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The Effects of Climate Change on Native Icelandic Plants: A Morphometric Analysis

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Iceland and Greenland: Climate Change and the Arctic

Fall 2018

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Lastly, I would like to thank my family for supporting me throughout this study abroad and research experience.

Abstract

This study seeks to evaluate the morphology of three native Icelandic plant species, *Alchemilla alpina*, *Arabidopsis petraea*, and *Silene uniflora*, in order to determine if changing climatic conditions have had an effect on Icelandic vegetation during the twentieth century. I measured herbarium specimens collected during a time period before 1950, and during the period from the late 1960s to the present. Using traditional morphometrics methods, I searched for changes in morphological traits such as plant height, leaf length to width ratio, and leaf size, then performed two-tailed t-tests to analyze the results of the analyses. I found significant changes in the plant height and in leaf length to width ratio of two of the species, but no significant differences in leaf area between the pre-1950 and post-1950 groups. Based on these results, I believe that future studies of this kind could benefit from more extensive data collection and contribute to our knowledge of the influence of climate change on sub-Arctic vegetation and its consequences.

Introduction

The vulnerable ecosystems of the Arctic and sub-Arctic regions are adversely susceptible to the effects of climate change; in fact, we are already observing the changes taking place in these terrestrial ecosystems. Vegetation has been shifting upslope in montane areas and boreal forests are expanding northward to colonize tundra (Trivedi et al., 2008). Positive feedback loops will exacerbate the effects and ecosystems are expected to reach tipping points from which populations cannot return. Mean near-surface temperature data from 1991 to 2010 and RCP 4.5 to 8.5 trajectories predict an increase of 3 to 4 degrees Celsius in northern Iceland and 2 to 3 degrees in southern Iceland by the period 2081 to 2100. Data from the IPCC's Fifth Assessment Report, published in 2014, show that mean precipitation in Iceland is expected to increase by 0 to 10 percent by the period 2081 to 2100.

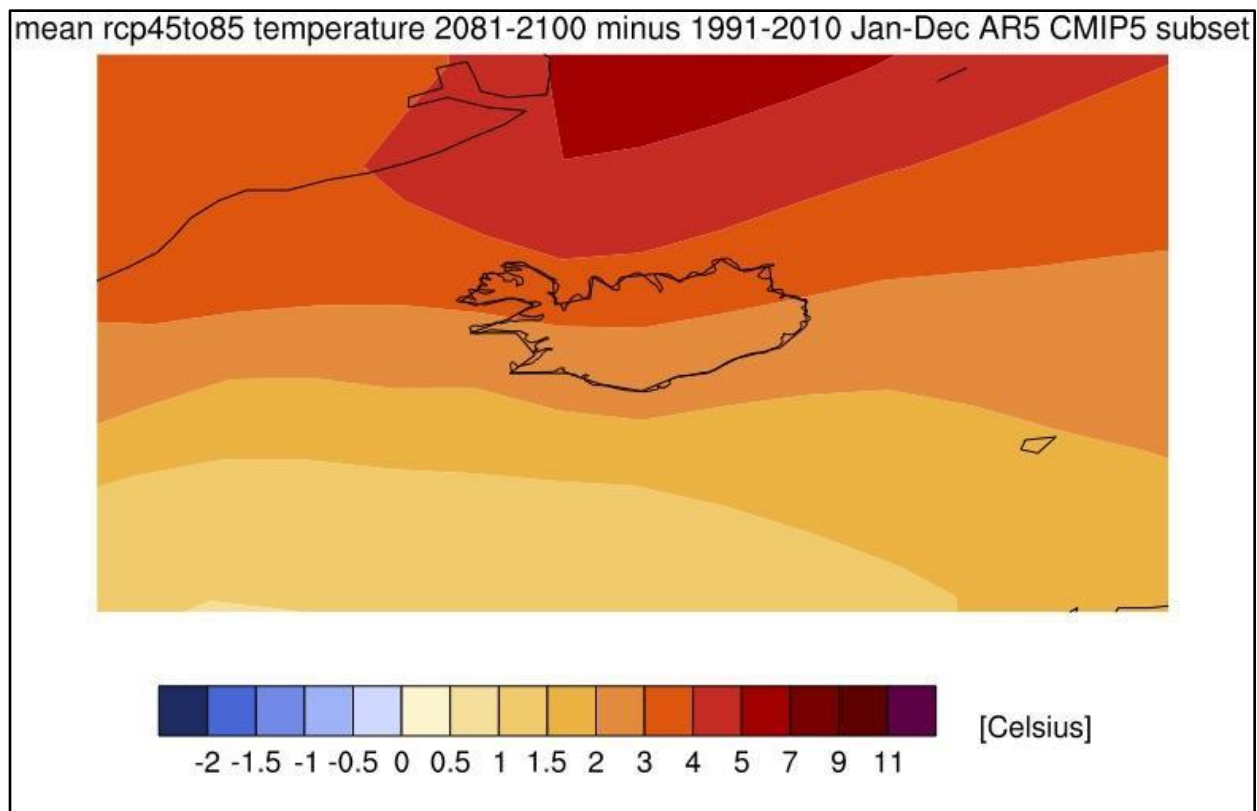


Figure 1. Predicted mean near-surface temperature in Iceland for the period 2081 to 2100, based on data from 1991 to 2010 and RCP 4.5 to 8.5 projections (KNMI Climate Explorer).

