Development Of Shrub And Lichen-Dominated Biocrust Propagation And Establishment Techniques For Reclamation In Northern Environments

by

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ABSTRACT

Resource exploration and extraction in the arctic causes long lasting disturbances as natural recovery is a long and slow process in the north. With three Canadian diamond mines expected to close in the next fifteen years, many hectares of land will require revegetating. Research conducted in the field at Diavik Diamond Mine Inc, Northwest Territories, Canada (Diavik), and in growth chambers at the University of Alberta, focused on propagation and establishment of shrub species and lichen biocrusts with the objective of developing integrated shrub heath tundra communities. To address the lack of previous research, we conducted a number of large scale studies to assess species behaviours under a variety of conditions that can be used to inform current reclamation practices and guide future research directions.

Two growth chamber experiments were conducted over 60 days to examine the effects of common and novel rooting techniques on adventitious and lateral root development on cuttings from eight arctic shrub species. The first experiment had six soaking times (0, 1, 3, 5, 10, 20 days), four indole-3-butyric acid (IBA) concentrations (0, 0.1, 0.4, 0.8 %), and three seasons (summer, fall, spring). The second had a control, three IBA concentrations (0.1, 0.4, 0.8 %), three *Salix* water extracts, or three smoke water extracts, in two seasons (summer, fall). All eight species developed at least primary and secondary roots in at least one season in one experiment, including one previously untested species, *Kalmia procumbens*. This is an important milestone for using vegetative propagation for shrub species that lack reliable seed sources. Rooting characteristics were highly variable, with maximum rooting percentages between 3 and 94, and maximum number of roots per cutting between 1 and 117, across species, seasons, and experiments. Dormant *Salix* cuttings should be collected for revegetation due to strong seasonal influences on rooting; only small seasonal effects were observed for the other seven species. Although rooting percentages were generally low, species specific interactions between season and *Salix* and smoke water extracts were observed. For *Salix*, common and novel treatments in

our study affected primary and secondary root development differently, indicating treatments must be carefully selected to optimize root system architecture for specific site conditions.

Field research focused on biocrust establishment on mining by-products (crushed rock, lake sediment, processed kimberlite), inoculant dispersal (dry placement, slurry), with habitat amelioration techniques (erosion control blanket, tundra soil, woody debris), and containment (jute mat) at Diavik. After three field seasons, uninoculated plots had significantly lower species richness and vegetation cover than inoculated plots. Biocrust retention was highest on plots with erosion control blanket, containment, woody debris, and crushed rock; larger scale application of these treatments should be assessed in future.

Growth chamber experiments were conducted to assess the effects of substrate (crushed rock, tundra soil), substrate depth (1, 1.5, 2 cm), substrate sterilization, lichen inoculation, and community composition (*Flavocetraria cucullata* alone, mixed sieved biocrust, unsieved mixed biocrust) and watering frequency (damp, 1 day, 2 day, 3 day, 10 day) on survival of arctic biocrusts collected from Diavik over six weeks. Mixed species had less decline in live lichen between the start and end of the experiment than *Flavocetraria cucullata*, and substrate interacted with species inoculation to affect species survival over time. We found that a three day watering frequency and a substrate depth of 1 cm had the least decline in live lichen. Sterilization did not affect lichen survival, and no contamination was observed. Our results highlighted the challenges of growing lichens under controlled conditions as only a few treatments increased live lichen.

Given the lack of research and limited success to date in restoring tundra vegetation communities, our research assessing novel propagation and establishment techniques for both shrub species and lichen biocrusts is foundational for community focused arctic revegetation. These results can guide future work incorporating different vegetation types, in conjunction with anthroposol development and placement, that meets the current and future needs of different species and communities, and can create new research opportunities assessing community assembly, vegetation succession, and recovery of ecosystem processes in the arctic.

PREFACE

Chapter II has been published as Ficko, S.A and M.A. Naeth. 2021. Root development on cuttings of seven arctic shrub species for revegetation. Arctic, Antarctic, and Alpine Research 53:237-251. S.A. Ficko and M.A. Naeth conceived and designed the research. S.A. Ficko collected the data, performed the analyses and developed the manuscript. M.A. Naeth procured funding and research site access, and supervised and edited the manuscript.

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What drives life is thus a little electric current, set up by the sunshine.

Albert Szent-Gyorgyi

This thesis is dedicated to my family.

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I. BACKGROUND

1. INTRODUCTION

Human activities in the north[1] have increased significantly over the past century with the discovery of resources such as oil and metals, increases in their value and requirements, and improvements in transportation to the north by land and air. Mineral extraction has played a large role in creating anthropogenic disturbances in the Canadian north. Sustainable and ethical development at all stages of mining from planning to closure can mitigate northern community concerns about long term impacts on their traditional lands and way of life, and reclaim disturbed tundra habitats following site closure.

Since the early 1990s, discovery of diamonds in kimberlite pipes near Lac de Gras, Northwest Territories (NWT) has led to construction of five diamond mines, Diavik Diamond Mines Inc. (Diavik), Ekati Diamond Mine, Gahcho Kué Diamond Mine, Jericho Diamond Mine, and Snap Lake Diamond Mine. Diavik is the largest and most productive mine, producing over 100 million carats of rough diamonds by 2016 (Figure 1.1) from four pipes (Shigley et al. 2016). While diamond mining is one of the cleanest forms of mining, above and below ground activities have a significant environmental footprint as they affect large areas of land through soil compaction and removal; construction of roads, gravel pads, and concrete pads; infrastructure development for accommodations, processing facilities, equipment storage and maintenance; water table lowering; and creation of waste rock piles (ABR Inc 1995, Couch 2002, Johnson et al. 2005, Naeth and Wilkinson 2011, Drozdowski et al. 2012). These activities leave the areas vulnerable to wind and water erosion, potentially unstable, and with limited ability to provide food or habitat for fauna. Without intervention, these areas could take hundreds to thousands of years to recover naturally due to the extreme environmental conditions and altered physical and chemical characteristics of the disturbed land (Billings 1987, Forbes and Jefferies 1999, Rausch and Kershaw 2007).

In this thesis, reclamation is defined as the process of assisting recovery of disturbed land to useful purposes, while restoration is defined as the process of assisting recovery of disturbed lands to pre-disturbance conditions. Revegetation is a specific component of reclamation that addresses assisted recovery of the vegetation community. Reclamation of tundra environments is necessary for timely plant community recovery; however, current revegetation practices are limited by lack of native plant material sources, harsh environmental conditions, high costs, and lack of regulations. Even with ongoing research since the 1960s, effective large scale methods to

[1]North in this thesis refers to arctic and subarctic regions with a cold climate, underlying permafrost and short growing season.

reclaim northern environments to pre-disturbed conditions have yet to be developed despite significant management strategy changes over time.

With approximately 3 years of mining remaining, Diavik is researching closure plans to reclaim disturbed areas through innovative, cost effective, and sustainable techniques with the goal of leaving positive community and environmental legacies (Diavik Diamond Mine Inc. 2011). Revegetation of land disturbed by mining and other anthropogenic activities in the north will require improvement and building of soils and substrate materials to support and sustain plant establishment, growth, and development, and acquisition and propagation of plant material that can tolerate harsh conditions while developing into an appropriate plant community (Kidd 1996, Kidd and Rossow 1998).

An understanding of the species in the current mosaic of tundra plant communities throughout the north is a foundation for reclamation work, and a baseline from which to document changes from climate change. Our research focusing on developing and improving methods for collection, propagation, and dispersal of native shrub species and lichen-dominated biocrusts from Diavik Diamond Mine will further current knowledge of how to accelerate revegetation of disturbed northern lands to conserve this unique ecosystem for future generations to call home, and create research opportunities to study community assembly and succession, and recovery of ecosystem processes.

2. LITERATURE REVIEW

2.1. Environmental Conditions At Diavik Diamond Mine

Diavik Diamond Mine is located on an island in the middle of Lac-de-Gras, approximately 320 km northeast of Yellowknife, Northwest Territories (64º49’ N, 110º27’ W), approximately 100 km north of the treeline and 200 km south of the arctic circle. Lac-de-Gras lies is in the Southern Arctic Ecozone, and the Point Upland Arctic Ecoregion (Ecosystem Classification Group 2012) with a short growing season between late May and mid August, near continuous daylight, mean annual rainfall of 128 mm (285 mm mean annual total precipitation) from 2011 to 2016 and mean annual temperature of -8.8 ºC. The landscape is dominated by large archean rock outcrops and remnants of glaciers in the form of boulders, till, and eskers (Drozdowski et al. 2012). Organic cryosolic soils dominate lowland areas, with sedges and mosses forming the dominant vegetation (Drozdowski et al. 2012). In upland areas, turbic and static cryosolic soils dominate with dwarf shrub heath tundra species, including *Arctous rubra* (Rehder & Wilson) Fernald (red bearberry), *Betula glandulosa* Michx. (bog birch), *Empetrum nigrum* L. (crowberry), *Kalmia procumbens*

(L.) Gift & Kron (alpine azalea), *Rhododendron tomentosum* Harmaja (marsh Labrador tea), *Salix* species (willow), *Vaccinium uliginosum* L. (bog bilberry), and *Vaccinium vitis-idaea*) L. (bog cranberry), and lichen dominated biocrust communities. Nomenclature for plant species from Diavik follows Northwest Territories Species Infobase (2021); nomenclature for all other species follows NatureServe (2021). Vegetation cover is 80 to 100 % in mesic to wet areas, to little cover in dry areas (Kidd 1996, Naeth et al. 2006, Ecosystem Classification Group 2012).

At Diavik, lichens and other micro biota are common components of the tundra ecosystem, with lichens providing 25 % or more ground cover in some areas (Naeth and Wilkinson 2008). Approximately 360 species of lichens have been identified in Northwest Territories (Goward and Björk 2012), and approximately 50 macrolichen species (not exhaustive) have been identified at Diavik from biocrust material collected in fall 2013 (Ficko, unpublished). Species included *Alectoria ochroleuca* (Hoffm.) A. Massal. (green witch's hair), *Bryocaulon divergens* (Ach.) Kärnefelt (heath foxhair lichen), *Bryoria nitidula* (Th. Fr.) Brodo & D. Hawksw. (tundra horsehair lichen), *Cetraria* Ach. species (Iceland lichens), *Cladonia* P. Browne species (including cupped species and reindeer lichens), *Dactylina arctica* (Hooker f.) Nyl. (Arctic finger lichen), *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell (curled snow lichen), *Flavocetraria nivalis* (L.) Kärnefelt & A. Thell (crinkled snow lichen), *Gowardia nigricans* (Ach.) P. Halonen, L. Myllys, S. Velmala, & H. Hyvärinen (gray witch's hair), *Masonhalea richardsonii* (Hooker) Kärnefelt (Arctic tumbleweed), *Melanelia stygia* (L.) Essl., *Parmelia* Ach. (alpine camouflage lichen), *Parmelia* species (shield lichens), *Sphaerophorus globosus* (Hudson) Vainio (coral lichen), *Stereocaulon* Hoffm. species (Easter lichens), and *Thamnolia vermicularis* (Sw.) Ach. Ex Schaerer (whiteworm lichen). Taxonomy follows Esslinger (2019). Eighteen species of mosses (Lamarre 2016) and three liverworts were present at Diavik. Other taxa present in biocrust communities were not characterized in this thesis.

2.2. Environmental Adaptations Of Northern Vegetation

Plants are an essential component of the global biogeochemical cycle, providing numerous ecosystem benefits, including soil stability, erosion control, water and infiltration capacity regulation, improved soil physical and chemical properties, oxygen, and improved air quality (Amézketa 1999, reviewed in Gyssels et al. 2005, reviewed in Reubens et al. 2007, de Groot et al. 2010, Bardgett et al. 2014). Plant functional type (life form, growth form, root type) or functional traits (architectural, morphological, physiological, biotic) may modulate interactions with the environment, including biological, chemical, hydrologic, microclimatic, and physical factors (Jonasson and Callaghan 1992, Schweingruber and Poschlod 2005, Gyssels et al. 2005, Marden

et al. 2007, Reubens et al. 2007, Pohl et al. 2011, Bardgett et al. 2014, Wang et al. 2016). In northern locations, plant growth is limited by short growing season, high wind, low temperature, low rainfall, desiccation, permafrost, limited seed production, unviable seeds, herbivory, low species diversity, soil compaction, and slow decomposition and nutrient turn over resulting in low soil fertility (Billings 1987, Forbes and Jefferies 1999, Rausch and Kershaw 2007, Deshaies et al. 2009, Ecosystem Classification Group 2012). Arctic and subarctic plant species biodiversity is limited to approximately 1,000 species that have adapted to the harsh conditions (Billings 1987).

In northern tundra environments, plants growing in exposed areas have low lying growth forms that maximize sunlight exposure and snow protection in winter, while minimizing effects of wind and low temperatures, potentially altering boundary layer effects. Root:shoot ratios, according to the optimality theory, reflect the dynamic carbon allocation between above and below ground tissues based on capturing the most limiting resources, particularly nitrogen in tundra environments, or storage of resources in fall (Chapin III 1980, Bloom et al. 1985, Chapin et al. 1986, 1987, Atkin 1996, Gedroc et al. 1996, Poorter et al. 2012, Zhu and Zhuang 2013, Reich et al. 2014). For example, Poorter et al. (2012) noted that many plants allocate resources to root development at the expense of shoot and leaf growth, particularly during times of water and nutrient stress, and Mokany et al. (2006) estimated a median root:shoot ratio of 4.8 for the tundra biome. Most plant species in northern locations have shallow roots that can have 20 times or more biomass than above ground shoots, and many species produce specialized below ground tissues such as stolons and rhizomes to store carbohydrates over winter and reproduce vegetatively to increase long term survival (Wielgolaski 1980, Chapin III et al. 1990, Archibold 1995, Densmore et al. 2000, Iversen et al. 2015). Since assessing below ground biomass is more challenging than assessing above ground biomass, various models use root:shoot ratio (or other similar ratios of plant biomass compartments) to estimate root biomass for a particular vegetation type. Below ground biomass of northern species are generally constricted to the top 30 cm of soil by underlying permafrost and soil temperature gradients in the active layer, though depth of rooting and timing of maximum root growth appears to be influenced by plant functional type and species (Jackson et al. 1996, Canadell et al. 1996, Iversen et al. 2015, Wang et al. 2016). Further research on the dynamics between resource acquisition and conservation strategies in fast or slow growing species, and on resource allocation at different times of year between short lived fine roots important for acquisition of water and nutrients and coarse roots for storage is necessary for assisting northern plant species recovery after disturbance and for understanding northern species responses to changing environmental conditions (Reich et al. 2014, Iversen et al. 2015, Blume-Werry et al. 2018).

Biological soil crusts (biocrusts) are common and often integral components of mature arid and semi arid ecosystems including polar environments, or as pioneers in primary and secondary succession pathways (Metting 1991, Bowker 2007). Biocrusts are important communities composed of various organisms such as algae, bacteria, cyanobacteria, fungi, lichens, liverworts, and mosses, that form a thin horizontal layer in association with the top few centimetres of soil (Eldridge and Greene 1994, Li et al. 2003, Bowker 2007, Belnap et al. 2016). Biocrusts are often called ecosystem engineers, and provide many beneficial functions, including reducing soil erosion, increasing soil stability, modifying infiltration and soil water retention, creating habitat for soil invertebrates, altering seedling establishment and plant productivity, and increasing soil fertility and nutrient cycling (Eldridge and Greene 1994, Lange et al. 1994, Mazor et al. 1996, Kidron and Yair 1997, Prasse and Bornkamm 2000, Harper and Belnap 2001, Belnap and Lange 2003, George et al. 2003, Elmarsdottir et al. 2003, Xiao et al. 2011, Lukešová et al. 2013, Weber et al. 2016a). Recent research has begun to assess the role of biocrusts in global and continental biogeochemical cycles and ecosystem functions, and to predict how changes to biocrust distribution from climate change may lead to a feedback cycle that further alters ecosystem structures and functions (Vile et al. 2008, Elbert et al. 2012, Pointing and Belnap 2012, Porada et al. 2013, 2014, Lenhart et al. 2015, Reed et al. 2016, Belnap and Lange 2017).

Abiotic and biotic environmental conditions, including soil and air temperatures, soil parent material, soil texture, soil chemistry, soil compaction, nutrient availability, vascular plant community structure, solar radiance and UV exposure, precipitation types and amount, wind, local climate conditions, and topography and microtopography, affect type and growth of biocrusts that develop on specific habitats (Benedict 1990, Rosentreter and Belnap 2003, reviewed in Bowker et al. 2016). In boreal and tundra environments, lichens and/or mosses are common in biocrusts. Large mats of fruticose lichens can constitute a significant portion of the winter diet of caribou in some regions, which are hunted or farmed by many northerners (Ahti 1977, Boertje 1984, Thomas and Hervieux 1986, Brodo et al. 2001, Kumpula 2001, Joly et al. 2007).

Soil crust organisms are poikilohydrous, with capacity to tolerate desiccation or xeric conditions, although biological activities such as growth, spore production (algae, lichen mycobionts, mosses), and cellular damage repair only occur when an organism achieved positive carbon balance after wetting by rain, dew, or fog (Kershaw and Rouse 1971, Lange et al. 1994, Green et al. 2011, Bidussi et al. 2013). Lange (2003) and Lange et al. (1994) found lichens moistened by overnight humidity or dew were generally only active for the first two to four hours of daylight, then dried out and become dormant as air temperature increases and humidity decreased with increasing light intensity. They found soil crust lichens hydrated to their maximum

water holding capacity by submerging in water for five minutes were air dry within 150 minutes. Biocrust organisms can be stressed by very brief periods of hydration, which favour respiration over photosynthesis, or excessive moisture which causes suprasaturation (Lange et al. 2001, Doherty et al. 2015). As biocrusts require sufficient water and nutrients for growth, they likely undergo pulses of growth under appropriate conditions followed by static growth or regression of biomass or cover (Weber et al. 2016a), although mean net annual growth is generally low.

In the only long-term study of biocrust lichens, biannual monitoring on the Colorado Plateau since 1967 demonstrated dynamic changes in individual lichen populations on a year to year basis (Belnap and Lange 2017). For example, while absolute cover values for lichens were low, cover of *Placidium* A. Massal. (Breuss 1996) species increased 400 % over two years, cover of *Circinaria hispida* (Mereschk.) A. Nordin, Savić & Tibell increased 420 % in one year, and cover of *Collema* F. H. Wigg. cyanolichens dropped from ~20 % to 4 % between 1967 and 2015. Lichen growth rates vary dramatically based on morphology, age, environmental conditions, and species specific rates, from as little as 0.1 mm to several centimetres radial growth in a year (Hale 1973, Nash 1996, Armstrong 2004, Sancho et al. 2007, Trenbirth and Matthews 2010). Growth rates between 3 and 5 mm per year have been recorded for some boreal and polar reindeer lichen species (Scotter 1963, Pegau 1968, Bliss 1971, Helle et al. 1983, Boudreau and Payette 2004, McMullin and Rapai 2020).

In northern environments, vegetative reproduction is generally more common than sexual reproduction due to the short growing season and harsh conditions; however, sexual reproduction in favourable years is a key factor in maintaining or increasing genetic diversity (Billings 1987). Many plant species are pollinated by insects and produce flower buds at the end of one growing season in preparation for favourable conditions in future years (Billings 1987, Totland 1993). Most non vascular species, including lichens (fungal partner), mosses, and algae, can reproduce sexually from diaspores or asexually by vegetative reproduction (Bowler and Rundel 1975, Bowker et al. 2000, Brodo et al. 2001, Roturier et al. 2007, Root and Dodson 2016). Mosses are totipotent and can reproduce from any vegetative tissue or propagule such as shoot fragments, bulbils, rhizomes, and gemmae (Memon and Lal 1981, Vitt et al. 1988). While frequency of natural lichenization is unknown, many lichen species are naturally dispersed by thallus fragmentation (trampling) or vegetative propagules such as isidia and soredia, then transported by wind, water, and animals which is facilitated by brittleness of dry thalli (Webb 1998, Heinken 1999, Brodo et al. 2001, Büdel and Scheidegger 2008). Following fragmentation, lichen thalli can resume growth by elongation of the apical portion, forming new branches at internodes between older branches or forming new podetia from undifferentiated thalli (Webb 1998).

In arctic and subarctic environments, effects of topography on micro, meso, and landscape scales significantly affect establishment, development, and survival of vascular and non vascular species. While northern species are adapted to growing at low temperatures, distribution of vegetation and biocrusts in relation to the surrounding landscape is affected by biogeographic, climatic, edaphic, topographic, and biotic forces, such as wind speed, snow pack, light, soil water, underlying parent material, and soil nutrients (Bliss 1962, Sohlberg and Bliss 1984, Billings 1987, Truett and Kertell 1992, Anderson and Bliss 1998, Kuntz and Larson 2006, Bowker et al. 2016). For germination and establishment, seeds need favourable micro sites or safe sites with appropriate physical and chemical properties and/or nurse species which can provide shelter from the wind, slightly raise soil and air temperatures, and increase water retention, to help overcome harsh environmental effects (Sohlberg and Bliss 1984, Jumpponen et al. 1999, Densmore et al. 2000, Elmarsdottir et al. 2003, Kuntz and Larson 2006).

Wildfires, while infrequent, play an important role in northern ecosystems (Racine et al. 1987). Knowledge of vegetation response to fire is limited to a few burns in Alaska and northern Canada which occurred since the 1970s, with some species adapting for survival following fire (Racine et al. 1987). Wildfires affect above and below ground physical, chemical, and biological properties of an ecosystem through changes to vegetation (vascular and non vascular species) and soils (Racine et al. 2006). In boreal forests, lichen succession is dependent on episodic fires to maintain an open woodland canopy, and culminates with almost complete cover by *Cladonia stellaris* or *Stereocaulon paschale* (Maikawa and Kershaw 1976, Kershaw 1977). These lichen species are common at high latitudes with open cover and acidic, xeric sandy soils or peat. Vegetation response to fire depends on fire severity, site conditions, time of year, plant species, and post fire time scale (Racine et al. 1987, 2006, Landhausser and Wein 1993).

2.3. Succession And Revegetation In The North

Anthropogenic disturbances, including climate change, infrastructure development, land management, recreational use, and resource extraction, can significantly impact function, integrity, and resilience of northern ecosystems by altering biodiversity, nutrient cycling, permafrost, water infiltration, and soil properties, increasing risk of erosion, and often removing sources of seeds or other inoculants found in the soil seedbank (Ebersole 1989, Belnap and Eldridge 2001, Forbes et al. 2001, Post et al. 2009, Lang et al. 2012, Chapin III et al. 2012, Schuur et al. 2015, Becker and Pollard 2016). Biocrusts are sensitive to disturbances such as trampling (humans, animals, vehicles), grazing, air temperature increases, changing climate, mining, pipeline construction, and fire (Eldridge and Greene 1994, Harper and Kershaw 1996, Marsh et

al. 2006, Lang et al. 2012, Escolar et al. 2012, Ferrenberg et al. 2015). Removal of crust material in severe disturbances will have a longer lasting detrimental impact than infrequent and localized disturbances that crush biocrusts in place creating a source of inoculants for recovery (Belnap and Lange 2017). Disturbance of micro biota can change vascular plant species abundance, which can cause further long term changes in the ecosystem (Jandt et al. 2008).

Following disturbances or creation of new habitat, plant communities develop and change through successional processes (Densmore et al. 2000). Vegetation development on newly exposed surfaces or severely disturbed sites is initially controlled by abiotic factors including soil, nutrients, water, and organic matter (Jumpponen et al. 1999, Mori 2011). The first plants to colonize are generally efficient seed or vegetative propagule producers, as soil generally lacks a source of plant material. In the north, slow growing woody perennials provide significantly less cover until later in succession (Babb and Bliss 1974, Klokk and Ronning 1987). The standard model of natural biocrust development and succession begins with colonization by large filamentous cyanobacteria, then smaller cyanobacterial and green algae, and finally mosses, and/or lichen species once the soil has sufficiently stabilized (Belnap and Eldridge 2001, Bowker 2007, Weber et al. 2016a, Read et al. 2016). Predictions for future succession in the north are more challenging and less reliable, as direct and indirect effects of anthropogenically induced climate change are expected to alter species composition through shrub expansion and increased growth, and species specific changes in biocrust composition (Henry and Molau 1997, Tape et al. 2006, Myers-Smith et al. 2011, Lang et al. 2012, Zamin and Grogan 2012, Chapin III et al. 2012). Recovery of ecosystems functions such as normal surface albedos, carbon fixation, and soil stability depends on which species recolonize after disturbance (Belnap and Lange 2017).

2.3.1. Natural revegetation

Disturbances in the north have long lasting environmental impacts as natural recovery is much longer and slower than in temperate climates (Billings 1987, Forbes and Jefferies 1999, Rausch and Kershaw 2007). Abiotic and biotic factors influencing recovery rates include type of soils, size and severity of disturbance, pre-disturbance vegetation, air temperature, soil water, and inoculation material availability (Belnap and Lange 2017). From long term studies of natural revegetation (35 to 50 years) at several arctic sites, researchers predicted that some disturbed sites may require several decades to hundreds of years or more to achieve similar plant diversity and cover as surrounding communities (Billings 1987, Klokk and Ronning 1987, Harper and Kershaw 1996, Forbes and Jefferies 1999, Rausch and Kershaw 2007). Methods of assessing recovery of mature soil biological crust ecosystems following disturbance have been variable and inconsistent, and often compare different types of biocrusts and different climates (Belnap and

Eldridge 2001, Belnap and Lange 2017), with estimates from a few to hundreds of years (Anderson et al. 1982, Johansen et al. 1982, 1984, Callison et al. 1985, Jeffries and Klopatek 1987, Cole 1990, Belnap 1993, Bowker 2007, reviewed in Weber et al. 2016, reviewed in Belnap and Lange 2017). Species that naturally established on disturbed areas such as gravel pads in arctic environments include grasses, forbs, shrubs, lichens, and mosses (Kershaw and Kershaw 1987, Bishop and Chapin III 1989, Walker 1996, Harvey Martens & Associates Inc. 2000).

In more temperate locations, (Xiao et al. 2014) found that a moss biocrust reformed on an artificially disturbed plot within two years on the Loess Plateau in China, and was similar in appearance to the undisturbed crust after seven years. Rola et al. (2014) assessed vegetation and cryptogamic (biocrust) recovery on contaminated sites of post-smelting dumps, and determined that *Cladonia rei* Schaerer (Syrek & Kukwa 2008, Dolnik et al. 2010, Pino-Bodas et al 2010) formed a distinct pioneer community in association with other species both in Poland and at other anthropogenic sites in Europe. In Wales, Dickinson et al. (2016) assessed interactions between vegetation and soil development on iron and coal mine wastes after 150 years of pedogenesis, and determined that plant-soil feedbacks affect biotic and abiotic conditions.

Vegetation growth after fire can originate from vegetative reproduction (sprouting), viable seeds in the soil or propagules invading the burned area (Johnson 1981). Rapid recovery, especially following mild or moderate burns, generally occurs by sprouting for species such as *Eriphorum vacinatum* L. (tussock cotton grass) and some dwarf shrubs including *Betula glandulosa*, *Empetrum nigrum*, *Rhododendron tomentosum, Salix* sp. (willow), *Vaccinium uliginosum,* and *Vaccinium vitis-idaea* (Racine 1981, Johnson 1981).

Compounds in smoke can promote seed germination (de Lange and Boucher 1990), with over 1,200 species in 80 genera, from fire prone and non fire prone environments showing enhanced germination in response to smoke (Roche et al. 1997, Bell 1999, Adkins and Peters 2001, Chiwocha et al. 2009). Some compounds isolated from smoke, such as 3-methyl-2H-furo[2,3-c]pyran-2-one (butenolide) and karrikins, had post germination stimulatory effects on seedlings similar to auxins and cytokinins (van Staden et al. 2006, Jain et al. 2008), and karrikins play a role in regulating root development (Chiwocha et al. 2009, Akeel et al. 2019, Swarbreck 2021). Vegetation composition shortly after fire is generally dominated by pioneering graminoid and bryophyte species from the seed bank or that invaded the site, with less shrub cover than in undisturbed areas (Racine 1981, Racine et al. 1987, 2006, Bret-Harte et al. 2013, Breen et al. 2015). Racine et al. (2006) found shrub cover increased as much as 65 % over 23 years, while grass and forb cover declined or disappeared. Severe fires can burn above and below ground vegetation and organic material, limiting recovery by sprouting, and facilitating colonization by

new species (Barrett et al. 2012). With climate change, the north will likely get warmer and drier, which could result in more frequent and severe fires, with long term vegetation shifts and altered succession trajectories.

2.3.2. Assisted revegetation

Assisted revegetation is a common reclamation technique to accelerate plant establishment, growth, and development on disturbed sites, though northern reclamation sites pose unique challenges and limitations for revegetation. Knowledge of expected successional pathways following disturbances can help accelerate revegetation by identifying factors limiting species establishment, growth, and development (Polster 1991). Revegetation in the north is complicated by limited access to equipment and lack of available resources. Few seed suppliers carry seeds for native arctic and alpine species, often in small quantities and/or consist of seeds for grasses and legumes which lack the diversity necessary for large scale revegetation projects of shrub-heath tundra areas (Vaartnou 1992, 2000, Wright 2008, Matheus and Omtzigt 2011). Seed purchased from distant resources may have significant transportation costs and may create issues of provenance for some species that could affect their long term success in revegetation projects (Densmore et al. 2000, Matheus and Omtzigt 2011).

Since the 1960s, research to accelerate revegetation in harsh environments has been conducted, including investigating natural recovery rates following disturbance in various types of habitats; selection, acquisition, propagation, and planting or dispersal of vegetation and propagules for assisted revegetation; and improvement of soils, substrates, and local microhabitats to support seed germination, biocrust establishment, and plant growth (Babb and Bliss 1974, Chapin III and Chapin 1980, Densmore 1987, Densmore et al. 1987, 2000, Younkin and Martens 1987, Ebersole 1989, Bishop and Chapin III 1989, De Grosbois et al. 1991, Macyk and Belts 1995, Bittman 1997, Withers 1999, Jones et al. 1999, Hagen 2002, Quinty and Rochefort 2003, Elmarsdottir et al. 2003, Gage and Cooper 2004, Walter et al. 2005, Kidd et al. 2006, Naeth et al. 2006, Holloway and Peterburs 2009, Duncan 2011, Matheus and Omtzigt 2011, Naeth and Wilkinson 2011, Ficko et al. 2015, Lamarre 2016).

Acquiring native species seed in sufficient quantities to reclaim large disturbances such as mine sites is difficult as nurseries and stores do not stock native seed for most northern shrub species. Common revegetation efforts often involved seeding early successional species that were readily available and provided rapid cover with large fibrous root systems to control erosion such as agronomic grasses and legumes, expecting later successional species to invade as soil and nutrient properties improve (Holloway and Zasada 1979, Claridge and Mirza 1981, Densmore 1992, Kidd and Rossow 1997, Forbes and Jefferies 1999, Withers 1999, Densmore et al. 2000,

Wright 2008). These species generally did not persist without repeated fertilizer application due to low nutrients in many northern soils and harsh environmental conditions (Webber and Ives 1978, Kershaw and Kershaw 1987, Klokk and Ronning 1987, Forbes and Jefferies 1999). When they did establish, large quantities of non native grasses and their litter hindered colonization and establishment of native species, leaving sites in a state of suspended succession (Densmore 1987, 1992, Younkin and Martens 1987, Bishop and Chapin III 1989, Forbes and Jefferies 1999, Withers 1999). In some cases, non native annual species such as *Lolium multiflorum* Lam. (annual rye grass) and *Hordeum vulgare* L. (barley) were seeded to quickly establish plant cover, decrease erosion, and act as a nurse crop for native seedlings by trapping blowing seeds, providing safe sites for germination, and increasing soil nutrients (Densmore et al. 2000, Cooper et al. 2004, Wright 2008).

In the past several decades, focus shifted from using southern agronomic species to using native plants and developing native cultivars adapted to the harsh environment, which can accelerate development of self sustaining plant communities, structurally and functionally integrated with the surrounding environment (Holloway and Zasada 1979, Forbes and Jefferies 1999, Kidd and Max 2000, Holloway and Peterburs 2009, Matheus and Omtzigt 2011). Desirable characteristics for woody, herbaceous, and non vascular species for revegetation of disturbed northern environments include tolerance of unfavourable environmental conditions such as coarse textured soils and low nutrients, organic matter, and water holding capacity, potential to improve soil compaction and stability, and biological properties such as low growth form, large root systems (vascular plants), perennial life form, native origin, and ability to provide habitat and food for local and transient wildlife (Rausch and Kershaw 2007, Zhao et al. 2016a). Species must be commercially or locally available in sufficient quantities for large scale projects, and success in previous revegetation studies is an asset.

Current assisted revegetation techniques include seeding commercial seed if available, collecting wild seed from native species, transplanting vegetation islands, planting nursery stock, collecting and propagating shrub cuttings, and using non vascular species (Kidd 1996, Densmore et al. 2000, Matheus and Omtzigt 2011). Choice of technique is influenced by various factors including quality and quantity of plant material necessary for revegetation, required plant diversity, site and climactic characteristics, desired end land use, jurisdictional regulations, labour requirements, knowledge development, and cost (Matheus and Omtzigt 2011, Zhao et al. 2016a). Broadcasting a purchased seed mix is the most common technique to increase site cover as it is fast, effective, and relatively inexpensive. Transplanting vegetation islands, shrubs, trees, or cuttings is labour intensive and costly, and is generally used on smaller sites or as a part of

revegetation plans to increase species diversity, preserve local genotypes, or accelerate natural recovery. Elmarsdottir et al. (2003) found biocrusts enhanced plant colonization and succession after reclamation in Iceland, indicating potential of non vascular species to improve revegetation. Despite the importance of non vascular species in northern ecosystems, little research has been conducted on how to incorporate them for revegetation of disturbed northern environments.

2.4. Selection And Acquisition Of Seeds For Northern Revegetation

When using early successional species, seed mixes and seeding rates must be carefully developed to prevent sod forming or aggressive species from out competing native species for space, nutrients, sunlight, and water and potentially preventing further succession (McTavish and Shopik 1983, Polster 1991, Forbes and Jefferies 1999, Withers 1999).

2.4.1. Commercial seed

Few companies supply seed for northern and alpine species, with most from northern grass cultivars and a few forb species. The northern seed industry has focused on grasses as they are easy to cultivate in breeder programs to develop certified seed, are natural colonizers, and can meet common revegetation goals such as rapid ground cover and erosion prevention (Vaartnou 1992, 2000, Matheus and Omtzigt 2011). Seed from other species is generally not available in sufficient quantities, not adapted to northern conditions, or does not meet reclamation objectives in sufficient time or within budget. Non native legume species, such as clover or alfalfa, were often included in seed mixes as it was thought they would increase available soil nitrogen. This practice is no longer recommended in revegetation manuals as application of fertilizer appears more effective at improving long term success, and some non native species have become persistent or invasive in some regions (Wright 2008, Matheus and Omtzigt 2011).

Yukon and Alaska have developed guidelines to select seed mixes with appropriate plant density adapted to soil and environmental conditions (Wright 2008, Matheus and Omtzigt 2011). Most of these native grass species grow in clumps (bunch grasses) rather than forming sod (turf grasses), which is beneficial for reclamation as bunch grasses are good nurse species for other native species. Sod forming species are beneficial for some projects as they have rhizomes and large fibrous root systems which help stabilize soil and decrease erosion. In Yukon, the industry practice is to include three to five complimentary species in a seed mix (10 to 40 % each), with final selection depending on factors such as desired ecological diversity and adaptability, visual considerations and site specific objectives, such as facilitating or preventing growth of natural vegetation. Seed mixes are generally developed based on number of species, desired density of species per unit area, pure live seed, germination tests, and seed weight.

Most seed purchased for revegetation projects will be common due to a lack of northern pedigreed seed. The revegetation expert is responsible for ensuring seed has been tested and graded and is not contaminated with invasive or noxious species (Wright 2008, Matheus and Omtzigt 2011). An emerging consideration when purchasing seed for revegetation is whether stock from a native cultivar is acceptable (even if propagated in a different region) or if it should be from a local genotype to prevent introduction of non-native traits (Densmore et al. 2000, Wright 2008, Matheus and Omtzigt 2011). In future, the use of seed transfer zones will likely be used more often to determine how far from a site seed can be purchased and still considered native.

2.4.2. Wild seed collection and storage

Seed production is an energy intensive process for northern plants, and many do not have appropriate environmental conditions to produce viable seeds each year (Bliss 1958). However, collecting local plant material is considered ideal for native plant revegetation (Vander Mijnsbrugge et al. 2010, Matheus and Omtzigt 2011). Locally collected wild seed reduces non native germplasm introduction, provides plants adapted to local conditions, and increases species diversity when seeds are not available commercially. Hand collection of wild seed is generally expensive, requiring extensive planning to collect at the right time of year for each species and high manual labour to collect, clean, store, and sow the seeds. While use of local seed is encouraged in many areas, it will likely only be applicable on a small scale due to high costs, unless regulatory changes require more extensive use (Wright 2008, Matheus and Omtzigt 2011).

When collecting wild seed, it is recommended to harvest < 10 % of seeds in < 10 % of years from any area to minimize impact on donor sites and increase genetic diversity of collected species (Native Plant Working Group 2000, Menges et al. 2004, Matheus and Omtzigt 2011). Collection methods vary with growth form and species (Matheus and Omtzigt 2011). Grass seed can be stripped from the stem, clipped as spikelets, or collected in a seed hopper by beating seed heads. Seed pods and heads from forbs and catkins from shrubs can be collected a few weeks before maturity and air dried in paper bags to avoid losing seeds. *Alnus* Mill. (alder), *Populus* L. (aspen, poplar), and *Betula* (birch) are commonly harvested shrub and tree species as they produce large numbers of seeds per catkin (Matheus and Omtzigt 2011). Collection of shrub and tree seeds must be timed for fall (most species) or spring (most *Salix* species) to harvest only ripe, viable seed (Densmore et al. 2000). Many species produce large seed crops periodically rather than yearly (Withers 1999). Seed collection is further complicated by short vitality times for species such as *Populus* and *Salix*, during which seed must be collected, processed, and sown or frozen (Walter et al. 2005). Shrub and tree seed are usually collected on or near the site then propagated in a greenhouse rather than directly planted. Berries can be hand picked and seeds

separated from the pulp by mashing and flotation (United States Forest Service 1974, Umarani 2014). To preserve vitality, all seeds should be air dried and kept cool or frozen prior to seeding.

2.4.3. Seed dormancy and seed bank development

Following dispersal, seeds require favourable conditions for germination. Many seeds, particularly those from non cultivated species, undergo a period of dormancy or arrested development prior to germination where they fail to germinate even under optimal conditions (Finch-Savage and Leubner-Metzger 2006). Dormancy can be endogenous (related to seed embryo) and caused by physiological, morphological or morphophysiological factors, or exogenous (related to seed coat or other surrounding tissue) and caused by physical, chemical, or mechanical factors (Baskin and Baskin 2004, Finch-Savage and Leubner-Metzger 2006). While dormancy is not well understood, environmental conditions, such as aeration, soil water, temperature, chemical signals, and light can break or change dormancy status (Bewley 1997, Baskin and Baskin 2004, Finch-Savage and Leubner-Metzger 2006).

Over time, dormant seed accumulation on or in soil and vegetative propagules form the soil seed bank, generally in the upper 5 to 10 cm of soil (Bakker et al. 1996). Seed banks are developed through a combination of inputs (seed rain, dispersal), outputs (germination, predation, decay, physical damage) and continuity (dormancy, persistence, viability). Seed banks generally contain a biased legacy of past surface vegetation, including transient (short term, <1 year) and persistent (long term, >1 year) seed banks (Bakker et al. 1996, Bossuyt and Hermy 2003). Future plant population dynamics are influenced by composition of the underlying seed bank, particularly following natural or anthropogenic disturbances (Chapin III and Chapin 1980, Freedman et al. 1982, Gartner et al. 1983, Ebersole 1989, Eager et al. 2013). Knowledge of potential species in the seed bank and their characteristics such as expected viability, longevity, and abundance can potentially be used to accelerate revegetation at disturbed sites (Bossuyt and Hermy 2003, Alsos et al. 2003). Prior to large scale anthropogenic disturbances, salvaging and stockpiling topsoil may help preserve the seed bank for future reclamation activities, although Mackenzie and Naeth (2019a) reported boreal seed viability was significantly impacted by stockpiling LFH material at depths greater than 1 m. The impact on seed vitality from stockpiling soil from tundra regions has yet to be determined.

2.5. Transplanting Vegetation Islands

Vegetation islands or clumps of soil, lichens, mosses, plants such as forbs, grasses, and sedges, roots, and soil, can be transplanted from undisturbed to disturbed areas to accelerate revegetation by increasing species diversity, providing micro sites to increase germination and

establishment of new species, introducing difficult to propagate species such as heath species to disturbed areas, and providing a source of native seed which can egress to unvegetated areas (Densmore et al. 2000, Walter et al. 2005, Matheus and Omtzigt 2011, Aradóttir 2012). Island transplants have been used to revegetate bryophyte species in peat land restoration (Rochefort and Lode 2006). Islands may be a source of microorganisms which are necessary for establishment and development of many native species (Perry and Amaranthus 1990, Gardes and Dahlberg 1996, Fujimura and Egger 2012, Thavamani et al. 2017). While expensive to translocate, vegetation islands are particularly useful in reclamation of large disturbances such as mine sites, where the interior of the disturbance may be too far from native tundra to receive naturally dispersed seeds or propagules (Matheus and Omtzigt 2011). Islands can be salvaged during development of new sites and used to revegetate nearby disturbed areas, although species composition and abundance may differ from the donor site (Aradóttir and Óskarsdóttir 2014).

Factors to consider when transplanting vegetation islands include size of islands to collect based on availability of heavy equipment, depth of islands, and if islands can be moved directly between locations or must be temporarily stored prior to planting (Densmore et al. 2000, Matheus and Omtzigt 2011). Deeper islands salvage more root material but require deeper receiving holes and may be in frozen ground. Current guidelines recommend that a suitable hole be prepared for the island so that vegetation is at ground level and has no air pockets, and that islands are watered as necessary while establishing to increase survival. In general, smaller, herbaceous species have higher survival rates than larger woody shrub species (Matheus and Omtzigt 2011).

2.6. Propagation Of Shrub Cuttings

Vegetative propagation of shrub species by cuttings is labour intensive but has good potential as a revegetation technique for reclamation of northern disturbances. Many northern shrub species have low, unknown or cyclic seed production; seed handling, collection, and storage challenges; few if any commercial seed suppliers; slow growth that may require multiple years to become established from seed; and high costs of transporting seedlings to northern reclamation sites from more southern greenhouses (Holloway and Zasada 1979, McTavish and Shopik 1983, Wright 2008, Matheus and Omtzigt 2011).

Planting stem cuttings will likely be a faster, more consistent, and effective method of establishing shrub species from multiple species on disturbed sites if adventitious root development can be promoted in the field in a timely manner. Adventitious root development on shrub cuttings has been documented for horticulturally important species and some circumpolar species, but there is limited research on evaluating factors to improve root development of

multiple species within a particular community. Northern shrub species such as *Populus balsamifera* L. (balsam poplar), *Salix alaxensis* (Andersson) Coville (Alaska willow), *Salix arctica* Pallas (arctic willow), and *Salix planifolia* Pursh (diamond leaf willow) are known to easily develop adventitious roots from root primordia along the stem (Houle and Babeux 1993, Densmore et al. 2000, Walter et al. 2005, Naeth and Wilkinson 2011, Ficko et al. 2015). Other species rarely or never root from cuttings, and some require more intensive assistance such as application of growth hormones, soaking prior to planting, use of bottom heat or intermittent mist or fog systems, and control of environmental conditions such as light, shade, air temperature, and substrate pH (Davies Jr et al. 2017). A few species are currently only known to grow from seed such as *Alnus viridis* (Chaix) DC. ssp. *crispa* (Ait.) Turrill (mountain alder)*, Betula glandulosa*, *Salix bebbiana* Sarg. (Bebb willow)*,* and *Salix scouleriana* Barratt ex Hook. (Scouler's willow) (Densmore and Zasada 1978, Densmore et al. 2000, Walter et al. 2005, Matheus and Omtzigt 2011).

Of the dominant shrub species at Diavik, *Salix glauca* L. (grayleaf willow) (Naeth and Wilkinson 2011), *Salix planifolia* Pursh. ssp. *planifolia* (Kartesz, J.T. 1994) (diamond leaf willow) (Houle and Babeux 1993, Densmore et al. 2000, Naeth and Wilkinson 2011), and *Vaccinium vitis-idaea* (Hagen 2002) consistently developed roots from stem cuttings under variable conditions, while *Betula glandulosa* (Holloway and Peterburs 2009, Naeth and Wilkinson 2011), *Rhododendron tomentosum* (Naeth and Wilkinson 2011), and *Vaccinium uliginosum* (Holloway and Zasada 1979) had poor rooting. Several studies found good rooting for *Empetrum nigrum* (Hagen 2002, Mallik and Karim 2008). Naeth and Wilkinson (2011) found poor rooting in different substrates and good root development, but poor survival for *Arctous rubra*. No information exists on collection and propagation of *Kalmia procumbens* by cuttings. In addition to the eight dominant shrub species at Diavik, *Dryas integrifolia* Vahl (entireleaf mountain avens) was found growing naturally on kimberlite parent material, making it a species of particular interest for diamond mine reclamation (Harvey Martens & Associates Inc. 2000). Current challenges for propagation of cuttings in the field at Diavik include lack of soil water and soil water holding capacity, altered hydrology, low organic matter, short growing season, and limited knowledge of effective propagation techniques for northern shrub species (Naeth and Wilkinson 2011).

