Plant species-specific Effects on Boreal Soil Fertility in Mature and Fire-Disturbed Forest

by

Emily Klapprat

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Abstract:

Soil fertility is the ability for soil to meet the requirements for plant growth. The soil fertility is influenced by both fire disturbance and plant species. Competitive species contribute higher quality leaf litter than stress-tolerant species in the boreal forest which influences aspects of soil fertility. The effect that plants with different life history strategies have on soil fertility has not been studied in the context of high-severity fire. Soil fertility variables including organic layer depth, soil temperature, soil respiration rate, pH, inorganic nitrogen content, percent soil organic matter, and percent water retention were compared between soil samples from replicate plots in the boreal forest near Churchill Manitoba, and soil samples from replicate plots in a fire-disturbed site in the boreal forest. Additionally, soil fertility variables were compared between soils sampled from competitive species (*Salix candida*) and stress-tolerant species (*Empetrum nigrum* and *Vaccinium uliginosum*) growing in the two sites. Statistical differences in soil variables were found between soil samples from the boreal forest and soil samples from a fire-disturbed site. High-severity fire reduces the organic layer depth and decreases the pH, soil respiration rate, and available nutrients. Inorganic nitrogen content and relative growth rate of sea lyme grass grown in soil samples were statistically different between the competitive plant *Salix candida* and the stress-tolerant plants. *Salix candida* influences soil fertility by increasing the inorganic nitrogen content and fostering soils that increase the relative growth rate of sea lyme grass. As the frequency, intensity, and severity of fires in the boreal forest are increasing due to climate change, it is important to understand how species impact soil fertility.

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Introduction:

Soil is an important component of the biosphere that performs a wide variety of ecosystem services such as carbon storage, nutrient cycling, growth medium for primary producers, habitat, and water retention. Soil fertility varies across biomes and is determined by the physical, chemical, and biological properties of the soil (Freyer *et al.*, 2023). Soil fertility is the ability to meet the requirements of plant growth, including optimal micro and macronutrients, water holding capacity, pH, cation exchange capacity, organic carbon, microbial activity, and fungal associations (Ottow, 2011; Clemmensen *et al.*, 2013). Although plants are dependent on soil fertility, they may also contribute to the local soil fertility by redistributing nutrients through roots, leaf litter, and fungal associations, and providing habitat for detritivores and fungi (Clemmensen *et al.*, 2013). Plant-soil relationships may affect biological processes like decomposition rates, soil respiration rates, and nutrient cycling. The contributions and role that plants play in influencing soil fertility may vary based on the relative abundance of certain groups of plants that differ in their life history strategy and general characteristics. The effect that plants have on soil fertility in the boreal forest has not been well studied in the context of disturbance by fire.

The boreal forest is an ecosystem that traditionally has low soil fertility and a variety of vegetation. This forest approaches the northern treeline and is limited in soil nutrients, especially available nitrogen (Vitousek & Howarth, 1991). The subarctic boreal forest has low productivity, low tree density, and poor-quality leaf litter resulting in slow nutrient turnover (Solantie, 2005). This coniferous forest is sometimes referred to as a lichen woodland from the abundance of reindeer lichen and semi-open canopy (Kershaw,

1977). The dominant tree types of the lichen woodland are white spruce, black spruce, and tamarack which provide a semi-open canopy for the lower-level deciduous shrubs like willows and dwarf birches. The coniferous tree species are examples of stress-tolerant plants while the deciduous shrubs are considered competitive for the biome; deciduous shrubs influence the biomass of understory plants through below-ground competition more than above-ground competition (Mudrak *et al.*, 2015). The understory is composed of prostrate and ericaceous shrubs often mixed and layered together. The lichen woodland forest community is cold tolerant with low soil temperature and slow decomposition rates with nutrient-poor acidic soils (Payette & Delwaide, 2018). Slow decomposition rates in boreal soils are due to the wet environment and acidic nature of the partially decomposing plant matter, mostly from stress-tolerant species (Kershaw, 1977). Mature open lichen woodland boreal forest has lower quality leaf litter compared to deciduous forests considering the prevalence of stress-tolerant coniferous trees, ericaceous plants, and mosses (Payette *et al.*, 2018).

Grime's theory of life history strategies addresses how plants can be divided into categories based on their strengths and trade-offs. The three categories of Grime's life history strategies are competitors, ruderals, and stress tolerators (Grime, 1977). Some plant species may exhibit characteristics of their life history strategy more strongly than others. Stress-tolerant ericaceous species such as *Vaccinium uliginosum* (Alpine Bilberry/Blueberry), and *Empetrum nigrum* (Crowberry) as well as competitive deciduous species such as *Salix candida* (Silver Willow) are common in the boreal forest. Willow species are more competitive than ericaceous plants and can form both arbuscular mycorrhizal and ectomycorrhizal associations which assist in nutrient cycling and organic

carbon sequestration (Baum *et al.*, 2020). In general, competitors have high resource requirements, so they allocate their resources towards early growth and increase in biomass requiring lots of nutrients and resources from the soil, however, they delay reproduction in the process (Grime, 1977). Competitive plants typically produce short-lived leaves and have a rapid growth rate allowing them to compete for resources more efficiently. The higher-quality tissue produced by competitive plants decomposes quickly which allows for more nutrient turnover and may create a positive feedback loop in soil fertility and plant productivity (Markham *et al.*, 2008; Kyaschenko *et al.*, 2018). High-intensity surface burns favor competitive plants that can grow on thin organic soils or in sandy mineral soils (Jorgensen *et al.*, 2023).

Ruderals also require high resources but must reproduce early and contribute readily to the seed bank. Ruderals take advantage of temporary good conditions as they are shorter-lived. Many ruderal species are found on moderately disturbed sites or nutrient rich fox dens in the boreal forest such as grasses and herbaceous perennials (Lang *et al.,* 2021). The ericaceous stress tolerators common in the boreal forest, *Empetrum nigrum* and *Vaccinium uliginosum* have similar characteristics to each other, however, *Vaccinium uliginosum* prefers acidic soils (Duan *et al.*, 2023; Yan *et al.*, 2019). Stress tolerators require fewer resources for survival but have a slower growth rate, drawing less nutrients from the soil than competitors and assimilating them into their tissues at a slower rate. Stress tolerators focus on using their energy for regular metabolism and survival instead of growth and delaying their reproduction (Grime, 1977). Stress-tolerant plants provide low-quality leaf litter compared to competitors or ruderals which slows the decomposition rate and reduces the amount of free nutrients in their habitat (Markham *et al.*, 2008). *Vaccinium uliginosum* leaf litter contributes a low amount of nitrogen due to the low N:P

ratio in the leaves (Duan *et al.*, 2022). *Empetrum nigrum* produces low-quality leaf litter since the plant produces phenolic compounds and waxes in the leaves which decrease the decomposition rate of the soil organic matter (Tybirk *et al.*, 2000). *Empetrum nigrum*, is predicted to increase in abundance as a fire-disturbed site matures as it requires higher light intensity than *Vaccinium uliginosum*, however, like *V. uliginosum,* it cannot easily outcompete other plants for light (Jorgensen *et al.*, 2023, Tybirk *et al.*, 2000). Characteristics attributed to stress-tolerant plants include leaf retention, low palatability to herbivores, and having a slow overall growth rate and metabolism (Bakker, 2002). Stress-tolerant plants dominate the boreal forest contributing a high proportion of low-quality leaf litter within the soil compared to other biomes.

The soils of a forest are divided into vertical layers called horizons. The O horizon is the surface layer that contains dead organic matter and newly deposited organic matter (Kenkel, 2022; Hilli *et al.*, 2008). The A horizon just below is commonly known as the topsoil and contains inorganic sand, silt, or clay and may contain some organic humus contributing organic acids (Kenkel, 2022). The quantity and quality of leaf litter and decomposing organic matter contribute to the composition of the O horizon and the soil fertility (Hilli *et al.*, 2008). Ericaceous stress-tolerant plants deposit organic matter less frequently by retaining their leaves longer than deciduous shrubs like *Salix candida*. Organic matter deposited by plants affects the fertility of the soil by the redistribution of carbon and nitrogen. However, boreal ecosystems are nitrogen-limited due to the high carbon-to-nitrogen ratio in the leaf litter (Kyaschenko *et al.*, 2018). Leaf litter, charcoal, fungi, and root mass make up a large proportion of the carbon in the soil (Clemmensen *et al.*, 2013). The effective carbon sequestration and build-up of the O horizon of the boreal forest is a function of the production and decomposition of leaf litter, root mass, and

associated fungi types. The O horizon has three stages of decomposing organic material including the newly deposited litter, the fragmented middle layer with partial decomposition and microbial activity, and the fully decomposed humus layer (Kenkel, 2022; Hilli *et al.*, 2008). The decomposition rate within the boreal forest is limited by factors such as temperature, seasonality, and soil moisture causing the decomposition rate to be much less than the litter and organic matter deposition rate (Kenkel, 2022). The build-up of the organic layer causes less nutrients to be available for the plant community. Soil fertility and plant-soil relationships can also be affected by the natural disturbance regime (Clemmensen *et al.*, 2013).

The primary disturbance in the boreal forest impacting the soil fertility and inherently the plants that occupy the soils is mid-intensity frequent fire (Monson, 2004). High-intensity fires are defined by the high amount of heat produced during the disturbance and often result in high-severity fires that greatly reduce the soil organic layer and biomass of the plant community (DellaSala, 2018; Jorgensen *et al.*, 2023). Low-intensity low-severity fires produce a low amount of heat during the fire event and cause less damage to the soil organic layer and plant community (DellaSala, 2018). The high-severity fires consume the organic layer of the soil and reduce the soil fertility for the post-fire plant community, often exposing the A horizon of the soil, increasing drainage, reducing water availability for biota, and slowing decomposition (Certini, 2005). The reduction of the O horizon and organic material increases the runoff of nutrients and risk of surface erosion. Time since last fire may influence the resulting species, fertility of the soil, and available nutrients, in addition to other factors like soil moisture, or intensity and severity of fire (Jorgensen, *et al.*, 2023).

The modified habitat and soil quality post-fire allow for investigation of how the plant community, life history types, and specific species enhance soil fertility. There are few details documented on the fire regime of the Hudson's Bay ecotone, however, it can be inferred from other similar boreal regions that the frequency of disturbance is high-intensity canopy fires every 50-100 years (Monson, 2004). High-severity surface fires burning deep into the organic layer are rare if they occur at all, meaning that the organic layer reduction, removal of biomass, large-scale redistribution of nutrients, and drastic changes in age structure are new occurrences for subarctic boreal forests and soils. The effects of wildfire on soil fertility provide a framework for evaluating how the plant community contributes to the enhancement of their associated soils. Variables like plant life history type, decomposition rate, pH, nutrient content, leaf litter quality, and fungal associations are all interrelated and contribute to the health of the soils (Grimes, 1977; Baum *et al.*, 2020; Clemmensen *et al.*, 2013). The development of soil fertility can be studied in fire-disturbed sites to better understand the connection between plant species and forest soil fertility.

The connection between soil fertility and life history of the dominant plants is not yet well understood, especially in the traditionally low-fertile, low-productivity forests. It is plausible that plant effects on soil may be just as important as the soil's effect on plants. Plants contribute to soil fertility differently depending on their life history characteristics, (Grimes, 1977; Duan *et al.*, 2022; Baum *et al.*, 2020) therefore a forest with mixed species composition may experience species-specific effects on soil fertility. Furthermore, soil fertility is known to be modified by fire disturbance (Certini, 2005); Observing the effect

of fire disturbance and species on soil fertility may provide an opportunity to better understand the development of soil fertility and the connections between plants and soil.

