Root development on cuttings of seven arctic shrub species for revegetation
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ABSTRACT
Vegetation removal during resource extraction in the Arctic causes long-lasting impacts requiring revegetation to accelerate plant reestablishment. This study focused on root development on shrub cuttings from seven common species at Diavik Diamond Mine, Northwest Territories. Two experiments were conducted; the first had six soaking times (zero, one, three, five, ten, twenty days), four indole-3-butyric acid (IBA) concentrations (0, 0.1, 0.4, 0.8 percent), and three seasons (summer, fall, spring). The second had a control, three IBA concentrations (0.1, 0.4, 0.8 percent) or alternative chemical compounds, either three Salix water or three smoke water extracts, in two seasons (summer, fall). After sixty days, all species developed at least primary and secondary roots in at least one season in one experiment, including one previously undocumented species, Kalnias procumbens. Rooting characteristics were highly variable, with maximum percentage of rooted cuttings from 3 to 55 percent and maximum number of roots per cutting from 1 to 117 across species, seasons, and experiments. Though rooting percentages were low, species-specific interactions between season and Salix water extract and smoke water extract were observed. Assessing multiple species highlights the potential of vegetative propagation to reforest northern disturbed sites with common species that lack reliable seed sources.

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 belowground mining activities, and waste rock piling (Couch 2002; Drozdowski, Naeth, and Wilkinson 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, Boudreau, and Harper 2009; Ficko, Smith, and Zeeb 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, Ebersole, and Strandberg 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 toward 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 that dominate many tundra communities (Elliott, McKendrick, and Helm 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).

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Vegetative propagation of shrub species by cuttings is labor 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; Wright 2008; McTavish and Shopik 2010; 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, Vander Meer, and Dunkle 2000; Walter et al. 2005; Naeth and Wilkinson 2011; Ficko, Smith, and Zeeb 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 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 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 belowground 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 have not been investigated to date as a stimulant for rooting of woody cuttings (Pierce, Esler, and Cowling 1995; Keely and Fotheringham 2000; Adkins and Peters 2001; Yao, Naeth, and Mollard 2017; Mackenzie and Naeth 2019). 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, Vander Meer, and Dunkle 2000; Walter et al. 2005). Soaking one to ten days has promoted adventitious root formation, mostly on *Salix* species, indicating the need to research the effect of soaking on multiple other species (Schaff, Pezeshki, and Shields 2002; Pezeshki et al. 2005; Walter 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 whether 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 whether 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.

**Materials and methods**

**Study site**

Diavik Diamond Mine (Diavik) is located approximately 320 km northeast of Yellowknife, Northwest Territories (64°30'41" N, 110°17'23" W), on an island in the middle
of Lac-de-Gras, 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 of 299 mm (45 percent as rain) and mean annual temperature of −9°C. Mean monthly temperatures in the growing season were 8°C, 14°C, and 11°C, 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, Anne Naeth, and Wilkinson 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, Anne Naeth, and Wilkinson 2012).

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 less than 10-cm 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 less than 5 cm to 25 cm. Nomenclature for species from Diavik follows Northwest Territories Species Infobase (Government of the Northwest Territories 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 stored at 4°C until planting within one week of collection.

Two screening experiments were conducted to investigate effects of common horticultural and novel treatments on root initiation and development over sixty days in a growth chamber (Table 1). The first experiment was three factorial with seventy-two 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 (zero, one, three, five, ten, and twenty days) and a concentration of IBA (0, 0.1, 0.4, and 0.8 percent) (Stim Root #1, #2, #3, respectively).

The second experiment was two factorial with nine treatments and one control (Table 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 percent 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 1,200 mL of cuttings in 2,400 mL boiling distilled water to soak for 12 hours to make three Salix water concentrations (0.5, 1, and 2, respectively). Smoke water extracts were prepared by placing 4 L distilled water in a smoker with 1.2 kg wood chips for 4 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).

Planting and soaking

Growth chamber conditions for both experiments mimicked growing conditions at Diavik. Conditions were set at 17°C during the day for 16 hours and 10°C at night for 8 hours for experiment 1 and at 17°C during the day for 20 hours and 10°C 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 1). For experiment 2, each cutting was planted in an individual container.