Methods to assess root development (primary, lateral, adventitious) may be destructive or non destructive, including determining proportions of plants or cuttings with roots and/or leaves, measuring number and biomass of roots and leaves, measuring longest root length, assessing root volume displacement, measuring root electrical capacitance, mean root diameter, root angle, and number of secondary roots, and calculating root to shoot biomass ratio, tensile strength, breaking strain, breaking stress, and resilience (Rein et al. 1991, Henry et al. 1992, Jonasson and

Callaghan 1992, Houle and Babeux 1993, 1998, Holt et al. 1998, Hagen 2002, Schaff et al. 2002, Carlson and Smart 2016). Holloway and Peterburs (2009) used a ranked scale to measure root quantity based on ease of propagation medium falling off the roots. Cuttings were rated as 1 (1-3 roots per cutting, medium falls off with gentle shake), 2 (4-8 roots per cutting, medium removed with vigorous shaking), or 3 (> 8 roots per cutting, medium difficult to remove without washing). Past experience indicated that cuttings rated 2 or above were more likely to survive transplanting. Root assessments generally occurred 30 to 60 days after planting (Densmore and Zasada 1978, Houle and Babeux 1998, Holloway and Peterburs 2009).

Commercial or open source root assessment software programs currently available that measure various properties including root architectural and anatomical traits such as root volume, total root length, root length density, and mean root diameter can be found at the Plant Image Analysis website (Lobet et al. 2013). Numerous environmental factors that may influence root and cutting development and growth are frequently measured, and include active layer and organic layer thickness, aggregation, soil respiration, pH, electrical conductivity, soil texture, air temperature, infiltration rate, moisture, bulk density, exchangeable nutrients, accumulation of metals, annual precipitation, solar irradiance, number of frost free days, and length of day (Arshad and Martin 2002, reviewed in Clark et al. 2005, Wang et al. 2016).

2.6.1. Current shrub collection and planting guidelines

Guidelines for using cuttings in northern revegetation are mostly from documents on stream bank restoration and slope bioengineering in northern boreal environments using easily rooted *Salix* and *Populus* species such as *Salix alaxensis* (Anderss.) Coville (feltleaf willow) and *Salix planifolia* (Densmore et al. 2000, Walter et al. 2005). Soil bioengineering is used in other parts of the world such as New Zealand (Marden et al. 2007), and mountainous regions in Nepal to stabilize soils and prevent landslides (Dhital et al. 2013). Identification of donor sites for cuttings is easiest in spring or summer when leaves are present and plants have catkins or blossoms. Cutting collection is normally recommended from dormant plants (Walter et al. 2005), although Holloway and Peterburs (2009) found cuttings from some Alaskan species developed roots throughout the growing season in a greenhouse. Recommendations for cuttings used in stream bank restoration and collected below the treeline include selecting branches no more than two to three years old, with leaf buds, 0.5 to 2.0 cm in diameter, and 50 to 150 cm or more in length (Densmore et al. 1987, Walter et al. 2005, Naeth and Wilkinson 2010, Matheus and Omtzigt 2011, Aboriginal Engineering Ltd. 2011). Cuttings longer than 50 cm may be trimmed into smaller cuttings prior to planting and lateral twigs removed, or longer cuttings may be planted if heavy equipment is available (Aboriginal Engineering Ltd. 2011). In research, cutting length varied from

5 to 50 cm depending on species and collection area (Morgenson 1991, Rein et al. 1991, Henry et al. 1992, Mudge et al. 1995, Gustavsson 1999, Hagen 2002, Schaff et al. 2002, Pezeshki et al. 2005, Kefeli et al. 2007, Tilley and Hoag 2009, Naeth and Wilkinson 2010, 2011, Schmidt 2012).

Cuttings have generally been planted directly into the field, rather than transferred to a greenhouse to develop roots prior to planting (Holloway and Peterburs 2009, Matheus and Omtzigt 2011). Cutting and planting stakes from local vegetation is generally more cost effective than planting nursery stock (Matheus and Omtzigt 2011). If soil is compacted during planting, rebar, a shovel, pick axe, or heavy equipment can be used to create holes vertically on a 45 º angle, or horizontally depending on the revegetation goal. To maximize root development, holes should be deep enough to bury ≥ 75 % of the cutting or to allow the cutting to be folded such that only a few leaf buds are visible above the surface (Densmore et al. 2000, Walter et al. 2005, Matheus and Omtzigt 2011, Ficko et al. 2015).

If large areas require revegetation, 20 to 30 cuttings can be planted in clusters or islands across the disturbed area (Bittman 1997, Ficko et al. 2015). Islands can significantly reduce time and cost of revegetation, decrease impact on donor sites, create micro topography to trap blowing seeds and provide safe sites for germination, accelerate revegetation of slow growing species, and promote long term success (Bittman 1997, Dona and Galen 2007, Ficko et al. 2015).

2.6.2. Storage of plant material

When collecting dormant cuttings in fall, guidelines recommend planting directly in the field if the ground is not frozen, or storing cuttings over winter for spring planting. Fall planting is preferred as cuttings can take advantage of soil water during spring snow melt and have up to a month more growing time as the site may not be accessible for spring planting.

Recommendations for cuttings to be stored over winter are to prevent drying and keeping cool to avoid mold or rotting. Cuttings can be packed in damp moss, vermiculite, snow, or damp material, then wrapped in plastic bags, tarps, or wet burlap (Densmore et al. 2000, Walter et al. 2005, Matheus and Omtzigt 2011). Cuttings can be refrigerated at 0 to 4 ºC, in a freezer at the warmest setting (Walter et al. 2005, Matheus and Omtzigt 2011), or under snow and sawdust, or staked in snow banks in the shade (Densmore et al. 2000, Matheus and Omtzigt 2011).

If stored outside, cuttings should be planted as soon as air temperature rises as arctic species can respire at close to freezing and may use carbohydrate reserves necessary for growth after planting (Densmore et al. 2000). Spring planting within 2 to 4 days of removal from cold storage is recommended for willow cuttings (Hansen and Phipps 1983, Bergkvist et al. 1996). As weather and soil conditions make large scale field work unpredictable, Volk et al. (2004) found cuttings from some *Salix* species could be planted up to 12 days after removal from storage with

no effect on viability or survival. Returning cuttings to supplemental cold storage at -4 to 2 ºC may extend viability if planting is delayed.

2.6.3. Horticulture conditions for propagation of shrub cuttings

Current methods to propagate shrub cuttings in horticultural settings include optimizing environmental factors such as air temperature, propagation medium, relative humidity, water, and amount of light to maximize rooting while minimizing growth of pathogens (Hartmann et al. 1990, Coggeshall and Van Sambeek 2003). Techniques have been developed based on species and ease of rooting, generally depending on time of year of collection and type of wood (soft, semi hard, hard). Growth media for cuttings should be firm and dense, with appropriate texture and composition of organic and inorganic matter, not shrink upon drying, retain water, be porous enough to permit oxygen to reach developing roots, and have low salinity and adequate nutrients (Hartmann et al. 1990). Common propagation media include mixes of sand, peat moss, perlite, vermiculite, and potting soil. Soils should be free from pathogens either by selecting an inert material or by treating with heat, water, or chemicals prior to planting. Containers should be suitable for the cutting size and shape. Once roots develop, cuttings should be transplanted into larger containers to avoid spiraling roots that will not anchor the plant properly in the field. For northern species, deep tap roots should be avoided due to underlying permafrost in many areas (Densmore et al. 2000).

Many large scale operations enhance root development using intermittent mist or fog with bottom heat (McTavish and Shopik 1983, Hartmann et al. 1990, Mudge et al. 1995, Aiello and Graves 1998, Gustavsson 1999, Lebude et al. 2004, Holloway and Peterburs 2009) or irrigation (Holt et al. 1998, Aiello and Graves 1998, Coggeshall and Van Sambeek 2003). As cuttings do not have roots when planted, maintaining high humidity through mist or fog can reduce plant stress by decreasing transpiration due to a lower vapour pressure gradient between leaves and surrounding air (Haissig 1986). These systems can be expensive, with high water use, nutrient leaching, and saturation of the medium which can decrease rooting (Regan and Henderson 1999). Cuttings may be soaked in water, or watered by hand on top or bottom of pots (Douglas 1966, Chmelar 1974, Densmore and Zasada 1978, Houle 1999). Photoperiod and air temperature (consistent or varying) for cuttings are generally species specific, although improved rooting occurred at high temperatures for some horticulture species (Haissig 1986, Geiss et al. 2009).

Only a few studies described greenhouse conditions used to propagate arctic shrub cuttings. Holloway and Zasada (1979) collected cuttings from 11 Alaskan species, which were grown using intermittent mist (5 second mist every 15 minutes) with 26.7 ºC bottom heat, 22 ºC air temperature, and supplemental lighting with 40 watt white fluorescent bulbs. Houle and

Babeux (1993, 1998) planted *Salix planifolia* and *Populous balsamifera* L. (balsam poplar) cuttings from northern Quebec in 110 cm^3 containers filled with sand and peat moss (3:1) which was generally watered twice a day and grown with a 16/8 hour light/dark photoperiod using sodium lamps, a maximum temperature of 20 ºC and 28 ºC, and a minimum temperature of 16 ºC. Hagen (2002) collected shrub cuttings from Svalbard and Norway and compared saturated moist air in a polyethylene tent to fog conditions under natural daylight at 22 ºC with an 18 hour photoperiod for five evergreen species (*Arctostaphylos uva-ursi* (L.) Spreng. (common bearberry)*, Cassiope tetragona* (L.) D. Don (arctic bell heather)*, Dryas octopetala* L. (eight petal mountain avens)*, Empetrum nigrum ssp hermaphroditum* (Lange ex Hagerup) (black crowberry)*, Vaccinium vitis-idaea*); two deciduous species (*Salix herbacea* L. (dwarf willow), *Salix polaris* Wahlenb. (polar willow) received similar conditions but only in saturated moist air. Holloway and Peterburs (2009) used intermittent mist with 26 ºC bottom heat with a minimum night greenhouse temperature of 15 ºC and natural daylight to grow 12 shrub species common in Alaska. Naeth and Wilkinson (2011) planted *Betula glandulosa, Salix glauca,* and *Salix planifolia* cuttings in root trainers filled with perlite and potting soil (1:1). Cuttings were covered with clear polyurethane plastic sheeting, watered as required, had a 16 hour photoperiod, and kept at 21 ºC. They kept *Arctous rubra, Empetrum nigrum, Rhododendron tomentosum, Salix planifolia,* and *Vaccinium vitis-idaea* under similar conditions, but planted in common mining substrates (gravel, potting soil, processed kimberlite, till).

2.6.4. Shrub root development and formation of adventitious roots

Plant growth normally occurs in apical meristems located at plant growing tips. Following cell division by mitosis, cell differentiation leads to development of specific structures including root, shoot, and leaf tissues. The root system is composed of primary roots initiated during embryogenesis which elongate after germination, and lateral and adventitious roots which are initiate and develop post embryonically from differentiated cells of roots, or shoot and leaf tissues, respectively (Barlow 1986, Lovell and White 1986, Hartmann et al. 1990, Geiss et al. 2009). Plant roots have important structural and functional purposes, including providing stability, resource acquisition from the growth substrate and transportation to the shoot system, storage of reserves, hormone synthesis, and propagation (Kramer and Kozlowski 1979, Schiefelbein and Benfey 1991, Pallardy 2008). Root functions and chemistry, species specific genetics, and above and below ground environmental conditions strongly affect root morphology, architecture, productivity, and lifespan, though development and branching patterns may take years to fully develop in tundra environments (Bell and Bliss 1978, Kramer and Kozlowski 1979, Schiefelbein and Benfey 1991, Jonasson and Callaghan 1992, Pregitzer et al. 2000, Pallardy 2008, Iversen et al. 2015).

Plants can reproduce by vegetative propagation as plant cells are totipotent, or contain genetic information necessary for growth and development of the whole plant, and because developed differentiated cells can return to a meristematic condition by dedifferentiation (Hartmann et al. 1990). Many angiosperms, from xerophytes to hydrophytes, develop different forms of adventitious roots from different sites of origin indicating that they likely help plants adapt to their environment (Barlow 1986).

Adventitious root formation may be initiated at a preformed potential root primordia site or require creation of a site through cell division and differentiation, often induced in response to wounding (Haissig 1974, Barlow 1986, Hartmann et al. 1990, Blakesley et al. 1991, de Klerk et al. 1999). Injury and exposure of cells and tissues by wounding causes different healing responses in plants (Hartmann et al. 1990). As outer cells die, a necrotic plate seals the wound to prevent desiccation and protect from pathogens. Callus formation by division of parenchyma cells forms a wound periderm, which may be necessary for adventitious root formation in some species. Plants go through three successive, interdependent physiological phases during adventitious root formation, namely induction, initiation, and expression, if they have preformed potential root primordia and a fourth stage, dedifferentiation, if root primordial formation is required (Geiss et al. 2009). Once a root primordia site is present, the adventitious root will emerge from the stem or leaf after further cell division, differentiation, and elongation, with a fully formed root cap and connection with stem vascular tissue (Hartmann et al. 1990). Time for root initiation, emergence, and development varies with species, especially for easy and difficult to root species.

Adventitious roots generally form from young secondary phloem in woody perennial species, but this depends on species and age of shoot material (Hartmann et al. 1990, Geiss et al. 2009). Ease of rooting varies with physiological factors including species, biological age, tissue, and growth form, with species separated into those that will root and those that will not (Lovell and White 1986, Geiss et al. 2009). Adventitious root development is an essential step for successful artificial vegetative propagation of cuttings (Geiss et al. 2009). Following severance, some species such as older woody cuttings require extensive treatment to promote rooting, while younger woody and herbaceous species, or species such as *Salix* with preformed potential primordial initial cells, generally require little or no assistance (Carlson 1938, 1950, Haissig 1974, Densmore and Zasada 1978, McTavish and Shopik 1983, de Klerk et al. 1997, 1999, Gage and Cooper 2004, Geiss et al. 2009).

2.6.5. Factors influencing formation of adventitious roots

Adventitious root development on shrub cuttings has been documented for various horticulturally important species and some circumpolar species. A common method to induce root

formation in cuttings is the use of growth hormones such as auxins. Auxins were the first group of hormones isolated in plants and have a wide variety of effects from stimulating adventitious root formation to production of ethylene and inhibition of lateral shoot formation (Blakesley et al. 1991, Pop et al. 2011). Auxin synthesis occurs mainly in young plant leaves and is then transported by bulk flow through the vascular system to various tissues in response to environmental stimuli and interactions with other hormones and growth regulators (Overvoorde et al. 2010, Pop et al. 2011). Directional movement into cells through integral membrane transport proteins creates local auxin gradients that play an essential role in regulating root architecture and development, including adventitious and lateral root formation, although specific mechanisms by which auxins stimulate rooting is unknown (Malamy 2005, Overvoorde et al. 2010, Olatunji et al. 2017). Two naturally produced endogenous auxins, indole-3-acetic acid (IAA) and indole-3-butyric acid (IBA), and one synthetic auxin, naphthalene-1-acetic acid (NAA), are commonly used to stimulate adventitious root formation in horticultural settings (Nanda et al. 1974a, Holloway and Zasada 1979, Kroin 1992, de Klerk et al. 1997, Houle and Babeux 1998, Simon and Petrášek 2011). Exogenous IBA application can improve rooting, root length, number of primary and secondary roots, root dry weight, time to root emergence, and survival in the field; timing and type of application, and optimal IBA concentration vary significantly with species (Sharma and Aier 1989, Rehana et al. 2020, Abdel-Rahman 2020).

Current recommendations for planting cuttings (usually easy to root *Salix* or *Populus* species) for environmental restoration, erosion control, land reclamation, streambank stabilization, and bioengineering include collecting dormant cuttings in fall or spring due to high carbohydrate reserves in tissues, and soaking up to 48 hours (Watson et al. 1997, Houle and Babeux 1998, Kuzovkina and Quigley 2005, Holloway and Peterburs 2009, Matheus and Omtzigt 2011). Longer soakings are less frequent in the literature, and have mixed results. For example, Pezeshki et al. (2005) found *Salix nigra* Marsh. (black willow) cuttings soaked for 7 days had greater survival, root development, and bud flush than 0 or 15 days soaking. Cuttings soaked 15 days did not survive longer than 42 days, and had significantly lower root and shoot biomass and number of buds and roots than unsoaked cuttings. Schaff et al. (2002) found soaking dormant *Salix nigra* cuttings for 10 days doubled cutting survival, and resulted in higher root, shoot, and leaf biomass than 0 or 3 days of soaking. Petersen and Phipps (1976) found soaking 17 and 20 days improved rooting and survival of hardwood cuttings of some *Populus* clones, while Miller-Adamany et al. (2017) found soaking and storing *Salix exigua* Nutt (coyote willow) cuttings for 17 days increased above ground biomass, with no differences between soaked and unsoaked for below ground biomass. In a large field study, Martin et al. (2005) found soaking *Salix nigra* cuttings

for 14 days significantly improved survival over 34 weeks relative to unsoaked cuttings. Soaking was hypothesized to improve cutting water status, enabling faster root development and better contact with soil even with low soil water conditions. In one study that investigated effects of season (fall, spring) and soaking time (0, 14 days) on *Salix amygdaloides* Andersson (peach leaf willow) and *Salix exigua* cuttings, soaking did not influence rooting percentages, but increased shoot and root biomass, respectively, for fall cuttings (Tilley and Hoag 2009).

Alternative methods to improve root development, such as soaking shoot cuttings in *Salix* water extract (soaking chopped pieces of *Salix* ssp. shoot tissue in water to allow salicylic acid to leach into water), have been recommended on some horticultural websites to improve rooting of shrub cuttings, and have recently been shown to improve rooting percentage and number of roots for *Olea europaea* L. (European olive), and plant height and above and below ground biomass for *Coleus scutellarioides* (L.) Benth. (common coleus) cuttings (Dudley and File 2007, Al-Amad and Qrunfleh 2016). Fire and fire by-products such as smoke water extract contain karrikins which induce germination in seeds from numerous plant species, especially seeds sown under drought conditions in arid and semi arid regions (Pierce et al. 1995, Keely and Fotheringham 2000, Adkins and Peters 2001, Kulkarni et al. 2011, Yao et al. 2017, Mackenzie and Naeth 2019b). Karrikins have recently been shown to play a role in regulating root development, but have not been investigated as a stimulant for rooting of woody cuttings (Taylor and van Staden 1998, Chiwocha et al. 2009, Akeel et al. 2019, Swarbreck 2021). The only research with cuttings demonstrated that smoke water extract had a positive effect on rooting of *Vigna radiata* (L.) R. Wilczek (mung bean) hypocotyl cuttings (Taylor and Van Staden 1996), highlighting an important research gap. Many shrub species form mycorrhizal fungi associations, although little is known for northern species about the effect or requirements for these associations (Kidd 1996, Kidd and Rossow 1997, Withers 1999, Kidd and Max 2000, Boldt-Burisch and Naeth 2017).

Other factors affecting root development of shrub cuttings include age (Henry et al. 1992)l. 1992), carbohydrate reserves (Fege and Brown 1984, Haissig 1986, 1989, Davies Jr et al. 2017, Tsafouros et al. 2019), cutting position (Saifuddin et al. 2013), cyclophysis (Hartmann et al. 1990), donor plant health (Hartmann et al. 1990), gender (Houle and Babeux 1998), geophysical location (Densmore and Zasada 1978, Holloway and Peterburs 2009), length (Densmore et al. 1987, Rossi 1999), light (reviewed in Geiss et al. 2009), mycorrhizae (Paschke et al. 2003), nutrients (Houle and Babeux 1998, Geiss et al. 2009), propagation environment (Gustavsson 1999), propagation media (Holloway and Zasada 1979, Rossi 1999), season (Tilley and Hoag 2009, Davies Jr et al. 2017), soil water (Rein et al. 1991, Houle and Babeux 1998, Schaff et al. 2002, Pezeshki et al. 2005), species (Chmelar 1974, Holloway and Zasada 1979, Holloway 1985,

Holloway and Peterburs 2009), temperature (Geiss et al. 2009), topophysis (Hartmann et al. 1990), and wounding (Holloway and Zasada 1979). Results within and between species were often variable and inconclusive indicating genotype and environmental conditions such as photoperiod, precipitation, and temperature that affect physiological status and health of the donor plant prior to harvesting may significantly impact root development (Andersen 1986, Holloway and Peterburs 2009, Bellini et al. 2014, Davies Jr et al. 2017).

2.6.6. Lateral root formation and root architecture development

In gymnosperms and dicotyledons, continued growth of the primary root produces a well developed taproot, or allorhizic root system from which lateral roots may emerge forming secondary and higher orders of root branches (Bellini et al. 2014, Atkinson et al. 2014). In monocotyledons, the primary root is short lived, and a fibrous or homorhyizic root system is derived postembryonically from adventitious roots that develop from the shoot, stems, or leaves, from which one or more orders of lateral roots may emerge (Lovell and White 1986, Kerk and Sussex 2007, Bellini et al. 2014). Primary, lateral, and adventitious roots are identical in structure, but have separate genetic pathways (Malamy 2005, Gutjahr et al. 2015, Yu et al. 2018). Research using model plants such as Arabidopsis (*Arabidopsis thaliana* L. Heynh. (thale cress)), rice, and maize have advanced understanding of mechanisms regulating initiation, morphogenesis, and emergence of new lateral and adventitious roots in eudicots and monocots (McCully 1999, Bellini et al. 2014, Atkinson et al. 2014). Regulation of different stages of lateral root formation including differentiation of pericycle founder cells, development of lateral root primordia, cell expansion leading to emergence of new lateral roots, and lateral root elongation in soil, leads to a characteristic root system architecture for different plant species (Malamy and Benfey 1997, Malamy 2005, Laplaze et al. 2007). However, research on plant regulation of root branching, particularly of diverse species grown in soil environments, is still needed.

Within a species, root architectural, morphological, physiological, and biotic traits may vary considerably due to phenotypic plasticity, whereby the expressed phenotype is a function of the underlying genotype and interactions with the surrounding environment (Nicotra et al. 2010, Bardgett et al. 2014, Lobet et al. 2019, Fromm 2019). Intrinsic genetic pathways control the root system architecture or the three dimensional volume of soil explored by roots, by regulating root length, growth, branch number, branching pattern, surface area, orientation, angle, and diameter (Malamy 2005, Jung and McCouch 2013, Morris et al. 2017). Lateral roots generally have a smaller diameter but similar anatomy to the primary, lateral, or adventitious parent root, with larger parent roots more likely to bear larger lateral roots (Doussan et al. 2003, Lecompte et al. 2005, Bellini et al. 2014, Wu et al. 2016). Extrinsic environmental response pathways modulate different

stages of the intrinsic genetic pathways in response to changing environmental conditions such as nutrient composition and distribution, soil density and compaction, type of soil particles, soil water availability and distribution, seasonal and climate changes, and interactions with soil micro biota (Malamy 2005, Jung and McCouch 2013). While the root organ structure is generally consistent within a given species, phenotypic plasticity gives immobile plants the ability to adapt to their environment to optimize anchorage, and nutrient and water uptake, creating diverse root system architecture even among genetically identical plants (Malamy 2005). However, as architectural and morphological root traits are challenging and costly to measure in situ, this has limited research in this area (Bardgett et al. 2014).

Fine roots are generally the shortest roots as they are usually the three most apical root branching orders from the root tip within a species. Fine roots are primarily involved in water and nutrient acquisition from soil, and are known to play key roles in ecosystem functions and biogeochemical cycling at local, regional, and global scales (Matamala et al. 2003, Pendall et al. 2004, Guo et al. 2008, Bardgett et al. 2014, reviewed in Iversen et al. 2015, McCormack et al. 2015). In northern locations, plant functions such as photosynthesis, nutrient uptake, and growth decrease as the mean environmental temperature decreases, and plants allocate a larger portion of total biomass to roots, reaching 70 % or more in tundra environments (Chapin et al. 1980, Poorter et al. 2012). As climate warming accelerates in northern latitudes, changes in root phenology due to changes in growing season length and shifts in plant community composition are expected to affect carbon cycling and other ecosystem processes, but most terrestrial biosphere models preferentially focus on above ground plant components with little to no inclusion of roots (Jackson et al. 2000, Iversen 2010, Bardgett et al. 2014, reviewed in Iversen et al. 2015). Limited research has been published on adventitiously derived root system architecture and morphology for various species from different ecosystems at different times of year, and if root systems have similar growth patterns to seed grown plants from the same species. With increasing exploration and resource extraction in the north, lack of knowledge about root development patterns and fine root systems of seed grown and adventitiously derived root systems for arctic species, is an important research gap.

2.7. Techniques For Revegetation Of Biocrusts

Biocrusts are integral to many ecosystem processes, and lichen dominated crusts in particular can be considered indicators of long term landscape health (Looman J. 1964, Scott and Hutchinson 1990, Klopatek 1992, Eldridge and Koen 1998, Eldridge and Rosentreter 1999, Bowker et al. 2008, Condon 2016, Antoninka et al. 2020b). Bowker (2007) hypothesized very little

research has been devoted to restoration and accelerating the recovery of biocrusts following disturbance as they are perceived to recover unassisted from disturbance, even though linear extrapolations of short term studies show recovery times from as little as a few years to millennia in the harshest environments (Anderson et al. 1982b, Cole 1990, reviewed in Belnap and Eldridge 2001, Dojani et al. 2011, reviewed in Weber et al. 2016).

When using biocrusts in reclamation and restoration of disturbed environments, it is important to determine a target and biogeographical scale to define success, often based on ecosystem structures such as biomass, cover, evenness, spatial clustering, richness, species composition, or ecosystem functions such as soil stabilization, erosion resistance, or nutrient cycling (Aronson et al. 1993, Maestre et al. 2005). Predictive model development for abundance, composition, and distribution of biocrusts using correlations between undisturbed crusts and local environmental factors may help develop appropriate structural targets for reclamation (Bowker et al. 2006a, 2006b). Realistic targets are a balance between the practical and desired reclamation goals, local environmental constraints, and reclamation costs (Zhao et al. 2016a).

While determining recovery of biocrusts is challenging (Belnap and Eldridge 2001), numerous methods have been used to assess natural and artificial biocrust health, growth, and success on scales from micro to global, in field, laboratory or growth chamber environments. Non-destructive assessment techniques include measuring cover (total plot, by vegetation layer, or by species) (Mueller-Dombois and Ellenberg 1974, Belnap 1993, Eldridge and Koen 1998), frequency or abundance of species present at a particular scale in a region (random or targeted selection) (Maestre et al. 2002, Li et al. 2005, Langhans et al. 2010), species density, length and/or height of crusts or particular organisms (Belnap 1993), thallus area (Bidussi et al. 2013), biocrust colour and classification (e.g. smooth (light or dark), rugose, pinnacle, rolling (thin, thick)) (reviewed in Colesie et al. 2016), soil water content and water retention (Xiao et al. 2011, 2014, reviewed in Chamizo et al. 2016), carbon cycling as carbon dioxide flux (net photosynthesis, dark respiration, net primary production) (Lange et al. 1984, Maestre et al. 2006, reviewed in Sancho et al. 2016), chlorophyll a fluorescence (Schroeter et al. 1992, Schlensog and Schroeter 2001, Bidussi et al. 2013, reviewed in Sancho et al. 2016), electrical resistance (proxy for active and inactive periods) (Proctor 2004, Weber et al. 2016a), environmental and climate data (precipitation, precipitation deficit, potential evapotranspiration, solar radiation, net radiation, mean maximum and minimum air temperature) (Bowker et al. 2005), and photographic analysis, including large scale landscape surveys using remote sensing (reviewed in Weber and Hill 2016) or more localized assessments of individual plots (Roturier et al. 2007, Dietz and Steinlein 2009, Vanha-Majamaa I. et al. 2009, Duncan 2011, Xiao et al. 2011, 2014, Lamarre 2016).

Destructive assessment methods include measurements of dry weight (proxy for positive net photosynthesis) (Bidussi et al. 2013), crust thickness (Belnap 1993), polysaccharide analysis (Cheshire 1979), soil aggregate stability (Davidson and Evans 1960), crust coherence (Eldridge and Koen 1998), microbial counts (Miles et al. 1938), chlorophyll a and b (Barnes et al. 1992), molecular community characterization (Maestre et al. 2006), molecular markers (eg., small ribosomal subunit RNA gene) (Roncero-Ramos et al. 2019), nitrogen cycling (Stewart et al. 1967, Maestre et al. 2006, reviewed in Barger et al. 2016), nuclear ribosomal internal transcribed spacer (Schoch et al. 2012) primer based sequencing (Zoller et al. 1999), soil chemistry and texture (pH, organic carbon, sand, silt, and clay, acid neutralizing potential, extractable micronutrients, electrical conductivity) (Gretarsdottir et al. 2004, Bowker et al. 2005), and resistance to wind and water erosion (McKenna Neuman et al. 1996, Kidron et al. 1999, McKenna Neuman and Maxwell 1999, 2002, Eldridge and Leys 2003). Understanding the impact of disturbances in the north on lichens and other components of biocrusts and investigating methods to accelerate recovery is necessary to reclaim tundra habitat for caribou and other fauna.

2.7.1. Environmental barriers limiting recovery of biocrusts and lichens

Assisted recovery can be grouped by methods to overcome increasingly challenging environmental barriers of propagule scarcity (inoculation), resource limitation (resource augmentation), and actively eroding soils (artificial soil stabilization), respectively (Bowker 2007). Factors such as type and extent of disturbance, likelihood of further disturbances, precipitation patterns and other environmental conditions, surface evaporation and water evaporation, proximity to inoculating material, soil type, and changes in soil texture due to compaction and wind erosion of fine particles are also thought to play a role in recovery of biocrusts (Belnap 1993, Eldridge and Greene 1994, Belnap and Eldridge 2001).

If disturbed areas such as abandoned mines, roads, or decommissioned power production facilities have actively eroding soils, stabilization is a priority to facilitate biocrust recovery, and has been accomplished using polyacrylamide application, coal fly ash and bioinoculant with filamentous cyanobacteria, coarse litter application (straw crimping), and stabilizing vascular plants, although cost, site, and species specific factors must be considered (Zhao et al. 2016a, Zaady et al. 2016, Fick et al. 2020). For example, Li et al. (2003) found artificial stabilization of sand dunes in China improved soil properties that provided favourable conditions for algae and mosses to propagate and establish.

Following soil stabilization, resource limitations, including lack of suitable micro sites and insufficient nutrient levels, may limit or prevent biocrust establishment. Maestre et al. (2006) found soil amendments such as composted sewage sludge enhanced recovery of biocrusts in a

Mediterranean semiarid environment. Tolpysheva and Timofeeva (2008) found chemical composition and texture of substrates and surface structure can affect lichen growth and size. In Sweden, Roturier et al. (2007) found substrates could affect *Cladonia arbuscula* ssp *mitis* (Sandst.) Ruoss success and recovery following disturbance. Keim et al. (2016) measured occupancy and abundance of terrestrial fruticose lichens important in reindeer and caribou diets in boreal forest in Northern Alberta, and determined that lichen presence increased with deeper ground water, shorter vegetation, and lower sphagnum moss cover, while abundance was negatively related to seasonal changes in photosynthetic capacity.

Field surveys have shown that ENE and NNW exposed slopes which tend to be more shaded, cooler and wetter, favour biocrust growth, as does microenvironmental properties such as presence of coarse woody debris, slope aspect, slope position, incident irradiance, light gradients, and position of vascular plants (Garcia-Pichel and Belnap 2001, Davidson et al. 2002, Bowker 2007). In Iceland, nitrogen, phosphorus, and potassium fertilizer promoted biocrust development (Gretarsdottir et al. 2004), while micronutrients such as magnesium and zinc increased biocrust abundance on the Colorado Plateau (Bowker et al. 2005), but few studies investigated nutrient and water requirements to promote establishment. Care must be taken when adding biological amendments such as manure that they do not add competitive or non-native species (Zhao et al. 2016a). Adding metabolically important substances such as glucose and mannitol, or other naturally occurring simple carbohydrates found in photosynthetic and metabolic pathways have been proposed to help damaged biocrusts survive stresses associated with rehydration, respiration, and photosynthesis (reviewed in Chiquoine 2012).

Biocrust establishment on disturbed sites is often limited by the lack of propagules or source material. Davidson et al. (2002) found that dispersal of mycobiont spores were often the limiting factor for natural lichenization in the field. Mass culturing crust organisms, such as blue green or green algae species or other target organisms such as the cyanobacterium *Microcoleus vaginatus,* is being researched as a method to initiate biocrust formation. Steps include isolating target organisms from natural biocrusts, mass culturing propagules to increase quantity for inoculation, preparing propagules for field application through concentration by evaporation or filtration, then application of cultivated material and establishment of propagules in the field (Zhao et al. 2016, reviewed in Rossi et al. 2017). Inoculation with cultivated biocrust organisms in the laboratory and field has shown some benefits for reclamation of contaminated soils (Ashley and Rushforth 1984), improvement of soil properties of agricultural lands (Metting and Rayburn 1983, Rao and Burns 1990, Rogers and Burns 1994, Falchini et al. 1996, Rossi et al. 2017), and establishment of cyanobacterial, moss, and lichen biocrusts on other disturbed soils (Chen et al.

2006, Xu et al. 2008, Wang et al. 2009, Muczynski 2014, Lan et al. 2014, Doherty et al. 2015, Antoninka et al. 2015, 2018, Bowker and Antoninka 2016, Rossi et al. 2017, Slate et al. 2019, Bowker et al. 2020).

An alternative method to establish biocrusts is to inoculate disturbed sites using crust material from another location, as this can introduce diverse species including cyanobacterial, algae, lichen fragments and thalli, fungal and moss spores, and other microorganisms to the disturbed area to accelerate recovery. Limited studies have documented crust material dispersal in drylands (see Sections 2.7.2 and 2.7.3), and may be beneficial only on a small scale as generally an undisturbed area must be disturbed to collect material (unless material can be salvaged prior to industrial activity or other planned disturbances). Development of techniques to propagate whole biocrust communities in greenhouses could address this lack of inoculant. Some research has indicated that irrigation after inoculation may be necessary to assist with biocrust re-establishment, but further research on the amount and frequency is still required (reviewed in Zhao et al. 2016).

As biocrusts can be stored for long periods of time with limited effect due to the desiccation tolerance (poikilohydric properties) of many of its species (Belnap et al. 2001, Bowker 2007, Chiquoine et al. 2016), changes in excavation techniques to salvage material may enhance future reclamation. While seed bank studies have shown that seed survival declines rapidly following stockpiling (Mackenzie and Naeth 2019a), biocrust propagules may have different survival patterns. The relationship between density of biocrust propagules in soil and recovery time has yet to be investigated (Bowker 2007). For large disturbances in the north such as mine sites, limited resources for revegetation and propagule scarcity, especially for internal areas far from undisturbed vegetative sources, are key barriers for reclamation.

2.7.2. Assisted dispersal and establishment of biocrusts and lichens in the field

Interest in assisted biocrust establishment using single or multiple biocrust species has recently increased, often to restore ecological benefits such as stabilize soil, increase nutrient cycling, and reduce erosion (Pointing and Belnap 2012, Bu et al. 2013, Zhao et al. 2016a). No field studies of propagation and dispersal of lichen biocrusts for reclamation in arctic tundra were found, although field site inoculation with native biocrust material containing a variety of species had higher species cover and diversity, biomass, chlorophyll a content, and improved soil properties on disturbed soils in alpine, arid, and semi arid areas in Australia, Canada, China, Germany, Spain and the USA (Belnap 1993, Scarlett 1994, Bowler 1999, Tian et al. 2006, Xiao et al. 2008, 2011, Campeau and Blanchard 2010, Chiquoine 2012, Zhao et al. 2016b, Chiquoine et al. 2016, Letendre et al. 2019).

In a field study in SE Australia, Scarlett (1994) mixed 150 cm^2 of crust pieces (3 to 5 mm thick) in 200 ml of water and spread the slurry at rates of 1:4.5, 1:9 and 1:19 on a slightly scarified soil in autumn-winter. After 18 months, eight moss and lichen species had high cover (not quantified), though many species from the original crust material failed to establish. St Clair et al. (1986) assessed recovery of burned areas in Utah six months after application of three slurry types (biocrust, subsoil, distilled water) on 0.25 m^2 plots. Slurries were prepared using 500 g biocrust or subsoil and 2,000 ml distilled water. Plots inoculated with biocrust slurries had significantly greater numbers of blue green algae than the other two treatments, although no difference between treatments was observed for green algae or diatoms. Belnap (1993) compared recovery of 0.25 m^2 scalped plots that were inoculated with 500 cc of dry and crumbled biocrust material, to scalped plots that were not inoculated, and surrounding undisturbed plots at four sites in Utah. Inoculated plots had significantly higher moss and lichen cover than uninoculated plots, higher chlorophyll a absorption, and higher lichen richness, although they were still significantly lower than undisturbed plots.

Chlorophyll a absorption was a better measure of recovery than visual assessment for cyanobacteria, but was only effective on dry, coarse grained soils, indicating other methods are required for assessment of different types of substrates. In a Canadian study, Campeau and Blanchard (2010) documented dispersal of moss, lichen, and plant propagules from donor sites onto disturbed plots along the Trans-Labrador highway. Over five years, control plots had less moss cover, fewer shrubs and seedlings, and generally lacked lichens relative to plots where propagules were introduced. In a four factorial experiment in Nevada, Chiquoine et al. (2016) assessed recovery of an abandoned road surface 18 months after inoculation with biocrust material that was salvaged and stored for two years, application of salvaged topsoil, amendment with wood shavings and planting of *Ambrosia dumosa* (Gray) Payne (white bursage), a dominant perennial shrub species. Inoculation with biocrust material significantly increased lichen and moss cover and composition on 1 x 1 m plots, recovered 43 % of cyanobacteria density, and improved soil fertility and stability.

To address lack of biocrust material for inoculation, Antoninka et al. (2017) compared growth of field collected and hand crumbled biocrust material on disturbed plots in Utah to biocrust material cultured in the laboratory under a variety of watering and hardening conditions. Inoculated plots initially showed greater recovery than control plots, though this was no longer significant at 26 months. Field collected biocrusts had less cover than cultivated biocrusts, but higher species richness, late successional cover, development level, and chlorophyll a concentrations. Further research is needed to determine the role and functions of various species

in healthy biocrust ecosystems (Bowker et al. 2010, Rosentreter et al. 2016), and if inoculation with biocrust material will be successful in arctic environments.

Assisted dispersal of lichen species has been studied (reviewed in Smith 2014) including for reindeer husbandry (Roturier et al. 2007, Roturier and Bergsten 2009), endangered species conservation (Lidén et al. 2004), or maintenance of lichen biodiversity in managed forests (Sillett and McCune 1998, Hazell and Gustafsson 1999, Hilmo 2002). Following assisted dispersal, Roturier et al. (2007) and Duncan (2011) found lichen fragments could be lost by subsequent dispersion by wind, water, or animals until fragments developed rhizines to anchor them. Roturier et al. (2007) found 70 % of fragments remained in 1 m^2 quadrats in a clear cut area after one year of growth relative to 94 % in a mature forest stand. Lichen movement was highest on mineral soil (7 % remaining), relative to 70 and 76 % remaining on moss and twig substrates, respectively, indicating the importance of site preparation and micro sites for lichen biocrust dispersal in windy areas like tundra. Slow recovery following disturbance is more likely due to long range dispersal limitations from donor populations than unfavourable conditions in the receiving environment.

Four studies focused on lichen dispersal for reclamation of disturbed land. Ballesteros et al. (2017) found water was the most suitable adhesive for attachment, retention, and vitality of *Diploschistes diacapsis* (Ach.) Lumbsch discs on gypsum spoil. Duncan (2011) transplanted fragments from late successional species *Cladonia arbuscula* ssp *mitis* onto substrates on reclaimed land in the oil sands in Alberta. After two growing seasons, moss and litter substrates retained more fragments than soil in 12 year old stands, although substrates had no significant impact in 24 year old stands. One year after dispersal, 41 % of fragments had hyphae, 23 % had apothecia, and 31 % had lateral branches, indicating fragments of this species can grow on different substrates following assisted dispersal. Turner et al. (2009) conducted research on land disturbed by coal mine exploration in British Columbia. Lichen fragments were introduced into several environments to investigate methods of dispersal, enhance micro sites, and improve lichen survival to reclaim land for woodland caribou. Krekula (2007, in Duncan 2011) assessed feasibility of distributing reindeer lichen thallus fragments ranging in size from a few millimetres to five centimetres using a leaf blower, at a rate of 10 g m^{-2} over five hectares in about eight hours.

2.7.3. Artificial propagation of lichens and biocrusts in controlled environments

In 1869, Schwendener found lichens formed by a symbiotic association between fungi and algae. Since the 1950s much research has been conducted on methods to cultivate lichens and/or induce lichenization under controlled laboratory conditions (Ahmadjian 1969, Lobakova and Smirnov 2012), as secondary metabolites produced by lichens such as antibiotics, ultra violet light absorbers, antioxidants, and pigments, have significant biotechnological potential (Yamamoto et

al. 1987, Lobakova and Smirnov 2012). Stages in lichen resynthesis include dissociation of lichen into mycobiont and photobiont components, obtaining monocultures of each component, mixed cultivation of components, and production of sa table morphogenetic association (Lobakova and Smirnov 2012). Low nutrient and hydrologic conditions, particularly wet-dry cycles, appear essential to symbiosis, but specific requirements of most lichen mycobionts continue to be elusive (Ahmadjian 1973, 1982). To date, five species form 60 % of lichens in successful resynthesis; 86 % have a green algal photobiont with 60 % from 3 species (Lobakova and Smirnov 2012).

Methods of growing whole lichen thalli in controlled environments from thallus fragments, soredia or isidia have been more successful than inducing lichenization (Bubrick and Galun 1986). For example, Yamamoto et al. (1985) artificially propagated *Usnea rubescens* and *Ramalina yasuda* using small sections of lichen thalli sterilized with water and cultured on a malt-yeast extract medium. Various lichen species from 52 genera in 22 families have been cultured on a variety of growth media selected on a species specific basis (Fahselt 1981, Stocker-Wörgötter and Türk 1988, 1991, Stocker-Wörgötter and Elix 2002, Lobakova and Smirnov 2012). Issues with these methods include maintaining an intact thallus, inducing thallus fragment germination, and preventing interference by contaminants (bacteria, bryophytes, fungi) due to lack of sterilization of donor material (Galun et al. 1972, Yoshimura et al. 1993, Lobakova and Smirnov 2012). Results from one reclamation focused study using slag from post smelting dumps, indicated that three of five *Cladonia* species have potential to form thali from powdered donor material (Rola and Osyczka 2017), and higher inoculation rates and weekly application of malt solution increased coverage and biomass of lichens over a year and a half.

Limited studies have investigated optimal growth chamber conditions for lichens or biocrusts as they are often considered slow growing and challenging to cultivate. However, better understanding of air temperature, photoperiod, light intensity, watering regimes, substrate preparation, inoculation method, and humidity requirements could improve recovery or ecological functions of lichens and biocrusts. For improved in vivo cultivation of lichens, Ott and Jahns (2002) recommended light intensities between 10 and 90 µmol photons m^{-2} s^{-1}, low air temperatures (15 ºC day, 10 ºC night), and alternating wet and dry phases lasting a minimum of two days to improve differentiation. High humidity was not recommended as it could lead to undifferentiated growth of the mycobiont, though in the field, Lange et al. (1988) found humid air alone is sufficient to cause photosynthetic activity in lichens with green algal photobionots, but does not activate lichens with a primary cyanobacterial photobiont.

Bidussi et al. (2013) cultivated *Lobaria pulmonaria* (L.) Hoffm. and *Lobaria scrobiculata* (Scop) DC. for 14 days at 200 µmol photons m^{-2} s^{-1} with 12 hour photoperiod, four air temperature

regimes (25/20, 21/16, 13/8, 6/1 ºC), and two watering regimes spraying lichens with deionized water (12 hour day hydration, 12 hour day and 12 hour night hydration). Hydration in both day and night resulted in higher growth rates for biomass and thallus area for both species. Kershaw and Millbank (1969) used a controlled growth chamber to maintain *Peltigera aphthosa* (L.) Willd. (felt lichen), a subarctic species from Scotland, in healthy condition over six months. Light and air temperature were field based; a prototype growth chamber determined it required a damp, drained environment with high humidity. Dibben (1971) investigated effects of 18 photoperiods and day-night temperature combinations on thalli growth for six lichen species over 18 months. Lichens were mixed with water and macerated in a blender for 15 seconds, then a 3 cm patch was poured onto the surface of a sterilized substrate. Temperatures that were > 30 ºC or prolonged high air temperatures and reversed day-night air temperatures had a negative effect on growth; other optimal conditions were species specific. All species produced new growth, but none produced complete fruiting bodies, indicating other conditions such as prolonged cold or drying may be required for mature fruiting bodies. Despite initial sterilization of equipment and soil, and washing plant-soil samples for four hours under running cold water, contaminants were an issue in some growth chambers containing other species, demonstrating challenges growing lichens in artificial environments.

Over the past few decades, research using biocrusts in controlled laboratory and growth chamber experiments has increased, to gain a better understanding of biocrust functions, and how to accelerate recovery of disturbed crusts in the field. Maestre et al. (2006) assessed type of inoculation (dry, slurry), fertilization (control, composted sewage sludge), and watering frequency (twice a week, five times a week) on biocrust recovery on semiarid degraded soils in SE Spain in a growth chamber over six months. Crusts were collected as 5 x 5 x 1 cm samples, fragmented into six pieces for a total surface area of 2.31 cm^2 that was placed directly on the surface of 18 g autoclaved soil in 22.06 cm^2 petri dishes (burying crusts so their surface was same height as the soil), or pulverized with 4 mL of water into a slurry then poured evenly on the soil. In half the dishes, 2 g of sterilized composted sewage sludge was mixed with soil prior to adding crust material, and dishes were then watered to 80 % field capacity on Monday and Friday, or Monday through Friday. Growth chamber conditions were maintained as a 12 hour photoperiod with 34/22 ºC day/night temperatures under 75 µmol $m^{-2}s^{-1}$ photosynthetic active radiation. Results varied by treatment and type of assessment, as net CO_2 exchange rate was highest with inoculation as a slurry and higher watering regime, and chlorophyll a and nitrogen fixation were highest with similar treatments but also with inclusion of sewage. However, there was a significant reduction in cyanobacterial species at the higher watering regime.

