Ecophysiology of Atlantic Coastal Shrubs in Response to Ocean Salt

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Abstract

Increased greenhouse gases in Earth's atmosphere are altering the global climate including changes in air temperature and precipitation patterns that are linked to increasing storms and sea-level rise. In coastal regions, more frequent storm surges and high-water levels can increase marine salt exposure on terrestrial ecosystems through waves and sea spray. There is a need to understand the physiological impacts of marine salt on plant species found in coastal habitats such as barrens and forests. These globally distributed habitats are dominated by woody plants, especially shrubs, and they represent a large portion of the Atlantic coast of Canada. Currently, there is a knowledge gap on how shrub species in these habitats are affected by salt stress. To address this gap, leaf and soil samples were collected from two sites: a rock barren, Chebucto Head, and a forest, Taylor Head, in Nova Scotia. This study examined leaf morphological and physiological traits related to salt tolerance and resource use in two dominant shrub species, the Northern Bayberry (*Morella pensylvanica*) and the Lowbush Blueberry (*Vaccinium angustifolium*). Individuals were sampled along a salinity gradient within 200 m of the Atlantic Ocean coastline. Traits included stomatal conductance, specific leaf area, leaf thickness, and leaf dry matter content; leaf nutrients included pH, electrical conductivity, sodium, potassium, nitrate, and calcium contents The soil characteristics and leaf traits were compared in relation to their proximity to the shore using three-way analysis of variance (ANOVA), linear regression, and a principal components analysis, providing more information on the differences between habitat, proximity to the shore, and species in response to ocean salt. This study found that there were differences in salt tolerance within the same species between the different habitats as well as a difference between species. In general, plants in the rock barren experienced higher salt loads and displayed more physiological stress than plants in the forest. The Northern Bayberry was more salt tolerant overall than the Lowbush Blueberry. This research has the potential to be applied in coastal restoration projects to inform which species may be most resilient to saltwater exposure and which habitats may be more vulnerable.

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1.0 Introduction

1.1 Climate Change, Storm Surge, and Sea-level Rise

Increased greenhouse gases in Earth's atmosphere are altering the global climate including changes in air temperature and precipitation patterns. These global changes can lead to shifts in species distributions and biodiversity loss (He and Silliman, 2019; Thuiller, 2007). As the mean global temperature increases, there is evidence for more powerful and frequent hurricanes being formed (Elsner, 2006; Hauser et al., 2015). Hurricanes and similar extreme weather events lead to storm surges and have the potential to cause serious damage to both infrastructure and the natural environment, including property damage, flooding, and coastal erosion (Davlasheridze et al., 2021; Morton and Barras, 2011). Although there are still uncertainties in the global relationship between climate change and the occurrence of extreme weather events, modelling relationships predict storm surge heights will increase with a warming climate in more localized areas (Davalsherize et al., 2021).

Climate change not only is related to an increased frequency of hurricanes and storm surge but rising sea level as well. Increased temperatures are leading to the thawing of sea ice and the thermal expansion of the oceans (Frederikse et al., 2020). Projections indicate that sea level rise will range from 0.26m to 0.77m globally by 2100, posing large risks for islands and low-lying coastal areas (Eamer et al., 2021). While these projected impacts are global, certain coastal regions experience sea level rise at faster rates than others including island countries, the Gulf Coast, and the Atlantic coast of North America (Titus and Richman, 2001; Wade, 2022).

The combined impacts of sea-level rise, coastal erosion, and increased storm surges from extreme weather events have the potential to increase salt stress in coastal ecosystems and associated organisms through increased exposure to sea water. These ecosystems are more likely to experience salt stress if they are exposed to more salt water and spray than they are adapted to, leading to an increase in the range and amount and of ocean salt that is deposited on land. Under this scenario, individuals that were once far enough away from the shoreline to experience limited to no influence from ocean water and spray would receive more ocean spray and deposition from waves, particularly for sessile organisms such as plants (He and Silliman, 2019; Hauser et al., 2015).

1.2 Salt Stress Responses in Plants

Plants face salt exposure from various sources including soil salinization (Isayenkov, 2012), sea spray, waves, and storm surge. It is known that the salt tolerance of plant species is variable, but broadly it is understood that increased salts in soil reduces the ability of the plant to properly absorb water and minerals required for growth. Water and nutrients are taken up by the roots via osmosis, so when there is a high concentration of salt in the soil, this shifts the osmotic gradient, reducing the flow of water and other essential nutrients in to the roots, leading to nutrient deficiencies (Lagerwerff, 1969).

Sodium (Na^+) is one of the most common salt-forming ions. Sodiumis considered to be a cytotoxic salt ion and is one of the most restricting substances to plant growth (Isayenkov, 2012 and Zhu, 2007). While the inhibition of plant growth is the primary symptom of excess sodium, it leads to other symptoms including the closure of stomata, resulting in reduced photosynthetic activity. There are also effects at the root level, as excess sodium interrupts the uptake of potassium, a necessary ion for plant function (Zhu, 2007). Additionally, nutrient deficiencies may occur such as calcium (Ca^{2+}) and nitrate (NO_3^-) deficiencies when exposed to saline conditions. In cases of high Na^+ in the soil, the uptake of the excess Na^+ restricts the ability of the roots to absorb water and essential nutrients such as Ca^{2+} and NO_3^- (Jouyban, 2012). Plants can actively avoid or tolerate salt stress by compartmentalizing excess sodium ions, and adjusting sodium-potassium ratios in their tissues. Compartmentalization is a mechanism through which salt is kept away from meristems and developing leaves that are actively photosynthesizing (Zhang, 2014). For example, many plants in naturally saline environments such as coastal and marine ecosystems (e.g., salt marshes), salt lakes and salt flats (Pessarakli, 1999) have specialized salt glands within their stems and leaves that sequester excess sodium ions (Isayenkov, 2012). Sodium is removed from cell cytoplasm via sodium/proton antiporters and stored within vacuoles. These vacuoles retain the sodium ions until they can be excreted by the leaves (Peng et al., 2016).

Compartmentalization of sodium in vacuoles also helps regulate the sodium-potassium ratio within the cells, further preventing salt toxicity (Mansour, 2023). Potassium (K) is a nutrient essential to cellular and enzymatic functions as it regulates the potential of cell membranes and maintains the homeostasis of cytoplasmic pH. Sodium has similar physiochemical properties to potassium which leads to competition between these nutrients and binding sites involved in important cellular function (Almeida et al., 2017). The ability of a plant to maintain a consistent sodium-potassium ratio (Na/K) under variable salinities is an indicator of the ability of the plant to maintain homeostasis under saline conditions and thus reflects relative salt tolerance (Kumar et al., 2011; Almeida et al., 2017).

1.3 Salt Stress and Coastal Ecosystems

Coastal ecosystems can be defined as terrestrial habitats that are influenced by ocean tides and ocean spray and are found within 100km from the coastline. These ecosystems are some of the most productive, yet threatened ecosystems around the globe, providing numerous ecosystem services (UNEP, 2006). The Atlantic Coastal Plain describes the land along the Atlantic Coast of the United States ranging from Florida to Massachusetts. The vegetation found within the Atlantic Coastal plain extends outside of this area, and can be found in Ontario, New Brunswick, and Nova Scotia, Canada (Environment Canada and Parks Canada Agency, 2015). Many Atlantic Coastal Plain plant species are found in habitats such as salt marshes, barrens, and forests (Querry, 2016).

Barren habitats can vary by environmental factors and represent some of the most extreme conditions for plant growth. Such environmental conditions include extreme temperatures, natural and anthropogenic disturbances, and soil conditions that are typically not ideal for plants including reduced organic matter, low pH, and increased salinity in coastal areas. Barrens are dominated by low shrubs and are known for their extreme climatic conditions (Porter et al., 2020). Barrens can be further classified by their surrounding environments (i.e., coastal, highland, and inland barrens) and the plant communities present. Generally, these habitats are occupied by ericaceous species and lichens, but communities vary (Davis,1996). This type of ecosystem is distributed globally and can be seen in places in which soils and/or exposed rock are dominant, with limited vegetation (Oberndorfer and Lundholm, 2009).

In Nova Scotia, there are multiple barrens situated near the coast which host around 173 species of plants and while there have been studies on barren or heathland biodiversity, these ecosystems tend to be overlooked when considering coastal development and other pressures

(Oberndorfer and Lundholm, 2009). Within Nova Scotia, there are patches of coastal barrens found within forested areas. These patches often are located on exposed bedrock and areas with a very thin layer of soil cover and are dominated by ericaceous species including *Vaccinium angustifolium* (Burley et al., 2010). In some cases, forest growth can overtake the barrens especially when the barren is located inland or in an area that is sheltered from sea spray and wind (Burley et al., 2010).

Forests can also be found throughout Nova Scotia and make up a large portion of Nova Scotia's coastal ecosystems. These coastal forests experience a cool and moist climate. Additionally, high humidity, strong winds, fog, and salt spray greatly influence plant species composition in Nova Scotia's coastal forests (Government of Nova Scotia, 2021). White Spruce (*Picea glauca*), Black Spruce (*Picea mariana*), Balsam Fir (*Abies balsamea*), Red Spruce (*Picea rubens*), Eastern Hemlock (*Tsuga canadensis*), and White Pine (*Pinus strobus*), as well as Maple (*Acer*), Birch (*Betula*), and shrubs are commonly found in Nova Scotia's coastal forests. Plant species in Nova Scotia's coastal forests may experience a krummholz condition, which is restricted tree growth that results in deformed and short vegetation which occurs in these mixed-wood forests in most coastal areas because they are exposed to wind and sea spray stress (Neily et al., 2004; Government of Nova Scotia, 2021). These forests are also often affected by natural disturbances including hurricanes, pests, and disease (Neily et al., 2004).

1.4 Study Purpose and Objectives

There is limited information on the effects of salt on plant species commonly found in barrens and forests of the Atlantic Coastal Plain. The objectives of this study are to determine:

1. If there are differences in leaf physiological and morphological traits between dominant shrub species along a salinity gradient from the coast-inland.
2. If there are differences in leaf traits among individuals of the same species growing along the coast versus further inland.
3. If there are differences in leaf traits among individuals of the same species growing in a coastal barren versus a coastal forest.

Understanding the impacts of salt stress on these plants, specifically by investigating whether there is variation in leaf physiology can be indicative of the plant's ability to grow and survive (Goud and Roddy, 2022). This study will emphasize the effects of sea spray and high-water levels as variations can indicate a response to environmental changes. Species found in these ecosystems are of economic value, such as *Vaccinium angustifolium* (Lowbush Blueberry) which is sold by the agricultural industry at an increasing rate making it an important crop for Eastern Canada and the US (Brazelton and Strik, 2007; Lafond, 2008). While the species found in these shrublands are tolerant of the poor soil and harsh conditions, there must be further investigation into how these species respond to salt stress, especially for ecosystems near the coast, as there is an increasing chance of salt exposure from sea spray and storm surge as a result of climate change (Hauser et al., 2015).

1.4.1 Focal Species: Northern Bayberry *(Morella pensylvanica*)

The Northern Bayberry (*Morella pensylvanica*, Family Myricaceae) is a deciduous to semi-evergreen shrub native to eastern Canada and the eastern United States. They thrive in moist, sandy, and acidic soils and prefer full sun environments. This shrub is quite versatile and can be found in regions that experience drought, strong winds, poor soil conditions, and ocean spray

(Flora of North America, 2020, Porter et al., 2020) including sand dunes, heathlands, barrens, and forests of the Atlantic coastal plain (Hauser, 2006). While often deciduous, this species can be semi-evergreen in regions with warmer winter climates. The leathery, aromatic leaves are dark green or a grey-green and glossy. They generally have lance or oval shaped leaves with teeth near the tip, or leaves may be smooth (Keen et al., 2005). The Northern Bayberry is dioecious, producing yellow-green catkins on both male and female plants that are not very showy. If pollinated, the female flowers produce gray-white drupes which are coated in an aromatic waxy coating (Flora of North America, 2020.; Hauser, 2006).

1.4.2 Focal Species: Lowbush Blueberry (*Vaccinium angustifolium*)

Lowbush Blueberry (*Vaccinium angustifolium*, Family Ericaceae) is a deciduous shrub species that can be found in forests, barrens, wetlands, and managed fields (Government of New Brunswick, 2012). This species prefers soils with a pH of 4.2-5.2 and thrives in full sun. Lowbush Blueberry has commercial value, particularly in the North American northeast (Government of New Brunswick, 2012). The Lowbush Blueberry is native to North America, ranging from Illinois to Minnesota and New England to Virginia in the United States, and from Newfoundland to Manitoba in Canada (Agriculture Canada, 1982; Tirmenstein, 1991). While the lowbush blueberry is found in harsh environments, the productivity of this species is reduced when exposed to road salt which can lead to economic losses (Eaton et al., 1999). Lowbush Blueberry has smooth, shiny, lanceolate leaves with toothed margins. The leaves are dark green and change to red in during autumn. The blue/bluish-black berries are not only harvested and consumed by people, but they are also consumed by several other species including black bears, deer, birds, and others (Tirmenstein, 1991).

2.0 Methods

2.1 Site Descriptions

2.1.1 Chebucto Head, Nova Scotia

Chebucto Head (Figures 1 and 2) is a coastal rock barren located on the Chebucto Peninsula, within the community of Duncan's Cove of Nova Scotia (44.50632, -63.52293). Climate of the region is humid and wet with mild temperatures, but due to the proximity to the coast temperatures tend to be cooler than inland Nova Scotia (Natural Resources Canada, 2010). Much of the area is exposed rock with thin layers of soil, with no tree canopy cover, leaving the area exposed to full sun and wind (Porter et al., 2020).

