappear from Site 3 as well.

Upland species were thriving on the three sites. *Populus* was dominant in each of the three woody plant categories (low shrubs, tall shrubs, trees). The only exception was *Salix* spp., which had relatively high numbers of low and tall shrubs. *Populus balsamifera* and *Populus tremuloides* are not characteristic of boreal lowlands so propagules of these two species would not be expected in the soil seed bank before or during substrate placement. Seeds would have migrated from areas surrounding the sites, germinated and established. Both of these species reproduce relatively quickly through root suckering. In the absence of significant competition from other trees or shrubs, these two species could have colonized the three sites relatively quickly, establishing their overstory dominance early. Overall, woody upland species outnumbered woody lowland species, both in number of species and number of individuals.

Cluster analysis and ISA differentiated several community types in Sites 1, 2, 3, and all sites combined (Table 2.11). Most MRPP pair wise comparisons between community types (Table 2.7) yielded no significant results. Like the 1 x 1 m quadrats in Sites 1 and 2, A values for significant comparisons were too low to consider the communities distinct. Thus at this sampling scale there are no distinct community types in any of the three sites and all sites combined. Several comparisons resulted in high A values, but non-significant p-values (Table 2.7). The relatively small sample sizes may not have been large enough to capture differences that may exist between these community types.

Monte Carlo permutation test results in RDA for each site and CCA for all sites combined indicated the first canonical ordination axis and all axes combined were significant (Table 2.8). Both canonical axes in the ordinations explained 7.3 to 23.3% of the variation in the species data (Table 2.10). However, species-environment correlations were not as strong as in the 1 x 1 m quadrats (Table 2.10), as indicated by the smaller eigenvalues for each axis in the ordinations (Figures 2.15, 2.16, 2.17, 2.18). Forward selection found several significant environmental variables within each ordination (Table 2.9). However, the association of community types within each site and all sites combined appears irrelevant as none of the communities are significantly different from one another.

In Site 1, forward selection in RDA determined that significant environmental variables were east west aspect (axis 1, correlation = 0.737), tree canopy cover (axis 2, correlation = -0.447), and medium sized hummocks (axis 2, correlation = 0.635) (Table 2.9, Figure 2.15). Species associated with higher canopy cover include *Orthilia secunda* (L.) House, *Galium boreale* L., *Fragaria virginiana*, and *Picea glauca* (low shrub). *Orthilia secunda*, *Galium boreale*, and *Fragaria virginiana* are known to prefer closed canopy forests (Moss 1994), and *Picea glauca* is known to establish in closed canopy broadleaf forests (Larsen 1980). East west aspect displayed a slightly stronger relationship with the plant species than tree canopy cover, as indicated by the longer vector. It is likely that, as in the 1 x 1 quadrats for Site 3, construction techniques biased the overall aspect of this site as well. This may explain the significance of this variable. Several upland species (*Corydalis aurea* Willd., *Trifolium repens* L., *Cornus canadensis*, *Aralia nudicaulis* L., and *Rosa acicularis* Lindl. (low shrub)) were associated with medium sized hummocks. This intermediate size of hummocks may provide the best habitat variability for these species.

In Site 2, forward selection in RDA determined that significant environmental variables were tree canopy cover (axis 2, correlation = -0.495), stem density of trees (axis 2, correlation = 0.618), and stem density of tall shrubs (axis 1, correlation = 0.954) (Table 2.9, Figure 2.16). Tall shrub stem density displayed a stronger relationship with the species data than tree stem density and canopy cover, as indicated by the longer vector in the ordination diagram (Figure 2.16). It is not known why tree canopy cover and tree stem density were negatively correlated, or why *Bromus inermis*, which is a species that prefers open and disturbed habitats, is associated with higher tree canopy cover. Species associated with higher tree stem density included *Populus tremuloides* (low shrub), *Populus balsamifera* (low shrub), *Ribes oxycanthoides* L. (low shrub), *Corydalis aurea*, *Astragalus canadensis* L., and fungus. *Populus tremuloides* and *Populus balsamifera* low shrubs could be associated with higher tree canopy cover because they may be regeneration from the parent trees, possibly through suckers or seeds. *Ribes oxycanthoides* is found in moist closed canopy forests (Moss 1994); the mesic conditions and closed canopy in this site may be conducive to the growth of this species. *Corydalis aurea* and *Astragalus canadensis* are both found in open woods (Moss 1994), which is contrary to the

closed canopy on this site. The association of fungus with higher tree stem density may be due to a symbiotic relationship of the fungus with the tree roots. Species associated with higher tall shrub stem density included *Carex* spp., *Populus balsamifera* (tall shrub), and *Equisetum arvense*. These species prefer wetter habitats (Moss 1994), and are likely associated with *Salix* and *Populus balsamifera* tall shrubs, which were the dominant tall shrub species in this site. Both *Salix* and *Populus balsamifera* prefer moist soil (Johnson et al. 1995), which is in agreement with the wetter conditions in this site; therefore, these species may be used as proxy indicators of the conditions that *Carex*, *Populus balsamifera* tall shrubs, and *Equisetum arvense* were found in.

Forward selection in RDA determined significant environmental variables in Site 3 were age of *Betula occidentalis* Hook. trees (axis 2, correlation = 0.702), tree canopy cover (axis 1, correlation = -0.800), medium sized hummocks (axis 1, correlation = 0.304), and stem density of tall shrubs (axis 1, correlation = 0.738) (Table 2.9, Figure 2.17). As in Site 2, species associated with greater tall shrub stem density (e.g. *Equisetum arvense*, *Parnassia palustris*, *Platanthera aquilonis* Sheviak, *Betula papyrifera*, *Salix* spp. (low shrub), and *Carex* spp.) are species that prefer moist habitats (Moss 1994). As *Salix* and *Populus balsamifera* were the dominant tall shrubs in this site as well, it is reasonable to conclude that the same moisture association exists in this site as in Site 2. It is not known why age of *Betula occidentalis* trees was selected as a significant environmental variable, or why *Rubus idaeus*, which is a species of open woods (Moss 1994), is associated with higher canopy cover.

When data from all sites were combined, forward selection in CCA determined significant environmental variables were north south aspect (axis 2, correlation = -0.559), age of *Betula occidentalis* trees (axis 1, correlation = 0.929), depressions (instead of hummocks) (axis 2, correlation = -0.404), and stem density of trees (axis 2, correlation = 0.718) (Table 2.9, Figure 2.18). Species associated with a north facing aspect and depressions, both of which tend to accumulate moisture, included wetland species such as *Salix* spp. (low shrub), *Ranunculus gmelinii* DC., *Hippuris vulgaris* L., *Schoenoplectus acutus* (Muhl. ex Bigel.) A. Löve & D. Löve, *Typha latifolia* L., *Rorippa islandica* (Oeder) Borbás, and *Platanthera aquilonis*. Stem density of tall shrubs did not exhibit the same relationship with

wetland species as in Sites 2 and 3 at this level of sampling. Species associated with greater tall shrub stem density included *Urtica dioica* L., fungus, *Galium boreale*, and *Caragana arborescens* (tall shrub). Again, it is not known why age of *Betula occidentalis* trees was chosen as a significant environmental variable.

4.5 Bryophytes

Site 1 contained five community types, determined by cluster analysis and ISA (Table 2.7). Pair wise comparisons using MRPP indicated most community types were not significantly different ($p = 0.005$) (Table 2.7). Comparisons between types 2 and 5, and 4 and 5 yielded significant and relatively strong separations. Based on numerical results there is one community type in this site: type 2 (*Ceratodon purpureus* (Hedw.) Brid. and *Bryum* spp. Hedw.). Several comparisons yielded high A values; however, the significances of these comparisons were all greater than the corrected alpha (0.005) (Table 2.7). The relatively small sample size may not have been large enough to capture differences between these community types (McCune and Grace 2002).

Although cluster analysis and ISA differentiated two community types (Table 2.12) in Site 2 ($A = 0.1348$, $p < 0.001$) (Table 2.7), the low A value indicated there was low separation between communities; therefore there were no distinct bryophyte community types.

Cluster analysis and ISA identified four community types in Site 3 (Table 2.12). MRPP comparisons showed types 1 and 2 exhibited significant and relatively strong differences in community composition (Table 2.7), and can therefore be considered separate community types. Pair wise comparisons between type 4 and types 1, 2 and 3 resulted in high A values, although p-values were greater than the corrected alpha (0.0083) (Table 2.7). This suggests the differences between types 1 and 2 were not strong and the sample size was likely not large enough to capture differences between these community types. Thus only 2 bryophyte community types existed: type 1 (*Amblystegium serpens* (Hedw.) Schimp.) and type 2 (*Pleurozium schreberi* (Brid.) Mitt.).

When all quadrats from all sites were combined, cluster analysis and ISA identified eight community types (Table 2.12); 13 of the 28 pair wise comparisons

indicated significant and strong differences between community types (Table 2.7). Nine of the 28 pair wise comparisons yielded strong A values, although p-values were greater than the corrected alpha (0.0018) (Table 2.7). Although sample size was relatively large (73 quadrats), the relatively small sample sizes for individual sites affected the ability of MRPP to capture differences between these community types. Due to the complex nature of the significant and non-significant differences between each of the 8 community types, it is concluded there were several, because types 1, 2, and 3 were different, types 5, 6, and 7 were different, and types 3, 5, and 7 were different.

Monte Carlo permutation test results in RDA for Sites 1 and 2 indicated all axes combined were significant. In Site 3 and all sites combined the first canonical axis and all axes combined were significant (Table 2.8), and the ordinations explained 8.1 to 30.8% of the variation (Table 2.10). As in the 5 x 5 m quadrat analyses, species-environment correlations were not as strong as in the 1 x 1 m quadrat analyses, as indicated by the smaller eigenvalues for each axis in the ordinations (Figures 2.19, 2.20, 2.21, 2.22). Forward selection found significant environmental variables within each ordination (Table 2.9).

Forward selection in RDA designated age of *Betula occidentalis* trees (axis 1, correlation = 1.000) as the only environmental variable being a significant descriptor of the relationship between species data and environmental variables in Site 1 (Table 2.9, Figure 2.19). Community type 2 was associated with younger *Betula occidentalis* trees, but this is not known why. The combination of species in this site is interesting, as they were indicative of a wide variety of habitats (Crum 1983). The most interesting were *Tortula mucronifolia* Schwägr., which is found on calcareous soil and rocks, and *Drepanocladus* spp. (Müll. Hal.) G. Roth, which is found in wet habitats such as fens, bogs, and swamps and is frequently submerged. The presence of *Sanionia uncinata* (Hedw.) Loeske is also interesting as it is characteristic of coniferous forests. This site does not contain appreciable mineral soil, rocks, or conifers, nor wet areas that would be submerged during the year; therefore these three species provide a hint at the type of vegetation prior to initial disturbance. Propagules of these species were likely in the diaspore bank at the time of substrate placement and were growing where they landed when the substrate was dumped onto the stockpile. Their

presence may a factor of substrate origin and random chance. It is not surprising to find the remaining species in this site as they can all be found in disturbed sites, on decaying wood or bare soil.

Forward selection in RDA designated tall shrub stem density (axis 1, correlation = 1.000) as a significant descriptor of the relationship between species data and environmental variables in Site 2 (Table 2.9, Figure 2.20). Species associated with greater tall shrub stem density include *Tomenthypnum nitens*, *Drepanocladus* spp., *Amblystegium serpens*, and *Aulacomnium palustre*. *Salix* spp. and *Populus balsamifera* were dominant low shrubs in this site, and as such could be indicators of more mesic conditions that support the growth of the above mentioned bryophyte species, all of which prefer moist to wet habitats (Crum 1983). The association of community types with the environmental vector does not appear relevant, as the two types were not significantly different.

In Site 3, forward selection in RDA determined depressions (not hummocks) (axis 2, correlation = 0.928) and tall shrub stem density (axis 1, correlation = 0.911) explained the most variation (Table 2.9, Figure 2.21). *Salix* spp. and *Populus balsamifera* dominated the tall shrub stem counts in this site, and could be used as proxy indicators of higher moisture conditions, as these species prefer moist habitats. Species associated with greater tall shrub stem density include *Leptobryum pyriforme* (Hedw.) Wilson, *Campylium stellatum*, *Pleurozium schreberi*, *Bryum* spp., and *Sanionia uncinata*, all of which can be found in moist to wet habitats. Community type 1 (characterized by *Amblystegium serpens*) was associated with decreased tall shrub stem density, and community type 2 (characterized by *Pleurozium schreberi*) was associated with greater tall shrub density. It is unclear why community type 1 was associated with lower tall shrub stem density, as *Amblystegium serpens* is generally found in swampy habitats.

When data from all three sites were combined, forward selection in RDA determined age of *Betula occidentalis* trees (axis 2, correlation = 0.350), depressions (not hummocks) (axis 2, correlation = 0.490), tree stem density (axis 2, correlation = -0.733), and tall shrub stem density (axis 1, correlation = 0.974) were significant (Table 2.9, Figure 2.22). Based on the correlation values of the environmental variables with the axes and vector length in the ordination diagram, tree stem and tall shrub stem densities show the strongest relationships

with the species data. Species associated with greater tall shrub stem density, which is dominated by *Salix* spp. and *Populus balsamifera* across sites, include *Sanionia uncinata*, *Leptobryum pyriforme*, *Campylium stellatum*, *Bryum* spp., *Amblystegium serpens*, and *Ceratodon purpureus*, all of which can be found in moist to wet habitats (Crum 1983). Species associated with greater tree stem density include *Bryum* spp., *Amblystegium serpens*, and *Ceratodon purpureus*.

4.6 Community development

Based on limited site histories, data collected on substrates, and current species compositions, the main pre-disturbance community on all three sites was likely a boreal wetland, such as a bog or fen. During site construction, the substrate was highly and very coarsely admixed (Figure 2.23), and little to no soil development has occurred, as expected for the relatively short time since the material was placed and time required for weathering and decomposition. However, an upland boreal forest plant community has developed from a lowland substrate on the three sites. Interpretation of the only picture taken during the first growing season following substrate placement (Figure 2.24) suggests the initial plant community may have been composed of early successional wetland species. Currently, the plant community on each site is composed mainly of early successional upland boreal species (Figure 2.25), but includes lowland and non-native species. It is clear that despite the odd substrate conditions present, succession is occurring. Dead individuals of *Salix* and *Betula papyrifera*, both early successional species, are suggestive of this. Several *Picea glauca* low shrubs were found in each site, a further indication succession is occurring, as this species co-dominates with *Populus* under normal upland boreal forest succession. Barring major disturbances such as fire or site deconstruction, the plant communities will likely continue to develop into mid successional mixed wood forests, and given time, will eventually become late successional upland boreal communities.

5. Conclusions

- Natural recovery of boreal forest vegetation on a hummocky admixed peat-mineral substrate is possible.
- Substrate chemical properties were within normal ranges for the region.

- Different environmental variables were chosen as significant environmental variables for each sampling level.
- Clay and sand substrate texture influenced vascular species cover at the 1 x 1 m sampling level.
- Tall shrub stem density influenced vascular and non-vascular species presence / absence at the 5 x 5 m sampling level.
- Canopy cover influenced vascular species presence / absence but not non-vascular species presence / absence at the 5 x 5 m sampling level, or vascular species cover at the 1 x 1 m sampling level.
- Age of *Betula occidentalis* trees influenced vascular and non-vascular species presence / absence at the 5 x 5 m sampling level.
- Overall, tall shrub stem density, tree canopy cover, and age of *Betula occidentalis* trees explained the most variation within the species data.
- Micro topographic (1 x 1 m) characteristics that did not show relationships with vascular species cover include degree of slope, percent cover bare ground, and litter depth. Micro topographic (1 x 1 m) characteristics that showed variable relationships with vascular species cover include aspect, hummock size, and location of 1 x 1 m quadrats in relation to topographic relief.
- Macro topographic (5 x 5 m) characteristics that did not show relationships with vascular species presence / absence include presence of rock and, with the exception of *Betula occidentalis*, age of all tree species. Macro topographic (5 x 5 m) characteristics that showed variable relationships with vascular species presence / absence include aspect and hummock size.
- Macro topographic (5 x 5 m) characteristics that did not show relationships with non-vascular species presence / absence include aspect, tree canopy cover, presence of rock, and age of all tree species except *Betula occidentalis*. Macro topographic (5 x 5 m) characteristics that showed variable relationships with non-vascular species presence / absence include hummock size and tree stem density.
- A mix of organic matter and mineral soil may provide an adequate substrate for some boreal species; the mix should be as homogeneous as possible to avoid large patches of bare, nutrient poor, mineral soil that do not support vegetation, and to ameliorate soil structure degradation.

- Donor soil seed and diaspore banks likely played a large role in revegetation. Species presence appears to be partly related to location of propagules in the seed / diaspore bank and where propagules landed after transport to the sites.
- Plant species were resilient and adaptive; they successfully grew in areas outside of their typical habitat range.
- With the exception of a few wet communities, vascular vegetation had not formed any distinct community types. Non-vascular species showed more distinct community types than vascular plants.
- After 26 to 34 years the research sites appear to be transitioning from early to mid successional communities.
- Plant community development appeared to be a product of several measured environmental variables and factors such as soil seed bank dynamics, propagule dispersal, germination conditions, and initial species composition, all of which likely played a role early in the history of these sites.

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7. Figures



Figure 2.1. Map showing the location of the Athabasca Oil Sands Region within Alberta, Canada (<http://www.grandsespaces.ch/>).



Figure 2.2. Map showing the location of research sites on the Suncor Energy Inc. mine, as indicated by the white circles (from Suncor Energy Inc).



Figure 2.3. Map of Site 1, as indicated by the black dashed line. Site is approximately 4 ha in size (from Suncor Energy Inc.).



Figure 2.4. Map of Site 2, as indicated by the black dashed line. Site is approximately 20 ha in size (from Suncor Energy Inc.).

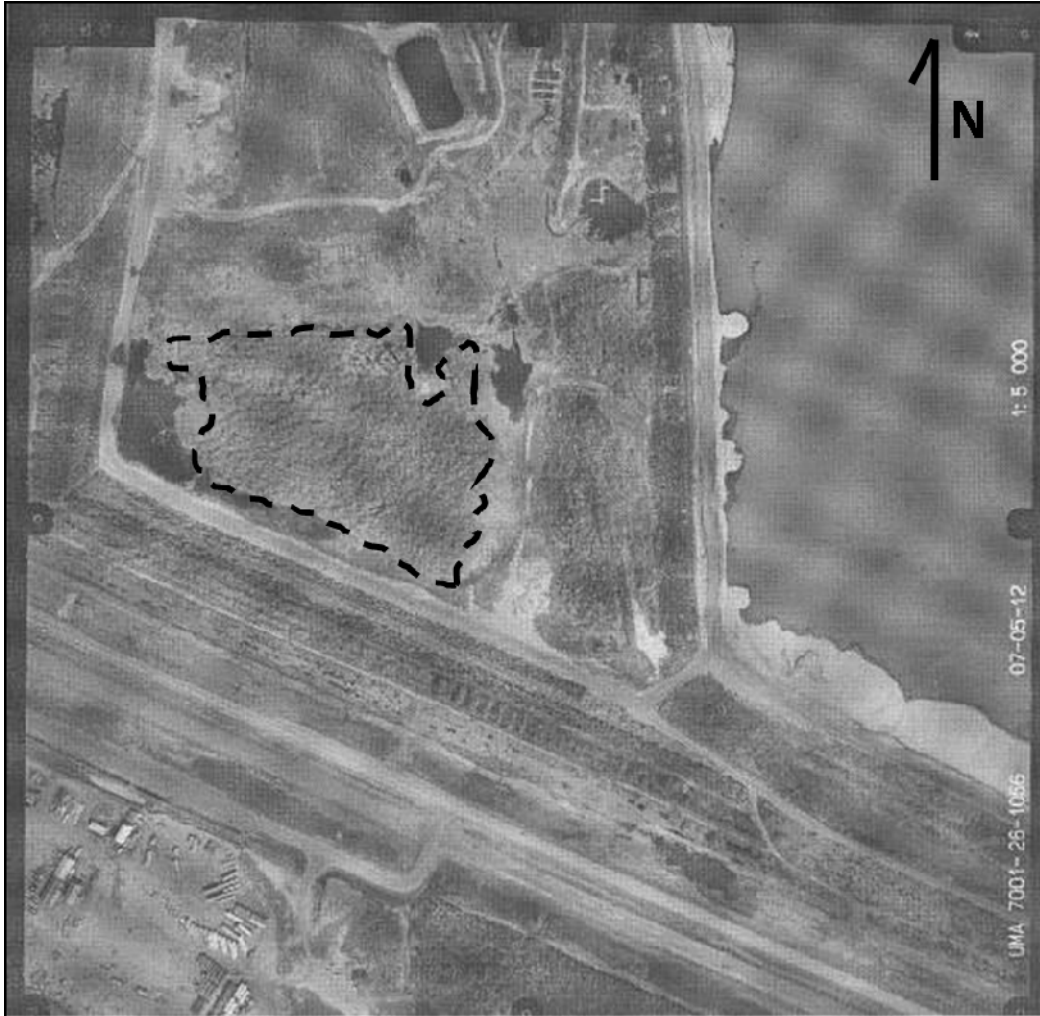


Figure 2.5. Map of Site 3, as indicated by the black dashed line. Site is approximately 6 ha in size (from Suncor Energy Inc.).