In Yukon, Stewart and Siciliano (2015) assessed how inoculation with slurries (mature biocrust from Husky SW mine, pure *Nostoc* commune culture, dried *Nostoc* spp. collected from grasslands in Yukon), application of biochar and substrate (Valley mine tailings, Husky SW mine impacted soil) could improve soil conditions and nitrogen input in a growth chamber experiment over 101 days. Substrates were autoclaved, then placed in petri dishes with 60.82 cm^2 surface area. To prepare the biocrust slurry, the top 2 to 3 cm of the surface crust were collected in the field, the soil layer removed, and then the remaining 1 cm of crust sieved through a 2 mm mesh. Six grams wet weight slurry was added to each dish. Experimental samples were maintained in a growth chamber with an 18 hour photoperiod, 19/10 ^oC day/night temperatures and light intensity of 200 $\mu mol\ m^{-2}s^{-1}$, and all samples were watered with 6 mL distilled water every second day. After 10 weeks of incubation, lichens, mosses, and *Nostoc* spp. were present on both substrates. Biocrust slurries had higher mean rates of nitrogen fixation than pure or dried *Nostoc* cultures on both substrates, with or without biochar.

Several other studies assessed cultivating mosses and moss biocrusts under controlled conditions to determine recovery times and functional properties of moss crusts, and to provide sufficient material for field inoculation with a lower impact on donor habitats (Antoninka et al. 2015, reviewed in Zhao et al. 2016a). Research has been conducted to compare inoculation methods for growing moss biocrusts (ground, pulverized), spores and vegetative fragments on a variety of substrates (Xu et al. 2008, Chen et al. 2009, Antoninka et al. 2015, Lamarre 2016, Bowker and Antoninka 2016). Optimal propagation conditions including water, fertilizer, and temperature requirements appear species specific (Chen et al. 2009, Doherty et al. 2015, Bowker and Antoninka 2016), indicating the complexity of propagating whole crust samples with numerous species under controlled conditions. However, while focusing on moss propagation, Bowker and Antoninka (2016) found a sixfold increase in biomass of two moss species after four months, and unintentionally cultivated lichens and cyanobacteria resulting in biocrusts that could fix nitrogen at rates similar to functionally mature biocrusts. Chamizo et al. (2016) noted that moving crusts from undisturbed areas in the field to disturbed areas or the laboratory will likely alter soil, water, and environmental variables influencing growth and functional properties of biocrusts, and should be taken into consideration when analyzing results and/or making recommendations.

2.8. Summary

Industrial disturbances are generally regulated federally and provincially. While more temperate regions such as Alberta have guidelines for returning disturbances to equivalent land capability, northern environments have many unknowns between the desire for reclamation and

the ability to reclaim (Campeau and Blanchard 2010). Reducing the scope, extent, and magnitude of anthropogenic disturbances in sensitive environments like the tundra is likely the best landscape management strategy to conserve and protect important and slow growing species in future (Dighton and White 2016). As native tundra is mainly composed of shrub heath and lichen biocrust species, it is vital to develop revegetation methods to accelerate their growth and development to natural community structure and function. Species must be selected to establish under current site conditions (disturbed soil, anthroposols) while allowing for an appropriate successional trajectory. Factors such as increased colonization by native plants, establishment of seedlings, increased species diversity, reproduction by colonizing species, establishment of mosses and lichens, accumulation of litter, and increased plant cover can be used to indicate success at different times following reclamation in the field and overall success of revegetation techniques (McKendrick 1987, Streever et al. 2003, Rausch and Kershaw 2007).

Unfortunately, even with many years of research, knowledge of effective revegetation strategies for large disturbances in arctic and subarctic environments continues to be elusive. Many questions still remain unanswered, including how to overcome seed dormancy; to accelerate germination, establishment, growth, and development of most northern plant species; to incorporate non vascular species and to recruit later successional species.

Shrub cuttings have high potential to create a consistent source of plant material for timely reclamation of large areas. Research is needed to adapt southern commercial techniques to reliably and practically root multiple species of shrub cuttings in quantities sufficient to reclaim northern disturbances. Techniques for cutting selection, storage, and rooting need modification due to differences between southern and northern species and local resources, and methods to create appropriate plant communities need to be developed. Research is needed to determine whether it is more effective to plant cuttings directly or to develop roots before field planting.

Although biocrusts are integral components of tundra ecosystems, their slow growth has limited research on their use in reclamation. Research is required on their large scale collection, propagation and dispersal in the north, and effects of fragment size, local micro biota, micro site size and type, and substrate on their establishment, growth, and survival.

3. RESEARCH PROGRAM OBJECTIVES

The objective of this PhD research program was to develop and assess revegetation techniques for creating integrated tundra communities with a similar mosaic of species as found in undisturbed areas. As very little research has been done on community focused revegetation

in the north, we conducted several large scale studies in the growth chamber and in the field to develop a baseline understanding of propagation and dispersion techniques for shrub species and lichen biocrusts, the dominant vegetation in shrub heath tundra. Results can be used to inform current reclamation practitioners and guide future research directions (Figure 1.2). The general research objectives were:

- To evaluate effectiveness of common and novel rooting techniques on cuttings from eight arctic shrub species in different seasons.
- To assess effectiveness of mining by-products with inoculant dispersal, habitat amelioration, and containment techniques for biocrust revegetation.
- To determine suitable growth chamber conditions for survival of lichen biocrusts.

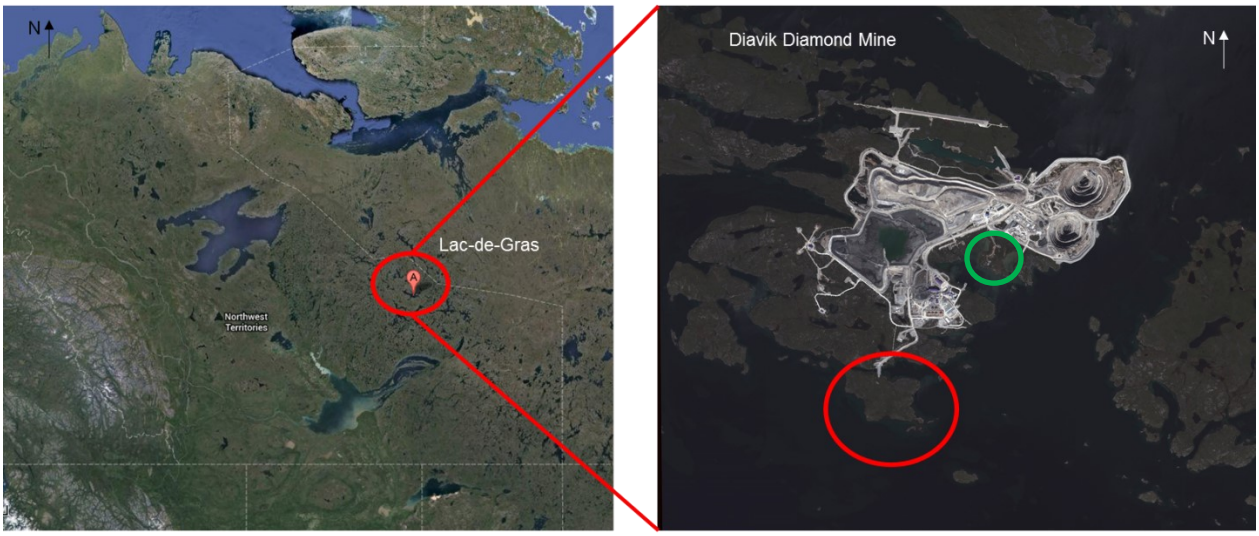

Figure 1.1. Location of Lac-de-Gras, Northwest Territories (left) and satellite image of Diavik Diamond Mine (right) with the vegetation collection area circled in red and the field research site circled in green.

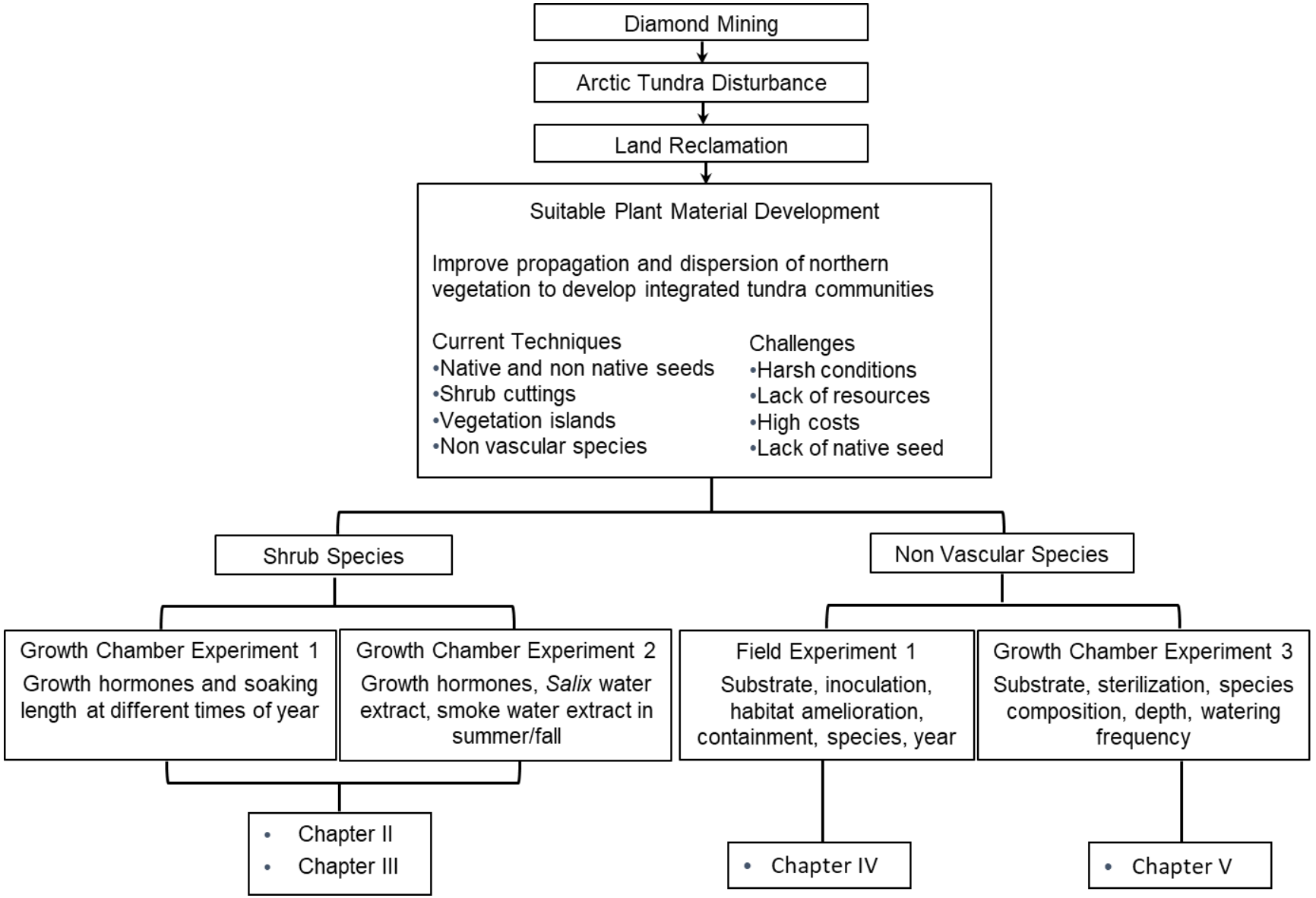

Figure 1.2. Schematic showing PhD research program.

II. ROOT DEVELOPMENT ON CUTTINGS OF SEVEN ARCTIC SHRUB SPECIES FOR REVEGETATION

1. INTRODUCTION

Exploration and extraction of mineral resources in the north has increased significantly over the past century, disturbing vast areas in Canada and around the world. Diamonds have been extracted from arctic mines since the mid 1990s, affecting the land through soil compaction and removal, road construction, infrastructure development, above and below ground mining activities, and waste rock piling (Couch 2002, Drozdowski et al. 2012). Vegetation removal and changes in soil properties due to disturbances can have long lasting impacts on northern landscapes, including on ecosystem services such as provision of food and habitat for fauna and indigenous communities (Johnson et al. 2005, Deshaies et al. 2009, Ficko et al. 2015). Natural recovery of these disturbances is predicted to take hundreds to thousands of years, as plant growth is inhibited by short growing seasons, low temperatures and rainfall, low species diversity, limited seed production and dispersal, low soil water, and low nutrient concentrations (Billings 1987, Harper and Kershaw 1996, Forbes et al. 2001, Miller and Naeth 2017).

Assisted revegetation is a common reclamation technique to accelerate plant establishment on disturbed sites. Successful revegetation of land in the north disturbed by mining and other anthropogenic activities will require development or amelioration of soil substrates and acquisition and propagation of plant material that can tolerate harsh conditions while allowing succession towards an appropriate plant community (Johnson 1987, Forbes and Jefferies 1999, Rausch and Kershaw 2007). Despite decades of research, few effective revegetation strategies have been developed for northern environments. Acquiring sufficient quantities of native species seed to reclaim large disturbances such as mine sites is challenging, as suppliers stock limited quantities of grass and forb seed, and rarely seed for northern shrub species which dominate many tundra communities (Elliott et al. 1987, Vaartnou 1992, Matheus and Omtzigt 2011). A common revegetation technique has been to seed available early successional species such as cold tolerant grasses and legumes, expecting later successional species to invade as soil and nutrient properties improve, although this is unreliable (Densmore 1992, Forbes and Jefferies 1999, Jorgenson et al. 2003, Naeth and Wilkinson 2014).

Vegetative propagation of shrub species by cuttings is labour intensive but has good potential as a revegetation technique for reclamation of northern disturbances. Many northern shrub species have low, unknown or cyclic seed production; seed handling, collection and storage

challenges; few if any commercial seed suppliers; slow growth that may require multiple years to become established from seed; and high costs of transporting seedlings to northern reclamation sites from more southern greenhouses (Holloway and Zasada 1979, McTavish and Shopik 1983, Wright 2008, Matheus and Omtzigt 2011). Planting stem cuttings will likely be a faster, more consistent, and effective method of establishing shrub species on disturbed sites if adventitious root development can be promoted directly in the field in a timely manner.

Adventitious root development on shrub cuttings has been documented for various horticulturally important species and some circumpolar species. Shrub species such as *Populus balsamifera* L. (balsam poplar), *Salix alaxensis* (Andersson) Coville (Alaska willow), *Salix arctica* Pallas (arctic willow), and *Salix planifolia* Pursh (diamond leaf willow) are known to easily develop adventitious roots from root primordia along the stem (Houle and Babeux 1993, Densmore et al. 2000, Walter et al. 2005, Naeth and Wilkinson 2011, Ficko et al. 2015). However, other species rarely or never root from cuttings, and some require more intensive assistance such as application of growth hormones, soaking prior to planting, use of bottom heat or intermittent mist or fog systems, and control of environmental conditions such as light, shade, air temperature, and substrate pH (Davies Jr et al. 2017).

A common method to stimulate root formation in cuttings is use of auxins such as indole-3-butyric acid (IBA), an endogenous growth hormone (Davies Jr et al. 2017). Exogenous IBA application can improve rooting, root length, number of primary and secondary roots, root dry weight, time to root emergence, and survival in the field; timing and type of application, and optimal IBA concentration vary significantly by species (Sharma and Aier 1989, Rehana et al. 2020, Abdel-Rahman 2020). Alternative methods such as soaking shoot cuttings in *Salix* water extract (chopped pieces of *Salix* ssp. shoot tissue in water; salicylic acid leaches into the water) have improved rooting percentage and number of roots for *Olea europaea* L. (European olive), and plant height and above and below ground biomass for *Coleus scutellarioides* (L.) Benth. (common coleus) cuttings. Fire and fire by products such as smoke water extract are known to induce germination in seeds from numerous plant species, but has not been investigated to date as a stimulant for rooting of woody cuttings (Pierce et al. 1995, Keely and Fotheringham 2000, Adkins and Peters 2001, Yao et al. 2017, Mackenzie and Naeth 2019b). The only research with cuttings demonstrated that smoke water extract had a positive effect on rooting of *Vigna radiata* (L.) R. Wilczek (mung bean) hypocotyl cuttings (Taylor and Van Staden 1996), highlighting an important research gap.

Guidelines for using cuttings in revegetation are mostly from documents on stream bank restoration and slope bioengineering in northern boreal environments using easily rooting *Salix*

and *Populus* species (Densmore et al. 2000, Walter et al. 2005). Soaking 1 to 10 days has promoted adventitious root formation, mostly on *Salix* species, indicating the need to research the effect of soaking on multiple other species (Schaff et al. 2002, Walter et al. 2005, Pezeshki et al. 2005). Current guidelines recommend collecting dormant cuttings in fall or spring due to high carbohydrate reserves in tissues, but little information exists on species specific optimal times of year for collection and planting to induce root formation in northern species (Densmore and Zasada 1978, Houle and Babeux 1998, Gustavsson 1999, Holloway and Peterburs 2009). To date, limited research has been published on adventitiously derived root system architecture and morphology for various species from different ecosystems at different times of year, and if the root systems have similar growth patterns to seed grown plants from the same species. With an increasing need for revegetation in the north, the lack of knowledge about root development patterns and fine root systems of seed grown and adventitiously derived root systems for arctic species is an important research gap.

In this study, effects of three common factors affecting rooting of stem cuttings of seven dominant shrub species at Diavik Diamond Mine Inc., Northwest Territories, were evaluated. The main objectives were to determine if concentration of common growth hormones or alternative chemical compounds, soaking time, and time of year of collection could promote root initiation and development in growth chamber experiments to produce a more consistent source of plant material for reclamation of disturbed northern sites. We expected all of these factors to have a positive impact on the species assessed.

2. MATERIALS AND METHODS

2.1. Study Site

Diavik Diamond Mine (Diavik) is located approximately 320 km northeast of Yellowknife, Northwest Territories (64º30´41´´ N, 110º17´23´´ W), on an island in the middle of Lac-de-Gras, approximately 100 km north of the treeline. Lac-de-Gras lies is in the Southern Arctic Ecozone, and the Point Upland Arctic Ecoregion (Ecosystem Classification Group 2012), with mean annual precipitation of 299 mm (45 % as rain) and mean annual temperature of -9 ºC. Mean monthly temperatures in the growing season were 8, 14, and 11 ºC, from June, July, and August, respectively. The landscape is dominated by large archean rock outcrops and the remnants of glaciers found as boulders, till, and eskers (Drozdowski et al. 2012). Turbic and static cryosolic soils dominate upland areas, with dwarf-heath shrubs and lichen species. Organic cryosolic soils dominate lowland areas, with sedges and mosses (Drozdowski et al. 2012).

2.2. Experimental Design

Cuttings from the ends of the growing tip of seven common tundra species were collected as we meandered across an undisturbed upland community at Diavik. *Betula glandulosa* Michx. (bog birch), a large erect species in this community, was collected as <10 to 42 cm cuttings. For the other six smaller species, *Arctous rubra* (Rehder & Wilson) Fernald (red bearberry), *Empetrum nigrum* L. (crowberry), *Kalmia procumbens* (L.) Gift & Kron & P.F. Stevens ex Galasso, Banfi & F. Conti (alpine azalea), *Rhododendron tomentosum* Harmaja (marsh Labrador tea), *Vaccinium uliginosum* L. (bog bilberry) and *Vaccinium vitis-idaea* L. (bog cranberry), cuttings were <5 to 25 cm. Nomenclature for species from Diavik follows Northwest Territories Species Infobase (2021); nomenclature for all other species follows NatureServe (2021). Cutting length varied based on available stem length from randomly selected plants for each species. Cutting stem diameter was 0.1 to 0.6 cm. Cuttings were transported in coolers and then stored at 4 ºC until planting within 1 week of collection.

Two screening experiments were conducted to investigate effects of common horticultural and novel treatments on root initiation and development over 60 days in a growth chamber (Table 2.1). The first experiment was three factorial with 72 treatments. Cuttings were collected at common work times for reclamation practitioners; in summer (25 to 26 June) during active growth, fall (19 to 23 September) at the end of the growing season, and spring (20 to 22 and 24 May) prior to plants fully emerging from dormancy. Cuttings from each species in each season were randomly assigned to be treated with a soaking time (0, 1, 3, 5, 10, and 20 days) and a concentration of IBA (0, 0.1, 0.4, and 0.8 %) (Stim Root® #1, 2, 3, respectively).

The second experiment was two factorial with nine treatments and one control (Table 2.1). Cuttings were collected in summer (2 July) and/or fall (27 to 28 September) based on species differences observed in experiment 1. Cuttings from each time period were randomly assigned to untreated, treated with a common growth hormone (0.1, 0.4, and 0.8 % IBA) (Stim Root® #1, 2, 3, respectively), or treated with an alternative chemical compound, either *Salix* water extract (*Salix* water), or smoke water extract (smoke water). *Salix* water extracts were prepared by cutting *Salix* shoots into 1 to 3 cm pieces and placing 300, 600, and 1200 mL of cuttings in 2,400 mL boiling distilled water to soak for 12 hours to make three *Salix* water concentrations (0.5, 1, 2, respectively). Smoke water extracts were prepared by placing 4 L distilled water in a smoker with 1.2 kg wood chips for four hours until all wood chips had been burned, and then diluting the extract with distilled water (1:20, 1:10, 1:1 volumes of extract to distilled water) to make three dilutions (0.05, 0.1, 0.5, respectively).

2.3. Planting And Soaking

Growth chamber conditions for both experiments mimicked growing conditions at Diavik. Conditions were set at 17 ºC during the day for 16 hours and 10 ºC at night for 8 hours for experiment 1; and at 17 ºC during the day for 20 hours and 10 ºC at night for 4 hours for experiment 2. Cuttings were planted in a mix of 50:50 by volume peat moss and horticultural potting soil. Soaking treatments in tap water were topped up as needed to keep the bottom 1 to 5 cm of each stem wet. The bottom 1 to 5 cm of each IBA treatment cutting was dipped in IBA powder prior to planting. Cuttings from all species were dipped to approximately the same depth, with cuttings from larger species dipped in more powder than cuttings from smaller species due to surface areas. The bottom 1 to 5 cm of each cutting for *Salix* water and smoke water treatments was soaked for 12 hours prior to planting.

Planting containers were based on size of cuttings and growth patterns. For experiment 1, three cuttings per species per treatment (season, soaking time, IBA concentration) were nested in the same container due to growth chamber space restrictions (Table 2.1). For experiment 2, each cutting was planted in an individual container.

2.4. Measurements

Shoot health and vigour of each cutting were assessed at 30 and 60 days using a five point scale with 1 = dead, 2 = poor (plant mostly dead or dying, < 30 % live green tissue), 3 = fair (average health and growth, 30 to 60 % live green tissue), 4 = good (plant healthy and growing, 60 to 90 % live green tissue), and 5 = excellent (plant robust and growing vigorously, 90 to 100 % live green tissue. Adventitious root development was assessed at 60 days. Cuttings were gently washed under running water to remove all substrate material. Primary roots refer to adventitious roots that emerged from the stem cutting; secondary and tertiary roots refer to successive orders of lateral root branches off the primary root (modified from Jung and McCouch 2013). The number of primary roots were counted under a microscope, length of the longest primary and secondary roots was measured, and presence of tertiary roots was noted.

2.5. Statistical Analyses

Interspecies comparisons were not conducted as different morphological and physiological characteristics could create confounding factors that affect interpretation of results. Cuttings in each season were assessed separately as modeling season as a fixed effect is problematic due to lack of season replication. Research has shown that many species likely have specific times of year that are more favourable for rooting than others (Teklehaimanot et al. 2004,

Araya 2007, Holloway and Peterburs 2009), thus season was not treated as a random effect. To analyze treatment effects, a threshold of 2/3 of cuttings with roots per species per season per experiment was selected for inclusion in a hurdle model, although due to low and/or inconsistent rooting, no species had sufficient rooting to meet this threshold. Given the exploratory nature of this screening study, results are presented graphically using ggplot2 (R, Version 4.0.2, 2020, Wickham 2016).

3. RESULTS AND DISCUSSION

3.1. Shoot Health

Determining trends in shoot health at different times of year can indicate which cuttings have rooted without needing to physically check for roots, saving time and disruption to the cutting. Shoot health was generally higher at day 30 than day 60 for each species, in each season, in each experiment. Shoot health of rooted cuttings was variable for most species, between season within an experiment, and between experiments within a season. Shoot health was not a good indicator of rooting for evergreen species in any season in either experiment. Increased shoot health between days 30 and 60 was observed for rooted *Betula glandulosa* fall cuttings in experiment 1, indicating this may be a useful technique for some deciduous species.

3.2. Adventitious Root Development

Reclamation of large scale northern disturbances requires development of an appropriate self sustaining and resilient plant community. All seven shrub species in our study produced adventitious roots in at least one season in one experiment; a significant milestone demonstrating future potential for plant propagation by arctic shrub cuttings. Maximum percentage of rooted cuttings was 3 to 55 % across species, seasons, and experiments, with season having the most influence on rooting for each species (Figures 2.1, 2.2, Table S2.1).

Although *Kalmia procumbens* cuttings had low rooting (< 10 % in all seasons and experiments), this was the first study to demonstrate development of adventitious roots (maximum 12 roots on one cutting in summer, experiment 1). Only one report was found describing rooting of *Arctous rubra* cuttings which had poor survival after four weeks (Naeth and Wilkinson 2011), similar to the low percentages in our study. Three other species, *Betula glandulosa, Rhododendron tomentosum,* and *Vaccinium uliginosum* had < 20 % rooting regardless of treatments, similar to previous research (Holloway and Zasada 1979, Holloway 2006, Holloway and Peterburs 2009, Naeth and Wilkinson 2011), although Calmes and Zasada (1982) observed

up to 77 % rooting for *Vaccinium uliginosum* summer cuttings. Despite low rooting for these five species, high variability in number of roots was common, with most cuttings having no roots and a few having a large number. Rooting is known to vary among species, individuals within species, and between clones of individuals, due to interactions among genetic, physiological, and environmental factors (Leakey 1985, Bellini et al. 2014).

Maximum number of roots on one cutting in our study was 1 to 117 across all species, seasons, and experiments. In experiment 1, 11 % of fall *Betula glandulosa* cuttings rooted; one cutting had 12 roots, which is promising for a hard to root species (Holloway and Peterburs 2009, Naeth and Wilkinson 2011). Roots on *Betula glandulosa* cuttings generally only initiated from the base, while roots emerged from multiple locations up the stem for the other species (Table 2.2). Seasonal rooting trends for maximum and mean number of roots, and maximum and mean length of the longest root, were not always consistent between experiments for a given species (SM Table 2.1). Due to the experimental design, differences between experiments, and low rooting, confirmatory statistical comparisons were not able to be conducted within an experiment or between experiments.

Rooting variability between years was more apparent for *Empetrum nigrum* and *Vaccininum vitis-idaea*, and similar to some previous research. For example, 55 % of *Vaccininum vitis-idaea* cuttings rooted in summer in experiment 1, but only 10 % rooted in summer in experiment 2. Gustavsson (1999) noted variability in rooting for *Vaccininum vitis-idaea* cuttings was likely related to effects of weather on shoot health and development in the preceding year, and interaction between year and seasonal rooting patterns for cuttings collected between April and August. Hagen (2002) observed 60 to 85 % rooting for *Vaccininum vitis-idaea* cuttings grown under saturated moist air and fog conditions, while Holloway (1985) observed 44 to 91 % rooting based on type of growth media and IBA treatment. Other studies have shown mixed results using softwood or hardwood cuttings, and increased rooting for cuttings collected before bud break in spring, or after shoot growth and berry production in fall (Lehmushovi 1975, Holloway 1985, Labokas and Budriuniene 1989).

No *Empetrum nigrum* cuttings rooted in fall in experiment 1; 40 % rooted in fall in experiment 2. Hagen (2002) observed 70 to 80 % rooting for *Empetrum nigrum* ssp *hermaphroditum* (Hagerup) Böcher cuttings in a peat, perlite, and sand mix under fog conditions or saturated moist air for two months. Other studies found good rooting capacity for *Empetrum nigrum* by stem cuttings, but did not provide details of techniques or rooting percentages (Monni et al. 2000, Holloway 2006, Mallik and Karim 2008).

Rooting variability across and within species highlights the need for research to determine what other factors are affecting rooting behaviour for these shrub species, as more consistency in rooting will make it a more effective reclamation technique. For example, conditions in our study were common for reclamation practitioners rather than typical horticultural procedures, so application of more specific techniques for hard to root species (e.g., mist chamber, bottom heat) may increase rooting and its consistency (Alder and Ostler 1989, Gustavsson 1999, Holloway and Peterburs 2009, Davies Jr et al. 2017). Other factors known to affect rooting and potentially needing further investigation for these shrub species include cutting ontogenetic age, cutting location on a donor plant (terminal or lateral shoot), donor plant physiological status (e.g., carbohydrate concentration, carbon:nitrogen ratio, nutrient status, water status), photoperiod, seasonal influences, and weather conditions the preceding year (Hess 1963, Andersen 1986, Gustavsson 1999, Bellini et al. 2014, Davies Jr et al. 2017).

In a horticultural setting, less than 25 to 50 % rooting is considered poor, depending on the species and grower, indicating a species would not be grown commercially (Holloway and Peterburs 2009, Davies Jr et al. 2017). However, for reclamation practitioners, other factors may take priority over low rooting, including re-establishment of keystone or rare species, or development of a heterogeneous plant community. In these cases, a higher cutting rate could be used to account for low rooting. When erosion control is a primary reclamation objective, selected species must provide sufficient live, litter, and ground cover to mitigate the impact of rain drops, with fibrous and deep taproots to stabilize surface and deeper soil layers (Hansen 1989). In northern environments, shrubs cuttings may be preferred for erosion control over seed grown shrubs, as their larger initial size provides greater ground cover. Cutting survival as low as 30 % has led to successful streambank stabilization in riparian environments (Watson et al. 1997), with similar benefits on large industrial disturbances in our experience.

3.2.1. Effect of treatment on adventitious root development

Determining treatment effects was challenging due to low rooting percentages, although responses to season, exogenous IBA concentration, and soaking length were species specific (Figures 2.1, 2.2). After wounding, exogenous auxins are taken up through the cut surface (Kenney et al. 1969), leading to an increase in endogenous auxin concentrations at the cutting base over time, which is needed for initiation of adventitious rooting (Gatineau et al. 1997, Benková et al. 2003, Yue et al. 2020). As cuttings in this study were treated with IBA up to seven days after collection, rooting for some species may have improved by rewounding the base of each cutting prior to treatment (Howard 1971). Timing for peak auxin levels following wounding likely occurs on a species specific basis.

Exogenous IBA concentration and time of year of application had variable effects in both experiments in our study, indicating a potential seasonal interaction effect between endogenous and exogenous auxins for different species. Studies of different species have shown that levels of endogenous growth hormones such as IAA vary naturally in roots of cuttings throughout the year, with some species needing application of different concentrations of exogenous auxin in different seasons for effective rooting (Nanda and Anand 1970, Blakesley et al. 1991, Joshi et al. 1992, Guo et al. 2009). Studies with *Arabidopsis thaliana* L. Heynh. (thale cress) mutants indicated IAA and IBA may play different roles in adventitious rooting, with interactions between endogenous IAA and exogenous IBA promoting rooting (Ludwig-Müller et al. 2005). However, species specific thresholds for auxin have been observed over which higher hormone concentrations can have a detrimental effect on rooting, number of roots, and root length (Houle and Babeux 1994, Lund et al. 1996, Ricci et al. 2008). Further research is required to determine levels of endogenous auxins in different species in our study throughout the growing season, and if interactions between endogenous and exogenous growth hormones are occurring.

Once cut from a donor plant, cuttings are susceptible to desiccation prior to new root development, which can lead to low survival (Martin et al. 2005). In our study, season influenced effect of soaking time in experiment 1. Only two other studies assessed effects of soaking cuttings in different seasons. Tilley and Hoag (2009) found soaking for 14 days, and fall or spring planting, did not affect rooting of either *Salix amygdaloides* Andersson (peach leaf willow) or *Salix exigua* Nutt (coyote willow) cuttings. However, fall *Salix exigua* cuttings soaked for 14 days had higher root biomass than other treatments, while fall *Salix amygdaloides* cuttings soaked for 14 days had higher shoot biomass. Pezeshki et al. (2005) found soaking nondormant *Salix nigra* Marsh. (black willow) cuttings for 7 days was beneficial for cutting survival, root development, and bud flush, with no cuttings surviving after 15 days of soaking. Results from these studies indicate a potential species specific interaction between season and soaking, likely due to cutting physiological status. More research is required to decipher how species specific differences in concentrations of various hormones, growth regulators, and carbohydrates between dormant and actively growing shrub cuttings influence adventitious rooting at different times of the year. While longer soaking times are not currently recommended for land reclamation, results indicate that ensuring cuttings are turgid on a species specific basis prior to planting will likely improve their long term survival in the field.

Rooting was generally low for the seven species in our study; however, species specific interactions between *Salix* water concentration and season, and smoke water concentration and season were observed in experiment 2 (Figure 2.2b). Similarly, Wise et al. (2020) determined that

concentration of a commercial willow bark extract that promoted root formation and root branching was species specific. Karrikins, the six active butenolide hormones isolated in plant derived smoke and smoke water extract have recently been shown to modulate root development, likely using a similar pathway as strigalactones (Swarbreck et al. 2019, 2020). Further research deciphering mechanisms of action for karrikins and strigolactones, and biostimulants such as *Salix* water extract may enhance adventitious rooting in northern shrub cuttings and other species.

3.3. Lateral Root Development

All species in our study developed secondary and tertiary order roots on at least one primary root, except *Arctous rubra* cuttings which did not develop tertiary roots in 60 days (Table 2.2, Figures 2.1, 2.2). Bell and Bliss (1978) and Billings et al. (1978) found lateral root development may take several years to begin in some arctic species. Roots on *Betula glandulosa* cuttings were long and thick, but easily broke into segments and had limited lateral root development. *Empetrum nigrum, Kalmia procumbens, Rhododendron tomentosum, Vaccinium uliginosum*, and *Vaccinium vitis-idaea* had small fine roots, and *Empetrum nigrum, Rhododendron tomentosum,* and *Vaccinium vitis-idaea* had considerable lateral root development. *Vaccinium vitis-idaea* roots had similar branching patterns as roots collected in the field in Alaska (Iversen et al. 2015), and was the only species to develop three or more orders of lateral roots in 60 days. *Rhododendron tomentosum* primary roots were easily detached from cuttings, similar to observations for *Rhododendron groenlandicum* (Oeder) Kron & Judd (bog Labrador tea) which developed tiny branched clumps of very thin roots, on a few roots (Holloway and Peterburs 2009). Maximum number of branching orders is likely controlled by species specific genetic factors, although interactions with the environment can create significant variation in root system architecture within individuals of a species (Doussan et al. 2003). Due to the slow growth of arctic plants, morphological characteristics and root branching patterns may require many years to develop fully (Billings et al. 1978, Bell and Bliss 1978), highlighting the need for further study of intact root systems of mature tundra plants to better understand growth, function, and phenology of arctic fine roots (Iversen et al. 2015), and how they compare to adventitiously developed root systems for different species.

3.3.1. Length of different root orders

Primary roots were longer than secondary roots for *Empetrum nigrum, Rhododendron tomentosum,* and *Vaccinium vitis-idaea* in our study (other species not assessed due to limited root development, Figure 2.3). Root elongation, followed by lateral root branching, is an iterative developmental process, and root growth varies between species and for different root orders

(Wilcox 1962, Pagès 1999, Malamy and Ryan 2001, Ito et al. 2006, Nibau et al. 2008). For example, Dittmer (1937) observed a decrease in mean length of four successive root orders for *Secale cereale* L. (cultivated rye), while Fan and Guo (2010) observed a similar decrease for six successive root orders for *Fraxinus mandshurica* Rupr. (Manchurian ash) and *Larix gmelinii* Rupr. (Dahurian larch). Basal diameter is correlated with potential root length, but many roots fail to reach their maximum potential (Wu et al. 2016). In northern locations, plants can allocate 70 % or more of their total biomass to roots (Chapin et al. 1980, Poorter et al. 2012), and since lateral roots make up the majority of root biomass for most plant species, their growth and longevity play an important role in shaping root system architecture, particularly arctic species (Nibau et al. 2008, Jung and McCouch 2013).

Within a specific root order in our study, experiment, season, and species influenced length of the longest root. Species specific genetic factors in conjunction with hormonal interactions and environmental factors control cell division and elongation, and determine growth and length of an emerged lateral root (Jung and McCouch 2013). Several studies demonstrated that elongation rates within a root order are related to root tip diameter as it reflects size of the root meristem where new elongating cells are produced (Cahn et al. 1989, Thaler and Pagès 1996, Lecompte and Pagès 2007).

Roots on cuttings in experiment 2 were generally longer than those in experiment 1 of a comparable root order for a specific season and species. Different results between experiments may have been influenced by experimental design, including cuttings growing individually versus together in one pot, photoperiod, and temperature. For example, *Cakile edentula* var. *lacustris* Fernald (Great Lakes sea rocket) plants can alter root growth if adjacent plants are related or not (Dudley and File 2007), while different species are known to have species specific photoperiod and temperature requirements. Soil temperature has a strong influence on various parameters affecting root architecture including initiation, growth, branching, and orientation (Wilcox and Pfeiffer 1990, Kaspar and Bland 1992, Nagel et al. 2009, reviewed in Rich and Watt 2013). While arctic species have adapted to growing at much lower optimal temperatures than related species in more temperate climates, tolerance for low temperatures still varies by species (Billings et al. 1978, Bell and Bliss 1978, Kummerow and Russell 1980).

Seasonal effects on root length varied by species in our study. Roots on summer cuttings in each experiment were generally shorter than roots of the same order on fall or spring cuttings, except for *Vaccinium vitis-idaea* cuttings in experiment 1 (Figure 2.3). Resource partitioning between different tissue types varies by season and species. While carbohydrate concentrations in cuttings are hypothetically considered an essential source of energy and material for

adventitious root development, mixed results in various studies were based on numerous factors including species, shrub type (deciduous, evergreen), donor plant maturity, cutting position (distal, basal), season (donor plant physiological status), and collection year, influencing carbohydrate type (soluble, insoluble) and quantity in different parts of a cutting (Fege and Brown 1984, reviewed in Haissig 1986, Haissig 1989, Davies Jr et al. 2017, Tsafouros et al. 2019). As plants have species specific requirements for macro and micro nutrients at different physiological stages throughout the growing season, plant roots must adapt their root system architecture to optimize nutrient uptake (Chapin and Shaver 1989, Clark and Boldingh 1991, Drossopoulos et al. 1996, Muhammad et al. 2015).

For reclamation practitioners, knowledge of species specific root architecture can help inform revegetation practices by determining depth of required substrate, substrate properties, species selection to meet revegetation goals (eg stabilize disturbed soil, community restoration; indigenous needs for specific species), and indicate environmental stressors affecting a plant due to changes in root architecture. Future research directly comparing root system architecture of shrubs grown in the field versus those grown from cuttings in pots and in the field will provide further insight into revegetation practices for disturbed environments.

4. CONCLUSIONS

All seven shrub species in our study developed at least primary and secondary roots, including previously undocumented *Kalmia procumbens*. Season had the most influence on rooting for all species, although results were highly variable within and between species, indicating factors other than those examined are likely influencing adventitious root development. Novel treatments of *Salix* water extract and smoke water extract were applied for the first time with cuttings from northern shrub species. While rooting percentages were generally low, species specific responses were apparent, highlighting the need for further research with these compounds.

To date, most propagation research has focused on individual and easy to root species such as *Salix* from northern plant communities. Our research addresses this critical gap by assessing multiple species, and highlights the potential to use vegetative propagation to accelerate re-establishment of plant communities on disturbed northern sites.

Table 2.1. Species, treatments, and replication for experiments (Exp) 1 and 2 in different seasons.

Species	Exp	Season	Treatment				Reps[1]	Pots[2]	Cuttings per species	Pot size (cm)
			Soak (d)	IBA (%)	Salix water	Smoke water				
Arctous rubra	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.8			3	1	54	6.5x6.5x6.5
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			3	1	72	6.5x6.5x6.5
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	6.5x6.5x6.5
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	4.2x4.2x6.2
Betula glandulosa	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			3	1	72	10x10x10
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			3	1	72	10x10x10
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	10x10x10
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	10x3x3
Empetrum nigrum	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			3	1	72	12x12x6
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			6	2	144	12x12x6
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	12x12x6
	2	Summer		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	28x2.7x 3.8
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	28x2.7x3.8
Kalmia procumbens	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			3	1	72	12x12x6
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			6	2	144	12x12x6
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	12x12x6
	2	Summer		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	28x2.7x 3.8
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	28x2.7x3.8
Rhododendron tomentosum	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.8			3	1	54	10x10x10
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			6	2	144	10x10x10
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	10x10x10
	2	Summer		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	4.2x4.2x6.2
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	4.2x4.2x6.2
Vaccinium uliginosum	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.8			3	1	54	6.5x6.5x6.5
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			6	2	144	6.5x6.5x6.5
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	6.5x6.5x6.5
	2	Summer		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	4.2x4.2x6.2
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	4.2x4.2x6.2
Vaccinium vitis-idaea	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.8[3]			3	1	72	6.5x6.5x6.5
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			6	2	144	6.5x6.5x6.5
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	6.5x6.5x6.5
	2	Summer		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	4.2x4.2x6.2
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	4.2x4.2x6.2

[1] Number of replicate cuttings per treatment
[2] Number of pots per treatment
[3] Missed planting *Vaccinium vitis-idaea* Soak 0, IBA 0.4 % cuttings

Table 2.2. Number of cuttings with primary, secondary, and tertiary roots for each species, and location of roots on cuttings.

Species	Total number of cuttings	Number of primary roots	Number of secondary roots	Number of tertiary roots	Location of roots relative to base
Arctous rubra	442	3	1	0	1-3 cm
Betula glandulosa	472	10	6	4	Generally at base, one root at 7 cm
Empetrum nigrum	632	66	45	25	0-11 cm
Kalmia procumbens	631	22	14	4	0-6 cm, on main and side branches
Rhododendron tomentosum	614	42	35	18	0-6 cm (most 0-3 cm)
Vaccinium uliginosum	610	28	21	14	0-5 cm
Vaccinium vitis-idaea	627	96	72	16	Generally 0-2 cm, some up to 10 cm

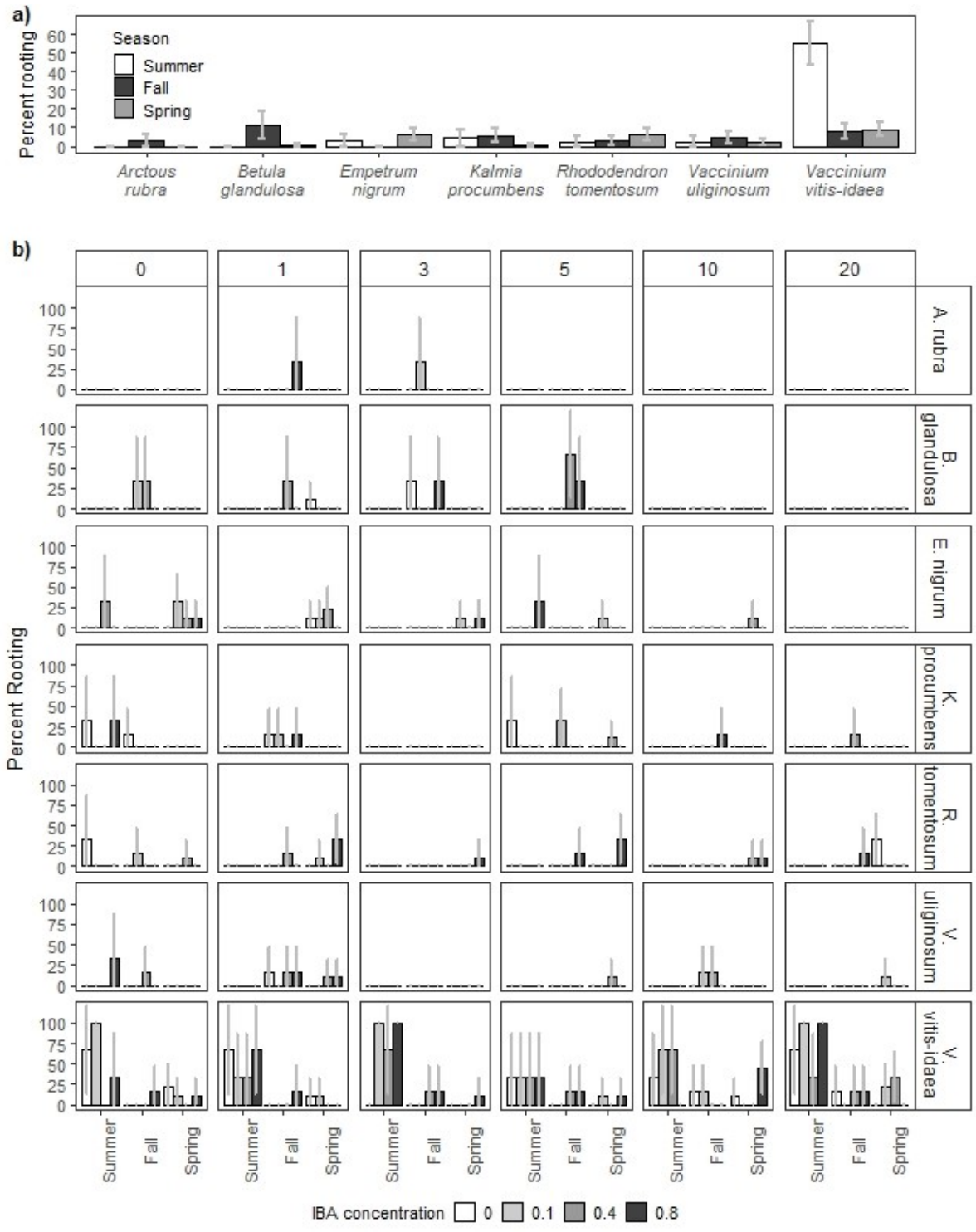

Figure 2.1. Percentage of rooted cuttings with 95 % confidence intervals in experiment 1, for a) each species (x-axis) grouped by time of year, and b) separated by all treatments; species (horizontal panels), time of year (x-axis), soaking time (vertical panels, 0, 1, 3, 5, 10, 20 days), and growth hormones (0, 0.1, 0.4, 0.8 % IBA). Summer cuttings of *Arctous rubra*, *Rhododendron tomentosum*, *Vaccinium uliginosum*, and *Vaccinium vitis-idaea* only received three IBA concentrations (0, 0.1, 0.8 % IBA). Number of cuttings in a) and b) are summarized in Table 2.1.