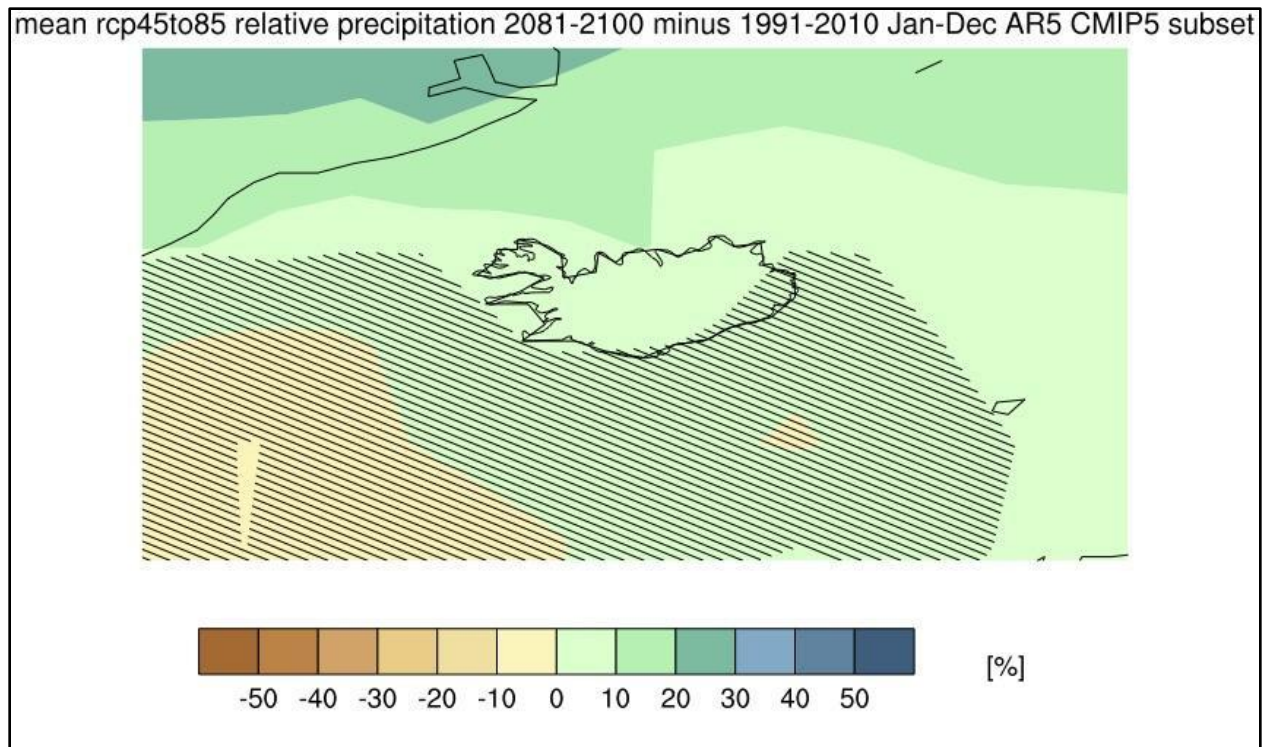


Figure 2. Predicted mean percent change in precipitation in Iceland for the period 2081 to 2100, based on data from 1991 to 2010 and RCP 4.5 to 8.5 projections (KNMI Climate Explorer).

Since the Industrial Revolution in the early 19th century, global atmospheric carbon dioxide levels have been steadily increasing (Etheridge et al., 1996), with a significant increase in the interannual trend after World War II, around 1950 (Figure 3). From the time period 1885 to 1934 and the period 1979 to 2018, data from the Goddard Institute for Space Studies Surface Temperature Analysis (GISTEMP) show a 1 to 1.5 degrees Celsius increase in near-surface temperature in southwest Iceland and an increase of 0.5 to 1 degree Celsius in the rest of Iceland (Figure 4). Data on precipitation collected by the Global Precipitation Climatology Centre (GPCC) state an increase of 10 to 20 percent in northern Iceland and 0 to 10 percent everywhere else in Iceland from the time period 1901 to 1950 to the period 1979 to 2018 (Figure 5). Based on this observation, I wanted to determine if there was a difference in the morphology of Icelandic plants grown and collected before 1950 and those collected two decades or more after 1950. Although any morphological differences would be partially due to natural intraspecific variation such as phenotypic plasticity, some differences may be a result of climatic variation,

such as changes in temperature, precipitation, and atmospheric carbon levels. Phenotypic plasticity is more frequently observed in species which are present across vast geographical areas and in regions with low biodiversity (Bjorkman et al. 2018). The plants analyzed in this study are common throughout Iceland and other parts of Europe, and they inhabit areas of different climatic conditions and elevations (“*Alchemilla alpina*,” n.d., “*Arabidopsis lyrata*,” 2018, “*Silene uniflora*,” 2018), so it is important to account for the environmental effects on plant morphology.

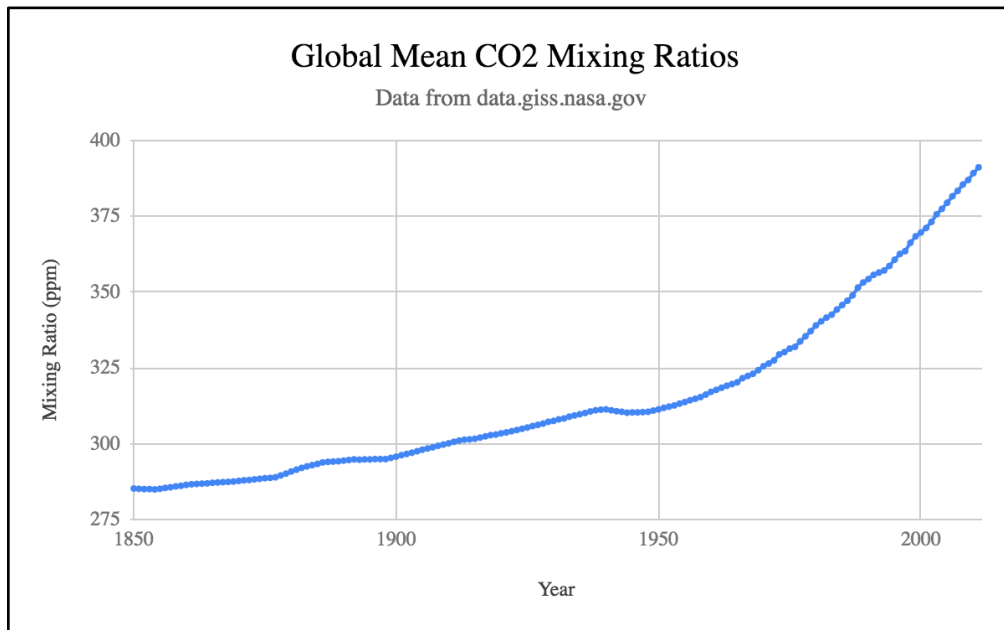


Figure 3. Levels of global atmospheric carbon dioxide in parts per million (ppm), from 1850 to 2011.

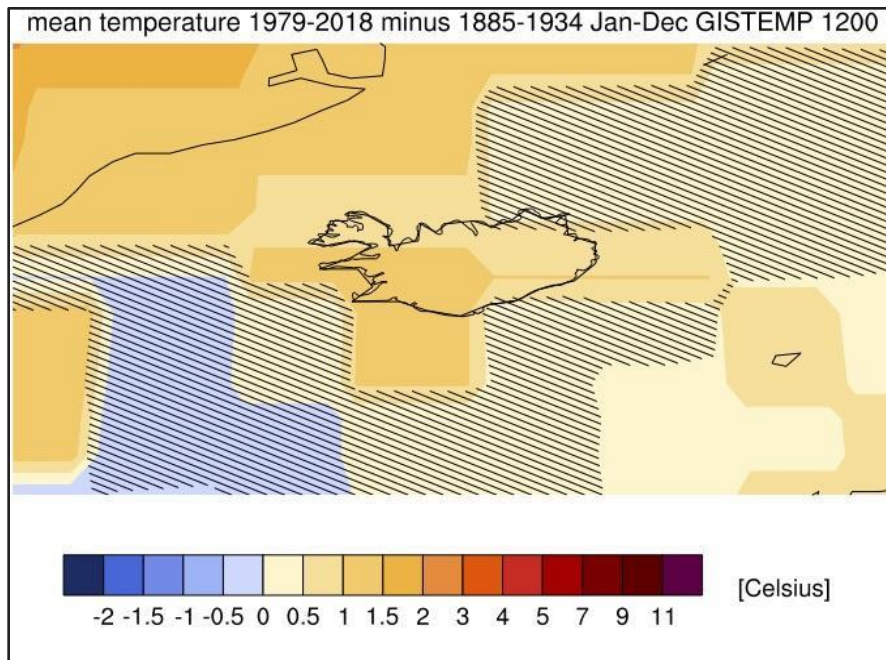


Figure 4. Mean near-surface temperature in Iceland from 1979 to 2018 minus the mean of 1885 to 1934 (KNMI Climate Explorer).