Purpose:

This study aims to increase our understanding of how stress-tolerant ericaceous plants and competitive woody shrubs affect soil fertility in the boreal forest by observing soil associated with three common plants occupying a mature forest habitat and fire-disturbed habitat. The development of soil fertility can be studied in disturbed sites to better understand the connection between plant species and forest soil fertility using homogenous patches as replicate plots. The species patches indicate enough resources for plant growth and survival and are ideal for targeting the effect a single plant species has on the soil fertility variables. The boreal forest recovers well from low-intensity frequent fires (Monson, 2004), however, the frequency, intensity, and severity of wildfires in the boreal forest are increasing due to climate change effects like earlier snowmelt, drought, and human activity (Walker *et al.*, 2019). Fire-disturbed areas are more susceptible to drought, nutrient leeching, and erosion which affects plant growth and species composition (Cooperdock, *et al.*, 2020). By studying three ubiquitous species within the boreal forest, we can better understand their reaction to the reduction in organic layer quality and quantity moving forward. The development of soil fertility associated with three species that vary in their stress tolerance and reactions to fire disturbance may differ in terms of soil fertility variables.

Hypothesis and Research Objectives:

The main objective of this research project is to observe the variability in the subarctic boreal soil fertility associated with three dominant plant species. This study compares soil fertility in undisturbed forest and forest disturbed by high-severity fire where monospecific patches of the dominant plants occur.

Differences in soil characteristics will be driven by plant species from their leaf litter quality, and tendencies to form mycorrhizal associations. I hypothesize that *Salix candida* associated soils will have higher organic layer depth, soil respiration rate, nutrient content, pH and water retention capacity than the stress-tolerant plants. *Vaccinium uliginosum* associated soils will be less fertile than soil associated with *Salix candida* as the leaf litter is lower quality in nutrients. Soil fertility associated with *Empetrum nigrum* will be lower due to the lower quality leaf litter, slow turnover in leaves and new roots, and high phenolic content which slows decomposition. Additionally, low concentrations of inorganic nitrogen are expected to be present in *Empetrum nigrum* associated soils due to the abundance of ericoid mycorrhizal associations that assist in the absorption of organic nitrogen (Tybirk *et al.*, 2000). I hypothesize that the differences in soil fertility between the disturbed and undisturbed sites are attributed to the depth and quality of the organic layer and the other soil variables tested. Fire alters the depth of the organic layer, amount of carbon, inorganic nitrogen levels, acidity, and soil respiration. I hypothesize that the soil fertility will be greater in the disturbed site from the observed nutrient levels (carbon and inorganic nitrogen) but soil respiration will be lower from a lack of organic matter housing microbial activity.

Relevance:

Soil fertility is a function of the production and decomposition of nutrient-rich leaf litter, roots, and fungi. The creation of a fertile soil is a dynamic process and is built by the plant community that occupies the soil. Climate change is threatening boreal soil fertility by increasing disturbance frequency, intensity, and severity (Monson, 2004; Walker *et al.,* 2019). By assessing the effect that stress-tolerant plants have on soil fertility we can better understand the reciprocal relationship between soils and plants. As wildfires, erosion, eutrophication, and climate change are impacting the north it is essential to unearth the plant-soil interactions that contribute to forest health.

Methods:

Forest Site Description:

The study area is classified by Brook (2001) as a spruce heath treed upland area with sand and gravel substrate, oligotrophic soils, and high lichen, shrub, and tree cover. The subarctic boreal is a spruce lichen woodland primarily forested with white spruce, black spruce, tamarack, and various willow species. Ericaceous and prostrate shrubs dominate the understory while feather moss (*Pleurozium*) and reindeer lichen (*Cladonia)* are the dominant ground cover.

The study is divided between two sites within the Churchill Wildlife Management Area, the undisturbed subarctic boreal forest, and the disturbed subarctic boreal (Fig. 14), approximate latitude and longitude 58°42'20.1"N, 93°50'34.0"W. The undisturbed forest is partially open stands of spruce and tamarack trees with high understory diversity and

density. The forest understory contains many shrub and ericaceous species layered and intermixed. The region experiences high humidity due to its coastal proximity and a high amount of moisture is retained by bryophytes and lichens on the forest floor.

Burn Site Description:

The disturbed site experienced a high-intensity fire in 1995 which consumed most of the organic layer of the soil down to the mineral layer. The fire is considered abnormal for the area as it was a high-severity surface burn rather than the typical low-severity canopy burn. Studying a high-severity burn is useful as drought conditions and earlier snowmelt can increase the chances of future high-severity surface burns in the area affecting the soil fertility, plant community, and species use of the area. Due to the fire, the remaining sandy well-draining soils have little organic layer protecting from surface erosion. There is no canopy coverage, however, the site contains mainly young spruce trees and tall willows (*Salix candida*) that have most likely regenerated vegetatively from the roots that survived the fire or germinated from seed post-fire. The spruce trees are estimated to be between 20-25 years old and reach 2-3 meters in height. The willows in the burned site were noticeably taller and thicker than the willows of the forest, often having multiple trunks. The understory is organized in monocultures of ericaceous and prostrate shrubs no larger than 2x2m with a mosaic of lichen, bare ground, star moss, and charred debris occupying most of the understory. These homogenous patches of single species were used to compare plant species and soil health.

Study design:

The soil under three study species: *Empetrum nigrum*, *Vaccinium uliginosum*, and *Salix candida,* were sampled between the forest site and the burn site to assess soil fertility. These species have been chosen because they are common throughout the boreal in the Churchill Wildlife Management Area and have an interesting post-fire response by growing in small circular monocrops. Assigning replicate plots and data collection in the field was done August 2023.

The two sampling sites had ten replicates of the three subject species. A total of 60 soil samples were collected from ten replicates of the three species in both the forest and burn sites (Fig. 15 & Fig. 16). The criteria for choosing a replicate included finding patches at least 60x60cm in area with greater than 80% coverage of the subject species. Replicate plots were at least 5 meters away from each other to reduce sampling of the same micro conditions. In the forest site, ten replicates of each species were spread over a distance of 2 kilometers (Fig. 15A). In the burn site, replicates were chosen following three transects until ten replicates of each species were found (Fig. 15B). Replicate plots had a maximum distance of 10 meters from the nearest replicate plot.

Soil respiration rate, organic layer depth, soil temperature, pH and hydrogen ion concentration, inorganic nitrogen content, carbon content and water retention were assessed for each replicate plot. The relative growth rate (Hunt, 1978) of sea lyme grass (*Leymus arenarius*) in soil samples from each replicate plot was used to assess overall soil fertility during a growth assay in the lab. Sea lyme grass was used as a model plant for assessing soil fertility since it is known to grow in nutrient-rich soils in the area such as fox dens and fertilized plots in northern Manitoba (Gharajehdaghipour *et al.*, 2016).

Forest Site Characterization: Each set of replicate plots containing one of each of the three species was visited in the forest site where the center of the set was located to measure an area with a 6 m radius. The circumference and height of trees over 5 cm in diameter within the 6 m radius were recorded. Species covering the highest percentage of the understory in the set were recorded and listed from most common to least common.

Burn Site Characterization: Transects running through the replicate plots of the burn site were measured. Species composition on the ground was recorded along the transect listed from most common to least common. Three transects were used to describe the area of the burn site which were 18 m, 44 m, and 74 m in length respectively.

Methods for Soil Fertility Variables

Organic layer Depth

Organic layer depth was measured at each replicate plot by digging down to the mineral layer and recording the distance from the mineral layer to the surface.

Soil Temperature

Soil temperature at each replicate plot was recorded using a standard thermometer with a 12 cm temperature probe while soil respiration data was collected at the replicate plots. Temperature measurements were taken at various times during the day between the two sites.

Soil Respiration

Soil respiration was measured using a Li Cor soil respiration chamber attached to a SenseAir K30 NDIR CO_2 sensor. Data was logged every three seconds when the

chamber was in use. Cylindric PVC collars that are 7.6 cm deep and 10.2 cm in diameter were inserted in the ground at each replicate plot. The collars were left for 24 hours to allow the soil to settle and minimize soil disturbance before measurements were taken. Readings began at ambient air levels before the soil respiration chamber was placed on the PVC collar. The respiration rate was then allowed to increase to 50 ppm above ambient CO2, and the chamber was then removed from the collar and allowed to vent back down to the ambient atmospheric level. This procedure was repeated three times for each collar (Fig. 17).

The soil respiration data was processed using JMP to calculate the respiration rate from the change in the CO2 in the soil chamber over time. For each PVC collar, the rate of CO2 increase was calculated for the three incubation periods using a least squares regression fit between carbon dioxide in ppm and time elapsed. The slope was calculated as the respiration rate in each subset and average slopes from the three subsets were used to determine the respiration rate at each collar (Fig. 17).

Soil samples were collected by carefully harvesting the soil contained within the PVC collars planted at each replicate plot. The PVC collars ensure that the same volume of soil is obtained from each replicate plot and the organic layer and mineral layer were separated upon collection. The volume of soil collected from each replicate plot was 618 cm^3. Soil samples were stored in a freezer before using for further analysis.

Soil pH

The pH of the soil was measured in the lab from a subsample of the soil collected and brought back to Winnipeg. Subsamples of the organic layer soil of each replicate plot were made into a slurry with distilled water. A pH probe was used to measure the pH of

each soil subsample. The pH values were converted into hydrogen ion concentration in micromolars (μM) for statistical analysis.

Inorganic Nitrogen Microdiffusion Assay

The inorganic nitrogen content within the soil was measured by performing a microdiffusion assay (Kahn, 2000) to measure the combined ammonium and nitrates of the soil samples. The microdiffusion assay was done for samples from the organic layers of the forest and burn site as well as the mineral layer of the burn site creating a total of 90 samples from three sample groups. Inorganic nitrogen was extracted from subsamples of soil from the forest and the burn site and stored in a freezer for about 6 weeks.

Ions were extracted from the soil using a concentrated (2M) NaCl solution. Devarda's alloy was used to convert nitrate to ammonium and magnesium oxide was used to volatilize the ammonium into ammonia as per the protocol (Kahn, 2000). Samples were left to incubate for a week allowing the ammonia to collect in a boric acid indicator. Titrations were done with a 0.0025 M sulfuric acid solution to measure the ammonia and nitrates in the incubated samples. Samples were compared with a 100 μg/ml nitrogen standard made with (NH4)2SO4 and KNO3.

Carbon Content

Carbon content was measured via loss on ignition to estimate the percent organic matter in the soil. Soil samples were dried in an oven at 100°C before being placed in a ceramic crucible. The crucibles containing soil samples were placed in a muffle furnace and covered for 3 hours to reduce the soil sample to charcoal. The cover was removed from each crucible and soil samples were burned in the muffle furnace for an additional 6

hours to reduce the soil samples to ash. The setpoint temperature of the muffle furnace was set to 707°F however the temperature displayed ranged between 700-850°F. The following formula (Robertson, 2011) was used to calculate the loss on ignition and carbon content in the soil:

% organic matter = preignition weight (g) – post ignition weight (g) / preignition weight (g) x100

Water retention

Soil samples from each sample site with a volume of 50 mL were dried in cylindrical Eppendorf tube in a drying oven at 65°C. A drainage hole was cut at the bottom of each tube containing dried soil samples and placed on a stand. 100 mL of water was poured over the dried soil samples and the amount of water recovered was recorded in mL. The percent water retained was calculated from the difference in water poured over the samples and water recovered.