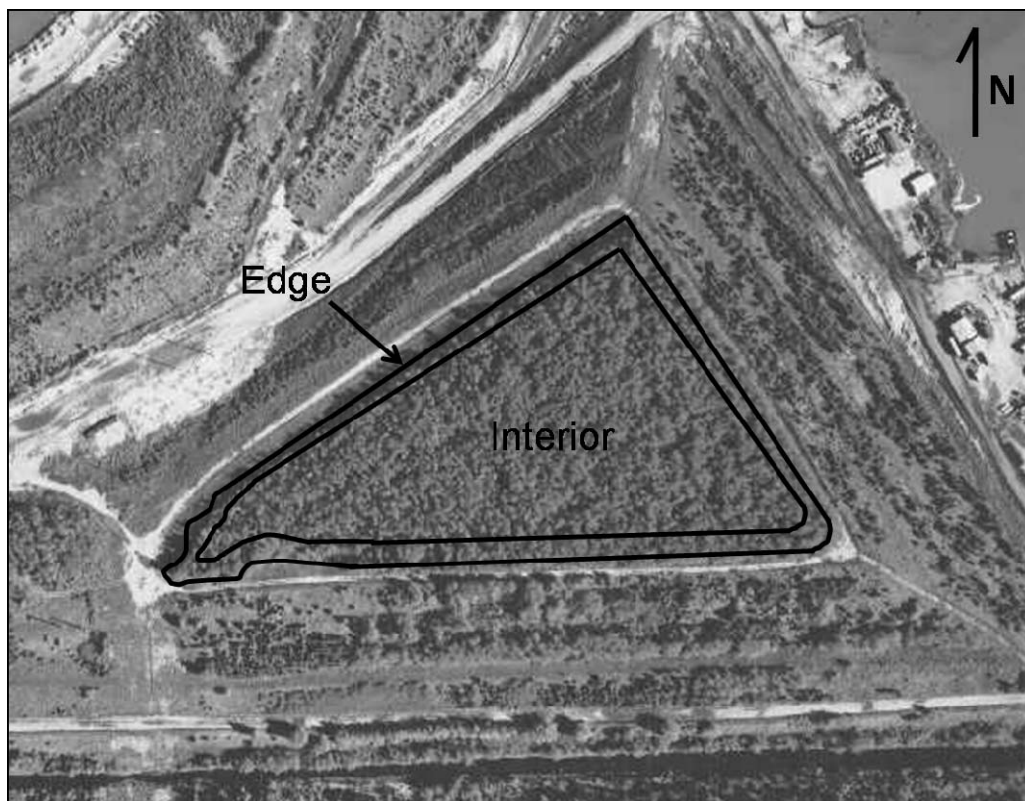


Figure 2.6. Stratification of Site 1 into an edge (5 m wide; not to scale) and an interior (from Suncor Energy Inc.).

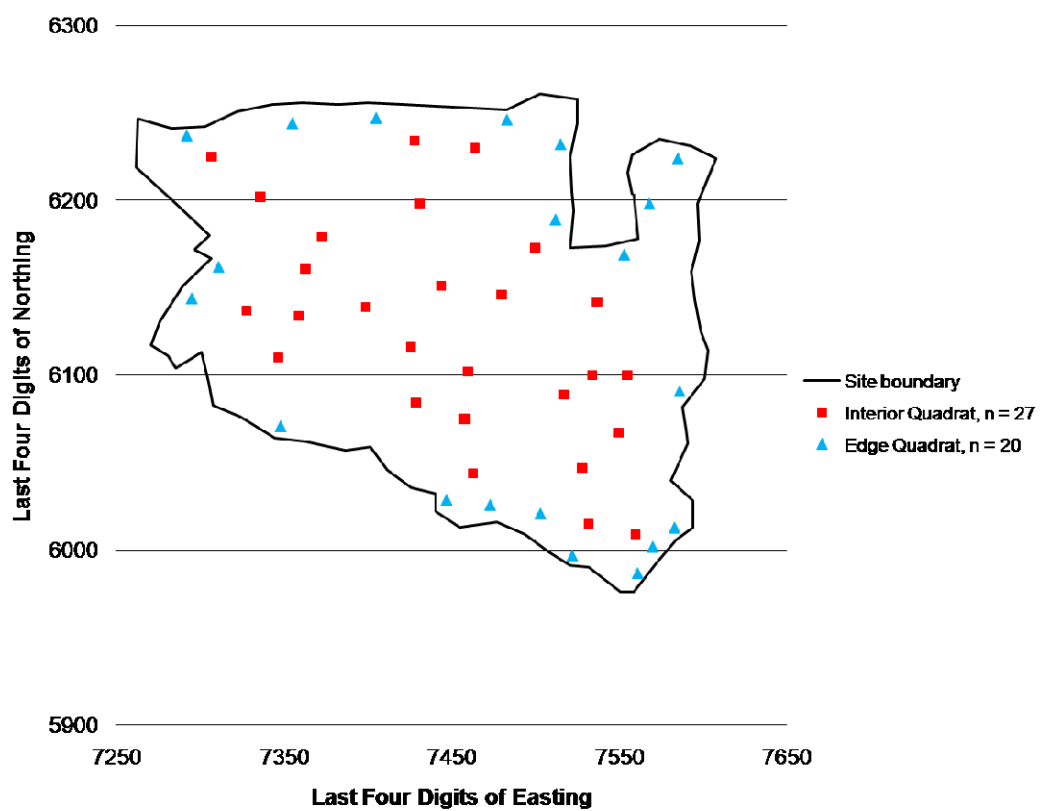


Figure 2.7. Map of Site 3 showing random locations of interior and edge quadrats.

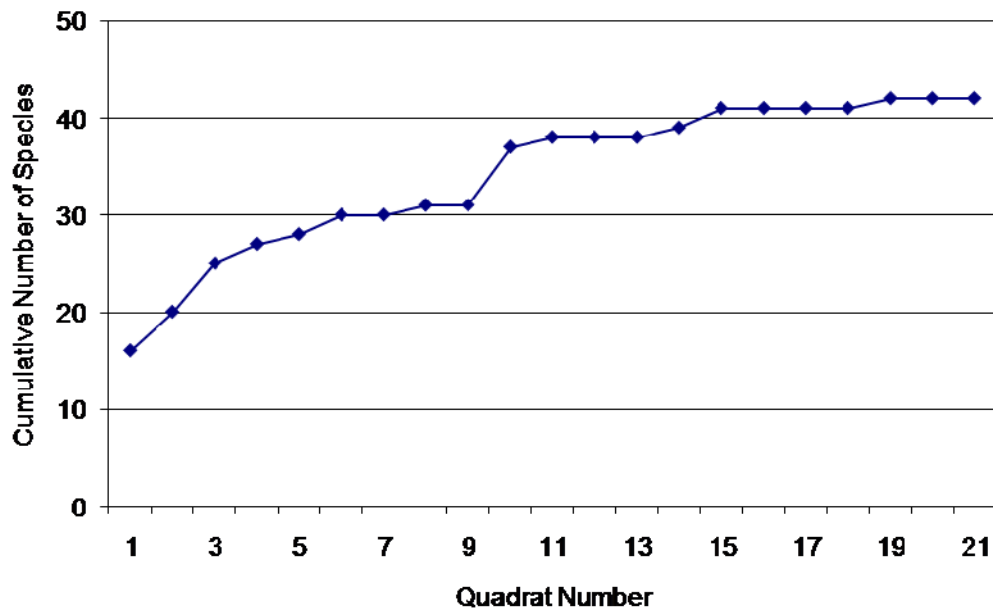


Figure 2.8a. Site 1 vascular species area curve for interior quadrats.

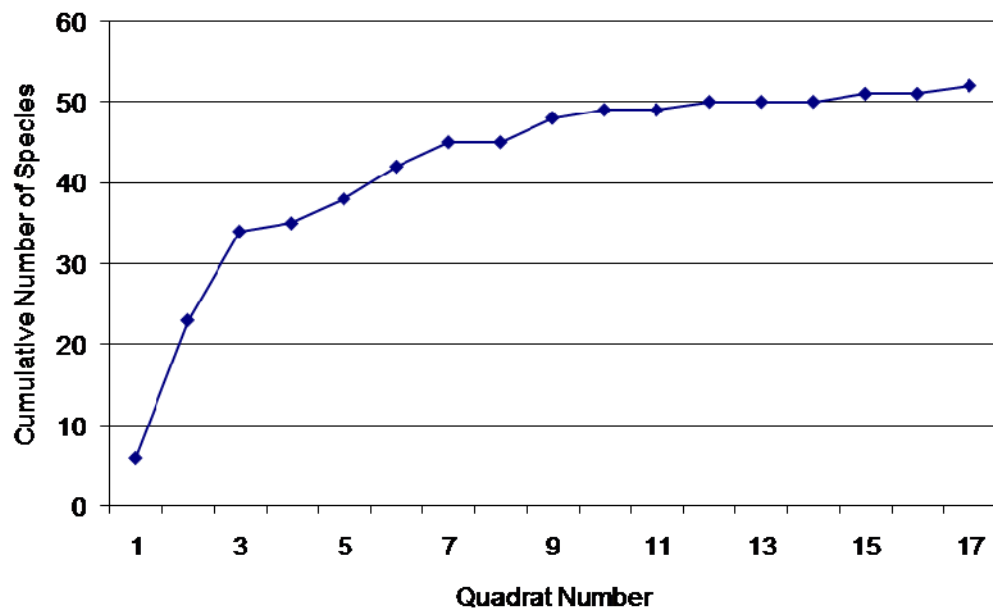


Figure 2.8b. Site 1 vascular species area curve for edge quadrats.

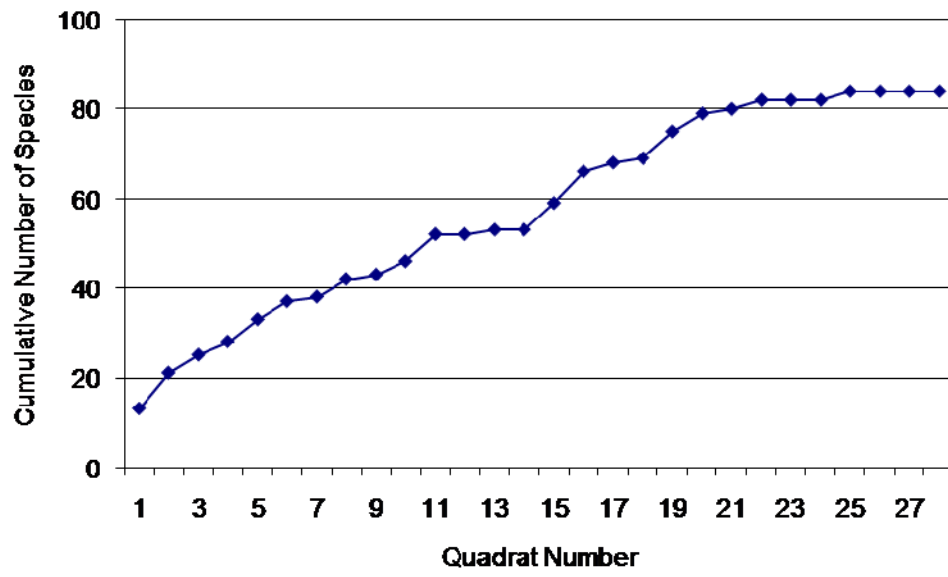


Figure 2.9a. Site 2 vascular species area curve for interior quadrats.

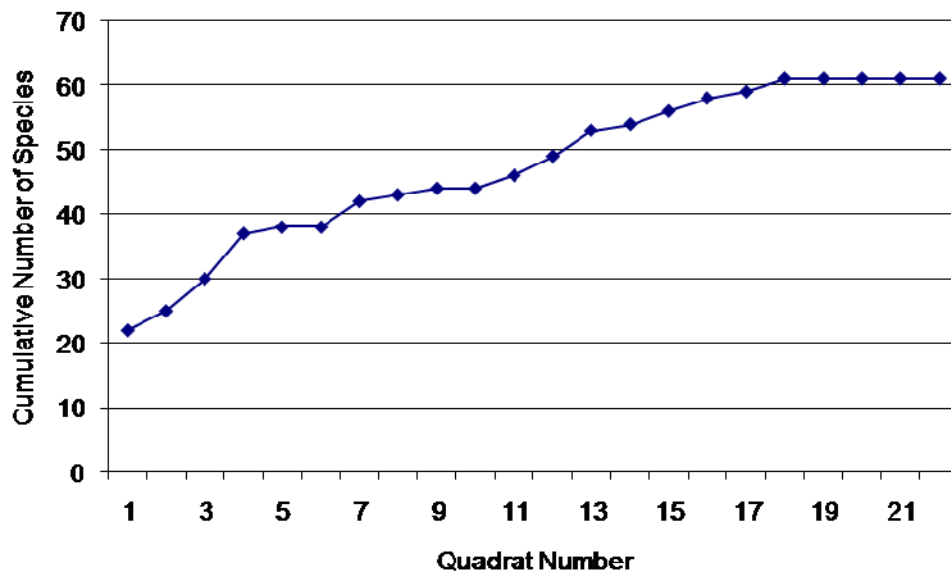


Figure 2.9b. Site 2 vascular species area curve for edge quadrats.

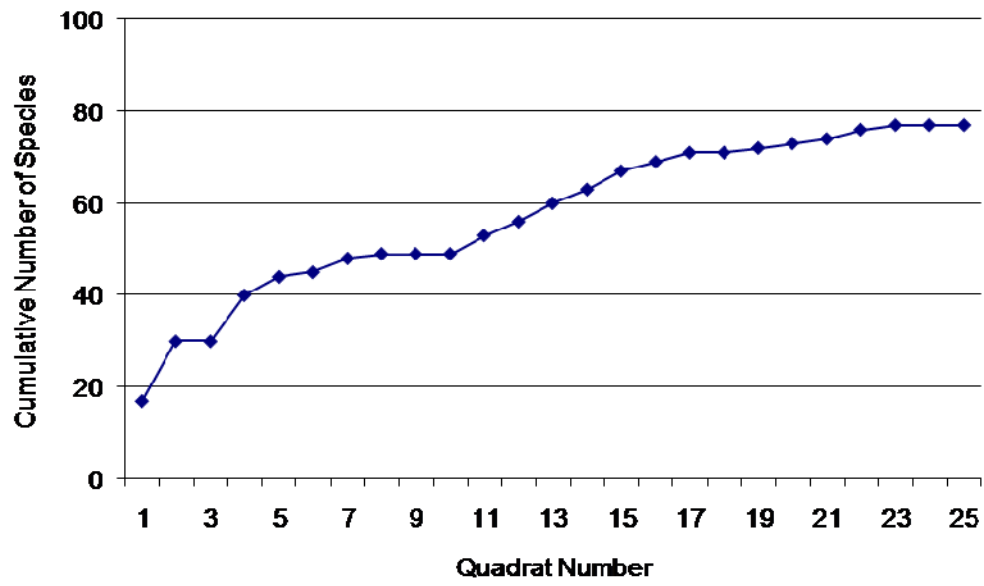


Figure 2.10a. Site 3 vascular species area curve for interior quadrats.

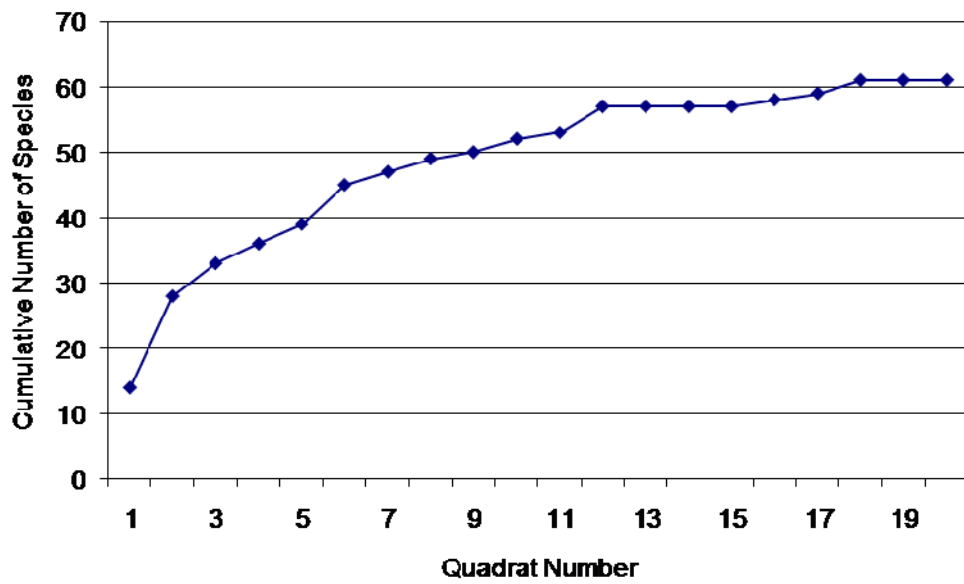


Figure 2.10b. Site 3 vascular species area curve for edge quadrats.