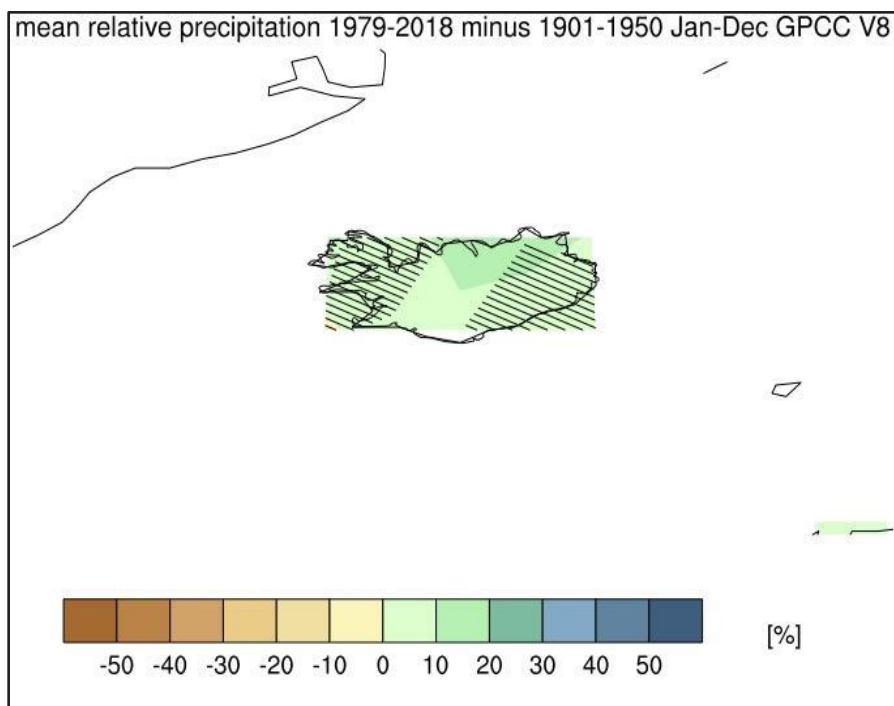


Figure 5. Mean relative precipitation in Iceland from 1979 to 2018 minus 1901 to 1950 (KNMI Climate Explorer).

Plants have been shown to have phenological and physiological responses to changes in climate (Lee et al. 2016), and I wanted to determine if there were morphological responses that could be detected in native Icelandic plants as well. Using morphometric software, I compared herbarium specimens of three species collected in northern Iceland between 1888 and 1934 to those collected between 1968 and 2013. By evaluating life form, plant height, ratio of leaf length to width, and leaf size, I hoped to find significant differences that might suggest morphological changes due to variations in climatic conditions. If morphological responses were to be detected in these three plant species, it may have implications for other Icelandic plant species or other sub-Arctic vegetation in the changing climate. As plants are the primary producers of ecosystems, changes in plant populations would have effects on other members of the ecosystem communities and may lead to positive feedback loops. Thus, it is important to gain a better understanding of plant responses using data from the past that is available in herbarium specimens, in order to make educated predictions about the future of ecosystems.

Studies which focus on morphology can help us gain an understanding of the way plants have responded to and interacted with ecosystem changes in the past, since phenological data may not be available. Herbarium specimens serve as an important resource for research on past climatic conditions and can contribute to a picture of what the environment looked like before researchers began collecting data to the extent that they do today. I chose to study *Alchemilla alpina*, *Arabidopsis petraea*, and *Silene uniflora* using specimens that are stored at the herbarium of the Icelandic Institute of Natural History in Akureyri, Iceland. These three plants are flowering, herbaceous perennials which are found all over Iceland (Kristinsson, 2010). *Alchemilla alpina*, also known as alpine lady's mantle, is found in forb meadow and grassland regions of Iceland ("Vegetation types," n.d.), as well as subarctic and mountainous regions of Europe and southern Greenland ("Alchemilla alpina," n.d.). *Alchemilla alpina* are 5 to 15 centimeters tall, topped with yellowish green flowers, and have palmate leaves made up of 5 to 7 leaflets which are each 1.5 to 2 centimeters long (Kristinsson, 2010). *Arabidopsis petraea*, commonly known as northern rock-cress, is present nearly everywhere in Iceland except on glaciers (Kristinsson, 2010) and has a circumpolar distribution which stretches south through the subarctic region ("Arabidopsis lyrata," 2018). This plant produces white flowers, and fruit that resembles bean pods which are usually 1.5 to 2 centimeters long. The individual plants are 5 to 12 centimeters tall, with elliptic leaves along the stems and lobed basal leaves, the latter of which

are 0.5 to 1 centimeter long (Kristinsson, 2010). The habitat of *Silene uniflora*, or sea campion, is sparsely vegetated land throughout Iceland (“Vegetation types,” n.d.) and coastal areas of western Europe (“*Silene uniflora*,” 2018). *S. uniflora* has distinct, white, bulb-shaped calyces (the sepals, collectively), and each plant has multiple, 10- to 15-centimeter long stems growing from its base, and 1- to 2-centimeter long narrowly-elliptical leaves along the stems (Kristinsson, 2010). *Alchemilla alpina* and *Silene uniflora* flower in June, while *Arabidopsis petraea* flowers in May (Kristinsson, 2010).