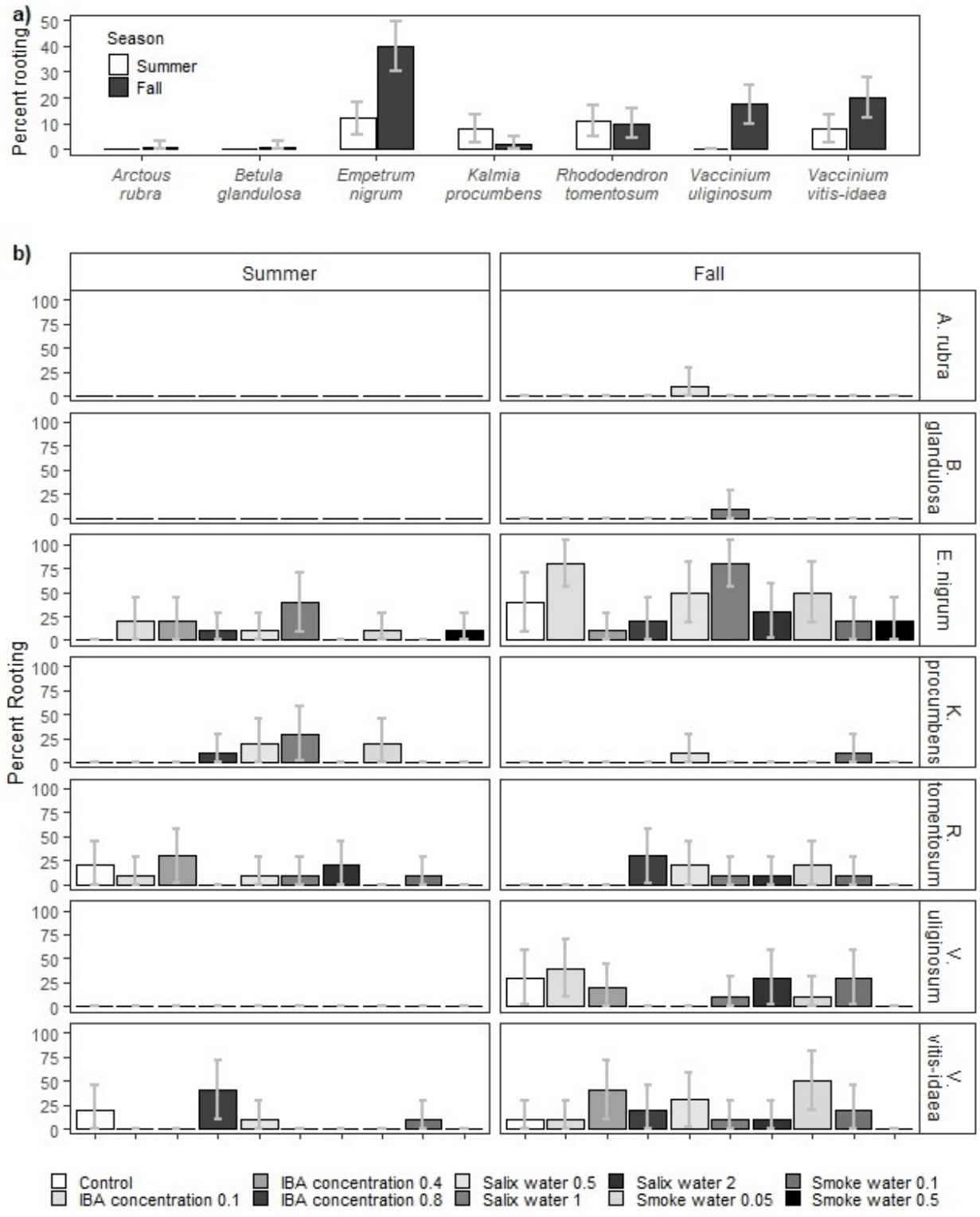

Figure 2.2. Percentage of rooted cuttings with 95 % confidence intervals in experiment 2, for a) each species (x-axis) grouped by time of year (n = 100), and b) separated by species (horizontal panels), time of year (vertical panels), and treatment group (n = 10); untreated (Control), growth hormone (0.1, 0.4, 0.8 % IBA), *Salix* water extract concentrations (0.5, 1, 2), or smoke water extract dilutions (0.05, 0.1, 0.5). *Arctous rubra* and *Betula glandulosa* were only collected in fall.

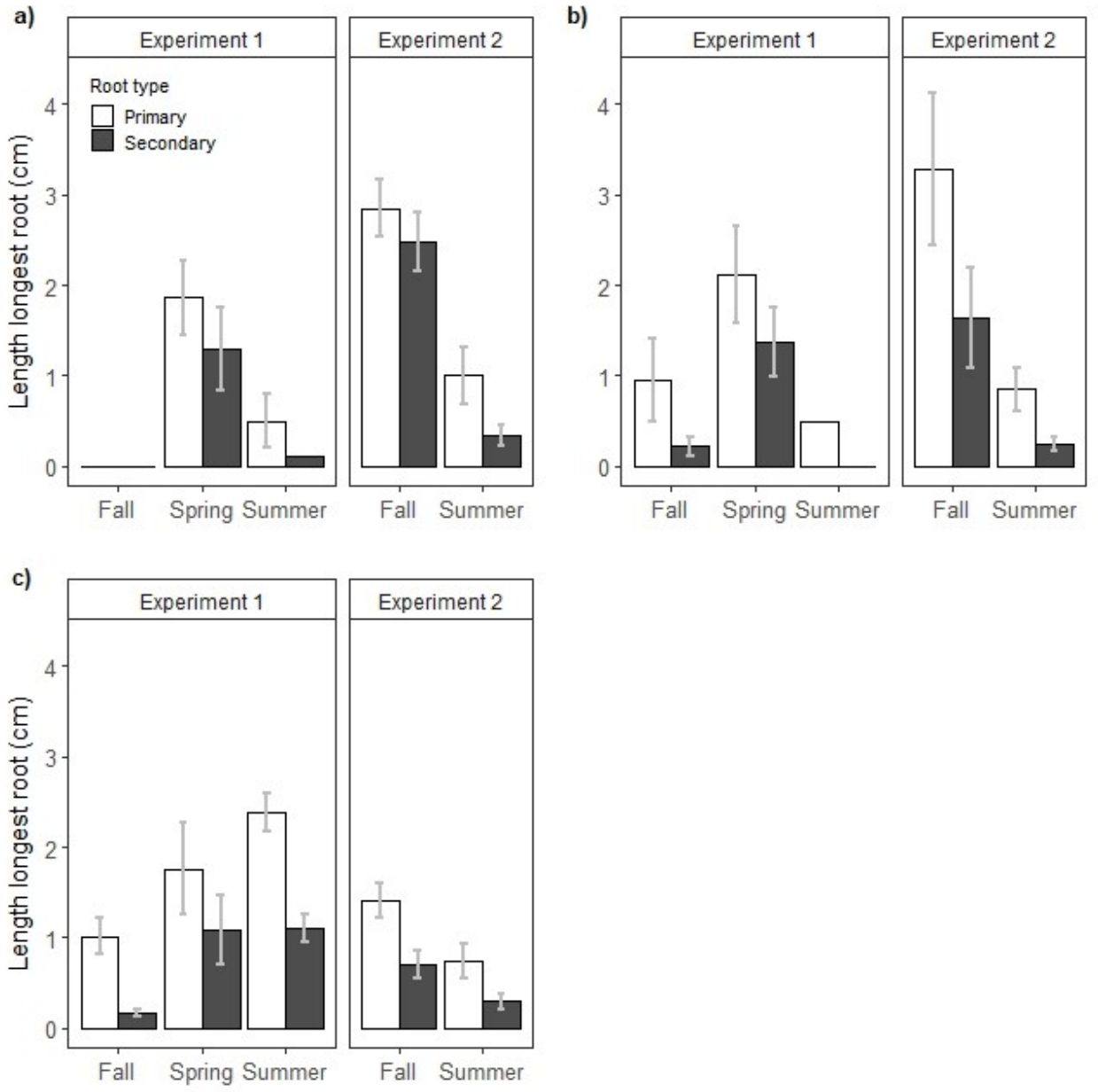

Figure 2.3. Length of longest primary and secondary roots at day 60 with 95 % confidence intervals for rooted a) *Empetrum nigrum*, b) *Rhododendron tomentosum*, and c) *Vaccinium vitis-idaea* cuttings in experiments 1 and 2 at different times of year. Number of rooted cuttings is summarized in Table 2.2 and Table S2.1.

Table S2.1. Summary statistics for maximum (max) and mean number of roots and length of the longest root for each species in experiments (Exp) 1 and 2 at different times of year. SE = standard error. NR = no roots.

Species	Exp	Season	Percent rooting	SE	Max # roots	Mean # roots (all cuttings)	SE	Mean # roots (rooted cuttings)	SE	Max length (cm)	Mean length (cm)	SE	n rooted	n planted
Arctous rubra	1	Summer	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0	54
		Fall	2.8	0.0	2	0.0	0.0	1.5	0.5	3.0	1.6	1.4	2	72
		Spring	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0	216
	2	Fall	1.0	0.0	1	0.0	0.0	1.0	NA	0.1	0.1	NA	1	100
Betula glandulosa	1	Summer	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0	73
		Fall	11.1	0.0	12	0.7	0.3	5.9	1.6	18.9	7.0	2.2	8	72
		Spring	0.4	0.0	1	0.0	0.0	1.0	NA	0.4	0.4	NA	1	227
	2	Fall	1.0	0.0	9	0.1	0.1	9.0	NA	0.2	0.2	NA	1	100
Empetrum nigrum	1	Summer	2.8	0.0	2	0.0	0.0	1.5	0.5	0.8	0.5	0.3	2	72
		Fall	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0	144
		Spring	6.0	0.0	49	0.5	0.2	8.5	3.6	5.9	1.9	0.4	13	216
	2	Summer	12.0	0.0	40	1.2	0.5	10.2	3.7	3.6	1.0	0.3	12	100
		Fall	40.0	0.0	80	4.9	1.3	12.2	2.9	8.1	3.1	0.3	40	100
Kalmia procumbens	1	Summer	4.2	0.0	12	0.3	0.2	6.7	2.7	0.2	0.2	0.0	3	71
		Fall	5.6	0.0	10	0.3	0.1	4.9	1.3	10.0	1.5	1.2	8	144
		Spring	0.5	0.0	8	0.0	0.0	8.0	NA	0.5	0.5	NA	1	216
	2	Summer	8.0	0.0	11	0.3	0.1	3.6	1.2	1.3	0.4	0.2	8	100
		Fall	2.0	0.0	4	0.1	0.0	2.5	1.5	0.4	0.3	0.1	2	100
Rhododendron tomentosum	1	Summer	1.9	0.0	1	0.0	0.0	1.0	NA	0.5	0.5	NA	1	54
		Fall	2.8	0.0	65	0.5	0.5	19.3	15.4	2.2	1.0	0.5	4	144
		Spring	6.5	0.0	16	0.3	0.1	5.1	1.4	7.7	2.1	0.5	14	216
	2	Summer	11.0	0.0	6	0.3	0.1	2.5	0.5	2.7	0.8	0.2	11	100
		Fall	10.0	0.0	117	3.1	1.4	31.2	11.3	9.3	3.3	0.8	10	100
Vaccinium uliginosum	1	Summer	1.9	0.0	4	0.1	0.1	4.0	NA	0.2	0.2	NA	1	54
		Fall	4.2	0.0	6	0.2	0.1	3.7	0.8	2.1	1.2	0.3	6	142
		Spring	1.9	0.0	23	0.2	0.1	8.3	5.2	6.0	3.0	1.1	4	216
	2	Summer	NR	NR	NR	NR	NR	NR	NR	NR	NR	NR	0	100
		Fall	17.3	0.0	49	2.3	0.7	13.0	3.1	7.2	3.9	0.4	17	100
Vaccinium vitis-idaea	1	Summer	55.1	0.1	30	6.3	0.9	11.4	1.2	4.7	2.4	0.2	38	69
		Fall	7.7	0.0	37	0.9	0.3	11.5	3.1	2.3	1.0	0.2	11	142
		Spring	8.8	0.0	14	0.5	0.1	5.9	1.0	8.0	1.8	0.5	18	216
	2	Summer	8.0	0.0	5	0.2	0.1	3.0	0.6	1.8	0.7	0.2	8	100
		Fall	20.0	0.0	23	1.6	0.4	8.0	1.6	3.0	1.4	0.2	20	100

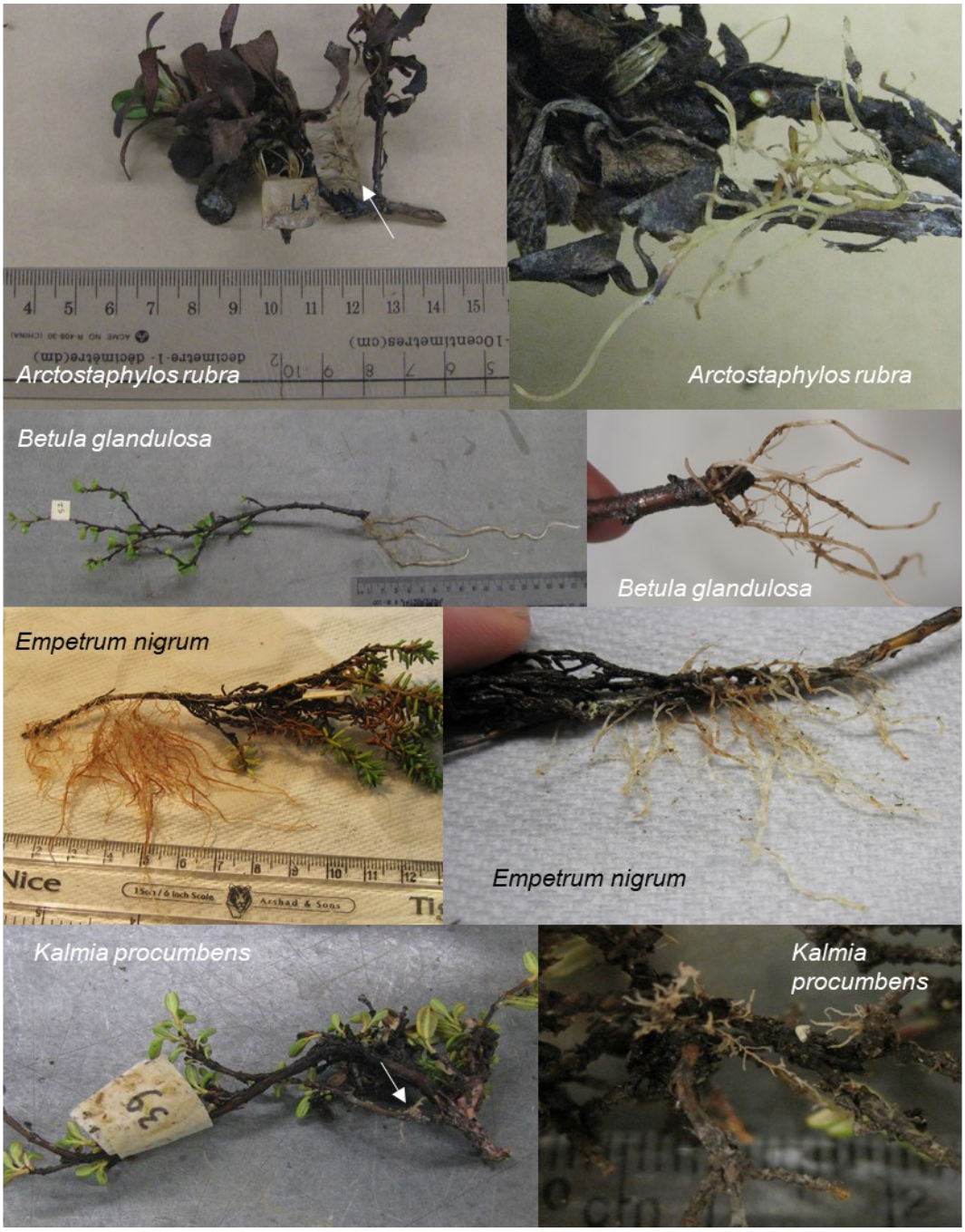

Figure S2.1. Representative images of roots on *Arctous rubra*, *Betula glandulosa, Empetrum nigrum,* and *Kalmia procumbens* cuttings.

Figure S2.2. Representative images of roots on *Rhododendron tomentosum, Vaccinium uliginosum,* and *Vaccinium vitis-idaea* cuttings.

III. INFLUENCE OF TREATMENT ON ROOTING OF ARCTIC *SALIX* SPECIES CUTTINGS FOR REVEGETATION

1. INTRODUCTION

Significant exploration and mineral resource extraction over the past century in the Canadian north has left large, long lasting disturbances in this unique ecosystem, highlighting the current need for effective revegetation techniques. As natural recovery may take decades or centuries, reclamation practitioners have often relied on seeding early successional species such as cold tolerant grasses and legumes to accelerate revegetation as they can be purchased commercially. However, this has been unreliable for developing appropriate shrub heath tundra communities, and determining techniques that consistently promote adventitious root development on arctic shrub cuttings could lead to faster and more effective revegetation in these harsh northern environments.

Plant roots play numerous structural and functional roles necessary for plant growth and survival, including anchorage and stability, resource acquisition and transportation, propagation, and storage of resources; and they provide important ecological benefits through assisting with local, regional, and global biogeochemical cycling of nutrients and water (Pendall et al. 2004, Bardgett et al. 2014, Austin and Zanne 2015). In northern locations, plant functions such as photosynthesis, nutrient uptake, and growth decrease as mean environmental temperature decreases, and plants allocate a larger portion of total biomass to roots, reaching 70 % or more in tundra environments (Chapin et al. 1980, Poorter et al. 2012).

Intrinsic genetic pathways control species specific traits such as root length and growth, branch number and pattern, and diameter, which may be modulated by changing environmental conditions (Malamy 2005, Jung and McCouch 2013, Morris et al. 2017). This phenotypic plasticity allows plants to adapt to their surrounding environment, and influences architectural, morphological, physiological, and biotic traits of the mature root system of even genetically identical plants (Nicotra et al. 2010, Bardgett et al. 2014, Fromm 2019). Growth of the primary root in dicotyledons such as *Salix* species, produces a well developed taproot, or allorhizic system from which lateral roots may emerge forming secondary and higher orders of root branches (Bellini et al. 2014, Atkinson et al. 2014). Regulation of different stages of lateral root formation leads to a characteristic root system architecture for different plant species (Malamy and Benfey 1997, Malamy 2005, Laplaze et al. 2007). Understanding these influences on root architecture can help us to develop successful revegetation techniques.

The ability to produce adventitious roots under natural or stressed circumstances such as wounding has been used by horticultural and forestry industries for food production, and economic and ecological benefits (Bellini et al. 2014, Steffens and Rasmussen 2016). In northern environments, revegetation of disturbed areas using shrub cuttings is a potentially promising reclamation technique as there are currently no commercial suppliers of seed for northern shrub species (Hagen 2002, Holloway and Peterburs 2009, Matheus and Omtzigt 2011, Ficko et al. 2015, Ficko and Naeth 2021). Shrub species such as *Salix alaxensis* (Andersson) Coville (felt leaf willow), *Salix arctica* Pall. (arctic willow), *Salix glauca* (gray willow), and *Salix planifolia* (diamond leaf willow), are known to quickly develop adventitious roots on cuttings with limited assistance as they have preformed root primordia, making them preferred species for northern revegetation (Densmore et al. 2000, Walter et al. 2005, Naeth and Wilkinson 2011, Ficko et al. 2015). Guidelines typically recommend collecting cuttings in fall or spring and soaking them for 24 to 48 hours before planting. However, limited research has been conducted on longer soaking times for cuttings that cannot be planted immediately due to work or environmental delays, or collecting cuttings in summer if the site is inaccessible in other months.

Growth hormones such as indole-3-butyric acid (IBA), a naturally produced endogenous auxin, are commonly applied to cuttings to stimulate adventitious rooting (Davies Jr et al. 2017). Auxin synthesis occurs mainly in young plant leaves and is transported by bulk flow through the vascular system to various tissues in response to environmental stimuli and interactions with other hormones and growth regulators (Overvoorde et al. 2010, Pop et al. 2011). Directional movement into cells through integral membrane transport proteins creates local auxin gradients that play an essential role in regulating root architecture and development, including adventitious and lateral root formation (Malamy 2005, Overvoorde et al. 2010, Olatunji et al. 2017). *Salix* water extract contains the phytohormone salicylic acid and a number of other compounds that have fungicidal, insecticidal, antibacterial, and root promoting properties (Sati et al. 2011, Al-Amad and Qrunfleh 2016, Singh et al. 2017, Deniau et al. 2019, Javed et al. 2020). It has commonly been used by home gardeners as an alternative treatment to improve rooting of cuttings, with several studies recently showing it can improve rooting for *Olea europaea* L. (European olive), *Coleus scutellarioides* (L.) Benth. (common coleus), *Chrysanthemum* sp. (chrysanthemum), *Lavandula* x hybrid ‘Frills’ PBR (lavender) and several arctic species (Al-Amad and Qrunfleh 2016, Koriesh et al. 2018, Wise et al. 2020, Ficko and Naeth 2021). Smoke water extract is another alternative treatment as karrikins in fire and smoke are known to improve germination for numerous species, and recently to play a role in regulating root development (Chiwocha et al. 2009, Akeel et al. 2019, Swarbreck 2021). The only study to assess use of smoke water extract on cuttings found species

specific interactions between season and smoke water extract for seven northern species (*Arctous rubra* (Rehder & Wilson) Fernald (red bearberry), *Empetrum nigrum* L. (crowberry), *Kalmia procumbens* (L.) Gift & Kron & P.F. Stevens ex Galasso, Banfi & F. Conti (alpine azalea), *Rhododendron tomentosum* Harmaja (marsh Labrador tea), *Vaccinium uliginosum* L. (bog bilberry) and *Vaccinium vitis-idaea* L. (bog cranberry), although results were limited by low rooting percentages (Ficko and Naeth 2021).

With increasing exploration and resource extraction in the north, developing a better understanding of root system architecture for *Salix* species grown from cuttings with different rooting techniques, and how their root system architecture compares to plants grown in undisturbed tundra is expected to improve revegetation success. The main objectives of our study were to assess effects of collection time, common rooting treatments (IBA concentration, soaking length), and novel rooting treatments (water extracts of *Salix* and smoke) on adventitious and lateral root development of *Salix* ssp. cuttings collected from Diavik Diamond Mine Inc. Northwest Territories, and grown under controlled conditions in a growth chamber. As lateral root development has rarely been studied on cuttings from arctic species, determining which treatments optimize root system architecture and not just adventitious rooting can improve revegetation of disturbed northern sites.

2. MATERIALS AND METHODS

2.1. Experimental Design

Cuttings were collected from growing tips of shrubs in an undisturbed upland dwarf heath tundra community at Diavik Diamond Mine, Northwest Territories (64º30´41´´ N, 110º17´23´´ W). *Salix glauca* L. (grayleaf willow) and *Salix planifolia* Pursh (diamond leaf willow) are the two main *Salix* species in the community, but were low in abundance relative to other shrub species, including *Arctous rubra* (Rehder & Wilson) Fernald (red bearberry), *Betula glandulosa* Michx. (bog birch), *Empetrum nigrum* L. (crowberry), *Kalmia procumbens* (L.) Gift & Kron & P.F. Stevens ex Galasso, Banfi & F. Conti (alpine azalea), *Rhododendron tomentosum* Harmaja (marsh Labrador tea), *Vaccinium uliginosum* L. (bog bilberry) and *Vaccinium vitis-idaea* L. (bog cranberry). Cuttings from both species were collected together for the experiments, similar to how a reclamation practitioner would collect them in the field. Cuttings were not separated by species as both successfully rooted with no significant differences in a preliminary trial (70 to 100 %) (Naeth and Wilkinson 2011). They grew together in the plant community making them difficult to separately identify in different seasons if leaves and/or catkins are not present. Cuttings varied in length from

10-40 cm based on stem length of available plants, and were planted in a 50:50 by volume peat moss and potting soil mix within 1 week at the University of Alberta.

The effects of common horticultural and novel treatments on adventitious and lateral root development were assessed in two screening studies. Cuttings in experiment 1 were collected in summer (25-26 June), fall (19-20 September), and spring (20-21 May), and treated with soaking times (0, 1, 3, 5, 10, 20 days) and indole3-butyric acid (IBA) concentrations (0, 0.1, 0.4, 0.8 %) for a total of 72 treatments (summer cuttings had no 0.4 % IBA due to growth chamber space restrictions, Table S3.1). There were 3, 6, and 9 cuttings per treatment group (soak x IBA concentration) in summer, fall, and spring for a total of 54, 144, and 216 cuttings, respectively. Experiment 2 cuttings were collected in fall (27-28 September), and untreated, or treated with IBA concentrations (0.1, 0.4, 0.8 %), *Salix* water extract (0.5, 1, 2), or smoke water extract (0.05, 0.1, 0.5). *Salix* water extracts were made by placing 300, 600, and 1200 mL of cuttings (1 to 3 cm pieces) in 2,400 mL boiling distilled water and soaking for 12 hours. Smoke water extracts were made by placing 4 L distilled water in a smoker with 1.2 kg wood chips for 4 hours, then diluting with distilled water (1:20, 1:10, 1:1 extract to distilled water by volume). There were 10 cuttings per treatment group for a total of 100 cuttings. Tap water was maintained at a depth of 5 cm in containers for soaking treatments. Approximately 5 cm of stem bottom was dipped in IBA powder prior to planting for IBA treatments, while for *Salix* and smoke water extract treatments the bottom 5 cm of cuttings was soaked for 12 hours prior to planting.

Three cuttings per species per treatment (soaking time x IBA concentration) were planted in the same 10 x 10 x 10 cm container in each season in experiment 1 due to growth chamber space restrictions. For experiment 2, each cutting was planted in an individual 10 x 3 x 3 cm root trainer. Cuttings were placed in a growth chamber for 60 days, then roots were gently rubbed under running water to remove all substrate. Growth chamber conditions were set at 17/10 ºC for 16/8 photoperiod in experiment 1 and 17/10 ºC for 20/4 photoperiod in experiment 2, to mimic different growing conditions at Diavik.

Primary root refers to the adventitious root that emerged from the stem cutting; secondary, tertiary, and quaternary roots refer to successive orders of lateral root branches off the primary root (Lecompte and Pagès 2007). To assess root development patterns, primary adventitious roots on each cutting were counted; lengths of longest primary, secondary, tertiary, and quaternary roots on each cutting were measured; and number of secondary roots on each primary root were assessed under a microscope and placed in categories (0, 1-24, 25-49, 50-74, 75-99, and >100) due to significant branching. Presence of callus was noted for cuttings in experiment 1, as callus is part of the wound response, and is a precursor for rooting in some (but not all)

species (Davies Jr et al. 2017). Shoot health and vigour of each cutting were assessed at 30 and 60 days using a five point scale with 1 = dead, 2 = poor (plant mostly dead or dying, < 30 % live green tissue), 3 = fair (average health and growth, 30 to 60 % live green tissue), 4 = good (plant healthy and growing, 60 to 90 % live green tissue), and 5 = excellent (plant robust and growing vigorously, 90 to 100 % live green tissue.

2.2. Statistical Analyses

All model estimation and statistical analyses were conducted using R (Version 4.0.2, 2020). One fall cutting in experiment 1 was removed from the data set prior to analysis as it had 80 roots; greater than 3 standard deviations from the mean. Cuttings were assessed separately by season since some species root more readily at certain times of year.

Due to low number of replicates per treatment, 2/3 of cuttings with roots per season per experiment was considered the minimum requirement for analysis in a hurdle model to determine treatment effects. Fall and spring cuttings in experiment 1 and fall cuttings in experiment 2 met this condition. The first step in the model was to predict probability that a cutting produced at least one root; the second step was to predict number of roots, longest root length, and proportion of rooted cuttings with shoot health 5. Mean shoot health, longest root length for different root orders at different times of year in each experiment, number of secondary roots per primary root, and number of roots and length of root with and without callus were presented graphically using ggplot2 (R, Version 4.0.2, 2020, Wickham 2016).

In experiment 1, a series of 10 models with combinations of the independent variables IBA concentration and soaking time was constructed for each dependent variable: 1) null model (no variables), 2) IBA concentration, 3) soak, 4) IBA concentration and soak, 5) IBA concentration and IBA concentration squared, 6) soak and soak squared, 7) IBA concentration, soak, and soak squared, 8) IBA concentration, soak, and IBA concentration squared, 9) IBA concentration, soak, IBA concentration squared, and soak squared, and 10) IBA concentration, soak, and IBA concentration x soak (interaction). All experiment 1 models were fitted with the glmmTMB package and glmmTMB function, with pot as a random variable. Models were compared using the Akaike Information Criterion (AIC), ranked by weight to determine probability of being the best model, and a cumulative probability of at least 0.9 was calculated for each dependent variable (Anderson 2008). As rooting is binary (present or absent), logistic regression was used to determine proportion of cuttings rooted in the first step for both experiments. For step 2, mean number of roots produced by cuttings with at least one root was predicted using zero truncated negative binomial regression as it could account for overdispersion, variability in distribution, and

count data. Mean length of the longest root was predicted by multiple linear regression, and proportion of cuttings with shoot health 5 was predicted by logistic regression.

In experiment 2, a fixed effects logistic regression model for proportion of cuttings that rooted with the control and nine treatments as independent variables was fitted with the MASS package and GLM function. For step 2, the Kruskal-Wallis rank sum test was used to compare the control group to nine treatment groups for mean number of roots per rooted cutting, and mean length of longest root, as models developed using parametric tests fit poorly. Dunnett's test for multiple comparisons with one control and a Hochberg adjustment was fitted from the PMCMR package to determine significant differences between the control group and each treatment group. The proportion of cuttings with shoot health 5 was predicted using logistic regression.

3. RESULTS AND DISUSSION

3.1. Shoot Health

Cuttings that rooted had higher shoot health than those that did not root regardless of treatment (Figure 3.1). Shoot health of rooted cuttings in experiment 1 was 3.3 to 5 for fall and spring cuttings across IBA concentration and soaking time. Only a few summer cuttings rooted, with shoot health variable. Shoot health of unrooted cuttings was 1 to 4 for fall and spring cuttings, and ≤ 2 for summer cuttings. In a preliminary study at Diavik, shoot health of five fall collected *Salix planifolia* cuttings (60 % rooted) was 1.4 (0.4 standard error) after 12 weeks in a growth chamber (Naeth and Wilkinson 2011). Since root development enables a plant to access nutrients and water from the soil, shoot health was stable or increased from day 30 to 60 for rooted cuttings in both experiments in all seasons (SM Figure 3.1). Fall and spring (but not summer) cuttings with higher shoot health at day 60 had more roots (data not shown). Using shoot health as a proxy for rooting could save time and minimize disruption to the cutting as roots do not need to be visually assessed; however, our results indicate that shoot health is not sufficiently correlated with rooting.

Percentage of rooted cuttings with shoot health 5 in experiment 1 was 42 to 75 for fall collected, and 53 to 75 for spring. The null model had most weight in both seasons, although soaking had a similar probability in spring, generally decreasing the percentage with shoot health 5 (Table 3.1). In experiment 2, shoots were typically very healthy, regardless of treatment. Percentage of rooted cuttings with shoot health 5 was 100 for all treatments except IBA 0.1 (89 %) and Salix water 2 (86 %). While none of the treatments had a strong effect on shoot health in this study, Houle and Babeux (1998) found that a 1 % IBA concentration decreased the percentage of *Salix planifolia* cuttings that developed leaves, lateral shoot number, and lateral

shoot biomass, while Schaff et al. (2002) found that *Salix nigra* cuttings soaked for 10 days had higher shoot and leaf biomass than unsoaked cuttings or cuttings soaked for three days. While scoring shoot health with a point scale is a faster method of assessing above ground growth, these results indicate that other methods such as counting shoot number or measuring shoot biomass may provide more information on treatment effects.

3.2. Root Development

Cuttings had consistently high rooting, with 82 % (421 of 514) cuttings developing adventitious roots across all experiments and treatments. Parent root elongation and subsequent lateral root branching is a complex process involving plant genetics, hormones, and environmental factors (Malamy 2005, Nibau et al. 2008, Atkinson et al. 2014). Cuttings generally had extensive branching, with some secondary through senary orders of lateral roots developing within 60 days. Of cuttings with primary roots, 396 developed secondary (94 %), 360 developed tertiary (86 %), and 117 developed quaternary roots (28 %) (quintenary and senary root orders not consistently assessed). *Salix* species (eg. *Salix alba* L. (white willow)*, Salix caprea* L. (goat willow)*, Salix cinerea* L. (European gray willow)*, Salix eleagnos* Scop. (hoary willow)*, Salix glabra* Scop. (smooth willow)*, Salix pulchra* Cham. (tea leaf willow)*,* and *Salix purpurea* L. (basket willow)) are known to produce numerous lateral roots (Kutschera and Lichtenegger 2002, Iversen et al. 2015), indicating intrinsic genetic factors likely determined extensive production of lateral roots in our study.

3.3. Response To Season

Season was most influential on callus formation with 75.7 ± 0.0 % of fall cuttings, 78.2 ± 0.0 % of spring cuttings, and 0 % of summer cuttings producing callus; and on adventitious root development, with 30 ± 0.1 % of summer cuttings and > 80 % of fall (both experiments) and spring cuttings rooted (Table S3.2). Our results were similar to those of Houle and Babeux (1993), with *Salix planifolia* cuttings having high rooting shortly before or after bud break in May and June and after dormancy in September and October, and significantly lower in July and August. Holloway and Peterburs (2009) found significant rooting (> 80 %) for two species in Alaska (*Salix alaxensis* var. *longistylis* (Rydb.) Schneid. (Alaska willow) and *Salix arbusculoides* Anderss. (little tree willow)) when collected mid to early July, and poor rooting (< 25 %) for one species (*Salix bebbiana* Sarg. (Bebb's willow)) regardless of collection time. Some *Salix* species, especially from riparian areas, have preformed root primorida, which allow cuttings to rapidly develop roots, while other *Salix* species must undergo cell dedifferentiation before induction of new root primordia

(Haissig 1974, Krasny et al. 1988, Davies Jr et al. 2017). While our cuttings were not identified to species, high rooting in fall and spring but not summer indicates a stronger influence of season on adventitious rooting than species, as all cuttings were collected in a similar manner from the same location each season. Environmental factors such as photoperiod, precipitation, and air temperature that affect physiological status and health of the donor plant prior to harvesting likely underly the species specific effect of season on adventitious rooting (Bellini et al. 2014, Davies Jr et al. 2017).

Lateral roots have greatest plasticity among different root types, allowing plants to respond in species specific ways to changing environmental conditions such as soil water, nitrogen, and phosphorus concentrations (Postma et al. 2014, Robbins and Dinneny 2015, Chen et al. 2018). Longest root length decreased with successive root orders for cuttings (Figure 3.3). Within a root order, season and experiment appeared to influence longest root length. For root branching, diameter of a parent root influences diameter and length of subsequent lateral roots (Lecompte and Pagès 2007, Wu et al. 2016). Summer cuttings in our study generally had smaller adventitious roots than fall or spring cuttings, and fewer and shorter lateral roots. As all cuttings in our study were grown in a similar soil mixture, differences in lengths between seasons within a root order in experiment 1, within a root order between fall experiment 1 and 2 cuttings, and number of roots in secondary root categories between experiment 1 and 2 (Figures 3.4, 3.5) are likely due to differences in growth chamber conditions, or differences in health and resources available in donor cuttings at different times of year or in different years. In comparison, there was little difference between number of roots in secondary root categories for fall and spring cuttings in experiment 1, except 75-99 category had twice as many spring cuttings with secondary roots as fall cuttings, (Figures 3.5, S3.2). As both number and length of lateral roots strongly affects root system architecture of a plant, selecting dormant *Salix* cuttings will likely be most successful in developing an extensive root system suitable for revegetation in the north.

Formation of callus and new roots requires input of carbohydrates solubilized from local sources or transported from distal portions of the cutting. Stored carbohydrates provide energy to enable a cutting to survive until it develops new roots, and building blocks for root formation (da Costa et al. 2013, Davies Jr et al. 2017). Dormant cuttings are thought to have higher carbohydrate reserves, although concentrations are not consistently correlated with rooting for different species (Fege and Brown 1984, Haissig 1986, Davies Jr et al. 2017, Tsafouros et al. 2019). Further research is required to determine factors affecting carbohydrate partitioning within a cutting at different times of year and in different species, and how this influences adventitious and lateral root development and callus formation. While summer is the best time for reclamation

practitioners to work, our results indicate that collecting cuttings from dormant *Salix* species will likely lead to more successful revegetation as cuttings have much higher rooting percentages and more developed root system architecture.

3.4. Response To IBA And Soaking

Fall and spring cuttings had sufficient adventitious rooting for treatment effects analysis; fall models generally had weaker treatment effects. Percentage of rooted cuttings in a dependent variable treatment group (IBA concentration or soaking time) in experiment 1 was 71 to 92 for fall cuttings, and 83 to 92 for spring (Figure 3.2). The null model had most weight in both seasons, although for fall cuttings soaking had similar weighting to the null model, indicating longer soaking times may increase rooting percentages (Table 3.1). In experiment 2, most fall cuttings rooted, regardless of treatment. Nine out of ten control cuttings, IBA 0.1 %, and IBA 0.4 % rooted, while ten out of ten IBA 0.8 % rooted.

Endogenous auxin concentrations naturally vary in plants throughout the growing season, and in cuttings an increase in endogenous auxin at the cut surface from polar auxin transport or application of different exogenous auxin concentrations, stimulates adventitious rooting in many species (Nanda and Anand 1970, Wiesman et al. 1988, Ludwig-Müller 2000, Štefančič et al. 2005). As cuttings in our study were not treated for up to seven days after collection, rewounding the cuttings prior to treatment may have resulted in different adventitious root percentages in different seasons based on interactions with seasonal endogenous auxin concentrations (Nanda and Anand 1970, Howard 1971, Blakesley et al. 1991). For instance, Nanda et al. (1974) found *Populus robusta* Schneid. cuttings developed more roots when treated with IBA at day 0 than at day 7 or 14. However, Lodama et al. (2016) found that delaying hormone application by one to two weeks improved rooting in *Lobostemon fruticosus* (L.) H. Buek (pyjama bush). Follow up research investigating endogenous auxin concentrations in *Salix* species from our study throughout the growing season can determine if interactions between endogenous and exogenous growth hormones are influencing root development.

Application of exogenous IBA in different forms and concentrations has species specific effects on numerous root parameters including callusing, timing of root emergence, number of primary and secondary roots, root length, dry weight, and field survival rates (Sharma and Aier 1989, Rehana et al. 2020, Abdel-Rahman 2020). In our study, cuttings with callus produced more roots than those without (Figure 3.6a). Increasing IBA concentration increased number of roots in fall and spring cuttings with callus and had a variable effect on cuttings without callus. Longer soaking increased number of roots for spring cuttings with callus and decreased them on fall

cuttings without callus. Spring cuttings with callus had longer roots than those without callus regardless of treatment (Figure 3.6b). In some species, such as *Lobostemon fruticosus* and *Arabidopsis thaliana*, root initials always developed from callus tissue (Ludwig-Müller et al. 2005, Lodama et al. 2016), but in *Prunus* GiSelA 5 (dwarf cherry), cuttings with callus had fewer and shorter roots than cuttings without callus (Štefančič et al. 2005). In two poplar species, the easy to root *Populus* x *euramericana* (Dode) Guinier cv. 1-78 developed roots from preformed root primordia and callus, while in the hard to root species, *Populus tremula* L., cuttings developed callus but not roots (Okoro and Grace 1976). Ludwig-Müller et al. (2005) and Nanda et al. (1974) both found that timing and concentrations of different auxins influenced whether cuttings developed callus and then roots, or just callus.

In experiment 1, the linear model with concentration best represented number of roots on fall cuttings, while the model with linear and quadratic terms for both concentration and soaking length best represented spring cuttings (Table 3.1, Figure 3.7). Number of roots increased with increasing IBA concentration until 0.4 % then decreased, decreased with shorter soaking (1, 3 days) than no soaking, and increased with longer soaking (5, 10, 20 days) (Table S3.3). Higher IBA concentrations in both seasons produced some cuttings with many roots (Figure 3.7). For longest root length, the null model had most weight for fall cuttings, followed by a linear soaking term (Table 3.1, Figure S3.5). Soaking generally decreased longest root length for fall cuttings relative to no soaking (Table 3.3). The model with linear concentration and soaking and quadratic concentration and soaking best represented spring cuttings (Table 3.1, Figure S3.5). Increasing IBA concentration generally decreased longest root length, while increasing soaking time up to 10 days slightly increased longest root length relative to no soaking (Table S3.3). In experiment 2, IBA 0.4 and 0.8 % had similar number of roots and root length as the control, while IBA 0.1 % had fewer and shorter roots (Figure 3.7e, Table S3.3, Figure S3.5e). Number of roots had only a weak correlation with longest root length for cuttings in both experiments (Figure S3.6).

For IBA concentrations similar to those in our study, Miller-Adamany et al. (2017) found no effects of application of 0.3 % IBA on below ground biomass of *Salix exigua* Nutt. (coyote willow) cuttings, while Hoag and Short (1992) found no improvement in rooting after applying 0.1 % IBA to cuttings from 10 willow species. In a subarctic study, Houle and Babeux (1998) found time of year did not affect rooting of *Salix planifolia* cuttings treated with 0.1 % IBA, although fall dormant cuttings produced more roots than August cuttings. Application of 0.01 and 0.1 % IBA to late May cuttings had similar rooting to dormant cuttings in our study. Higher concentrations of IBA (1 %), above the concentration used in our study, decreased rooted cuttings and number of

roots indicating a potential auxin threshold for *Salix* species (Houle and Babeux 1994, Lund et al. 1996, Ricci et al. 2008).

For soaking duration, only one other study was found that specifically investigated effects of season (fall, spring), and soaking time (0, 14 days) on *Salix* cuttings (*Salix amygdaloides* Andersson (peach leaf willow) and *Salix exigua* cuttings) (Tilley and Hoag 2009). Soaking did not influence rooting percentages, but increased shoot and root biomass of fall cuttings, respectively. Ficko and Naeth (2021) found species specific responses to soaking and season for seven other shrub species from Diavik, but rooting percentages were low. In another study, soaking dormant *Salix nigra* cuttings for 10 days doubled cutting survival, and resulted in higher root, shoot, and leaf biomass than 0 or 3 days of soaking which was similar to the pattern for number of roots on spring cuttings in our study (Schaff et al. (2002). Miller-Adamany et al. (2017) found soaking and storing *Salix exigua* cuttings for 17 days increased above ground biomass, with no differences between soaked and unsoaked cuttings for below ground biomass; Martin et al. (2005) found soaking *Salix nigra* cuttings for 14 days in a large field study significantly improved cutting survival over 34 weeks. Soaking was hypothesized to improve cutting water status which enabled faster root development and better contact with soil even with low soil water conditions. Further research is necessary to decipher the physiological mechanism underlying how soaking time impacts rooting, and how this varies by season.

Endogenous IAA concentrations in the rooting zone are known to affect all stages of lateral root initiation, primordia development, and emergence (Bhalerao et al. 2002, De Smet et al. 2007). In our study, application of exogenous IBA had a variable effect on lateral root development by generally increasing number of cuttings with fewer than 50 secondary roots, and decreasing number of cuttings with greater than 75 secondary roots, although this varied by season and experiment (Figures 3.4, 3.5, S3.3). Soaking time did not strongly influence number of secondary roots (Figure S3.4). In *Arabidopsis thaliana*, lateral root formation is promoted by increasing exogenous auxin concentrations until a maximum after which further lateral root formation is decreased or inhibited (Péret et al. 2009, Ivanchenko et al. 2010). In *Cucurbita pepo* L. (pumpkin), application of exogenous auxins decreased primary root growth, but had no effect on lateral root initiation (Ilina et al. 2018). IBA application in our study likely decreased the rate of parent root elongation, and potentially exceeded the maximum concentration which decreased number of secondary roots. Given root system architecture of cuttings is shaped by both adventitious and lateral root development, use of auxins must be carefully balanced to optimize both adventitious and lateral root development to cultivate plants with healthy and well developed root systems suitable for reclamation.

3.5. Response To *Salix* And Smoke Water Extracts

In experiment 2, 100 % of cuttings rooted for all three smoke water treatments, and 0.5 and 1 *Salix* water extracts relative to 90 % for control cuttings (Figures 3.7e, S3.5e). However, the highest concentration of *Salix* water extract (2) only had 70 % of cuttings root. Ficko and Naeth (2021) found differences in rooting percentages between season and *Salix* water extract, and season and smoke water extract for seven northern species also collected from Diavik; but rooting percentages were generally < 25 %. Smoke water extract and low concentrations of *Salix* water extract increased secondary root number between 25 and 74 relative to the control (Figure 3.4).

In our study, *Salix* cuttings may not have responded strongly to *Salix* water extract if they already contained the same compounds (salicylic acid) as those in the extract, or if the *Salix* water extracts were not optimal concentrations to stimulate adventitious rooting. Recent research has determined that karrikins, found in smoke water extract, use similar signaling pathways as strigolactones, a newly discovered class of plant hormone. Karrikins and strigolactones inhibited adventitious and lateral root formation in *Arabidopsis thaliana*, although low phosphorus conditions or high auxin concentrations overrode the inhibitory effect on lateral root formation (Kapulnik et al. 2011, Ruyter-Spira et al. 2011, Rasmussen et al. 2012). Given there were differences in response between adventitious and lateral root development in our study, understanding how compounds in these extracts affect different pathways in the plant may improve revegetation efforts in future by selecting treatments that optimize root system architecture for the local soil conditions of the reclamation site.