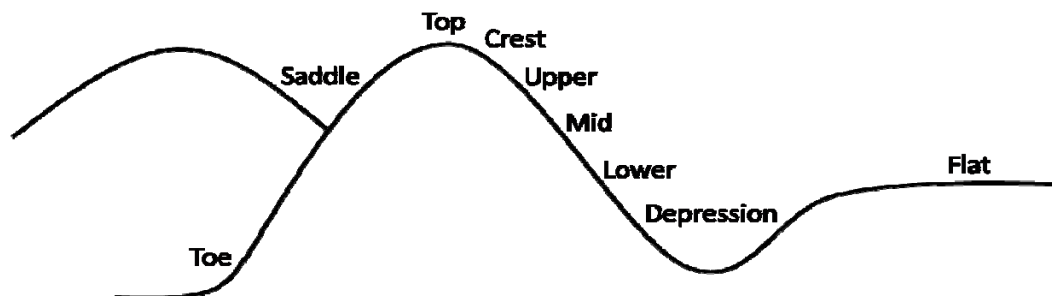
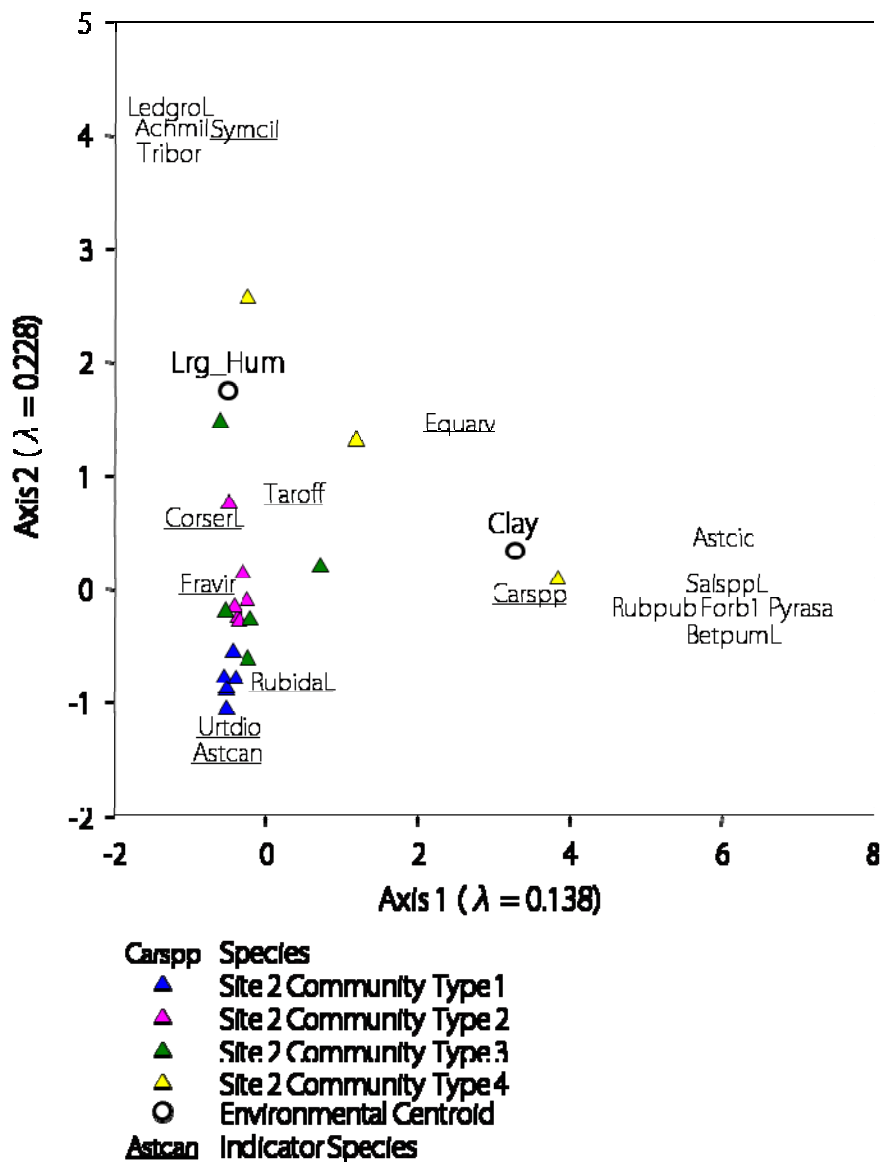
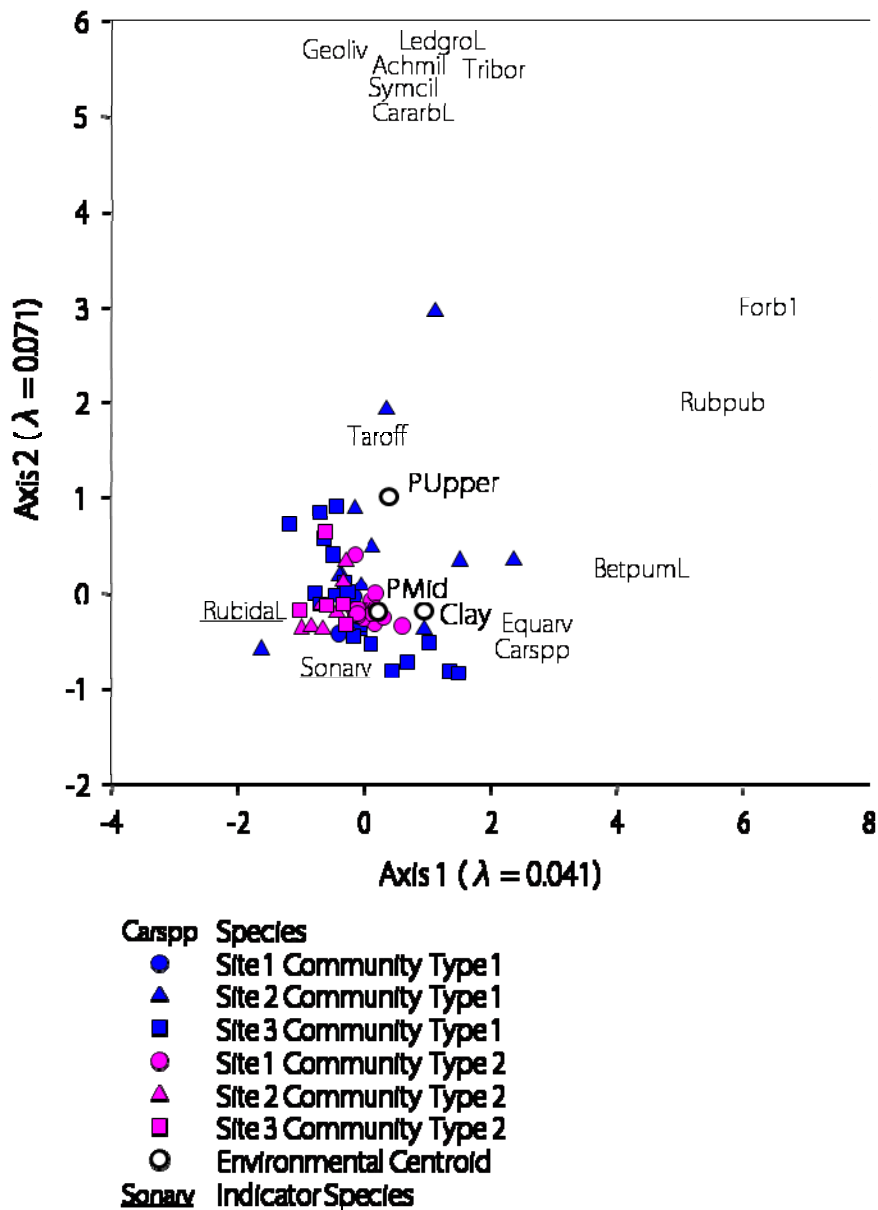


Figure 2.11. Topographic positions for 1 x 1 quadrat positions.



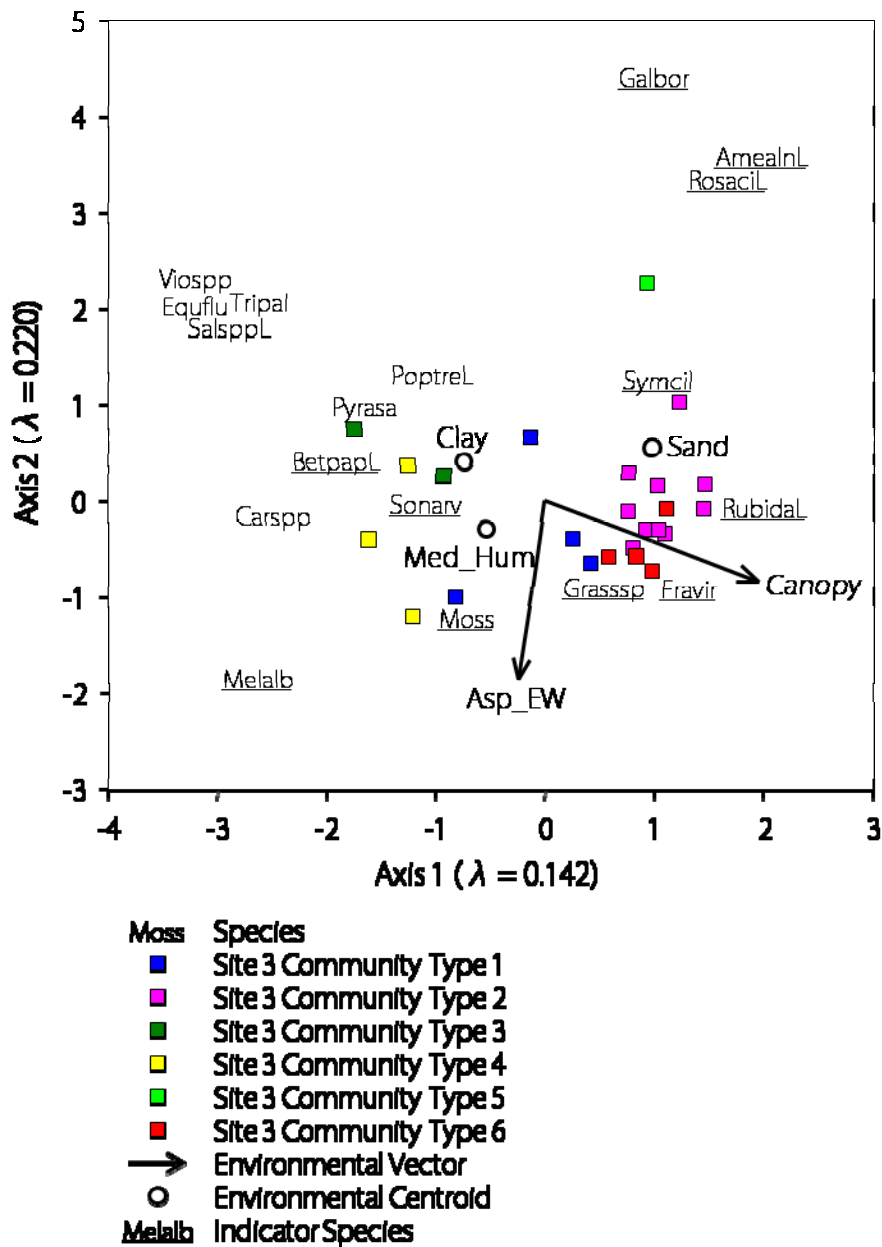
Clay = clay substrate texture; Large_Hum = large sized hummocks; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.12. Canonical correspondence analysis ordination of vascular species data and significant environmental variables for 1 x 1 m interior quadrats at Site 2.



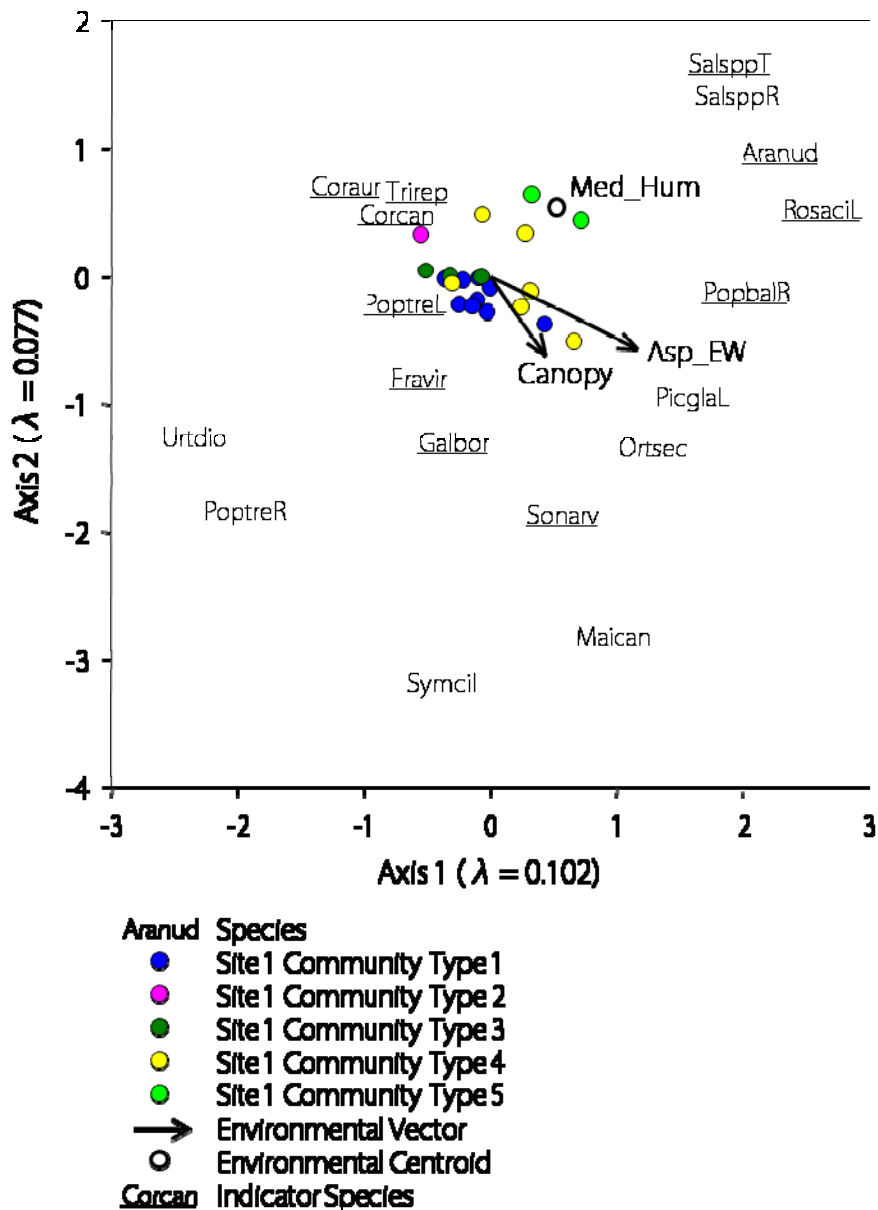
Clay = clay substrate texture; PMid = mid slope position of the quadrat; PUpper = upper slope position of the quadrat; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.13. Canonical correspondence analysis ordination of vascular species data and significant environmental variables for 1 x 1 m interior quadrats for all sites combined.



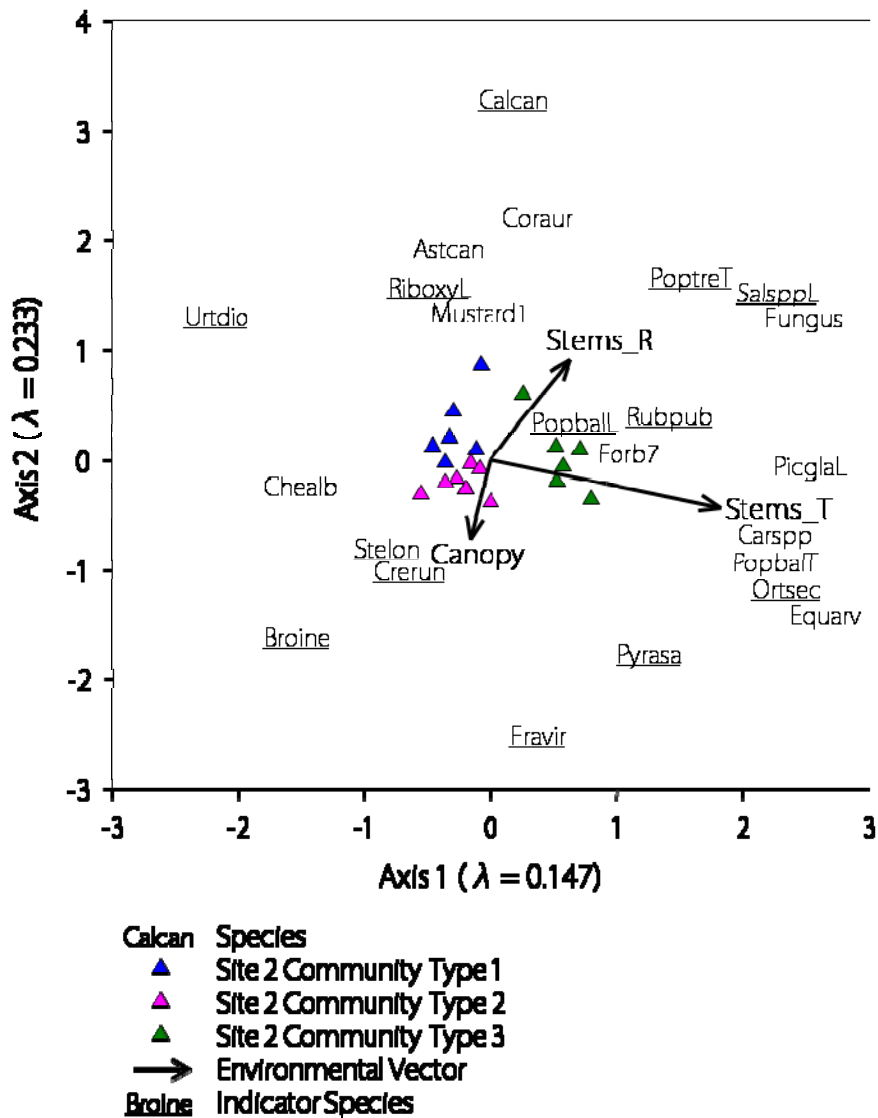
Asp_EW = east west aspect of the quadrat; Canopy = percent tree canopy cover; Clay = clay substrate texture; Med_Hum = medium sized hummocks; Sand = sand substrate texture; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.14. Canonical correspondence analysis ordination of vascular species data and significant environmental variables for 1 x 1 m interior quadrats at Site 3.



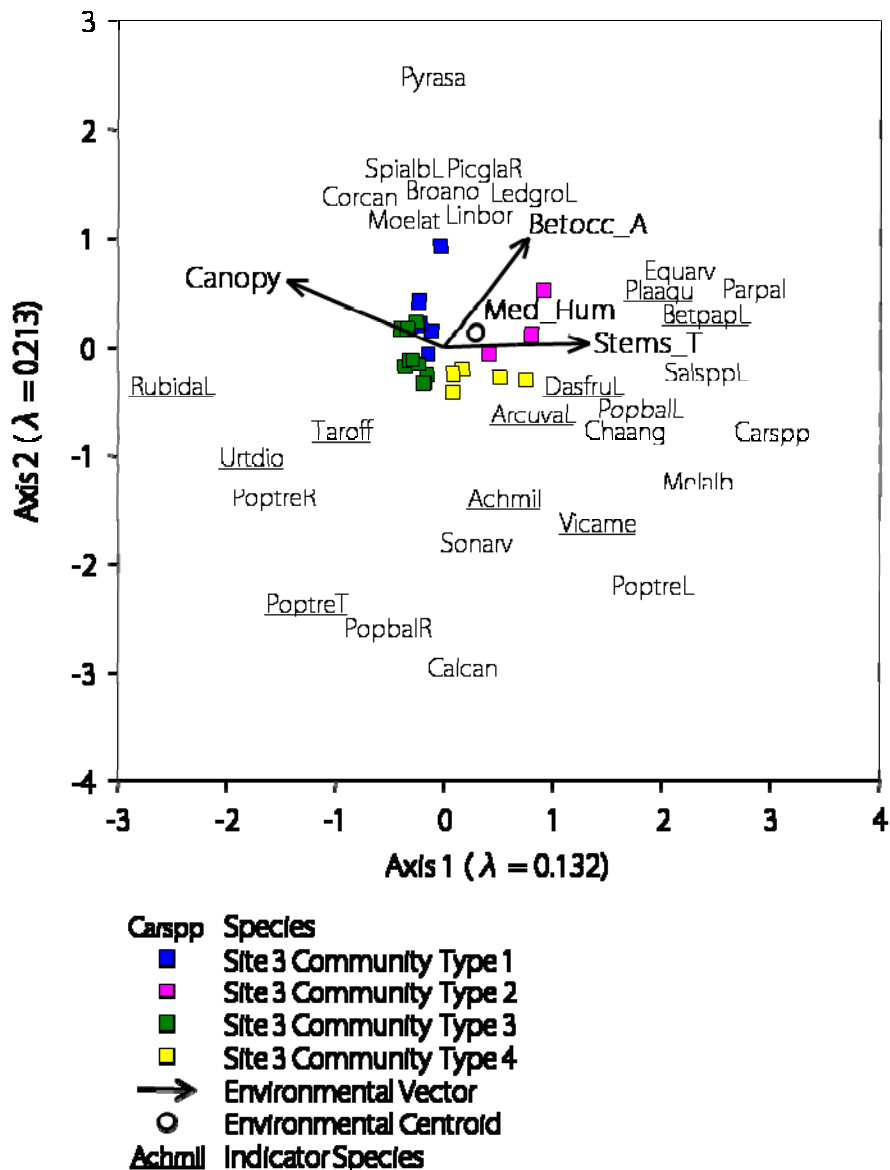
Asp_EW = east-west aspect of the quadrat; Canopy = percent tree canopy cover; Med_Hum = medium sized hummocks; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.15. Redundancy analysis ordination of vascular species data and significant environmental variables for 5 x 5 m interior quadrats at Site 1.