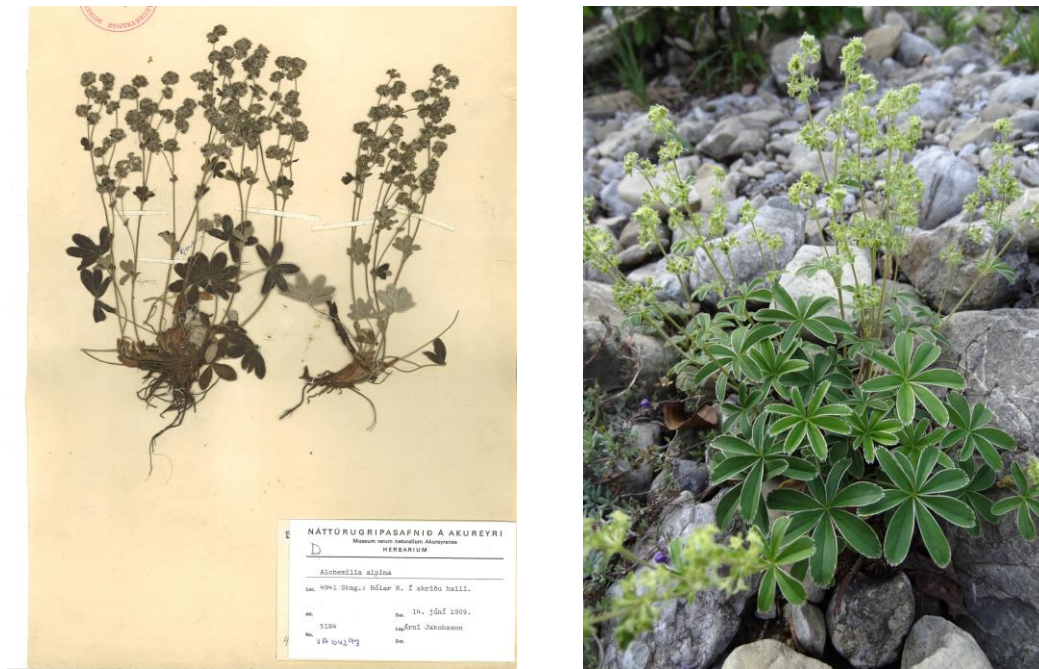


Figure 6. Herbarium specimens of *Alchemilla alpina* from the Icelandic Institute of Natural History (IINH) and an individual plant photographed in the wild (Schmidt, 2012).



Figure 7. Herbarium specimen of *Arabidopsis petraea* scanned at the IINH, and an individual plant photographed growing in the wild (*Arabidopsis petraea* sl1, 2013).



Figure 8. Herbarium specimens of *Silene uniflora* from the IINH, and an individual plant growing in the wild (Allday, 2009).

For this study, I chose to evaluate morphological traits that have been found to be responsive to changes in climatic conditions. Plant height is a trait sensitive to temperature increases, especially in Iceland (Bjorkman et al., 2018), and short plant height is associated with harsh growing environments (Cornelissen et al., 2003). The Raunkiær plant life form method is used to describe a plant's growth in relation to its structure, categorizing plants by height, lifespan, and whether they grow in the ground or in water (Cornelissen et al., 2003). Life form can indicate plant responses to climate based on the perennating tissue, or meristematic tissue, which is active during the growth season. The location of the perennating tissue on the plant affects the survival of the plant, such that those growing in harsher climates tend to have this tissue closer to the soil in order to limit its exposure to climatic conditions or herbivore grazing (Cornelissen et al., 2003). Based on this relationship between life form, plant height, and climate, if the near-surface temperature and precipitation in Iceland were to continue to increase, we might see an increase in plant height and distance of meristematic tissue from the ground in the future.

There has also been a connection found between leaf size and climate. Leaf size is the area of an individual leaf or lamina and is different from specific leaf area, which takes into account the mass of the leaf. Smaller leaf size is associated with more extreme environments in which plants endure drought conditions, or severely high or low temperatures (Cornelissen et al., 2003). Since temperature is expected to increase in Iceland, the average leaf size may become smaller, but precipitation is also projected to increase, which may suggest a shift towards larger average leaf size. Leaf size and plant height also have an effect on the albedo of the vegetation and the ability of the vegetation to sequester carbon (Bjorkman et al., 2018); therefore, it is important to gain a thorough understanding of these changes as they have ripple effects throughout the ecosystem.

Methods

When evaluating morphology of *Alchemilla alpina*, *Arabidopsis petraea*, and *Silene uniflora*, it is important to take phenotypic plasticity into consideration as a confounding

variable. In order to account for this variation, I chose to focus on herbarium specimens from the Icelandic Institute of Natural History that were collected in the northeastern and northwestern regions and northern highlands of Iceland. I accessed the Institute's herbarium in Akureyri, Iceland, and scanned every herbarium sheet for these three species excluding those with specimens that had not been collected in the specified regions of Iceland. I used a Canon flatbed scanner set at 300 dpi to capture digital images of the herbarium sheets in jpeg format.

My objective was to compare the changes in morphology of these plants between two time periods, so I used the Climate Explorer climate modelling tool from the Koninklijk Nederlands Meteorologisch Instituut (KNMI) website to assess how the climate had changed in Iceland, in terms of near-surface temperature and precipitation. I then analyzed the data on atmospheric carbon levels from the Goddard Institute for Space Studies (GISS) website. Based on the significant increases in temperature, precipitation, and carbon levels, I decided to compare the herbarium specimens collected during the time period of 1888 to 1934, to the specimens collected from 1968 to 2013 (the oldest specimen was collected in 1888 and the most recent specimen was collected in 2013). The analysis of *Alchemilla alpina* included twenty individuals from before 1950 and seven from after 1950. I used nineteen individuals from before 1950 and twenty-six from after 1950 in the analysis of *Arabidopsis petraea*, and included nine from before 1950 and twenty from after 1950 in the dataset for *Silene uniflora*.

A 2003 paper by Cornelissen et al. details the methods for studying plant traits, and the authors evaluate the traits on their associations with different aspects of environmental and climatic change. They state that growth form, life form, plant height, and photosynthetic pathway, among others, have connections to both climate response and carbon dioxide response. Leaf size and ratio of leaf length to width are associated with climate response, but their relation to carbon dioxide response is uncertain (Cornelissen et al. 2003). I used literature to evaluate the life forms of the three species, and assessed the plant height, leaf size, and ratio of leaf length to leaf width with morphometrics. Plant height is defined as the height measured from the base of the plant at ground level to the uppermost photosynthetic structures, not including flowers or fruit that may be higher up on the plant. Specific leaf area takes into account the mass of a leaf and expresses the area as a unit divided by the mass, and thus is a clearer indicator of a relationship between morphology and carbon dioxide response than leaf area alone. However, as

I was not able to weigh the herbarium specimens, I focused on leaf size, which is the area of a single lamina or leaf.

I performed the morphometric analysis in ImageJ (Rasband, 2015), measuring plant height and leaf length and width with the segmented line tool and the leaf size with the polygon selection tool. Measurements of leaf length were taken down the midvein of the leaf, excluding the rachis and petiole, and leaf width was measured at the midpoint of the length, perpendicular to the length measurement. As there was a lot of variation in how the leaves of *Alchemilla alpina* were pressed and in how many leaflets make up each leaf, measuring the length and width of the entire leaf would not have produced a correct measurement, so I measured the length and width of the middle leaflet in each cluster (Figure 9a). I measured the length and width of individual basal leaves on the *Arabidopsis petraea* and *Silene uniflora* plants (Figure 9b, c, e, f), as the leaves higher up on the stems tended to have different shapes.