Growth Assay

Sea lyme grass seeds (*Leymus arenarius*) were germinated on paper towels in plant trays under an artificial light for 3 weeks (Sept 15-Oct 5, 2023). 20 cm x 5.5 cm cylindric plant pots were prepared by lining the bottom with clay spheres for adequate drainage and placing the collected mineral and organic soil from each plot replicate within the pots. The initial fresh mass of the sea lyme grass seedlings was recorded as they were planted in the pots and watered before being placed in the growth chamber. For the first few days, plastic cups were placed over the plant pots to increase the humidity around the sea lyme grass seedlings to help them adjust to the growth chamber conditions.

The growth chamber contains three plasma lights to provide light for the six trays of growing sea lyme grass seedlings. The plants received 14 hours of light per day and the lights were turned off for 10 hours of night similar to the August photoperiod in Churchill, Manitoba. Temperatures were 20°C during the day and 10°C at night. The average light intensity across the three plasma lights at the height of the plant pots was 218 μmol s-1 m-2. The trays containing the pots growing the sea lyme grass were rotated twice a week and each plant received 60-70 mL of distilled water or watered until their saturation point twice a week. Water that drained from the plant pots was collected and poured back into the tube to prevent over leeching of nutrients from the soil.

Sea lyme grass seedlings were allowed to grow for 49-55 days or 7.5 weeks (Oct 5-Nov 29, 2023) to assess their relative growth rate. The final fresh mass of the roots and the shoots of each seedling were recorded at the time of harvest. The final dry mass of the roots and shoot was recorded after drying the tissue in a drying oven at 60°C. The initial dry mass of seedlings was calculated from the dry root mass:dry shoot mass ratio. The relative growth rate was calculated by the natural logarithm of the change in mass divided by the number of days.

Statistics:

A two-factor ANOVA test using species and habitat type (forest and burn) was used to assess the effect of species on soil fertility in the two habitats. Due to the large variability between the forest site and the burn site, they violate the ANOVA assumptions for evaluating the species effect. Species effect at each site was run separately from the site to account for the variability between the two sites. Variables included in the ANOVA are soil respiration, organic layer depth, pH, inorganic nitrogen content, relative growth rate,

carbon content, and water retention capacity. An all-pairwise comparison was performed by a student's t-test to determine the significant differences in soil variables due to species with a sample size of 30 in each site and 56 degrees of freedom. In-text descriptions of results from the soil fertility variables and growth assay show the mean and standard deviation (mean $\pm$ standard deviation) and refer to figures containing the mean and standard error. Soils from the sample replicate plots were compared using Principal Component Analysis for soils from both the forest site and burn site together and separately.

Results:

Organic Layer depth

Site type had a significant effect on the organic layer depth ($p < 0.0001$). No statistical differences in organic layer depth were found between the species of the forest site or of the burn site. The mean organic layer depth between all the forest plot replicates was 22.59 $\pm$ 11.08 cm, while the mean depth of the burn replicate plots was one-tenth of the forest organic layer depth with a mean of 2.63 $\pm$ 1.04 cm (Fig. 1).

A positive correlation was found between the % SOM and Organic Layer Depth; for each centimeter of depth, the % SOM increases by 1.2597 ($R^2 = 0.511$).

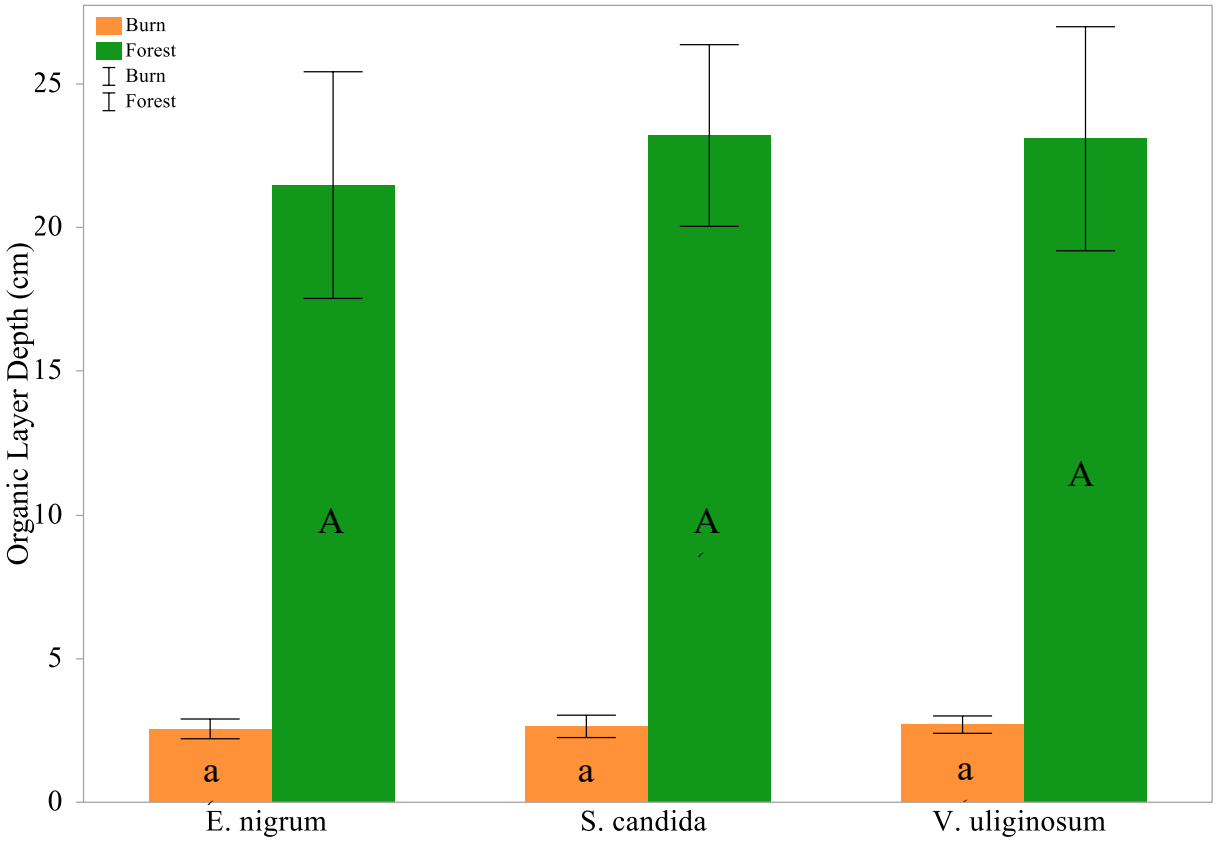

Figure 1: Mean organic layer depth for *E. nigrum*, *S. candida*, and *V. uliginosum* in centimeters of the burn site (orange) and forest site (green). Error bars show the standard error. Bars with same character label are not statistically significantly different.

Soil Temperature

Site type had a significant effect on the soil temperature ($p < 0.0001$). No statistical differences in soil temperature were found between the species of the forest site or of the burn site. The mean soil temperature of the forest site was 8.8 $\pm$ 1.3°C while the burn site had a higher mean soil temperature at 14.2 $\pm$ 1.6°C (Fig. 2).

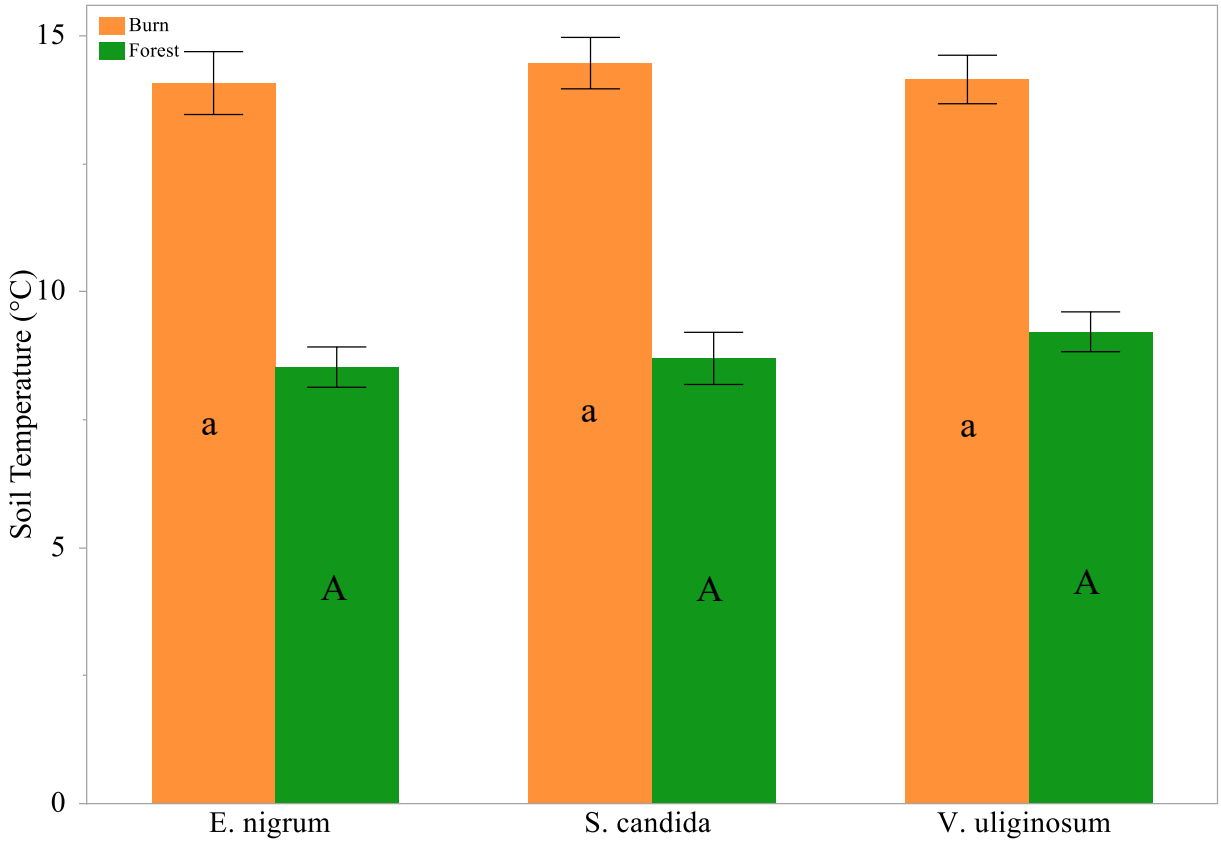

Figure 2: Mean soil temperature in °C at the replicate plots of *E. nigrum*, *S. candida* and *V. uliginosum* in the burn site (orange) and the forest site (green). Error bars show the standard error. Bars with same character label are not significantly different.

Soil Respiration

Site type had a significant effect on the soil respiration rate ($p < 0.0001$). In general, the mean soil respiration of the forest was three times higher than the soil respiration rate of the burn site at 1.705 ± 1.772 ppm CO2 s-1 (Fig. 3).

No statistical differences in soil respiration rate were found between the species considering both sites, however when analysing soils from both sites together, soils from *Salix candida* were approaching significance for differences in soil respiration rate ($p = 0.08$). No statistical differences in soil respiration rate were found between the species of

the forest site, however in the burn site there were statistically significant differences in soil respiration rate between the species. Largest difference in species of the burn site was between *Vaccinium uliginosum* and *Empetrum nigrum* (p = 0.0053).