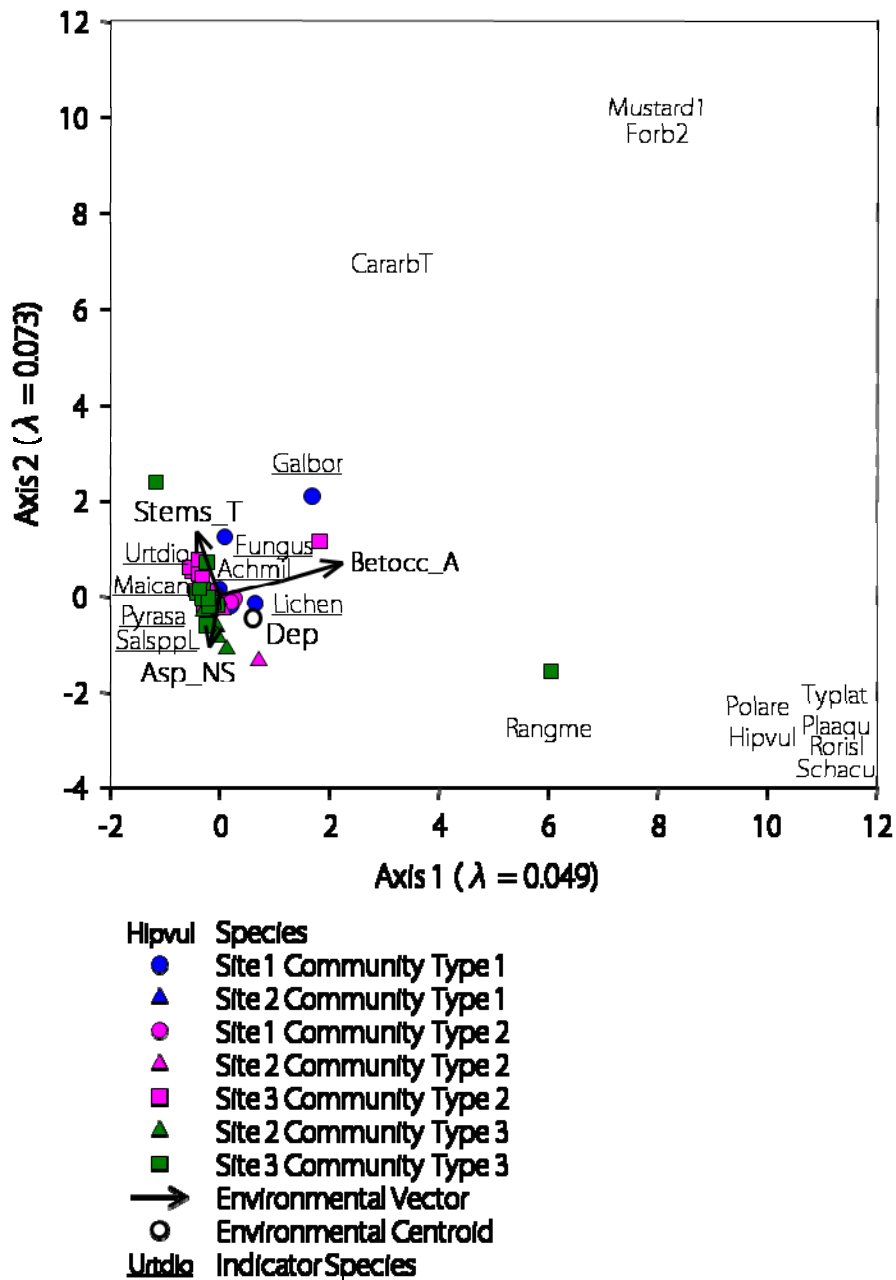
Canopy = percent tree canopy cover; Stems_R = tree stem density; Stems_T = tall shrub stem density; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.16. Redundancy analysis ordination of vascular species data and significant environmental variables for 5 x 5 m interior quadrats at Site 2.



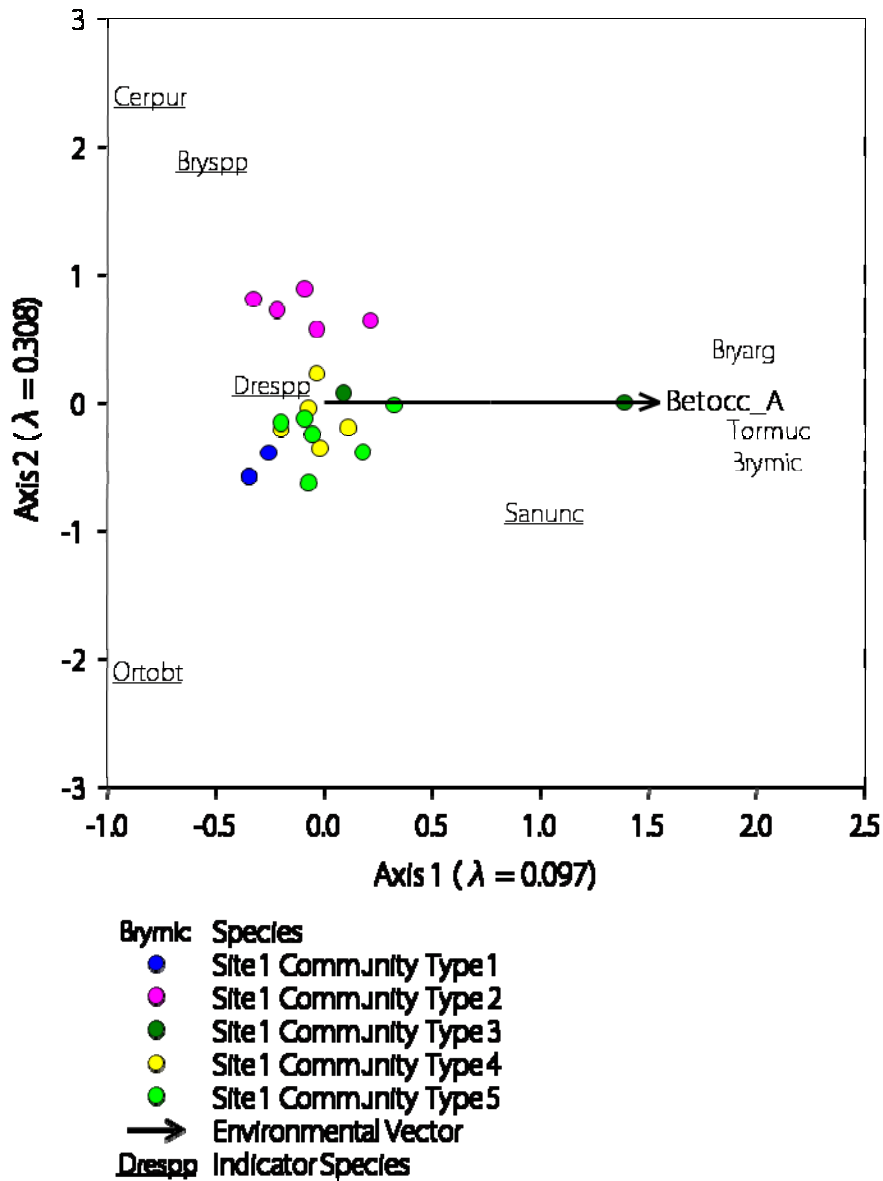
Betocc_A = age of *Betula occidentalis* trees; Canopy = percent tree canopy cover; Med_Hum = medium sized hummocks; Stems_T = tall shrub stem density; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.17. Redundancy analysis ordination of vascular species data and significant environmental variables for 5 x 5 m interior quadrats at Site 3.



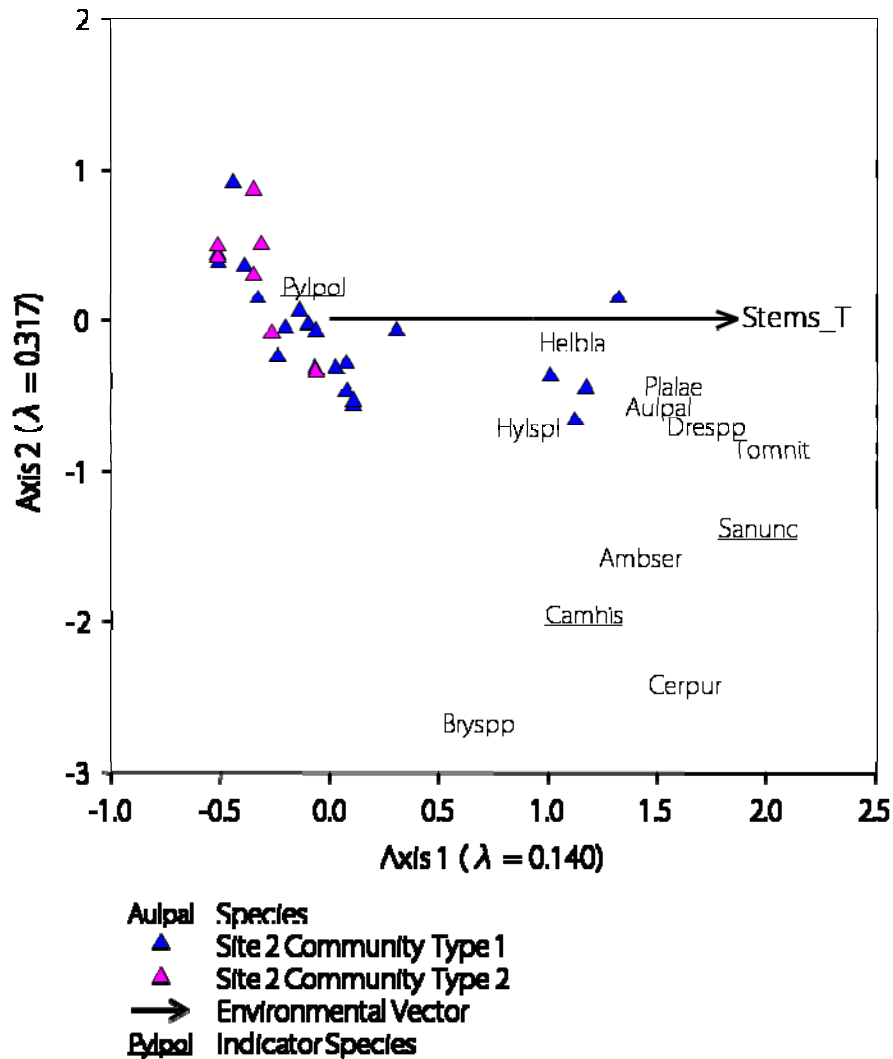
Asp_NS = north south aspect of the quadrat; Betocc_A = age of *Betula occidentalis* trees; Dep = depression (no hummocks); Stems_T = tall shrub stem density; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.18. Canonical correspondence analysis ordination of vascular species data and significant environmental variables for 5 x 5 m interior quadrats for all sites combined.



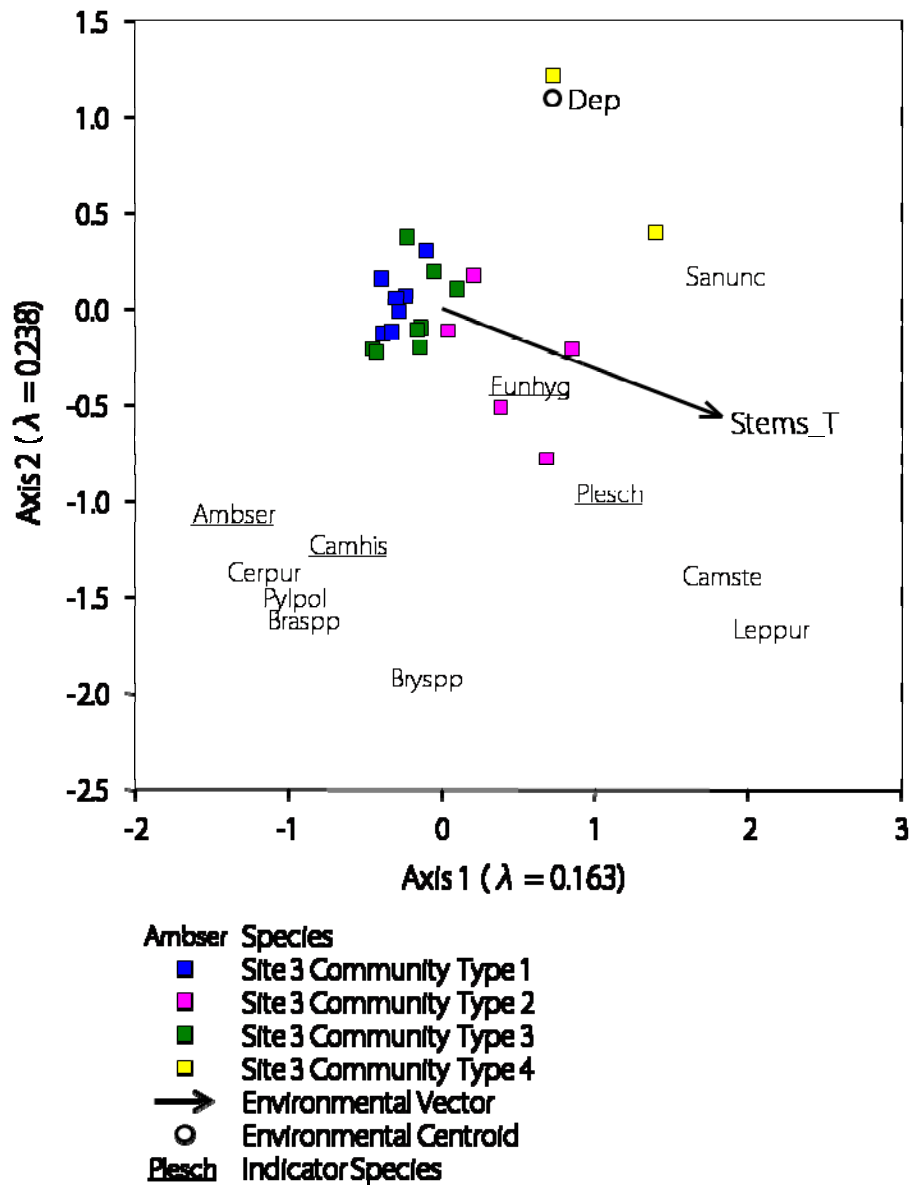
Betocc_A = age of *Betula occidentalis* trees; some species have been moved from their original location increase clarity of the ordination; see Table A6 for species codes

Figure 2.19. Redundancy analysis ordination of non-vascular species data and significant environmental variables for 5 x 5 m interior quadrats at Site 1.



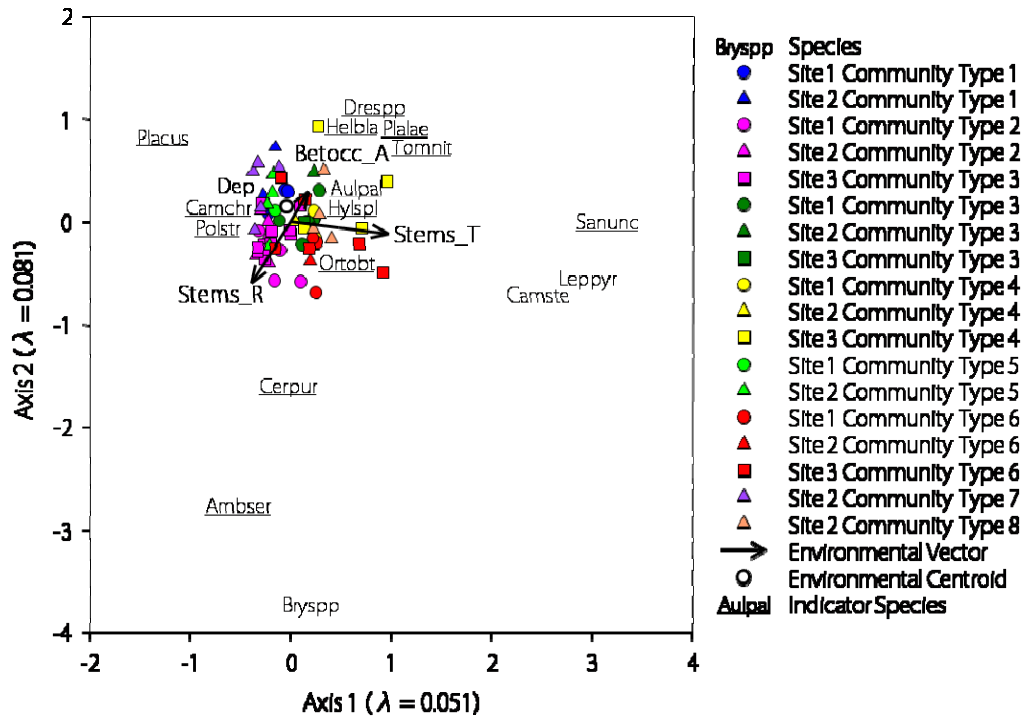
Stems_T = tall shrub stem density; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.20. Redundancy analysis ordination of non-vascular species data and significant environmental variables for 5 x 5 m interior quadrats at Site 2.



Dep = depression (no hummocks); Stems_T = tall shrub stem density; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.21. Redundancy analysis ordination of non-vascular species data and significant environmental variables for 5 x 5 m interior quadrats at Site 3.



Betocc_A = age of *Betula occidentalis* tree; Dep = depression (no hummocks); Stems_R = tree stem density; Stems_T = tall shrub stem density; some species have been moved from their original location to increase clarity of the ordination; see Table A6 for species codes

Figure 2.22. Redundancy analysis ordination of non-vascular species data and significant environmental variables for 5 x 5 m interior quadrats in all sites combined.



Figure 2.23. Picture of Site 3 profile illustrating admixed substrate.



Figure 2.24. Picture of Site 1 looking southeast; initial conditions during spring 1976 after winter placement of water logged substrate.



Figure 2.25. Picture of Site 1 illustrating average plant community growth that could be found in all sites in summer 2007.

8. Tables

Table 2.1. Topographic position classes of 1 x 1 m quadrats.

Description	Class
Top	1
Crest	2
Upper	3
Mid	4
Lower	5
Toe	6
Saddle	7
Depression	8
Flat	9

Table 2.2. Lengths of the longest detrended correspondence analysis gradient for each sampling scale and each site, and the chosen ordination method.