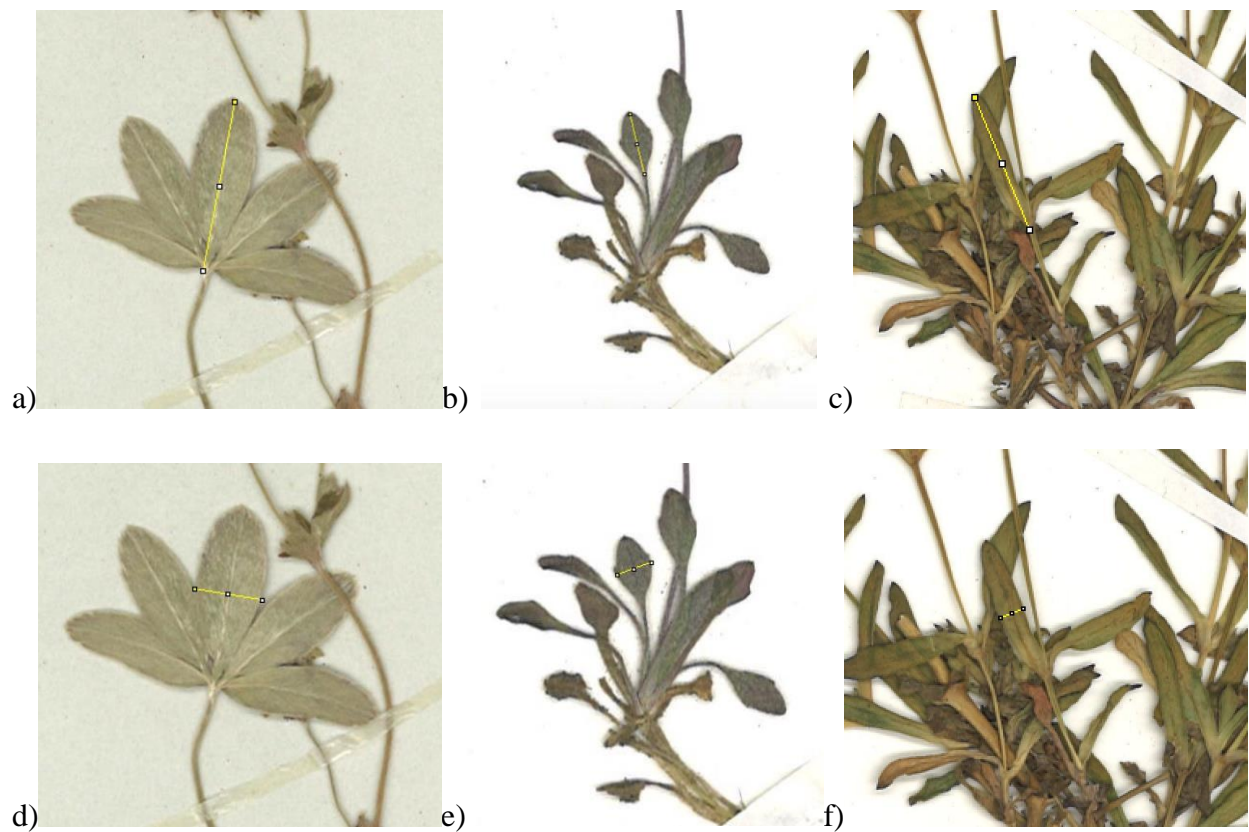




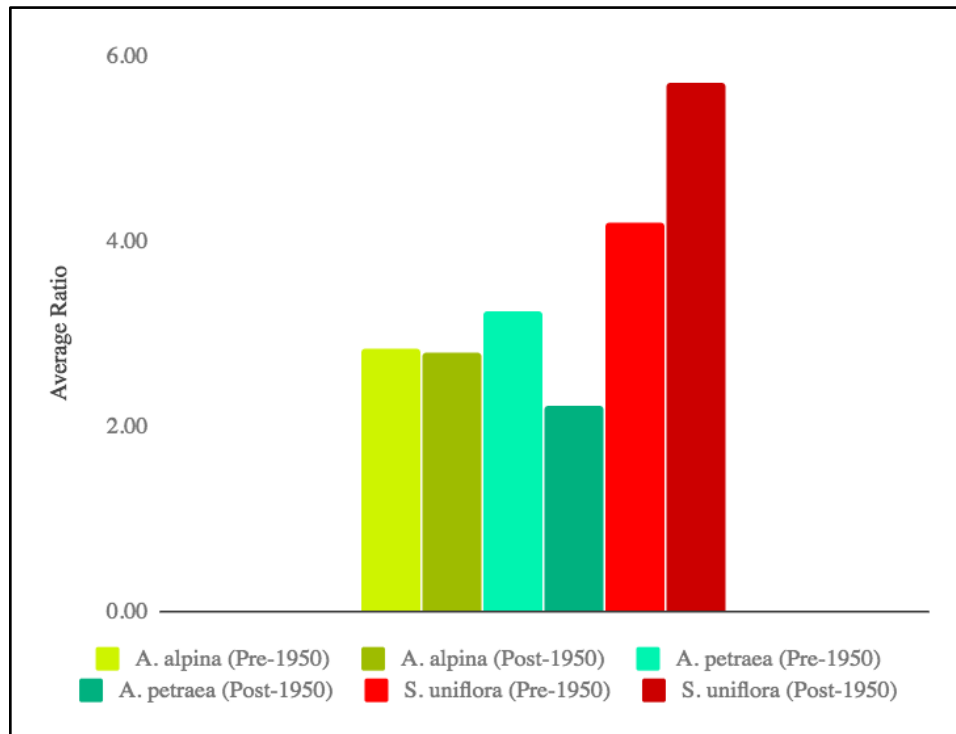
Figure 9. Measuring plant traits in ImageJ. Leaf length (a), leaf width (d), plant height (g), and leaf size (j) of *Alchemilla alpina*; leaf length (b), leaf width (e), plant height (h) and leaf size (k) of *Arabidopsis petraea*; and leaf length (c), leaf width (f), plant height (i), and leaf size (l) of *Silene uniflora*.

Ethics

This was a collections and literature based study, so there were no human, animal, or live plant subjects involved in this study. Care was taken to preserve the condition of the herbarium specimens during the scanning process.