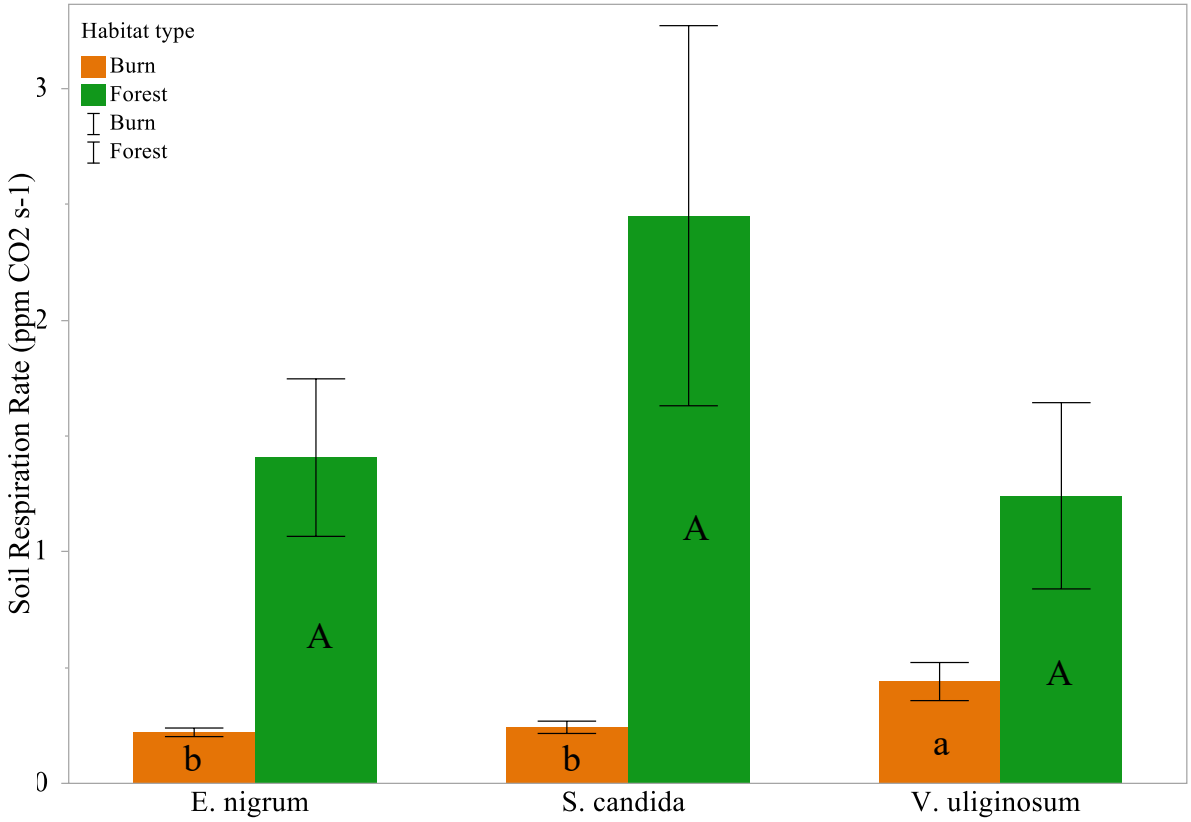

Figure 3: Mean soil respiration rate for *E. nigrum*, *S. candida* and *V. uliginosum* in ppm CO2 s-1 in the burn site (orange) and the forest site (green). Error bars show the standard error. Bars with same character label are not significantly different.

Soil pH and hydrogen ion concentration

Site type had a significant effect on soil pH (p = 0.0467). Soil hydrogen ion concentration in the burn site was twice the hydrogen ion concentration of the forest site (Fig. 4). The mean pH of the burn site was 4.1 while the mean pH of the forest site was

4.4. *Salix candida* had a significant effect on soil pH ($p = 0.0306$) with a mean hydrogen ion concentration of 27.93 ± 40.7 µM between the two sites, which is a pH value of 4.5.

In the burn site there were statistically significant differences in pH between the species. Largest difference in species of the burn site was between *Salix candida* and *Empetrum nigrum*($p = 0.0063$). No statistical differences in soil pH were found between the species of the forest site.

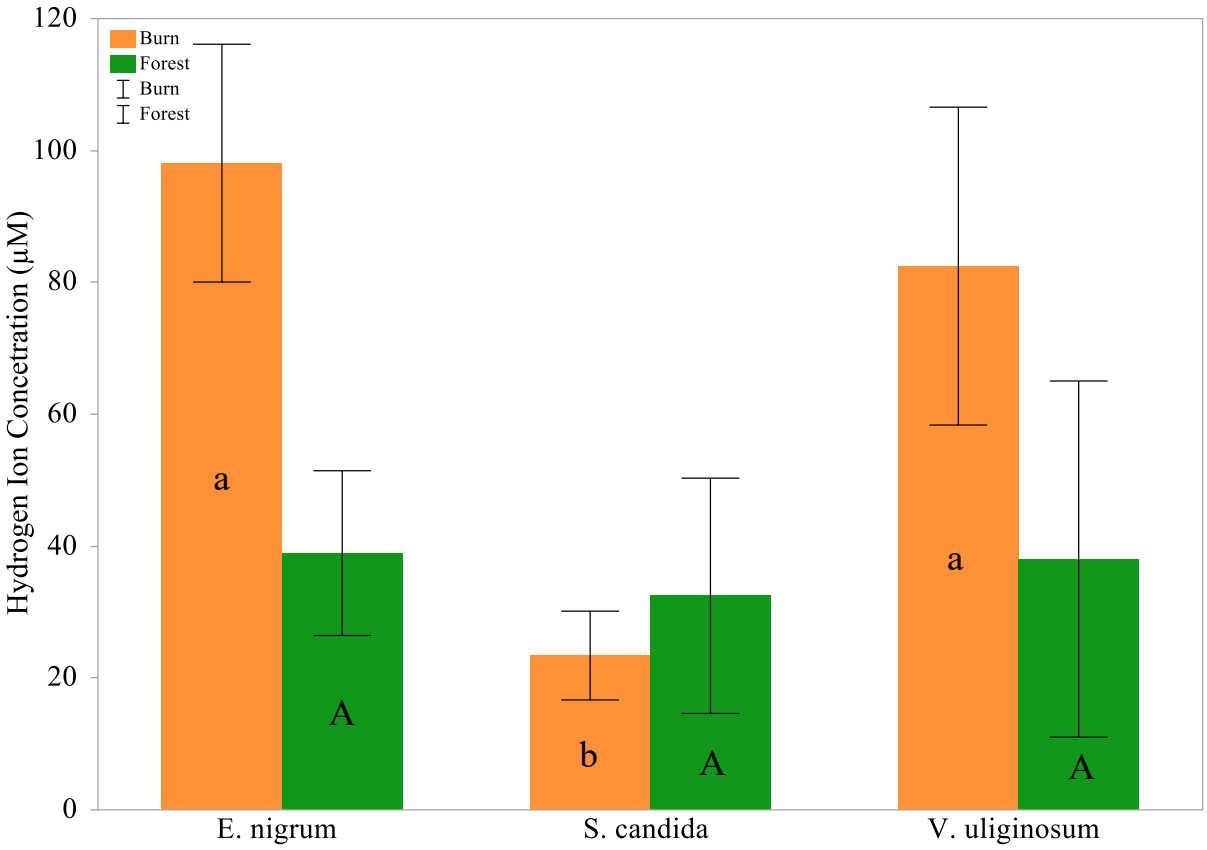

Figure 4: Mean hydrogen ion concentration for *E. nigrum*, *S. candida*, and *V. uliginosum* in the burn site (orange) and the forest site (green). Error bars show one standard deviation from the mean. Bars with same character label are not significantly different.

Inorganic Nitrogen

Site type had a significant effect on inorganic nitrogen content ($p < 0.0001$). Overall, species also had a significant effect on inorganic nitrogen content ($p = 0.0299$).

Salix candida of both sites had a significant effect on inorganic nitrogen content ($p = 0.0092$) with a mean inorganic nitrogen content of 63 ± 62.69 µg N g-1. *Empetrum nigrum* soils had the least mean inorganic nitrogen content at 25.78 ± 34.79 µg N g-1 while *Vaccinium uliginosum* soils had an intermediate mean inorganic nitrogen content at 32.31 ± 41.84 µg N g-1.

Statistical differences for inorganic nitrogen content of the organic layer of the burn site were found between species with the highest difference between *Empetrum nigrum* (low inorganic N) and *Salix candida* (high inorganic N) ($p = 0.0467$) (Fig. 6). The same pattern and direction of differences was observed for the statistical differences in inorganic nitrogen content of the mineral layer of the burn site; the highest difference was between *Empetrum nigrum* (low inorganic N) and *Salix candida* (high inorganic N) ($p = 0.048$) (Fig. 7).

The pattern of statistical differences between species for inorganic nitrogen content in the organic layer of the forest site repeated with the highest difference between *Empetrum nigrum* (low inorganic N) and *Salix candida* (high inorganic N) ($p = 0.05$) (Fig. 6).

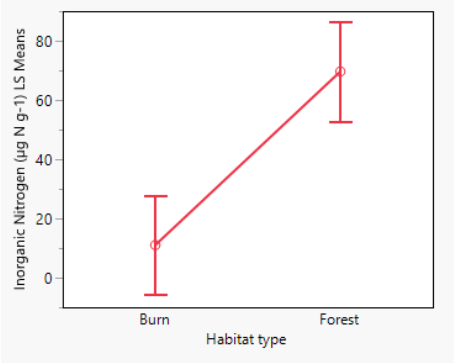

Figure 5: Mean inorganic nitrogen between sites measured in µg N g-1 for the organic layer of the burn site and the organic layer of the forest site.

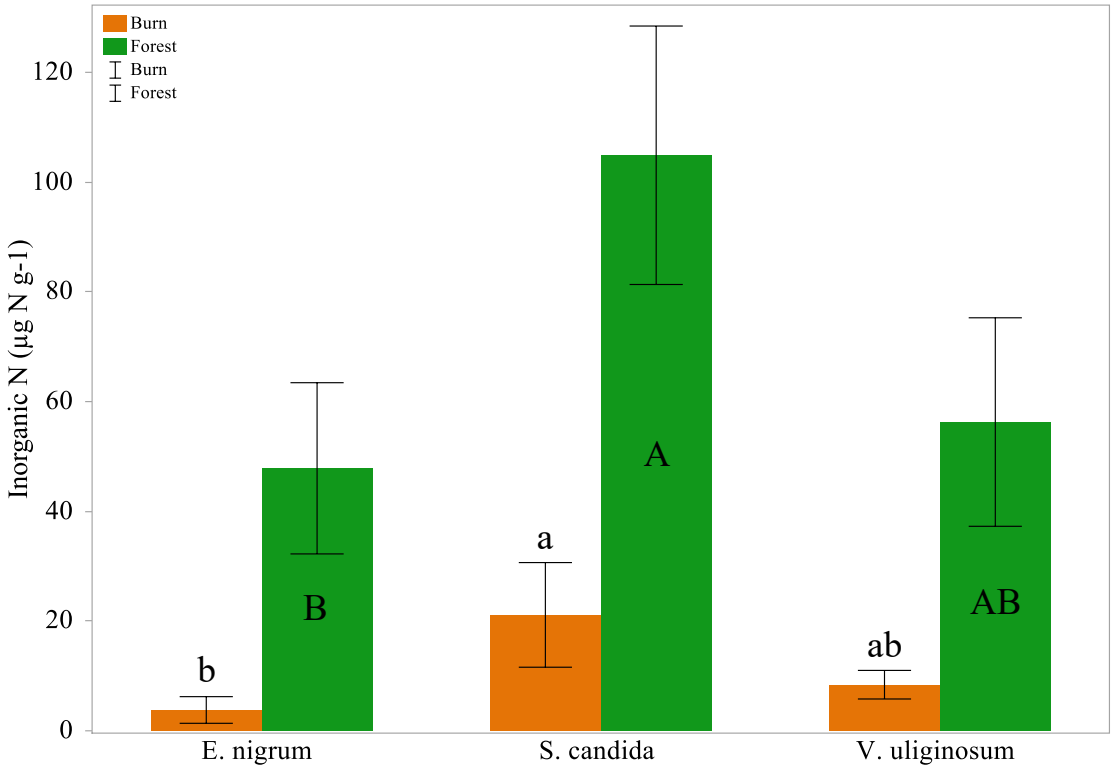

Figure 6: Mean inorganic nitrogen content (organic layer) for *E. nigrum*, *S. candida* and *V. uliginosum* in the burn organic layer (orange), and the forest organic layer (green). Inorganic nitrogen content is measured in µg N g-1. Error bars show the standard error. Bars with same character label are not significantly different.