4. CONCLUSIONS

For successful northern revegetation, cuttings must develop an appropriate root system architecture that can respond to harsh and changing environmental conditions. Our *Salix* ssp. cuttings developed extensive root system architecture within 60 days, with some cuttings developing up to six orders of roots. A high shoot health rating was not a good indicator of rooting. Root length decreased with increasing root order in all seasons, although length differed within a root order between seasons and experiments. Season strongly influenced rooting percentages, with > 80 of fall and spring cuttings and only 30 of summer cuttings developing primary roots, indicating collection of dormant *Salix* cuttings will be most successful for reclamation. Cuttings with callus developed more roots than cuttings without callus. Application of IBA increased number of primary roots per cutting, varying with season; and increased number of cuttings with < 50 secondary roots per primary root and decreased number of cuttings with > 75 secondary

roots per primary root. Longer soaking times increased number of primary roots per cutting in different seasons, and soaking up to 10 days increased longest root length. Application of *Salix* and smoke water extracts did not improve adventitious rooting of cuttings, but increased number of cuttings with 25 to 74 secondary roots. As few studies have investigated treatment effects on both adventitious and lateral root development of arctic cuttings, this research highlights the importance of selecting treatments that optimize root system architecture for the local environmental conditions to maximize revegetation success at disturbed northern sites.

Table 3.1. Experiment 1 model rankings and probabilities for fall and spring cuttings predicting proportion of cuttings that rooted, and for cuttings with at least one root, predicting number of roots, longest root length, and proportion with shoot health 5. Models were compared using the AIC and ranked by weight to determine probability of being the best model for the data. A cumulative probability of at least 0.9 is presented for each dependent variable, along with the null model probability.

Fall models rankings	Model probability	Spring models rankings	Model probability
Proportion rooted			
Null	0.272	Null	0.393
Soaking	0.234	Concentration	0.168
Concentration	0.111	Soaking	0.152
Concentration + Soaking	0.095	Concentration + Soaking	0.068
Soaking + Soaking^2	0.091	Concentration + Concentration^2	0.068
Concentration + Soaking + Concentration*Soaking	0.071		
Concentration + Concentration^2	0.041		
Root number			
Concentration	0.228	Concentration + Concentration^2 + Soaking + Soaking^2	0.760
Concentration + Concentration^2	0.206	Concentration + Soaking + Concentration^2	0.218
Concentration + Soaking	0.161	Null	0.000
Concentration + Soaking + Concentration*Soaking	0.138		
Concentration + Soaking + Concentration^2	0.113		
Concentration + Soaking + Soaking^2	0.093		
Null	0.002		
Root length			
Null	0.276	Concentration + Soaking + Soaking^2	0.568
Soaking	0.205	Concentration + Concentration^2 + Soaking + Soaking^2	0.220
Concentration	0.130	Soaking + Soaking^2	0.140
Soaking + Soaking^2	0.097	Null	0.001
Concentration + Soaking	0.092		
Concentration + Concentration^2	0.053		
Concentration + Soaking + Concentration*Soaking	0.046		
Shoot health of 5			
Null	0.404	Null	0.250
Concentration	0.156	Soaking	0.204
Soaking	0.156	Soaking + Soaking^2	0.144
Soaking + Soaking^2	0.070	Concentration	0.096
Concentration + Soaking	0.063	Concentration + Soaking + Concentration*Soaking	0.092
Concentration + Concentration^2	0.060	Concentration + Soaking	0.075

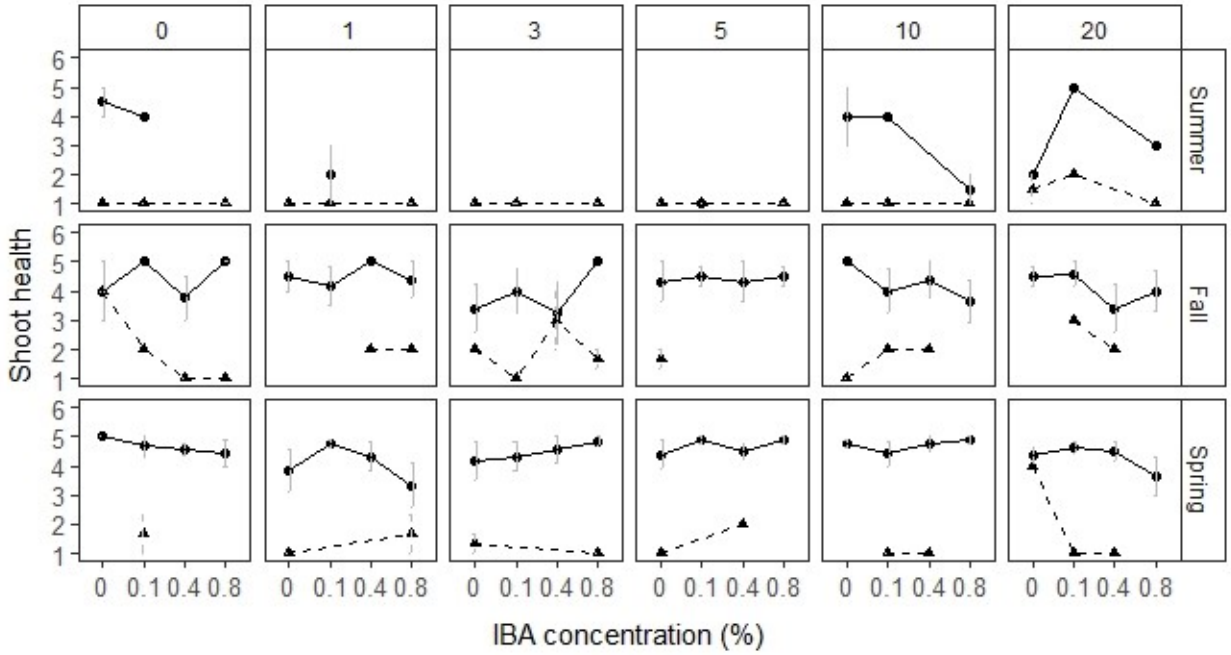

Figure 3.1. Shoot health at day 60 for *Salix* ssp. cuttings in experiment 1 that rooted (circle, solid line) and did not root (triangle, dashed line) by IBA concentration (%) (x-axis), season (horizontal panels), and soaking time (days) (vertical panels) with standard error of the mean. There were n = 3 (summer), n = 6 (fall), and n = 9 (spring) cuttings for each soaking x IBA treatment. Shapes without error bars represent a single cutting.

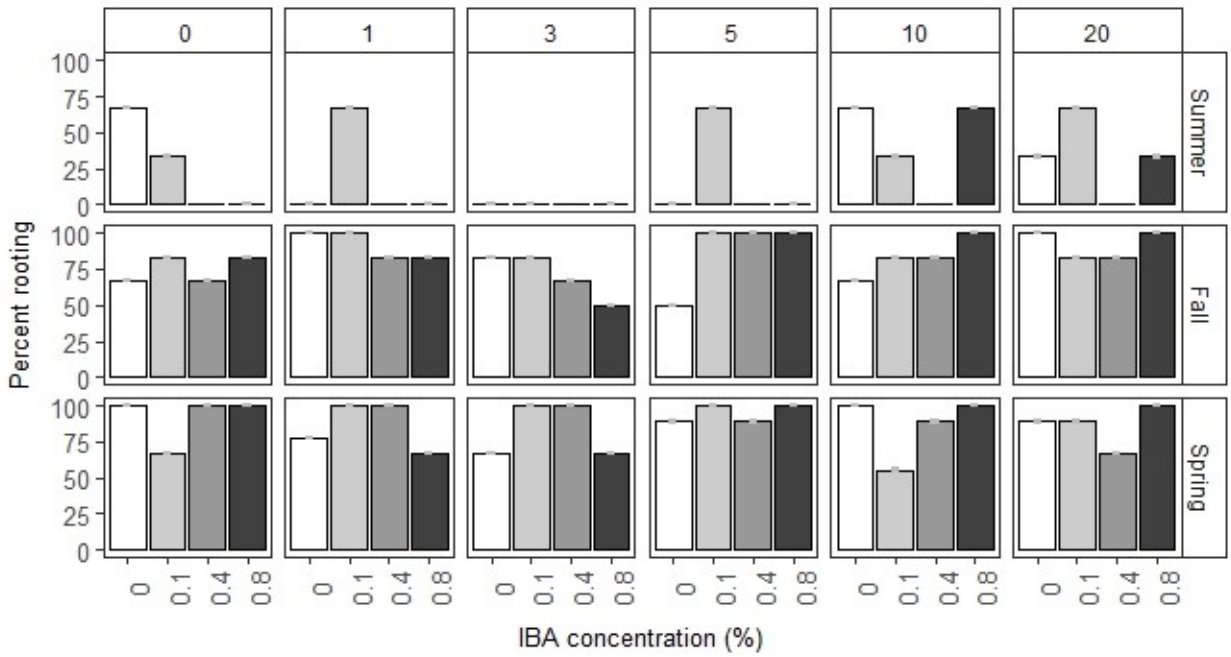

Figure 3.2. Percentage of rooted *Salix* ssp. cuttings with standard error in experiment 1 by soaking time (vertical panels, 0, 1, 3, 5, 10, 20 days), IBA concentration (0, 0.1, 0.4, 0.8 % IBA) and at different times of year (horizontal panels) Summer cuttings received three IBA concentrations (0, 0.1, 0.8 % IBA). Each bar is n = 3 (summer), n = 6 (fall), and n = 9 (spring).

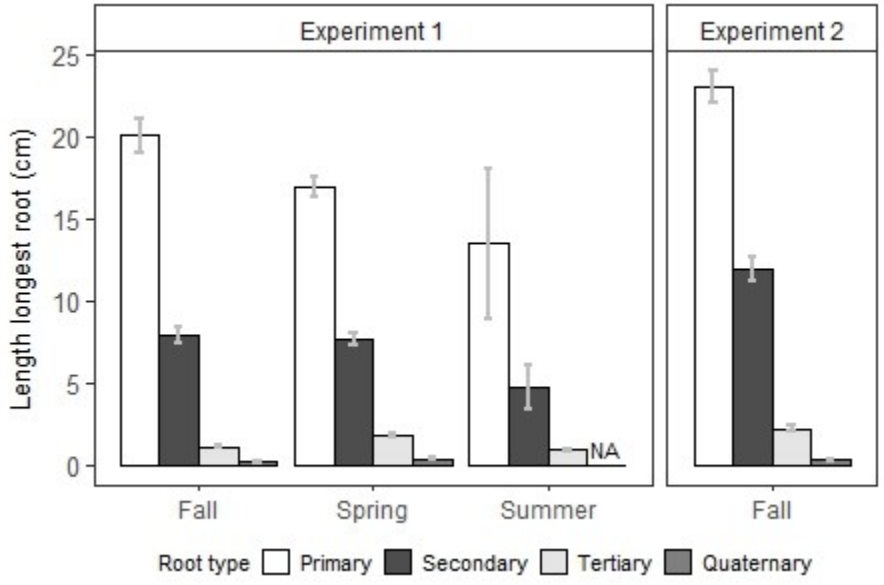

Figure 3.3. Length of longest primary, secondary, tertiary, and quaternary roots with standard error at day 60 for rooted *Salix* ssp. cuttings in experiments 1 and 2 at different times of year. Length of longest quaternary roots was not assessed for summer cuttings in experiment 1.

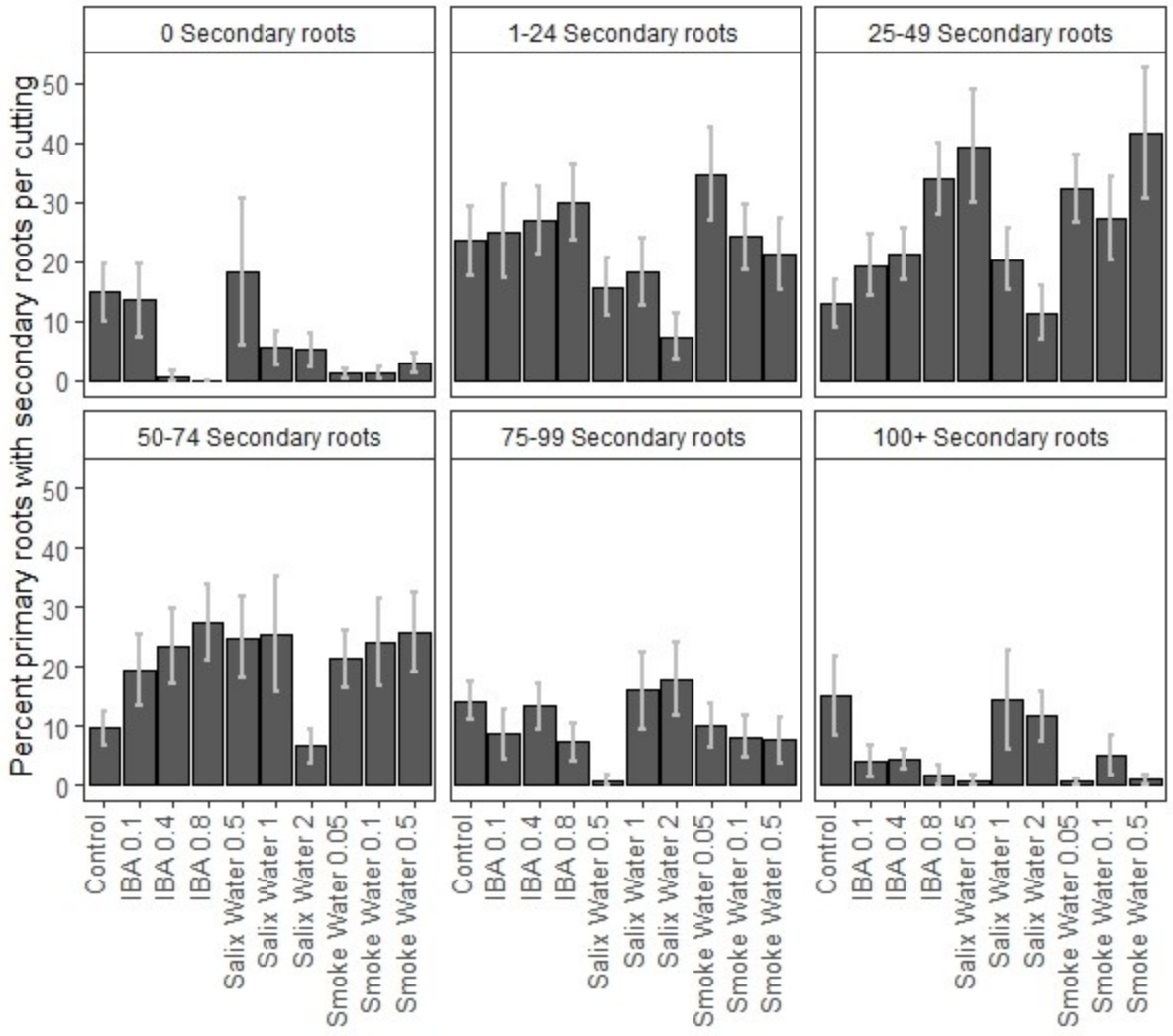

Figure 3.4. Percent of fall *Salix* ssp. primary roots with secondary roots per cutting in experiment 2 with secondary roots in different secondary root categories by treatment (x axis) with standard error. All cuttings are present in each root category. Each bar is n = 10 (all rooted cuttings are represented in each secondary root box).

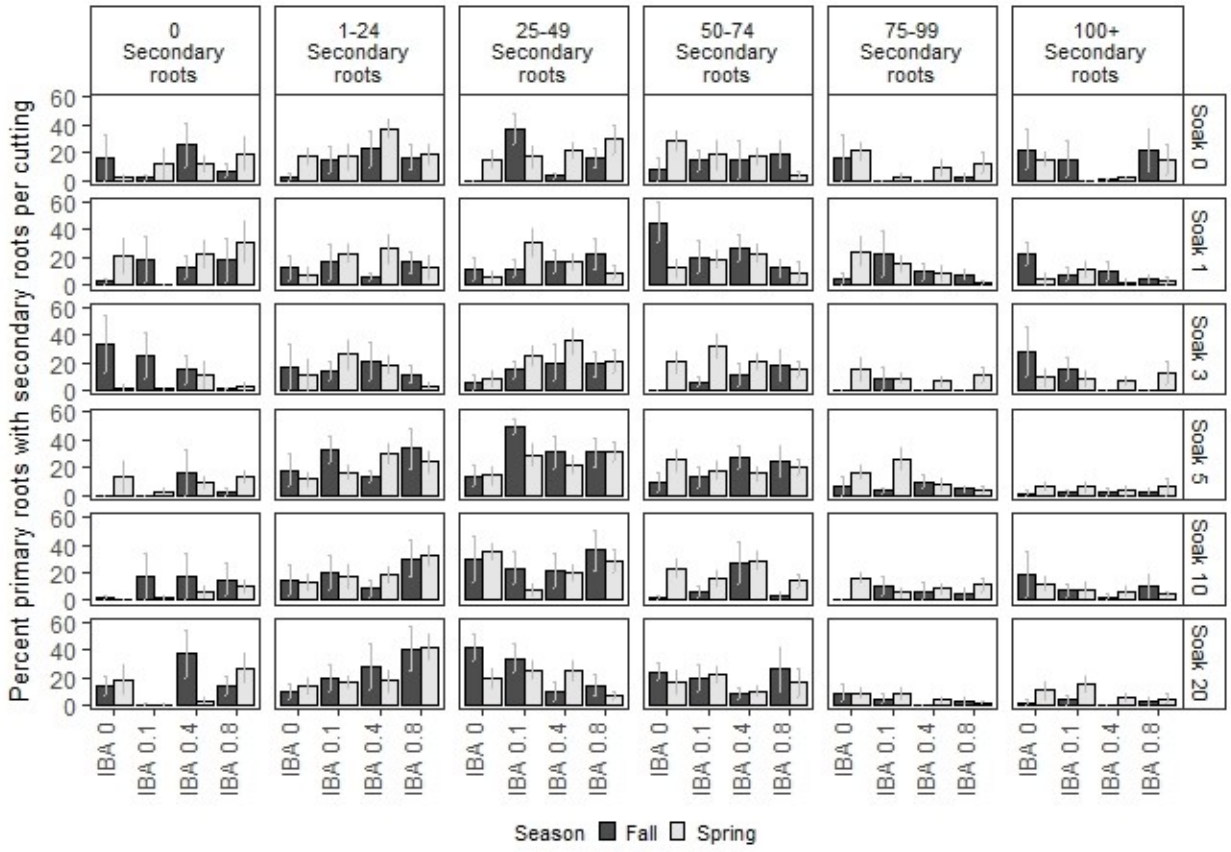

Figure 3.5. Percent of fall and spring *Salix* ssp. primary roots with secondary roots per cutting in different secondary root categories (vertical panels) in experiment 1 by IBA concentration (%) (x axis) and soaking time (days) (horizontal panels) with standard error. All cuttings are present in each secondary root category (vertical panel). Each bar is n = 6 (fall) and n = 9 (spring).

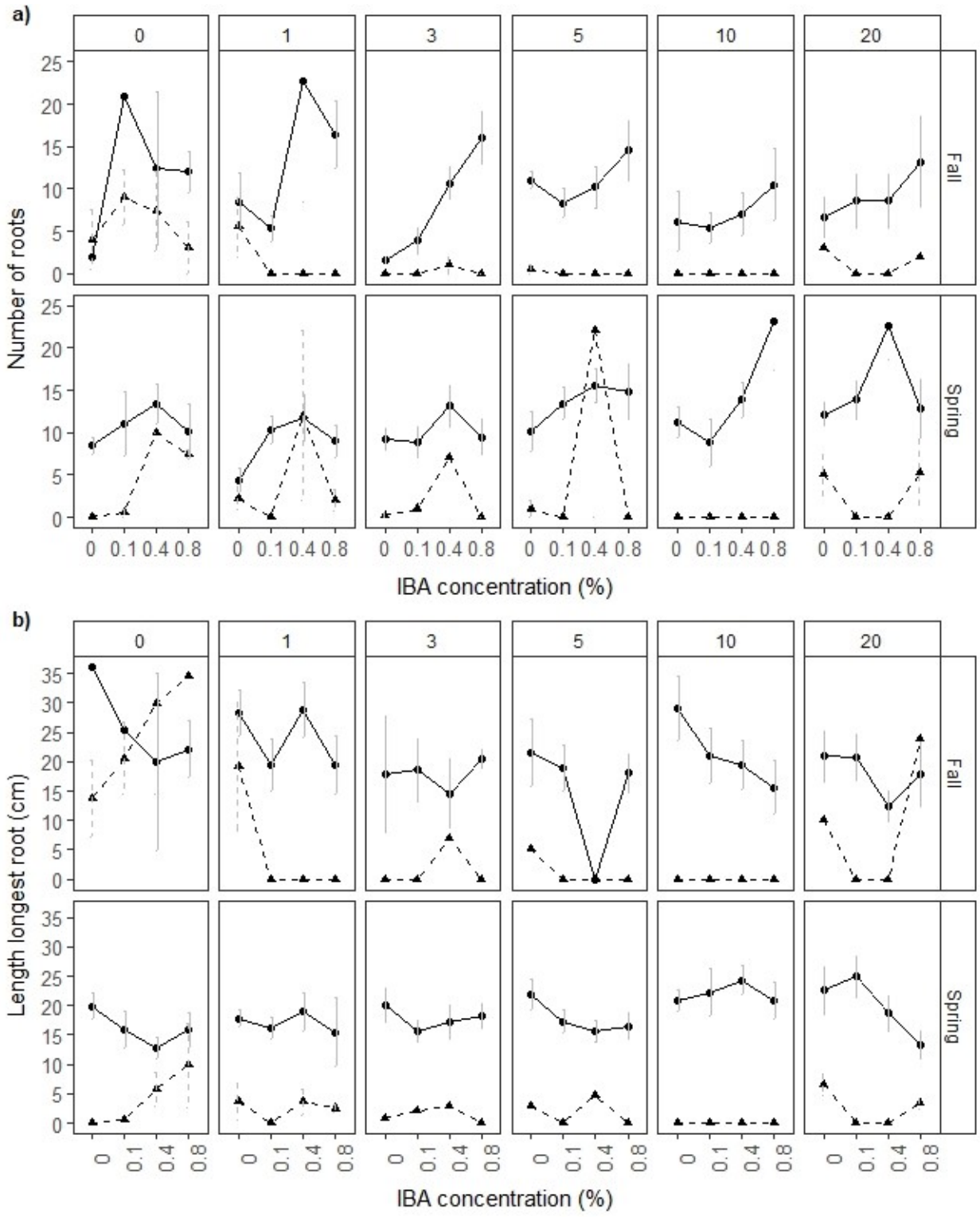

Figure 3.6. Number of roots (a) and length longest root (b) with standard error at day 60 for all *Salix* ssp. cuttings in experiment 1 that had callus (solid line) and did not callus (dashed line) by IBA concentration (%) (x axis), season (horizontal panels), and soaking time (days) (vertical panels).

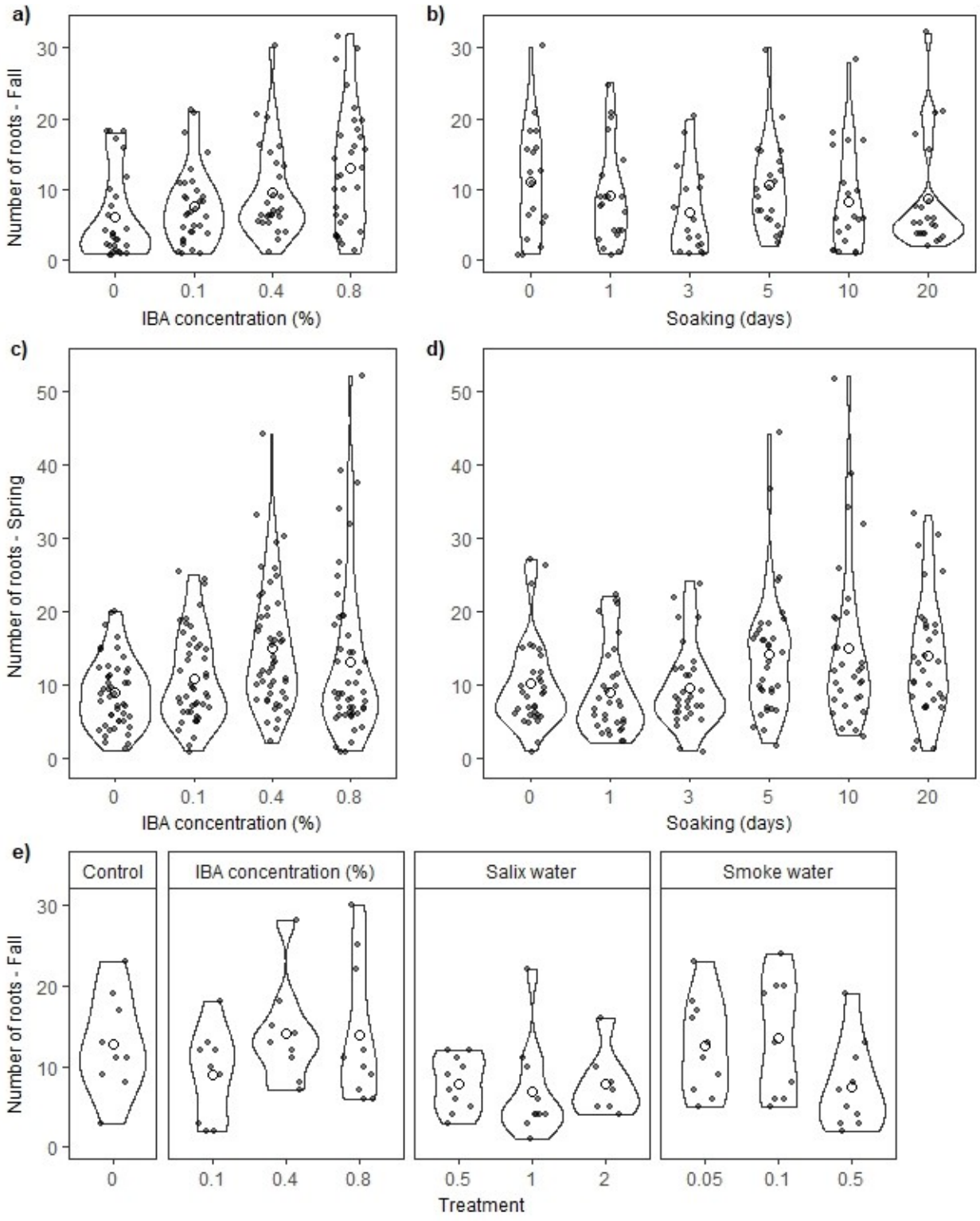

Figure 3.7. Violin and jitter plots for number of roots in fall (a, b, e) and spring (c, d) on rooted *Salix* ssp. cuttings from experiment 1 for IBA concentration (%) (a, c), soaking time (days) (b, d), and from experiment 2 by treatment (e). Closed circles represent individual roots, open circles represent treatment means. Each closed circle in the jitter plot had a small value (between 0 and 0.2) added to the value on the x axis to visually separate points. Black lines for each violin plot use density curves to show data distribution, with wider areas having higher frequency of data points than narrower areas.

Table S3.1. Treatments, replication, and planting containers for experiments (Exp) 1 and 2 in different seasons.

Species	Exp	Season	Treatment				Reps per treat[2]	Pots per treat[3]	Cuttings per species	Pot size (cm)
			Soak (d)	IBA (%)	Salix water	Smoke water				
Salix ssp.	1	Summer	0, 1, 3, 5, 10, 20	0, 0.1, 0.8			3	1	54	10x10x10
	1	Fall	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			6	2	144	10x10x10
	1	Spring	0, 1, 3, 5, 10, 20	0, 0.1, 0.4, 0.8			9	3	216	10x10x10
	2	Fall		0, 0.1, 0.4, 0.8	0.5, 1, 2	0.05, 0.1, 0.5	10	10	100	10x3x3

[1] Number of replicate cuttings per treatment
[2] Number of pots per treatment

Table S3.2. Summary statistics for maximum (max) and mean number of roots and longest root length for *Salix* ssp. cuttings in experiments (Exp) 1 and 2 at different times of year. SE = standard error. NR = no roots.

Species	Exp	Season	Percent rooting ± SE	Max # roots	Mean # roots (all cuttings) ± SE	Mean # roots (rooted cuttings) ± SE	Max length (cm)	Mean length (cm) ± SE	n rooted	n planted
Salix ssp.	1	Summer	29.6 (0.1)	9	0.9 (0.3)	3.1 (0.6)	55.5	13.5 (4.6)	16	54
		Fall	83.3 (0.0)	80	8.1 (0.8)	9.7 9 (0.9)	45.6	19.9 (1.0)	120	144
		Spring	88.0 (0.0)	52	10.5 (0.6)	11.9 (0.6)	41.0	17.0 (0.6)	190	216
	2	Fall	93.9 (0.0)	30	9.9 (0.7)	10.5 (0.7)	42.4	23.0 (0.9)	93	100

Table S3.3. Number of roots and longest root length for *Salix* ssp. cuttings separated by treatment (IBA concentration (%), soaking time (day), *Salix* water extract, smoke water extract) in fall and spring in experiments 1 and 2. Maximum (max) and minimum (min) number of roots and length of roots on second line in brackets.

Treatment	Number roots ± SE (max/min)		Length longest root (cm) ± SE (max/min)		N	
Experiment 1						
	Fall	Spring	Fall	Spring	Fall	Spring
IBA %						
0	6.1±1.1 (18/1)	8.9±0.7 (20/1)	21.3±2.5 (42.0/0.1)	18.5±1.2 (33.7/0.6)	28	47
0.1	7.7±1.0 (21/1)	10.8±0.9 (25/1)	20.0±1.7 (38.0/ 0.1)	17.8±1.2 (41.0/0.6)	32	46
0.4	9.5±1.2 (30/1)	14.9±1.2 (44/2)	19.0±2.4 (45.6/2.5)	16.4±1.2 (33.0/1.3)	28	49
0.8	12.9±1.5 (32/1)	13.0±1.6 (52/1)	19.3±1.7 (34.5/2.5)	15.3± (32.0/1.8)	31	48
Soaking (day)						
0	11.2±1.9 (30/1)	10.1±1.1 (27/1)	22.6±2.9 (45.0/0.6)	14.9±1.3 (29.5/0.6)	18	33
1	9.1±1.5 (25/1)	8.9±1.1 (22/2)	23.1±2.4 (45.6/0.1)	14.5±1.5 (32.0/0.6)	21	31
3	6.7±1.5 (20/1)	9.6±1.0 (24/1)	17.3±3.3 (42.0/0.1)	15.9±1.4 (31/0.8)	17	30
5	10.6±1.4 (30/2)	14.1±1.5 (44/2)	17.7±2.3 (43.3/2.5)	16.9±1.2 (31.5/2.9)	21	34
10	8.4±1.7 (28/1)	15.0±2.0 (52/3)	20.6±2.4 (40.4/4.8)	22.0±1.4 (33.0/6.6)	20	31
20	8.6±1.7 (32/2)	13.8±1.5 (33/1)	17.9±1.9 (31.6/2.9)	17.8±1.9 (41.0/2.3)	22	31
Experiment 2						
Control	12.7±2.0 (23/3)		23.8±2.2 (36.3/14.2)		9	
IBA						
0.1	9.0±1.9 (18/2)		17.5±3.1 (33.8/2.9)		9	
0.4	14.0±2.1 (28/7)		25.5±2.0 (37.2/19.0)		9	
0.8	13.8±2.7 (30/6)		23.0±2.7 (41.8/11.5)		10	
Salix water						
0.5	7.9±1.1 (12/3)		19.2±3.8 (42.1/4.0)		10	
1	6.9±1.9 (22/1)		26.2±3.1 (40.8/8.9)		10	
2	7.9±1.6 (16/4)		26.2±4.9 (42.4/2.2)		7	
Smoke water						
0.05	12.5±1.9 (23/5)		20.1±2.1 (33.0/11.3)		10	
0.1	13.4±2.5 (24/5)		30.7±2.1 (38.0/20.2)		9	
0.5	7.5±1.7 (19/2)		19.6±1.9 (28.5/12.9)		10	

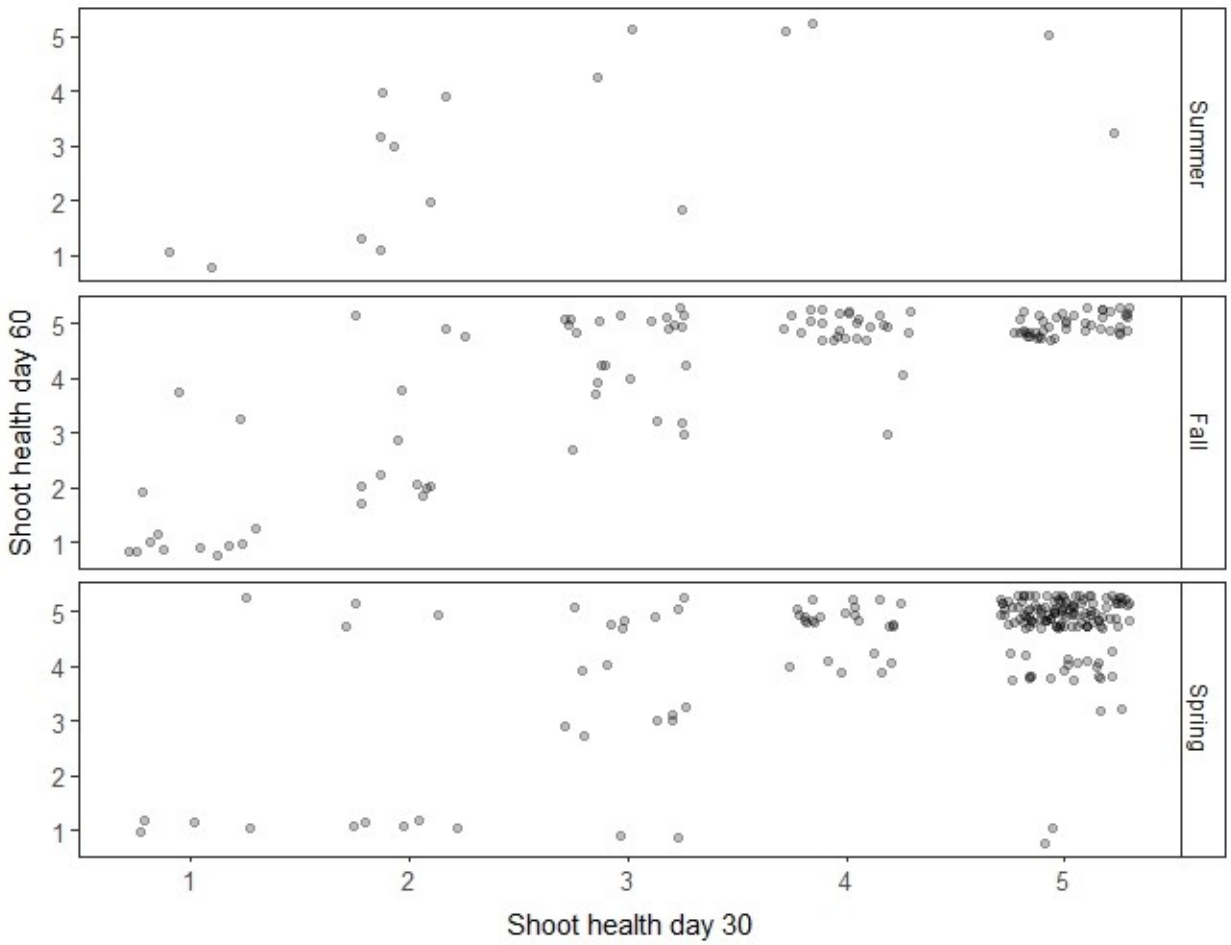

Figure S3.1. Jitter plot for correlation between shoot health at day 60 and shoot health at day 30 for rooted *Salix* ssp. cuttings in summer, fall, and spring in experiment 1. Each point in a jitter plot had a small value (between 0 and 0.3) added to both values on x and y axes to visually separate points.

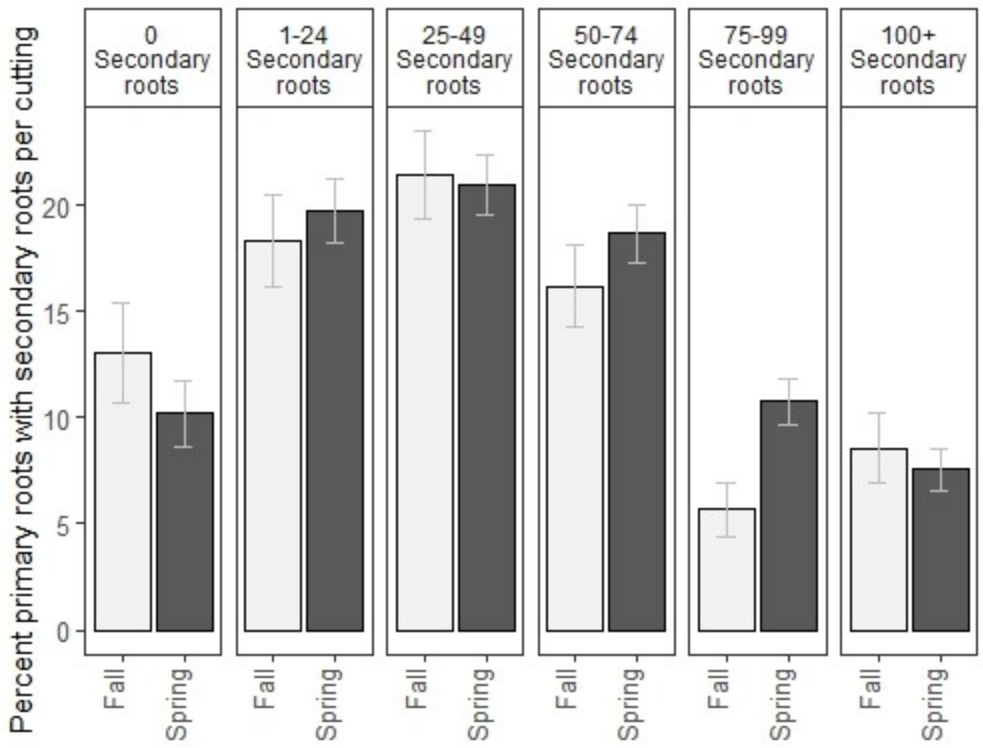

Figure S3.2. Percent of *Salix* ssp. cuttings with standard error in experiment 1 with secondary roots in different categories (vertical panels) in different seasons (x-axis). Fall bars are n = 120, spring bars are n = 190.

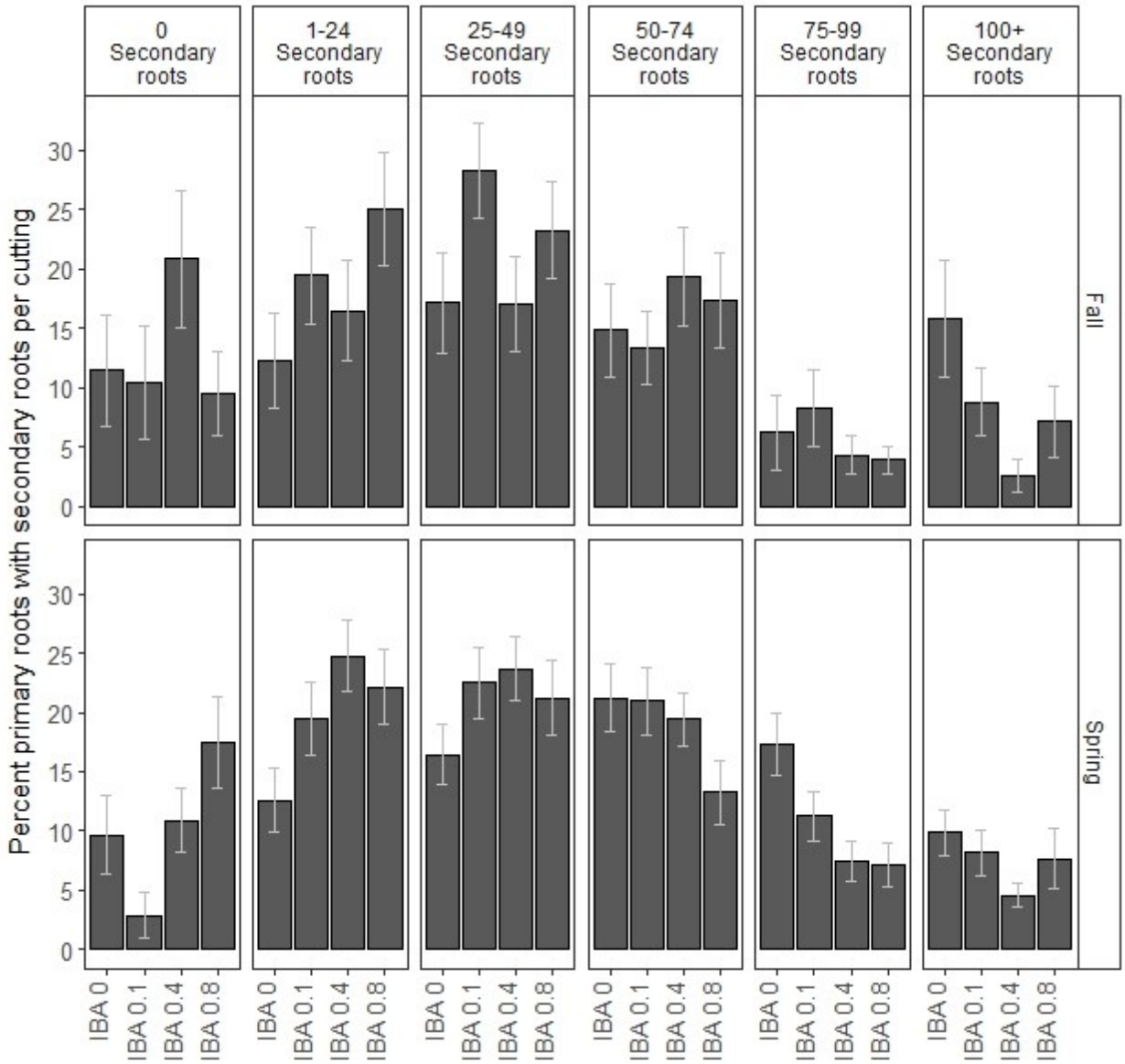

Figure S3.3. Percent of *Salix* ssp. cuttings with standard error in experiment 1 with secondary roots in different categories (vertical panels) by IBA concentration (%) (x axis) in different seasons (horizontal panels). Fall bars are n = 36 and spring bars are n = 54.

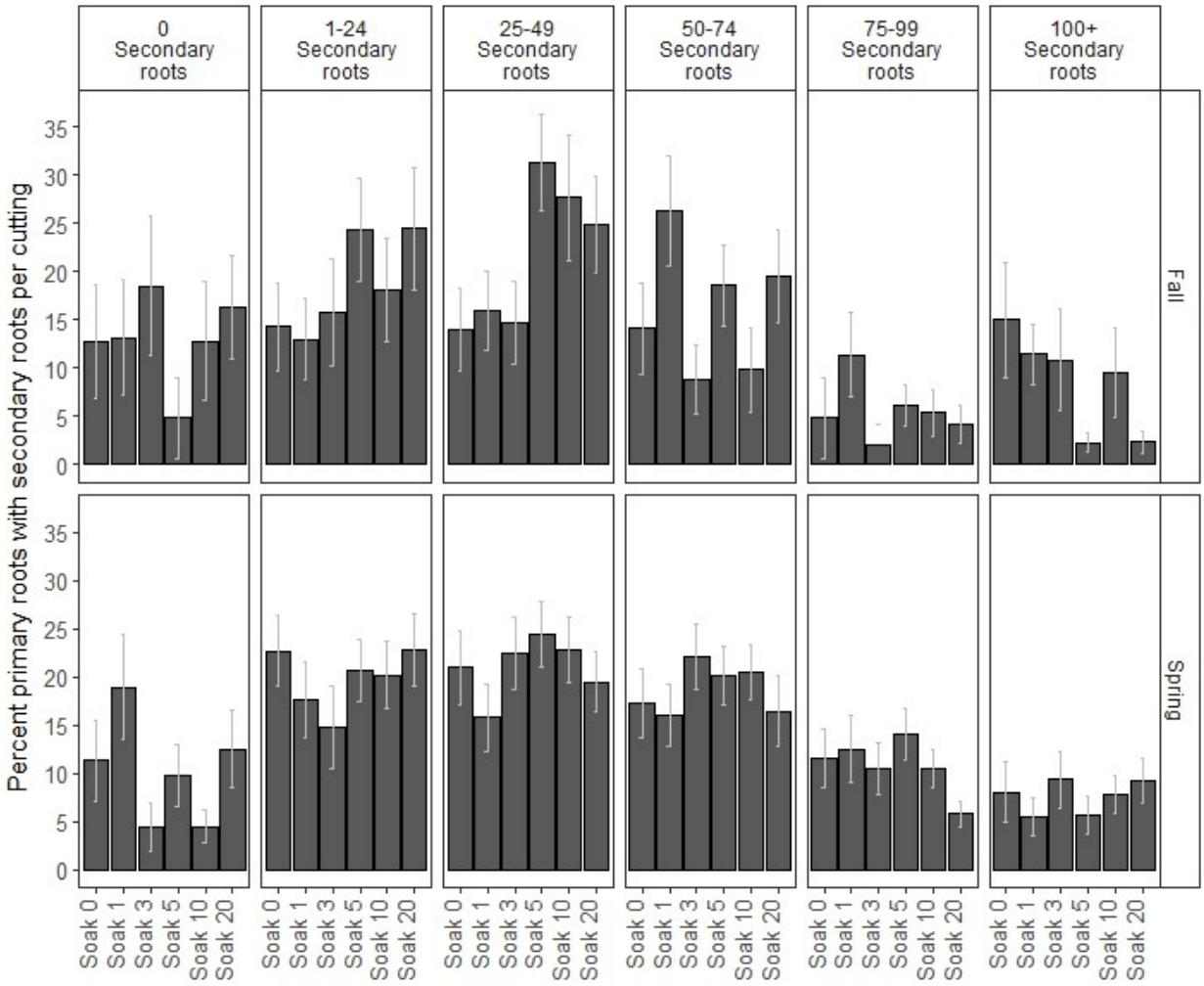

Figure S3.4. Percent of *Salix* ssp. cuttings with standard error in experiment 1 with secondary roots in different categories (vertical panels) by soaking time (days) (x axis) in different seasons (horizontal panels). Fall bars are n = 24 and spring bars are n = 36.