Measurements

Shoot height and vigor of each cutting were assessed at thirty and sixty days using a five-point scale with 1 = dead, 2 = poor (plant mostly dead or dying, <30 percent live green tissue), 3 = fair (average health and
Table 1. Species, treatments, and replication for experiments 1 and 2 in different seasons.

| Species            | Experiment | Season | Soak (d) | Treatment | Replicate cuttings per treatment | Pots per treatment | Cuttings per species | Pot size (cm) |
|--------------------|------------|--------|----------|-----------|----------------------------------|-------------------|---------------------|---------------|
| Arctous rubra      | 1          | Summer | 0, 1, 3, 5, 10, 20 | IBA (%) 0, 0.1, 0.8 | 3 | 1 | 54 | 6.5 × 6.5 × 6.5 |
|                    | 1          | Fall   | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 3 | 1 | 72 | 6.5 × 6.5 × 6.5 |
|                    | 1          | Spring | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 9 | 3 | 216 | 6.5 × 6.5 × 6.5 |
|                    | 2          | Fall   | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 4.2 × 4.2 × 6.2 |
| Betula glandulosa  | 1          | Summer | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 3 | 1 | 72 | 10 × 10 × 10 |
|                    | 1          | Fall   | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 3 | 1 | 72 | 10 × 10 × 10 |
|                    | 1          | Spring | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 9 | 3 | 216 | 10 × 10 × 10 |
|                    | 2          | Fall   | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 10 × 3 × 3 |
| Empetrum nigrum    | 1          | Summer | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 3 | 1 | 72 | 12 × 12 × 6 |
|                    | 1          | Fall   | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 6 | 2 | 144 | 12 × 12 × 6 |
|                    | 1          | Spring | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 9 | 3 | 216 | 12 × 12 × 6 |
|                    | 2          | Summer | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 28 × 2.7 × 3.8 |
|                    | 2          | Fall   | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 28 × 2.7 × 3.8 |
| Kalmia procumbens  | 1          | Summer | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 3 | 1 | 72 | 12 × 12 × 6 |
|                    | 1          | Fall   | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 6 | 2 | 144 | 12 × 12 × 6 |
|                    | 1          | Spring | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 9 | 3 | 216 | 12 × 12 × 6 |
|                    | 2          | Summer | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 28 × 2.7 × 3.8 |
|                    | 2          | Fall   | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 28 × 2.7 × 3.8 |
| Rhododendron tomentosum | 1          | Summer | 0, 1, 3, 5, 10, 20 | 0.1, 0.8  | 3 | 1 | 54 | 10 × 10 × 10 |
|                    | 1          | Fall   | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 6 | 2 | 144 | 10 × 10 × 10 |
|                    | 1          | Spring | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 9 | 3 | 216 | 10 × 10 × 10 |
|                    | 2          | Summer | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 4.2 × 4.2 × 6.2 |
|                    | 2          | Fall   | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 4.2 × 4.2 × 6.2 |
| Vaccinium uliginosum| 1          | Summer | 0, 1, 3, 5, 10, 20 | 0.1, 0.8  | 3 | 1 | 54 | 6.5 × 6.5 × 6.5 |
|                    | 1          | Fall   | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 6 | 2 | 144 | 6.5 × 6.5 × 6.5 |
|                    | 1          | Spring | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 9 | 3 | 216 | 6.5 × 6.5 × 6.5 |
|                    | 2          | Summer | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 4.2 × 4.2 × 6.2 |
|                    | 2          | Fall   | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 4.2 × 4.2 × 6.2 |
| Vaccinium vitis-idaea| 1          | Summer | 0, 1, 3, 5, 10, 20 | 0.1, 0.8  | 3 | 1 | 72 | 6.5 × 6.5 × 6.5 |
|                    | 1          | Fall   | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 6 | 2 | 144 | 6.5 × 6.5 × 6.5 |
|                    | 1          | Spring | 0, 1, 3, 5, 10, 20 | 0.1, 0.4, 0.8 | 9 | 3 | 216 | 6.5 × 6.5 × 6.5 |
|                    | 2          | Summer | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 4.2 × 4.2 × 6.2 |
|                    | 2          | Fall   | 0, 0.1, 0.4, 0.8  | 0.5, 1.2 0.05, 0.1, 0.5 | 10 | 10 | 100 | 4.2 × 4.2 × 6.2 |

Note. *Missed planting Vaccinium vitis-idaea soak 0, IBA 0.4 percent cuttings.
growth, 30 to 60 percent live green tissue), 4 = good (plant healthy and growing, 60 to 90 percent live green tissue), and 5 = excellent (plant robust and growing vigorously, 90 to 100 percent live green tissue). Adventitious root development was assessed at sixty days. Cuttings were gently washed under running water to remove all substrate material. Primary roots refers to adventitious roots that emerged from the stem cutting; secondary and tertiary roots refers 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.

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 because 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 favorable 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 two-thirds 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, v4.0.2; Wickham 2016).

Results and discussion
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 that this may be a useful technique for some deciduous species.

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 percent across species, seasons, and experiments, with season having the most influence on rooting for each species (Figures 1 and 2; Supplementary Table 1).

Although Kalmia procumbens cuttings had low rooting (<10 percent in all seasons and experiments), this was the first study to demonstrate development of adventitious roots (maximum twelve roots on one cutting in summer, experiment 1). Only one report was found describing rooting of Arctous rubra cuttings that 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 less than 20 percent 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 percent 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, among individuals within species, and between clones of individuals, due to interactions among genetic, physiological, and environmental factors (Leakey 1985; Bellini, Pacurar, and Perrone 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 percent 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, whereas roots emerged from multiple locations up the stem for the other species (Table 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 (Supplementary Table 1). Due to the experimental design, differences between experiments, and low rooting,
confirmatory statistical comparisons were not conducted within an experiment or between experiments.