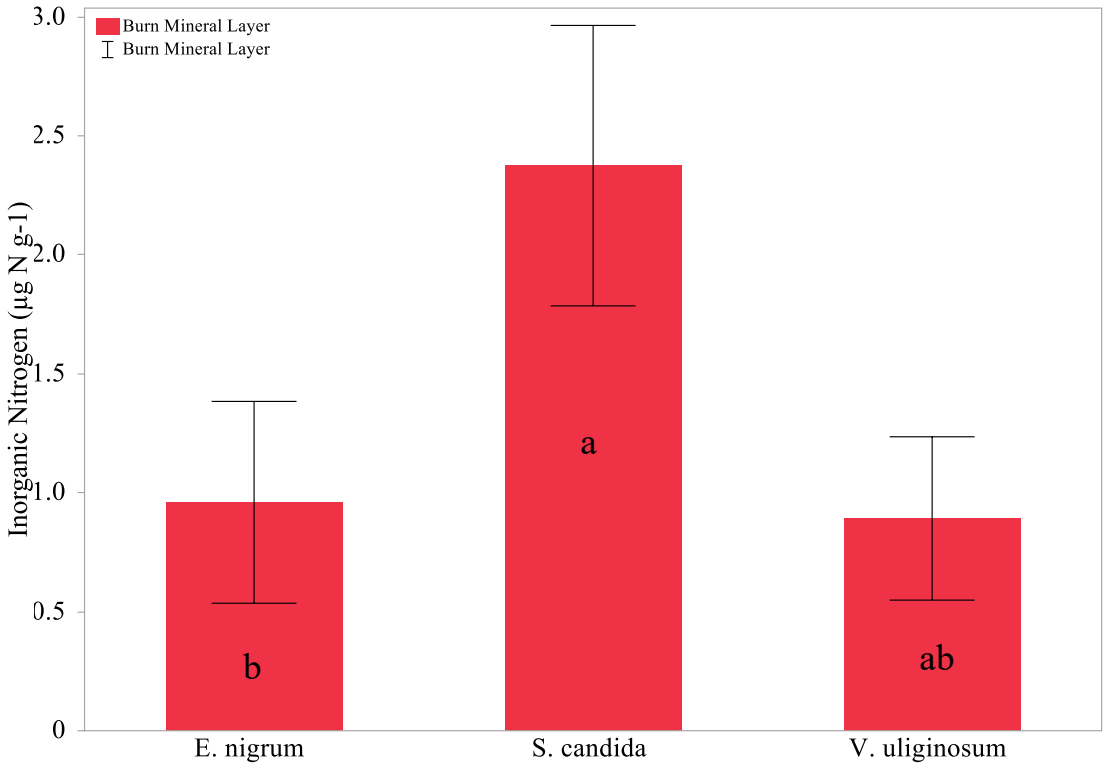

Figure 7: Mean inorganic nitrogen content (mineral layer) in µg N g-1 for *E. nigrum*, *S. candida* and *V. uliginosum* in the burn mineral layer (red). Error bars show one standard deviation from the mean. Bars with same character label are not significantly different.

Percent Soil Organic Matter (Carbon content)

Site type had a significant effect on the percent Soil Organic Matter (% SOM) ($p < 0.0001$), however, species did not have a significant effect on the % SOM (Fig. 8).

In the burn site there were statistically significant differences in % SOM between the species with the largest difference between *Empetrum nigrum* and *Salix candida* ($p = 0.0411$). *Empetrum nigrum* and *Vaccinium uliginosum* also had significant differences from one another for the % SOM ($p = 0.0433$). In the forest site there were no statistically significant differences in % SOM between the species. The mean % SOM of soil from species in the forest site was $78.22 \pm 20.88\%$ which was almost twice the % SOM of soil

from the species of the burn site which had a mean of 39.46 ± 20.64%. No significant correlation was found between the soil temperature and the %SOM.

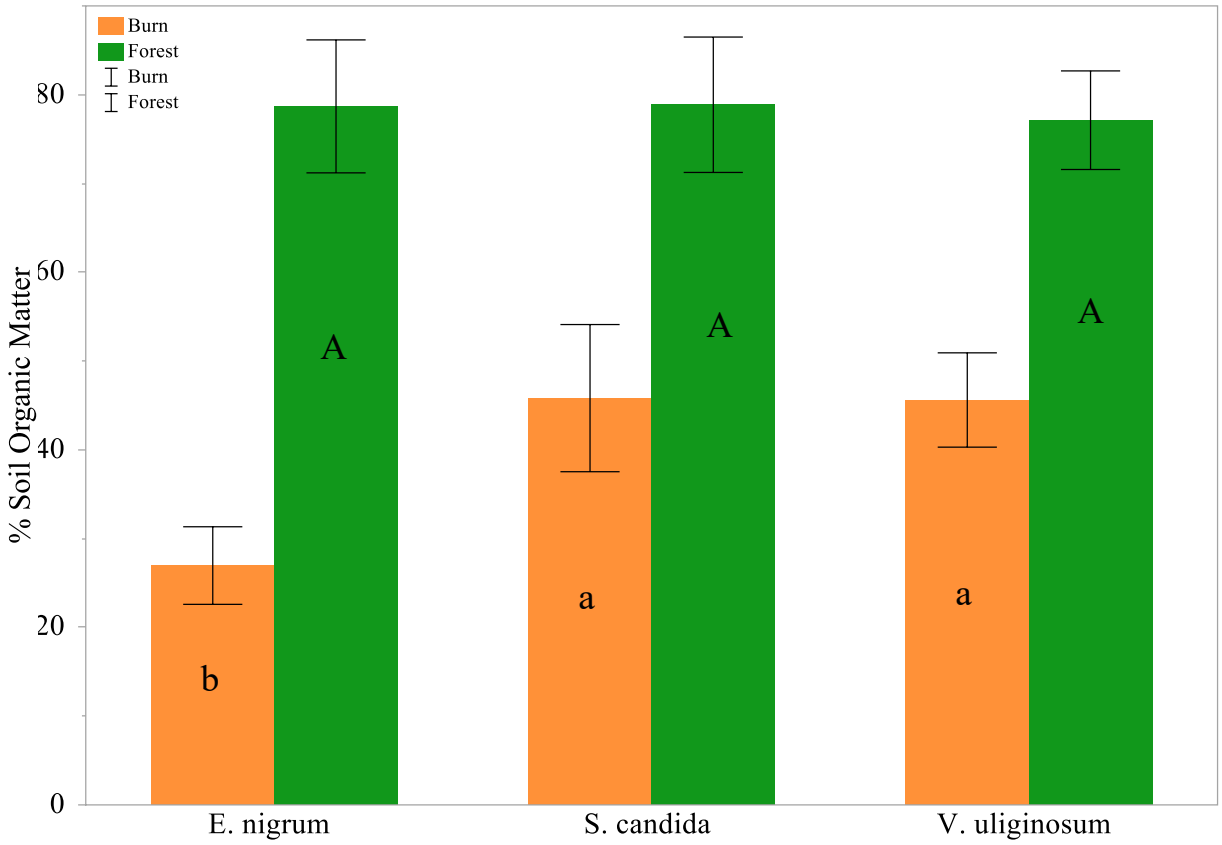

Figure 8: Mean percent Soil Organic Matter (%SOM) of soils samples from *E. nigrum*, *S. candida* and *V. uliginosum* in the burn site (orange) and the forest site (green). Error bars show the standard error. Bars with same character label are not significantly different.

Percent Water Retention

Site type had a significant effect on the percent water retention of soil ($p < 0.0001$) (Fig. 9). The mean water retention was twice as high in the burn site compared to the forest site. Species did not have a significant effect on the percent water retention of soil,

with *Empetrum nigrum* soils retaining 11.15 ± 6.33%, *Vaccinium uliginosum* soils retaining 10.9 ± 4.71% *Salix candida* soils retaining 10.75 ± 5.96%.

No statistically significant differences were found between species and their percent water retention in the burn site or the forest site when analyzed separately.

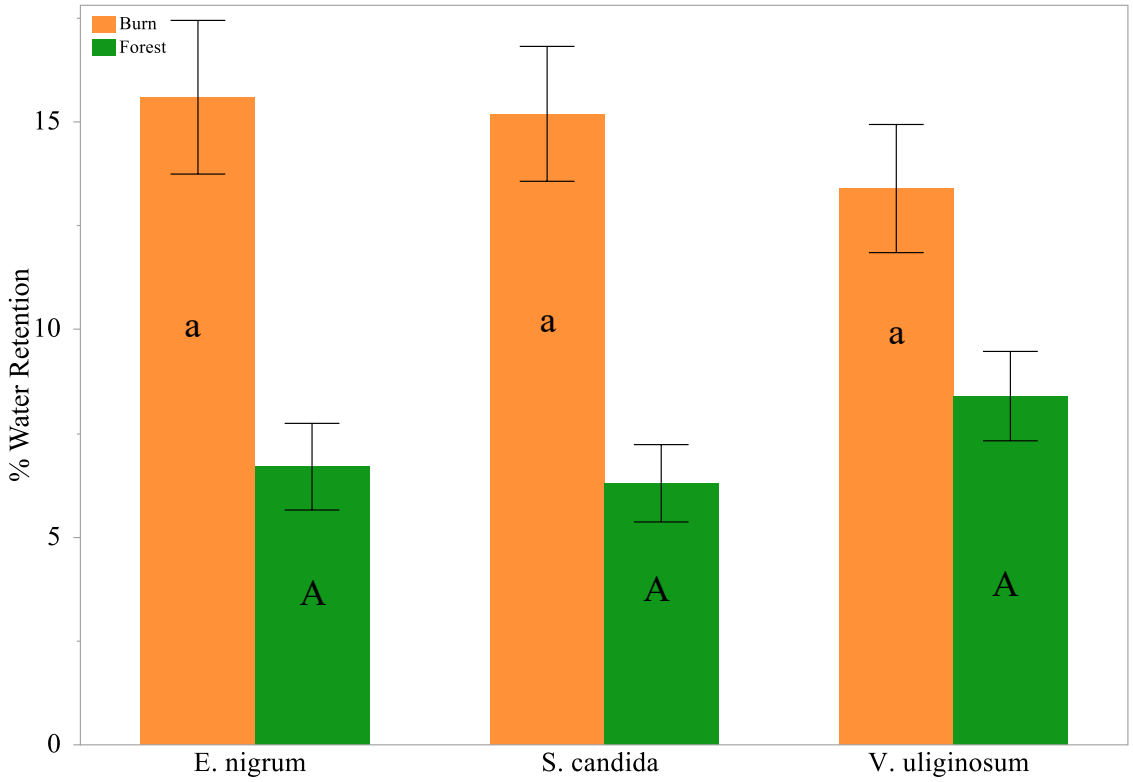

Figure 9: Mean percent water retention of soil sampled from *E. nigrum*, *S. candida* and *V. uliginosum* in the burn site (orange) and the forest site (green). Error bars show the standard error. Bars with same character label are not significantly different.