Coastal barrens at this site host several distinct plant communities compromised of different abundances of bryophytes, ferns, shrubs, small trees, and grasses. Within the study area, the dominant species were low-growing shrubs such as Northern Bayberry (*Morella pensylvanica*), Black Huckleberry (*Gaylussacia baccata*), Common Juniper (*Juniperus communis*), and Black Crowberry (*Empetrum nigrum*). The Lowbush Blueberry (*Vaccinium angustifolium*) and Bog Cranberry (*Vaccinium oxycoccus*) are also abundant (Porter et al., 2020).

2.1.2 Taylor Head, Nova Scotia

Taylor Head (44.83717, - 62.57728)(Figures 1 and 3) is a coastal mixed forest dominated by Balsam Fir (*Abies balsamea*) and Spruce (*Picea*). It is located on the Eastern Shore of Nova Scotia within the Taylor Head Provincial Park. The climate of the area is humid with mild temperatures, and experiences higher winds than inland Nova Scotia due to the proximity to the ocean (Natural Resources Canada, 2010). Various shrub species grew under the conifer and hardwood canopy. Within the study area, the dominant shrub species were the Northern

Bayberry and the Lowbush Blueberry. Mountain Cranberry (*Vaccinium vitis-idaea*) and Black Crowberry (*Empetrum nigrum*) were also present. There were areas of exposed rock and variation in soil depth. A gravel road transected the site and individual plants along the road had particulates from the road deposited on their leaves.

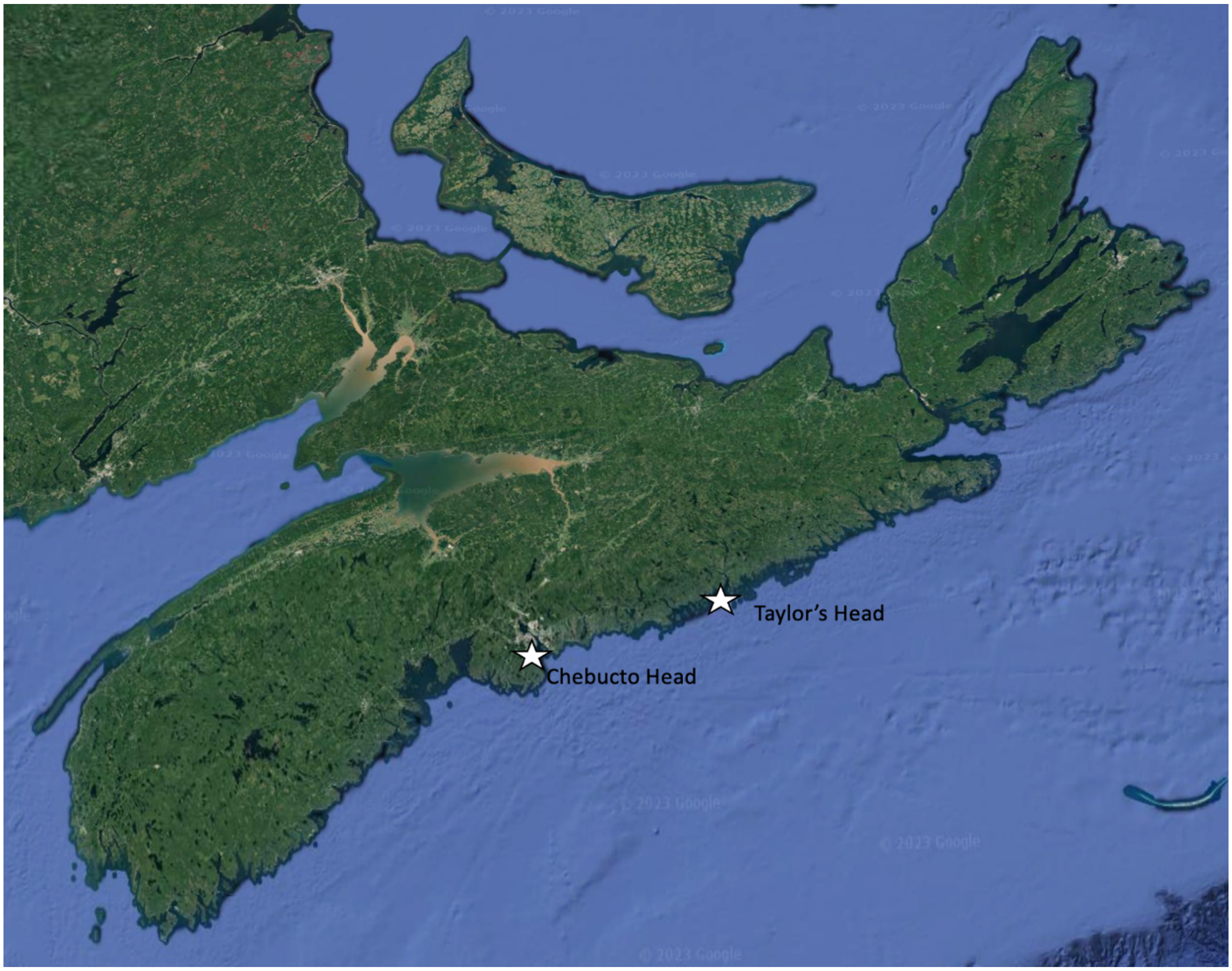

Figure 1: A map of Nova Scotia highlighting the two study sites: Chebucto Head, a coastal barren, and Taylor Head, a coastal forest.

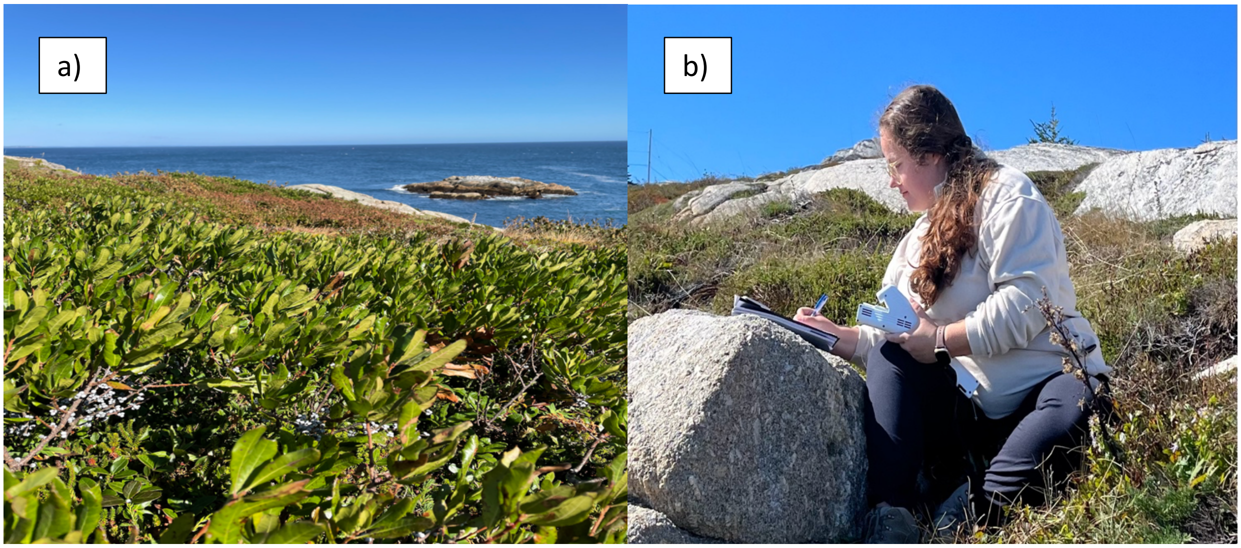

Figure 2: Chebucto Head. Photo a) shows the dense areas of shrubs and exposed rock near the ocean. Image b) shows exposed rock and shallow soils in which some of the samples were taken.

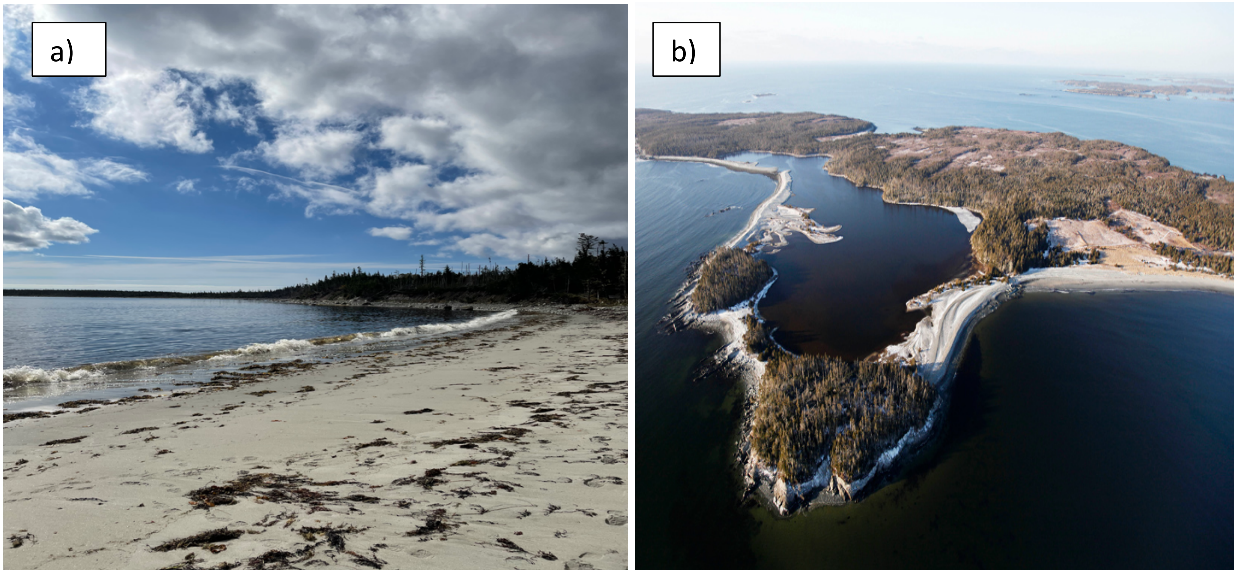

Figure 3: A portion of the Taylor Head area showing the (a) sandy beach and (b) the mixed-wood forest. Photo b) taken from Tourism Nova Scotia (2023)

2.2 Experimental Design

At each site location, a transect was outlined beginning at the point on the shoreline where plants first appear then moving further inland. Three plots at the Chebucto Head site were outlined to represent a coastal (25m from the coast), intermediate (92m from the coast), and inland area (130m from the coast). At Taylor Head, the intention was to sample from three plots as well, but the target species were not easily found in what was intended to be the intermediate plot, so only two plots were used: coastal (39m from the coast) and inland (320m from the coast). Each plot was approximately 25m^2 in size. Throughout this thesis, barren and forest locations are classified as habitats, plots closest to the shore are classified as 'coastal' sites and plots furthest from the shore are classified as 'inland' sites.

2.2.1 Soil and Leaf Sampling

Within each plot, three surface soil samples were taken at different spots within the plots using a small trowel. This was done to gather information about the average soil characteristics of each plot. The soil samples were stored in Ziploc bags and placed in a refrigerator upon returning to the lab to avoid drying until in-lab measurements could be completed. Standing water samples were also collected from the coast and inland plots at Chebucto Head as well as ocean water samples from both study locations (Appendix 5).

Leaf samples were taken from four species: Lowbush Blueberry*,* Northern Bayberry, Black Crowberry and Bog Cranberry (Appendices 1-3 and 6). For each species, leaf samples were taken from 6 individuals within each plot.

Stomatal conductance was measured in the field using a LI-600 Porometer/Fluorometer (LI-COR, Lincoln, NE). For each individual plant, I recorded the stomatal conductance (g_{sw})

from three leaves under ambient conditions. Selected leaves were fully expanded and did not show any signs of disease, herbivory, or other damage. The average g_{sw} was calculated and used to represent the stomatal conductance of that individual. Leaves were then collected from that same individual and placed in a refrigerator for storage until analyses could be done in the lab. This process was repeated for six individuals of each species, within each plot. Measurements of stomatal conductance (g_{sw}, mmol m^{-2} s^{-1}) where taken from the same individuals from which leaf samples were collected, but g_{sw} was only measured in the Lowbush Blueberry and Northern Bayberry as the leaves of the other two species were too small to be recorded using the available equipment.

2.3 Lab Analysis

2.3.1 Soil and Water Characteristics

Fresh soil samples were weighed and then placed in a drying oven at 60°C for 48 hours. Once the soils were dry, they were weighed once more. This data was used to calculate the gravimetric water content (measured in grams) of the soil using the following formula:

$$WC = (mass_{wet} - mass_{dry}) / mass_{dry}$$

To determine the water-soluble nutrient content in the soil, a 2:1 ratio of distilled water and soil was placed in microcentrifuge tubes, shaken, and then allowed to sit for one hour. 1mL of solution was then pipetted into portable nutrient meters ((LAQUA-Twin, TestAgro, Phoenix, AZ, Appendix 4). Between samples, the meters were rinsed with distilled water and after every third sample, the meters were recalibrated. Water samples were measured in the same way (Appendix 5).