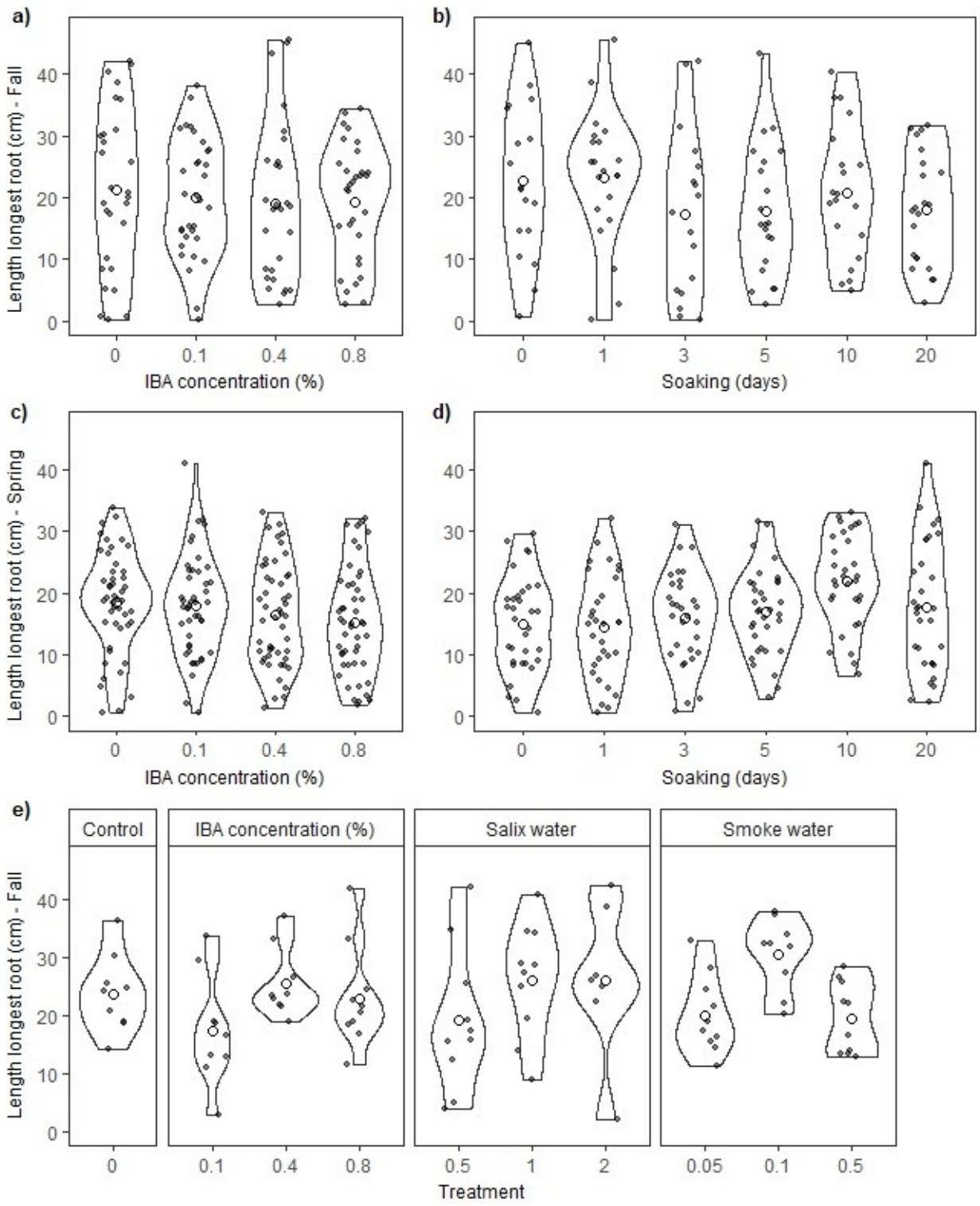

Figure S3.5. Violin and jitter plots for longest root length (cm) in fall (a, b, e) and spring (c, d) on rooted *Salix* ssp. cuttings from experiment 1 for IBA concentration (%) (a, c), soaking time (days) (b, d), and from experiment 2 by treatment (e). Closed circles represent individual roots, open circles represent treatment means. Each closed circle in the jitter plot had a small value (between 0 and 0.2) added to the value on the x axis to visually separate points. Black lines for each violin plot use density curves to show the data distribution, with wider areas having a higher frequency of data points than narrower areas.

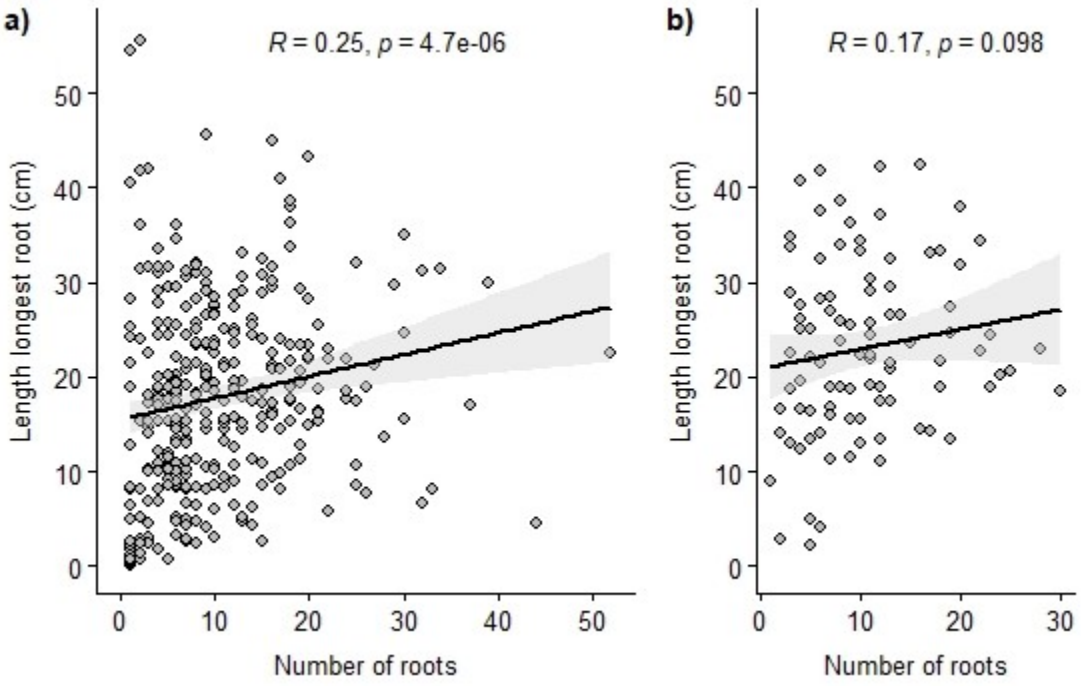

Figure S3.6. Correlation between number of roots and longest root length for rooted *Salix* ssp. cuttings in experiment 1 a) (n = 326) and experiment 2 b) (n = 100).

IV. ASSISTED DISPERSAL AND RETENTION OF LICHEN BIOCRUST MATERIAL FOR NORTHERN RECLAMATION

1. INTRODUCTION

Resource extraction by mining and oil and gas companies leaves large environmental footprints, and continues to expand in Canada's north. Diamond mining creates vast piles of crushed rock and processed kimberlite, leaving previously vegetated areas exposed to wind and water erosion and unable to support the unique, native tundra species (Rausch and Kershaw 2007). To restore ecological function to these environments when they are disturbed, reclamation either by natural or assisted revegetation is needed for dominant communities including shrub-heath species (Ficko and Naeth 2021) and biological soil crusts (biocrusts).

Biocrusts are complex communities of poikilohydric organisms such as algae, bacteria, cyanobacteria, fungi, lichens, liverworts, and mosses, that form a thin horizontal layer in association with the top few centimetres of the soil surface (Eldridge and Greene 1994, Belnap and Lange 2003, Belnap et al. 2016). Biocrusts may be pioneer communities in primary and secondary succession pathways or components of mature arid and semi-arid ecosystems, including polar environments, where they often have higher species diversity than vascular plants (Bowker 2007, Rosentreter et al. 2016, Wietrzyk-Pełka et al. 2021). Biocrusts reduce soil erosion and increase soil stability, modify infiltration and soil water retention, create habitat for soil invertebrates, alter seedling establishment and plant productivity, and increase soil fertility and nutrient cycling (West 1990, Eldridge and Greene 1994, Belnap and Lange 2003, Weber et al. 2016). In boreal and tundra environments, biocrusts can form mats of fruticose lichens, contributing a significant portion of the winter diet of caribou which are hunted or farmed by many northerners (Ahti 1977, Thomas and Hervieux 1986, Kumpula 2001).

Biocrusts are sensitive to trampling, grazing, mining, pipeline construction, climate change, invasive species, and fire (Eldridge and Greene 1994, Harper and Kershaw 1996, Ferrenberg et al. 2015, Weber et al. 2016b). Biocrust disturbances can affect terrestrial biogeochemical cycling, which can cause long term changes in local (potentially global) ecosystems (Jandt et al. 2008, Ferrenberg et al. 2015, 2017). Despite their importance, few studies on northern biocrust restoration exist, perhaps because biocrusts are perceived to recover unassisted from disturbance (Bowker 2007). However, linear extrapolations of short term studies show recovery times from as little as six years to as long as millennia in the harshest environments (Weber et al. 2016a). Kidron et al. (2020) suggested that most types of crusts can recover within

20 years following disturbance, unless abiotic factors such as soil recovery are also necessary following disturbance, in which case recovery may take thousands of years.

Potential factors affecting succession and recovery of biocrusts include type and extent of disturbance, likelihood of further disturbances or threats to establishment, proximity to inoculating material, reproductive strategies of component species, environmental conditions, and habitat and substrate including soil type, soil stability, and soil texture (Eldridge and Greene 1994, Belnap and Eldridge 2001, Smith 2014). While lichens, bryophytes, and algae can reproduce by sexual diaspores, asexual reproduction by fragmentation and vegetative diaspores is more common for many species (Bowler and Rundel 1975, Vitt et al. 1988, Brodo et al. 2001, Root and Dodson 2016). Assisted recovery must address propagule scarcity (inoculation), resource limitations (resource augmentation), and actively eroding soils (artificial soil stabilization, Bowker 2007), with the latter two interventions recently referred to as habitat ameliorations (Antoninka et al. 2020a, Bowker et al. 2020). For large disturbances such as mine sites, substrate composition, limited resources for revegetation, propagule scarcity, especially for internal areas far from undisturbed vegetation sources, and high transportation costs are key reclamation barriers.

Interest in assisted biocrust establishment using single or multiple biocrust species has recently increased, often to restore ecological benefits (Pointing and Belnap 2012, Bu et al. 2013, Zhao et al. 2016a, Antoninka et al. 2018). No known research addresses propagation and dispersal of lichen biocrusts for reclamation in arctic tundra, although studies assessed assisted dispersal of lichens in other ecosystems (reviewed in Smith 2014) including reindeer husbandry (Roturier et al. 2007, Roturier and Bergsten 2009), endangered species conservation (Lidén et al. 2004), lichen biodiversity maintenance in managed forests (Sillett and McCune 1998, Hazell and Gustafsson 1999, Hilmo 2002), and reclamation (Duncan 2011, Gypser et al. 2015, Ballesteros et al. 2017, Lorite et al. 2020). Inoculation with field collected, mixed species biocrust material accelerated recovery on disturbed soils, with higher species coverage and diversity, chlorophyll content, and improved soil properties (Belnap 1993, Scarlett 1994, Bowler 1999, Maestre et al. 2006, Xiao et al. 2008, Chiquoine et al. 2016, Antoninka et al. 2018, Bowker et al. 2020). Given increasing northern resource exploration and extraction, further evaluation of inoculation techniques and methods to assess recovery and restore crusts to severely disturbed areas in remote field locations are needed.

In this study we began to redress that knowledge gap, using biocrust material collected in a tundra ecosystem at Diavik Diamond Mine Inc., Northwest Territories, Canada. We hypothesized that substrate, inoculation, habitat amelioration, and containment techniques would enhance northern biocrust reclamation. We evaluated the impact of i) available substrates from

mining by-products (crushed rock, lake sediment, processed kimberlite), ii) dry and wet (slurry) inoculant dispersal to introduce propagules, iii) habitat amelioration techniques to enhance inoculant retention and establishment (erosion control blanket, tundra soil, woody debris), and iv) containment (jute mat) on biocrust establishment. We assessed cover, species richness, and species composition changes over three field seasons after biocrust inoculation.

2. MATERIALS AND METHODS

2.1. Research Site Description

Diavik Diamond Mine is located on an island in Lac-de-Gras, 320 km northeast of Yellowknife, Northwest Territories (64º30´41´´ N, 110º17´23´´ W), approximately 100 km north of the treeline. Lac-de-Gras is in the Southern Arctic Ecozone, and the Point Upland Arctic Ecoregion (Ecosystem Classification Group 2012), with mean annual precipitation 285 mm (over half snow) and mean annual temperature -9 ºC, from 2011 to 2016. In upland areas, turbic and static cryosolic soils dominate (Drozdowski et al. 2012), with dwarf heath shrubs, including *Arctous rubra* (Rehder & Wilson) Fernald (red bearberry), *Betula glandulosa* Michx. (bog birch), *Empetrum nigrum* L. (crowberry), *Kalmia procumbens* (L.) Gift & Kron (alpine azalea), *Rhododendron tomentosum* Harmaja (marsh Labrador tea), *Salix* sp. (willow), *Vaccinium uliginosum* L. (bog bilberry) and *Vaccinium vitis-idaea*) L. (bog cranberry), and lichen dominated biocrust communities.

Northern biocrust species diversity often exceeds vascular plant diversity. Approximately 360 lichen species are documented for the Northwest Territories (Goward and Björk 2012), with over 50 macro-lichen species identified at Diavik during the course of the research at that site (Ficko, unpublished). Dominant lichens included *Alectoria ochroleuca* (Hoffm.) A. Massal., *Bryocaulon divergens* (Ach.) Kärnefelt, *Bryoria nitidula* (Th. Fr.) Brodo & D. Hawksw., *Cetraria* Ach. sp., *Cladonia* P. Browne sp. (cupped species, reindeer lichens), *Dactylina arctica* (Hooker f.) Nyl., *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell, *Flavocetraria nivalis* (L.) Kärnefelt & A. Thell, *Gowardia nigricans* (Ach.) P. Halonen, L. Myllys, S. Velmala, & H. Hyvärinen, *Masonhalea richardsonii* (Hooker) Kärnefelt, *Melanelia* stygia (L.) Essl., *Parmelia* Ach. sp., *Sphaerophorus globosus* (Hudson) Vainio, *Stereocaulon* Hoffm. sp., and *Thamnolia vermicularis* (Sw.) Ach. Ex Schaerer. Taxonomy follows Esslinger (2019). Eighteen species of mosses (Lamarre 2016) and three liverworts were present at Diavik. Other biocrust taxa were not characterized in this study.

2.2. Experimental Design And Treatments

A split-split-plot experimental design embodied four crossed factors. There were three substrates (crushed rock, lake sediment, processed kimberlite) x three inoculation treatments (dry, slurry, none) x four habitat amelioration treatments (erosion control blanket, tundra soil, woody debris, none) x two containment treatments (jute mat, none; Figure 4.1).

Three blocks of raised gravel beds of crushed granite waste rock had been established in 2008 on natural eskers and were re-mixed with an excavator to loosen compact soil and remove any vegetation prior to our research. Each block was divided into three equal sized main plots, which randomly received one of three mine waste materials as substrate; crushed rock (no substrate over gravel bed), lake sediment (from mining pits after diking and water pumping), or fine processed kimberlite (released as slurry, then dried). Crushed rock (particle size < 1 mm to < 50 cm) contained the largest portion of coarse fragments, followed by lake sediment (particle size < 1 mm to < 30 cm), then processed kimberlite (particle size < 1 mm). Processed kimberlite had highest sand content; lake sediment had greatest silt and clay (Miller et al. 2021).

Fifteen 24 m^2 sub-plots were established in main plots in the available space around other research program plots (five replicates per substrate). These sub-plots were divided into 1 x 1 m sub-sub-plots to accommodate 24 combinations of inoculation, habitat amelioration, and containment treatments, which were randomly allocated and applied to a 50 x 50 cm quadrat in the centre of each sub-sub-plot. Thus there were 360 sub-sub-plots (24 treatment combinations x 3 substrates x 5 replicates).

Habitat amelioration and containment treatments were used to assess common techniques for vascular plant revegetation. Jute mat is often used to prevent erosion, retain moisture, and suppress weeds. Jute mat was considered a containment treatment as it was placed on top of other treatments. Coconut fibre erosion control blankets and jute mat were obtained from Cascade Geotechnical Inc. and cut into 60 x 60 cm squares. Erosion control blankets and jute mat were anchored by a border of rocks; this rock border was placed around all plots for consistency.

Tundra soil was collected from an unmined area at Diavik. A mix of mineral soil and humus soil was collected to a depth of 10 to 15 cm. Soil was mixed on a tarp using shovels to increase homogeneity. Large clods were broken into smaller pieces. Each soil treatment received approximately 3 L of soil evenly spread to a depth of 1 cm.

Woody debris was collected from tundra surrounding the plots. Cuttings were collected from *Betula glandulosa, Empetrum nigrum,* and *Rhododendron tomentosum*, 5 to 45 cm long. A mix of all three species was spread on each plot. Small handfuls of substrate material were placed

on top of cuttings to help prevent litter movement. Approximately 75 % cover was achieved using cuttings as leaves were present.

Biocrust samples were collected with a trowel from the same area as tundra soil by removing 1 to 2 cm deep patches with visible macro-lichens where the crust naturally split when disturbed. Material was air dried and sieved (1 cm grid) to increase propagule number from donor thalli using the natural fragmentation capacity of lichens. Sieved material (28,200 g) was hand mixed in large bins to create a homogenous mixture of species which was placed in paper bags and stored at 4 °C prior to dispersal on July 1 to 2. Baseline inoculation species richness was determined from 10 % of bags.

Inoculation treatments mimicked natural vegetative fragment dispersal and common revegetation techniques for seeding. Dry placement material was dispersed by evenly scattering 100 g of sieved lichen dominated biocrust in a thin layer across the surface of each sub-sub-plot. Slurries were prepared by mixing 100 g of sieved biocrust material with 1 L of untreated lake water. After 5 min the slurry was poured as evenly as possible across the sub-sub-plot. Material in large clumps was gently spread with a hand rake evenly across the surface. Biocrust material was spread on top of erosion control blanket, tundra soil, woody debris, and unamended sub-sub-plots. Jute mat was placed on top of each applicable sub-sub-plot.

2.3. Biocrust Assessment

Non-destructive assessment of macro-lichens allowed for multi-year monitoring of sub-sub-plots. While cyanobacteria and algae are frequently early colonizers of disturbed plots and have frequently been used in biocrust assessment, we focused specifically on whether macro-lichens can be used in land reclamation, as they are dominant, visible species in the mature tundra communities.

Sub-sub-plots were visually assessed during the third week of August in years 1 (1 month after set up), 2, and 3 (2014-2016) of the research. Each sub-sub-plot was monitored for presence or absence of bryophytes and 14 species, genus, and/or morphology of lichens (hereafter lichens), including *Cetraria*, cupped *Cladonia,* reindeer *Cladonia* (previously genus *Cladina*), wand *Cladonia*, *Dactylina*, *Flavocetraria cucullata, Flavocetraria nivalis,* foliose lichens, brown hair lichens, yellow hair lichens, *Masonhalea richardsonii, Sphaerophorus, Stereocaulon,* and *Thamnolia vermicularis*, to determine species richness. Nadir pictures were taken of each sub-sub-plot at 100 cm height with a manual focus digital camera. A coloured toothpick marked the north facing corner of each plot, and a 30 cm ruler lined up with the toothpick each year to show scale. In year 3, total cover was assessed for each sub-sub-plot, and lichens were further

quantified into four categories: none, tiny (1 to 4 fragments), some (5 to 19 fragments), or lots (greater than 20 fragments).

2.4. Statistical Analyses

Responses to treatment effects for year 3 data for species richness and cover were analyzed using mixed effect models (Proc Mixed) in SAS 9.4 (SAS Institute Inc 2013). Data for no lichen inoculation treatments were removed prior to modelling as they had a mean cover of less than 1, and residuals were markedly smaller than those of any other treatment. Optimization of models was assessed using the AICc. Substrate, lichen dispersal technique, habitat amelioration, containment treatments, and all two way, three way, and four way interactions among them were designated fixed effects in the models. Substrates were randomly applied to plots on three blocks, and then subdivided into sub-plots prior to application of treatments. For species richness, heterogenous residuals for substrate and habitat amelioration were included in the final model used to determine p-values for fixed effects, along with block and block x substrate as random effects. For cover, heterogenous residuals for substrate and amendment were included in the final model with block, block x substrate, and sub-plot included as random effects. Pre-planned orthogonal contrasts were conducted for significant main effects ($p \leq 0.05$) and adjusted for interactions by comparing relevant pairs of experimental variables for species richness and cover, respectively. Measurements are presented as means ± 1 standard error.

Year 3 biocrust species composition was visualized using NMDS ordinations with Bray-Curtis dissimilarity indices using the metaMDS function in the R vegan package (Oksanen et al. 2020) and with a Sorenson distance matrix in PC-ORD (McCune and Mefford 2016). After removing no lichen inoculation treatments, dry and slurry treatments were combined as they were not different in univariate analyses. A two-dimension solution was consistently indicated as having lowest stress so we solved for the best solution. Points (sub-sub-plots) and vectors (percent cover, species richness) were made using ggplot2 package in R (Wickham 2016). Ellipses were made using stat_ellipse function in ggplot2, and represent 70 % of the data. To determine differences between treatment groups, we used the adonis function in the vegan package to calculate Permuational Analysis of Variance (PerMANOVA, 9,999 permutations) with Bray-Curtis distance matrix, permuted within block. Pair-wise comparisons with a holm adjustment for multiple comparisons were conducted using pairwise.perm.manova function in the RVAideMemoire package in R (Hervé 2021). As PerMANOVA cannot distinguish between differences in centroid location or dispersion, we tested differences in beta-diversity between treatment groups using Betadisper function in the vegan package by examining homogeneity of group dispersions with

spatial medians as the group centroid for different treatments. Pair-wise comparisons within each treatment were conducted with a Tukey post hoc test, adjusted for multiple comparisons. Negative eigenvalues in Betadisper were corrected by the Lingoes method (Legendre and Anderson 1999).

Change in individual species presence was calculated by subtracting probability of presence in year 2 from year 3, and was presented graphically using ggplot2. Differences with year 1 data were not included as assessments were only done by one person rather than two people as in years 2 and 3. For pictographic analysis, photos were cropped and edited to enhance colour contrast and minimize shadows. A 15 x 15 grid (225 points) in SamplePoint (Booth et al. 2006) was overlaid on top of each picture to identify lichen species, litter, or substrate manually at each point. As the distance of 1 m above the sub-sub-plots did not provide sufficient focus to clearly identify biocrust material to species or from non-biocrust material for analysis of cover, and could not be compared to field measurements, those results are not discussed further.

3. RESULTS

3.1. Inoculation

In year 3, lichens were detected on 100 % of inoculated plots and 70 % of uninoculated plots. Species richness in inoculated plots (n = 240) was 13.4 ± 0.1 with a maximum of 15 species, relative to 1.9 ± 0.2 with a maximum of 9 for uninoculated plots (n = 120), and initial species richness of 14.8 ± 0.1 (calculated from 10 % of material in inoculant sample bags). Cover for inoculated plots was 9.9 ± 0.6 across all treatments, and < 1 (maximum 2) on uninoculated plots.

Lichen dispersal (dry vs wet slurry) did not significantly impact species richness or cover after uninoculated plots were removed from year 3 data analysis (Table 4.1, Figures 4.2, 4.3). A significant three way interaction indicated greater cover with dry inoculant than with slurry on lake sediment with containment; slurry inoculant on lake sediment without containment had greater cover than dry inoculant. Change in individual species presence between years 2 and 3 showed greatest declines (up to 70 %) on processed kimberlite without containment and no habitat amelioration or tundra soil (Figure 4.4). *Cetraria*, *Dactylina, Flavocetraria cucullata, Flavocetraria nivalis*, *Stereocaulon*, *Thamnolia vermicularis*, and yellow hair species declined 50 to 70 % for some treatments; wand and cup *Cladonia* and bryophytes declined the least (maximum 11 %).

3.2. Substrate

Cover on crushed rock (mean 9.2 ± 0.9, maximum 35) and lake sediment (mean 7.9 ± 0.9, maximum 45) was greater than on processed kimberlite (mean 3.1 ± 0.4, maximum 20, Tables

4.1, S4.1) by year 3. Similarly, species richness was greater on crushed rock (14.3 ± 0.1) and lake sediment (13.9 ± 0.1) than on processed kimberlite (12.0 ± 0.3, Table S4.2).

A significant three way interaction occurred between substrate, habitat amelioration, and containment for cover and species richness, and between substrate, inoculation technique, and containment for cover (Table 4.1, Figures 4.2, 4.3). All plots on crushed rock had greater cover than on processed kimberlite, regardless of inoculation, containment, or habitat amelioration treatments, while species richness on crushed rock was generally greater than processed kimberlite regardless of habitat amelioration or containment treatments, except with erosion control blanket and containment (Tables S4.1, S4.2). Cover and species richness on lake sediment were either similar to crushed rock or an intermediary between crushed rock and processed kimberlite across habitat amelioration and containment treatments (except species richness for plots with no habitat amelioration and no containment was in between crushed rock

kimberlite had and processed kimberlite and significantly different from both), and across inoculation and containment treatments for cover.

Species composition and dispersion (beta-diversity, variance in multivariate space) were significantly different among substrates in year 3, except crushed rock and lake sediment only differed in species composition (Figure 4.5, Table 4.2). Crushed rock had the least variance of the three substrates, and was more strongly associated with greater cover, while processed the most dispersion.

3.3. Habitat Amelioration

Erosion control blanket was the most successful habitat amelioration treatment rather than tundra soil, the natural habitat for biocrusts, with greatest species richness (14.4 ± 0.1) and cover (16.9 ± 1.3) in year 3 (Figure 4.2). Erosion control blanket and woody debris had similar trends for species richness; however, woody debris had similar cover (5.7 ± 0.6) to no habitat amelioration (8.0 ± 1.0), as it was more difficult to detect lichen species under woody debris. No habitat amelioration and tundra soil had similar trends, with lower species richness and cover than erosion control blanket.

Three way interactions for substrate, habitat amelioration, and containment treatments were noted for species richness and cover (Table 4.1, Figures 4.2, 4.3). Species richness did not differ with habitat amelioration on each substrate with containment (Table S4.2). Cover for sub-sub-plots with containment was more variable depending on substrate and habitat amelioration treatment (Table S4.1). Erosion control blanket and containment always had greater cover than woody debris, while cover for no habitat amelioration and tundra soil varied with substrate.

Without containment, erosion control blanket treatments generally had greater species richness and cover than other habitat amelioration treatments on all substrates. Lichens were frequently observed clustered in dips on erosion control blanket with no containment. Erosion control blanket and woody debris had greater species richness than no habitat amelioration and tundra soil on crushed rock with no containment, while erosion control blanket > woody debris > tundra soil > no habitat amelioration on lake sediment or processed kimberlite with no containment.

Species composition was significantly different among habitat amelioration treatments, except between no habitat amelioration and tundra soil (Table 4.2, Figure 4.5). Erosion control blanket had the least variance, and was more highly associated with cover. No habitat amelioration and tundra soil had most dispersion, and were not significantly different from each other. Erosion control blanket versus woody debris, and woody debris versus tundra soil, differed in species abundance but not dispersion, while all other treatments differed in dispersion.

3.4. Containment

Containment often had more evenly distributed lichens and had greater cover and species richness than no containment. Species richness had more variability without containment. A three-way interaction between substrate, habitat amelioration, and containment was significant for species richness and cover, and between substrate, inoculation technique, and containment for cover (Table 4.1, Figures 4.2, 4.3). Containment on lake sediment with dry inoculant had greater cover than no containment (Table S4.1). However, with containment and woody debris, it was often visually challenging to detect lichens.

Species composition and dispersion were significantly different with and without containment in year 3 (Table 4.2, Figure 4.5). Containment had less variance in dispersion than no containment, and was more highly associated with greater species richness.

4. DISCUSSION

4.1. Inoculation To Optimize Biocrust Establishment

Our study is the first to demonstrate effective inoculation with lichen dominated biocrust material on mining by-products at a disturbed site in the arctic over three field seasons. The persistence of lichens on all substrates, and decreased presence of some species by year 3 is similar to results from other locations and disturbances. In a more southern location, Belnap (1993) found inoculated plots had significantly greater species richness and cover than uninoculated plots at four sites in Utah after two to five years, although values were significantly

lower than undisturbed control sites. Chiquoine et al. (2016) found inoculation with biocrust material was the only treatment to restore moss and lichen species to abandoned road surfaces after 18 months. Antoninka et al. (2018) found greater initial cover with inoculation than without in two field experiments, with convergence after 12 or 26 months indicating natural recovery could occur. However, inoculated plots had greater cover of late successional species and species richness after six months, and higher soil aggregate stability, indicating the value of inoculation to accelerate restoration of ecosystem functions by biocrusts.

Proximity to undisturbed crusts has been considered important for natural recovery of disturbed areas (Belnap 1993, Bowker 2007, Weber et al. 2016a, Antoninka et al. 2018). Our results show that inoculation significantly increased species richness and cover relative to uninoculated plots, indicating the importance of assisted reclamation to accelerate biocrust establishment in the north. Lichens on uninoculated sub-sub-plots likely blew in from adjacent sub-sub-plots rather than from the tundra surrounding the experimental areas, as lichen fragments similar to sieved pieces were observed blowing between sub-sub-plots in the field, and spray painted lichen fragments were observed up to 10 m away from plots in the predominant wind direction after 24 hours (Ficko, unpublished).

We expected slurry dispersal would have had the best response, as lichens are only metabolically active when wet (Lange 2001, Lange et al. 2001, Rajeev et al. 2013). Being wet during dispersal may have had a priming effect, as lichens would have been heavier, softer, and more likely to settle into habitat ameliorants, hooking into the substrate as they changed shape with drying. Lack of differences between inoculation treatments may result from saturation with water hindering photosynthesis during establishment as thallus saturation slows absorption and movement of O_2 and CO_2 (Cowan et al. 1992, Lange et al. 2001). Saturation would have had a greater impact on species in our study, as most lichens were green algal dominants, which have a low threshold for water and can often start photosynthesizing from dew or high ambient humidity (Lange et al. 1994, reviewed in Nash 1996). Similarly, Antoninka et al. (2020) found watering biocrust inoculant during application did not significantly increase establishment, but noted above average rain and snow throughout their experiment. Maestre et al. (2006) found microcosms inoculated with biocrust slurry and composted sewage sludge, and watered five days per week, had highest nitrogen fixation and chlorophyll a content relative to no inoculation, dry inoculation, no sewage sludge, or watering twice a week after six months in a growth chamber. Microcosms inoculated with a slurry and watered five times a week had increased net CO_2 exchange rate. Differences in results for inoculation type relative to our study may be due to a one time application of water versus repeated watering, how slurries were prepared (sieving to 1 cm and mixing with

water in our study versus grinding biocrust material with water in a mortar and pestle), which variables were assessed, and field versus growth chamber conditions.

While high watering frequency improved biocrust growth in the growth chamber, likely by initiating frequent photosynthesis, facilitating repeated watering on a large scale at a remote arctic site with low rainfall would be significantly more challenging. Methods to increase moisture retention could improve this limitation. For large disturbances such as mine sites, particularly in the north, inoculation will be necessary to ensure biocrust establishment due to changes in substrates from the surrounding environment, lack of proximity to natural biocrust material, and harsh environmental conditions with a short growing season. As we found no difference in main effects between dispersal of dry biocrust inoculant or slurry, both should be further explored for large scale application in the north.

4.2. Substrate, Habitat Amelioration, And Containment Influences On Biocrust Growth And Functions

Stable soils with little disturbance are necessary for lichen dominated biocrust establishment due to slow growth. At our site, crushed rock and lake sediment were more stable substrates than sandy textured processed kimberlite, and generally had more microtopographic variability. Decreased richness and cover, and presence of individual species on processed kimberlite in year 3 is likely due to loss of lichens by burial or wind (Ficko, observations). Large photosynthetic organisms in biocrusts, such as lichens and bryophytes, can die if buried too deeply, or for too long (Jia et al. 2008). Processed kimberlite, the main by-product of diamond mining, is likely not a suitable long term substrate for biocrusts by itself as it has highest pH and sand content of the three substrates (Miller et al. 2021).

Much research has been conducted on ecological benefits of biocrusts for soils, but relatively little on how environmental and substrate properties, such as temperature, humidity, slope, aspect, microtopography, salinity, and nutrients, affect biocrust growth and succession (Zhao et al. 2016a). Soil texture and pH influence species composition and distribution (Robinson et al. 1989, Belnap and Eldridge 2001), indicating that the specific biocrust species and community composition may respond differently to various substrates, and decreases in presence of individual species in our study may have been due to the interaction with substrate properties. For example, there was a higher frequency of various lichen and liverwort species on loamy than sandy soils at undisturbed sites in Australia (Eldridge and Greene 1994). Two studies on disturbed sites in Utah found better crust development on substrates with higher silt content (Anderson et al. 1982a), or on fine textured clay loam soil than coarse textured sandy loam soil (Antoninka et

al. 2020a), with fine textured soil benefiting more from surface roughening to increase microtopography than coarse textured soil. Robinson et al. (1989) and Gould and Walker (1999) decreased lichen species richness as pH increased from 4 to 9 in different environments in the NWT. Löbel et al. (2006) found a linear increase in lichen species richness as pH increased from 3 to 8 in dry grasslands in Sweden. Zraik et al. (2018) found species specific associations with soil pH, sand shape (angular, round), and percent sand for lichens in Manitoba, indicating the importance of substrate properties to improve biocrust reclamation. Crushed rock and lake sediment are also by-products of northern mining, and have potential as substrates for biocrusts when combined with habitat amelioration such as erosion control blanket.

Our results determined that habitat amelioration techniques can increase species diversity, abundance, and cover on disturbed sites. While tundra soil is the natural habitat of lichen biocrusts, erosion control blanket and woody debris increased microtopography and were more successful in retaining lichens than no habitat amelioration or tundra soil, which were more exposed and susceptible to wind and weathering over time. Similarly, Roturier et al. (2007) found differences in fragment movement and re-establishment of *Cladonia arbuscula* ssp*. mitis* on habitat amelioration treatments, with less movement of fragments placed on moss, twigs, or bark, than on bare soil. Jute mat on the soil surface prior to inoculation increased total biocrust cover for lichens and mosses after 6 and 18 months, but slightly decreased late successional cover (Bowker et al. 2020). Jute mat likely provides benefits other than containment, such as increasing microtopography, attachment sites for lichens, and/or water retention. Condon and Pyke (2016) found greater cover with jute mat for two moss species from biocrusts in Idaho and Oregon.

These results suggest habitat amelioration practices that increase microtopography such as erosion control blanket, or containment treatments such as jute mat, can also increase soil stability on some surfaces such as processed kimberlite, addressing two barriers for biocrust re-establishment as outlined by Bowker (2007). Although our results indicate application of erosion control blanket provided the most consistent and predictable response, followed by containment, and then woody debris, further research is required to determine if larger scale application of these treatments has the same effect on biocrust survival as our small 0.5 x 0.5 m plots.

In this research we focused on assessing macro-lichens from field collected biocrusts over time, since appropriate species richness and cover, and sufficient quantities of various species are necessary for restoration of important ecological functions provided by biocrusts. While only a few lichens had bleached by year 3, habitat amelioration and containment treatments made it too challenging to quantify specific growth patterns by photographic analyses. Similarly, habitat amelioration techniques such as woody debris combined with containment made even visual

assessments of species richness and cover challenging. We attempted to improve accuracy and consistency of results by having two people do assessments in years 2 and 3, including a lichen expert. As we did not measure changes in lichen growth, we recommend addition of other methods to assess if lichens are alive and to quantify how ecological functions are changing as a result of biocrust development, such as chlorophyll a (common proxy for biocrust biomass, Castle et al. 2011), chlorophyll fluorescence (index for biocrust health and recovery, Maxwell and Johnson 2000), soil aggregate stability, available nitrogen, and/or nitrogen fixation. Longer term monitoring is necessary as mature biocrusts can take many decades to establish fully.

4.3. Biocrust Application In The North

Very few techniques to scale up dispersal of biocrust inoculant for large scale disturbances such as mine sites have been tested, especially for lichen dominant biocrusts. Reclamation techniques have generally focused on seeding vascular plants to accelerate recovery of disturbed sites by drill, broadcast, aerial, or hydro seeding, although implementation in the north still faces many challenges (Matheus and Omtzigt 2011). As collection of natural biocrust material for reclamation creates new disturbances, methods to rapidly mass cultivate cyanobacteria from biocrusts have been developed to increase the number of propagules, and can be applied in powdered or slurry form in the field (reviewed in Zhao et al. 2016, Giraldo-Silva et al. 2019). However, methods to mass propagate bryophytes and lichens have not been developed, and suitable species compositions for different environments are unknown. For planned disturbances such as mine sites like Diavik, salvaging biocrust material prior to disturbances could ensure appropriate material for use during mine closure, although research on appropriate storage and dispersal techniques is needed (reviewed in Tucker et al. 2020). Doherty et al. (2020) recently determined that manually broadcasting moss fragments on imprinted soil had small, but significant, increases in cover after two years at a disturbed site in Montana, but drill seeding moss fragments was unsuccessful, possibly due to burial.

Of our three substrates studied, processed kimberlite was least effective, alone or in combination with habitat amelioration or containment treatments. Given the extent of planned and current disturbances in the north, development of anthroposols from mining by-products mixed with organic or inorganic amendments (e.g. Reid and Naeth 2005a, 2005b, Larney and Angers 2012, Miller and Naeth 2017) may improve tundra reclamation by creating suitable substrates for biocrusts from by-products currently stored on site. Other techniques to investigate to decrease stress and potentially to improve biocrust recovery include use of shade to decrease direct UV exposure, choosing season of dispersal to maximize preferred environmental factors such as

times with higher moisture and lower air temperatures, regular watering of crusts following dispersal, creation of microtopography using furrows or imprinting, and dispersing larger fragments or even mats of biocrust material (Lamarre 2016, Zhao et al. 2016a, 2021, Antoninka et al. 2020a). Creation of suitable substrates and habitats are necessary to support establishment and recovery of vascular plants and biocrusts following disturbances in the north. Given the logistical challenges and costs with transporting anything to the arctic, integration of management and revegetation strategies will be necessary to ensure successful reclamation and restoration of disturbed ecological functions.

5. IMPLICATIONS FOR PRACTICE

- Arctic macro-lichens and bryophytes in biocrusts survived for three field seasons on three diamond mining by-products; biocrust survival was greater on crushed rock and lake sediment than on processed kimberlite. Thus unamended processed kimberlite is not recommended for reclamation.
- Biocrust application is necessary to ensure sufficient species composition and abundance on mining by-products in northern environments.
- Habitat amelioration and containment techniques that increased microtopographic variability, including erosion control blanket, jute mat, and woody debris, had more consistent and predictable responses for retaining lichen dominated biocrust material on small field plots. Larger scale field application of these techniques should be investigated to accelerate biocrust reclamation of disturbed arctic environments.

Table 4.1. Mixed model results for cover and species richness. Statistically significant results are shown in bold (α = 0.05). Lowest AICc was 1259.8 for cover and 643.9 for species richness.

		Cover (%)		Species richness	
	DF	F	P	F	P
Containment (Contain)	1	14.29	**<0.001**	71.55	**<0.001**
Habitat amelioration (Hab)	3	32.81	**<0.001**	36.75	**<0.001**
Inoculation (Inoc)	1	0.02	0.898	0.93	0.337
Substrate (Sub)	2	8.37	**0.048**	26.87	**0.002**
Contain*Hab	3	12.21	**<0.001**	20.31	**<0.001**
Contain*Inoc	1	1.70	0.195	0.39	0.532
Contain*Sub	2	1.57	0.216	10.84	**<0.001**
Hab*Inoc	3	0.26	0.852	1.04	0.385
Hab*Sub	6	3.14	**0.009**	7.36	**<0.001**
Inoc*Sub	2	0.07	0.937	1.61	0.206
Contain*Hab*Inoc	3	1.04	0.380	1.65	0.188
Contain*Hab*Sub	6	2.89	**0.015**	2.40	**0.037**
Contain*Inoc*Sub	2	3.69	**0.030**	2.78	0.067
Hab*Inoc*Sub	6	0.89	0.510	0.83	0.551
Contain*Hab*Inoc*Sub	6	1.94	0.089	1.56	0.175

Table 4.2. Changes in multivariate species composition abundance for containment, habitat amelioration, and substrate treatments in year 3. Significant PerMANOVA analyses indicate differences in centroid location and/or dispersion, while significant Betadisper analyses indicate differences in dispersion.

			Permanova			Betadisper				
	N	DF	Pseudo F	R^2	P	Pseudo F	P	Diff[1]	Lwr	Upr
Containment (Contain)	240	1	19.35	0.047	**<0.001**	13.99	**0.001**			
None-Jute	120				**<0.001**		**<0.001**	0.022645	0.010719	0.03457
Habitat amelioration (Hab)	240	3	14.65	0.108	**<0.001**	7.562	**0.001**			
None-EB	60				**<0.001**		**<0.001**	0.034331	0.012773	0.055888
Soil-EB	60				**<0.001**		**<0.001**	0.030716	0.00907	0.052362
WD-EB	60				**<0.001**		0.528	0.011396	-0.01034	0.033134
Soil-None	60				0.5874		0.973	-0.00361	-0.02517	0.017942
WD-None	60				**0.0081**		**0.033**	-0.02293	-0.04458	-0.00129
WD-Soil	60				**0.0364**		0.101	-0.01932	-0.04106	0.002418
Substrate (Sub)	240	2	36.15	0.177	**<0.001**	33.85	**0.001**			
LS-CR	80				**<0.001**		0.388	0.007272	-0.00577	0.020311
PK-CR	80				**<0.001**		**<0.001**	0.042526	0.029487	0.055565
PK-LS	80				**<0.001**		**<0.001**	0.035254	0.022215	0.048293
Contain*Hab		3	6.12	0.045	**<0.001**					
Contain*Sub		2	5.17	0.025	**<0.001**					
Hab*Sub		6	3.14	0.046	**<0.001**					
Contain:Hab:Sub		6	1.59	0.023	0.0777					
Residuals		216		0.529						
Total		239		1						

[1]Diff = difference in dispersion for pair-wise comparisons, Lwr = lower limit, Upr = upper limit

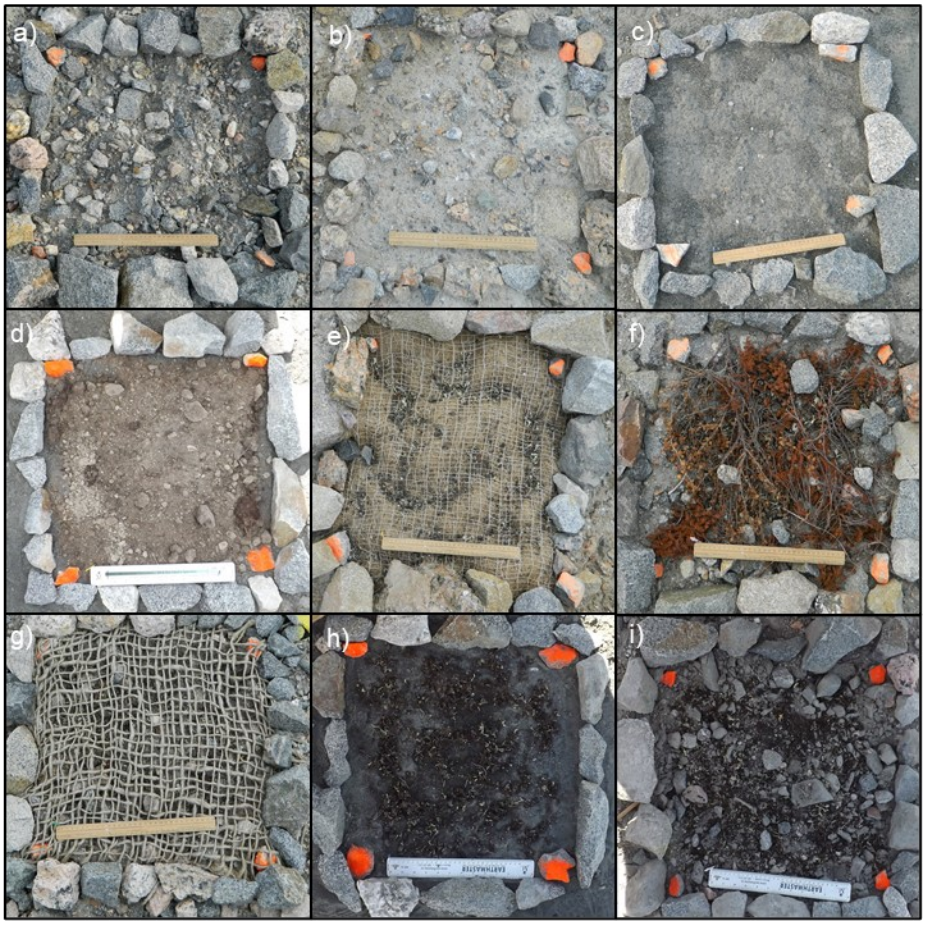

Figure 4.1. Images for four biocrust treatments, substrate [a) crushed rock, b) lakebed sediment, c) processed kimberlite], amendment [d) tundra soil, e) erosion control blanket, f) woody debris], containment [g) jute], and inoculation [h) slurry, i) dry placement]. A 30 cm ruler is shown for scale. All pictures were taken at the first assessment period except h) and i) which are from immediately after dispersal.