Growth Assay

Site type did not have a significant effect on the relative growth rate of sea lyme grass; however, species had a significant effect on the relative growth rate ($p = 0.0006$).

Salix candida soils had a significant effect on the relative growth rate of sea lyme grass ($p < 0.0001$). Grass grown in *Salix candida* soils had the highest mean relative growth rate at 43.41 ± 22.13 mg g-1 day-1. *Empetrum nigrum* soils also had a significant effect on the relative growth rate of sea lyme grass ($p = 0.0409$). Grass grown in *Empetrum nigrum* soils had the lowest mean relative growth rate of 23.56 ± 11.61 mg g-1 day-1

From the burn site, soils associated with the different species had a statistically significant difference in the relative growth rate of sea lyme grass planted in those soils. The largest difference in relative growth rate is between sea lyme grass grown in *Vaccinium uliginosum* soils and *Salix candida* soils ($p = 0.0016$). There was also a significant difference in relative growth rate between sea lyme grass grown in *Empetrum nigrum* soils and *Salix candida* soils ($p = 0.0022$).

From the forest site, there was no significant difference in the relative growth rate of sea lyme grass grown in soils from different species. The mean relative growth rate of sea lyme grass growing in forest soils was 31.52 ± 17.38 mg g-1 day-1 which was slightly higher than the mean relative growth rate of sea lyme grass grown in soils from the burn (Fig. 10), however, habitat type did not affect the relative growth rate of sea lyme grass.

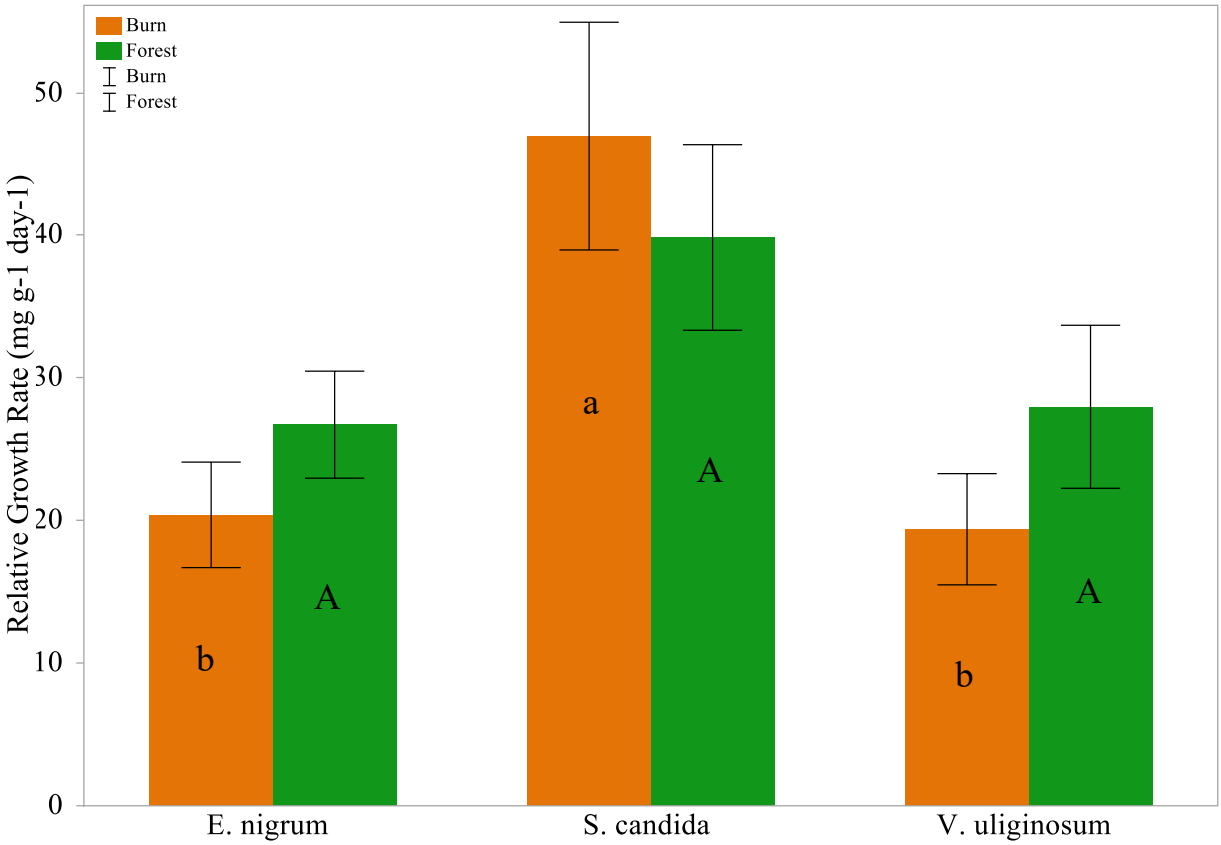

Figure 10: Mean relative growth rate of sea lyme grass grown in soils sampled from *E. nigrum*, *S. candida* and *V. uliginosum* in the burn site (orange) and the forest site (green). Relative growth rate is measured mg g-1 day-1. Error bars show the standard error. Bars with same character label are not significantly different.

Principle Component Analysis of Soil Fertility Variables

After performing a Principal Component Analysis (Fig. 11), 52.7% of the variation was explained by component 1 which showed positive associations with the soil respiration rate, organic layer depth and % SOM and negative associations with soil temperature and water retention. Component 2 explained 14.9% of the variation which showed positive associations with soil Hydrogen ion concentration.

The burn site and the forest site data points for the soil variables are clearly divided on the PCA space (Fig. 11). The burn site soil data points occupy the negative space of component 1 where high temperature and high water retention were observed. The forest site soil data occupy the positive space of component 1 where high respiration rate, high organic layer depth and high % SOM were observed. This separation corresponds with the results concerning statistical significance in the burn site for high soil temperature and water retention and low respiration rate, organic layer depth and % SOM.

Component 1 (Fig. 11) shows that soils from the forest are more likely to have higher soil respiration, organic layer depth, % SOM and to an extent inorganic nitrogen. Component 2 shows how *Empetrum nigrum* soils from the burn are more likely to have a high H ion concentration and acidic pH. *Salix candida* and *Vaccinium uliginsosum* soils from the burn site are being pulled by the Hydrogen ion concentration and inorganic nitrogen concentration on component 1. No correlation was found between the PCA axis values of and the growth rate of sea lyme grass.

PCA was also done for the forest site and burn site separately (Fig. 12 & Fig. 13). The PCA for the forest site (Fig. 12) shows that 27% of the variation is explained by component 1 which is strongly influenced by the organic layer depth and % SOM. The PCA for the burn site (Fig. 13) shows 33% of the variation is explained by component 1 which is strongly influenced by the % SOM and water retention. No obvious clusters separating the three species were apparent on the components of the PCA for the forest or the burn.

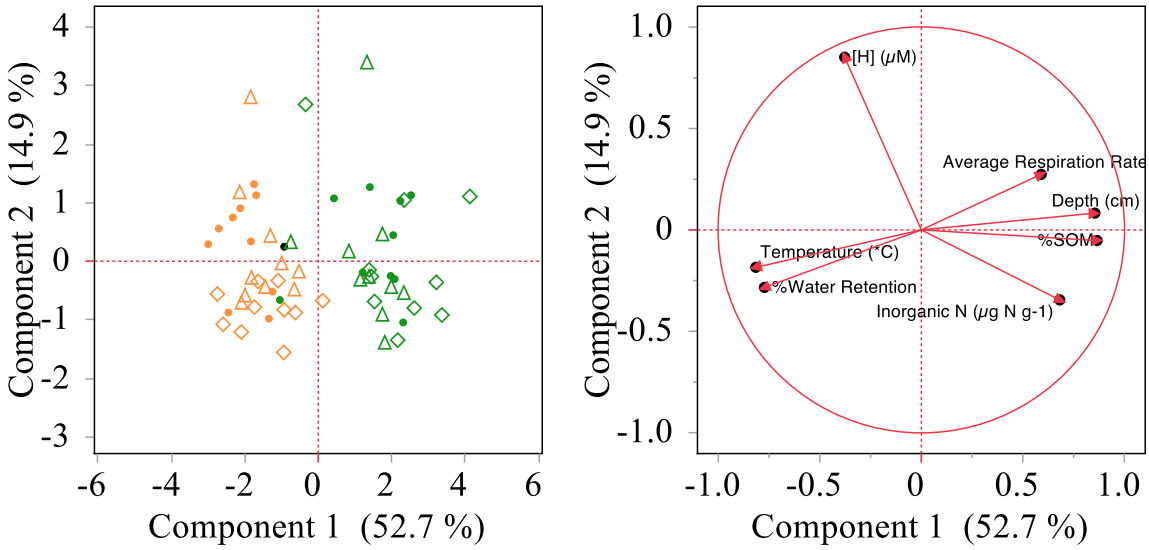

Figure 11: Principal Component Analysis A. Principal Component Analysis showing Burn site data points (orange) and Forest site data points (green) for soils associated *with E. nigrum* (point), *S. candida* (Diamond) and *V. uliginosum* (triangle). B. Principal Component Analysis with component 1 explaining 52.7% of the variation and component explaining 14.9% of the variation.

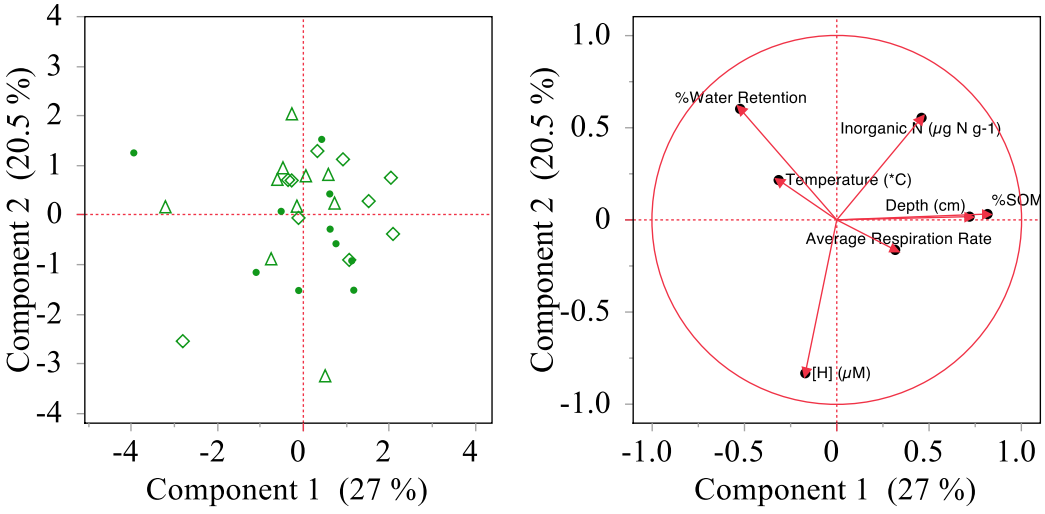

Figure 12: Principal Component Analysis of the Forest Site. A. Data points for soils associated with *E. nigrum* (point), *S. candida* (Diamond) and *V. uliginosum* (triangle) in the forest site. B. Principal Component Analysis of forest soils with component 1 explaining 27% of the variation and component explaining 20.5% of the variation.