2.3.2 Leaf Morphology

To investigate variation in leaf function within a species, the following morphological traits were measured: leaf size (LS, cm^2), specific leaf area (SLA, cm^2g^{-1}), leaf thickness (Lth, mm), and leaf dry matter content (LDMC). Using a LI-3000C Portable Leaf Area Meter (LI-COR, Lincoln, NE) and a scale, the average leaf area, length, width, maximum width, and fresh mass were recorded for all leaves collected from each individual plant (Appendices 1-4). After fresh mass was recorded, the leaf samples were placed in a drying oven at approximately 60°C for a minimum of 48 hours, which is a standardised procedure for leaf drying (Pérez-Harguindeguy et al., 2013). Once dry, the leaf dry mass was recorded, and samples were stored in a sealed container at room temperature to avoid rehydration.

2.3.3 Leaf Nutrient Content

An analysis of the water-soluble nutrient concentrations within the leaves can help to better understand how much salt is in the leaves as well as the concentrations of other nutrients that can indicate plant health and function. Leaf pH, electrical conductivity (EC, µS/cm), sodium (Na, ppm), potassium (K, ppm), nitrate (NO_3, ppm), and calcium (Ca, ppm) were measured.

The dried leaves were finely ground using a regular coffee grinder which was rinsed with ethanol between samples to avoid contamination. Once complete, a solution was prepared using a 2:1 ratio of distilled water and ground leaves placed in a microcentrifuge tube. The sample was shaken and then placed in a refrigerator for one hour. After the time has elapsed, a pipette was used to dispense 1mL of the solution into each of the nutrient meters (LAQUA-Twin, TestAgro, Phoenix, AZ). After every third measurement, the meters were recalibrated as they drifted from the standard after three uses. Meters were rinsed after every sample, and this was repeated until all samples were processed.

2.4 Statistical Analyses

Using the statistical software R (R Core Team, 2022), linear regressions were performed to determine if there were relationships between the environmental variables and leaf traits. Analysis of variance (ANOVA) was done to determine if the variance between leaf traits and soil variables were statistically significant between habitats, sites, and species. Lastly, a principal components analysis (PCA) ordination was used to see similarities and differences among all measured leaf traits within the habitats, sites, and species. The data from the intermediate plot at Chebucto Head was excluded from the analyses as there was not an intermediate plot at Taylor head with which to compare it. Additionally, data were collected for all four species, but this study only statistically analyzed data for the Lowbush Blueberry and Northern Bayberry due to time constraints The raw data for all species are in Appendices 1-4 and Appendix 6.

3.0 Results

3.1 ANOVA

3.1.1 Soil Variation

There was not a significant difference in the concentrations of soil Na, K and Ca between sites and habitats, but the concentration of NO_3 in the soil was significantly different between sites ($p = 0.0296$) and habitat ($p = 0.0051$). Additionally, the site x habitat interaction was significant for NO_3 ($p = 0.00039$), where the concentrations were highest in the barren coast and the forest inland sites (Table 1 and 3).

The pH varied significantly between both sites ($p = 0.0276$) and habitats ($p = 0.0344$). The habitat x site interaction was also significant ($p = 0.0344$). pH was highest at the barren coast. Neither the water content nor the electrical conductivity of the soils varied significantly between sites and habitat (Table 1).

3.1.2 Leaf Trait Variation

The leaf Na/K ratio varied between habitats ($p <0.0001$), with plants in the barren site having a higher Na/K ratio than those in the forest (Figure 7). Similarly, there was a difference in Na/K ratio between sites ($p = 0.0002$), with plants found on the coast having a higher Na/K ratio. The variation between species was not significant ($p= 0.0590$).

Variation in stomatal conductance (g_{sw}) was not significant between habitat ($p = 0.7036$) or site ($p= 0.9024$), but it varied significantly between species ($p < 0.0001$), in which the Northern Bayberry had a higher g_{sw} than the Lowbush Blueberry (Figure 8).

Specific leaf area (SLA) varied between species ($p <0.0001$) and between habitats ($p < 0.0001$). The Northern Bayberry had a higher SLA than the Lowbush Blueberry (Figure 6) and samples taken from the forest had a higher SLA than the barren (Table 2, Figure 6). SLA was not significantly different between inland and coastal sites ($p = 0.0704$).

Leaf dry matter content (LDMC) varied significantly between sites ($p = 0.0015$). The samples from the inland site had higher LDMC than samples from the coast (Figure 9). Variation was also significant between species ($p <0.0001$) in which the Lowbush Blueberry leaves had a higher LDMC than the Northern Bayberry leaves (Table 2, Figure 9). Variation between habitats was not significant ($p = 0.6649$), but the habitat x site interaction was significant ($p = 0.0314$).

Leaf electrical conductivity (EC) did not vary significantly by site ($p = 0.1789$), but it did vary by species ($p<0.0001$) and by habitat ($p <0.0001$). The EC of the Northern Bayberry was higher than the Lowbush Blueberry. The samples taken from the barren showed higher EC than those from the forest (Table 2, Figure 11).

The pH of the leaves varied significantly by species ($p <0.0001$). The Lowbush Blueberry had more acidic leaves than the Northern Bayberry (Table 2, Figure 13). The difference between the pH of leaves significantly varied by site ($p = 0.0296$) with the plants on the coastal site having a higher leaf pH than the inland site (Table 2 and Figure 13).

The concentration of Na in the leaves was significantly different between the species ($p<0.0001$) and between habitats ($p <0.0001$). The Na concentration in the Northern Bayberry was higher than that of the Lowbush Blueberry (Table 2; Figure 4). For both species, the individuals growing in the barren habitat had higher concentrations of Na in the leaves when compared to the individuals growing in the forest. Additionally, the Na concentrations varied based on the site in which the individuals grew ($p = 0.0040$) as the Na concentration of the leaves was higher in the coast than inland.

The potassium concentration in the leaves was dependent on the species ($p <0.0001$). There was a higher concentration of potassium in the Northern Bayberry than in the Lowbush Blueberry (Table 2; Figure 5). The habitat ($p = 0.1324$) and the site ($p = 0.5401$) did not have a significant effect on the concentration of potassium in the leaves. There is however a relationship between the effects of site and species combined ($p =0.0305$) on the concentration of potassium found in the leaves.

Nitrate (NO_3) concentration in the leaves did not vary between sites ($p = 0.0846$), but there was significant variation between habitats ($p <0.0001$), in which the concentration of NO_3

in the leaves was higher in the barren than in the forest. Similarly, the concentration of NO_3 was higher in the Northern Bayberry than in the Lowbush Blueberry (Figure 12).

The concentrations of calcium (Ca) varied significantly between species ($p < 0.0001$), site ($p = 0.046$), and habitat ($p < 0.0001$). The Lowbush Blueberry had higher Ca concentrations in the leaves than the Northern Bayberry (Table 2; Figure 10). In terms of the differences between habitats, the plants in the forest had higher Ca concentrations than those in the barren. Additionally, the leaf samples from the coastal site had lower concentrations of Ca than the inland sites.

Table 1: Variation in soil nutrient contents, pH, electrical conductivity and water content between habitats and sites. Data are plot means with standard deviation for soil variables within each site (coast and inland) for the barren (Chebucto Head) and forest (Taylor Head) habitats. Groups that share the same letter are statistically similar based on Tukey post-hoc tests.

Soil Variable	**Barren Coast**	**Barren Inland**	**Forest Coast**	**Forest Inland**
Sodium	99 (87.58) a	26 (7.21) a	22 (10.82) a	13.33 (6.03) a
Potassium	29.33 (13.58) a	58 (12.49) a	58.67 (30.55) a	45.33 (14.47) a
Calcium	7.00 (3.61) a	6.67 (1.15) a	11.33 (2.89) a	16 (6.93) a
Nitrate	140 (20)a	30.667 (8.622) b	28.667 (13.614) b	54 (30.61) b
pH	5.73 (0.29) a	4.5 (0.1) b	4.53 (0.71) b	4.5 (0.26) b
Electrical Conductivity	567 (326.92) a	430.67 (141.21) a	291.67 (131.54) a	268.33 (70.81) a
Gravimetric Water Content	0.511 (0.247) a	1.744 (1.127) a	1.727 (1.675) a	0.695 (0.234) a

Table 2: ANOVA statistics of leaf trait analyses for *Vaccinium angustifolium* and *Morella pensylvanica* across sites and habitats. Traits analyzed: Leaf pH, electrical conductivity (EC), sodium (Na), potassium (K), nitrate (NO_3), calcium (Ca), specific leaf area (SLA), stomatal conductance (g_{sw}), sodium-potassium ratio (Na/K Ratio), and leaf dry matter content (LDMC).

Trait		Df	Sum Sq	Mean sq	F value	Pr(>F)
g_{sw}	Habitat	1	0.0005	0.0005	0.147	0.7036
	Site	1	0.00005	0.00005	0.015	0.9024
	Species	1	0.07855	0.07855	22.892	2.35E-05
	Habitat:Site	1	0.01111	0.01111	3.238	0.0795
	Habitat:Species	1	0.00797	0.00797	2.323	0.1354
	Site:Species	1	0.06961	0.06961	20.287	5.66E-05
	Habitat:Site:Species	1	0.00368	0.00368	1.073	0.3066
	Residuals	40	0.13725	0.00343		
SLA	Habitat	1	205.24	205.24	44.727	5.11E-08
	Site	1	15.86	15.86	3.456	0.0704
	Species	1	231.51	231.51	50.454	1.35E-08
	Habitat:Site	1	0.53	0.53	0.116	0.7348
	Habitat:Species	1	16.47	16.47	3.59	0.0654
	Site:Species	1	23.3	23.3	5.078	0.0298
	Habitat:Site:Species	1	29.96	29.96	6.53	0.0145
	Residuals	40	183.55	4.59		
Na	Habitat	1	302736	302736	84.37	2.11E-11
	Site	1	33496	33496	9.335	0.003991
	Species	1	116427	116427	32.447	1.26E-06
	Habitat:Site	1	47251	47251	13.168	0.000798
	Habitat:Species	1	2002	2002	0.558	0.45945
	Site:Species	1	1951	1951	0.544	0.465224
	Habitat:Site:Species	1	2883	2883	0.803	0.375421
	Residuals	40	143528	3588		
K	Habitat	1	15769	15769	2.36	0.1324
	Site	1	2552	2552	0.382	0.5401
	Species	1	574219	574219	85.934	1.64E-11
	Habitat:Site	1	4602	4602	0.689	0.4115
	Habitat:Species	1	252	252	0.038	0.847
	Site:Species	1	33602	33602	5.029	0.0305
	Habitat:Site:Species	1	52	52	0.008	0.9301
	Residuals	40	267283	6682		
Ca	Habitat	1	30351	30351	165.849	8.18E-16
	Site	1	776	776	4.24	0.046
	Species	1	32918	32918	179.874	<2.00E-16
	Habitat:Site	1	35	35	0.191	0.6641
	Habitat:Species	1	5786	5786	31.617	1.60E-06
	Site:Species	1	32	32	0.173	0.6796
	Habitat:Site:Species	1	842	842	4.599	0.0381
	Residuals	40	7320	183		
NO_3	Habitat	1	98645	98645	72.499	1.61E-10
	Site	1	4256	4256	3.128	0.084576
	Species	1	41301	41301	30.354	2.31E-06
	Habitat:Site	1	15987	15987	11.75	0.001423
	Habitat:Species	1	1365	1365	1.003	0.322501
	Site:Species	1	23763	23763	17.464	0.000154
	Habitat:Site:Species	1	10920	10920	8.026	0.00719
	Residuals	40	54426	1361		

pH	Habitat	1	0.083	0.083	3.012	0.090347
	Site	1	0.141	0.141	5.09	0.029595
	Species	1	22.141	22.141	800.271	<2.00E-16
	Habitat:Site	1	0.441	0.441	15.934	0.000273
	Habitat:Species	1	0.021	0.021	0.753	0.390701
	Site:Species	1	0.003	0.003	0.12	0.730332
	Habitat:Site:Species	1	0.013	0.013	0.482	0.491563
	Residuals	40	1.107	0.028		
Na/K Ratio	Habitat	1	4.386	4.386	68.722	3.21E-10
	Site	1	1.042	1.042	16.318	0.000236
	Species	1	0.241	0.241	3.777	0.059026
	Habitat:Site	1	0.948	0.948	14.858	0.000411
	Habitat:Species	1	1.06	1.06	16.599	0.000213
	Site:Species	1	0.666	0.666	10.442	0.002468
	Habitat:Site:Species	1	0.072	0.072	1.133	0.293518
	Residuals	40	2.553	0.064		
EC	Habitat	1	6.457	6.457	26.892	6.54E-06
	Site	1	0.45	0.45	1.872	0.17888
	Species	1	7.769	7.769	32.356	1.30E-06
	Habitat:Site	1	1.122	1.122	4.673	0.03668
	Habitat:Species	1	0.002	0.002	0.01	0.91956
	Site:Species	1	2.29	2.29	9.539	0.00365
	Habitat:Site:Species	1	0.601	0.601	2.503	0.12151
	Residuals	40	9.604	0.24		
LDMC	Habitat	1	0.00016	0.00016	0.19	0.66489
	Site	1	0.00974	0.009739	11.597	0.00152
	Species	1	0.01607	0.016071	19.137	8.47E-05
	Habitat:Site	1	0.00418	0.004179	4.976	0.03138
	Habitat:Species	1	0.00143	0.001435	1.709	0.19862
	Site:Species	1	0.00013	0.000131	0.156	0.69478
	Habitat:Site:Species	1	0.00058	0.00058	0.69	0.411
	Residuals	40	0.03359	0.00084		

Table 3: Variation in soil properties across sites (coast and inland), habitats (barren and forest), and their interaction