Sample Scale	Site	Longest Gradient	Method	Chosen Method
1x1	Site 1	3.008	Linear/Unimodal	RDA
	Site 2	4.541	Unimodal	CCA
	Site 3	3.487	Unimodal	CCA
	All Sites	4.484	Unimodal	CCA
5x5	Site 1	2.344	Linear	RDA
	Site 2	2.336	Linear	RDA
	Site 3	3.150	Linear/Unimodal	RDA
	All Sites	4.491	Unimodal	CCA
Bryophytes	Site 1	2.308	Linear	RDA
	Site 2	2.592	Linear	RDA
	Site 3	3.362	Linear/Unimodal	RDA
	All Sites	3.476	Linear/Unimodal	RDA

Table 2.3. Species richness by growth form for interior and edge quadrats in each site.

Growth Form	Site 1			Site 2			Site 3		
	Interior	Edge	Overlap ¹	Interior	Edge	Overlap	Interior	Edge	Overlap
Liverwort	2	2	2	4	3	3	2	4	2
Bryophyte	15	15	13	22	18	11	17	22	13
Sedge	0	0	0	2	0	0	1	1	1
Grass	6	8	5	10	10	7	6	5	3
Forb	25	31	21	40	24	20	48	29	22
Low Shrub	13	18	11	17	16	13	20	21	17
Tall Shrub	9	10	8	6	11	6	8	8	8
Tree	6	4	4	3	5	3	8	6	6
Sum ²	66	80	64	101	76	63	100	89	72
Combined Sum ³	90			120			126		

¹ Overlap indicates the number of species that occur in the edge and interior quadrats of each site

² Sum of species for interior and edge quadrats takes into account duplication of species that occur in the low shrub, tall shrub, and tree growth form categories.

³ Combined sum of species found in the interior and edge quadrats takes into account duplication of species that occur in both stratifications, as well as duplication of species in the low shrub, tall shrub, and tree growth form categories

Table 2.4. Hummock size classes for 1 x 1 m and 5 x 5 m quadrats.

Class	Description
1	Depression
2	Flat
3	Small
4	Medium
5	Large
6	Very large
7	Very, very large

Table 2.5. Substrate texture classes for 1 x 1 m quadrats.

Class	Description
1	Sand
2	Silt
3	Clay
4	Organic matter

Table 2.6. Vascular community types and significant differences, as determined by cluster analysis and indicator species analysis from the 1 x 1 m interior quadrats.

Site	Community Type	Significant Differences	Species	Indicator Value	P-Value
1	1	a	<i>Salix</i> spp. (L ¹)	0.462	0.024
			<i>Symphyotrichum ciliolatum</i>	0.370	0.032
	2	b	<i>Rubus idaeus</i>	0.592	0.001
2	1	a	<i>Rubus idaeus</i>	0.414	0.006
			<i>Urtica dioica</i>	0.524	0.033
	2	b	<i>Fragaria virginiana</i>	0.810	0.002
			<i>Taraxacum officinale</i>	0.517	0.033
			<i>Astragalus canadensis</i>	0.400	0.014
	3	c	<i>Cornus sericea</i> (L)	0.400	0.017
			<i>Equisetum arvense</i>	0.765	0.001
			<i>Symphyotrichum ciliolatum</i>	0.667	0.015
			<i>Carex</i> spp.	0.540	0.031
	4	abc			
3	1	ac	<i>Amelanchier alnifolia</i> (L)	0.250	0.584
	2	b	<i>Rubus idaeus</i> (L)	0.427	0.001
	3	abc	<i>Salix</i> spp. (L)	1.000	0.008
			<i>Betula papyrifera</i> (L)	0.848	0.018
			Grass spp.	0.691	0.034
	4	a	<i>Melilotus albus</i>	1.000	0.001
			Moss	0.543	0.026
	5	abc	<i>Rosa acicularis</i> (L)	0.954	0.003
			<i>Symphyotrichum ciliolatum</i>	0.765	0.007
			<i>Galium boreale</i>	1.000	0.05
	6	c	<i>Fragaria virginiana</i>	0.751	0.001
All	1	a	<i>Sonchus arvensis</i>	0.464	0.001
	2	b	<i>Rubus idaeus</i> (L)	0.732	0.001

¹ L = low shrub

Table 2.7. Multi-response permutation procedure pair wise comparisons of community types in each site.

Sampling Scale	Significance	Site	Comparison	A	P	Corrected Alpha
1x1	Significant P-Value and High A Value	3	2 vs 4	0.2747	0.001998	0.0033
			4 vs 6	0.4148	<0.001	
	Significant P-Value and Low A Value	1	1 vs 2	0.09073	<0.001	0.05
			1 vs 2	0.1901	0.001998	
		2	1 vs 3	0.1122	<0.001	0.0083
			2 vs 3	0.1175	<0.001	
		3	1 vs 2	0.154	<0.001	0.0033
			2 vs 6	0.1652	<0.001	
		All	1 vs 2	0.1272	<0.001	0.05
			1 vs 4	0.2514	0.017982	
	Not Significant P-Value and High A Value	3	1 vs 3	0.2523	0.012987	0.0033
			1 vs 6	0.2253	0.024975	
			3 vs 5	0.2835	0.32867	
			4 vs 5	0.2785	0.25774	
			5 vs 6	0.3582	0.18981	
			2 vs 4	0.1981	0.01998	
	Not Significant P-Value and Low A Value	2	3 vs 4	0.1189	0.015984	0.0083
			1 vs 4	0.1149	0.027972	
		3	1 vs 5	0.1543	0.21179	0.0033
			2 vs 3	0.1916	0.016983	
			2 vs 5	0.1192	0.1039	
			3 vs 4	0.16	0.08991	
			3 vs 6	0.331	0.06993	
5x5	Significant P-Value and Low A Value	1	1 vs 3	0.05659	0.002997	0.005
			1 vs 4	0.04278	0.002997	
		2	1 vs 2	0.1022	0.001998	0.017

Table 2.7. Multi-response permutation procedure pair wise comparisons of community types in each site (continued).

Sampling Scale	Significance	Site	Comparison	A	P	Corrected Alpha
5x5	Significant P-Value and Low A Value	2	1 vs 3	0.1439	0.002997	0.017
			2 vs 3	0.1339	< 0.001	
		3	1 vs 3	0.08593	0.001998	0.0083
			1 vs 4	0.111	0.003996	
			2 vs 3	0.1685	0.004995	
			3 vs 4	0.1233	< 0.001	
	Not Significant P-Value and High A Value	All	1 vs 2	0.04678	< 0.001	0.017
			1 vs 3	0.09501	< 0.001	
			2 vs 3	0.0364	< 0.001	
		1	2 vs 5	0.4184	0.33766	0.005
			3 vs 5	0.208	0.095904	
		Not Significant P-Value and Low A Value	1 vs 2	0.09047	0.093906	
			1 vs 5	0.1349	0.017982	
			2 vs 3	0.1161	0.24575	
			2 vs 4	0.1176	0.23177	
			3 vs 4	0.09777	0.021978	
			4 vs 5	0.0908	0.050949	
		3	1 vs 2	0.1275	0.011988	0.0083
			2 vs 4	0.1125	0.010989	
	Significant P-Value and High A Value	1	2 vs 5	0.2496	0.002997	0.005
			4 vs 5	0.207	0.001998	
		All	1 vs 2	0.2584	< 0.001	0.0018
			1 vs 3	0.243	< 0.001	
			1 vs 4	0.3217	< 0.001	
			1 vs 6	0.3439	< 0.001	
			2 vs 3	0.2608	< 0.001	
Bryophytes	Significant P-Value and High A Value	1	2 vs 5	0.2496	0.002997	0.005
			4 vs 5	0.207	0.001998	
		All	1 vs 2	0.2584	< 0.001	0.0018
			1 vs 3	0.243	< 0.001	
			1 vs 4	0.3217	< 0.001	
			1 vs 6	0.3439	< 0.001	
			2 vs 3	0.2608	< 0.001	

Table 2.7. Multi-response permutation procedure pair wise comparisons of community types in each site (continued).

Sampling Scale	Significance	Site	Comparison	A	P	Corrected Alpha
Bryophytes	Significant P-Value and High A Value	All	2 vs 4	0.2036	< 0.001	0.0018
			2 vs 5	0.2207	< 0.001	
			3 vs 5	0.2129	< 0.001	
			3 vs 7	0.3149	< 0.001	
			3 vs 8	0.2889	< 0.001	
			5 vs 6	0.3316	< 0.001	
			5 vs 7	0.2326	< 0.001	
			6 vs 7	0.3984	< 0.001	
	Significant P-Value and Low A Value	2	1 vs 2	0.1348	< 0.001	0.05
		3	1 vs 2	0.2161	0.002997	0.0083
			1 vs 3	0.1523	< 0.001	
			2 vs 3	0.1253	< 0.001	
		All	2 vs 6	0.124	< 0.001	0.0018
			2 vs 7	0.1997	< 0.001	
			2 vs 8	0.1854	< 0.001	
			3 vs 4	0.1718	< 0.001	
			3 vs 6	0.1796	< 0.001	
	Not Significant P-Value and High A Value	1	4 vs 6	0.1923	< 0.001	0.005
			1 vs 2	0.4249	0.017982	
			1 vs 3	0.3471	0.097902	
			1 vs 4	0.2921	0.01998	
			1 vs 5	0.2551	0.00999	
		3	2 vs 4	0.2977	0.013986	0.0083
			1 vs 4	0.3898	0.020979	
			2 vs 4	0.2013	0.054945	
			3 vs 4	0.278	0.021978	
			1 vs 5	0.2912	0.001998	
		All				0.0018

Table 2.7. Multi-response permutation procedure pair wise comparisons of community types in each site (continued).

Sampling Scale	Significance	Site	Comparison	A	P	Corrected Alpha
Bryophytes	Not Significant P-Value and High A Value	All	1 vs 7	0.295	0.001998	0.0018
			1 vs 8	0.4347	0.003996	
			4 vs 5	0.2689	0.002997	
			4 vs 7	0.2362	0.001998	
			4 vs 8	0.2134	0.001998	
			5 vs 8	0.3978	0.003996	
			6 vs 8	0.2057	0.003996	
			7 vs 8	0.3956	0.00999	
	Not Significant P-Value and Low A Value	1	2 vs 3	0.1437	0.052947	0.005
			3 vs 4	0.1562	0.048951	
			3 vs 5	0.07005	0.21079	

Table 2.8. Monte Carlo permutation test results of ordination axes for each site.

Sampling Scale	Site	Test of Significance of First Canonical Axis		Test of Significance of All (Canonical) Axes	
		F-Ratio	P-Value	F-Ratio	P-Value
1x1	1	- ¹	-	-	-
	2	2.711	0.012	2.505	0.002
	3	2.976	0.002	2.160	0.002
	All	2.535	0.042	2.100	0.002
5x5	1	1.939	0.004	1.770	0.002
	2	2.756	0.002	2.015	0.002
	3	2.883	0.002	2.166	0.002
	All	3.049	0.002	1.730	0.002
Bryophytes	1	- ²	-	2.032	0.036
	2	-	-	4.218	0.002
	3	4.082	0.004	3.271	0.002
	All	3.673	0.004	2.267	0.002

¹ No result because no significant environmental variables

² No result because only 1 significant environmental variable

Table 2.9. Results of forward selection of significant environmental variables in 1 x 1 m interior quadrats (non-significant variables not included).

Sampling Scale	Site	Variable	Extra Fit	P-Value	Intra-Set Correlations of Environmental Variables with Axes	
					Axis 1	Axis 2
1x1	1	- ¹	-	-	-	-
	2	Clay ²	0.5473	0.008	0.989	0.149
		Lrg_Hum ³	0.3656	0.012	-0.138	0.991
	3	Asp_EW ⁴	0.2195	0.034	-0.099	-0.816
		Canopy ⁵	0.4128	0.002	0.780	-0.367
		Clay	0.1967	0.050	-0.449	-0.398
		Med_Hum ⁶	0.2869	0.006	-0.604	0.537
		Sand ⁷	0.2428	0.024	0.458	0.427
	All	Clay	0.2444	0.008	0.840	-0.406
		PMid ⁸	0.1800	0.002	0.271	-0.286
		PUpper ⁹	0.2075	0.030	0.318	0.932
5x5	1	Asp_EW	0.0855	0.002	0.737	-0.413
		Canopy	0.0684	0.026	0.279	-0.447
		Med_Hum	0.0842	0.004	0.530	0.635
	2	Canopy	0.0674	0.024	-0.084	-0.495
		Stems_R ¹⁰	0.0653	0.048	0.331	0.618
		Stems_T ¹¹	0.1415	0.002	0.954	-0.300
	3	Betocc_A ¹²	0.0756	0.008	0.432	0.702
		Canopy	0.1078	0.002	-0.800	0.426
		Med_Hum	0.0519	0.042	0.304	0.174
		Stems_T	0.0779	0.002	0.738	0.019
	All	Asp_NS ¹³	0.1463	0.030	-0.080	-0.559
		Betocc_A	0.3367	0.002	0.929	0.362
		Dep ¹⁴	0.1565	0.048	0.329	-0.404
		Stems_R	0.1520	0.046	-0.172	0.718
Bryophytes	1	Betocc_A	0.0966	0.048	1.000	0.000
	2	Stems_T	0.1396	0.002	1.000	0.000
	3	Dep	0.0899	0.034	0.374	0.928
		Stems_T	0.1476	0.002	0.911	-0.415
	All	Betocc_A	0.0208	0.042	0.156	0.350
		Dep	0.0204	0.042	0.182	0.490
		Stems_R	0.0242	0.030	-0.365	-0.733
		Stems_T	0.0472	0.002	0.974	-0.161

¹ No significant variables in Site 1

² Clay = clay substrate texture

³ Lrg_Hum = large sized hummocks

⁴ Asp_EW = east west aspect

⁵ Canopy = tree canopy cover

⁶ Med_Hum = medium sized hummocks

⁷ Sand = sand substrate texture

⁸ PMid = mid slope quadrat position

⁹ PUpper = upper slope quadrat position

¹⁰ Stems_R = tree stem density

¹¹ Stems_T = tall shrub stem density

¹² Betocc_A = age of *Betula occidentalis* trees

¹³ Asp_NS = north south aspect

¹⁴ Dep = depression (no hummocks)

Table 2.10. Redundancy analysis and canonical correspondence analysis results for each sampling scale and each site.

Sampling Scale	Site	All Canonical Axes		Cumulative Percent Variance of Species Data				Cumulative Percent Variance of Species-Environment relation				Species-Environment Correlations	
		Sum of all Eigenvalues	Sum of Canonical Eigenvalues	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2	Axis 3	Axis 4	Axis 1	Axis 2
1x1	1	- ¹	-	-	-	-	-	-	-	-	-	-	-
	2	4.01	0.913	13.8	22.8	36.5	48.1	60.4	100.0	0	0	0.945	0.864
	3	3.724	1.396	14.2	22.0	29.0	33.9	37.8	58.8	77.3	90.4	0.907	0.837
	All	6.652	0.063	4.1	7.1	9.5	17.8	42.7	74.3	100	0	0.804	0.744
5x5	1	1	0.238	10.2	17.9	23.8	34.2	43.0	75.4	100.0	0	0.922	0.940
	2	1	0.274	14.7	23.3	27.4	37.3	53.6	85.1	100.0	0	0.954	0.925
	3	1	0.313	13.2	21.3	27.3	31.3	42.1	67.9	87.2	100.0	0.950	0.898
	All	7.421	0.779	4.9	7.3	9.2	10.5	46.5	69.1	87.2	100.0	0.893	0.811
Bryophytes	1	1	0.097	9.7	30.8	45.7	60.3	100.0	0	0	0	0.868	0
	2	1	0.140	14.0	31.7	44.6	54.7	100.0	0	0	0	0.719	0
	3	1	0.238	16.3	23.8	38.7	50.5	68.5	100.0	0	0	0.855	0.754
	All	0.944	0.113	5.1	8.1	10.2	11.9	43.0	68.0	85.8	100.0	0.749	0.532

¹ No result because no significant environmental variables

Table 2.11. Vascular community types and significant differences, as determined by cluster analysis and indicator species analysis from the 5 x 5 m interior quadrats.

Site	Community Type	Significant Differences	Species	Indicator Value	P-Value
1	1	a	<i>Salix</i> spp. (T ¹)	0.353	0.001
			<i>Populus tremuloides</i> (L ²)	0.353	0.019
	2	ab	<i>Corydalis aurea</i>	0.818	0.015
			<i>Fragaria virginiana</i>	0.474	0.040
			<i>Trifolium repens</i>	1.000	0.044
			<i>Cornus canadensis</i>	1.000	0.045
			<i>Galium boreal</i>	0.720	0.004
	3	b	<i>Sonchus arvensis</i>	0.367	0.024
			<i>Populus balsamifera</i> (R ³)	0.391	0.038
	5	ab	<i>Rosa acicularis</i> (L)	0.692	0.026
			<i>Aralia nudicaulis</i>	0.750	0.040
2	1	a	<i>Ribes oxycanthoides</i> (L)	0.694	0.001
			<i>Urtica dioica</i>	0.522	0.001
			<i>Calamagrostis canadensis</i>	0.381	0.001
	2	b	<i>Bromus inermis</i>	0.735	0.001
			<i>Fragaria virginiana</i>	0.557	0.001
			<i>Crepis runcinata</i>	0.375	0.001
			<i>Stellaria longifolia</i>	0.375	0.001
			<i>Populus balsamifera</i> (L)	0.375	0.001
			<i>Salix</i> spp. (L)	0.571	0.001
	3	c	<i>Rubus pubescens</i>	0.500	0.001
			<i>Pyrola asarifolia</i>	0.427	0.001
			<i>Populus tremuloides</i> (T)	0.370	0.006
			<i>Orthilia secunda</i>	0.667	0.029
3	1	a	<i>Rubus idaeus</i> (L)	0.357	0.001
	2	ab	<i>Betula papyrifera</i> (L)	0.714	0.007
			<i>Platanthera aquilonis</i>	0.513	0.025
	3	c	<i>Urtica dioica</i>	0.736	0.001
			<i>Taraxacum officinale</i>	0.353	0.014
	4	b	<i>Populus tremuloides</i> (T)	0.390	0.005
			<i>Vicia americana</i>	0.800	0.005
			<i>Dasiphora fruticosa</i>	0.400	0.041
			<i>Arctostaphylos uva-ursi</i> (L)	0.400	0.043
			<i>Achillea millefolium</i>	0.417	0.044

¹ T = tall shrub

² L = low shrub

³ R = tree

Table 2.11. Vascular community types and significant differences, as determined by cluster analysis and indicator species analysis from the 5 x 5 m interior quadrats (continued).

Site	Community Type	Significant Differences	Species	Indicator Value	P-Value
All	1	a	Fungus	0.838	0.001
			Lichen	0.573	0.001
			<i>Galium aparine</i>	0.672	0.001
			<i>Maianthemum canadense</i>	0.469	0.001
	2	b	<i>Salix</i> spp. (L)	0.315	0.025
			<i>Urtica dioica</i>	0.316	0.056
	3	c	<i>Achillea millefolium</i>	0.335	0.004
			<i>Pyrola asarifolia</i>	0.330	0.010

¹ T = tall shrub

² L = low shrub

³ R = tree

Table 2.12. Non-vascular community types and significant differences, as determined by cluster analysis and indicator species analysis from the 5 x 5 m interior quadrats.