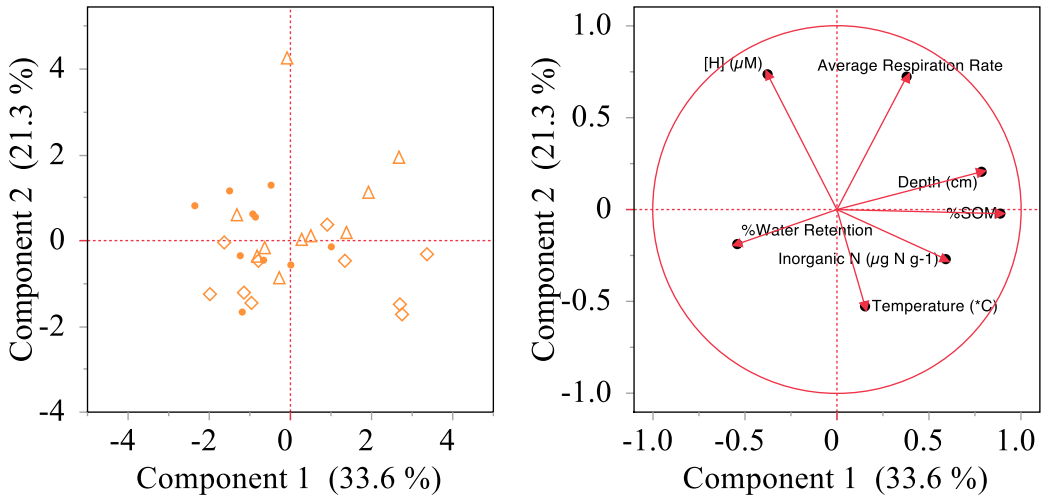

Figure 13: Principal Component Analysis of the Burn Site 13a. Data points for soils associated with *E. nigrum* (point), *S. candida* (Diamond), and *V. uliginosum* (triangle) in the burn site. 13b. Principal Component Analysis of fire-disturbed soils with component 1 explaining 33.6% of the variation and component explaining 21.3% of the variation.

Discussion:

Differences between the two sites and the three subject species that were either stress-tolerant or competitive were evident for the soil fertility variables such as soil respiration, organic layer depth, pH, % SOM and water retention. The soil from three species had a significant effect on the relative growth rate of sea lyme grass. Previous studies support the interconnectedness of soil fertility variables, recovery from fire disturbance, and species effects on soil as outlined below. Soil fertility is a balance between the production and decomposition of organic matter (Zang, 2020). The decomposition rate of the soil is influenced by how plant species affect abiotic factors of the soil (pH, temperature, texture, and other chemical properties) and biotic factors (leaf litter quality, microbial activity, % SOM) (Zhang, 2020).

Principal Component 1 from Figure 11 shows that most variability is due to high % SOM, increased depth and soil respiration rate. All soil fertility variables (organic layer depth, respiration rate, pH inorganic nitrogen content, % SOM, water retention, and soil temperature) were statistically significantly different between the forest site and the burn site. The soils from the burn site subjected to a high-severity wildfire had a statistically significant decrease in all the soil fertility variables except for temperature and water retention which increased (Fig. 2 and Fig. 9). The high-severity fire caused an unexpectedly low pH and may have contributed to the overall reduction in fertility (Fig. 4). The sustained low pH after a wildfire is different from other studies, however, these primarily focus on the mid-intensity, mid-severity fires characteristic of the boreal forest (Certini, 2005, Clemmensen *et al.*, 2013). Additionally, higher temperatures in the burn site did not correlate with an increase in respiration rate contradictory to previous studies (Lloyd & Taylor, 1994). The species-specific effects on soil fertility and soil fertility variables in the subarctic boreal forest are apparent. The relative growth rate of sea lyme grass was species driven rather than site driven for testing overall soil fertility (Fig. 10). As expected, the competitive species *Salix candida* significantly increased the respiration rate, the amount of inorganic nitrogen, and showed resistance to low pH in the burn site. As a result, soils associated with *Salix candida* contributed to a higher relative growth rate of sea lyme grass compared to soils from the stress-tolerant plants.

The depth of the O horizon influences the decomposition of organic matter and the rate at which nutrients are redistributed (O'Donnell *et al.*, 2016); in turn, the depth of the organic layer is influenced by the rate of decomposition, microbial community composition, temperature, precipitation, water retention, and disturbance (Barreto, 2018).

Unsurprisingly the organic layer depth of in the forest was deeper than the organic layer depth of replicate plots in the burn. Stress-tolerant species like *Empetrum nigrum* produce leaf litter that decomposes slower than the leaf litter of other ericaceous plants or competitive plants (Tybirk, *et al.*, 2000), therefore a deeper organic layer would be expected among *Empetrum nigrum* replicate plots from lack of decomposition, acidic pH, and organic matter buildup. However, in this study organic layer depth was not significantly influenced by species even though *Empetrum nigrum* had a low % SOM compared to the other species (Fig. 8). The lack of variation in organic layer depth among species is from the larger effect that the site has on the soil variables such as soil respiration rate, % SOM, temperature, and water retention. Higher nitrogen content in the forest may inhibit colonization of fungal detritivores whose role is to accelerate decomposition (Baldrian *et al.,* 2023); reducing detritivore activity from low nitrogen supply compared to other forest types allows for the increase in both organic layer depth and % SOM.

Temperature is an important control on the production of organic material from plants as well as the decomposition of organic matter within the soil (O'Donnell *et al.*, 2016). Lower temperatures favor the build-up of SOM, however, from this study, no correlation was found between temperature and % SOM, likely due to the dramatic differences between the two sites.

In general, temperature impacts soil respiration rates, especially in summer months when microbial density is high; As the temperature of the soil increases, soil respiration rate increases (Shibistova *et al.*, 2002). No apparent correlation was found between the soil temperature and respiration rate from the results above, however, temperature

differences between the forest and the burn site are likely from the shade from forest trees and the insulative effect of bryophytes and lichens on the forest floor (Porada *et al*., 2016). Bryophytes have been found to decrease soil temperature and are more efficient as an insulative layer in summer (Porada *et al*., 2016). The high respiration rate in the forest is more likely to be driven by the quality and depth of organic matter, higher nitrogen content, and habitat for microbes rather than temperature (Anjum & Ahmed Khan, 2021). High respiration rates within the forest site are a part of the carbon cycling of the forest and measurements were taken during the annual peak in soil respiration for the boreal forest (Shibistova *et al.*, 2002). The daily assimilation of CO2 in the boreal forest is 20 μmol m -2 s -1, therefore the forest site can help balance the amount of CO2 being respired and reassimilated better than the burn site where there is considerably less vegetation, less nitrogen, and more ericaceous plants (Jarvis et al. 1997).

Microbes are important to soil fertility as they fix nitrogen, and increase the mobilization of nutrients like phosphorus, potassium, and iron by converting them into organic acids (Rashid *et al.*, 2016). Microbial biomass and productivity suffer from wildfire activity, and it may take up to 12 years for microbial biomass to reach pre-fire levels again (Certini, 2005). However, this fire occurred over 25 years ago, and the mean respiration rate of the burn is still less than half that of the mean respiration rate of the forest. The respiration rate after high-intensity fires may take longer to rebound due to the near complete reduction in the organic layer, highly acidic pH and low % SOM.

Vaccinium uliginosum soils have the highest mean respiration rate of the species in the burn site potentially from mycorrhizal associations, affinity for microbes, or high root density (Högberg *et al.*, 2001). However, it has been reported that under low soil

microbial conditions, *Vaccinium uliginosum* reduces its foliar N:P ratio and consequently its leaf litter quality (Duan *et al.*, 2023). When comparing the respiration rate of *Vaccinium uliginosum* compared to soils fostered by other species or within the forest, *Vaccinium uliginosum* respiration rates are relatively low which may be creating a positive feedback loop that contributes to more low-quality leaf litter deposited in the soil. This positive feedback loop mechanism may also be the case for *Empetrum nigrum* leaf litter since this ericaceous stress-tolerant plant had soils with the lowest respiration rate in the burn site.

Respiration rates in the forest site were higher due to increased habitat for microbial activity and the presence of live roots. As indicated by the PCA (Fig. 11) respiration rate, organic layer depth, and % SOM have a similar drive in the same direction. Plants themselves contribute to the respiration rate as root respiration accounts for up to half of the soil respiration (Högberg *et al.*, 2001), and CO2 efflux increases linearly with fine root density (Shibistova *et al.*, 2002). Considering the density of roots in the forest soils observed when measuring organic layer depth and the quantified % SOM, it follows that soil respiration would be higher on average in the forest compared to the burn.

Soil respiration is a biological process that releases CO2 and has been estimated to contribute 80 Gt of CO2 per year (Shibistova *et al.*, 2002). Soil respiration may affect the carbon content of the soil, especially in sandy fire-disturbed soils (Shibistova *et al.*, 2002). Soil respiration may be impacting the amount of carbon in the soil to a degree, but the deposition of organic material, temperature, and depth of the organic layer would have a greater effect on the carbon content of the soil. In this study, no apparent correlation was

found between soil respiration and % SOM. The site had a statistically significant effect on soil respiration with a depressed respiration rate in the burn site compared to the forest site. Some studies related to fire disturbance indicate that pH, temperature, C:N ratio in the soil, and fire history were the best indicators of respiration rate (Cooperdock *et al.*, 2020). Other variables such as temperature, microhabitat for microbial and detritivore activity, carbon content, organic layer depth containing respiring roots, and quality of leaf litter may be driving these site differences in respiration rate together (Jarvis et al. 1997; Laganière, 2012).

The boreal forest is known for its acidic soils and slow decomposition rate, the buildup of peat contributes to the acidity and the refinement of the active layers of soil (Beaulne, 2021), however, no correlation was found between % SOM and respiration rate of the soil. Post-low-severity fire soils have more electrical conductivity due to the release of ions in the burning organic matter; and the pH of the soil increases from the denaturation of organic acids and the release of bases into the environment as organic matter burns down (Certini, 2005). Under low-severity conditions, a liming effect occurs in the soils as low-intensity burning releases bases in an otherwise acidic medium. During the liming effect, the bases released from low-intensity fire interact with the existing acids in the soil allowing for the soil to neutralize within a couple of years if microbial activity and plant growth rebound steadily after the disturbance has passed (Certini, 2005; Granath *et al.*, 2021). However, in this study, the acidity of the burn site is higher than the acidity of the forest site. The sustained low pH of the burn site after over 25 years in this study is different from previous results, possibly due to the leaching of ions in the soil or the high severity of the fire and extent of O horizon consumed. Other factors apart from fire

severity such as lichen composition, high soil temperature or microbes may be influencing the high acidity of the burn site and must be investigated.

The overall high acidity in the burn site may cause the leaf litter of the three subject species to decompose slower and reduce the variability in organic layer depth. The openness of the burn site may influence the organic layer depth as the burn site is susceptible to surface erosion of soil reducing the build-up of humus and litter, especially after a high-severity fire (Carcaillet *et al.*, 2006). The charred material remaining on the burn site is hydrophobic and contributes to the loss of moisture and erosion of the soil (Köster *et al.*, 2021). Forest soils are protected from erosion by a higher density in tree coverage and moss coverage of the soil helping retain moisture and soil particles. Water retention of the burn site and the forest site was generally low, however, the burn site retained about double the percentage of water retained in burn soils compared to forest soils indicating that the organic matter is not retaining as much water as previously thought and other factors like compaction and the accumulation of waxy or hydrophobic organic matter, may be influencing water retention (Huang & Hartemink, 2020, Tybirk *et. al*, 2000). Lower hydrogen ion concentration found in soils associated with *Salix candida* may be explained by the ability for deciduous shrubs and trees to buffer the acidity and bring up calcium from deeper soil horizons (Berger *et al*., 2006; Prietzel *et al*., 2021). Leaf litter deposited by competitive plants such as *Salix candida* may contain higher amounts of calcium which counteracts the acidity of the soil (Berger *et al*., 2006).