Trait		Df	Sum Sq	Mean Sq	F value	Pr(>F)
Na	Habitat	1	6030	6030	3.062	0.118
	Site	1	5002	5002	2.54	0.15
	Habitat:Site	1	3104	3104	1.576	0.245
	Residuals	8	15753	1969		
K	Habitat	1	208.3	208.3	0.562	0.475
	Site	1	176.3	176.3	0.476	0.5099
	Habitat:Site	1	1323	1323	3.568	0.0956
	Residuals	8	2966	370.8		
Ca	Habitat	1	140.08	140.08	7.929	0.0226
	Site	1	14.08	14.08	0.797	0.398
	Habitat:Site	1	18.75	18.75	1.061	0.3331
	Residuals	8	141.33	17.67		
NO_3	Habitat	1	5808	5808	14.55	0.00513
	Site	1	5292	5292	13.26	0.006578
	Habitat:Site	1	13601	13601	34.07	0.000388
	Residuals	8	3193	399		
pH	Habitat	1	1.08	1.08	6.48	0.0344
	Site	1	1.203	1.2033	7.22	0.0276
	Habitat:Site	1	1.08	1.08	6.48	0.0344
	Residuals	8	1.333	0.1667		
WC	Habitat	1	0.021	0.021	0.02	0.891
	Site	1	0.03	0.03	0.029	0.8688
	Habitat:Site	1	3.845	3.845	3.667	0.0918
	Residuals	8	8.387	1.048		
EC	Habitat	1	143664	143664	3.853	0.0853
	Site	1	19120	19120	0.513	0.4943
	Habitat:Site	1	9577	9577	0.257	0.626
	Residuals	8	298264	37283		

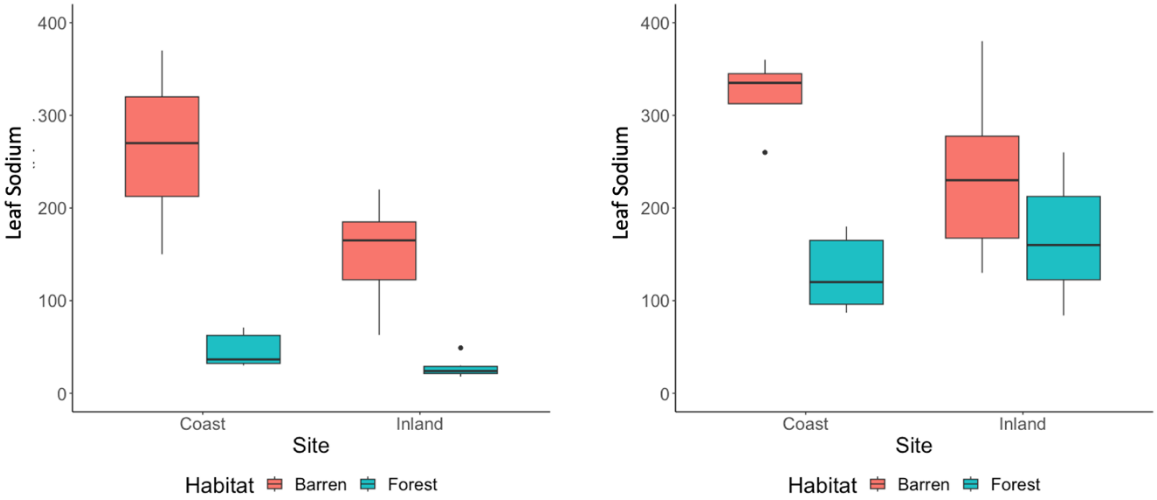

Figure 4: Variation in leaf water-soluble sodium (Na) concentration in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

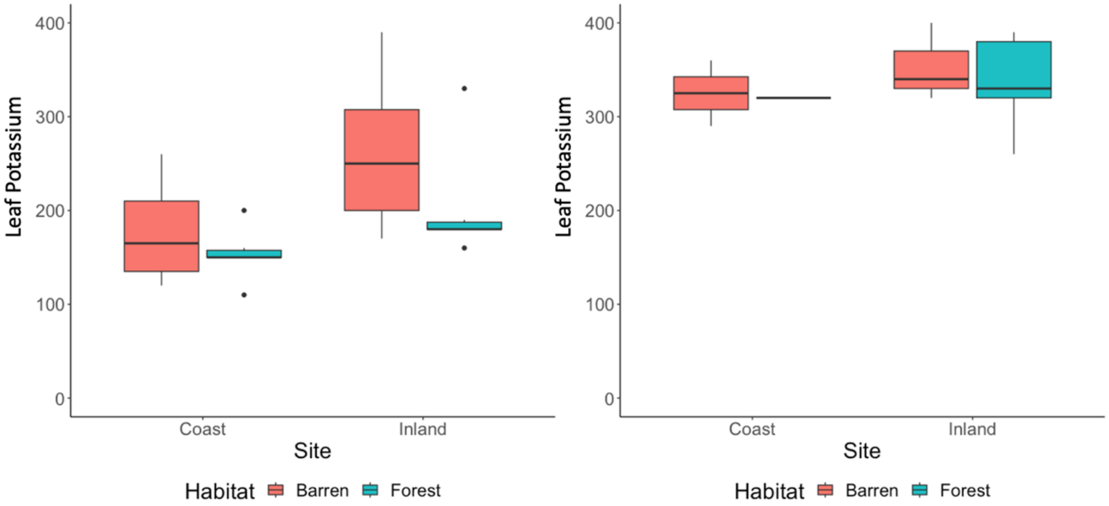

Figure 5: Variation in leaf water-soluble potassium (K) concentration in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

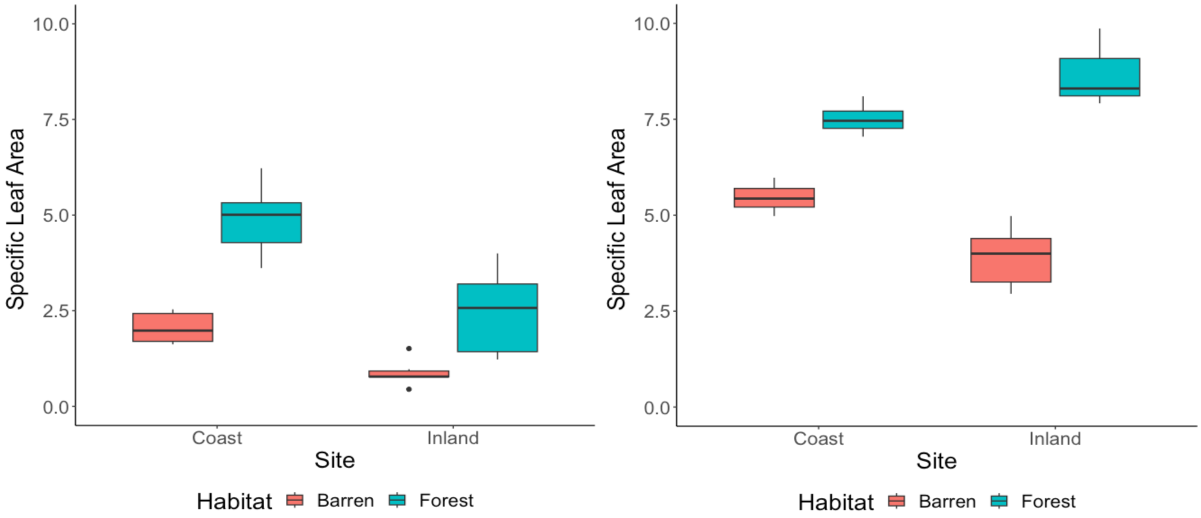

Figure 6: Variation in specific leaf area (SLA) in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

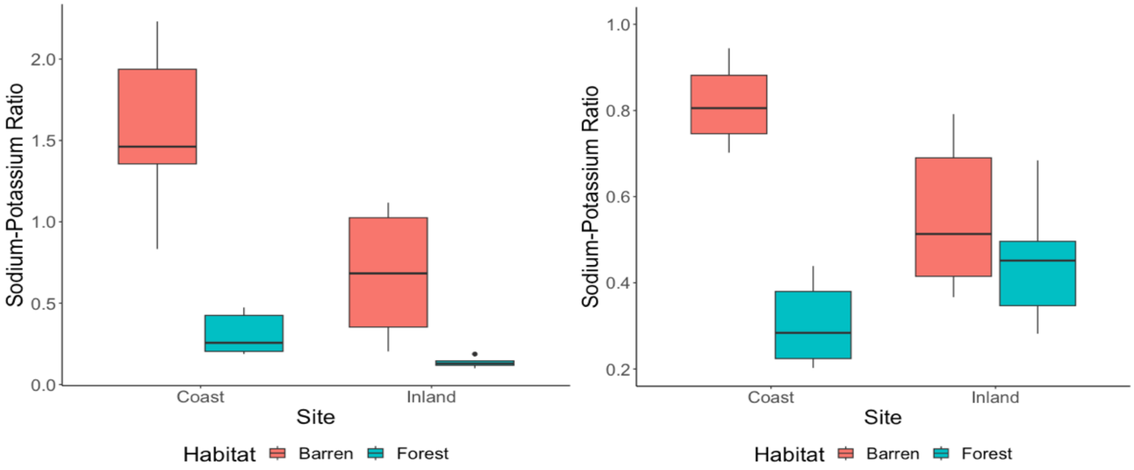

Figure 7: Variation in leaf water-soluble sodium (Na)/potassium (K) ratio in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

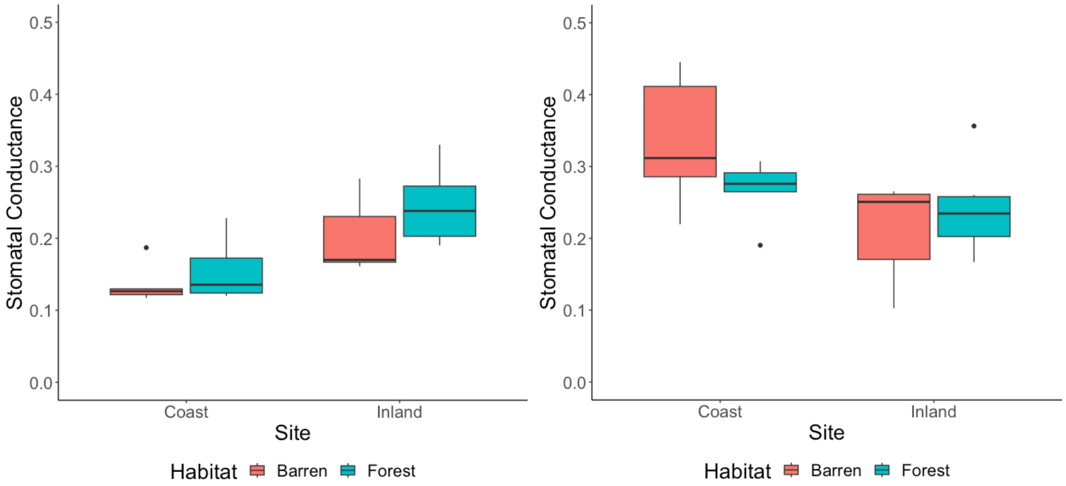

Figure 8: Variation in leaf stomatal conductance (gsw) in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

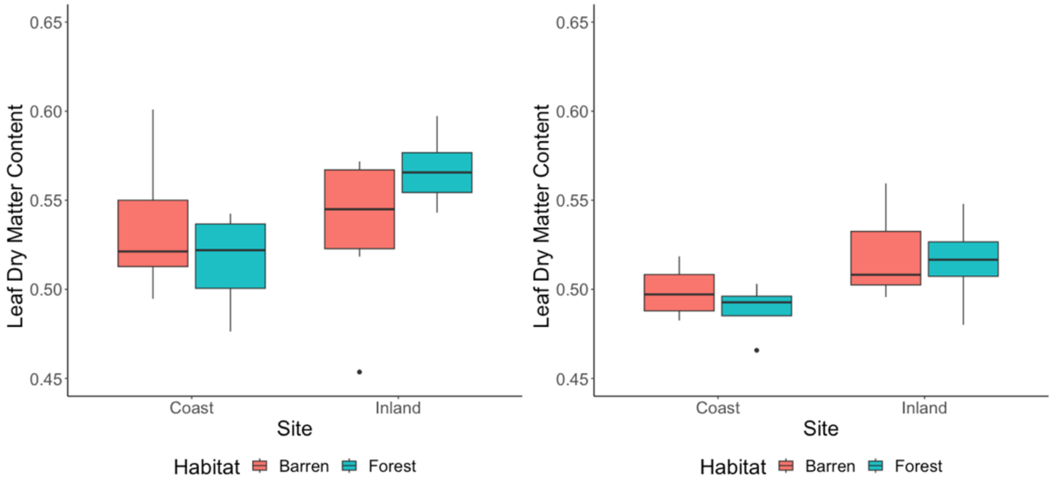

Figure 9: Variation in leaf dry matter content (LDMC) in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