Site	Community Type	Significant Differences	Species	Indicator Value	P-Value
1	1	ab	<i>Orthotrichum obtusifolium</i>	0.545	0.005
	2	a	<i>Ceratodon purpureus</i>	0.662	0.007
			<i>Bryum</i> spp.	0.652	0.001
			<i>Drepanocladus</i> spp.	0.500	0.094
	4	a	- ¹	-	-
5	b	<i>Sanionia uncinata</i>	0.435	0.019	
2	1	a	<i>Campylium hispidulum</i>	0.667	0.002
			<i>Sanionia uncinata</i>	0.429	0.019
	2	b	<i>Pylaisiella polyantha</i>	0.525	0.063
3	1	a	<i>Amblystegium serpens</i>	0.417	0.001
	2	b	<i>Pleurozium schreberi</i>	0.600	0.013
	3	c	<i>Campylium hispidulum</i>	0.476	0.006
	4	abc	<i>Funaria hygrometrica</i>	0.500	0.084
All	1	ab	<i>Orthotrichum obtusifolium</i>	0.335	0.010
	2	f	<i>Ceratodon purpureus</i>	0.255	0.001
	3	g	<i>Campylium chrysophyllum</i>	0.090	0.497
	4	cdh	<i>Sanionia uncinata</i>	0.263	0.029
	5	ac	<i>Polytrichum strictum</i>	0.143	0.217
	6	ei	<i>Amblystegium serpens</i>	0.224	0.002
	7	bd	<i>Plagiomnium cuspidatum</i>	0.354	0.004
	8	bce	<i>Aulacomnium palustre</i>	0.750	0.001
			<i>Plagiothecium laetum</i>	0.750	0.001
			<i>Tomenthypnum nitens</i>	1.000	0.001
			<i>Helodium blandowii</i>	0.500	0.004
			<i>Drepanocladus</i> spp.	0.435	0.005
			<i>Hylocomium splendens</i>	0.417	0.007

¹ Indicator species for this community type were not given due to a glitch in the program used to run the indicator species analysis

III. HYPOTHETICAL PLANT COMMUNITY DEVELOPMENT SCENARIO

1. Introduction

Prior to the initiation of this research in 2007, no research had been conducted on the three study sites. Given that data from repeated measurements through time are not available, the following is a hypothetical account of what may have occurred during plant community development of these sites, and is based on data collected during the research. Although speculative and theoretical, it draws on scientifically sound principles regarding plant biology, plant ecology, and ecosystem development.

2. Possible Community Development Scenario

Based on limited site histories, collected on substrates data, and current species composition, the main pre-disturbance community on all three sites was likely a boreal wetland, such as a bog or fen, with a black spruce and larch overstory. The sites are currently in transition from an early to mid successional upland boreal community, and contain species belonging to upland and lowland habitats; however, community development has not followed typical secondary successional pathways.

Due to soil salvage and stockpile construction operations, the substrate is highly admixed. Many propagules in the upper undisturbed soil may have been buried at depths lower than ideal for plant germination and / or growth. Patches of viable propagules may have been exposed on the stockpile surface where they germinated, were consumed by wildlife, or damaged by the elements. All of these factors would have affected revegetation.

Some colonizing species can be ascertained from the only picture taken during the first growing season following substrate placement on Site 1 (Figure 3.1). Standing water can be seen in depressions between hummocks, and grass-like species and low shrubs (interpreted as sedges, grasses and willows) had begun to grow in lower areas and around the edges of the standing water. These species likely emerged from the soil seed bank. Areas of bare mineral soil and the tops of hummocks were mostly devoid of vegetation, so the establishing

species likely preferred wetter habitats (hummocks may have drained too much to support wetland species). Construction techniques and substrate types were similar among sites, thus at that stage Sites 2 and 3 likely were similar to Site 1.

Hydrophilic and disturbance loving bryophytes may have begun to colonize shortly after substrate placement. Gametophytic tissue may have remained intact during salvage and construction operations. Spores may have germinated from the diaspore bank if within an optimal distance from the substrate surface.

Spores are known to be transported long distances (even intercontinentally) (Miles and Longton 1992, Miller and McDaniel 2004, Muñoz et al. 2004, Frahm 2008) and may have come from undisturbed areas around the mine or quite distant. Spores were less likely to have been transported by animals as there is a high noise level and physical disturbance on the mine that would deter wildlife from the sites, which at that time lacked suitable habitat, foraging or hiding areas. Bryophyte spores may have been transported from undisturbed areas by flies (Goffinet and Shaw 2004), assuming the flies could fly that far. The most likely method of colonization was emergence from the diaspore bank (Caners et al. 2009), as bryophyte spores can remain viable for decades (Frahm 2008), and from wind transport, with spores carried on warm air currents as they are ejected from capsules (Miles and Longton 1992, Schofield 2001).

Non-native cosmopolitan vascular species such as *Cirsium arvense* (L.) Scop. (Canada thistle), *Sonchus arvensis*, *Poa pratensis* L. (Kentucky bluegrass), *Bromus inermis*, and *Taraxacum officinale* F.H. Wigg. (common dandelion) may have launched an early invasion from adjacent disturbed areas. These species are adapted to highly disturbed and low nutrient conditions (Johnson et al. 1995), and are able to grow rapidly and disseminate large amounts of seed (Stevens 1932, Wilson 1979, Johnson et al. 1995, Bubar et al. 2000), thus multiplying quickly and increasing their rate of spread. In the absence of competition from native forbs and with ample organic matter on the sites, these species would have had few obstacles to overcome while firmly establishing their presence.

Vegetated areas adjacent to the sites may have served as a source of seed and propagules, thus playing a large role in revegetation and plant community development. Site 1 is bordered to the northwest by a *Caragana arborescens* hedge and to the east and southwest by *Populus* spp. L. (poplar), *Caragana*

arborescens, and a grass-legume reclamation mix of *Agropyron cristatum*, *Agropyron elongatum* (Host) P. Beauv. (tall wheatgrass), *Bromus* spp. L. (brome), *Festuca rubra* L. (red fescue), *Medicago sativa*, *Trifolium hybridum* L. (alsike clover), and *Trifolium repens* L. (white clover) (Shopik and Klym 1978). Several of these species were observed in this site. Along the west edge of Site 2, dense patches of *Astragalus cicer* L. (chickpea milkvetch) were found, which likely invaded from the reconstructed Highway 60, where it may have been part of a ditch seed mix. As the prevailing wind in Alberta is from the west, seeds could have been blown into the edge of the site and spread from there. North of Site 3 is a reclaimed area supporting *Populus* trees and forbs, including *Melilotus officinalis*, which is found on site.

With time, early colonizing *Salix* shrubs could have continued to grow and thrive and *Betula papyrifera* may have begun to establish. Many *Salix* and *Betula papyrifera* snags were found in all three sites, indicating that as excess water drained from the sites, conditions for these two species, which prefer moist habitats (Moss 1994), became undesirable and they could no longer survive. *Salix* shrubs were still growing or had replaced the ones that died; however, with the exception of Site 3 which is more mesic than the other two sites (observations and inferences from species composition), there was no recruitment of *Betula papyrifera*. Competition from *Populus balsamifera* and *Populus tremuloides* may have contributed to the ongoing demise of *Salix* and *Betula papyrifera* in Sites 1 and 2.

Propagules likely arrived the first growing season after substrate placement and continued to arrive to the present. It may have taken a couple growing seasons before the propagules germinated, hence the two to five year delay in growth of *Populus balsamifera* and *Populus tremuloides*. Upland forb propagules may have arrived on the wind, and shrub propagules may have arrived via digestive systems of birds; both may have germinated after a delay. Species likely not present in the seed bank (e.g. *Arctostaphylos uva-ursi* (L.) Spreng. (kinnikinnick)) may have been transported by birds, and at the time of sampling could be found growing outside their typical habitat range. Unusual combinations of species were found growing together, such as *Betula papyrifera* and *Arctostaphylos uva-ursi*, which are indicative of different soil, water and nutrient conditions

(Beckingham and Archibald 1996). If non-native weeds were present in the early years, they have successfully maintained their presence. They are currently found in dense patches or thinly dispersed throughout the three sites. Upland bryophytes such as *Pylaisiella polyantha* (Hedw.) Grout, which grows on the base of *Populus tremuloides* trunks, could have arrived at the same time as upland forbs and shrubs via one of the previously discussed transport mechanisms. In Sites 2 and 3 periodically wet depressions continue to sustain isolated communities of hydrophilic species.

Soil has not developed, as expected for the relatively short time since the material was placed and the long time required for weathering and decomposition. The substrate was admixed (Figure 3.2); thus a typical soil with definable horizons will not form within the near future. Little to no decomposition has taken place in the large chunks of peat that remain intact on and below the surface. An LFH horizon is beginning to develop; leaf and twig litter is accumulating on the surface and breaking down. Where pockets of organic matter are at or near the surface, an A horizon may gradually develop; however, where mineral soil is exposed, an A horizon or even development of an LFH layer will take an appreciable longer time as many exposed hummocks of mineral soil lack vascular vegetation cover. Bryophytes may be growing in these areas, but in many cases the hummocks are devoid of vegetation. It will take time for litter to accumulate and for a hospitable environment to be created for seed germination. The mineral substrate was salvaged from below the peat pockets, and as such has very little to no structural development as it is basically parent material. As vascular plants begin to colonize the bare areas, their roots will assist in developing soil structure, and as the roots die and are replaced they will contribute organic matter to the nutrient poor mineral soil.

The most interesting part of the development of these plant communities is that, with the exception of a few localized wet depressions supporting lowland type communities, an overall upland community has developed on a lowland substrate on the sites (Figure 3.3). There is no documented evidence of this phenomenon occurring elsewhere in the boreal forest and thus these sites may be relatively unique. When a disturbance is reclaimed, the usual intent is to mimic the original soil and vegetation. Developing an upland community from a lowland substrate

would not likely be proposed, but as demonstrated on these sites, is possible.

Populus tremuloides is often the first tree to colonize harvested boreal forest. Over time *Picea glauca* seedlings establish in the understory and eventually become co-dominant with *Populus*, creating a mixedwood canopy (Larsen 1980). As succession progresses, *Populus* is outcompeted for light and other nutrients and a coniferous forest replaces the mixedwood forest. Contradictory to what Clementsian (Clements 1916) and Gleasonian (Gleason 1926) successional theories predict, this is not the end point of succession, otherwise known as the climax. Succession in the natural boreal forest is a site specific cyclical process influenced by physical site conditions (e.g. relief and depth to water table), climate (e.g. annual precipitation and growing season length), and disturbances (e.g. insect and pathogen outbreaks and fire return interval). In some boreal communities the high disturbance frequency prevents the community from reaching the later successional stages of development (Larsen 1980).

It is clear that despite the odd substrate conditions present, succession is occurring on the three sites. Snags of *Salix* and *Betula papyrifera*, both of which are early successional species, are suggestive of this. Several *Picea glauca* low shrubs were found in each site, a further indication succession is occurring. Relative species abundances have changed since initial revegetation of each site (eg Figure 3.1 vs. Figure 3.3), and species may have arrived, established, and faded from the communities prior to this study, which is all part of the successional process. These three communities will likely continue from primary successional to mid successional upland boreal forest communities, and, given time, will eventually become late successional upland boreal communities.

These sites appear to support a combination of succession theories. In the early stages of succession on the research sites, initial floristics (Egler 1954) may have played an important role. Current species composition indicates that upland species that likely were not present in the soil seed bank prior to initial disturbance colonized the sites relatively quickly after substrate placement. These species, some of which are characteristic of mid and later successional stages, have persisted, despite the sites being currently in transition from an early to mid successional stage. As the community develops, entry by new species may be inhibited by canopy closure and competition for resources by the

established plants; thus the theory of inhibition could be supported (Connell and Slatyer 1977). Barring major disturbances, the sites will likely remain in climax state on a stand scale, with *Picea glauca* eventually dominating the overstory and shade tolerant species dominating the understory, which could support the theory of tolerance (Connell and Slatyer 1977). However, as demonstrated many times, boreal communities are not static; they are adapted to disturbance, and often require it for community renewal (Larsen 1980). Small disturbances on a patch scale (e.g. tree throw) will create openings in the canopy and forest floor, allowing early successional shade intolerant species (which may persist in the soil seed bank or invade from surrounding areas) to establish, resetting the successional timeline. This could support the theory of patch associated succession (Watt 1947) and the theory that in some situations a climax community is unattainable (McCune and Cottam 1985).

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4. Figures



Figure 3.1. Picture of Site 3 profile illustrating admixed substrate.



Figure 3.2. Picture of Site 1 looking southeast; initial conditions during spring 1976 after winter placement of water logged substrate.



Figure 3.3. Picture of Site 1 illustrating average plant community growth that could be found in all sites in summer 2007.

IV. SYNTHESIS AND FUTURE RESEARCH

1. Summary

Reclamation in the Alberta Oil Sands Region (AOSR) has focused on capping disturbed areas with a salvaged peat-mineral mix substrate and planting trees, forbs, and grasses to establish ground cover and prevent erosion. Little is known about natural recovery of vegetation from a peat-mineral mix, especially in the long term. It was hypothesized that natural recovery could be an option for reclamation in the AOSR.

This research used an ex post facto (i.e. retrospective) approach to investigate the unintentional natural recovery of upland boreal forest vegetation on a salvaged lowland peat-mineral mix substrate. Using three natural recovery sites aged 26 to 34 years, the effects of environmental variables (pH, electrical conductivity, substrate texture, topographic position, litter depth, hummock size, aspect, degree of slope, tall shrub and tree stems densities, canopy cover, and tree ages) on the composition and cover of upland boreal vegetation were investigated. Three sampling scales were used: vascular vegetation within 1 x 1 m and 5 x 5 m quadrats, and bryophytes within 5 x 5 m quadrats.

Vascular and non-vascular vegetation was assessed for development of community types within each site. With the exception of Site 3, which had two community types, vascular vegetation was homogeneous. Non-vascular vegetation showed several communities in each site, with the greatest number of types occurring when data from all three sites were combined in one analysis.

Electrical conductivity and pH of the substrate were within normal ranges for the region. The substrate was highly admixed and texture varied greatly within the sites. Across all three sites, three macro topographic environmental variables (tall shrub stem density, tree canopy cover, and age of *Betula occidentalis* trees) explained the most variation within the species data at the 5 x 5 m sampling level. Other significant macro topographic environmental variables included aspect and hummock size. Significant micro topographic environmental variables included clay and sand substrate texture, aspect, hummock size, and location of 1 x 1 m quadrats in relation to topographic relief.

Vegetation on each site was considered to be in transition from an early to a mid successional upland community. Bringing together information regarding site histories, substrate characteristics, and current species compositions, it is hypothesized that these communities developed from early successional lowland communities, and that development will continue to late successional upland communities with a few pockets of lowland communities. It was concluded that community development was a product of several measured environmental variables plus factors such as soil seed bank dynamics, propagule dispersal, germination conditions, and initial species composition, all of which likely played a role in community development early in the history of these sites.

2. Reclamation Applications

Results from this study indicate that natural recovery of upland boreal forest vegetation on a lowland substrate is possible and that a highly admixed peat-mineral substrate can support self-sustaining and evolving plant communities. Current reclamation of disturbances in the AOSR using conventional techniques requires intense inputs such as equipment, plant propagules, and human hours. Natural recovery can reduce the resources needed to reclaim a site, and may facilitate development of healthier ecosystem processes than traditionally reclaimed sites.

One of the limitations associated with natural recovery is the long time required for development of a suitable plant community. This longer time frame may not suit developers and regulators. However, natural recovery is a viable option for reclamation on the AOSR, particularly as part of a progressive reclamation plan and in areas where a native plant community is desired for the end land use.

3. Future Research

No information is available regarding community development leading up to the present day; therefore interpretations and conclusions from this research are based on limited site history information and two years of data collected many years after salvaged substrate was placed on each site. It is inevitable that change will occur within the communities, as this is the nature of succession. The

presence of later successional species found in the understory will likely increase, some non-native species may eventually be outcompeted, and species richness in lowland communities within the sites may increase.

Long term sampling is needed to determine what changes have occurred and when. The sites in this research represent a unique opportunity to conduct further research that would increase the understanding of succession and the trajectory and timeframe of natural recovery. This research can be used as a building block for further investigation, including:

- Characterization of microfauna, mesofauna, and mycorrhizal fungi as indicators of ecological success.
- Characterization of coarse woody debris and whether it has an influence on community composition.
- Determination of rooting depth of species within different growth forms in relation to substrate texture, and the assessment of rooting restrictions within the soil profile.
- Soil development, including development of the LFH layer, an A horizon, and decomposition of large chunks of peat on and below the soil surface.
- Long term soil water trends in hummocks vs. depressions and how they relate to community development.
- Soil nutrient trends in organic matter vs. mineral soil and how they relate to long term community development.
- Resistance of naturally recovered plant communities to invasion of non-native plant species.
- Successional development of the communities as an indicator of ecological success.

V. APPENDIX

Table A1. Substrate reconnaissance data from 5 x 5 quadrats

Site	Sample	Field Electrical Conductivity (dS/m)	Lab Electrical Conductivity (dS/m)	Field pH	Lab pH
1	1a	0.08	0.29	5.4	5.1
	1b	0.14	0.36	5.6	5.7
	2a	0.14	0.37	6.0	5.8
	2b	0.17	0.38	6.6	6.3
	3a	0.17	0.41	7.2	6.9
	3b	0.24	0.65	7.5	7.0
2	1a	0.12	0.14	5.3	5.3
	1b	0.14	0.29	5.4	5.3
	2a	0.18	0.36	5.6	5.4
	2b	0.18	0.39	5.8	5.7
	3a	0.20	0.46	7.5	7.0
	3b	0.25	0.47	7.8	7.7
3	1a	0.15	0.51	7.3	6.7
	1b	0.20	0.58	7.5	6.8
	2a	0.26	0.67	7.6	6.9
	2b	0.30	0.69	7.7	7.1
	3a	0.50	0.84	7.8	7.1
	3b	0.73	1.85	7.8	7.2

Table A2. All vascular and non-vascular species identified within the research sites.