Higher than average inorganic nitrogen content associated with *Salix candida* soils may be caused by a combination of the high leaf litter quality and lower microbial activity among the other species. Studies on *Salix* species suggest that their higher nutrients in the

leaves affects the decomposition rate and soil fertility more than other climatic effects (Hoeber *et al.,* 2020). Low inorganic nitrogen in soils associated with *Empetrum nigrum* may be attributed to the thick waxy cuticle of the leaves in the leaf litter that slows decomposition and contribute fewer nutrients. *Empetrum nigrum* is known to be a nitrogen-limited species thriving in nutrient-poor acidic soils (Tybirk *et al.*, 2000). The severity of fire in the burn site may be a factor in the loss of inorganic nutrients since the removal of vegetation and an increase in temperature can increase the mineralization of nutrients (Turner *et al.*, 2007). Since much of the organic nitrogen in the burn area was volatilized after the high-intensity fire, little nitrogen was left to be mineralized and stored in inorganic forms (Certini, 2005; Turner *et al.*, 2007). The reduction in microbes may contribute to the low inorganic nitrogen content as few microbes are converting organic nitrogen to inorganic forms.

The reduction in plant biomass and organic layer due to severe fire significantly reduces the carbon content of post-high-severity, high-intensity fire (Pellegrini *et al.*, 2022). Carbon can be further reduced after fire from wind erosion and low C inputs from vegetation (Pellegrini *et al.*, 2022). The openness of the burn site and mosaic of isolated vegetation may account for the low input and retention of carbon in the soil contributing to the low % SOM. Low % SOM in soils associated with *Empetrum nigrum* was expected and is reflected by the low leaf litter quality, acidic pH, and low decomposition rate from phenolic compounds and waxes (Tybirk *et al.,* 2000; Markham *et al.*, 2008). In general, post-fire soils in the boreal experience an increase in pyrogenic carbon relative to other forms of carbon (Pellegrini *et al.*, 2022), however little charcoal was observed in soil samples from the burn site due to the fire severity nearly 30 years ago.

Species had a significant effect on the relative growth rate of sea lyme grass and that was especially prominent in *Salix candida* soils. High relative growth rates of sea lyme grass grown in *Salix candida* soils from the burn and the forest site indicate that *Salix candida* soils are more fertile for the nutrient-requiring grasses and have been found growing together on moderately disturbed nutrient rich sites (Lang *et al.,* 2021). The higher fertility of *Salix candida* soils comes from a combination of adequate microbial activity, % SOM, pH, and inorganic nitrogen. The contribution to soil fertility by stress-tolerant plants like *Empetrum nigrum* and *Vaccinium uliginosum* have similar effects on the relative growth rate of plants that occupy those soils with low biomass accumulation regardless of disturbance.

Conclusion:

Significant differences among soil variables were found between the forest site and the burn site, however plant species and their life history strategy characteristics have an impact on soil fertility. Even in low fertile soils such as the burn site, *Salix candida* is a competitive plant that significantly increases the amount of inorganic nitrogen of the soil, can buffer the soil acidity and produces soils with high growth rate of sea lyme grass.

Fire severity is an important parameter that affects soil fertility variables and has dramatically different effects when comparing soils exposed to high-severity fire and no disturbance. The acidity and the respiration rate of the soil are two soil fertility variables that are unexpectedly altered by the high severity nature of wildfire as soil pH remains more acidic rather than basic and respiration rate depressed after post high-severity fire.

Low severity fires are a part of the natural disturbance regime, and the subarctic boreal forest has maintained its resilience against high-intensity and high-severity fires by being an ecosystem that supports a thick organic layer, high water tables, and permafrost that retain moisture and buffer the effects of drought and fire disturbance (Bill *et al.*, 2023). The warming of the north by climate change is shifting the natural fire disturbance regime allowing high-severity fires to consume large amounts of soil organic matter on the surface and plant biomass which has consequences to soil fertility.

Altered soil conditions with the increase in high-intensity surface burns, allow for the establishment of deciduous tree species such as willows or dwarf birches (Bill *et al.*, 2023). Broader consequences to soil fertility and the boreal ecosystem as climate change increases the frequency, intensity, and severity of fire disturbance. As fire disturbance is changing the prevalence of competitive deciduous trees rather than ericaceous plants, oligolectic pollinators may be changing their range of host plants. For example, in Manitoba, the bee *Andrena bradleyi* is an ericaceous plant specialist but has been observed carrying 95.84% *Salix* pollen grains in the absence of ericaceous plants or ericaceous blooms (Watson & Bartel, 2024). The change in vegetation type and vegetation form may be influencing the carbon and nitrogen cycling in the soil.

Soil fertility is changing due to increased frequency of high-severity, high-intensity fire and the reduction on soil fertility has consequences to the plant community in terms of organic layer, soil temperature, pH conditions, microbial activity, carbon quality and nitrogen content. However, the positive effect that competitive species, such as *Salix candida*, have on soil fertility in the boreal forest can impact the future of the soils and their ability to support the establishment of other vegetation.

Additional Figures

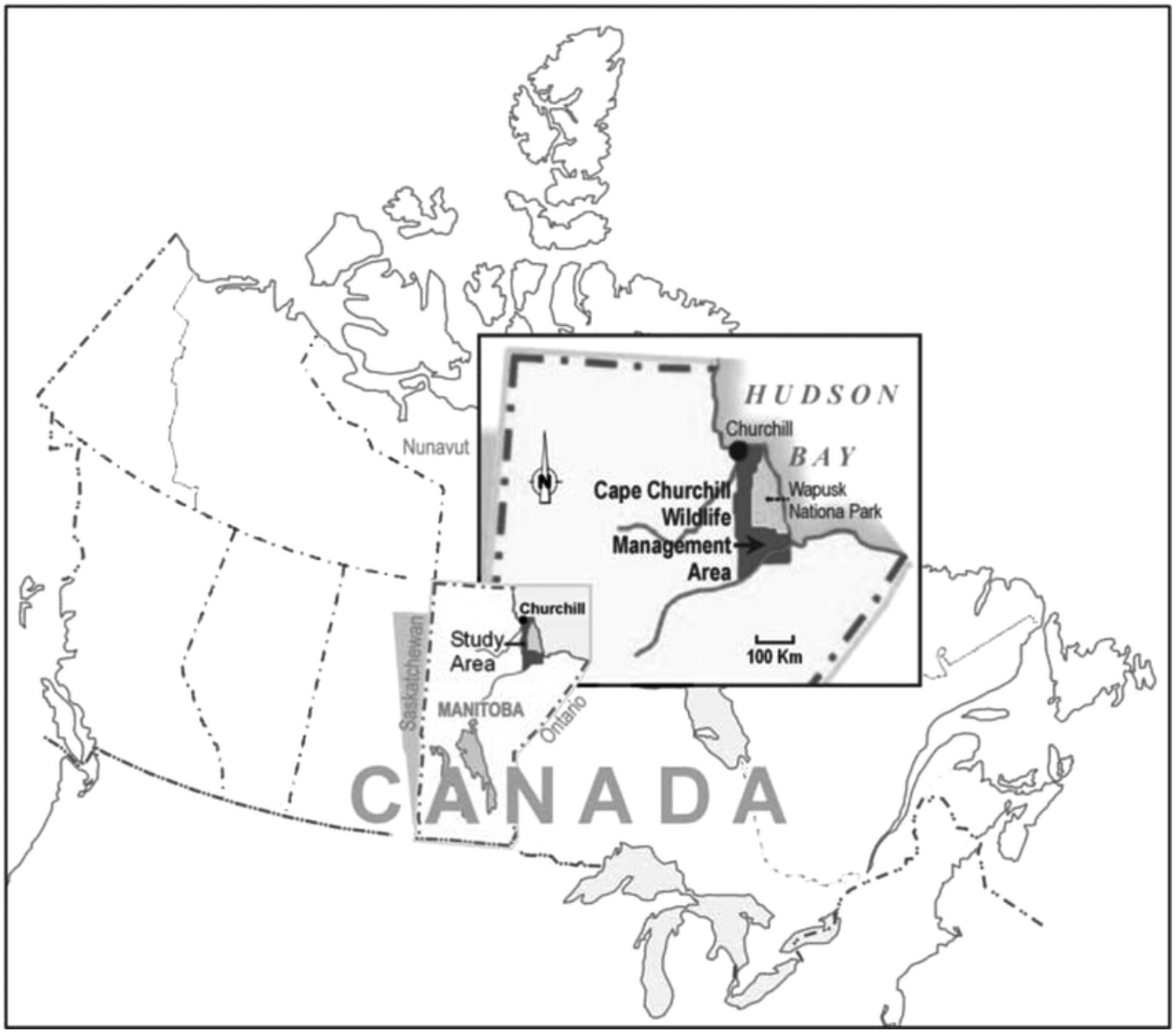

Figure 14: Study Area located in northern Manitoba, Canada in Churchill Wildlife Management Area near the town of Churchill, Manitoba. (© Ryan, 2001). Used with permission.



Figure 15: Study area satellite images. A. Forest site satellite image with coordinates and scale bar; replicate samples of the three species were taken within the red circle. B. Burn site satellite image coordinates and scale bar; replicate samples of the three species were taken within the red circle.



Figure 16: Schematic of the Study Design that included two sample sites, the Forest Site and the Burn Site. Each sample site contained 10 sets of replicate plots with the three subject species. From the forest site there are ten *Empetrum nigrum* (C), ten *Vaccinium uliginosum* (V), and ten *Salix candida* (W) replicate plots. From the burn site there are ten *Empetrum nigrum* (C), ten *Vaccinium uliginosum* (V), and ten *Salix candida* (W) replicate plots, creating a total of 60 replicate plots.

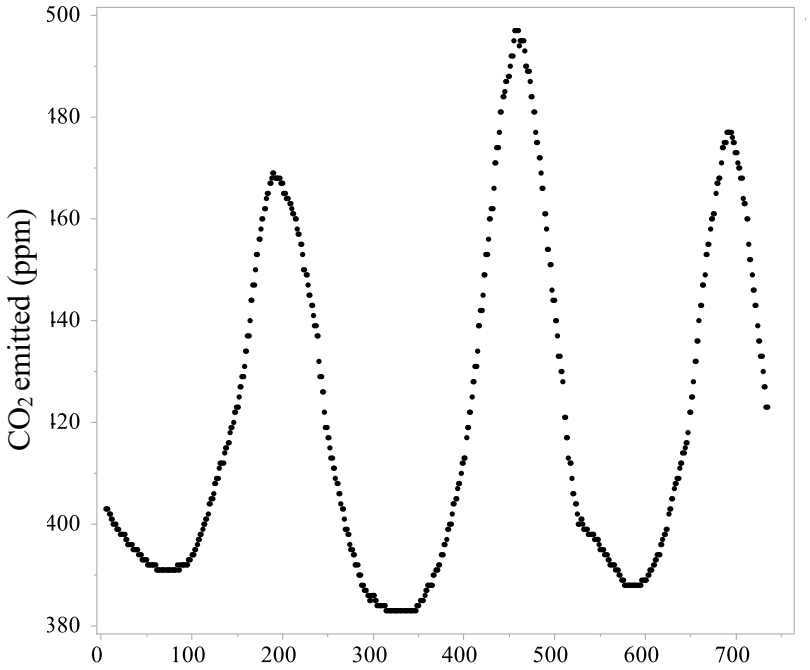

Figure 17: Example of respiration rate slopes with CO_2 emitted from the soil in ppm over time in seconds. The bold data points represent the increase and decrease in respiration rate while enclosed in the soil respirator.

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