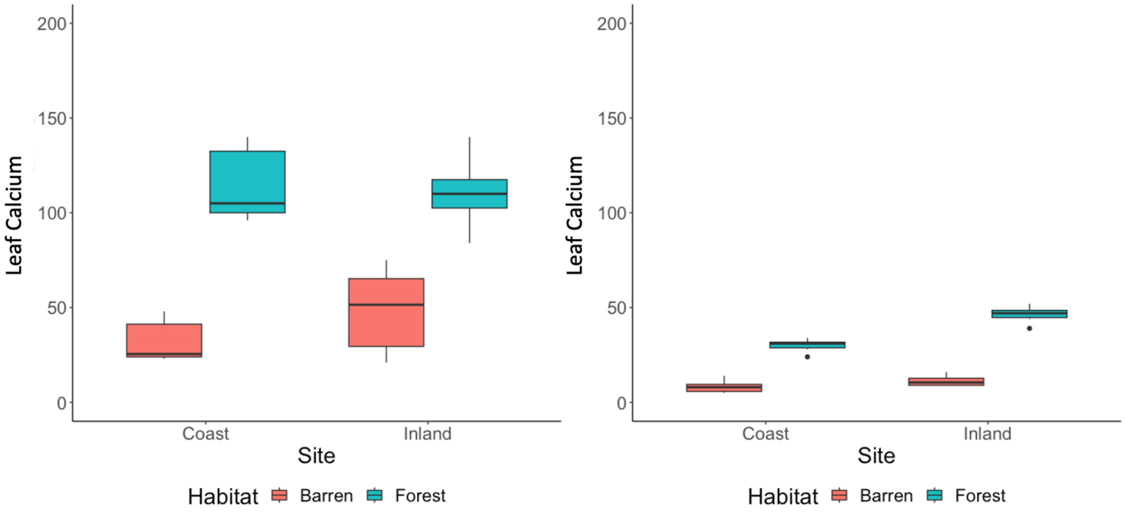

Figure 10: Variation in leaf water-soluble Calcium (Ca) concentration in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

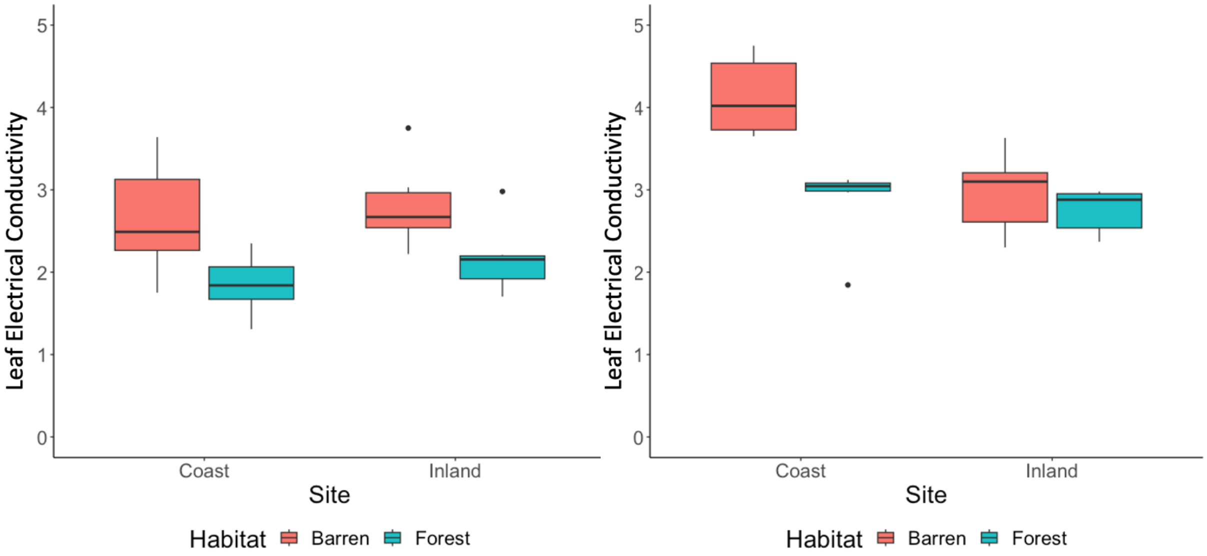

Figure 11: Variation in leaf electrical conductivity (EC) in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

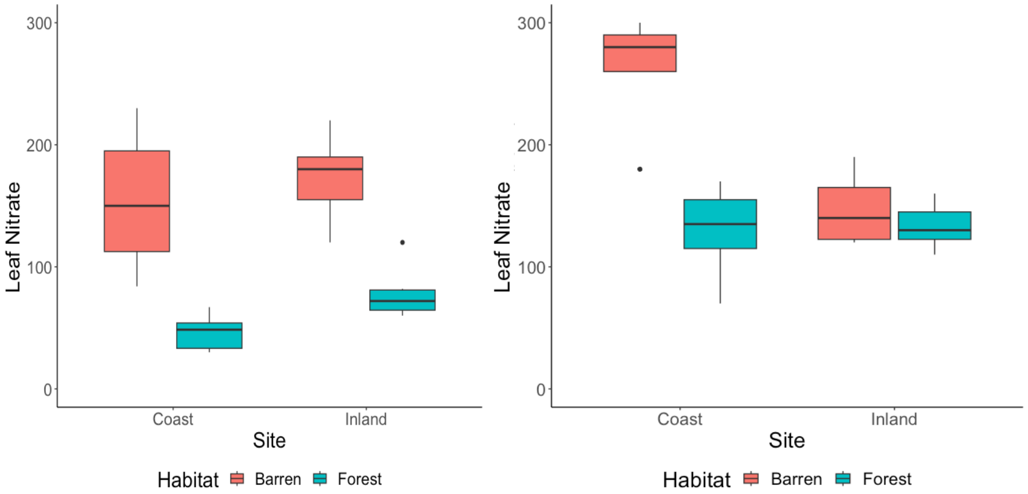

Figure 12: Variation in leaf water-soluble nitrate (NO_3) concentration in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

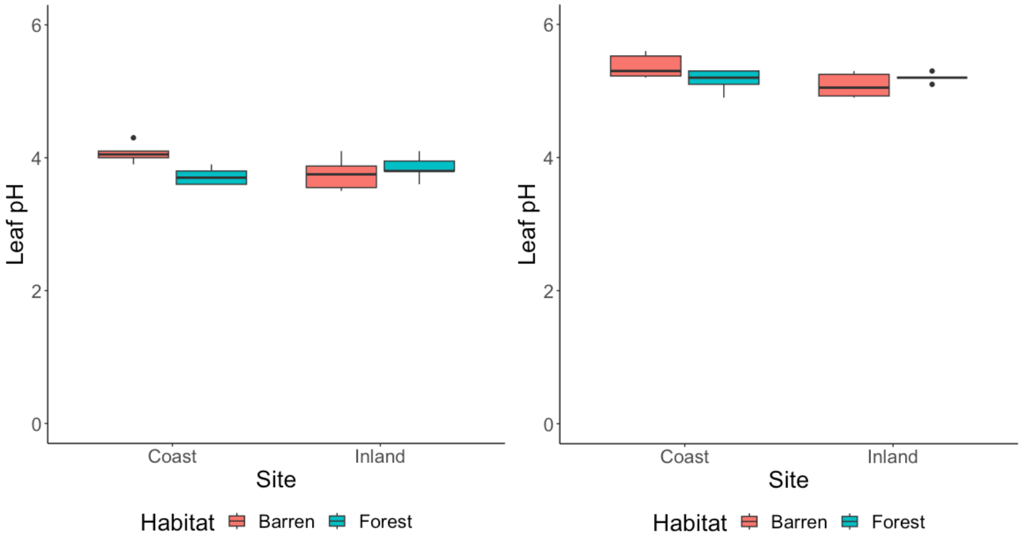

Figure 13: Variation in leaf pH in Lowbush Blueberry (left) and Northern Bayberry (right) across coastal and inland sites between barren and forest habitats in southern Nova Scotia.

3.2 Linear Regressions

For select leaf traits, a linear regression was completed to see the relationship between leaf traits and soil properties (Table 3). For stomatal conductance (g_{sw}), none of the soil variables had a significant relationship (Table 4). Specific leaf area (SLA) was not significantly correlated with soil calcium (p=0.7437), soil electrical conductivity (EC) (p=0.4473), or soil sodium (p= 0.06141). SLA was positively correlated with soil potassium (p=0.0024), and negatively correlated with soil nitrate (p=0.0074), soil pH (p=0.0092), and water content (WC) of the soil (p=0.0006). The salt tolerance of the species in this study is the ratio of sodium to potassium and is referred to as "Tolerance" (Table 3). Each soil trait measured in this study had a significant relationship with the tolerance of the plants (Table 3).

Table 4: Linear regression statistics for leaf and soil trait relationships: stomatal conductance (g_{sw}), specific leaf area (SLA), sodium-potassium ratio (Na/K ratio), electroconductivity (EC), calcium (Ca), potassium (K), sodium (Na), nitrate (NO_3), gravimetric water content (WC), and pH.

Treatment	Coefficient	R-squared adjusted	p-value	f-statistic	standard error
g_{sw} ~ WC	0.001461	-0.02165	0.9492	0.004109	0.08192
g_{sw} ~ Ca	0.03191	0.008584	0.2417	1.4017	0.0807
g_{sw} ~ EC	0.001291	-0.003941	0.3712	0.8155	0.08121
g_{sw} ~ K	0.0003126	-0.01992	0.7761	0.08186	0.08185
g_{sw} ~ Na	0.0001336	-0.01938	0.7458	0.1063	0.08183
g_{sw} ~ NO_3	-7.19E-05	-0.02044	0.8096	0.0587	0.08187
g_{sw} ~ pH	-0.008005	-0.01971	0.7637	0.09144	0.08184
SLA ~ K	0.15175	0.1652	0.002423	10.3	3.542
SLA ~ Ca	-0.4292	-0.01934	0.7437	0.1082	3.914
SLA ~ EC	-0.005254	-0.008856	0.4473	0.5874	3.804
SLA ~ Na	-0.3619	0.05387	0.06141	3.676	3.771
SLA ~ NO_3	-0.0368	0.1272	0.007413	7.85	3.622
SLA ~ pH	-3.201	0.1199	0.009155	7.404	3.637
SLA ~ WC	3.5299	0.2112	0.0005997	13.58	3.443
Na/K ratio ~ WC	-0.6695	0.3354	4.97E-09	51.49	0.3354
Na/K ratio ~ Ca	0.5122	0.1982	0.0008957	12.62	0.4326
Na/K ratio ~ EC	0.0035881	0.3652	3.24E-06	28.04	0.3849
Na/K ratio ~ K	-0.031087	0.4836	2.49E-08	45.01	0.3472
Na/K ratio ~ pH	0.7423	0.4688	4.84E-08	42.47	0.3521
Na/K ratio~ Na	0.012303	0.5411	1.57E-09	56.41	0.3273
Na/K ratio~ NO_3	0.008512	0.4915	1.73E-08	46.43	0.3445

3.3 Multivariate Principal Component Analysis: Ordination

The first principal component axis (PC1) explained 45% of the total variation among plants, and was primarily associated with g_{sw}, pH, EC, K, Na, LS, LDMC, Ca, and NO_3 (Table 5). The second principal component axis (PC2) explained 23% of the total variation among plants, and was primarily associated with SLA, Na/K ratio, and L_{th}, (Table 5). Figure 16a) shows a clear separation between barren and forest habitats, as well as a difference between the focal dominant shrub species. Similarly, Figure 16b) shows a clear separation of the species, but there is less differentiation between the coast and inland sites for the same species.

Table 5: Loadings for the first two principal components analysis (PCA) axes. This describes the strength of associations between *Vaccinium angustifolium* and *Morella pensylvanica* and twelve leaf traits.

Traits	**vPC1**	**vPC2**
Stomatal Conductance	0.69	-0.1379
pH	1.229	-0.3829
Electrical Conductivity (EC)	1.1459	0.5534
Potassium (K)	1.1802	-0.1857
Sodium (Na)	1.0553	0.7707
Leaf Size (LS)	1.0108	-0.7782
Specific Leaf Area (SLA)	0.625	-1.0614
Sodium-Potassium Ratio (Na/K)	0.2315	0.997
Leaf Dry Matter Content (LDMC)	-0.8532	0.3287
Leaf Thickness (L_{th})	-0.5371	0.9046
Calcium (Ca)	-1.1204	-0.459
Nitrate (NO_3)	1.0498	0.7702

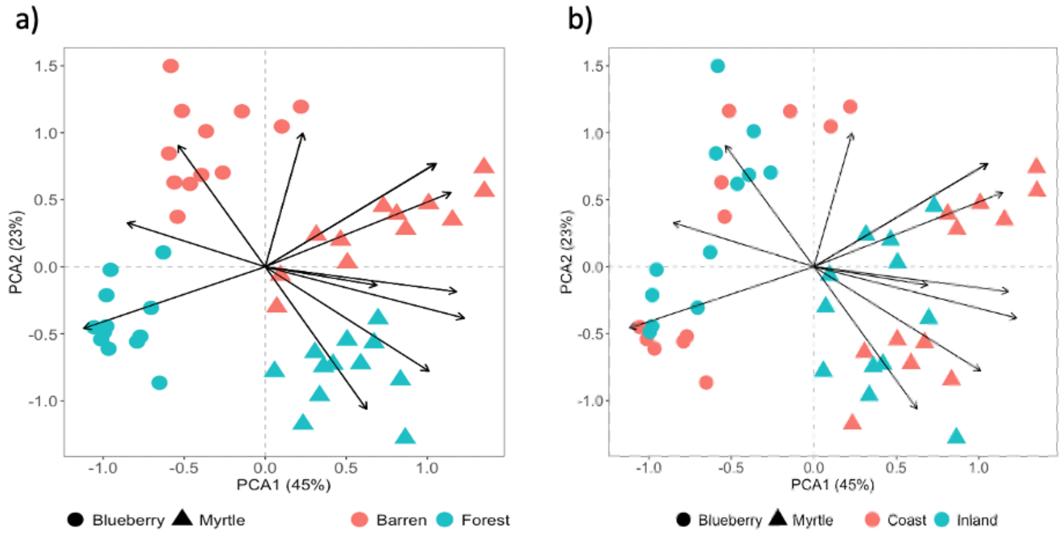

Figure 14: Variation of (a) species (*Morella pensylvanica* and *Vaccinium angustifolium*) and habitat (barren and forest) and (b) species and site (coast and inland) based on leaf pH, electrical conductivity (EC), sodium (Na), potassium (K), nitrate (NO_3), calcium (Ca), specific leaf area (SLA), stomatal conductance (g_{sw}), sodium-potassium ratio (Na/K Ratio), leaf dry matter content (LDMC), leaf size (LS) and leaf thickness (L_{th}). The strength of association is shown along the PC1 axis (45%) and the PC2 axis (23%).