Rooting variability between years was more apparent for *Empetrum nigrum* and *Vaccinium vitis-idaea* and similar to some previous research. For example, 55 percent of *Vaccinium vitis-idaea* cuttings rooted in summer in experiment 1 but only 10 percent rooted in summer in experiment 2. Gustavsson (1999) noted that variability in rooting for *Vaccinium 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 percent rooting for Vaccinium vitis-idaea cuttings grown under saturated moist air and fog conditions, and Holloway (2009) observed 44 to 91 percent 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 2009; Labokas and Budriuniene 1989).

No Empetrum nigrum cuttings rooted in fall in experiment 1; 40 percent rooted in fall in experiment 2. Hagen (2002) observed 70 to 80 percent rooting for Empetrum nigrum ssp. hermaphroditum (Hagerup)
Table 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                        | 23                       | 0–11 cm                           |
| Kalnia procarbous           | 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-idea        | 627                      | 96                      | 72                        | 16                       | Generally 0–2 cm, some up to 10 cm |

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, Salemaa, and Millar 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 behavior for these shrub species, because 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 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, Pucarar, and Perrone 2014; Davies et al. 2017).

In a horticultural setting, less than 25 to 50 percent rooting is considered poor, depending on the species and grower, indicating that a species would not be grown commercially (Holloway and Peterburs 2009; Davies et al. 2017). However, for reclamation practitioners, other factors may take priority over low rooting, including reestablishment of keystone or rare species or development of a heterogenous 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, because their larger initial size provides greater ground cover. Cutting survival as low as 30 percent has led to successful streambank stabilization in riparian environments (Watson, Abt, and Derrick 1997), with similar benefits on large industrial disturbances in our experience.

**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 1 and 2). After wounding, exogenous auxins are taken up through the cut surface (Kenney, Sudi, and Blackman 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). Because 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 Indole-3-acetic acid (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 Anind 1970; Blakesley, Weston, and Elliott 1991; Joshi et al. 1992; X. 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, Vertocnik, and Town 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, Smith, and Hackett 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 whether 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, Pezeshki, and Shields 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 fourteen 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 fourteen days had higher root biomass than other treatments, and fall Salix amygdaloides cuttings soaked for fourteen days had higher shoot biomass. Pezeshki et al. (2005) found that soaking nondormant Salix nigra Marsh. (black willow) cuttings for seven days was beneficial for cutting survival, root development, and bud flush, with no cuttings surviving after fifteen 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 year. Though longer soaking times are not currently recommended for reclamation, results indicate that ensuring cuttings are turgid on a species-specific basis prior to planting will likely improve 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 2b). Similarly, Wise, Gill, and Selby-Pham (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 strigolactones (Swarbreck et al. 2019; Swarbreck, Mohammad-Sidik, and Davies 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.

**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 sixty days (Table 2; Supplementary Figures 1 and 2). Bell and Bliss (1978) and Billings, Peterson, and Shaver (1978) found that 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 branching patterns similar to those of 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 sixty 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, Pagès, and Pierret 2003). Due to the slow growth of arctic plants, it can take years for morphological characteristics and root branching patterns to fully develop (Bell and Bliss 1978; Billings, Peterson, and Shaver 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.

**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 3). Root elongation followed by lateral root branching is an iterative developmental process, and root growth varies between species and for different root orders (H.
For example, Dittmer (1937) observed a decrease in mean length of four successive root orders for *Secale cereale* L. (cultivated rye), and 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, Pagès, and Wu 2016). In northern locations, plants can allocate 70 percent or more of their total biomass to roots (Chapin, Johnson, and McKendrick 1980; Poorter et al. 2012), and because 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, Gibbs, and Coates 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 because they reflect the size of the root meristem where new elongating cells are produced (Cahn, Zobel, and Bouldin 1989; Thaler and Pagès 1996; Lecompte and Pagès 2007).

**Figure 3.** Length of longest primary and secondary roots at day 60 with 95 percent 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 and Supplementary Table 1.
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), and 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 (G. E. Wilcox and Pfeiffer 1990; Kaspar and Bland 1992; Nagel et al. 2009; reviewed in Rich and Watt 2013). Though 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 (Bell and Bliss 1978; Billings, Peterson, and Shaver 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 3). Resource partitioning between different tissue types varies by season and species. Though 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, 1989; Davies et al. 2017; Tsafouros et al. 2019). Because plants have species-specific requirements for macro- and micronutrients 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, Kouchaji, and Bouranis 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 and species selection to meet revegetation goals (e.g., 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.

**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 that other factors 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. Though 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 reestablishment of plant communities on disturbed northern sites.

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