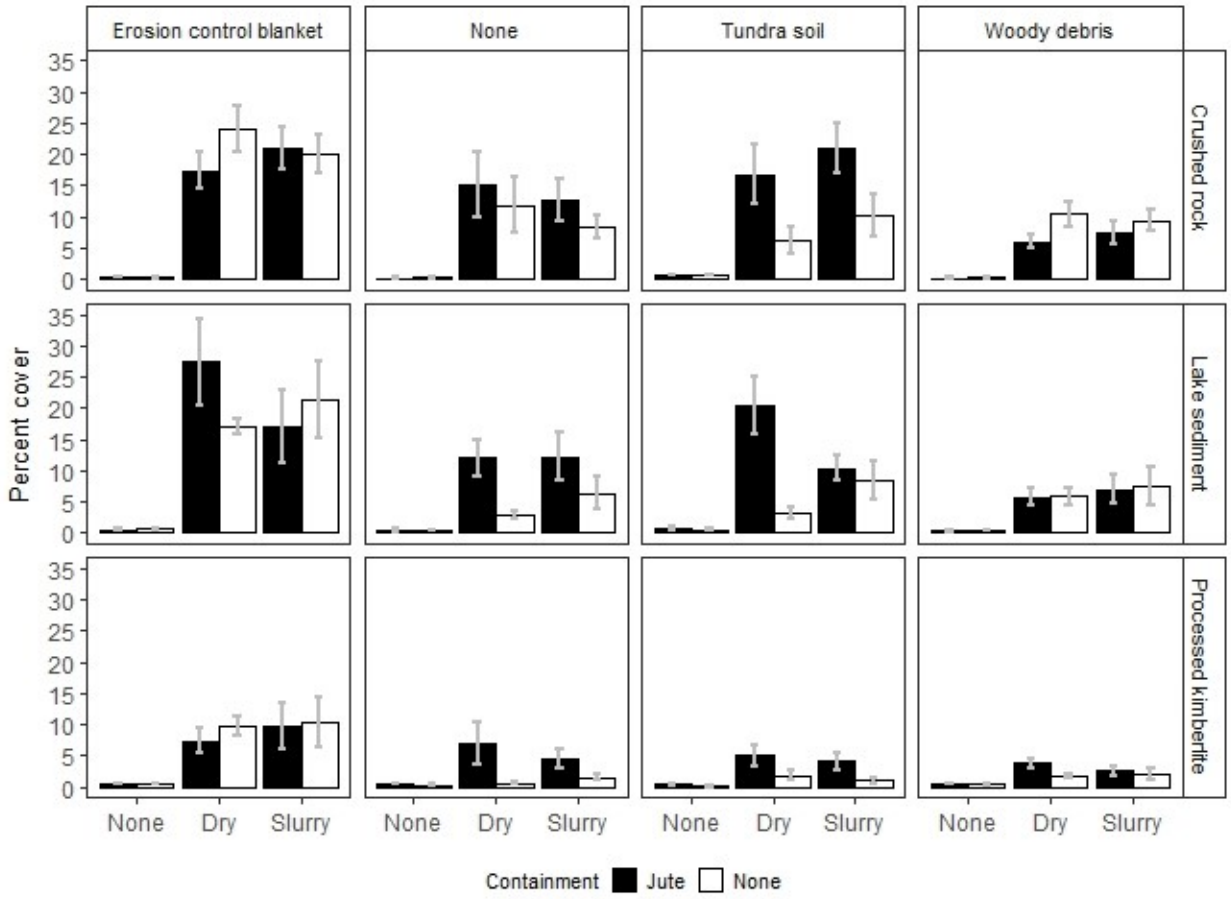

Figure 4.2. Year 3 cover by inoculation (x-axis), substrate (horizontal panels), habitat amelioration (vertical panels), and containment treatments. Each bar represents the mean, error bars are ± standard error, n = 5. See Tables 4.1. and S4.1. for significantly different treatments.

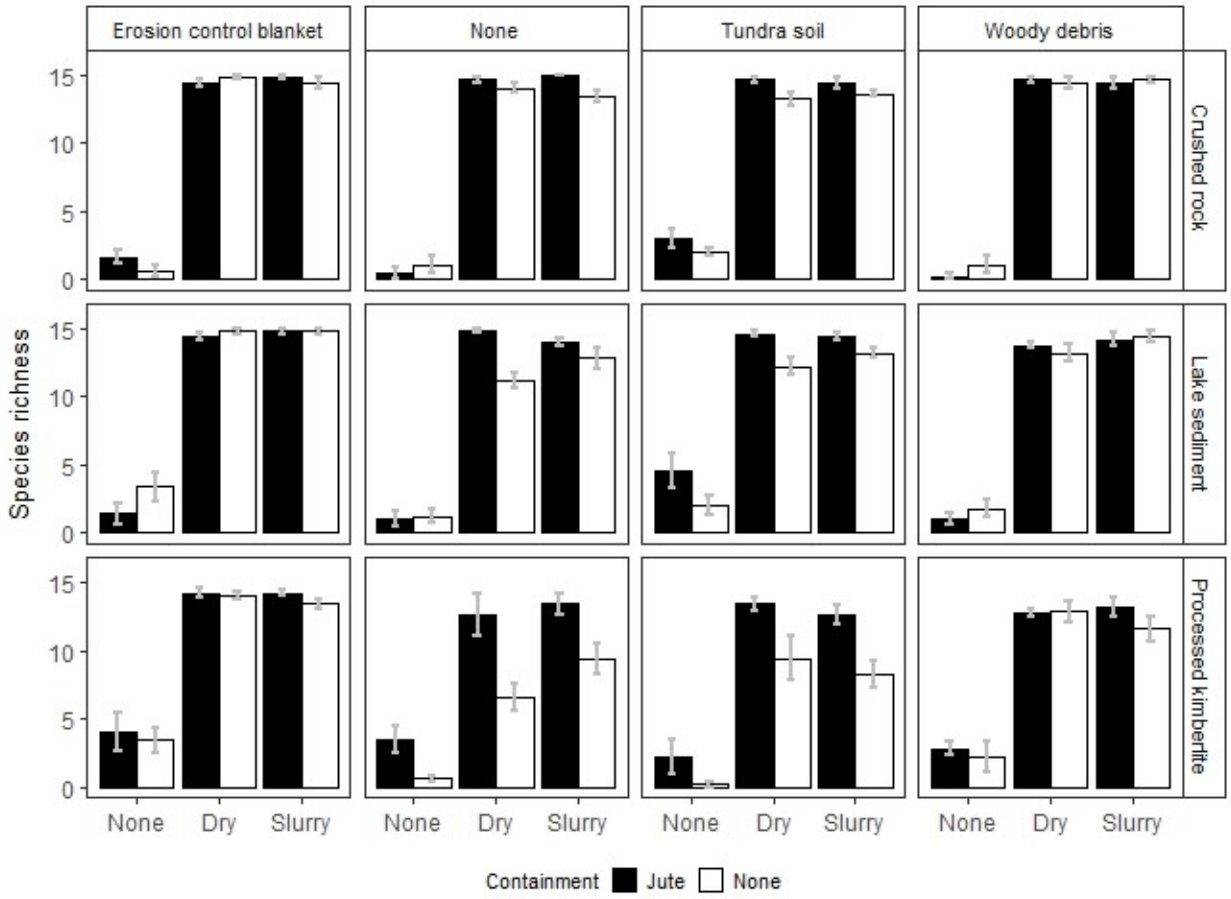

Figure 4.3. Year 3 species richness by inoculation (x axis), substrate (horizontal panels), habitat amelioration (vertical panels), and containment treatments. Each bar represents the mean, error bars are ± standard error, n = 5. See Tables 4.1. and S4.2. for significantly different treatments.

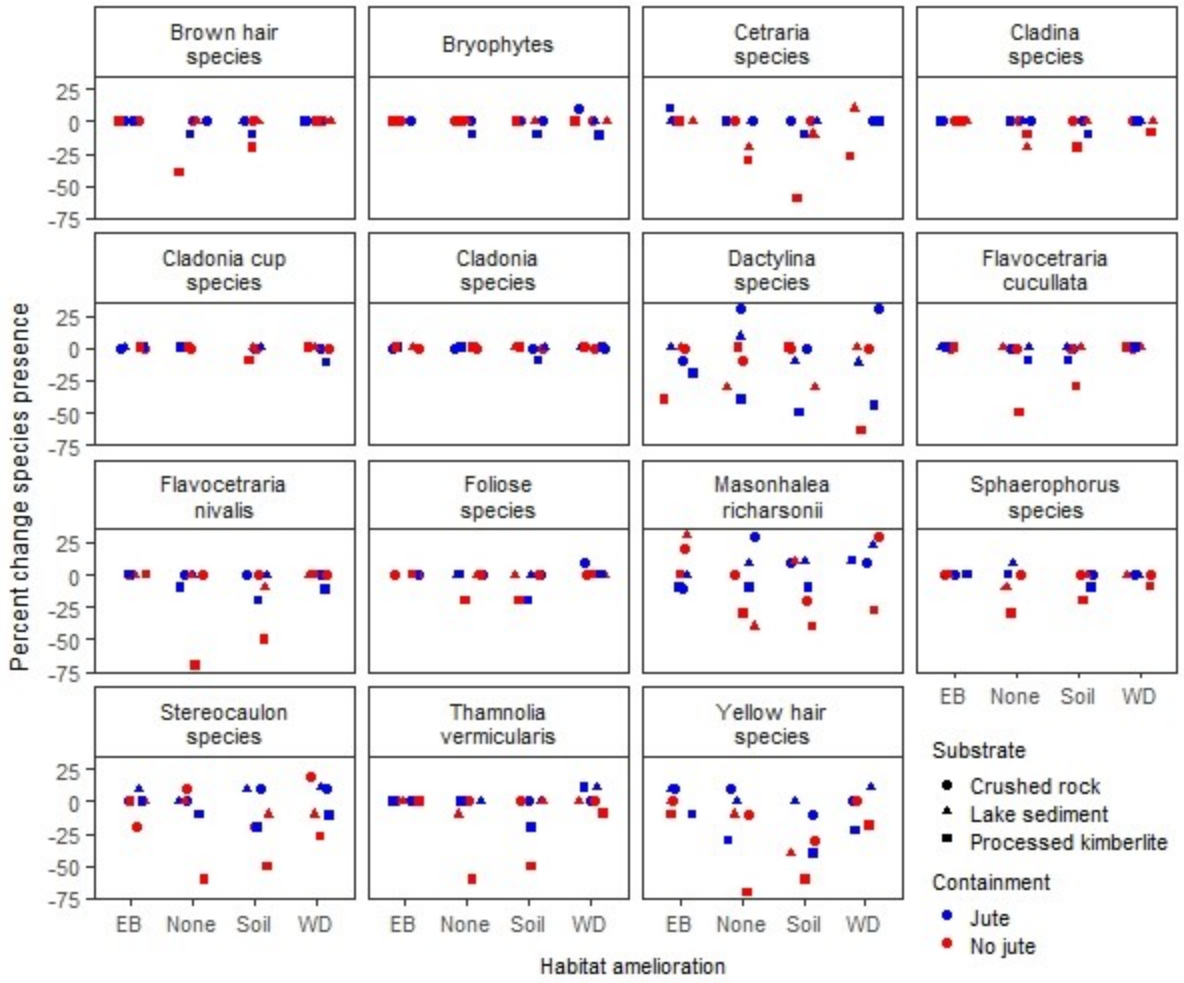

Figure 4.4. Percent change in individual species presence between years 2 and 3 for habitat amelioration (x-axis; EB = erosion control blanket, none = no habitat amelioration, Soil = tundra soil, WD = woody debris), substrate (shape), and containment (colour) treatment. Each shape in the jitter plot had a random value (between 0 and ± 0.1) added to the value on the x axis to visually separate shapes. Each shape represents the mean, n = 10.

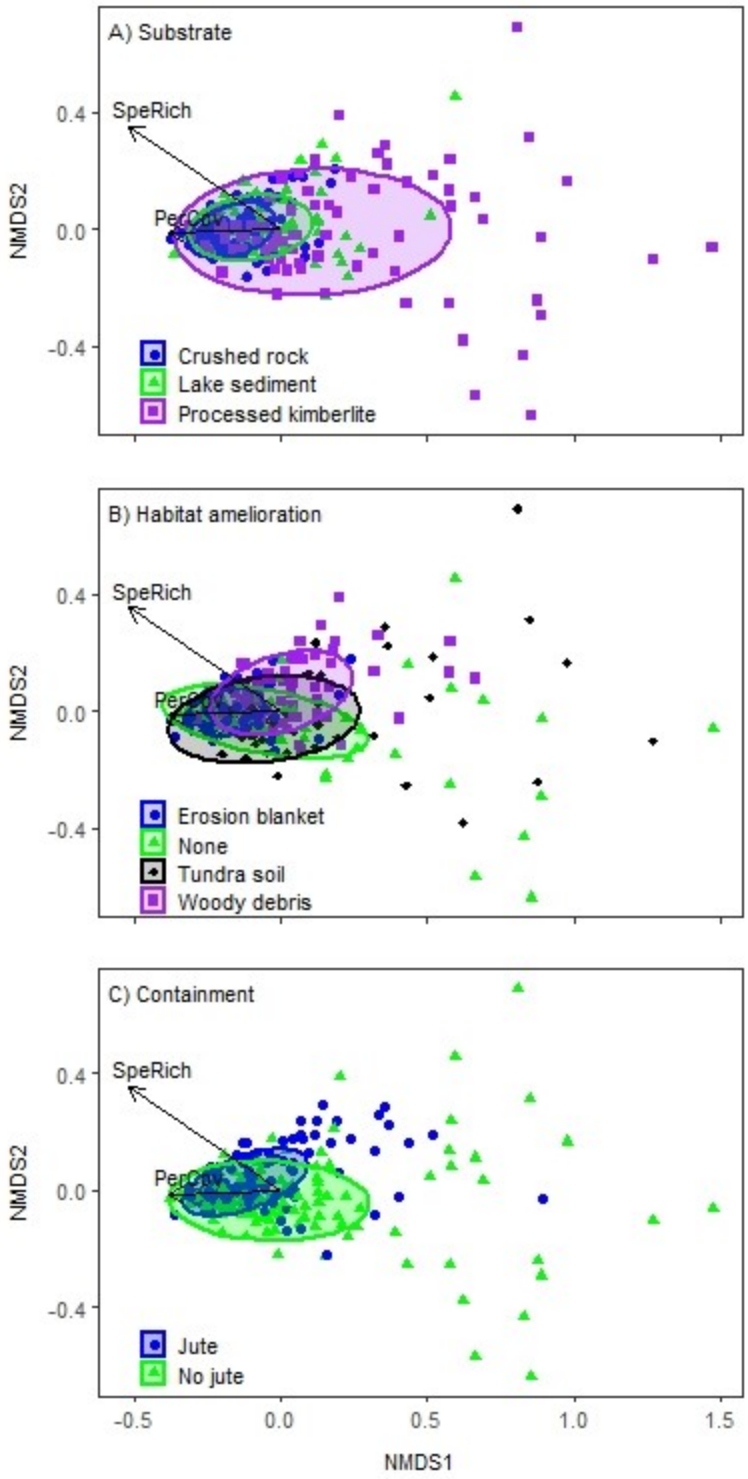

Figure 4.5. NMDS two-dimensional visualization of year 3 species composition for a) substrate, b) habitat amelioration, and c) containment treatments. Arrows are scaled (0.65) and represent relative length and direction for cover (PerCov) and species richness (SpeRich). Ellipses represent 70 % of the data. Stress = 0.10252.

Table S4.1. Mixed model pair wise comparisons for cover comparing relevant pairs from significant main effects and interactions. Statistically significant results are shown in bold (α = 0.05). Lowest AICc was 1259.8. Sub = substrate: CR = crushed rock, LS = lake sediment, PK = processed kimberlite; lichen = lichen inoculation: DP = dry placement; amend = habitat amelioration technique: EB = erosion control blanket, soil = tundra soil, WD = woody debris; jute = containment technique.

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
1) Jute vs no jute in sub=CR/lichen=DP	0.7000	2.3117	52.3	0.30	0.7632	-3.9381	5.3381
2) Jute vs no jute in sub=CR/lichen=slurry	3.5500	2.3117	52.3	1.54	0.1306	-1.0881	8.1881
3) Jute vs no jute in sub=LS/lichen=DP	9.0420	2.0700	27.6	4.37	**0.0002**	4.7992	13.2849
4) Jute vs no jute in sub=LS/lichen=slurry	0.7000	2.0740	27.7	0.34	0.7383	-3.5502	4.9502
5) Jute vs no jute in sub=PK/lichen=DP	2.2227	1.1992	29.7	1.85	0.0738	-0.2275	4.6728
6) Jute vs no jute in sub=PK/lichen=slurry	1.5750	1.1973	29.5	1.32	0.1985	-0.8718	4.0218
7) CR vs LS in lichen=DP/jute=Jute	-2.0847	3.1851	9.72	-0.65	0.5280	-9.2097	5.0402
8) CR vs PK in lichen=DP/jute=Jute	8.0379	2.8805	6.43	2.79	**0.0293**	1.1032	14.9726
9) LS vs PK in lichen=DP/jute=Jute	10.1226	2.6582	7.94	3.81	**0.0052**	3.9854	16.2598
10) CR vs LS in lichen=DP/jute=No jute	6.2573	3.1863	9.76	1.96	0.0787	-0.8660	13.3806
11) CR vs PK in lichen=DP/jute=No jute	9.5605	2.8789	6.42	3.32	**0.0145**	2.6255	16.4956
12) LS vs PK in lichen=DP/jute=No jute	3.3032	2.6586	7.97	1.24	0.2494	-2.8321	9.4385
13) DP vs Slurry in substrate=CR/jute=Jute	-1.7500	2.3117	52.3	-0.76	0.4524	-6.3881	2.8881
14) DP vs Slurry in substrate=CR/jute=No jute	1.1000	2.3117	52.3	0.48	0.6362	-3.5381	5.7381
15) DP vs Slurry in substrate=LS/jute=Jute	4.6420	2.0700	27.6	2.24	**0.0331**	0.3992	8.8849
16) DP vs Slurry in substrate=LS/jute=No jute	-3.7000	2.0740	27.7	-1.78	0.0854	-7.9502	0.5502
17) DP vs Slurry in substrate=PK/jute=Jute	0.4811	1.1999	29.8	0.40	0.6913	-1.9702	2.9324
18) DP vs Slurry in substrate=PK/jute=No jute	-0.1666	1.1960	29.4	-0.14	0.8902	-2.6112	2.2781
19) CR vs LS in lichen=slurry/jute=Jute	4.3073	3.1863	9.76	1.35	0.2069	-2.8160	11.4306
20) CR vs PK in lichen=slurry/jute=Jute	10.2690	2.8794	6.42	3.57	**0.0106**	3.3341	17.2038
21) LS vs PK in lichen=slurry/jute=Jute	5.9617	2.6591	7.98	2.24	0.0554	-0.1735	12.0968
22) CR vs LS in lichen=slurry/jute=No jute	1.4573	3.1863	9.76	0.46	0.6574	-5.6660	8.5806

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
23) CR vs PK in lichen=slurry/jute=No jute	8.2940	2.8794	6.42	2.88	**0.0260**	1.3591	15.2288
24) LS vs PK in lichen=slurry/jute=No jute	6.8367	2.6591	7.98	2.57	**0.0332**	0.7015	12.9718
25) Jute vs no jute in amend=EB	-0.4167	2.2140	37.2	-0.19	0.8517	-4.9020	4.0687
26) jute vs no jute in amend=none	5.4273	1.4993	26.6	3.62	**0.0012**	2.3487	8.5059
27) Jute vs no jute in amend=soil	7.8167	1.4716	26.1	5.31	**<.0001**	4.7927	10.8407
28) Jute vs no jute in amend=WD	-0.9675	0.7276	26.7	-1.33	0.1949	-2.4614	0.5264
29) EB vs None in jute=Jute	5.9394	1.8887	60.6	3.14	**0.0026**	2.1622	9.7166
30) EB vs Soil in jute=Jute	3.7000	1.8798	61.4	1.97	0.0536	-0.05842	7.4584
31) EB vs WD in jute=Jute	11.4452	1.6500	45.2	6.94	**<.0001**	8.1223	14.7680
32) None vs Soil in jute=Jute	-2.2394	1.4829	52.3	-1.51	0.1370	-5.2147	0.7359
33) None vs WD in jute=Jute	5.5058	1.1790	39.3	4.67	**<.0001**	3.1216	7.8900
34) Soil vs WD in jute=Jute	7.7452	1.1637	38.7	6.66	**<.0001**	5.3908	10.0995
35) None vs Soil in jute=No jute	0.1500	1.4880	52.8	0.10	0.9201	-2.8348	3.1348
36) None vs WD in jute=No jute	-0.8890	1.1785	39.1	-0.75	0.4552	-3.2725	1.4946
37) Soil vs WD in jute=No jute	-1.0390	1.1576	38.1	-0.90	0.3751	-3.3823	1.3044
38) EB vs None in jute=No jute	11.7833	1.8927	61	6.23	**<.0001**	7.9986	15.5681
39) EB vs Soil in jute=No jute	11.9333	1.8798	61.4	6.35	**<.0001**	8.1749	15.6918
40) EB vs WD in jute=No jute	10.8944	1.6457	44.7	6.62	**<.0001**	7.5792	14.2095
41) Jute vs no jute in sub=CR/amend=EB	-2.8000	3.3239	15.2	-0.84	0.4126	-9.8762	4.2762
42) Jute vs no jute in sub=CR/amend=None	3.8000	3.8153	14.8	1.00	0.3352	-4.3408	11.9408
43) Jute vs no jute in sub=CR/amend=Soil	10.7000	3.7446	15.1	2.86	**0.0119**	2.7215	18.6785
44) Jute vs no jute in sub=CR/amend=WD	-3.2000	1.7677	14	-1.81	0.0917	-6.9902	0.5902
45) jute vs no jute in sub=LS/amend=EB	3.0000	5.0155	15.7	0.60	0.5583	-7.6501	13.6501
46) Jute vs no jute in sub=LS/amend=None	7.7818	1.8116	14.8	4.30	**0.0007**	3.9162	11.6474
47) Jute vs no jute in sub=LS/amend=Soil	9.6000	2.1545	15	4.46	**0.0005**	5.0078	14.1922

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
48) Jute vs no jute in sub=LS/amend=WD	-0.8977	1.1340	11.5	-0.79	0.4445	-3.3797	1.5843
49) Jute vs no jute in sub=PK/amend=EB	-1.4500	2.8132	15.7	-0.52	0.6134	-7.4230	4.5230
50) Jute vs no jute in sub=PK/amend=None	4.7000	1.5465	15.4	3.04	**0.0081**	1.4108	7.9892
51) Jute vs no jute in sub=PK/amend=Soil	3.1500	0.9087	13.8	3.47	**0.0038**	1.1984	5.1016
52) Jute vs no jute in sub=PK/amend=WD	1.1954	0.5956	11.5	2.01	0.0689	-0.1089	2.4996
53) EB vs None in sub=CR/jute=Jute	5.3000	3.5780	29.4	1.48	0.1492	-2.0134	12.6134
54) EB vs Soil in sub=CR/jute=Jute	0.3000	3.5405	31.2	0.08	0.9330	-6.9191	7.5191
55) EB vs WD in sub=CR/jute=Jute	12.5000	2.6620	22.7	4.70	**0.0001**	6.9890	18.0110
56) None vs Soil in sub=CR/jute=Jute	-5.0000	3.7801	29.8	-1.32	0.1960	-12.7222	2.7222
57) None vs WD in sub=CR/jute=Jute	7.2000	2.9733	21.2	2.42	**0.0245**	1.0205	13.3795
58) Soil vs WD in sub=CR/jute=Jute	12.2000	2.9280	21.5	4.17	**0.0004**	6.1197	18.2803
59) EB vs None in sub=LS/jute=Jute	9.7182	3.7618	19.4	2.58	**0.0180**	1.8546	17.5817
60) EB vs Soil in sub=LS/jute=Jute	6.8000	3.8599	21.3	1.76	0.0924	-1.2195	14.8195
61) EB vs WD in sub=LS/jute=Jute	16.3977	3.6422	17.5	4.50	**0.0003**	8.7287	24.0667
62) None vs Soil in sub=LS/jute=Jute	-2.9182	1.9733	29.1	-1.48	0.1499	-6.9537	1.1173
63) None vs WD in sub=LS/jute=Jute	6.6795	1.5102	26.1	4.42	**0.0002**	3.5758	9.7832
64) Soil vs WD in sub=LS/jute=Jute	9.5977	1.7346	22	5.53	**<.0001**	6.0008	13.1947
65) EB vs None in sub=PK/jute=Jute	2.8000	2.2700	24.1	1.23	0.2293	-1.8841	7.4841
66) EB vs Soil in sub=PK/jute=Jute	4.0000	2.0904	18.9	1.91	0.0709	-0.3767	8.3767
67) EB vs WD in sub=PK/jute=Jute	5.4378	2.0373	17.3	2.67	**0.0160**	1.1446	9.7310
68) None vs Soil in sub=PK/jute=Jute	1.2000	1.2684	24	0.95	0.3535	-1.4176	3.8176
69) None vs WD in sub=PK/jute=Jute	2.6378	1.1786	20.5	2.24	**0.0365**	0.1829	5.0927
70) Soil vs WD in sub=PK/jute=Jute	1.4378	0.7786	25.6	1.85	0.0764	-0.1638	3.0394
71) EB vs None in sub=CR/jute=No jute	11.9000	3.5780	29.4	3.33	**0.0024**	4.5866	19.2134
72) EB vs Soil in sub=CR/jute=No jute	13.8000	3.5405	31.2	3.90	**0.0005**	6.5809	21.0191

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
73) EB vs WD in sub=CR/jute=No jute	12.1000	2.6620	22.7	4.55	**0.0001**	6.5890	17.6110
74) None vs Soil in sub=CR/jute=No jute	1.9000	3.7801	29.8	0.50	0.6189	-5.8222	9.6222
75) None vs WD in sub=CR/jute=No jute	0.2000	2.9733	21.2	0.07	0.9470	-5.9795	6.3795
76) Soil vs WD in sub=CR/jute=No jute	-1.7000	2.9280	21.5	-0.58	0.5675	-7.7803	4.3803
77) EB vs None in sub=LS/jute=No jute	14.5000	3.7798	19.7	3.84	**0.0011**	6.6069	22.3931
78) EB vs Soil in sub=LS/jute=No jute	13.4000	3.8599	21.3	3.47	**0.0022**	5.3805	21.4195
79) EB vs WD in sub=LS/jute=No jute	12.5000	3.6298	17.2	3.44	**0.0030**	4.8497	20.1503
80) None vs Soil in sub=LS/jute=No jute	-1.1000	2.0074	29.4	-0.55	0.5878	-5.2031	3.0031
81) None vs WD in sub=LS/jute=No jute	-2.0000	1.5189	24.4	-1.32	0.2001	-5.1320	1.1320
82) Soil vs WD in sub=LS/jute=No jute	-0.9000	1.7085	21.3	-0.53	0.6038	-4.4496	2.6496
83) EB vs None in sub=PK/jute=No jute	8.9500	2.2700	24.1	3.94	**0.0006**	4.2659	13.6341
84) EB vs Soil in sub=PK/jute=No jute	8.6000	2.0904	18.9	4.11	**0.0006**	4.2233	12.9767
85) EB vs WD in sub=PK/jute=No jute	8.0831	2.0281	17	3.99	**0.0010**	3.8037	12.3626
86) None vs Soil in sub=PK/jute=No jute	-0.3500	1.2684	24	-0.28	0.7849	-2.9676	2.2676
87) None vs WD in sub=PK/jute=No jute	-0.8669	1.1627	19.6	-0.75	0.4648	-3.2957	1.5620
88) Soil vs WD in sub=PK/jute=No jute	-0.5169	0.7542	24.1	-0.69	0.4997	-2.0732	1.0395
89) CR vs LS in amend=EB/jute=Jute	-2.5927	4.8406	25.9	-0.54	0.5968	-12.5454	7.3601
90) CR vs PK in amend=EB/jute=Jute	10.6190	3.7926	16	2.80	**0.0128**	2.5789	18.6591
91) LS vs PK in amend=EB/jute=Jute	13.2117	4.5539	25.9	2.90	**0.0075**	3.8489	22.5745
92) CR vs LS in amend=None/jute=Jute	1.8255	3.7610	14.1	0.49	0.6349	-6.2347	9.8857
93) CR vs PK in amend=None/jute=Jute	8.1190	3.6574	12.5	2.22	**0.0456**	0.1842	16.0538
94) LS vs PK in amend=None/jute=Jute	6.2935	2.6357	7.72	2.39	**0.0451**	0.1763	12.4106
95) CR vs LS in amend=Soil/jute=Jute	3.9073	3.8290	15.3	1.02	0.3234	-4.2408	12.0554
96) CR vs PK in amend=Soil/jute=Jute	14.3190	3.5109	11	4.08	**0.0018**	6.5925	22.0454
97) LS vs PK in amend=Soil/jute=Jute	10.4117	2.6338	7.3	3.95	**0.0051**	4.2347	16.5886

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
98) CR vs LS in amend=WD/jute=Jute	1.3050	2.7630	5.07	0.47	0.6563	-5.7696	8.3797
99) CR vs PK in amend=WD/jute=Jute	3.5568	2.5803	4.03	1.38	0.2397	-3.5885	10.7020
100) LS vs PK in amend=WD/jute=Jute	2.2517	2.2628	3.96	1.00	0.3765	-4.0545	8.5579
101) CR vs LS in amend=EB/jute=No jute	3.2073	4.8406	25.9	0.66	0.5135	-6.7454	13.1601
102) CR vs PK in amend=EB/jute=No jute	11.9690	3.7926	16	3.16	**0.0061**	3.9289	20.0091
103) LS vs PK in amend=EB/jute=No jute	8.7617	4.5539	25.9	1.92	0.0654	-0.6011	18.1245
104) CR vs LS in amend=None/jute=No jute	5.8073	3.7838	14.4	1.53	0.1465	-2.2876	13.9022
105) CR vs PK in amend=None/jute=No jute	9.0190	3.6574	12.5	2.47	**0.0290**	1.0842	16.9538
106) LS vs PK in amend=None/jute=No jute	3.2117	2.6661	8	1.20	0.2628	-2.9368	9.3601
107) CR vs LS in amend=Soil/jute=No jute	2.8073	3.8290	15.3	0.73	0.4746	-5.3408	10.9554
108) CR vs PK in amend=Soil/jute=No jute	6.7690	3.5109	11	1.93	0.0800	-0.9575	14.4954
109) LS vs PK in amend=Soil/jute=No jute	3.9617	2.6338	7.3	1.50	0.1745	-2.2153	10.1386
110) CR vs LS in amend=WD/jute=No jute	3.6073	2.7368	4.95	1.32	0.2452	-3.4512	10.6658
111) CR vs PK in amend=WD/jute=No jute	7.9521	2.5731	3.98	3.09	**0.0368**	0.7915	15.1127
112) LS vs PK in amend=WD/jute=No jute	4.3448	2.2268	3.77	1.95	0.1270	-1.9860	10.6756

Table S4.2. Mixed model pair wise comparisons by orthogonal contrasts for species richness comparing relevant pairs from significant main effects and interactions. Statistically significant results are shown in bold (α = 0.05). Lowest AICc was for the model was 643.9. Sub = substrate: CR = crushed rock, LS = lake sediment, PK = processed kimberlite; lichen = lichen inoculation: DP = dry placement; amend = habitat amelioration technique: EB = erosion control blanket, soil = tundra soil, WD = woody debris; jute = containment technique.

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
1) Jute vs no jute in sub=CR/amend=EB	-144E-16	0.2882	15.2	-0.00	1.0000	-0.6138	0.6138
2) Jute vs no jute in sub=CR/amend=None	1.1000	0.2529	14.8	4.35	**0.0006**	0.5603	1.6397
3) Jute vs no jute in sub=CR/amend=Soil	1.1000	0.3634	15.9	3.03	**0.0081**	0.3292	1.8708
4) Jute vs no jute in sub=CR/amend=WD	4.37E-14	0.3065	15.4	0.00	1.0000	-0.6518	0.6518
5) Jute vs no jute in sub=LS/amend=EB	-0.2000	0.2123	15.5	-0.94	0.3606	-0.6512	0.2512

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
6) Jute vs no jute in sub=LS/amend=None	2.4336	0.4597	16.3	5.29	**<.0001**	1.4606	3.4065
7) Jute vs no jute in sub=LS/amend=Soil	1.8000	0.4129	15.9	4.36	**0.0005**	0.9244	2.6756
8) Jute vs no jute in sub=LS/amend=WD	0.1496	0.4990	15	0.30	0.7684	-0.9140	1.2133
9) Jute vs no jute in sub=PK/amend=EB	0.5000	0.3258	15.7	1.53	0.1448	-0.1918	1.1918
10) Jute vs no jute in sub=PK/amend=None	5.0000	1.0935	15.3	4.57	**0.0003**	2.6735	7.3265
11) Jute vs no jute in sub=PK/amend=Soil	4.2000	1.0032	15.4	4.19	**0.0008**	2.0668	6.3332
12) Jute vs no jute in sub=PK/amend=WD	0.7660	0.7816	15.9	0.98	0.3418	-0.8921	2.4240
13) EB vs None in sub=CR/jute=Jute	-0.2000	0.2711	31.2	-0.74	0.4663	-0.7528	0.3528
14) EB vs Soil in sub=CR/jute=Jute	0.1000	0.3280	29.3	0.30	0.7626	-0.5704	0.7704
15) EB vs WD in sub=CR/jute=Jute	0.1000	0.2975	31.7	0.34	0.7390	-0.5062	0.7062
16) None vs Soil in sub=CR/jute=Jute	0.3000	0.3131	28.4	0.96	0.3460	-0.3409	0.9409
17) None vs WD in sub=CR/jute=Jute	0.3000	0.2810	28	1.07	0.2948	-0.2756	0.8756
18) Soil vs WD in sub=CR/jute=Jute	-144E-17	0.3362	31	-0.00	1.0000	-0.6856	0.6856
19) EB vs None in sub=LS/jute=Jute	0.1664	0.3517	23.3	0.47	0.6405	-0.5606	0.8935
20) EB vs Soil in sub=LS/jute=Jute	0.1000	0.3283	23.7	0.30	0.7633	-0.5780	0.7780
21) EB vs WD in sub=LS/jute=Jute	0.6504	0.3932	20	1.65	0.1137	-0.1698	1.4705
22) None vs Soil in sub=LS/jute=Jute	-0.06643	0.4318	31.8	-0.15	0.8787	-0.9461	0.8133
23) None vs WD in sub=LS/jute=Jute	0.4839	0.4836	30.6	1.00	0.3248	-0.5029	1.4707
24) Soil vs WD in sub=LS/jute=Jute	0.5504	0.4662	29.2	1.18	0.2473	-0.4028	1.5035
25) EB vs None in sub=PK/jute=Jute	1.2000	0.8068	18	1.49	0.1542	-0.4951	2.8951
26) EB vs Soil in sub=PK/jute=Jute	1.2000	0.7458	18.6	1.61	0.1245	-0.3632	2.7632
27) EB vs WD in sub=PK/jute=Jute	1.2204	0.6241	20.7	1.96	0.0641	-0.07850	2.5193
28) None vs Soil in sub=PK/jute=Jute	3.18E-13	1.0493	29.6	0.00	1.0000	-2.1443	2.1443
29) None vs WD in sub=PK/jute=Jute	0.02042	0.9666	28.9	0.02	0.9833	-1.9567	1.9975
30) Soil vs WD in sub=PK/jute=Jute	0.02042	0.9163	29.9	0.02	0.9824	-1.8511	1.8920

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
31) EB vs None in sub=CR/jute=No jute	0.9000	0.2711	31.2	3.32	**0.0023**	0.3472	1.4528
32) EB vs Soil in sub=CR/jute=No jute	1.2000	0.3280	29.3	3.66	**0.0010**	0.5296	1.8704
33) EB vs WD in sub=CR/jute=No jute	0.1000	0.2975	31.7	0.34	0.7390	-0.5062	0.7062
34) None vs Soil in sub=CR/jute=No jute	0.3000	0.3131	28.4	0.96	0.3460	-0.3409	0.9409
35) None vs WD in sub=CR/jute=No jute	-0.8000	0.2810	28	-2.85	**0.0082**	-1.3756	-0.2244
36) Soil vs WD in sub=CR/jute=No jute	-1.1000	0.3362	31	-3.27	**0.0026**	-1.7856	-0.4144
37) EB vs None in sub=LS/jute=No jute	2.8000	0.3643	22.7	7.69	**<.0001**	2.0460	3.5540
38) EB vs Soil in sub=LS/jute=No jute	2.1000	0.3283	23.7	6.40	**<.0001**	1.4220	2.7780
39) EB vs WD in sub=LS/jute=No jute	1.0000	0.3735	20.5	2.68	**0.0143**	0.2221	1.7779
40) None vs Soil in sub=LS/jute=No jute	-0.7000	0.4420	31.5	-1.58	0.1233	-1.6009	0.2009
41) None vs WD in sub=LS/jute=No jute	-1.8000	0.4766	31.2	-3.78	**0.0007**	-2.7717	-0.8283
42) Soil vs WD in sub=LS/jute=No jute	-1.1000	0.4497	29.8	-2.45	**0.0206**	-2.0186	-0.1814
43) EB vs None in sub=PK/jute=No jute	5.7000	0.8068	18	7.06	**<.0001**	4.0049	7.3951
44) EB vs Soil in sub=PK/jute=No jute	4.9000	0.7458	18.6	6.57	**<.0001**	3.3368	6.4632
45) EB vs WD in sub=PK/jute=No jute	1.4864	0.5719	21.8	2.60	**0.0165**	0.2996	2.6732
46) None vs Soil in sub=PK/jute=No jute	-0.8000	1.0493	29.6	-0.76	0.4519	-2.9443	1.3443
47) None vs WD in sub=PK/jute=No jute	-4.2136	0.9337	27.3	-4.51	**0.0001**	-6.1284	-2.2988
48) Soil vs WD in sub=PK/jute=No jute	-3.4136	0.8816	28.5	-3.87	**0.0006**	-5.2179	-1.6094
49) CR vs LS in amend=EB/jute=Jute	0.003669	0.3290	7.96	0.01	0.9914	-0.7555	0.7629
50) CR vs PK in amend=EB/jute=Jute	0.3321	0.3733	11.9	0.89	0.3913	-0.4820	1.1461
51) LS vs PK in amend=EB/jute=Jute	0.3284	0.3351	11.9	0.98	0.3466	-0.4024	1.0592
52) CR vs LS in amend=None/jute=Jute	0.3701	0.4201	18.4	0.88	0.3896	-0.5109	1.2511
53) CR vs PK in amend=None/jute=Jute	1.7321	0.8214	19.5	2.11	**0.0481**	0.01606	3.4481
54) LS vs PK in amend=None/jute=Jute	1.3620	0.8573	22.8	1.59	0.1259	-0.4123	3.1362
55) CR vs LS in amend=Soil/jute=Jute	0.003669	0.4421	19.4	0.01	0.9935	-0.9203	0.9277

Orthogonal Contrasts	Estimate	Standard Error	DF	t Value	Pr > |t|	Lower	Upper
56) CR vs PK in amend=Soil/jute=Jute	1.4321	0.7835	22.4	1.83	0.0809	-0.1911	3.0552
57) LS vs PK in amend=Soil/jute=Jute	1.4284	0.7906	23.3	1.81	0.0837	-0.2060	3.0628
58) CR vs LS in amend=WD/jute=Jute	0.5540	0.4737	20	1.17	0.2559	-0.4340	1.5421
59) CR vs PK in amend=WD/jute=Jute	1.4525	0.6539	21.4	2.22	**0.0372**	0.09418	2.8108
60) LS vs PK in amend=WD/jute=Jute	0.8985	0.7112	27.7	1.26	0.2170	-0.5592	2.3561
61) CR vs LS in amend=EB/jute=No jute	-0.1963	0.3290	7.96	-0.60	0.5672	-0.9555	0.5629
62) CR vs PK in amend=EB/jute=No jute	0.8321	0.3733	11.9	2.23	**0.0459**	0.01805	1.6461
63) LS vs PK in amend=EB/jute=No jute	1.0284	0.3351	11.9	3.07	**0.0098**	0.2976	1.7592
64) CR vs LS in amend=None/jute=No jute	1.7037	0.4316	19.2	3.95	**0.0008**	0.8010	2.6063
65) CR vs PK in amend=None/jute=No jute	5.6321	0.8214	19.5	6.86	**<.0001**	3.9161	7.3481
66) LS vs PK in amend=None/jute=No jute	3.9284	0.8630	23.3	4.55	**0.0001**	2.1444	5.7123
67) CR vs LS in amend=Soil/jute=No jute	0.7037	0.4421	19.4	1.59	0.1276	-0.2203	1.6277
68) CR vs PK in amend=Soil/jute=No jute	4.5321	0.7835	22.4	5.78	**<.0001**	2.9089	6.1552
69) LS vs PK in amend=Soil/jute=No jute	3.8284	0.7906	23.3	4.84	**<.0001**	2.1940	5.4628
70) CR vs LS in amend=WD/jute=No jute	0.7037	0.4562	19.4	1.54	0.1391	-0.2497	1.6571
71) CR vs PK in amend=WD/jute=No jute	2.2184	0.6050	21.8	3.67	**0.0014**	0.9630	3.4739
72) LS vs PK in amend=WD/jute=No jute	1.5148	0.6542	27.9	2.32	**0.0281**	0.1746	2.8550

V. OPTIMIZING GROWTH CHAMBER CONDITIONS FOR MAINTAINING NORTHERN LICHEN-DOMINATED BIOCRUSTS

1. INTRODUCTION

Biocrusts are complex communities of poikilohydric species including algae, bacteria, bryophytes, cyanobacteria, lichens, and microfungi. They are important in ecological processes of polar and other arid environments worldwide, including seedling establishment, infiltration, plant production, and soil temperatures; creating habitat, improving soil stability, and carbon and nitrogen fixation (Eldridge and Greene 1994, Belnap and Lange 2003). In the north, wild and farmed caribou herds rely on fruticose lichens for winter food (Thomas and Hervieux 1986, Kumpula 2001). Natural and anthropogenic disturbances such as climate change, grazing, infrastructure development, resource extraction, and trampling can have significant, long term, adverse effects on biocrusts (Eldridge and Greene 1994, Harper and Kershaw 1996, Ferrenberg et al. 2015).

The perception that biocrusts recover unassisted after disturbance has limited research on techniques for assisted recovery, even though estimates for natural recovery are years to millennia (Bowker 2007, Weber et al. 2016a, Kidron et al. 2020). Over the past few decades, inoculation techniques relying on vegetative reproductive strategies of biocrust organisms have been explored in the field for single or multiple crust species to accelerate biocrust re-establishment (Bu et al. 2013, Zhao et al. 2016, Antoninka et al. 2018, Ficko et al., in prep). No studies on accelerating recovery of northern lichen biocrusts have been published, although a few investigated using individual lichen species in mine site reclamation (Duncan 2011, Ballesteros et al. 2017). As lichens make up a large portion of primary producers in tundra ecosystems (Wielgolaski 1972, Kjelvik and Kärenlampi 1975, Asplund and Wardle 2017), inclusion of their recovery in reclamation is critical.

Reclamation practitioners need to understand the factors that are limiting recovery of disturbed sites. As northern sites have both short growing seasons and harsh environmental conditions (Rausch and Kershaw 2007b), growing northern lichen biocrusts in controlled conditions can optimize techniques to accelerate field recovery, augment donor material for field application, test how disturbances (such as climate change) may alter ecological function, and may predict impacts. However, studies conducted in optimal conditions such as growth chambers for lichen species are sparse (Kershaw and Millbank 1969, Dibben 1971, Galun et al. 1972, Xiao et al. 2011, Bidussi et al. 2013, Bu et al. 2013, Zhao et al. 2016); only two assessed lichen

biocrusts in a controlled environment for land reclamation purposes (Maestre et al. 2006, Bowker and Antoninka 2016).

Common inoculation techniques in the field and growth chamber included selecting individual species, transplanting intact crust pieces, or artificial fragmentation of crust material (sieving). Watering regimes were daily, every few days, to once a month, with several studies emphasizing importance of alternating wet and dry periods. Lichens are sensitive to substrate properties including pH, texture, and nutrients (Robinson et al. 1989, Belnap and Eldridge 2001, Bowker et al. 2005). Lichen cultivation was often on artificial media such as agar, although lichen and moss biocrust growth has occurred on soil and sand (Maestre et al. 2006, Xu et al. 2008, Zhao et al. 2016a, Bowker and Antoninka 2016). Although substrate sterilization before experimental set up is common to limit algae, bacteria, and fungi, contamination was attributed to external sources rather than experimental material (Dibben 1971, Duckett et al. 2004, Xu et al. 2008, Zhao et al. 2014). Duckett et al. (2004) found contamination often started within one week. Substrate depth was rarely examined, but may affect water retention. Lichens grow slowly, but growth within a few to 9 weeks for individual lichen species and various biocrusts indicate short term studies can assess treatments (Dibben 1971, Galun et al. 1972, Xu et al. 2008, Bidussi et al. 2013, Zhao et al. 2014).

Better understanding of factors affecting lichen dominated biocrust growth under controlled conditions could enable investigations of their recovery or ecological functions. To address this knowledge gap, we assessed effects of substrate, substrate depth, substrate sterilization, lichen inoculation, community composition, and watering frequency on survival of arctic lichens in biocrusts from Diavik Diamond Mine Inc., Northwest Territories, Canada in a six week growth chamber experiment. We hypothesized that tundra soil would be a better substrate than crushed rock, and greater depths of substrate better than shallow; that autoclaved substrates would reduce contamination by other biota; that a sieved mix of biocrust material, similar to natural fragment dispersal, would be better than an unsieved mix or single species; and that moderate watering regimes would be best.