Results

I analyzed the measurements obtained from ImageJ with two-tailed t-tests on the VassarStats Statistical Computation website. According to the results of the t-tests, *Arabidopsis petraea* and *Silene uniflora* showed a significant difference in leaf length to width ratio between



the two time periods. The mean ratio of leaf length to width in *A. petraea* increased by 1.023 ($p < .0001$, $t = 6.92$, $df = 127$), and decreased by 1.498 in *S. uniflora* ($p = 0.00014$, $t = -4.07$, $df = 60$). *Alchemilla alpina* and *Arabidopsis petraea* both displayed significant differences over time with respect to plant height. The means of the two groups of *Alchemilla alpina* had a difference of 2.776 cm ($p = 0.039$, $t = 2.17$, $df = 26$) and *Arabidopsis petraea* had a positive difference of 3.063 cm between the group means ($p = 0.011$, $t = 2.72$, $df = 27$). There were no significant differences in leaf size between the pre-1950 and post-1950 groups for any of the three species examined. *Alchemilla alpina* had a difference of 41.254 cm in means from the older group to the more recent group ($p = 0.281$, $t = 1.09$, $df = 100$), *Arabidopsis petraea* showed a difference of 7.114 cm between the group means ($p = 0.076$, $t = 1.80$, $df = 72$), and there was a difference of 0.744 cm between the two group means ($p = 0.944$, $t = 0.07$, $df = 48$) for *S. uniflora*.

Figure 10. The average ratio of leaf length to leaf width, divided by species and time period collected, to compare individuals collected before 1950 to those collected after 1950.

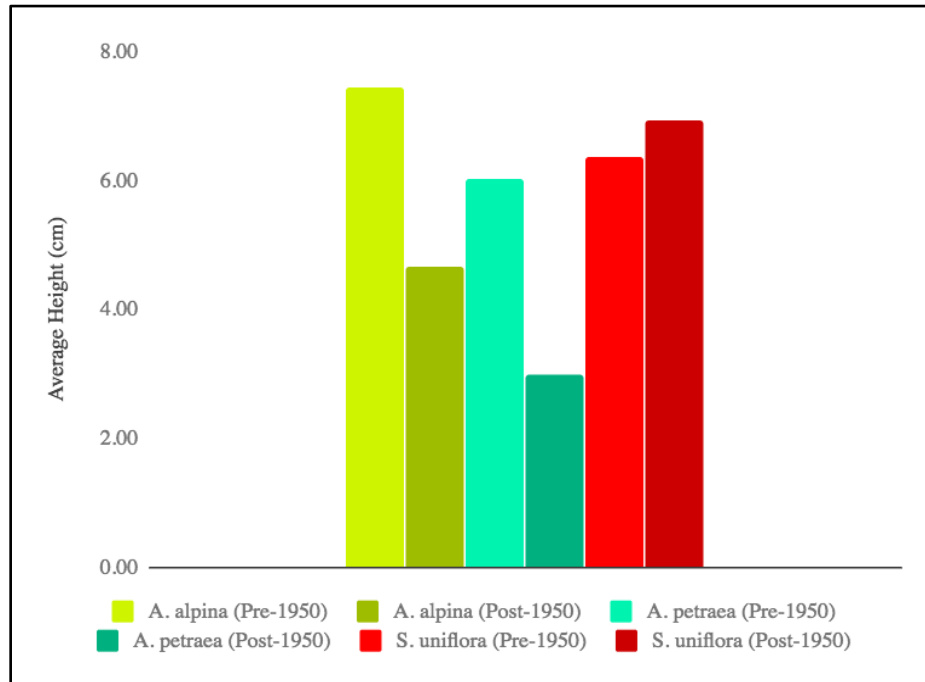


Figure 11. The average plant height of each species, comparing the average height of the pre-1950 specimens to the post-1950 specimens.

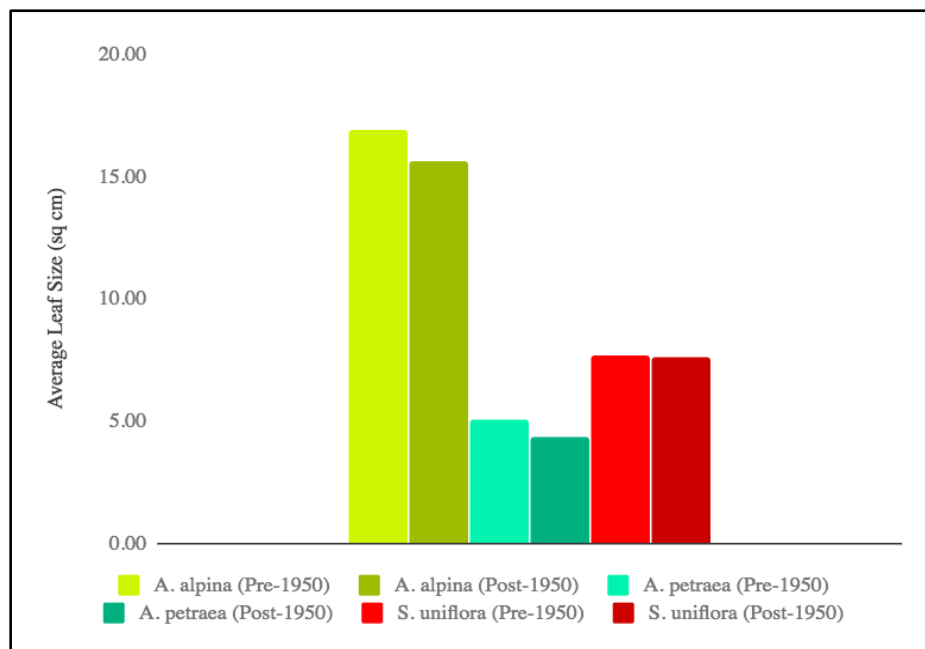


Figure 12. Comparison of average leaf size (area of lamina, expressed in centimeters squared) between the pre-1950 and post-1950 groups for each species.

Discussion

The results of the t-tests do not indicate any significant difference between pre-1950 and post-1950 leaf size. This is unexpected based on the relationship between climate and leaf size described in the article by Cornelissen et al. (2003). However, it is consistent with the findings of the paper by Bjorkman et al. (2018). Using data from 117 sites throughout the Arctic, the amount of change in leaf size that Bjorkman et al. observed during their study was not statistically significant, and the minimum (RCP2.6) and maximum (RCP8.5) IPCC carbon emission scenarios do not project significant change in leaf area. This may suggest that specific leaf area is a more effective indicator of ecosystem disruption by temperature increases, as specific leaf area is expected to increase based on IPCC estimates of climate change (Bjorkman et al., 2018).