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Fungus				fungus	x	x	x	x	x	x
Lichen				lichen	x	x	x	x	x	x
Liverwort	Geocalycaceae	<i>Lophocolea</i> spp.			x	x	x	x	x	x
	Jungermanniaceae	<i>Mylia anomala</i>					x			x
	Pterigynandraceae	<i>Myurella julacea</i>					x	x		x
	Ptilidiaceae	<i>Ptilidium pulcherrimum</i>			x	x	x	x	x	x
Moss	Amblystegiaceae	<i>Amblystegium serpens</i>			x	x	x	x	x	x
	Amblystegiaceae	<i>Campyllum chrysophyllum</i>		goldenleaf campyllum moss	x	x	x	x	x	x
	Amblystegiaceae	<i>Campyllum hispidulum</i>		hispid campyllum moss						x
	Amblystegiaceae	<i>Campyllum stellatum</i>		star campyllum moss			x			
	Amblystegiaceae	<i>Campyllum</i> spp.			x	x	x	x	x	x
	Amblystegiaceae	<i>Drepanocladus</i> spp.					x			x
	Amblystegiaceae	<i>Sanionia uncinata</i>			x					
	Aulacomniaceae	<i>Aulacomnium palustre</i>			x	x	x		x	x
	Brachytheciaceae	<i>Brachythecium</i> spp.			x	x		x	x	x
	Brachytheciaceae	<i>Eurhynchium pulchellum</i>				x	x	x	x	x
	Brachytheciaceae	<i>Tomenthypnum nitens</i>					x			
	Bryaceae	<i>Bryum argenteum</i>		silvergreen bryum moss				x		
	Bryaceae	<i>Bryum</i> spp.						x	x	x
	Bryaceae	<i>Leptobryum pyriforme</i>						x		
	Ditrichaceae	<i>Ceratodon purpureus</i>					x			
	Ditrichaceae	<i>Ditrichum</i> spp.							x	

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Moss	Fissidentaceae	<i>Fissidens bryoides</i>		bryoid fissidens moss			x			
	Funariaceae	<i>Funaria hygrometrica</i>					x	x	x	
	Grimmiaceae	<i>Schistidium apocarpum</i>								x
	Helodiaceae	<i>Helodium blandowii</i>		Blandow's helodium moss				x		
	Hylocomiaceae	<i>Hylocomium splendens</i>		splendid feather moss	x	x	x	x	x	x
	Hylocomiaceae	<i>Pleurozium schreberi</i>		Schreber's big red stem moss	x	x	x	x	x	x
	Hypnaceae	<i>Hypnum lindbergii</i>		Lindberg's hypnum moss					x	x
	Hypnaceae	<i>Hypnum pratense</i>			x	x	x			
	Hypnaceae	<i>Pseudotaxiphyllum elegans</i>							x	
	Hypnaceae	<i>Pylaisiella polyantha</i>		aspen stalking moss			x			x
	Leskeaceae	<i>Bryohaplocladium microphyllum</i>			x	x	x	x	x	x
	Mniaceae	<i>Plagiomnium cuspidatum</i>		toothed plagiomnium moss	x			x		x
	Mniaceae	<i>Plagiomnium ellipticum</i>		elliptic plagiomnium moss	x	x	x		x	
	Orthotrichaceae	<i>Orthotrichum obtusifolium</i>		obtuseleaf aspen moss		x	x			x
	Plagiotheciaceae	<i>Plagiothecium denticulatum</i>		toothed plagiothecium moss	x					
	Plagiotheciaceae	<i>Plagiothecium laetum</i>					x	x		x
	Plagiotheciaceae	<i>Plagiothecium</i> spp.			x	x	x	x	x	x
	Polytrichaceae	<i>Polytrichum juniperinum</i>		juniper polytrichum moss		x				
	Polytrichaceae	<i>Polytrichum strictum</i>					x			
	Pottiaceae	<i>Barbula</i> spp.			x	x	x	x	x	x
	Pottiaceae	<i>Tortula mucronifolia</i>		mucronleaf tortula moss				x		x
	Thuidiaceae	<i>Thuidium recognitum</i>								x
Sedge	Cyperaceae	<i>Carex brunnescens</i>		brownish sedge				x		

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Sedge	Cyperaceae	<i>Carex</i> spp.		sedge			x		x	x
	Cyperaceae	<i>Schoenoplectus acutus</i>		great bulrush					x	
Grass	Poaceae	<i>Agropyron cristatum</i>		crested wheatgrass		x				
	Poaceae	<i>Agrostis scabra</i>		rough hair grass	x	x	x	x	x	x
	Poaceae	<i>Bromus anomalus</i>		nodding brome					x	x
	Poaceae	<i>Bromus ciliatus</i>		fringed brome			x			x
	Poaceae	<i>Bromus inermis</i>		smooth brome	x	x	x	x		x
	Poaceae	<i>Bromus</i> spp.		brome			x			
	Poaceae	<i>Calamagrostis canadensis</i>		marsh reed grass	x	x	x	x	x	x
	Poaceae	<i>Deschampsia cespitosa</i>		tufted hairgrass			x			
	Poaceae	<i>Elymus trachycaulus</i>	<i>trachycaulus</i>	slender wheatgrass					x	
	Poaceae	<i>Festuca saximontana</i>		Rocky Mountain fescue		x		x		
	Poaceae	<i>Leymus innovatus</i>		hairy wild rye		x		x		
	Poaceae	<i>Pascopyrum smithii</i>		western wheatgrass			x	x		
	Poaceae	<i>Phleum pratense</i>		timothy				x		
	Poaceae	<i>Poa palustris</i>		fowl bluegrass	x	x	x	x	x	
	Poaceae	<i>Poa pratensis</i>		Kentucky bluegrass			x	x	x	
	Poaceae	<i>Poa</i> spp.		bluegrass	x	x	x	x		
	Poaceae	<i>Schizachne purpurascens</i>		false melic	x					
	Poaceae	Grass spp.			x	x	x		x	x
Forb	Asteraceae	<i>Achillea millefolium</i>		common yarrow		x	x	x	x	x
	Asteraceae	<i>Achillea sibirica</i>		Siberian yarrow			x			
	Asteraceae	<i>Aster</i> spp.		aster					x	

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Forb	Asteraceae	<i>Cirsium arvense</i>		Canada thistle			x			
	Asteraceae	<i>Crepis runcinata</i>		fiddleleaf hawksbeard			x			
	Asteraceae	<i>Crepis tectorum</i>		narrowleaf hawksbeard		x				
	Asteraceae	<i>Erigeron glabellus</i>		smooth fleabane			x		x	x
	Asteraceae	<i>Erigeron</i> spp.		fleabane		x				
	Asteraceae	<i>Hieracium</i> spp.		hawkweed				x		
	Asteraceae	<i>Hieracium cynoglossoides</i>		woolly hawkweed			x			
	Asteraceae	<i>Packera paupercula</i>		balsam groundsel				x		
	Asteraceae	<i>Packera</i> spp.		groundsel	x	x		x	x	x
	Asteraceae	<i>Petasites frigidus</i>		palmate-leaved coltsfoot	x				x	
	Asteraceae	<i>Petasites sagittatus</i>		arrow-leaved coltsfoot						x
	Asteraceae	<i>Solidago canadensis</i>		Canada goldenrod		x	x		x	
	Asteraceae	<i>Sonchus arvensis</i>		perennial sow thistle	x	x	x	x	x	x
	Asteraceae	<i>Symphyotrichum ciliolatum</i>		Lindley's aster	x	x	x	x	x	x
	Asteraceae	<i>Taraxacum officinale</i>		dandelion	x	x	x	x	x	x
	Araliaceae	<i>Aralia nudicaulis</i>		wild sarsaparilla	x	x		x		
	Brassicaceae	<i>Arabis</i> spp.		rockcress			x			x
	Brassicaceae	<i>Rorippa islandica</i>		marsh yellow cress					x	
	Brassicaceae	<i>Sisymbrium loeselii</i>		small tumbleweed mustard	x					
	Caprifoliaceae	<i>Linnaea borealis</i>		twinlineflower					x	
	Caryophyllaceae	<i>Moehringia lateriflora</i>		bluntleaf sandwort	x	x	x	x	x	
	Caryophyllaceae	<i>Stellaria calycantha</i>		northern starwort			x			
	Caryophyllaceae	<i>Stellaria longifolia</i>		long-leaved chickweed	x	x	x	x		

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Forb	Chenopodiaceae	<i>Chenopodium album</i>		lambsquarters	x	x	x	x	x	
	Chenopodiaceae	<i>Chenopodium capitatum</i>		strawberry blite						
	Cornaceae	<i>Cornus canadensis</i>		bunchberry	x		x		x	
	Equisetaceae	<i>Equisetum arvense</i>		common horsetail	x	x	x	x	x	x
	Equisetaceae	<i>Equisetum fluviatile</i>		water horsetail			x		x	
	Fabaceae	<i>Astragalus canadensis</i>		Canadian milkvetch		x	x		x	
	Fabaceae	<i>Astragalus cicer</i>		chickpea milkvetch			x	x		
	Fabaceae	<i>Lathyrus venosus</i>		veiny peavine					x	
	Fabaceae	<i>Medicago sativa</i>		alfalfa	x	x	x	x	x	x
	Fabaceae	<i>Melilotus officinalis</i>		yellow sweet clover			x	x	x	x
	Fabaceae	<i>Trifolium repens</i>		white clover	x	x			x	x
	Fabaceae	<i>Vicia americana</i>		American vetch			x		x	x
	Fumariaceae	<i>Corydalis aurea</i>		golden corydalis	x	x	x	x	x	x
	Hippuridaceae	<i>Hippuris vulgaris</i>		common mare's-tail					x	
	Juncaginaceae	<i>Triglochin palustris</i>		marsh arrowgrass					x	
	Lamiaceae	<i>Galeopsis tetrahit</i>		hemp nettle					x	x
	Liliaceae	<i>Maianthemum canadense</i>		wild lily-of-the-valley	x	x				x
	Onagraceae	<i>Chamerion angustifolium</i>		fireweed	x	x	x	x	x	x
	Onagraceae	<i>Epilobium ciliatum</i>		fringed willowherb					x	
	Onagraceae	<i>Epilobium</i> spp.		fireweed			x	x		x
	Orchidaceae	<i>Platanthera aquilonis</i>		northern green orchid					x	x
	Polygonaceae	<i>Eriogonum</i> spp.		buckwheat					x	
	Polygonaceae	<i>Polygonum arenastrum</i>		common knotweed					x	

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Forb	Primulaceae	<i>Trientalis borealis</i>		northern starflower	x	x	x			
	Pyrolaceae	<i>Orthilia secunda</i>		one-sided wintergreen	x		x		x	x
	Pyrolaceae	<i>Pyrola asarifolia</i>		common pink wintergreen	x	x	x	x	x	x
	Pyrolaceae	<i>Pyrola chlorantha</i>		greenish-flowered wintergreen					x	
	Pyrolaceae	<i>Pyrola</i> spp.		wintergreen						
	Ranunculaceae	<i>Actaea rubra</i>		red and white baneberry		x				
	Ranunculaceae	<i>Aquilegia brevistyla</i>		blue columbine					x	
	Ranunculaceae	<i>Ranunculus gmelinii</i>		Gmelin's buttercup			x		x	
	Rosaceae	<i>Fragaria vesca</i>		woodland strawberry	x	x	x		x	
	Rosaceae	<i>Fragaria virginiana</i>		wild strawberry	x	x	x	x	x	x
	Rosaceae	<i>Geum aleppicum</i>		yellow avens			x			
	Rosaceae	<i>Geum triflorum</i>		old man's whiskers			x	x		
	Rosaceae	<i>Potentilla norvegica</i>		Norwegian cinquefoil		x	x	x	x	
	Rosaceae	<i>Rubus arcticus</i>	acaulis	dwarf raspberry		x			x	x
	Rosaceae	<i>Rubus pubescens</i>		dewberry			x		x	
	Rubiaceae	<i>Galium aparine</i>		cleavers	x	x	x			
	Rubiaceae	<i>Galium boreale</i>		northern bedstraw	x	x	x	x	x	x
	Rubiaceae	<i>Galium</i> spp.		bedstraw; cleavers					x	
	Santalaceae	<i>Geocaulon lividum</i>		false toadflax		x	x			x
	Saxifragaceae	<i>Parnassia palustris</i>		northern grass-of-parnassus					x	x
	Scrophulariaceae	<i>Castilleja raupii</i>		Raup's Indian paintbrush						x
	Typhaceae	<i>Typha latifolia</i>		cattail					x	

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Forb	Urticaceae	<i>Urtica dioica</i>		stinging nettle	x	x	x	x	x	x
	Violaceae	<i>Viola adunca</i>		early blue violet		x			x	
	Violaceae	<i>Viola renifolia</i>		kidney-leaved violet						x
	Violaceae	<i>Viola</i> spp.		violet					x	
		Forb 2			x					
		Forb 6				x				
		Forb 7				x	x			x
		Forb 10					x	x	x	x
		Forb 12								x
		Forb 15					x			
		Forb 17					x			
Low Shrub	Aceraceae	<i>Acer negundo</i>		Manitoba maple				x		
	Betulaceae	<i>Betula glandulosa</i>		bog birch		x				
	Betulaceae	<i>Betula occidentalis</i>		water birch		x			x	x
	Betulaceae	<i>Betula papyrifera</i>		paper birch			x		x	x
	Betulaceae	<i>Betula pumila</i>		dwarf birch			x	x	x	x
	Caprifoliaceae	<i>Lonicera dioica</i>		twining honeysuckle					x	x
	Caprifoliaceae	<i>Symphoricarpos occidentalis</i>		western snowberry	x	x			x	x
	Cornaceae	<i>Cornus sericea</i>		red osier dogwood	x	x	x	x	x	x
	Elaeagnaceae	<i>Elaeagnus commutata</i>		silver willow					x	
	Elaeagnaceae	<i>Shepherdia canadensis</i>		soopolallie		x				x
	Ericaceae	<i>Arctostaphylos uva-ursi</i>		kinnikinnick					x	
	Ericaceae	<i>Ledum groenlandicum</i>		Labrador tea			x	x	x	x

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Low Shrub	Ericaceae	<i>Vaccinium vitis-idaea</i>		bog cranberry			x	x		
	Fabaceae	<i>Caragana arborescens</i>		caragana	x	x	x	x		
	Grossulariaceae	<i>Ribes glandulosum</i>		skunk currant	x		x		x	x
	Grossulariaceae	<i>Ribes hudsonianum</i>		northern black current		x		x		
	Grossulariaceae	<i>Ribes oxycanthoides</i>		northern gooseberry	x	x	x	x	x	x
	Grossulariaceae	<i>Ribes triste</i>		wild red currant	x	x	x			x
	Pinaceae	<i>Larix laricina</i>		larch						
	Pinaceae	<i>Picea glauca</i>		white spruce	x	x	x	x	x	x
	Pinaceae	<i>Picea pungens</i>		blue spruce						x
	Rhamnaceae	<i>Rhamnus alnifolia</i>		alder-leaved buckthorn		x				
	Rosaceae	<i>Amelanchier alnifolia</i>		Saskatoon	x	x	x	x	x	x
	Rosaceae	<i>Dasiphora fruticosa</i>	<i>floribunda</i>	shrubby cinquefoil			x		x	x
	Rosaceae	<i>Prunus virginiana</i>		chokecherry		x		x		x
	Rosaceae	<i>Rosa acicularis</i>		common wild rose	x	x	x	x	x	x
	Rosaceae	<i>Rubus idaeus</i>		wild red raspberry	x	x	x	x	x	x
	Rosaceae	<i>Spiraea alba</i>		white meadowsweet					x	
	Salicaceae	<i>Populus balsamifera</i>		balsam poplar	x	x	x	x	x	x
	Salicaceae	<i>Populus tremuloides</i>		trembling aspen	x	x	x	x	x	x
	Salicaceae	<i>Salix</i> spp.		willow	x	x	x	x	x	x
Tall Shrub	Aceraceae	<i>Acer negundo</i>		Manitoba maple				x		
	Betulaceae	<i>Betula occidentalis</i>		water birch	x	x	x	x	x	x
	Betulaceae	<i>Betula papyrifera</i>		paper birch	x	x			x	x
	Betulaceae	<i>Betula pumila</i>		dwarf birch			x	x	x	x

¹ I = interior quadrat² E = edge quadrat

Table A2. All vascular and non-vascular species identified within the research sites (continued).

Growth Form	Family	Genus and Species	Subspecies	Common Name	Site 1		Site 2		Site 3	
					I ¹	E ²	I	E	I	E
Tall Shrub	Caprifoliaceae	<i>Lonicera dioica</i>		twining honeysuckle				x		
	Cornaceae	<i>Cornus sericea</i>		red osier dogwood	x	x	x	x	x	x
	Fabaceae	<i>Caragana arborescens</i>		caragana	x	x		x		
	Grossulariaceae	<i>Ribes triste</i>		wild red currant		x				
	Pinaceae	<i>Picea glauca</i>		white spruce	x			x	x	x
	Rosaceae	<i>Amelanchier alnifolia</i>		Saskatoon		x				
	Rosaceae	<i>Rubus idaeus</i>		wild red raspberry	x	x		x		
	Salicaceae	<i>Populus balsamifera</i>		balsam poplar	x	x	x	x	x	x
	Salicaceae	<i>Populus tremuloides</i>		trembling aspen	x	x	x	x	x	x
	Salicaceae	<i>Salix</i> spp.		willow	x	x	x	x	x	x
Tree	Betulaceae	<i>Betula occidentalis</i>		water birch	x				x	x
	Betulaceae	<i>Betula papyrifera</i>		paper birch				x	x	x
	Betulaceae	<i>Betula pumila</i>		dwarf birch					x	
	Pinaceae	<i>Larix laricina</i>		larch	x	x		x	x	x
	Pinaceae	<i>Picea glauca</i>		white spruce	x				x	
	Salicaceae	<i>Populus balsamifera</i>		balsam poplar	x	x	x	x	x	x
	Salicaceae	<i>Populus tremuloides</i>		trembling aspen	x	x	x	x	x	x
	Salicaceae	<i>Salix</i> spp.		willow	x	x	x	x	x	x
Sum					80	93	110	91	115	102
Combined Sum ³						106		135		140

¹ I = interior quadrat² E = edge quadrat³ Combined sum takes into account overlap of species within the low shrub, tall shrub and tree growth form categories

Table A3. Environmental variable data collected in 1 x 1 quadrats in each site.

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Slope (degrees)	Litter Depth (cm)	Bare Ground (%)	Litter Cover (%)	Rock Cover (%)	Position (class)	Topography (class)	Texture (class)
1	1	0	1.00	0.00	3	7	0	88	0	1	7	4
	2	140	-0.77	0.64	14	3.5	0	85	0	4	4	4
	3	130	-0.64	0.77	14	2	0	93	0	4	4	4
	4	0	1.00	0.00	0	3.5	1.5	95	1	1	7	4
	5	336	0.91	-0.41	4	3	0	97	0	9	0	4
	6	150	-0.87	0.50	11	2	0.1	98	0	4	4	4
	7	138	-0.74	0.67	11	3.5	0	96	0	6	3	4
	8	318	0.74	-0.67	12	3	0	94	0.5	4	4	4
	9	104	-0.24	0.97	12	4	0	98	0	2	6	4
	10	115	-0.42	0.91	20	3	0	95	0	4	4	4
	11	316	0.72	-0.69	14	3.5	1	94	0	2	6	4
	12	300	0.50	-0.87	5	2.5	0	82	0	9	1	4
	13	0	1.00	0.00	14	1.5	1	95	0.5	4	4	4
	14	350	0.98	-0.17	10	7	0	94	0	7	0	4
	15	0	1.00	0.00	0	5.5	0	99	0	1	7	4
	16	116	-0.44	0.90	21	3.5	0	97	0	4	4	4
	17	0	1.00	0.00	8	5	0	96	0	7	0	4
	18	294	0.41	-0.91	17	2	1	95	0	4	4	4
	19	150	-0.87	0.50	12	7	0	85	0	6	0	4
	20	130	-0.64	0.77	12	3	0	99	0	5	4	4
	21	0	1.00	0.00	0	5	0	98	0	1	7	4

¹ Aspect NS = north south aspect² Aspect EW = east west aspect

Table A3. Environmental variable data collected in 1 x 1 quadrats in each site (continued).

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Slope (degrees)	Litter Depth (cm)	Bare Ground (%)	Litter Cover (%)	Rock Cover (%)	Position (class)	Topography (class)	Texture (class)
2	1	230	-0.64	-0.77	0	2.4	0	94	0	1	7	4
	2	180	-1.00	0.00	12	4	0	95	0	5	3	4
	3	150	-0.87	0.50	10	4.1	4	95	0	8	2	4
	4	315	0.71	-0.71	3	1.6	0.1	95	0.5	2	6	4
	5	330	0.87	-0.50	8	3.1	0	98	0	6	3	4
	6	95	-0.09	1.00	9	2	20	65	8	7	0	1
	7	55	0.57	0.82	13	4.8	0	97	0	4	4	1
	8	210	-0.87	-0.50	22	3	0.1	90	1.5	6	4	1
	9	20	0.94	0.34	21	2.5	0	90	0	4	4	1
	10	0	1.00	0.00	0	1.5	0	90	0	1	7	0
	11	220	-0.77	-0.64	13	5	0	87	0	1	7	1
	12	205	-0.91	-0.42	22	5.5	0	100	0	4	4	4
	13	180	-1.00	0.00	5	5	0	95	0	4	4	1
	14	120	-0.50	0.87	9	6.5	2	95	0	1	7	4
	15	310	0.64	-0.77	25	2.8	1	95	0.5	3	5	1
	16	100	-0.17	0.98	22	2.0	0	96	0	3	5	1
	17	340	0.94	-0.34	17	1.9	0	99	0	3	5	3
	18	180	-1.00	0.00	19	3.2	0	97	0	3	5	1
	19	285	0.26	-0.97	11	1.2	0	95	0	3	0	3
	20	290	0.34	-0.94	24	1.9	0	98	0	5	3	4
	21	55	0.57	0.82	12	4.6	0	97	0	4	4	1
	22	285	0.26	-0.97	19	5.2	2	95	0	4	4	4

¹ Aspect NS = north south aspect² Aspect EW = east west aspect

Table A3. Environmental variable data collected in 1 x 1 quadrats in each site (continued).