2. METHODS

2.1. Biocrust Source Characteristics

Diavik Diamond Mine is located 100 km north of the treeline and 320 km northeast of Yellowknife, Northwest Territories (64º30´41´´ N, 110º17´23´´ W), on an island in Lac-de-Gras. Lac-de-Gras lies in the Point Upland Arctic Ecoregion (Ecosystem Classification Group 2012);

mean annual precipitation is 285 mm (over half snow) and mean annual temperature -9 ºC from 2011 to 2016. Uplands are vegetated by dwarf-heath shrubs and lichen dominated biocrust communities. More than 50 species of macrolichens have been identified at Diavik, including *Alectoria ochroleuca* (Hoffm.) A. Massal., *Bryocaulon divergens* (Ach.) Kärnefelt, *Bryoria nitidula* (Th. Fr.) Brodo & D. Hawksw., *Cetraria* Ach. species, *Cladonia* P. Browne species (including cupped species and reindeer lichens), *Dactylina arctica* (Hooker f.) Nyl., *Flavocetraria cucullata* (Bellardi) Kärnefelt & A. Thell, *Flavocetraria nivalis* (L.) Kärnefelt & A. Thell, *Gowardia nigricans* (Ach.) P. Halonen, L. Myllys, S. Velmala, & H. Hyvärinen, *Masonhalea richardsonii* (Hooker) Kärnefelt, *Sphaerophorus globosus* (Hudson) Vainio, *Stereocaulon* Hoffm. species, and *Thamnolia vermicularis* (Sw.) Ach. Ex Schaerer. Taxonomy follows Esslinger (2019).

2.2. Experimental Design

Four experiments assessed lichen survival over time on substrates available at Diavik (crushed rock, tundra soil). Experiment 1 assessed substrate sterilization (autoclaved, unautoclaved), experiment 2 lichen species composition (*Flavocetriaria cucullata*, none, sieved mixed species, unsieved mixed species), experiment 3 substrate depth (1, 1.5. 2 cm), experiment 4 watering frequency (damp; 1, 2, 3, 10 days) (Table 5.1, Figure 5.1). Each treatment was replicated five times totaling 130 experimental units, and placed in clear plastic germination dishes (microcosms, 11 x 11 x 3 cm). Some treatments overlapped experiments as baseline conditions were autoclaved substrate, sieved mixed species, 2 cm substrate, and two day watering.

Tundra soil was collected from an undisturbed area on the southernmost tip of the island. A mix of mineral and organic soil was collected from a depth of 5 to 30 cm after removing surface vegetation. Crushed rock, the most common mining by-product at Diavik, was collected from stockpiles in October. Substrates were transported in sealed 20 L buckets. Tundra soil and crushed rock were sieved to 2 cm to increase homogeneity by removing clods, plant roots, and rocks. Crushed rock had pH 7.8, loamy sand texture, and total organic carbon 0.1 %; tundra soil had pH 4.5, sandy loam texture, and total organic carbon 2.7 % (Miller and Naeth 2017). Sterilized substrates were autoclaved twice at 121 ºC for 3 h. Most microcosms received 242 mL of substrate (2 cm), except the depth treatments which only received 182 mL (1.5 cm), or 121 mL substrate (1 cm).

Biocrusts with visible macrolichens were hand collected using a trowel on September 24 and 25. 2014 from a similar area as tundra soil. A biocrust species mix (sieved, unsieved) was used, as multiple species naturally grow together in tundra communities. The mix was compared to *Flavocetraria cucullata*, the most frequent lichen on site, to determine if an individual species

can be used as an indicator of crust growth and survival. Crust material was air dried for five days, then transported in brown paper bags and frozen at -10 ºC prior to use. Biocrust material was hand mixed then sieved on a 1 cm grid. Sieved fragments were weighed (6 g) and refrigerated in paper bags at 4 ºC until placement. *Flavocetraria cucullata* was hand picked and weighed (4 g for similar coverage as sieved mixes). For unsieved mixes, 6 g of intact crust (one or more pieces) were weighed. Microcosms were inoculated by evenly scattering a thin layer of dry crust material (sieved mix or *Flavocetraria cucullata*) across substrate surfaces, or placing intact pieces on the surface and gently pushing them down to ensure good substrate contact.

Microcosms were placed in a growth chamber with a day temperature of 17 ºC for 20 h and a night temperature 10 ºC for 4 h based on mean mid-May to mid-June Diavik temperatures. To determine a watering regime with suitable wet/dry cycles for normal growth, samples were watered every one, two, three or 10 days or visually kept damp. Watering was before daylight with 40 mL distilled water, except the one day treatment that received 30 mL so it was not flooded.

2.3. Statistical Analyses

Microcosms were photographed after set up and six weeks later to assess changes in live biocrust cover over time. Pictures were cropped and edited to enhance colours and minimize shadows, then analyzed using SamplePoint (Booth et al. 2006). A 12 x 12 grid was overlaid on each picture (144 points), and each point was manually identified as live or dead lichen species, mosses, other, or litter, substrate, or unknown (unidentifiable). Dead lichens were identified by changes in colour and form. The number of live lichen points was divided by [total number of points minus number of unknown points] to estimate percent live lichen in each microcosm, then the difference between the start and end values were analyzed to determine effects on lichen survival over time.

Model estimation and statistical analyses were conducted using R (Version 4.0.2, 2020). ‘No lichen’ inoculation treatments used as a negative control for the experiment did not contain or develop live lichen at either time in any replicate, so were removed prior to statistical analysis. Models were fitted with the lm function and analyzed for all two-way interactions. Fixed effects were substrate and sterilization in Experiment 1, substrate and lichen community composition in experiment 2, substrate and substrate depth in experiment 3, and substrate and watering treatment in experiment 4. Pair-wise comparisons within each treatment or interaction were conducted with a Tukey post hoc test, adjusted for multiple comparisons. Substrate P values were adjusted using a Bonferroni correction to account for use in four separate tests. Plots were made using the ggplot2 package (Wickham 2016).

3. RESULTS

Percent live lichen cover declined in almost every treatment over six weeks. The exceptions were sieved mix on tundra soil watered every 3 days, and 1 cm depth sieved mix (Figure 5.2).

The decline in live lichen cover did not differ between substrates for either sterilization treatment (Table 5.2, Figure 5.2a). The numerically larger decline for live lichen cover on sterilized than unsterilized substrates was not significant.

A two way interaction was significant for substrate and lichen species composition (Table 5.2, Figure 5.2b). Change in lichen cover for *Flavocetraria cucullata* on crushed rock was the main driver for interaction, as it decreased 40.7 %, with approximately six times greater decline than *Flavocetraria cucullata* on tundra soil, and was significantly different from all other treatments. (Table 5.2, Figure 5.3b). While unsieved mix on crushed rock declined nine times more than unsieved mix on tundra soil, no other treatments were significantly different.

Substrate and the two way interaction between substrate and substrate depth were not significant (Table 5.2, Figure 5.2c). Live lichen cover increased on 1 cm substrate (4.3 %, Figure 5.3a), but decreased for 1.5 cm (0.9 %) and 2 cm (6.8 %). A 2 cm depth was significantly different from 1 cm but not 1.5 cm.

The two way interaction between substrate and watering on change in live lichen cover between weeks 0 and 6 was not significant (Table 5.2, Figure 5.2d). Damp crushed rock exhibited the greatest decline in live lichen cover (44.1 %); three day watering on tundra soil was the only watering frequency to increase lichen cover (2.6 %). Substrate and watering treatments were each significant. Crushed rock had greater decreases in live lichen cover (18.1 %) than tundra soil, (9.3 %). Damp treatments had largest decreases in live lichen cover (32.8 %), followed by one day watering (22.3 %). Damp and one day watering were not significantly different, but were significantly different from all other treatments. Two, three, and ten days between waterings were not significantly different (decreases 6.8, 1.7, 3.5 %, respectively).

4. DISCUSSION

4.1. Sterilization

Autoclaving of substrates prior to growth chamber experiments is common and sometimes required to prevent overgrowth of algae or other microbiota in substrates (Dibben 1971, Maestre et al. 2006). Sterilization was not necessary for our substrates as we did not observe any

contamination, and unsterilized microcosms did not exhibit significantly greater lichen loss. Zhao et al. (2014) did not sterilize substrates and had no issues with contamination after 10 weeks. Muczynski (2014) found unautoclaved treatments had more chlorophyll a than autoclaved after mixed culture inoculation with cyanobacteria and green algae, indicating soil organisms may be beneficial for biocrust growth.

4.2. Lichen Species Composition

The large decline of *Flavocetraria cucullata* on crushed rock relative to the smallest decline of unsieved mix on tundra soil indicates reclamation experiments must account for specific species' survival, which may depend on substrate, and that biocrust survival is likely higher as a mix than as individual species. This was similar to our field study results (Ficko et al., in prep), where substrates affected species composition and persistence after three field seasons.

Effect of substrate properties on biocrust survival has not been well studied, although several studies showed soil pH can influence lichen composition and distribution (Gould and Walker 1999, Löbel et al. 2006, Zraik et al. 2018). The much higher pH of crushed rock than tundra soil may account for greater decline of *Flavocetraria cucullata* relative to sieved and unsieved mixes, as greater species diversity in mixes meant some species may have been less affected by higher pH. Differences in substrate texture and organic matter may have influenced lichen survival. Several studies found lichen species prefer loamy or fine textured clay loam soil over sandy or coarse textured sandy loam soil (Eldridge and Greene 1994, Antoninka et al. 2020a). While crushed rock had a loamy sand texture, and tundra soil a sandy loam texture, crushed rock visually formed a hard surface crust after wetting and drying, likely due to lower organic matter and sedimentation. Water was unable to infiltrate as quickly on crushed rock, likely due to the surface crust, which left lichens wetter for longer (see Watering Frequency below). *Flavocetraria cucullata* fragments generally lie closer to the surface than sieved or unsieved mixes, as shape and size were more uniform so had less variable microtopography to lift them off the substrate surface.

4.3. Substrate Depth

As distance from the overhead lights in the chambers was not standardized between depth treatments, differences in results may be due to substrate depth and/or environmental factors such as surface substrate temperature and drying rates. Substrates in 1 cm treatments likely dried faster than deeper substrates. Crusts on 2 cm depth were closer to tops of microcosms, with potentially greater air flow than more sheltered 1 cm microcosms. In our experiment, 1 cm

substrate depth was most suitable; our selected 2 cm baseline may have negatively influenced results in other experiments.

4.4. Watering Frequency

Water on crushed rock was not absorbed as rapidly as on tundra soil, so lichens had a greater chance of longer suprasaturation (Lange 2001). Lichens are poikilohydric organisms, and many species tolerate extensive desiccation with few physiological effects (Kranner et al. 2008, Green et al. 2018). However, high thallus water content hinders net photosynthesis for numerous species by increasing CO_2 diffusion resistance, with maximum net photosynthesis occurring over a very small thallus hydration range (Lange 2001). Many green algae lichens can photosynthesize from dew or high humidity alone (Lange et al. 1986). As species in our study were mostly green algal lichens and naturally grow with low precipitation, frequent watering (damp, one day) with humidity 65-75 % in the growth chamber, likely suprasaturated the thallus and decreased net photosynthesis, which negatively affected lichen survival. Lichens with ten day watering may not have declined in cover as they are physiologically inactive when dry (Kranner et al. 2008). Lichen with three day watering and tundra soil increased cover; we hypothesize that this treatment had adequate water and humidity, while also minimizing suprasaturation.

5. IMPLICATIONS FOR PRACTICE

- Substrate properties and species composition must be considered in future biocrust growth chamber experiments, as mixed species declined less than single species, and substrate affected survival over time.
- We recommend using a three day watering frequency and a 1 cm substrate depth for microcosms similar to the ones in our study; substrate sterilization was unnecessary, at least in the short term.
- Only a few treatments increased live lichen cover, demonstrating the challenges of growing lichen biocrusts under controlled conditions.
- Assessment of reclamation treatments in short term growth chamber experiments has potential to screen and select treatments prior to field experimentation.

Table 5.1. Experimental design for Experiments 1-4. Experiment 1 assessed substrate sterilization (autoclaved, unautoclaved), Experiment 2 assessed lichen species composition (*Flavocetriaria cucullata*, none, sieved mixed species, unsieved mixed species), Experiment 3 assessed substrate depth (1, 1.5, 2 cm), Experiment 4 assessed watering frequency (damp; 1, 2, 3, 10 day).

Treatment #	Substrate	Sterilization	Inoculation	Watering	Depth (cm)	Reps
Experiment 1: Substrate Sterilization						
2	Crushed rock	Not autoclaved	None	2-day	2	5
10			Sieved mix	2-day	2	5
1		Autoclaved	None	2-day	2	5
5			Sieved mix	2-day	2	5
14	Tundra soil	Not autoclaved	None	2-day	2	5
22			Sieved mix	2-day	2	5
13		Autoclaved	None	2-day	2	5
17			Sieved mix	2-day	2	5
Experiment 2: Lichen Species Composition						
1	Crushed rock	Autoclaved	None	2-day	2	5
6			*F. cucullata*	2-day	2	5
5			Sieved mix	2-day	2	5
7			Unsieved mix	2-day	2	5
13	Tundra soil	Autoclaved	None	2-day	2	5
18			*F. cucullata*	2-day	2	5
17			Sieved mix	2-day	2	5
19			Unsieved mix	2-day	2	5
Experiment 3: Substrate Depth						
8	Crushed rock	Autoclaved	Sieved mix	2-day	1	5
9					1.5	5
5					2	5
20	Tundra soil	Autoclaved	Sieved mix	2-day	1	5
21					1.5	5
17					2	5
Experiment 4: Watering Frequency						
3	Crushed rock	Autoclaved	Sieved mix	Damp	2	5
4				1-day	2	4
5				2-day	2	5
11				3-day	2	4
12				10-day	2	5
15	Tundra soil	Autoclaved	Sieved mix	Damp	2	5
16				1-day	2	5
17				2-day	2	5
23				3-day	2	5
24				10-day	2	5

Table 5.2. ANOVA and Tukey test pair-wise comparisons where applicable for change in live lichen cover between week 0 and week 6 for each experiment. CR = crushed rock, TS = tundra soil, FC = *Flavocetraria cucullata*, SM = sieved mixed species, UM = unsieved mix species.

	DF	F	Adj R^2	P	diff	lwr	upr	P adj
Experiment 1: Substrate Sterilization			-0.1591					
Substrate	1	0.0097		1.0000				
Sterilization	1	0.3526		0.5610				
Substrate x sterilization	1	0.0302		0.8643				
Residuals	16							
Experiment 2: Lichen Species Composition			0.6532					
Substrate	1	18.742		**0.0009**				
Species composition	2	11.602		**0.0003**				
Substrate x species composition	2	8.832		**0.0013**				
TS:FC-CR:FC					0.3406	0.1591	0.5220	**<0.0001**
CR:SM-CR:FC					0.3382	0.1568	0.5197	**<0.0001**
TS:SM-CR:FC					0.3408	0.1594	0.5223	**<0.0001**
CR:UM-CR:FC					0.2986	0.1172	0.4801	**0.0004**
TS:UM-CR:FC					0.3955	0.2140	0.5770	**<0.0001**
CR:SM-TS:FC					-0.0024	-0.1838	0.1791	1.0000
TS:SM-TS:FC					0.0002	-0.1812	0.1817	1.0000
CR:US-TS:FC					-0.0420	-0.2234	0.1395	0.9782
TS:UM-TS:FC					0.0549	-0.1265	0.2364	0.9331
TS:SM-CR:SM					0.0026	-0.1789	0.1841	1.0000
CR:UM-CR:SM					-0.0396	-0.2211	0.1419	0.9831
TS:UM-CR:SM					0.0572	-0.1242	0.2387	0.9211
CR:UM-TS:SM					-0.0422	-0.2237	0.1393	0.9777
TS:UM-TS:SM					0.0547	-0.1268	0.2361	0.9342
TS:UM-CR:UM				0.5750	0.0969	-0.0846	0.2783	0.5750
Residuals	24							
Experiment 3: Substrate Depth			0.0984					
Substrate	1	0.0036		1.0000				
Depth	2	4.0353		**0.0309**				
1.5-1					-0.1502	-0.1502	0.0455	0.3897
2-1					-0.1113	-0.2091	-0.0134	**0.0237**
2-1.5					-0.0589	-0.1568	0.0390	0.3072
Substrate x depth	2	0.0456		0.9555				
Residuals	24							

	DF	F	Adj R^2	P	diff	lwr	upr	P adj
Experiment 4: Watering Frequency			0.6553					
Substrate	1	10.0470		**0.0120**				
Watering	4	19.9778		**<0.0001**				
Damp-1					-0.1005	-0.2246	0.2360	0.1613
Damp-2					-0.2604	-0.3811	-0.1396	**<0.0001**
Damp-3					-0.3067	-0.4308	-0.1826	**<0.0001**
Damp-10					-0.2930	-0.4138	-0.1722	**<0.0001**
2-1					0.1599	0.0358	0.2840	**0.0060**
3-1					0.2062	0.0789	0.3335	**0.0004**
10-1					0.1925	0.0684	0.3166	**0.0007**
3-2					0.0463	-0.0778	0.1704	0.8211
2-10					-0.0326	-0.1534	0.0882	0.9368
3-10					0.0137	-0.1104	0.1378	0.9977
Substrate x watering	4	2.1001		0.0998				
Residuals	38							

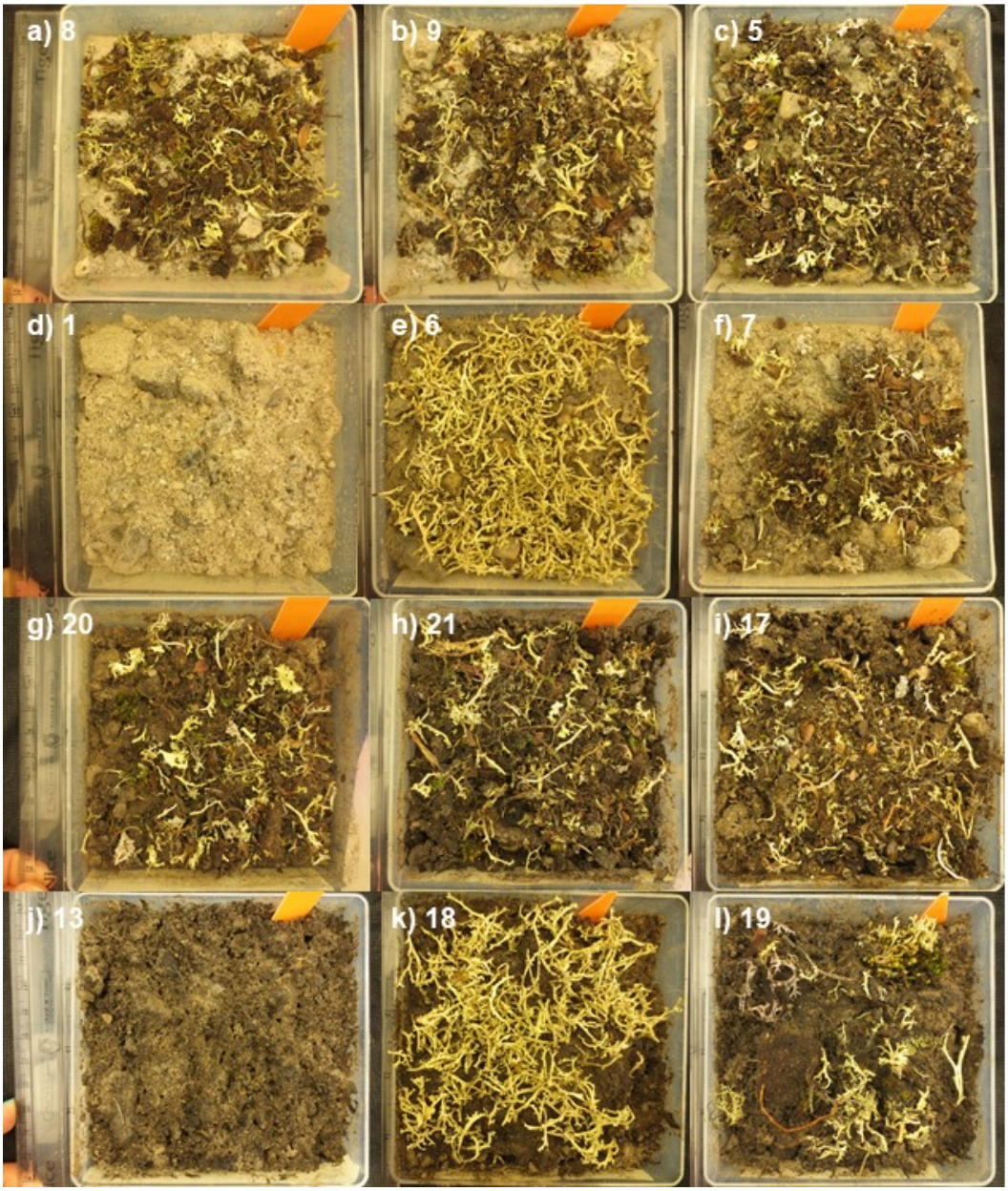

Figure 5.1. Images of microcosms at start of the experiment on crushed rock (a-f) and tundra soil (g-l), by depth (a and g = 1 cm, b and h = 1.5 cm, c and i = 2 cm) and lichen species composition (d and j = none, e and k = *Flavocetraria cucullata*, c and l = sieved mix, f and l = unsieved mix). Numbers after the letter correspond to treatments in Table 5.1.

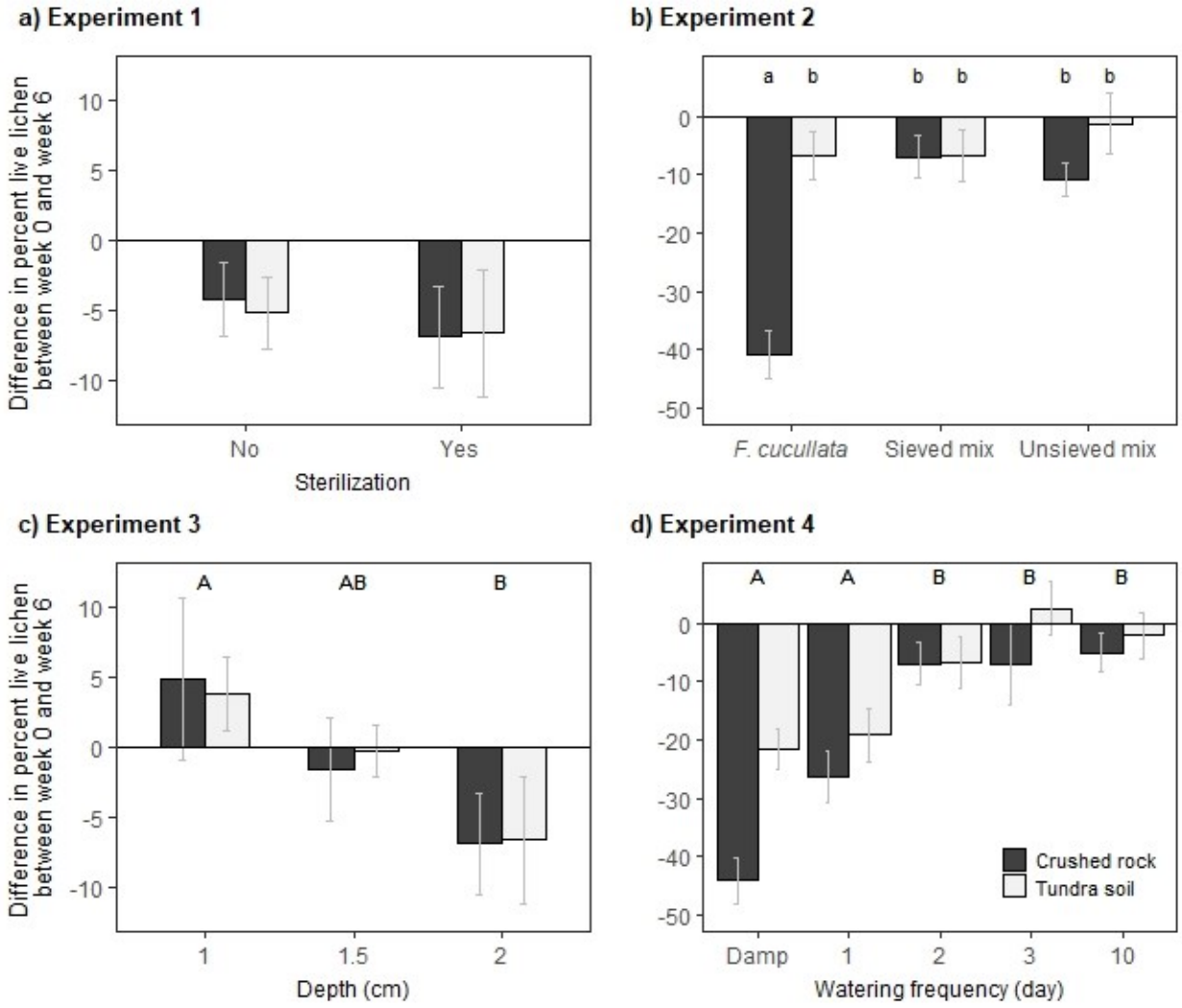

Figure 5.2. Change in live lichen cover between weeks 0 and 6 for a) sterilization, b) lichen species composition (*Flavocetraria cucullata*, sieved mixed lichen, unsieved mixed lichen), c) substrate depth (cm), and d) watering frequency (day) on crushed rock (black bars) and tundra soil (grey bars). Each bar represents the mean (n = 5) and error bars represent standard errors. Upper case letters above bars (c, d) indicate significance for the x-axis treatment; lower case letters above bars (b) indicate significance for the interaction between lichen species composition and substrate. Pair-wise comparisons are listed in Table 5.2. Baseline conditions were autoclaved substrate, sieved mixed species, 2 cm substrate, and two day watering.

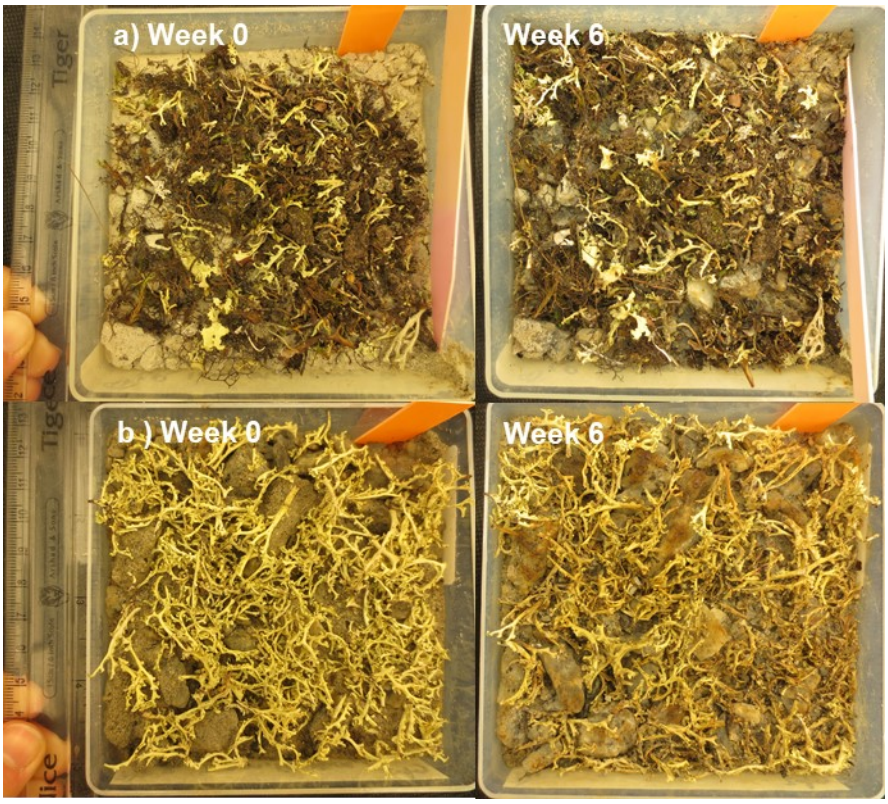

Figure 5.3. Images showing examples of change in live lichen cover between week 0 and week 6 for a) sieved mix species on 1 cm depth crushed rock (increase in live cover of 4.9 %), and b) *Flavocetraria cucullata* on crushed rock (decrease in live cover of 40.7 %).

VI. SYNTHESIS OF RESEARCH

1. INTRODUCTION

Vegetation removal and changes in soil properties due to increased exploration and resource extraction in northern environments can create long lasting disturbances that can affect arctic ecosystem functions and services. While most research to date has focused on a single plant species or a few at a time, successful revegetation of these disturbed environments requires acquisition and propagation of plant material from multiple vascular and non vascular species that can tolerate current site conditions (disturbed soils and/or anthroposols), while facilitating succession towards the desired plant community. Northern revegetation practices are inherently limited by harsh environmental conditions, and currently exacerbated by lack of sources of native plant material, high transportation costs, and lack of reclamation regulations. Even with decades of research, effective large scale methods to reclaim disturbed northern environments to pre-disturbance plant communities have yet to be developed despite significant changes in management strategies over time. The critical need for northern revegetation methods continues to grow as northern exploration and development rapidly increase.

2. RESEARCH SUMMARY

This research program was designed to begin to address the major gaps in northern revegetation by assessing and developing techniques for integrated tundra communities with a mosaic of species similar to that in undisturbed areas. Our research conducted in the field at Diavik Diamond Mine Inc, Northwest Territories, Canada (Diavik), and in growth chambers at the University of Alberta, focused on shrub species and lichen biocrusts, the dominant vegetation in shrub heath tundra in upland areas at Diavik. As very little research has been done on community focused reclamation in the north, we conducted a number of large scale growth chamber and field studies to develop a baseline understanding of species behaviours under a variety of conditions that can be used to inform current reclamation practitioners and guide future research directions. We focused on developing and improving methods to propagate and grow cuttings from native shrub species and lichen biocrusts for reclamation of harsh northern environments.

2.1. Shrub Cutting Research

Shrub cuttings were selected for this research, rather than seeds, as they have a high potential to provide a consistent source of plant material for timely reclamation of large areas. We

conducted two growth chamber experiments to examine the effects of common and alternative rooting techniques on adventitious and lateral root development on cuttings from eight arctic shrub species to optimize root system architecture for revegetation. After 60 days in a growth chamber, all eight species developed at least primary and secondary roots in at least one season in one experiment, including one previously undocumented species, *Kalmia procumbens* (L.) Gift, Kron, & P.F. Stevens ex Gala (alpine azalea). Rooting characteristics were highly variable, with 3 to 94 % of cuttings that rooted, and 1 to 117 roots per cutting across species, seasons, and experiments. Novel treatments of *Salix* water extract and smoke water extract were applied for the first time with cuttings from northern shrub species. While rooting percentages were low for seven of the eight species, species specific interactions between season and *Salix* water extract and smoke water extract occurred.

Over 80 % of fall and spring *Salix* cuttings developed adventitious roots, yet only 30 % of summer cuttings rooted, indicating strong seasonal influences. Many cuttings developed extensive root system architecture in 60 days; some developed up to six orders of roots. Root length decreased with increasing root order in all seasons, and season influenced length within root orders. Application of IBA increased number of primary roots per cutting per season, and number of cuttings with < 50 secondary roots per primary root. Longer soaking times increased the number of primary roots per cutting in different seasons, and soaking up to 10 days increased the longest root length. *Salix* and smoke water extract applications increased number of cuttings with 25 to 74 secondary roots per primary root.

2.2. Lichen Biocrust Research

2.2.1. Field research

No known research addressed propagation and dispersal of lichen dominated biocrusts for reclamation in arctic tundra. We assessed establishment of lichens associated with lichen biocrusts on mining by-products (crushed rock, lake sediment, processed kimberlite), with inoculant dispersal (dry placement, slurry), habitat amelioration techniques (erosion control blanket, tundra soil, woody debris), and jute mat containment over three field seasons at Diavik. Three years after inoculation, lichens were detected on 100 % of inoculated plots and 70 % of uninoculated plots (likely blown in from inoculated plots). Uninoculated plots had significantly lower species richness and vegetation cover than inoculated plots. Biocrust retention was greatest on plots with erosion control blanket, jute mat containment, woody debris, and crushed rock. Plots with processed kimberlite, no habitat amelioration or tundra soil, and no jute mat containment had lowest cover, species richness, and individual species abundance. Our research was the first to

highlight the importance and effectiveness of inoculation and habitat amelioration techniques for biocrust reclamation on different mining by-products in the north.

2.2.2. Growth chamber research

Optimal growth chamber conditions for lichens and lichen biocrusts have rarely been assessed, and no known studies using northern biocrusts were found. To enable further investigations of reclamation treatments under controlled conditions with northern biocrusts, we assessed the effects of substrate, substrate depth, substrate sterilization, lichen inoculation and community composition, and watering frequency on survival of arctic biocrusts collected from Diavik in a six week growth chamber experiment. Mixed species (sieved or unsieved) had less decline in live lichen cover than an individual species (*Flavocetraria cucullata*), and substrate interacted with species inoculation to affect species survival over time. We found that a three day watering frequency and a substrate depth of 1 cm resulted in the lowest decline in live lichen cover. Sterilization of substrates by autoclaving did not affect lichen survival, and no contamination was observed over six weeks on either sterilized or unsterilized substrates. Our results highlighted the challenges of growing lichens under controlled conditions as in only a few treatments did live lichen cover increase.

3. RESEARCH APPLICATIONS FOR RECLAMATION

Three northern diamond mines in Canada are slated to close within the next fifteen years, and will require revegetation of multiple hectares of disturbed land, as will other northern disturbances. Developing effective community focused revegetation strategies is vital to ensure future ecological structure and functions of these areas. The multi-faceted research we conducted investigating reclamation techniques for both shrubs and lichen biocrusts provides an important stepping stone on the pathway towards community focused revegetation of disturbed areas.

3.1. Shrub Research

All eight shrub species studied have the capacity to grow adventitious roots from cuttings, including multiple higher orders of roots for most species. This is an important finding for using vegetative propagation for shrub species that lack reliable seed sources, as reclamation practitioners could use a higher cutting rate to account for low rooting percentages in some circumstances. For five species (*Arctous rubra* (Rehder & Wilson) Fernald (red bearberry), *Betula glandulosa* Michx. (bog birch), *Kalmia procumbens* (L.) Gift & Kron & P.F. Stevens ex Galasso, Banfi & F. Conti (alpine azalea), *Rhododendron tomentosum* Harmaja (marsh Labrador tea),

Vaccinium uliginosum) L. (bog bilberry), maximum rooting potential never exceeded 20 % within a season, indicating that common revegetation techniques using indole-3-butyric acid (IBA) growth hormones and/or soaking, and novel treatments of *Salix* water and smoke water, were insufficient to promote consistent root development. As there were small but observable differences in rooting between seasons, season of collection may be a critical factor to enhance rooting in the future once other treatments or management strategies can be found that induce more reliable rooting. *Empetrum nigrum* L. (crowberry) and *Vaccinium vitis-idaea* L. (bog cranberry) had variable rooting, with 40 and 55 % rooting, respectively, in one season in one experiment, but 0 and 10 %, respectively, in the corresponding season in another experiment. Similarly, all seven species had highly variable numbers of roots per cutting, indicating the need to better understand what other genetic, physiological, and/or environmental factors are affecting and potentially controlling rooting behaviour of these shrub species.

Salix species are frequently used in research experiments as many readily develop adventitious roots on cuttings, so the high rooting in both experiments was not unexpected. Based on our results, collection of dormant *Salix* cuttings is recommended to maximize reclamation success, as season had the strongest influence on rooting. Given that neither IBA concentration nor soaking strongly influence rooting percentages for *Salix* cuttings, reclamation practitioners can choose to directly plant *Salix* cuttings without application of either treatment. However, if logistical issues arise after collection but prior to planting, our results indicate that *Salix* cuttings could be soaked for up to three weeks without significant adverse effects. To date, the effects of treatments on both adventitious and lateral root development from adventitiously derived root systems have rarely been presented in the literature for any species, especially arctic species. Our results demonstrate that the common and novel treatments used in our study affected primary and secondary root development differently. This is an important finding as it means that reclamation practitioners can, and must, carefully select and balance treatments to optimize root system architecture for specific site conditions.

3.2. Biocrust Research

Biocrust inoculation effectively increased species richness and cover on three mining by-products in the first study using lichen biocrusts in the arctic. Lichens on inoculated plots were observed blowing between plots in our study, dispersing propagules to uninoculated areas. As biocrust collection presently creates further disturbances, creating small islands with biocrust inoculant and allowing wind dispersal to distribute crust material to adjacent areas could reduce the amount of material required for larger scale projects. Biocrust survival was greater on crushed

rock and lake sediment than on processed kimberlite, and similar to results with graminoids and bryophytes previously conducted in the Naeth lab, we do not recommend unamended processed kimberlite for reclamation. Habitat amelioration and containment techniques that increased microtopographic variability, including erosion control blanket, jute mat, and woody debris, had more consistent and predictable responses for retaining biocrust material on our small field plots. As species specific responses to treatments were observed between years 2 and 3, longer term assessments are needed to determine if species composition can be maintained and if the inoculated species can provide desired ecological functions in future. We recommend assessment and a cost-benefit analysis for larger scale field application of biocrust inoculation on erosion control blanket, jute mat, and woody debris on different substrates or amended substrates, to determine the treatment with greatest potential for effective biocrust reclamation at Diavik and other disturbed arctic environments.

Results from the growth chamber experiment provide guidance for desirable growth chamber conditions for future experiments with lichen biocrusts. We found that substrate sterilization was not necessary, and recommend inoculating with a mix of biocrust species, a substrate depth of 1 cm, and a three day watering frequency for microcosms, similar to those used in our study. As lichens generally had a greater decline in live cover on crushed rock than on tundra soil, we recommend that future studies assess different amendments mixed with crushed rock such as tundra soil, sewage, compost, or peat to lower pH and increase organic matter to determine if amended mining by-products can provide suitable substrate material for lichen biocrusts.

Overall, the information gained from this research is foundational for developing community focused revegetation plans at Diavik. Results can be extrapolated to reclamation of other northern disturbances with similar pre-disturbance vegetation communities.

4. RESEARCH LIMITATIONS AND FUTURE CONSIDERATIONS

Resource extraction and exploration over the past two centuries in Canada’s north have created numerous large scale disturbances, significantly affecting above and below ground ecosystems. Reducing the scope, extent, and magnitude of future projects using sustainable and ethical development practices can help conserve and protect slow growing tundra species that are already under stress due to climate change. For current and past disturbances, closure plans must balance site design, local environmental conditions, practical and desired reclamation goals, and logistical challenges and costs associated with reclamation. Current guidelines in North West

Territories, Canada require sites to be left safe for animals and people, but do not specify specific revegetation requirements. Successful reclamation will require improving soils or building new substrates with suitable properties to support and sustain establishment and growth of desired species, and development of revegetation techniques for the acquisition, propagation, and management of plant material for the creation of extensive, integrated tundra communities with appropriate structure and ecological functions. For future projects, collaboration with Indigenous communities and incorporation of their traditional ecological knowledge to help guide location and scope of large scale projects, and minimize their potential impacts, will be vital to meet the long term needs of the communities who live on and use the land.

4.1. Substrate Source And Properties

Development of anthroposols (human made soils) to support vegetation is an important step in mine closure plans, particularly for remote sites where importing large amounts of materials is not cost effective. Properties of materials available on site in large quantities for substrate development must be evaluated to determine if they meet the needs of various species in different plant communities. For example, substrate nitrogen, phosphorus, and organic matter are generally most important for vascular plants, while substrate pH, texture, and organic matter can affect biocrust species composition. Given the lack of precipitation at Diavik, substrate water holding capacity and changes in hydrology due to mining must also be considered. In some cases, substrate properties such as elevated metals in processed kimberlite, or high sulphur content in some soils, must be taken into consideration to ensure accumulation in the food chain does not occur. If needed, substrates can be amended to address deficits in substrate properties, preferably using materials available on site, such as sewage, compost, or tundra soil, although importing amendments may be necessary in some cases. If sufficient amendments are unavailable, creating islands across the reclamation sites with amended areas interspersed among unamended areas has potential to allow egress of species over time. Anthroposol development is a growing area of research in the Naeth lab and elsewhere, and future studies are needed to investigate how environmental and substrate properties such as temperature, humidity, slope, aspect, microtopography, salinity, and nutrients in amended or unamended substrates interact to support growth and succession of different species.

4.2. Vegetation Response And Material Limitations

Vegetation recovery following disturbances in the north are influenced by abiotic and biotic factors such as soils, disturbance footprint, air temperature, precipitation, soil water content, pre-

disturbance vegetation, and availability of seeds and propagules for colonization. Natural recovery in the north is a much longer and slower process than in more temperate climates, and large scale disturbances remove access to natural seedbanks and proximity to vegetation sources that could inoculate substrates. Assisted revegetation is often used to accelerate vegetation establishment and growth, but is limited by lack of seed suppliers carrying sufficient quantities of seeds for native species, and appropriate species diversity for shrub heath tundra environments. Past efforts to revegetate using agronomic grasses and legumes have rarely been effective, as many such species did not survive the harsh northern environments, or rapidly developing large fibrous root systems prevented establishment and growth of native species. Current assisted revegetation techniques, such as seeding commercial or wild collected native seed, propagating native shrub cuttings, transplanting vegetation islands, and inoculating with non vascular species, seek to overcome these issues, but continue to face significant challenges; this research focused on two of those areas, but many questions still need to be addressed.

4.2.1. Shrubs

From this research, variability in rooting within many species highlights the need to determine what other physiological, genetic, and environmental factors are affecting rooting behaviour, including cutting ontogenetic age, location on a donor plant (terminal or lateral shoot), donor plant physiological status (carbohydrate concentration, carbon:nitrogen ratio, nutrient status, water status), photoperiod, seasonal influences, and weather conditions the preceding year. Questions specifically raised by our research include determining levels of endogenous auxins in different species throughout the growing season, and if interactions between endogenous and exogenous growth hormones are occurring; deciphering how species specific differences in concentrations of various hormones, growth regulators, and partitioning of carbohydrates between dormant and actively growing shrub cuttings influence adventitious and lateral root development and callus formation at different times of year in different species; deciphering the physiological mechanisms underlying how soaking time impacts rooting, and how this varies by season; and deciphering mechanisms of action for karrikins and strigolactones, and biostimulants such as *Salix* water extract given there were differences in response between adventitious and lateral root development in our study. For *Salix* species, field trials should be conducted to determine if cuttings planted directly in the field still have high rooting percentages and survival over multiple growth seasons. Research is needed to compare root system architecture of mature shrubs from different species grown in the field versus adventitiously developed root systems on plants grown from cuttings in pots and transplanted into the field to provide further insight into revegetation practices for disturbed environments.

Assessment of different photoperiods, propagation media, and air temperatures, and use of common horticultural procedures for hard to root species such as intermittent mist chambers, bottom heat, and high humidity, should be investigated to determine if they improve rooting. If consistent rooting can be induced, a cost-benefit analysis must take into account costs associated with collection, propagation, and transportation of sufficient quantities of cuttings to greenhouse facilities and rooted cuttings back to site, versus development of greenhouse facilities onsite or in nearby communities. Costs associated with labour for planting must also be included. If consistent rooting cannot be induced, collection of native shrub seeds and research to ensure consistent germination in sufficient quantities for large scale seeding at appropriate times for reclamation will become necessary.

4.2.2. Biocrusts

Despite the importance of biocrusts in many ecosystems, little research has been conducted on how to incorporate them into revegetation plans, particularly for disturbed northern environments. The majority of studies support use of biocrust inoculation to increase species richness, cover, and abundance following disturbances, particularly for interior areas far from vegetative sources of propagules. While techniques to mass culture various biocrust species are being investigated, culturing lichen species has yet to be successful, and suitable species compositions for different environments are still unknown. At present, inoculation generally requires collecting crust material from an undisturbed area for use on the reclamation site creating further disturbances, unless material can be salvaged prior to disturbance from the site or a nearby location. As biocrust organisms have high desiccation tolerance, future research investigating propagule density and species survival in stockpiles may lead to methods to preserve salvaged material as an inoculant source for reclamation. Collection methods and costs must be considered as tundra soil is rarely preserved due to challenges of working with heavy equipment on rocky terrain, and current techniques for seeding vascular plants, such as drill, broadcast, aerial, or hydroseeding, have yet to be adapted for dispersing large quantities of inoculant. As our results showed no difference in survival between dry and slurry inoculation, both techniques can be explored for large scale inoculation on northern sites.

Assessing the effect of different reclamation techniques on lichen biocrust growth is challenging in the north due to short growing seasons, harsh conditions, and slow growth for many species. Understanding factors limiting recovery under controlled conditions can accelerate recovery in the field. Our growth chamber results provided initial conditions for northern biocrust species, but factors that require further investigation include light intensity, daylight length, air temperature, humidity, and longer growing times. Field techniques to be investigated include large

scale application of erosion control blankets, jute mats, and woody debris to determine their effects on biocrust survival. Other strategies to be assessed include shading plots to decrease direct UV exposure; dispersing inoculant in seasons with higher precipitation, soil water, and lower temperatures; irrigating biocrusts following dispersal although amount and frequency of irrigation are unknown. There are challenges with large scale irrigation, creating microtopographic variability, and dispersing larger fragments or mats of biocrust material. Techniques for non destructive long term monitoring of plots will be required to ensure development of desired ecological functions over time, for mitigation implementation if desired successional trajectories are not being achieved.

4.2.3. Development of integrated tundra communities

Revegetation in the north has evolved over the past half century from avoiding using any vegetation to prevent erosion; to seeding early successional agronomic species to quickly provide cover, improve soil properties, and prevent erosion; seeding early successional native species adapted to the harsh northern conditions; and most recently, using a variety of techniques, including seeding native species, propagating native shrub cuttings, and transplanting salvaged vegetation islands to accelerate development of self sustaining plant communities. However, our desire to revegetate disturbed areas to pre-disturbance conditions has yet to be achieved based on our current strategies and techniques. Specifically, the lack of inclusion of non vascular species in reclamation plans is a serious limitation for development of shrub heath tundra. Our research on shrub cuttings and lichen biocrusts provides a critical foundation for future work that specifically investigates how to build integrated tundra communities. Future steps include understanding how to incorporate different vegetation types, either together or at different times, in conjunction with anthroposol development and placement that meets the current and future needs of different species and communities.

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