4.0 Discussion

The objectives of this study were to determine if there are differences in leaf physiological and morphological traits between individuals growing in a coastal barren versus a coastal forest; to determine if there are differences between leaf traits between species in the same environment (coastal sites versus inland sites), and to determine if there are differences in leaf physiological and morphological traits between dominant species along a salinity gradient. In general, this study found that the Northern Bayberry is more tolerant to salt stress than the Lowbush Blueberry, and that there was physiological and morphological variation between individuals growing in the different habitats (barren versus forest).

4.1 Salt Tolerance

The ratio between Na and K is an important ratio that reflects plant salt tolerance via the ability to maintain cytosolic homeostasis, which allows for optimal plant function. Potassium is an essential nutrient for plants, but when there are high levels of Na present, Na ions can outcompete K at binding sites, reducing the ability of the individual to uptake K (Zhang et al., 2018). This ratio is a measurement of tolerance; a higher ratio indicates that there is more sodium present in the leaves than potassium. This study shows that individuals within the barren have higher Na/K, indicating that they have more difficulty taking up enough potassium to balance the concentrations of sodium compared to individuals within the forest, as well as those in the coast compared to inland. The ability to maintain a lower Na/K ratio is important for plants who experience salt stress as K is required by plants and if the Na is inhibiting the ability of the plant to acquire enough K, salt toxicity may occur (Zhang et al., 2018). In this study the Na/K ratio was higher within the leaves of the species within the barren compared to those in the forest and was also higher within the leaves on the coast than the inland sites (Table 2; Figure 7).

Additionally, the Na/K ratio had a positive relationship with Ca and, EC, pH, Na, and NO_3 in the soil, and a negative relationship with WC and K. Other studies have shown that higher concentrations of Na within soil reduce K uptake, resulting in high Na/K ratios (Cassaniti et al., 2009). The concentration of Na in the soils was higher at the barren than the forest (Table 1), which is reflected in the higher Na/K ratio within leaves collected in the barren.

4.2 Stomatal Conductance

Stomatal conductance is a measure of leaf water loss through stomatal pores. A higher g_{sw} indicates that the stomata are open, and transpirational water loss is occurring at a higher rate than smaller values of g_{sw}. Soils with high salinity can reduce water availability and root water uptake, which may cause stomata to close in an effort to reduce transpirational water loss. In this study, the Northern Bayberry had a higher overall g_{sw} than the Lowbush Blueberry (Table 2, Figure 8), indicating that the Northern Bayberry has more water loss through open stomata relative to the Lowbush Blueberry. This could suggest that the Northern Bayberry is not experiencing as much physiological stress than the Lowbush Blueberry in the same environment. This may be due to different responses of the species to water availability (Davies and Kozlowski, 1977) or differences in salt toleranceA study investigating the effects of salt water on Green Ash (*Fraxinus pennsylvanica* Marsh.) found that stomatal conductance was reduced by up to 72%, and net photosynthesis was reduced up to 82% in response to salt stress (Pezeshki and Chambers, 1986). It is possible that the Lowbush Blueberry had a lower g_{sw} than the Northern Bayberry because it is less tolerant to Na and must reduce water loss via transpiration to conserve water availability.

4.3 Leaf Morphology

SLA was higher in the Northern Bayberry than the Lowbush Blueberry, and there was also a difference between habitats, as the SLA of individuals in the forest was higher than those within the barren. SLA was negatively correlated with pH, NO_3, and WC of the soil (Table 4). SLA is the ratio of leaf area to leaf dry mass, which relates to the availability of nutrients and often has a positive relationship with the amount of nitrogen in the leaves (Pérez-Harguindeguy et al., 2013) which may explain why the SLA is larger in leaves that have higher concentrations of NO_3 (Table 2; Figures 6 and 12). An additional factor to consider is L_{th}, which mainly varies with differences in light intensity (Hodgson et al., 2011), and is related to SLA. A study on mangroves and their response to salt stress showed that higher concentrations of Na induced the thickening of leaves as a method of water conservation, which would contribute to a decrease in SLA (Nandy et al., 2007). As the Lowbush Blueberry was the species with a lower salt tolerance, this may have caused this species to conserve water thus potentially reducing the SLA in response to salt stress.

Additionally, soil water content had a positive relationship with SLA (Table 4). When there is less water available, plants may have reduced leaf size to reduce water loss via transpiration (Liu et al., 2017). Soil water content was statistically similar across both sites and habitats on average, but this may be due to the small sample size, as there still is variation in the data from individual plots. It is expected that in an area with a higher soil water content, SLA would also increase as the plant is less restricted by the need to conserve water (Liu et al., 2017). Variation in SLA between the Northern Bayberry and Lowbush Blueberry may reflect the differences between species for handling water stress and nutrient deficient soils (Goud and Roddy, 2022) .

LDMC is the ratio of leaf dry mass to fresh mass, and is a measure of leaf density and water content. LDMC was higher in individuals growing within the inland sites than the coast sites (Table 2, Figure 9). This is in contrast to a study done on the salt tolerance of the Blue Leaf Wattle shrub (*Acacia saligna*), which found that LDMC increased with increasing soil Na, as Na would accumulate in the leaves (Elfeel and Bakhashwain, 2012). LDMC also reflects the resource use of a plant as there is a trade-off between the ability to produce biomass and to conserve nutrients (Garnier et al., 2001; Saura-Mas and Lloret, 2007). The higher LDMC for inland plants in this study could indicate that these inland sites have more nutrient availability within the soil than the coast sites (Domínguez et al., 2012; Goud and Roddy, 2022). LDMC also varied between species; the Lowbush Blueberry had a higher LDMC then the Northern Bayberry (Table 2; Figure 9). This suggests that the Lowbush Blueberry may need to conserve more nutrients than the Northern Bayberry within the environmental conditions at the study locations indicating the Northern Bayberry is more tolerant to these conditions.

4.4 Leaf Chemistry

The concentration of Na in leaves varied between species, site, and habitat (Table 1 and 2). The concentration of leaf sodium was higher in the barren compared to the forest (Figure 4), which was expected as the shrubs in the barren had no protection/cover from sea spray, unlike the forest which had shelter provided by the tree canopy. The samples from the coast had more sodium in the leaves than the inland samples, which was also expected as the inland sites were further away from the ocean and thus would receive less direct sea spray. Lastly, the interspecific variation of the leaves was significant with the Northern Bayberry having the higher concentration of Na than the Lowbush Blueberry. This may reflect the strategy of that species to resist salt stress. Higher sodium in the leaves of the Northern Bayberry may reflect this species ability to accumulate Na and compartmentalize it within the leaves, reducing cytosolic Na, which is an indicator of a salt tolerant species (Liang et al. 2018).

The concentration of K was also higher in the Northern Bayberry than the Lowbush Blueberry (Table 2, Figure 5), which could reflect the ability for the Northern Bayberry to avoid salt toxicity as the Northern Bayberry is able to uptake K despite having a higher Na concentration, as this can inhibit the ability of the plant to acquire K. This further reflects the greater salt tolerance of the Northern Bayberry compared to that of the Lowbush Blueberry, especially where the availability of soil K was similar across both habitats and sites (Table 1 and 3).

The leaf electrical conductivity (EC) of the Northern Bayberry was higher than that of the Lowbush Blueberry (Table 2, Figure 11) which reflects the overall ion content, and potential nutrient content within the leaves, which was generally higher in the Northern Bayberry. Because the Lowbush Blueberry generally had a lower concentration of nutrients within the leaves, it was expected that the EC would also be lower than the Northern Bayberry. EC is an indicator of nutrient availability of the plant in which a low EC indicates a potential nutrient deficiency, but a high EC can indicate toxicity (Ding et al., 2018). In this case, the lower EC of the Lowbush Blueberry may suggest that in this environment, the species has a reduced ability to uptake nutrients.

The pH of the leaves was variable between sites and species. The leaves in the coast had a higher pH than the inland leaves (Table 2; Figure 13), which could be related to the proximity of the ocean, which has a basic pH of around 8. Furthermore, the Lowbush Blueberry leaves were more acidic than those of the Northern Bayberry. The variation between species was expected as Lowbush Blueberry is known to have acidic leaves (Kramer and Schrader, 1945). The interspecific variation may be explained by components not measured during this study, such as tannins present in the leaves (Pérez-Harguindeguy et al., 2013). Variation in leaf pH between sites may also be related to the pH of the soil, as the sites with the highest leaf pH also had the highest soil pH.

Nitrate (NO_3) and calcium (Ca) are other important nutrients for plant growth; nitrogen is an important component of proteins, chlorophylls, and nucleic acids and Ca plays a role in the permeability of cellular membranes along with other necessary functions When a plant becomes deficient of these nutrients, symptoms include leaf and root tip death (Raven et al., 2013). If high soil sodium concentrations reduce root water uptake and the ability of these shrubs to absorb NO_3 and Ca, such deficiencies may lead to diseased leaves and reduced survival of the plant. There was a difference between leaf Ca between habitat, site, and species. While the Northern Bayberry had a higher concentration of all other nutrients, the Lowbush Blueberry had higher concentration of Ca. A calcium deficiency is more likely to occur in acidic soils (White and Broadley, 2003), a condition in which the Lowbush Blueberry can thrive; this may reflect an adaptation of the Lowbush Blueberry to conserve Ca as it has adapted to acidic, potentially low Ca soils.

4.5 Limitations and Moving Forward

This study does not account for the influence of other environmental factors such as light and wind exposure, which can impact the growth of a plant and could explain variation in measured traits such as stomatal conductance. The limitation of this study was that the statistical power of linear regressions between plant traits and the soil properties was low because the replicates were not paired to each individual plant that was sampled, leading to an unbalanced analysis as there were fewer replicates for soil samples than plant samples. Three samples were taken from each plot, but if this study were repeated, soil samples should be taken from directly below each individual plant that is sampled. This limitation could be why there was not a significant variation in sodium in the soil at the site or habitat level (Table 3) despite the coast having more sodium present than the inland site. If this study was to be repeated, leaf samples would be collected at different times throughout the day such as once in the morning, once in the afternoon, and once in the evening to better reflect plant physiology as there may be variations throughout the day in response to light intensity and temperature. If another field study were to be completed, there should be three plots along the transect to observe the differences between individuals within the same habitat that are impacted by sea spray greatly, moderately, and not at all. Moving forward, a greenhouse study could be done as a complimentary study. This would allow a controlled exposure to ocean salt and allow observation of the immediate response to salt stress as well as the prolonged response in several test groups.

4.6 Implications

This study found that Northern Bayberry is more tolerant to ocean salt from sea spray and waves than the Lowbush Blueberry. Additionally, there was a significant difference in leaf traits between coastal barren and coastal forest habitats. At the species level, this shows that species have different ways of dealing with salt stress, and some are more tolerant than others. In this case, the Northern Bayberry is more tolerant of salt stress than the Lowbush Blueberry.

The differences between habitats (Table 1, 4 and 5; Figure 14) are also important to consider. The barrens generally had lower nutrient availability than the forest and if these coastal areas experience more frequent ocean salt exposure, individuals growing in this habitat are at an increased risk of salt toxicity as higher concentrations of salts inhibit the uptake of essential nutrients such a K, which is already limited in these areas. Barrens are also exposed habitats meaning there is no coverage from tree canopies and are thus exposed to direct light, wind, and have less protection from sea spray than a coastal forest.

In agriculture, toxicity from saline soils limits agricultural productivity by reducing the occurrences of seed germination and negative impacts on overall plant growth and productivity (Isayenkov, 2012). Salinity in soil has been shown to negatively impact tree growth and survival by damaging roots and other tissues, as well as reducing the individual's ability to absorb nutrients and water (Zhang, 2014). As the Lowbush Blueberry is an economically valuable crop in Atlantic Canada (Government of New Brunswick, 2012), it can be inferred that if this species is not salt tolerant and continues to be exposed to salt from sea spray and waves, it could result in the loss of wild blueberry crops in coastal habitats and thus a source of income.

Coastal regions such as Atlantic Canada are threatened with climate related phenomena including sea level rise and increasing frequency and intensity of storms that cause sea spray and storm surges. These can lead to coastal erosion and salt toxicity among plant communities close to the shore (Mansour, 2023;). To mitigate these effects, a knowledge of salt tolerant species is useful for coastal restoration projects as plants can provide stability to the soils through their roots, provide habitat for wildlife (Gracia et al., 2018).