According to a paper authored by Wang and Ni (2005), plant traits such as phyllotaxy, leaf type, and ratio of leaf length to width influence a plant's ability to endure drought and perform carbon fixation. This is likely due to the way in which the surface area and position of leaves expose a plant to precipitation, sunlight, and gases in the environment. Even if the ratio of leaf length to width changes, the area of the lamina may remain the same, which may have an effect on how the plant responds to changes in its environment. *Alchemilla alpina* did not display a significant difference in ratio of leaf length to width over time, but the ratio decreased in *Arabidopsis petraea* and increased in *Silene uniflora*. There were significant changes in leaf length to width ratio for two of the species but no significant differences in leaf size for any of the species, which may be accounted for by clarifying that the proportions of the leaves changed whereas the size did not change notably. This may have implications for the physiological processes of the plants that are affected by precipitation or carbon levels.

The plant height actually displayed a significance decrease for *Alchemilla alpina* and *Arabidopsis petraea* between the two time periods, which conflicted with what some of the literature suggested. This could have been due to errors in measurement or sampling, or it may suggest another event occurring in the ecosystem. Although there are several examples of literature reporting an increase in tundra or Arctic plant height due to climate change, one article

in particular, by Bjorkman et al. (2018) suggests that Arctic vegetation is not taller because the native plants themselves are taller, but because they are being replaced by taller plant species migrating from lower latitudes. One reason that the native Icelandic plants might be shorter than before could be due to competition with invasive species. Species not native to the Arctic and sub-Arctic tend to be taller than those which are native (Bjorkman et al., 2018), providing them the competitive advantage of being able to reach more sunlight and other resources, and limit the amount of sunlight that smaller, native plants are exposed to. This accelerates the colonization of the ecosystem and has lasting effects on the structure of the community. This shift in vegetation can also disrupt relationships between plants and the herbivores that feed on them, and affect plant-pollinator interactions. Nonnative plant species might have different flower morphology that could prevent the native pollinators from pollinating them, or their phenology might be incompatible, leading to a mismatch in period of pollination and flowering time, which would harm both populations (Hegland et al., 2009).

Taller vegetation would also affect abiotic factors in the ecosystem, such as soil temperature. One of the negative feedback effects of this change would be the shade that taller plants would provide for the soil, decreasing the temperature and decomposition rates (Bjorkman et al., 2018). However, positive feedback loops could also be set into motion, and are expected to be more damaging to ecosystems. The increased carbon sequestration and lower albedo from the taller vegetation would lead to warmer soil and increase near-surface temperatures. As the climate would continue to warm, tundra ecosystems would become more habitable for plants migrating from southern regions. A warmer climate would melt permafrost in the Arctic and increase the depth of the active layer, releasing methane gas and contributing to the greenhouse gas effect (Anthony et al. 2012).

In addition to soil temperature, snowpack could be affected by the shift to taller vegetation, in conflicting ways. If the taller plants have larger leaf areas, then the albedo would be decreased, leading to higher soil temperatures and less snowpack. However, taller and larger plants provide more surface area for snow to fall on, thus increasing snowpack. A thicker layer of snowpack would insulate the ground and increase soil temperatures and rates of decomposition (Bjorkman et al., 2018).

The decreased height of *Alchemilla alpina* may put it at a competitive disadvantage when colonization by nonnative plants is concerned. Based on the literature, this species' height would put it at risk of having limited access to resources in the ecosystem, as taller plants would limit its sunlight and water uptake. However, this is more likely to be a long-term effect on *Alchemilla alpina*, as it is currently a very common plant throughout Iceland (Kristinsson, 2010). *Arabidopsis petraea* may face similar competitive issues, as the results indicated that the average height of the plant decreased during the twentieth century. Although the mean leaf size of this species did not decrease, the ratio of length to width did, suggesting that the average leaf shape is shorter and wider than in the past. This may provide an advantage for accessing resources with the projected increase in amount of precipitation. The leaves of *Silene uniflora* were longer and narrower in the post-1950 group, but it is uncertain what effect this would have on the productivity and survival of the species for the projected climatic conditions, as leaves with relatively large length to width ratios are generally associated with drought tolerance. This incongruity of results between the species suggests that the plants are either not affected by changing climatic conditions, or that they may have begun adapting to these conditions, such as in the decreased leaf length to width ratio of *Arabidopsis petraea* plants.

These changes in the plant traits do not indicate that climate change has had an effect on the morphology of the plants, or perhaps imply that the effect is too minute to detect at this time. It would require a long-term study to collect enough data points to determine whether or not changes in climatic conditions influence the morphological traits of native Icelandic plants. However, some of the changes in the traits were statistically significant, meaning that the differences in measurements were not due to chance. These differences could be the result of measurement error, which would be able to be ruled out by replication of methods in future studies. At this point in time, the results of this study are not applicable to other native Icelandic plants. The three plants analyzed in this project are all herbaceous perennials with similar, broad distributions throughout the country, and are not representative of the plants native to Iceland. The results were inconclusive and inconsistent across species, signifying the need for more breadth of sampling across plant families and regions in the future.

Study Limitations

Experimental and measurement errors may have been introduced into the study design and had an effect on the results of the analysis. The majority of the herbarium specimens were collected during the summer months of June, July, and August, but a small number of the specimens had been collected outside of the growing season, during May or September. Comparing the leaf size or height of plants from different seasons may show more of a difference between specimens than actually exists. Specimens from the same species varied greatly in physical appearance, with differences in form and presence or lack of flowers, which may have led to inconsistencies in measurements. For example, one specimen of *Arabidopsis petraea* had several flowering stems growing out of the same root system, whereas most of the other plants only had one stem on each root system. The number of leaflets on each compound leaf of *Alchemilla alpina* also varied, within a range of five to seven leaflets clustered together, which may have been indicative of the age of the individual plant and might have had an effect on leaf size or ratio of length to width. Plant age was likely a confounding variable as well, as it would have had an effect on the plant height and leaf size, and may have skewed the data. There is also the matter of phenotypic plasticity, mentioned previously. A plant collected in the highlands would likely be smaller than a plant of the same species and age collected in the lowlands or coastal areas, because of differences in climatic conditions and resource availability (E. Kuttner, personal communication, 25 October, 2018).

The specimens were collected by a number of different botanists, who may not have selected all of the plants randomly. The plants collected may have been the tallest or the least affected by herbivore grazing, and might not necessarily be representative of the plants from that region and year, making it difficult to apply the results of this study to the species in Iceland overall. Additionally, the collected specimens had been mounted to the herbarium sheets by several different botanists over the years, each with slightly different preferences for mounting techniques. This may have prevented specimens from being measured and analyzed in a consistent manner, especially if there was variation in whether the abaxial or adaxial side of a lamina was face-up on the sheet, or if a leaf was folded and its boundaries were not clear. For some of the specimens, the roots or rhizomes of the plant were pressed in a way that made it

difficult for the basal leaves to be measured. While potentially leading to errors in measurement, this also decreased the number of data points that could have been collected.