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Slope (degrees)	Litter Depth (cm)	Bare Ground (%)	Litter Cover (%)	Rock Cover (%)	Position (class)	Topography (class)	Texture (class)
2	24	150	-0.87	0.50	17	4.9	0	98	0	6	4	3
	26	270	0.00	-1.00	13	3.7	0	95	0	4	4	3
	27	110	-0.34	0.94	19	4.5	0	95	0	4	4	4
	29	315	0.71	-0.71	12	3.5	0	95	0	4	4	4
	28	80	0.17	0.98	10	6.3	0	90	0	4	4	1
	30	270	0.00	-1.00	20	4.9	0	95	0	4	4	0
3	1	150	-0.87	0.50	17	2.8	0	0	0	4	4	3
	2	280	0.17	-0.98	11	4.3	0	0	0	3	5	4
	3	60	0.50	0.87	13	3.3	0	0	0	2	6	3
	4	190	-0.98	-0.17	16	3.8	0	0	0	4	4	4
	5	345	0.97	-0.26	2	2.9	0	0	0	1	7	4
	6	325	0.82	-0.57	16	2.5	0	0	0	4	4	0
	7	335	0.91	-0.42	22	3.4	0	0	0	4	4	1
	8	350	0.98	-0.17	10	4.2	0	0	0	3	5	4
	9	130	-0.64	0.77	7	2.5	0	0	0	2	6	4
	10	0	1.00	0.00	0	3.4	0	0	0	1	7	4
	11	100	-0.17	0.98	12	0.2	0	0	0	6	3	3
	12	180	-1.00	0.00	11	2.6	0	0	0	3	5	1
	13	295	0.42	-0.91	22	3.0	0	0	0	4	4	1
	14	220	-0.77	-0.64	16	3.2	0	0	0	4	4	1
	15	275	0.09	-1.00	5	1.2	0	0	0	7	2	3
	16	40	0.77	0.64	11	3.3	0	0	0	3	5	4

¹ Aspect NS = north south aspect² Aspect EW = east west aspect

Table A3. Environmental variable data collected in 1 x 1 quadrats in each site (continued).

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Slope (degrees)	Litter Depth (cm)	Bare Ground (%)	Litter Cover (%)	Rock Cover (%)	Position (class)	Topography (class)	Texture (class)
3	17	0	1.00	0.00	0	2.4	0	0	0	9	1	1
	18	85	0.09	1.00	22	2.8	0	0	0	2	6	1
	19	0	1.00	0.00	0	3.4	0	0	0	8	1	3
	20	270	0.00	-1.00	27	2.1	0	0	0	4	4	3
	21	250	-0.34	-0.94	10	1.6	0	95	0	1	7	3
	22	180	-1.00	0.00	8	2.7	0	95	0	3	5	4
	23	350	0.98	-0.17	23	1.4	2	90	0	4	4	3
	24	130	-0.64	0.77	18	0.5	3	82	0	4	4	3

¹ Aspect NS = north south aspect

² Aspect EW = east west aspect

Table A4. Environmental variable data collected in 5 x 5 quadrats in each site.

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Canopy Cover (%)	Rock	Topography (class)	Tall Shrubs (density)	Trees (density)	Betpap ³ (age)	Betocc (age)	Popbal (age)	Poptre (age)	Salspp (age)
1	1	210	-0.015	0.008	42.7	0	5	17	0				30	
	2	150	0.012	-0.012	30.2	1	5	2	0				30	
	3	305	-0.017	-0.005	42.7	1	3	3	14		22	23	22	17
	4	186	-0.014	-0.011	37.5	0	5	3	0				29	
	5	117	-0.013	-0.012	56.3	0	3	3	5			30	29	
	6	280	-0.016	-0.007	61.5	1	5	6	9			29	27	
	7	204	-0.017	0.004	52.1	0	3	3	0			29		16
	8	0	0.000	0.000	49	0	1	9	6			29	27	
	9	0	0.000	0.000	72.9	0	5	3	3				28	
	10	45	0.009	0.015	58.3	1	5	3	6			22		22
	11	0	0.000	0.000	81.3	0	3	5	12			32		
	12	0	0.000	0.000	52.1	0	3	5	1			23		26
	13	324	-0.016	-0.007	64.6	0	4	5	4			29		
	14	32	0.015	0.010	59.4	0	6	13	5				26	
	15	0	0.000	0.000	83.3	0	4	7	6			32		25
	16	32	0.015	0.010	55.2	1	6	2	1			27		
	17	0	0.000	0.000	59.4	0	2	3	3					19
	18	0	0.000	0.000	0	0	5	7	3			32	23	18
	19	26	0.011	0.013	0	1	5	4	4				29	
	20	170	0.016	0.006	66.7	1	5	3	9				24	22
	21	0	0.000	0.000	62.5	0	1	19	8			29		
2	1	0	1.000	0.000	92.7	0	5	9	7			17		

¹ Aspect NS = north south aspect² Aspect EW = east west aspect³ See Table A6 for species codes

Table A4. Environmental variable data collected in 5 x 5 quadrats in each site (continued).

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Canopy Cover (%)	Rock	Topography (class)	Tall Shrubs (density)	Trees (density)	Betpap ³ (age)	Betocc (age)	Popbal (age)	Poptre (age)	Salspp (age)
2	2	150	-0.866	0.500	85.4	0	5	0	1				18	
	3	160	-0.940	0.342	43.8	0	5	6	1			15	24	
	4	180	-1.000	0.000	43.8	0	6	4	1			19	18	
	5	150	-0.866	0.500	50	0	5	3	2				23	
	6	0	1.000	0.000	82.3	0	5	9	4			24	20	
	7	190	-0.985	-0.174	87.5	0	5	2	5					
	8	320	0.766	-0.643	80.2	0	5	6	4				25	
	9	350	0.985	-0.174	81.3	0	4	2	4				23	
	10	0	1.000	0.000	84.4	0	5	14	7			22	25	
	11	180	-1.000	0.000	43.8	0	4	2	1				19	16
	12	0	1.000	0.000	40.6	0	5	1	3			19	22	
	13	300	0.500	-0.866	55.2	0	3	0	12			20	18	
	14	0	1.000	0.000	77.1	0	7	1	4			18	23	
	15	0	1.000	0.000	53.1	0	5	8	9			21	19	
	16	290	0.342	-0.940	58.3	0	5	19	3			18	13	
	17	0	1.000	0.000	75	0	4	19	10			19		15
	18	0	1.000	0.000	76	0	5	18	5			14		
	19	310	0.643	-0.766	40.6	0	4	15	3			17	21	17
	20	0	1.000	0.000	65.6	0	1	27	3			20		
	21	0	1.000	0.841	0	0	4	12	2					
	22	200	-0.940	-0.807	0	0	4	2	6			28	24	
	24	0	1.000	0.841	0	0	4	17	1			22	22	
	26	51	0.629	0.589	0	0	4	4	4				22	

¹ Aspect NS = north south aspect² Aspect EW = east west aspect³ See Table A6 for species codes

Table A4. Environmental variable data collected in 5 x 5 quadrats in each site (continued).

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Canopy Cover (%)	Rock	Topography (class)	Tall Shrubs (density)	Trees (density)	Betpap ³ (age)	Betocc (age)	Popbal (age)	Poptre (age)	Salspp (age)
2	27	305	0.574	0.543	0	1	5	2	6			20	17	
	29	0	1.000	0.841	0	0	5	1	5			18	19	
	28	140	-0.766	-0.693	0	0	5	9	6			22		
	30	210	-0.866	-0.762	0	0	5	2	2				22	
3	1	325	0.819	-0.574	81.3	0	5	13	8	19			19	
	2	335	0.906	-0.423	94.8	0	4	19	5	14	14		18	
	3	230	-0.643	-0.766	89.6	0	5	10	12				20	18
	4	0	1.000	0.000	14.6	0	1	16	0	20	21		14	
	5	260	-0.174	-0.985	89.6	0	5	17	12			21	22	
	6	0	1.000	0.000	88.5	0	5	12	2	17		13	17	
	7	240	-0.500	-0.866	82.3	0	5	8	10	16		18	21	
	8	0	1.000	0.000	93.8	0	5	18	7			18	19	
	9	0	1.000	0.000	91.7	0	5	25	9			15	17	
	10	0	1.000	0.000	90.6	0	5	22	11			15	19	16
	11	130	-0.643	0.766	46.9	0	5	60	0	14		19	17	
	12	280	0.174	-0.985	40.6	0	4	12	0			15	15	
	13	0	1.000	0.000	46.9	1	5	11	8			18	21	
	14	5	0.996	0.087	67.7	0	5	5	15			14	18	
	15	275	0.087	-0.996	62.5	0	5	3	7			16	21	
	16	235	-0.574	-0.819	64.6	1	5	17	9	17		22	21	15
	17	310	0.643	-0.766	63.5	0	3	12	11			17		
	18	0	1.000	0.000	60.4	0	5	4	7				19	

¹ Aspect NS = north south aspect² Aspect EW = east west aspect³ See Table A6 for species codes

Table A4. Environmental variable data collected in 5 x 5 quadrats in each site (continued).

Site	Quadrat	Aspect (degrees)	Aspect NS ¹	Aspect EW ²	Canopy Cover (%)	Rock	Topography (class)	Tall Shrubs (density)	Trees (density)	Betpap ³ (age)	Betocc (age)	Popbal (age)	Poptre (age)	Salspp (age)
3	19	0	1.000	0.000	71.9	0	5	7	9				19	
	20	0	1.000	0.000	43.8	0	5	49	3	12				
	21	150	-0.866	0.500	47.9	1	4	78	2			14		
	22	0	1.000	0.000	59.4	1	3	5	4			21	16	21
	23	0	1.000	0.000	56.3	1	2	14	13			18	20	
	24	0	1.000	0.000	49	1	5	42	0	16			19	

¹ Aspect NS = north south aspect

² Aspect EW = east west aspect

³ See Table A6 for species codes

Table A5. Ages of cored trees in each site.

Site	Quadrat	BetoccR ¹	BetpapR	LarlarR	PicglaR	PopbalR	PoptreR	SalsppR
1	1						30	
	2						30	
	3		22			23	22	17
	4				23		29	
	5					30	29	
	6					29	27	
	7					29		16
	8					29	27	
	9						28	
	10					22		22
	11					32		
	12					23		26
	13					29		
	14						26	
	15					32		25
	16			29		27		
	17							19
	18					32	23	18
	19						29	
	20						24	22
	21					29		
2	1					17		
	2						18	
	3					15	24	
	4					19	18	
	5						23	
	6					24	20	
	7							
	8						25	
	9						23	
	10					22	25	
	11						19	16
	12					19	22	
	13					20	18	
	14					18	23	
	15					21	19	
	16					18	13	
	17					19		15
	18					14		
	19					17	21	17
	20					20		
	21							
	22					28	24	
	24					22	22	
	26						22	
	27					20	17	
	28					22		

¹ See Table A6 for species codes

Table A5. Ages of cored trees in each site (continued).

Site	Quadrat	BetoccR ¹	BetpapR	LarlarR	PicglaR	PopbalR	PoptreR	SalsppR
2	29					18	19	
	30						22	
3	1	19					19	
	2	14	14				18	
	3						20	18
	4	20	21	18			14	
	5					21	22	
	6	17				13	17	
	7	16				18	21	
	8			17		18	19	
	9					15	17	
	10					15	19	16
	11	14				19	17	
	12					15	15	
	13					18	21	
	14					14	18	
	15					16	21	
	16	17				22	21	15
	17					17		
	18						19	
	19						19	
	20	12						
	21					14		
	22					21	16	21
	23					18	20	
	24	16					19	
SUM ²		9	3	3	1	48	54	15
MAX ³		20	22	29	23	32	30	26
MIN ⁴		12	14	17	23	13	13	15
AVERAGE ⁵		16.1	19.0	21.3	23.0	21.1	21.4	18.9

¹ See Table A6 for species codes

² Total number of individuals of each species

³ Maximum age of each species

⁴ Minimum age of each species

⁵ Average age of each species

Table A6. Species codes. Nomenclature as per United States Department of Agriculture PLANTS database.

Growth Form	Genus and Species	Common Name	Code
Moss	<i>Amblystegium serpens</i>		Ambser
	<i>Aulacomnium palustre</i>		Aulpal
	<i>Brachythecium</i> spp.		Braspp
	<i>Bryohaplocladium microphyllum</i>		Brymic
	<i>Bryum argenteum</i>	silvergreen bryum moss	Bryarg
	<i>Bryum</i> spp.		Bryspp
	<i>Campylium chrysophyllum</i>	goldenleaf campylium moss	Camchr
	<i>Campylium hispidulum</i>	hispid campylium moss	Camhis
	<i>Campylium stellatum</i>	star campylium moss	Camste
	<i>Ceratodon purpureus</i>		Cerpur
	<i>Drepanocladus</i> spp.		Drespp
	<i>Funaria hygrometrica</i>		Funhyg
	<i>Helodium blandowii</i>	Blandow's helodium moss	Helbla
	<i>Hylocomium splendens</i>	splendid feather moss	Hylspl
	<i>Leptobryum pyriforme</i>		Leppyr
	<i>Orthotrichum obtusifolium</i>	obtuseleaf aspen moss	Ortobt
	<i>Plagiomnium cuspidatum</i>	toothed plagiomnium moss	Placus
	<i>Plagiothecium laetum</i>		Plalae
	<i>Pleurozium schreberi</i>	Schreber's big red stem moss	Plesch
	<i>Polytrichum strictum</i>		Polstr
	<i>Pylaisiella polyantha</i>	aspen stalking moss	Pylpol
	<i>Sanionia uncinata</i>		Sanunc
	<i>Tomenthypnum nitens</i>		Tomnit
	<i>Tortula mucronifolia</i>	mucronleaf tortula moss	Tormuc
Sedge	<i>Carex</i> spp.	sedge	Carspp
	<i>Schoenoplectus acutus</i>	great bulrush	Schacu
Grass	<i>Bromus anomalus</i>	nodding brome	Broano
	<i>Bromus inermis</i>	smooth brome	Broine
	<i>Calamagrostis canadensis</i>	marsh reed grass	Calcan
Forb	<i>Achillea millefolium</i>	common yarrow	Achmil
	<i>Aralia nudicaulis</i>	wild sarsaparilla	Aranud
	<i>Astragalus canadensis</i>	Canadian milkvetch	Astcan
	<i>Astragalus cicer</i>	cicer milkvetch	Astcic
	<i>Chamerion angustifolium</i>	fireweed	Cahang
	<i>Chenopodium album</i>	lambsquarters	Chealb
	<i>Cornus canadensis</i>	bunchberry	Corcan
	<i>Corydalis aurea</i>	golden corydalis	Coraur
	<i>Crepis runcinata</i>	fiddleleaf hawksbeard	Crerun
	<i>Equisetum arvense</i>	common horsetail	Equarv
	<i>Equisetum fluviatile</i>	water horsetail	Equflu
	<i>Fragaria virginiana</i>	wild strawberry	Fravir
	<i>Galium boreale</i>	northern bedstraw	Galbor
	<i>Geocaulon lividum</i>	northerb bastard toadflaw	Geoliv
	<i>Hippuris vulgaris</i>	common mare's-tail	Hipvul
	<i>Linnaea borealis</i>	twinflor	Linbor
	<i>Maianthemum canadense</i>	wild lily-of-the-valley	Maican
	<i>Melilotus albus</i>	yellow sweet clover	Melalb

Table A6. Species codes. Nomenclature as per United States Department of Agriculture PLANTS database (continued).

Growth Form	Genus and Species	Common Name	Code
Forb	<i>Moehringia lateriflora</i>	bluntleaf sandwort	Moelat
	<i>Orthilia secunda</i>	one-sided wintergreen	Ortsec
	<i>Parnassia palustris</i>	northern grass-of-parnassus	Parpal
	<i>Platanthera aquilonis</i>	northern green orchid	Plaaqu
	<i>Polygonum arenastrum</i>	common knotweed	Polare
	<i>Pyrola asarifolia</i>	common pink wintergreen	Pyrasa
	<i>Ranunculus gmelinii</i>	Gmelin's buttercup	Rangme
	<i>Rorippa islandica</i>	marsh yellow cress	Rorisl
	<i>Rubus pubescens</i>	dewberry	Rubpub
	<i>Sonchus arvensis</i>	perennial sow thistle	Sonarv
	<i>Stellaria longifolia</i>	long-leaved chickweed	Stelon
	<i>Symphyotrichum ciliolatum</i>	Lindley's aster	Symcil
	<i>Taraxacum officinale</i>	dandelion	Taroff
	<i>Trientalis borealis</i>	northern starflower	Tribor
	<i>Trifolium repens</i>	white clover	Trirep
	<i>Triglochin palustris</i>	marsh arrowgrass	Tripal
	<i>Typha latifolia</i>	cattail	Typlat
	<i>Urtica dioica</i>	stinging nettle	Urtdio
	<i>Vicia americana</i>	American vetch	Vicame
	<i>Viola</i> spp.	violet	Viospp
Low Shrub	<i>Amelanchier alnifolia</i>	Saskatoon	AmealnL
	<i>Arctostaphylos uva-ursi</i>	kinnikinnick	ArcuvaL
	<i>Betula papyrifera</i>	paper birch	BetpapL
	<i>Betula pumila</i>	dwarf birch	BetpumL
	<i>Caragana arborescens</i>	caragana	CararbL
	<i>Cornus sericea</i>	red-osier dogwood	CorserL
	<i>Dasiphora fruticosa</i>	shrubby cinquefoil	DasfruL
	<i>Ledum groenlandicum</i>	Labrador tea	LedgroL
	<i>Picea glauca</i>	white spruce	PicglaL
	<i>Populus balsamifera</i>	balsam poplar	PopbalL
	<i>Populus tremuloides</i>	trembling aspen	PoptreL
	<i>Ribes oxycanthoides</i>	northern gooseberry	Riboxyl
	<i>Rosa acicularis</i>	common wild rose	RosaciL
	<i>Rubus idaeus</i>	wild red raspberry	RubidaL
	<i>Salix</i> spp.	willow	SalsppL
	<i>Spiraea alba</i>	white meadowsweet	SpialbL
Tall Shrub	<i>Caragana arborescens</i>	caragana	CararbT
	<i>Populus balsamifera</i>	balsam poplar	PopbalT
	<i>Populus tremuloides</i>	trembling aspen	PoptreT
	<i>Salix</i> spp.	willow	SalppT
Tree	<i>Picea glauca</i>	white spruce	PicglaR
	<i>Populus balsamifera</i>	balsam poplar	PopbalR
	<i>Populus tremuloides</i>	trembling aspen	PoptreR
	<i>Salix</i> spp.	willow	SalsppR