There is a difference between leaf traits of the same species found in coastal barrens versus those found in coastal forests, and the Northern Bayberry and Lowbush Blueberry respond differently to saline conditions. As we can expect to see more frequent and intense storms than in the past because of climate change (Elsner, 2006; Hauser et al., 2015), more and more individual plants will be exposed to levels of ocean salt that exceed their normal conditions. This can lead to a change in coastal habitat composition as salt toxicity inhibit key functions leading to the death of the plant (Isayenkov, 2012; Zhu 2007). This study found that the Lowbush Blueberry is less tolerant to ocean salt than the Northern Bayberry, and that within a species, those growing in a coastal barren experience more stress than those growing in the coastal forest. While these ecologically and economically important species are growing in a salt-stressed habitat, further studies should be done concerning the extent of the species salt tolerance, and how these indirect effects of climate change may impact the success of these coastal shrubs.

5.0 Acknowledgements

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6.0 Appendices

Appendix 1: Raw leaf measurement data for *Vaccinium angustifolium* (all ID's containing "vaccang") and Morella pensylvanica (all ID's containing "Myrtle"). The first letter of the ID corresponds to the location (A= Chebucto Head, B= Taylor Head), the first number corresponds to the plot (1= coast, 2= inland), and the last number corresponds to the individual plant.

ID	Site	Habitat	Species	Leaf Count	Leaf Area (cm^2)	Fresh Mass (g)	Dry Mass (g)	Length (cm)	Avg Width (cm)	Max Width (cm)	Stomatal Conductance (mmol m^{-2} s^{-1})
A1.vaccang.1	Coast	Barren	Blueberry	58	129.11	2.4045	1.2711	148.1	0.8	1.8	0.13
A1.vaccang.2	Coast	Barren	Blueberry	48	113.16	2.0758	1.0668	127.2	0.8	1.7	0.129
A1.vaccang.3	Coast	Barren	Blueberry	40	81.58	1.569	0.804	91.5	0.8	2.1	0.117
A1.vaccang.4	Coast	Barren	Blueberry	37	99.43	2.1725	1.0747	103.0	0.9	1.8	0.121
A1.vaccang.5	Coast	Barren	Blueberry	56	98.64	1.8801	1.0475	125.5	0.7	1.5	0.187
A1.vaccang.6	Coast	Barren	Blueberry	58	69.78	1.2354	0.7424	113.9	0.6	1.2	0.124
A3.vaccang.1	Inland	Barren	Blueberry	83	39.71	0.5906	0.3166	95.7	0.4	1	0.166
A3.vaccang.2	Inland	Barren	Blueberry	176	102.28	1.651	0.7489	210.1	0.4	1.1	0.161
A3.vaccang.3	Inland	Barren	Blueberry	204	131.09	1.6106	0.8349	270.1	0.4	2.1	0.25
A3.vaccang.4	Inland	Barren	Blueberry	106	104.19	1.8263	1.0116	187.8	0.5	1.2	0.169
A3.vaccang.5	Inland	Barren	Blueberry	139	133.08	2.1441	1.2253	219.5	0.6	1.4	0.171
A3.vaccang.6	Inland	Barren	Blueberry	255	136.22	2.0876	1.1936	259.7	0.5	1.5	0.283
B1.vaccang.1	Coast	Forest	Blueberry	60	76.9	0.6590	0.3545	130.3	0.5	1.2	0.124
B1.vaccang.2	Coast	Forest	Blueberry	46	73.99	0.7355	0.3758	95.8	0.7	1.6	0.12
B1.vaccang.3	Coast	Forest	Blueberry	14	23.5	0.2438	0.1212	35.3	0.6	1.2	0.124
B1.vaccang.4	Coast	Forest	Blueberry	32	51.03	0.5379	0.2562	79.6	0.6	1.9	0.147
B1.vaccang.5	Coast	Forest	Blueberry	35	75.75	0.7965	0.4321	97.7	0.7	1.7	0.181
B1.vaccang.6	Coast	Forest	Blueberry	29	54.6	0.6638	0.3538	73.2	0.7	2.6	0.228
B2.vaccang.1	Inland	Forest	Blueberry	31	69.23	0.9351	0.5585	90.5	0.7	1.3	0.19
B2.vaccang.2	Inland	Forest	Blueberry	117	162.35	1.9714	1.1096	253.2	0.6	2.2	0.201
B2.vaccang.3	Inland	Forest	Blueberry	48	66.56	0.7968	0.4327	95.3	0.6	1.8	0.33
B2.vaccang.4	Inland	Forest	Blueberry	60	109.56	0.9902	0.5738	137.7	0.7	1.6	0.208
B2.vaccang.5	Inland	Forest	Blueberry	93	75.76	0.7298	0.4148	133.3	0.5	1.9	0.268
B2.vaccang.6	Inland	Forest	Blueberry	147	144.59	1.4550	0.8025	254.9	0.5	2	0.274
A1.myrtle.1	Coast	Barren	Myrtle	14	85.04	1.9598	1.0162	75.8	1.1	2.3	0.2917
A1.myrtle.2	Coast	Barren	Myrtle	14	103.86	2.6857	1.296	84.7	1.2	2.8	0.3317
A1.myrtle.3	Coast	Barren	Myrtle	15	124.88	3.0517	1.4828	91.7	1.3	2.6	0.4453
A1.myrtle.4	Coast	Barren	Myrtle	16	125.53	3.1911	1.5761	94.1	1.3	2.7	0.2197
A1.myrtle.5	Coast	Barren	Myrtle	15	94.58	2.4239	1.2129	82.4	1.1	2.4	0.2837
A1.myrtle.6	Coast	Barren	Myrtle	19	107.90	2.1159	1.0812	103.6	1.0	2.3	0.438
A3.myrtle.1	Inland	Barren	Myrtle	26	116.43	2.8132	1.5173	127.4	0.9	2.2	0.264

A3.myrtle.2	Inland	Barren	Myrtle	24	109.57	2.6443	1.4795	111	0.9	2.2	0.2483
A3.myrtle.3	Inland	Barren	Myrtle	22	112.92	2.4221	1.2155	99	1.1	2.6	0.1447
A3.myrtle.4	Inland	Barren	Myrtle	18	135.2	3.3478	1.6883	104.3	1.2	2.8	0.1027
A3.myrtle.5	Inland	Barren	Myrtle	23	115.09	2.6747	1.3258	127.3	0.9	2	0.253
A3.myrtle.6	Inland	Barren	Myrtle	18	78.59	1.7126	0.877	90.7	0.8	1.7	0.2653
B1.myrtle.1	Coast	Forest	Myrtle	17	84.33	1.2175	0.6125	66.3	1.2	2.4	0.3073
B1.myrtle.2	Coast	Forest	Myrtle	13	135.22	1.7984	0.8841	75.7	1.7	3.3	0.2927
B1.myrtle.3	Coast	Forest	Myrtle	20	211.59	2.9941	1.3947	125.8	1.6	3.6	0.2867
B1.myrtle.4	Coast	Forest	Myrtle	22	155.53	2.0314	1.0032	107.8	1.4	2.8	0.265
B1.myrtle.5	Coast	Forest	Myrtle	16	188.74	2.186	0.9823	109.1	1.7	3.6	0.2647
B1.myrtle.6	Coast	Forest	Myrtle	28	302.69	3.4206	1.4735	180.5	1.6	3.8	0.1903
B2.myrtle.1	Inland	Forest	Myrtle	10	158.19	1.683	0.8579	79.9	1.9	3.8	0.218
B2.myrtle.2	Inland	Forest	Myrtle	20	191.46	2.5187	1.2092	124	1.5	3.1	0.3563
B2.myrtle.3	Inland	Forest	Myrtle	13	200.28	2.5424	1.3416	107.2	1.8	3.5	0.167
B2.myrtle.4	Inland	Forest	Myrtle	14	133.68	1.9105	0.9677	87.9	1.5	3.6	0.1973
B2.myrtle.5	Inland	Forest	Myrtle	15	166.08	2.4334	1.3335	100	1.6	3.3	0.251
B2.myrtle.6	Inland	Forest	Myrtle	14	170.88	2.322	1.2155	99.2	1.7	3.6	0.2603

Appendix 2: Leaf chemistry data for *Vaccinium angustifolium* (all ID's containing "vaccang") and Morella pensylvanica (all ID's containing "Myrtle"). The first letter of the ID corresponds to the location (A= Chebucto Head, B= Taylor Head), the first number corresponds to the plot (1= coast, 2= inland), and the last number corresponds to the individual plant.

ID	Site	Habitat	Species	pH	Electrical Conductivity (μS/cm)	Potassium (ppm)	Calcium (ppm)	Nitrate (ppm)	Sodium (ppm)	Sodium Potassium Ratio
A1.vaccang.1	Coast	Barren	Blueberry	4	1.752	180	24	110	150	0.83333333
A1.vaccang.2	Coast	Barren	Blueberry	4.1	3.64	260	27	230	370	1.42307692
A1.vaccang.3	Coast	Barren	Blueberry	4.1	2.43	130	24	180	290	2.23076923
A1.vaccang.4	Coast	Barren	Blueberry	3.9	3.32	220	23	200	330	1.5
A1.vaccang.5	Coast	Barren	Blueberry	4	2.21	150	48	84	200	1.33333333
A1.vaccang.6	Coast	Barren	Blueberry	4.3	2.55	120	46	120	250	2.08333333
A3.vaccang.1	Inland	Barren	Blueberry	4.1	2.57	200	68	220	160	0.8
A3.vaccang.2	Inland	Barren	Blueberry	3.5	3.03	390	24	150	110	0.28205128
A3.vaccang.3	Inland	Barren	Blueberry	3.5	2.22	310	21	190	63	0.20322581
A3.vaccang.4	Inland	Barren	Blueberry	3.9	2.53	200	75	120	220	1.1
A3.vaccang.5	Inland	Barren	Blueberry	3.7	3.75	300	46	170	170	0.56666667
A3.vaccang.6	Inland	Barren	Blueberry	3.8	2.77	170	57	190	190	1.11764706
B1.vaccang.1	Coast	Forest	Blueberry	3.6	1.616	160	100	30	30	0.1875
B1.vaccang.2	Coast	Forest	Blueberry	3.8	1.309	110	96	30	33	0.3
B1.vaccang.3	Coast	Forest	Blueberry	3.6	2.14	150	100	43	70	0.46666667
B1.vaccang.4	Coast	Forest	Blueberry	3.6	1.841	150	110	54	71	0.47333333
B1.vaccang.5	Coast	Forest	Blueberry	3.9	1.839	150	140	54	32	0.21333333
B1.vaccang.6	Coast	Forest	Blueberry	3.8	2.35	200	140	67	40	0.2
B2.vaccang.1	Inland	Forest	Blueberry	4.1	2.15	180	140	64	21	0.11666667
B2.vaccang.2	Inland	Forest	Blueberry	3.8	2.21	180	100	78	22	0.12222222
B2.vaccang.3	Inland	Forest	Blueberry	3.6	2.16	190	84	82	26	0.13684211
B2.vaccang.4	Inland	Forest	Blueberry	4	1.704	180	110	60	18	0.1
B2.vaccang.5	Inland	Forest	Blueberry	3.8	1.843	160	110	66	30	0.1875
B2.vaccang.6	Inland	Forest	Blueberry	3.8	2.98	330	120	120	49	0.14848485
A1.myrtle.1	Coast	Barren	Myrtle	5.6	3.93	430	14	180	360	0.8372093
A1.myrtle.2	Coast	Barren	Myrtle	5.3	4.68	530	8	300	410	0.77358491
A1.myrtle.3	Coast	Barren	Myrtle	5.6	3.66	360	10	290	340	0.94444444
A1.myrtle.4	Coast	Barren	Myrtle	5.3	4.75	570	8	350	420	0.73684211
A1.myrtle.5	Coast	Barren	Myrtle	5.2	4.11	470	5	280	330	0.70212766
A1.myrtle.6	Coast	Barren	Myrtle	5.2	3.65	290	5	260	260	0.89655172
A3.myrtle.1	Inland	Barren	Myrtle	5.3	2.46	340	16	120	150	0.44117647
A3.myrtle.2	Inland	Barren	Myrtle	5.3	3.06	410	13	150	240	0.58536585
A3.myrtle.3	Inland	Barren	Myrtle	4.9	3.23	600	12	170	220	0.36666667
A3.myrtle.4	Inland	Barren	Myrtle	5.1	2.3	320	9	120	130	0.40625

A3.myrtle.5	Inland	Barren	Myrtle	5	3.14	400	9	130	290	0.725
A3.myrtle.6	Inland	Barren	Myrtle	4.9	3.63	480	9	190	380	0.79166667
B1.myrtle.1	Coast	Forest	Myrtle	5.1	2.97	430	34	110	87	0.20232558
B1.myrtle.2	Coast	Forest	Myrtle	5.1	1.845	320	24	70	88	0.275
B1.myrtle.3	Coast	Forest	Myrtle	5.3	3.12	410	31	130	120	0.29268293
B1.myrtle.4	Coast	Forest	Myrtle	4.9	3.06	580	28	140	120	0.20689655
B1.myrtle.5	Coast	Forest	Myrtle	5.3	3.09	440	32	170	180	0.40909091
B1.myrtle.6	Coast	Forest	Myrtle	5.3	3.03	410	31	160	180	0.43902439
B2.myrtle.1	Inland	Forest	Myrtle	5.2	2.96	550	47	130	230	0.41818182
B2.myrtle.2	Inland	Forest	Myrtle	5.3	2.98	380	39	150	260	0.68421053
B2.myrtle.3	Inland	Forest	Myrtle	5.2	2.44	320	44	110	160	0.5
B2.myrtle.4	Inland	Forest	Myrtle	5.2	2.83	390	49	160	110	0.28205128
B2.myrtle.5	Inland	Forest	Myrtle	5.1	2.37	260	52	120	84	0.32307692
B2.myrtle.6	Inland	Forest	Myrtle	5.2	2.93	330	47	130	160	0.48484848

Appendix 3: Leaf morphological data calculated based on measured traits of *Vaccinium angustifolium* (all ID's containing "vaccang") and Morella pensylvanica (all ID's containing "Myrtle"). The first letter of the ID corresponds to the location (A= Chebucto Head, B= Taylor Head), the first number corresponds to the plot (1= coast, 2= inland), and the last number corresponds to the individual plant.