Future Research

If I were to make improvements to this study, I would measure specific leaf area, in addition to leaf size, as it is a better indicator of environmental change than leaf size alone. However, this would require the collection and drying of new plant specimens since herbarium specimens cannot be weighed accurately. The ratio of leaf length to width changed over time for two of the species, but the leaf size did not change significantly, so it would be helpful to analyze leaf outline in the future, in order to determine how the leaf shape has changed. This would require more advanced morphometric methods, such as a digital landmark analysis and geometric morphometrics. I would also increase the diversity of sub-Arctic plant species sampled, so that the results would have a better chance of representing different growth forms and families of plants. The three species analyzed in this project have fairly broad distributions throughout Iceland, so sampling species which are only present in specific areas of Iceland may provide insight into the different ways plants are affected by climate change. Obtaining more localized climate data and focusing on additional aspects of climate such as soil temperature, humidity, and solar radiation would more accurately represent the climate of Iceland and supply more validity to the morphometric analyses.

There is some uncertainty in the literature about how tundra ecosystems will experience negative and positive feedback loops (Bjorkman et al. 2018), so more data are needed to understand how the abiotic factors of sub-Arctic ecosystems are affected by vegetation changes and to interpret the changes in plant morphology. Continued collection of Arctic and sub-Arctic plants would help to build herbaria, which in turn would further aid future collections-based studies.

Conclusions

Although this study provided conflicting results with unclear implications, I believe that further exploration of the methods to evaluate more traits would yield more significant, useful results. A broader study of native Icelandic plant morphology could provide researchers with the insight to understand the effects of climate change on Icelandic and other sub-Arctic ecosystems.

Literature sources have already detected changes in the vegetation of tundra ecosystems using experimental methods in long term studies, and morphological studies of herbarium specimens could serve to complement those findings, as they represent another dataset and perspective with which to determine the effects of climate change on sub-Arctic vegetation. As the influence of changing climatic conditions on plant phenology and physiology have already been observed (Lee et al., 2016; Sayed, 1995), the effects on morphology would further aid researchers in understanding the implications of climate change on community structure and dynamics in Arctic and sub-Arctic ecosystems.

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Appendix

Additional Figures

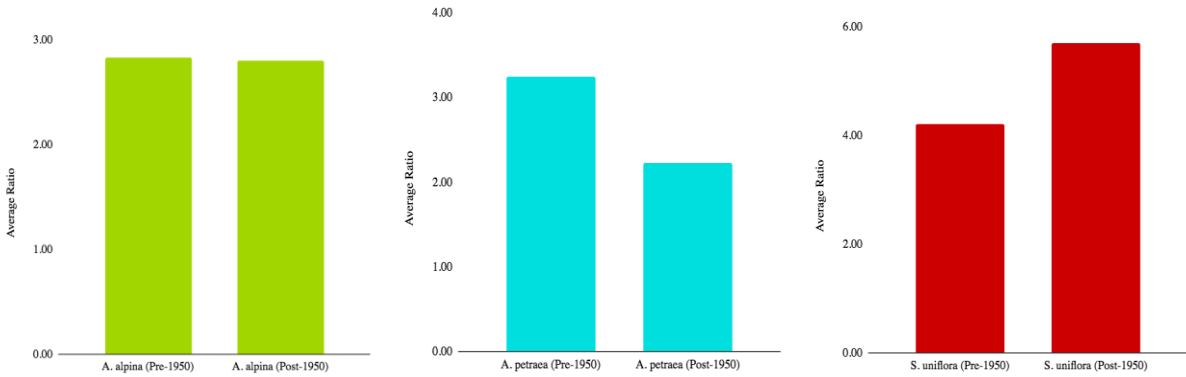


Figure A. Expands on the results of Figure 10.

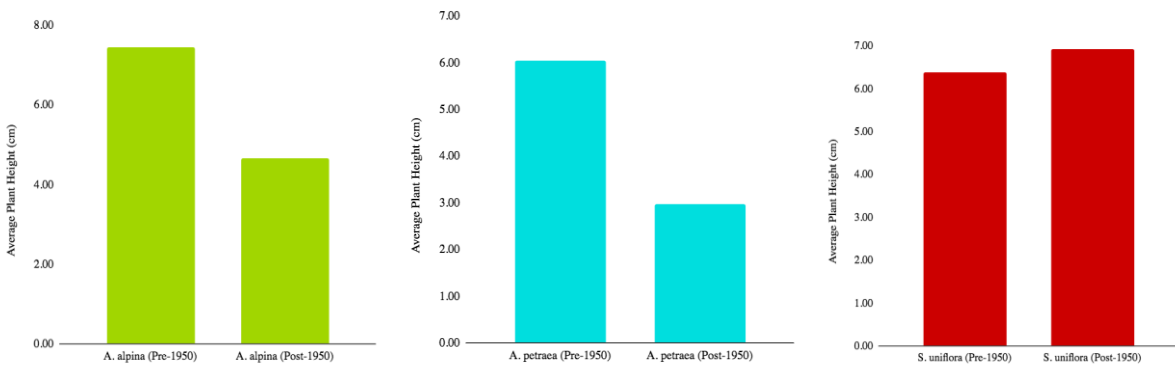


Figure B. Expands on the results of Figure 11.

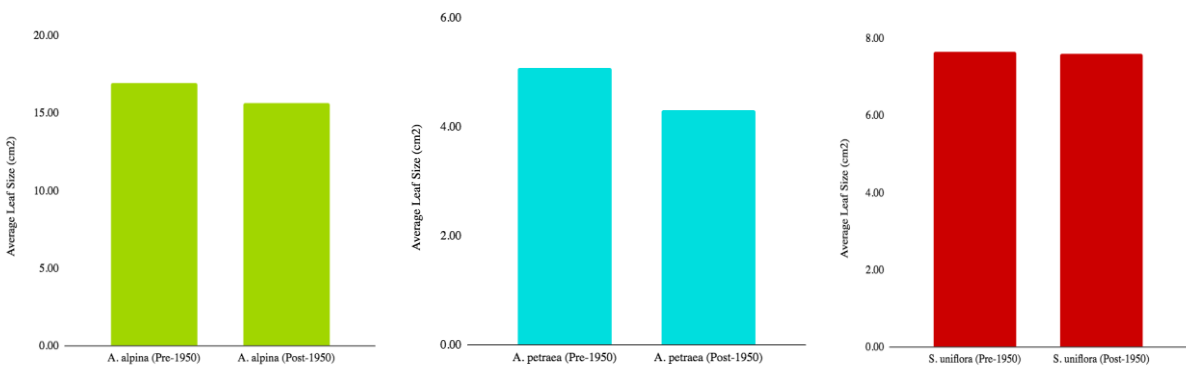


Figure C. Expands on the results of Figure 12.