ID	Site	Habitat	Species	Avg area (cm^2)	Leaf Dry Matter Content (g/cm^2)	Leaf Thickness (mm)	Specific Leaf Area (cm^2*g^{-1})
A1.vaccang.1	Coast	Barren	Blueberry	2.22603448	0.52863381	1.08017195	1.75126621
A1.vaccang.2	Coast	Barren	Blueberry	2.3575	0.51392234	0.88050901	2.20988001
A1.vaccang.3	Coast	Barren	Blueberry	2.0395	0.5124283	0.7693062	2.53669154
A1.vaccang.4	Coast	Barren	Blueberry	2.6872973	0.49468354	0.80843307	2.50050926
A1.vaccang.5	Coast	Barren	Blueberry	1.76142857	0.55715122	1.06737226	1.68155472
A1.vaccang.6	Coast	Barren	Blueberry	1.20310345	0.60093897	1.02684437	1.6205596
A3.vaccang.1	Inland	Barren	Blueberry	0.47843373	0.53606502	1.23444472	1.51116151
A3.vaccang.2	Inland	Barren	Blueberry	0.58113636	0.45360388	2.84098553	0.7759866
A3.vaccang.3	Inland	Barren	Blueberry	0.64259804	0.51837824	2.50638798	0.76967067
A3.vaccang.4	Inland	Barren	Blueberry	0.98292453	0.55390681	1.85802668	0.97165335
A3.vaccang.5	Inland	Barren	Blueberry	0.95741007	0.57147521	2.23947926	0.78136789
A3.vaccang.6	Inland	Barren	Blueberry	0.53419608	0.57175704	3.90792835	0.44755033
B1.vaccang.1	Coast	Forest	Blueberry	1.28166667	0.53793627	0.51417425	3.61542078
B1.vaccang.2	Coast	Forest	Blueberry	1.60847826	0.51094494	0.4572645	4.28014439
B1.vaccang.3	Coast	Forest	Blueberry	1.67857143	0.49712879	0.14524255	13.8495992
B1.vaccang.4	Coast	Forest	Blueberry	1.5946875	0.47629671	0.33730747	6.22438525
B1.vaccang.5	Coast	Forest	Blueberry	2.16428571	0.54249843	0.3680198	5.0087612
B1.vaccang.6	Coast	Forest	Blueberry	1.88275862	0.53299187	0.35256777	5.32153369
B2.vaccang.1	Inland	Forest	Blueberry	2.23322581	0.59726233	0.41872165	3.9986138
B2.vaccang.2	Inland	Forest	Blueberry	1.38760684	0.56284874	1.42071943	1.2505469
B2.vaccang.3	Inland	Forest	Blueberry	1.38666667	0.54304719	0.57461539	3.20468377
B2.vaccang.4	Inland	Forest	Blueberry	1.826	0.57947889	0.5422782	3.18229348
B2.vaccang.5	Inland	Forest	Blueberry	0.81462366	0.5683749	0.89587381	1.96389502
B2.vaccang.6	Inland	Forest	Blueberry	0.98360544	0.55154639	1.47925168	1.22567656
A1.myrtle.1	Coast	Barren	Myrtle	6.07428571	0.5185223	0.32263876	5.97745101
A1.myrtle.2	Coast	Barren	Myrtle	7.41857143	0.48255576	0.36202388	5.72420635
A1.myrtle.3	Coast	Barren	Myrtle	8.32533333	0.48589311	0.36655589	5.614603
A1.myrtle.4	Coast	Barren	Myrtle	7.845625	0.49390492	0.40673624	4.9778726
A1.myrtle.5	Coast	Barren	Myrtle	6.30533333	0.50039193	0.3844206	5.19855993
A1.myrtle.6	Coast	Barren	Myrtle	5.67894737	0.51098823	0.37258665	5.25244855
A3.myrtle.1	Inland	Barren	Myrtle	4.47807692	0.53935021	0.6282161	2.95134576

A3.myrtle.2	Inland	Barren	Myrtle	4.56541667	0.55950535	0.57920234	3.08578349
A3.myrtle.3	Inland	Barren	Myrtle	5.13272727	0.50183725	0.47189338	4.22272914
A3.myrtle.4	Inland	Barren	Myrtle	7.51111111	0.50430133	0.44571302	4.44891969
A3.myrtle.5	Inland	Barren	Myrtle	5.00391304	0.49568176	0.53452168	3.77425935
A3.myrtle.6	Inland	Barren	Myrtle	4.36611111	0.51208689	0.39224838	4.97846193
B1.myrtle.1	Coast	Forest	Myrtle	4.96058824	0.50308008	0.2454346	8.09891957
B1.myrtle.2	Coast	Forest	Myrtle	10.4015385	0.49160365	0.1728975	11.7651153
B1.myrtle.3	Coast	Forest	Myrtle	10.5795	0.46581611	0.28300959	7.58550226
B1.myrtle.4	Coast	Forest	Myrtle	7.06954545	0.49384661	0.28734521	7.04699507
B1.myrtle.5	Coast	Forest	Myrtle	11.79625	0.44935956	0.18531313	12.0088059
B1.myrtle.6	Coast	Forest	Myrtle	10.8103571	0.43077238	0.31641878	7.33651655
B2.myrtle.1	Inland	Forest	Myrtle	15.819	0.5097445	0.10639105	18.439212
B2.myrtle.2	Inland	Forest	Myrtle	9.573	0.48008894	0.26310457	7.9168045
B2.myrtle.3	Inland	Forest	Myrtle	15.4061538	0.52769037	0.16502497	11.4834182
B2.myrtle.4	Inland	Forest	Myrtle	9.54857143	0.50651662	0.20008229	9.86728473
B2.myrtle.5	Inland	Forest	Myrtle	11.072	0.54799869	0.21977962	8.30296213
B2.myrtle.6	Inland	Forest	Myrtle	12.2057143	0.52347115	0.19023876	10.041723

Appendix 4: Soil data for Chebucto Head and Taylor Head.

Location	ID	Fresh Mass (g)	Dry Mass (g)	Habitat_Site	pH	Electrical Conductivity (μS/cm)	Nitrate (ppm)	Potassium (ppm)	Sodium (ppm)	Calcium (ppm)	Gravimetric Water Content
Chebucto Head	A1.1	2.1624	0.2067	Barren_Coast	5.9	942	160	21	200	11	0.78906628
Chebucto Head	A1.2	1.0253	0.7455	Barren_Coast	5.4	342	120	22	53	6	0.42937626
Chebucto Head	A1.3	0.7133	0.3903	Barren_Coast	5.9	417	140	45	44	4	0.31437356
Chebucto Head	A3.1	0.2926	0.1663	Barren_Inland	4.5	321	29	48	24	8	2.03307276
Chebucto Head	A3.2	0.4005	0.1469	Barren_Inland	4.6	381	40	54	34	6	2.69843431
Chebucto Head	A3.3	2.253	0.7854	Barren_Inland	4.4	590	23	72	20	6	0.49987268
Taylor Head	B1.1	0.9441	0.3754	Forest_Coast	4.4	288	44	52	34	13	1.20245072
Taylor Head	B1.2	1.6486	0.9756	Forest_Coast	5.3	162	18	32	13	13	0.37607626
Taylor Head	B1.3	1.1944	0.2435	Forest_Coast	3.9	425	24	92	19	8	3.60123203
Taylor Head	B2.1	0.9908	0.3519	Forest_Inland	4.2	276	51	36	14	12	0.87610117
Taylor Head	B2.2	1.1623	0.4327	Forest_Inland	4.7	335	86	62	19	24	0.7788306
Taylor Head	B2.3	2.1977	0.938	Forest_Inland	4.6	194	25	38	7	12	0.43113006

Appendix 5: Water chemistry from the ocean and standing water at Chebucto Head and Taylor Head. The letter listed in the ID corresponds to the location (A= Chebucto Head, B= Taylor Head), the number within the ID corresponds to the plot (0 = ocean, 1= coast, 2= inland).

ID	Site	pH	Sodium (ppm)	Calcium (ppm)	Potassium (ppm)	Nitrate (ppm)	Electrical Conductivity (μS/cm)
A0	Ocean	7.4	9900	1000	390	580	-
A1	Coast	6.4	80	15	-	22	655
A3	Inland	4.8	39	-	-	13	217
B0	Ocean	6.6	7500	-	350	490	-

Appendix 6: Data collected for Bog Cranberry (*Vaccinium oxycoccus*) and Black Crowberry (*Empetrum nigrum*).

ID	Site	Habitat	Species	Number of Leaves	Leaf Area (cm2)	Fresh Mass (g)	Dry Mass (g)	Length (cm)	Avg Width (cm)	Max Width (cm)
A1.Empnig.2	Coast	Barren	Black Crowberry	518	18.03	0.4288	0.2878	-	-	-
A1.Empnig.5	Coast	Barren	Black Crowberry	567	19.62	0.6252	0.3884	-	-	-
A2.Empnig.1	Intermediate	Barren	Black Crowberry	523	16.06	0.3979	0.2496	-	-	-
A2.Empnig.2	Intermediate	Barren	Black Crowberry	412	11.35	0.3021	0.2162	-	-	-
A2.Empnig.4	Intermediate	Barren	Black Crowberry	189	5.72	1.511	0.0882	-	-	-
A2.Empnig.6	Intermediate	Barren	Black Crowberry	386	10.72	0.2484	0.1817	-	-	-
B1.Empnig.1	Coast	Forest	Black Crowberry	219	7.21	0.1643	0.0929	-	-	-
B1.Empnig.2	Coast	Forest	Black Crowberry	215	5.37	0.1065	0.0665	-	-	-
B1.Empnig.3	Coast	Forest	Black Crowberry	110	3.94	0.0585	0.0362	-	-	-
B1.Empnig.4	Coast	Forest	Black Crowberry	56	1.06	0.0114	0.0017	-	-	-
B1.Empnig.5	Coast	Forest	Black Crowberry	42	1.05	0.0142	0.0043	-	-	-
B1.Empnig.6	Coast	Forest	Black Crowberry	62	1.66	0.0203	0.0079	-	-	-
B2.Empnig.1	Inland	Forest	Black Crowberry	307	7.79	0.0889	0.0776	-	-	-
B2.Empnig.3	Inland	Forest	Black Crowberry	68	1.83	0.0213	0.0182	-	-	-
B2.Empnig.5	Inland	Forest	Black Crowberry	82	1.89	0.0224	0.0195	-	-	-
B2.Empnig.6	Inland	Forest	Black Crowberry	103	2.07	0.274	0.0233	-	-	-
A1.Vaccoxy.1	Coast	Barren	Bog Cranberry	480	93.95	2.0277	-	226.3	0.4	2.2
A1.Vaccoxy.2	Coast	Barren	Bog Cranberry	739	110.7	2.2842	-	421.5	0.2	1.4
A1.Vaccoxy.3	Coast	Barren	Bog Cranberry	813	119.41	2.6774	-	293.4	0.4	2
A1.Vaccoxy.4	Coast	Barren	Bog Cranberry	873	158.26	3.2986	-	457	0.3	1.7
A1.Vaccoxy.5	Coast	Barren	Bog Cranberry	764	169.28	3.6357	-	411.6	0.4	2.1
A1.Vaccoxy.6	Coast	Barren	Bog Cranberry	297	62.48	1.6251	-	134.9	0.4	1.9
A2.Vaccoxy.1	Intermediate	Barren	Bog Cranberry	263	46.8	1.035	-	125	0.3	1.5
A2.Vaccoxy.2	Intermediate	Barren	Bog Cranberry	354	64.51	1.4252	-	175.8	0.3	2
A2.Vaccoxy.3	Intermediate	Barren	Bog Cranberry	207	38.14	0.8465	-	100.7	0.3	1.5
A2.Vaccoxy.4	Intermediate	Barren	Bog Cranberry	292	55.98	1.1208	-	56.01	0.4	2.8
A2.Vaccoxy.5	Intermediate	Barren	Bog Cranberry	348	81.65	1.8829	-	176.8	0.4	2.9
A2.Vaccoxy.6	Intermediate	Barren	Bog Cranberry	140	21.06	0.4991	-	62.7	0.3	1.2
A3.Vaccoxy.1	Inland	Barren	Bog Cranberry	1004	56.32	2.461	-	140.2	0.4	2.4
A3.Vaccoxy.2	Inland	Barren	Bog Cranberry	677	105.64	2.0746	-	311.7	0.3	1.4
A3.Vaccoxy.3	Inland	Barren	Bog Cranberry	726	51.17	2.61201	-	151.4	0.3	1.7
A3.Vaccoxy.4	Inland	Barren	Bog Cranberry	376	75.08	1.6591	-	179.9	0.4	1.7
A3.Vaccoxy.5	Inland	Barren	Bog Cranberry	335	75.82	1.3407	-	170.4	0.4	2
A3.Vaccoxy.6	Inland	Barren	Bog Cranberry	707	128.42	2.8975	-	294.3	0.4	1.8

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